

## The effects of the fungus-growing ant, *Trachymyrmex jamaicensis*, on soil fertility and seed germination in a subtropical dry forest

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**Abstract:** The fungus-growing ant, *Trachymyrmex jamaicensis*, is common in the Guánica dry forest of Puerto Rico and uses the pulp of fleshy fruits of many plant species as the primary substrate on which its fungal symbiont is cultivated. The ants discard the seeds and often intact fruits in refuse piles located on the soil surface near the nest entrance. Nest construction activities of *T. jamaicensis* result in deposition of subsoil over the surface leaf litter, altering the soil profile. The distribution of *T. jamaicensis* nests is aggregated. The ants preferred to nest where the soil was in a ravine and were absent from areas with shallow soils. Concentrations of Ca, Mg, Na, P, Fe, Mn, K, C and N tend to be higher in the ant refuse piles than in the surface soil or the subsoil. The differences in nutrient concentrations depend on the geological origin of the soil. Germination studies show higher seed germination in the refuse piles than in control areas, but seedling survivorship is lower in refuse piles.

**Resumen:** La hormiga *Trachymyrmex jamaicensis* es común en el Bosque Seco de Guánica (Puerto Rico) y utiliza la pulpa de las frutas como principal sustrato para cultivar un hongo que constituye su fuente alimenticia. Luego descarta las semillas y en muchas ocasiones las frutas enteras en sus vertederos de desperdicios. En sus actividades de construcción de nidos, estas hormigas traen partículas del subsuelo que depositan sobre la hojarasca del bosque alterando el perfil del suelo. Encontramos que la distribución de nidos de esta especie exhibe un patrón de agregación, prefiriendo anidar en una hondonada del bosque y a estar ausente de lugares donde el suelo es poco profundo. Un análisis de los nutrientes del subsuelo, suelo y el área de desperdicios indica que la presencia de varios elementos es mayor en las áreas de desperdicios que en el suelo o el subsuelo. Las diferencias dependen del origen geológico del suelo. Los estudios de germinación muestran que hay mayor germinación en las áreas de desperdicios comparadas a áreas de control, pero la sobrevivencia es menor en las áreas de desperdicios que en las de control.

**Resumo:** A formiga criadora de fungos, *Trachymyrmex jamaicensis*, é comum na floresta seca de Guánica em Porto Rico e usa a polpa dos frutos frescos de muitas espécies como o substrato primário onde o fungo simbionte é cultivado. A formiga descarta as sementes e muitas vezes frutos intactos em montes de refugio localizados à superfície do solo próximo da entrada da ninho. As atividades de construção dos ninhos da *T. jamaicensis* implica a deposição de subsolo sobre a camada de folhada superficial de que resulta uma alteração do perfil do solo. A distribuição dos formigueiros da *T. jamaicensis* é do tipo agregado. As formigas preferem nidificar onde o solo seja ravinoso e não seja profundo. A concentração do Ca, Mg, Na, P, Fe, Mn, K, C e N tendem a ser maiores nos montes de refugio das formigas do que na superfície do solo ou no subsolo. As diferenças na concentração em nutrientes depende da rocha mãe do solo. Estudos de germinação mostraram maior germinação das sementes nos refugos do que nas áreas de controle, se bem que a sobrevivência seja menor nos refugos.

**Key words:** Ants, attine, dry forest, germination, Guánica forest, nutrients, Puerto Rico, soil, tropics.

## Introduction

Few studies have been conducted on the effects of animals on nutrient cycling, soil properties and seed germination in tropical dry forests even though 42% of the world's tropical forests are tropical or subtropical dry forests (Butcher *et al.* 1989; Brown & Lugo 1982; Castilleja 1991; Vázquez & Orozco 1984; Westoby *et al.* 1991). Ants and termites are the dominant animals of soils in arid and semi-arid regions (Lee 1981). Ant activities affect soil turnover, profile development, create micro-relief by mounding and excavation, modify soil texture, regulate the movement of air and water, affect rates of soil erosion and the cycling of nutrients (Beattie & Culver 1983; Eldridge & Pickard 1994; Hole 1961; Humphreys 1981; Le Houérou 1981; Lee & Foster 1991; Mitchell 1988). Termites, ants and earthworms are among the most important bioturbation agents, but earthworms are rare in dry soils and under these circumstances termites and ants assume a more important role. As many tropical and subtropical forests have been disturbed or destroyed (Murphy *et al.* 1995), it is important from the standpoint of conservation and management to know the roles of animals in dry forest recovery following disturbances.

Fruit and seed production is common in the deciduous plant association of the Guánica dry forest of Puerto Rico and with little seasonal pattern (Castilleja 1988, 1991; Murphy *et al.* 1995). Many species fruit intermittently throughout the year, but seed germination rarely occurs. Most canopy trees are rare as seedlings. The average seedling density of all tree species at Guánica is 0.8 seedlings/m<sup>2</sup> (Castilleja 1991). Successful seedling establishment in the Guánica dry forest is affected by moisture availability and the small seeds (mean longest axis is 6.4 mm with sd of 4.2 mm) produced by trees in this forest increase the vulnerability of seedlings to inadequate moisture supply (Castilleja 1991). Coppicing has been suggested as the predominant strategy of recovery following cutting (Murphy & Lugo 1986). Although coppicing is a natural phenomenon in dry forests with shallow soils, human intervention through cutting may increase its occurrence. Molina

(1998) found that seed germination was the main mechanism for tree regeneration in secondary dry forests with a long history of human induced stress, and that recovery depends on the specific stresses received in the past. However, recruitment is perhaps different under non-disturbance conditions.

There are approximately 42 species of ants in the Guánica dry forest (Torres, Snelling & Canals unpublished data). *Trachymyrmex jamaicensis* and *Cyphomyrmex minutus* (a yeast-culturer) are the only fungus-growing ants in the Guánica forest. *Cyphomyrmex minutus* uses mainly insect fecal pellets but rarely seeds on which to cultivate its symbiont yeast (Torres 1984; Wheeler 1910; Wilson 1971). *Trachymyrmex jamaicensis* by contrast collects fruits of *Crossopetalum rhacoma*, *Erithalis fruticosa*, *Guettarda elliptica*, *Coccoloba microstachya* and *Bouyeria succulenta* and uses the flesh to grow their fungus gardens (Torres 1989). Seeds are discarded on the soil surface near the entrances to the nests in waste piles, where seeds are concentrated at levels several times higher than in the adjacent soil. It is common to see intact fruits in the refuse piles. It appears that these fruits are somehow unfit for manuring the fungus and are discarded along with the seeds. Following the passage of Hurricane Hortense over Puerto Rico (September 1996), we observed *T. jamaicensis* carrying to their nests green leaves that fell to the forest floor, which indicates the opportunistic feeding habits of this species. *Trachymyrmex jamaicensis* also collects flowers of *Capparis cynophallophora* and *Gymnanthes lucida*, and brown dead leaves of *Leucaena leucocephala* to cultivate its fungus. The maximum foraging distance that we have recorded in this ant is 4.1 m from the nest entrance.

*Trachymyrmex jamaicensis* occurs throughout the Bahamas and the Greater Antilles primarily in dry and scrub forests (Torres 1989; Weber 1967). The external indication of a nest is a largely circular mound (20-55 cm across and 3-14 cm high) about 3 cm from the nest entrance (2-17 mm in diameter). The mound consists of subsoil and clearly shows the color of the subsoil. One to several underground nest cham-

bers can be found at depths of 2.7 to 70 cm (Weber 1967), and the gardens are suspended from rootlets. The refuse pile is located 17-35 cm from the nest entrance. In the Guánica forest, *T. jamaicensis* has a patchy distribution with areas of high abundance in the deciduous and alluvial forests, but it is almost absent from the scrub forest.

Although *T. jamaicensis* gathers, transports and manipulates fruits from different plant species (Torres 1989) for use as a fungal substrate, there are no studies of the potential benefits to the plants. Fruit removal by ants can potentially benefit plants by (1) hiding seeds from predators and in some cases, the effects of fire, (2) reducing competition among seedlings under the parent canopy, (3) promoting seed dispersal and (4) repositioning seeds in microsites more conducive to germination (Buckley 1982; Beattie 1985; Westoby *et al.* 1991). Also, ant removal of fruit pulps from seeds could increase seed germination (Farji & Silva 1996; Oliveira *et al.* 1995). Many studies report higher concentrations of nutrients on ant hills and their benefits to the plants (Beattie 1985), but ant hills can have a lower concentration of some nutrients and ant activities can adversely affect the establishment of some plant species (Haines 1975; King 1977). Here, we report on the fungus-growing ant, *Trachymyrmex jamaicensis*, in the Guánica subtropical dry forest and the effects this ant has on: (1) soil nutrient dynamics, (2) soil profile, and (3) seed germination and seedling survivorship.

### Study site

The study site was located in the subtropical dry forest (Ewel & Whitmore 1973; sensu Holdridge 1967) of Guánica in southwestern Puerto Rico (18°N and 66°55'W). The substrate of the forest is derived from limestone and about 25% of the surface is exposed rock or outcropping. The maximum soil depth is approximately 120 cm (Wadsworth 1990). Soils in the forest are alkaline and have low water retention (Castilleja 1991; Medina & Cuevas 1990). The Guánica forest is structurally smaller than many tropical and subtropical dry forests because of low and variable annual rainfall (772 mm, CV of 35.1) (Castilleja 1991), long dry season (six months) and, on some sites, the large amount of surface limestone rock. Soil moisture deficits occur during 10 months of the year (Murphy & Lugo 1990). Forty-five percent of the annual precipitation occurs during the months of September, October and November with

an annual coefficient of variation of 49.8 (Castilleja 1991). The maximum mean temperature (28°C) occurs from August to October and the minimum mean temperature (24°C) between January and February. Three major intergrading plant associations compose the vegetation of the forest: scrub in sandy, shallow limestone outcroppings, semi-evergreen vegetation on sites with deeper alluvial and coal-luvial soils, and deciduous forest on intermediate sites (Murphy *et al.* 1995). Our study site is representative of the deciduous vegetation that cover about 58% of the Guánica forest (Lugo *et al.* 1978).

### Methods

We studied the pattern of nest distributions of *Trachymyrmex jamaicensis* in the 1.4 ha plot (17°58.240'N, 66°52.456'W, near "Camino El Fuerte" K5, H3.44) where several studies on nutrient dynamics and vegetation structure have been conducted in this forest (Lugo & Murphy 1986; Murphy & Lugo 1986; Murphy *et al.* 1995). The plot was subdivided into 576 (5 x 5 m) subplots and the number of ant nests counted in each subplot. We also determined the dry weight from the refuse and the nest soil mound of 15 ant nests that ranged from small to large. In addition, the refuse and the mound soil were examined for the presence of roots.

To determine the effects of *T. jamaicensis* on soil nutrient concentrations we took 10 g samples from the refuse pile, the subsoil brought to the surface during nest construction, and from a surface location 30 cm from the refuse pile of 20 ant nests (N=60). The surface locations were selected in the N, S, E, and W directions with the use of a table of random numbers. Ten of the nests were located within 20 m from the southwest corner of the 1.4 ha plot where the subsoil was yellow and calcimorphic (mollisol soil order, Munsell 2.5 Y-7/4). The other ten in an area 230 m from the plot (17°58.164'N, 66°52.558'W, near "Camino El Fuerte" K5, H1.51) where the subsoil was red (Ensenada clay soil, Munsell 5YR-5/6) (Lugo *et al.* 1996; Munsell soil color charts 1994; Roberts 1942). Nests were studied in areas with different soil types (calcimorphic and clay soils) to see if the effects of *T. jamaicensis* differed between soil types. Soil samples were collected in Hubco Protexco sand sample bags. Samples were crushed with a Dynacrush Soil Crusher and passed through 10 and 20-mesh sieves. Nitrogen was determined using the semi-micro Kjeldahl procedure (Chapman & Pratt

1979). Calcium, Mg, Na and Al were extracted in 1 N KCl and Fe, Mn, K and P with  $\text{NH}_4\text{-EDTA-NaHCO}_3$  (Olsen modified, Olsen 1982) and quantitated in a Beckman plasma emission spectrometer (Spectra Span V). Organic matter was determined using the modified Walkley & Black (1934) method (Nelson & Sommers 1982). All nutrient concentrations are reported on an oven-dry basis ( $105^\circ\text{C}$  for 48 hr). Two refuse samples from the calcimorphic soil did not contain sufficient refuse to conduct all the element determinations. One of these samples was used to estimate Ca, Mg and Na and the other for P, Fe, Mn, K, and Al. Two-way ANOVAs with soil regions (refuse, surface and subsoil) and soil type (calcimorphic and clay soil) as factors were conducted for all the elements. Because the refuse from the calcimorphic soil contained 9 replicates for each element, a replicate was randomly removed from the refuse collected in the red clay soil to have proportional subclass sizes (Underwood 1981; Zar 1996).

To study the effects of the activities of *Trachymyrmex jamaicensis* on seed germination we systematically searched for 26 nests with refuse piles greater than  $400\text{ cm}^2$  in area. On November 10, 1996, a  $20 \times 20\text{ cm}$  quadrat was marked in each refuse pile; and at a distance 1 m from the refuse pile another  $20 \times 20\text{ cm}$  quadrat was established as a control. The control quadrats were located in one of the following directions: N, NE, E, SE, S, SW, W and NW with the use of a table of random numbers. Every two months (first 6 months), thereafter monthly (for 13 months), the quadrats were visited and the number of seedlings recorded.

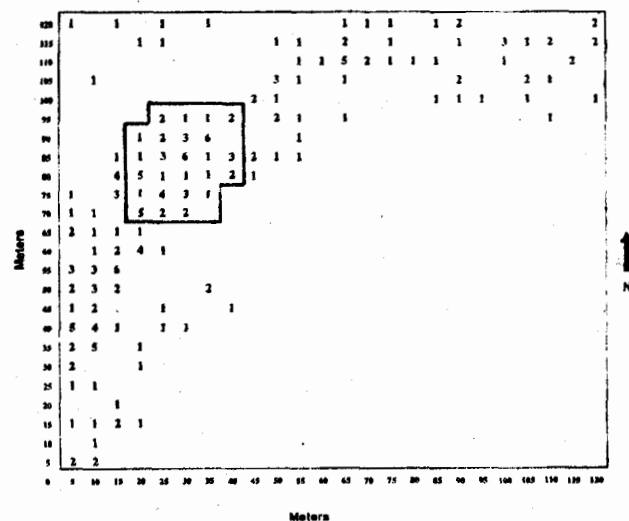
## Results

We observed 219 nests in the 1.4 ha study area (Fig. 1). Nests were aggregated ( $X^2 = 124.69$ ,  $df = 3$ ,  $P < 0.001$ ) and concentrated in areas with deep soils and where the soil was in a shallow ravine. Nests were absent from shallow rocky soil on limestone outcrops and areas with deep litter accumulation. The refuse dry weight ranges from 36.0 to 1435.2 g ( $\bar{X} = 388.5$ ,  $SE = 135.8$ ) and the mound soil from 179.0 to 4434.2 g ( $\bar{X} = 1547.0$ ,  $SE = 428.3$ ). We found 0.5 mm roots at the interface of the refuse pile and the soil of two nests and 0.5 mm roots at the base of three ant mounds ( $N = 15$ ).

Ant refuse piles contained the highest concentrations of all elements measured, independent of soil type (Table 1). The surface soil in both soil types was

slightly richer in nutrients than the subsoil, but most differences were not significant. The red clay was significantly higher in Fe and N, and the calcimorphic soil was higher in C. Although the concentrations of Ca, Mg, Mn, and the percent Al saturation tend to be higher in the red clay soil, the differences depend on the soil region (interactions between soil region and soil type are significant). The interactions emerge because the magnitude of the differences between means from different soil types depend on the soil regions compared, although the mean differences generally indicate a higher nutrient content in the regions from the red clay soil (Underwood 1981). When interactions were significant, we conducted one way ANOVA to compare differences among soil regions in each soil type. Tukey HSD (Day & Quinn 1989; SYSTAT 1998) were used in the pairwise mean comparisons (Table 1).

Seed germination occurred 11 months later (October 26, 1997) when several rainfall events terminated a long dry season. A total of 98 seedlings (89 dicots and 9 monocots) were found in the refuse piles and 31 (24 dicots and 7 monocots) in the controls. The mean seed germination was 3.77 per  $20\text{ cm}^2$  ( $SE = 1.11$ ,  $N = 26$ ) in the refuse piles and 1.19 per  $20\text{ cm}^2$  ( $SE = 0.28$ ,  $N = 26$ ) in the control quadrats. The median (2.0) seed germination in the refuse piles was



**Fig. 1.** Distribution of nests of *Trachymyrmex jamaicensis* in a 1.4 ha plot in Guánica, Puerto Rico. Numbers represent the nests in  $5 \times 5\text{ m}$  subplots. Nests in the dotted area were located in a shallow ravine. The large area in the southeastern portion of the plot without nests was mostly limestone outcrop with very thin soil.

**Table 1.** Available nutrient concentrations ( $\bar{X} \pm SE$ ) in soil regions located in two soil types. Two-way Anovas with soil region and soil type as factors were done for each nutrient. When interactions between factors were significant, One-Way Anovas were conducted on the soil regions of each soil type. Means with the same letters are not significantly different (Tukey HSD, soil region factor,  $P > 0.05$ ). When interactions are present only the means with the same letters, within the same soil type, are not significantly different. The center row (soil type effects) shows the P-values of the differences among means from different soil types (disregarding the soil region classification) or interaction between soil type and soil region. N = 10 for each group, except refuse from the yellow soil type (N=9).

Soil region	Ca (mg/g)	Mg (mg/g)	Na (mg/g)	P (mg/g)	Fe (mg/g)	Mn (mg/g)	K (mg/g)	Al Saturation (%)	C (%)	N (%)
<b>Red clay soil</b>										
Refuse	7.65 $\pm$ 0.36 <sup>a</sup>	0.72 $\pm$ 0.06 <sup>a</sup>	0.25 $\pm$ 0.056	0.040 $\pm$ 0.011	0.04 $\pm$ 0.013 <sup>a</sup>	0.15 $\pm$ 0.020	1.79 $\pm$ 0.14	2.93 $\pm$ 0.59	22.90 $\pm$ 1.72	1.55 $\pm$ 0.15
Surface	7.70 $\pm$ 0.30 <sup>a</sup>	0.53 $\pm$ 0.06 <sup>ab</sup>	0.09 $\pm$ 0.004 <sup>a</sup>	0.007 $\pm$ 0.003 <sup>a</sup>	0.02 $\pm$ 0.012 <sup>a</sup>	0.05 $\pm$ 0.007 <sup>a</sup>	0.46 $\pm$ 0.12 <sup>a</sup>	0.16 $\pm$ 0.03 <sup>a</sup>	10.29 $\pm$ 0.63 <sup>a</sup>	0.79 $\pm$ 0.10
Subsoil	6.81 $\pm$ 0.53 <sup>a</sup>	0.37 $\pm$ 0.05 <sup>b</sup>	0.11 $\pm$ 0.010 <sup>a</sup>	0.005 $\pm$ 0.002 <sup>a</sup>	0.02 $\pm$ 0.015 <sup>a</sup>	0.05 $\pm$ 0.013 <sup>a</sup>	0.21 $\pm$ 0.02 <sup>a</sup>	0.23 $\pm$ 0.06 <sup>a</sup>	7.05 $\pm$ 0.42 <sup>a</sup>	0.51 $\pm$ 0.06
Soil type effects	Interaction	Interaction	NS	NS	P<0.05	Interaction	NS	Interaction	P<0.001	P<0.05
<b>Yellow calcimorphic soil</b>										
Refuse	6.70 $\pm$ 0.47	0.73 $\pm$ 0.09	0.29 $\pm$ 0.021 <sup>a</sup>	0.021 $\pm$ 0.004	0.01 $\pm$ 0.004 <sup>a</sup>	0.06 $\pm$ 0.009	1.93 $\pm$ 0.15	1.62 $\pm$ 0.15	28.77 $\pm$ 2.48	1.55 $\pm$ 0.17
Surface	4.95 $\pm$ 0.25	0.25 $\pm$ 0.02 <sup>c</sup>	0.07 $\pm$ 0.009 <sup>a</sup>	0.005 $\pm$ 0.000 <sup>a</sup>	0.01 $\pm$ 0.001 <sup>a</sup>	0.04 $\pm$ 0.004	0.26 $\pm$ 0.04 <sup>a</sup>	0.27 $\pm$ 0.05 <sup>b</sup>	13.09 $\pm$ 0.58 <sup>a</sup>	0.57 $\pm$ 0.04
Subsoil	2.47 $\pm$ 0.22	0.17 $\pm$ 0.02 <sup>c</sup>	0.05 $\pm$ 0.006 <sup>a</sup>	0.003 $\pm$ 0.000 <sup>a</sup>	0.01 $\pm$ 0.001 <sup>a</sup>	0.01 $\pm$ 0.002	0.28 $\pm$ 0.05 <sup>a</sup>	0.30 $\pm$ 0.04 <sup>b</sup>	11.00 $\pm$ 0.35 <sup>a</sup>	0.18 $\pm$ 0.04

higher than in the control quadrats (1.00) ( $U = 480$ ,  $P < 0.01$ ). Most of the seedlings were *Stenandrium tuberosum* (Acanthaceae), *Croton humilis* (Euphorbiaceae) and *Lantana camara* (Verbenaceae). Two months later total seedling survivorship was higher (0.70) in the controls than in the refuse piles (0.19) ( $X^2 = 11.38$ ,  $df = 1$ ,  $P < 0.001$ ). This statistical test was done under the assumption that seedling survivorship was independent, a reasonable assumption due to the low seedling densities. Some of the individuals belonging to *Stenandrium tuberosum* may represent established perennials, not newly germinated seeds. *Stenandrium tuberosum* can lose their leaves during the dry season, leaving a very reduced underground stem (Acevedo 1997; Liogier 1997). Deleting *S. tuberosum* from the above analyses does not alter any of the main conclusions. Seven months later (June 6, 1998) there was a total of seven dicot seedlings in refuse piles as compared to 14 in the controls. Only two seedlings of *C. humilis* (both in the control) were taller than 8 cm and could have a possibility of establishment.

### Discussion

The study of invertebrate effects on soil processes and plant dynamics is a neglected aspect of tropical and subtropical dry forest ecology. We found that the ant *Trachymyrmex jamaicensis* could have important, although localized, effects in soil processes at the Guánica dry forest. The localized effects are the result of the pattern of nest aggregation and the patchy distribution of this ant throughout the forest. We were unable to demonstrate short term effects of the activities of this ant in seedling survival, but we cannot rule out the possibility of long term effects due to the mineralization of the organic matter in the refuse piles or seed germination under better humidity conditions.

The concentration of *Trachymyrmex jamaicensis* nests in deep soil and in the shallow ravine could be related to the need for a humid environment for establishment and maintenance of the fungal gardens required by this ant. Many ant species are highly sensitive to lack of humidity (Hölldobler & Wilson 1990) and dry weather promotes inactivity in attine species (Weber 1979). In addition, growth rates of attine fungal symbionts are temperature dependent (Weber 1979). It is likely that nests with chambers deep in the soil could provide greater stability in humidity and temperature. Some of the nests had

galleries that contact porous limestone bedrock. We believe that water from the limestone may stabilize the humidity and temperature of the fungus garden environment. Although we did not encounter nests in areas with deep leaf litter in the study site, nests of *T. jamaicensis* do occur in this microhabitat in other areas of the forest.

The activities of *Trachymyrmex jamaicensis* created pockets of higher nutrient concentrations in their refuse piles, which in turn influenced the spatial distribution of nutrient concentrations at the soil surface. An important feature of nutrient concentrations in arid areas is that vertical and horizontal heterogeneity is stronger than in most other ecosystems (West 1981). We found higher concentrations of nutrients in the waste piles, but low concentrations in the mounds formed by *T. jamaicensis*. This is contrary to the findings of other studies that report higher levels of nutrients in ant mounds (Beattie 1985). The reason for the difference is that *T. jamaicensis* generally does not mix its refuse with soil brought to the surface during nest excavation.

Although *Trachymyrmex jamaicensis* transports soil from the subsoil to the surface, which tends to invert the soil profile, the significance in terms of nutrient distributions is slight because the differences in nutrient concentrations between the soil and subsoil are relatively minor, except for N, Mn, and Ca. Probably the most important effect resulting from the movement of the soil by the ants to the surface is the burial of leaf litter. This change in the profile of leaf litter is important in arid zones because soil organic matter produced by roots or soil organisms is distributed quite uniformly, but the organic matter derived from litter remains concentrated near the soil surface because rains are too infrequent or low in intensity to carry it far into the soil (Binet 1981). Weathering of parental rock is generally low in arid zones because of lack of water for chemical reactions (West 1981). Under arid conditions the activities of organisms can become important to enrich the soil in the lower horizons. We believe that movement of fruits, flowers and occasionally leaves, which are among the richest plant parts in terms of nutrients (Lugo & Murphy 1986), into *T. jamaicensis* nests makes only a minor contribution to the enrichment of lower soil horizons in this forest, because most of these materials are removed to the waste piles. Also, the soil movement by *T. jamaicensis* affects the surface texture because soil brought to the surface from the lower horizons



consists of clay grading into silty loam and is low in porosity (Murphy *et al.* 1995).

The effect of *Trachymyrmex jamaicensis* on soil nutrient distribution is similar in the calcimorphic and red clay soils. In both soil types it increases surface heterogeneity in nutrient concentrations more than the depth heterogeneity. The red clay soil seems to be a better soil for plant growth. The higher total content of C in the refuse from the calcimorphic soil probably reflects differences in organic C, but the higher content of C in the surface and subsoil of the calcimorphic soil could also reflect the higher  $\text{CaCO}_3$  in this soil. The higher Fe content in the regions from the red clay soil reflects the presence of iron oxides in this soil. The low percent Al saturation indicates a high alkalinity in the Guánica forest with alkalinity greater in the surface and subsoil of the calcimorphic soil. Although Ca distribution is quite uniform in the regions of red clay soil, the distribution of Ca is significantly different in the regions of the calcimorphic soil. The high Ca concentration in the Guánica soils can result in the partial immobilization of P due to the formation of low soluble calcium phosphate (Mengel & Kirkby 1982) and the immobilization of iron and manganese (Medina & Cuevas 1990). Also, low phosphorus levels may restrict the capability of plants to fix nitrogen and the transformation of N from the organic to inorganic pool (Lee 1981; West 1981). It is possible that the higher concentration of P in the ant refuse piles might enhance seedling survivorship when germination occurs under better moisture conditions, which occur infrequently in this forest (US Department of Commerce 1961).

Germination under field conditions is low in dry forests (Ray & Brown 1994). We expected higher seed germination and seedling survivorship in the refuse piles, because the concentration of seeds was several times higher than in nearby surface soil, and because of the higher nutrient content of these sites. Low seed germination eliminated the possibility of competition as a cause of seedling mortality, although there may exist the possibility of competition from the established trees which possess extensive root systems (Murphy *et al.* 1995) that can concentrate minerals and collect water from a large volume of soil (Binet 1981). However, refuse piles were almost devoid of leaf litter; and evaporation may be greater in these microsites than in sites covered by leaf litter, which could have adversely affected small seedlings. Similarly, Haines (1975) working in a wet forest in Barro Colorado (Panamá)

found higher nutrient concentrations in *Atta colombica* refuse dumps compared to the forest floor, but poor growth and survival of seedlings on refuse-dump soil, probably due to poor water retention, high temperatures (due to decomposition) and disturbance by faunal activity (S. Rehner pers. com.). At very low matric potentials, the *A. colombica* refuse can deliver very little water in comparison to adjacent forest soil.

Surface layers of organic matter are as porous as the coarsest sands, and clay has a high moisture equivalent (Daubenmire 1974). The refuse piles of *Trachymyrmex jamaicensis* are high in organic matter and lack clay which may contribute to the low survival of seedlings in these refuse piles. Haines (1975) found that refuse stimulated the production of roots from nearby trees that removed water from the refuse dumps to levels detrimental to the seedlings. Water removal by tree roots and the unusual water-retention properties of refuse soils made the refuse dump sites of *A. colombica* a desert for the seedlings during the dry season (Haines 1975). Contrary to the findings of Haines (1975) roots in the *T. jamaicensis* refuse piles were scarce. In some cases plant diversity is higher in ant mounds enriched with debris, several years after the ants had abandoned the mounds, owing to gradual mineralization of the debris (Buckley 1982).

The importance of water to seedling survivorship in the Guánica forest has been implied by Castilleja (1991) who found that seedlings in the Guánica forest are confined to moisture-retaining microsites and are practically nonexistent in forest gaps. Canopy cover results in a decrease of direct incident radiation on the ground and a reduction of evaporation from the soil surface. Numerous studies show that maximum seedling mortality, as observed in this study, occurs shortly after germination (Castilleja 1991). Tevis (1958), in studies of desert vegetation, found that even when germination was abundant after above-average precipitation, seedling recruitment was dependent on the onset of the following rainy season. We agree with Castilleja (1991) that high species richness in this forest could be the result of long-term accretion of plants that become established stochastically and that field monitoring of seedling establishment over many seasons is needed to evaluate the initial stages of dry forest regeneration (Ray & Brown 1994).

In this study we did not find a positive effect of *Trachymyrmex jamaicensis* on seedling survivor-

ship. Long term studies are needed to determine how seedling survival varies from year to year in this dry forest. One question that needs to be answered is why do plant species produce seeds and fruits with such high frequency (Castilleja 1991) if seedling establishment is so difficult in the Guánica forest? Perhaps some plant species are following a bet-hedging strategy (Stearns 1976; Yodzis 1989) or may be the reproductive patterns in some species reflect ancestral characters and not reproductive adaptations for life in dry forests (Brooks & McLennan 1991).

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