SPECIES COMPOSITION OF ROOT-FEEDING MACROARTHROPODS IN A SUBALPINE GRASSLAND ASSOCIATED WITH PINE FOREST IN MEXICO

A. MORÓN-RÍOS,[1] V.J. JARAMILLO, and R. DIRZO

Centro de Ecología, UNAM, Ap. Postal 70-275, C.P. 04510 Ciudad Universitaria, México, D.F. México

Abstract

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Below-ground herbivores have been poorly studied regardless of their importance for the establishment and composition of plant communities. In a subalpine grassland associated with a 3200-m-elevation pine forest in central Mexico, the composition and vertical and horizontal distribution of the macroarthropod root-feeding community was studied for 14 months. The root-feeding community included six species of Coleoptera and one species of Diptera. The dominant species were *Phyllophaga* spp. (subgenus *Phytallus*, "macrophylla" group) and *Trachyploeomimus* aff. *spurcus* Champion. Mean density and biomass of this community were 101 individuals and 3 g per square metre, respectively. These values were low when compared with those reported for other communities. Species were most abundant in the first 10 cm of the soil all year around. Dominant species showed a clumped horizontal distribution most of the year.

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Résumé

Les herbivores souterrains ont été peu étudiés, nonobstant l'importance qu'ils peuvent avoir dans l'establissement et la composition des communautés végétales. Dans un pâturage sous-alpin situé dans une forêt de conifères dans le centre de Mexique, on a étudié pendant 14 mois la composition et la distribution verticale et horizontale de la communauté de macroarthropodes rhizophages. La communauté des rhizophages est constituée par six espèces de l'ordre Coleoptère et une espèce de l'ordre Diptère. Les espèces dominantes ont été *Phyllophaga* spp. (sous-genre *Phytallus*, groupe "macrophylla") et *Trachyploeomimus* aff. *spurcus* Champion. La densité et la biomasse moyenne annuale des "taxa" rencontrés ont été de 101 individus et 3 g par mètre carré respectivement. Ces valeurs sont faibles quand on les compare avec les décrit pour d'autres localités. La distribution verticale des espèces se concentre dans les premiers 10 cm du sol durant toute l'année. Les espèces dominantes ont un patron de distribution horizontal inégal durant la plupart de l'année.

Introduction

Soil arthropods constitute one of the most abundant components of the edaphic fauna. Root-feeders longer than 2 mm are classified as macroarthropods (Eisenbeis and Wichard 1987). Knowledge of the identity of species and their biology is mostly restricted to those that either damage crops, ornamentals, and forage species (Cherry 1985; Graber et al. 1931; Islas 1964; King et al. 1981; Lim et al. 1980; Reinhard 1946; Ritcher 1957; Rodríguez del Bosque 1981, 1988; Weiner and Capinera 1980) or can be used for the biological control of weeds (Blossey 1993).

The ecology of root-feeding macroarthropods has been poorly studied. Other than investigations related to agriculture, few species, such as the root fauna associated with *Centaurea maculosa* Lam. in Europe (Müller 1989) and the below-ground herbivores of a short-grass prairie (Lloyd and Kumar 1977), have been intensively studied. In Mexico, only the Coleoptera of soil at Laguna Verde, Veracruz (Villalobos and Lavelle 1990) and other soil arthropods at the same site (Lavelle et al. 1981) and at Bonampak, Chiapas (Lavelle and

[1] Current address: ECOSUR, Depto. de Ecología y Sistemática Terrestre, Ap. Postal 63, C.P. 29290, San Cristóbal de las Casas, Chiapas, México.

Kohlmann 1984) have been described. Assessments of the role that below-ground herbivores may play on the composition of plant communities and the establishment of plant species and their interactions (Brown and Gange 1989; Brown 1989; Ramsell et al. 1993) are limited to some temperate sites.

To understand the role of root-feeding macroarthropods on plant community dynamics and to assess the effects of above-ground herbivory on the root-feeding community, an investigation was made in a subalpine grassland (Morón-Ríos 1995). An initial and key component of this study was the assessment of the composition and abundance of root-feeding species and their temporal and spatial patterns of distribution. Herein we address the following questions: (*a*) What is the species composition of macroarthropod root-feeders in a subalpine grassland and how do their density and biomass fluctuate during the year? (*b*) What is the spatial distribution (horizontal and vertical) of this fauna in the soil profile and how does this distribution vary seasonally?

Materials and Methods

Study Area. The study site was located in the Forest Experimental Station of Zoquiapan, 98°45′W and 19°30′N (División de Ciencias Forestales of the Universidad Autónoma Chapingo). The station lies within the Zoquiapan National Park in the Neovolcanic Belt of Central Mexico. Altitude fluctuates between 3000 and 3500 m (Franco and Búrquez 1981). Mean annual precipitation is 1169 mm and mean annual temperature is 11°C (average of 20 years from the Río Frío climatological station, located 8 km NNW of Zoquiapan). Precipitation is concentrated between the months of April and October with maxima in July and September. Maximum temperatures are registered in April and August and the frost period occurs between October and March. The soil has low cohesion and good drainage and aeration. The dominant texture is sandy (Franco and Búrquez 1981).

The vegetation is pine forest dominated by *Pinus hartwegii* Lindl. with the co-occurrence of *P. montezumae* Lamb., *P. leiophylla* Schl. & Cham., *P. ayacahuite* Ehr., *P. pseudostrobus* Lindl., *Abies religiosa* (H.B.K.) Cham. & Schl., *Cupressus lindleyi* Klotzsch., *Quercus crassipes* H. & B., *Q. rugosa* Née., *Q. laurina* H. & B., and *Alnus firmifolia* Fern. The understory is dominated by the grasses *Muhlenbergia quadridentata* (H.B.K.) Kunth and *Festuca tolucensis* H.B.K. which form a characteristic grassland-like plant community known locally as a "zacatonal". Other grass species of the same genera are also present along with several herbaceous species. The maximum number of herbaceous species has been recorded in July and November, and decreases have been recorded in February and March (Obieta and Sarukhán 1981).

Grazing by cattle is frequent in the area. Grazed sites have greater plant diversity than experimentally protected ones (Obieta and Sarukhán 1981). The dicot *Alchemilla procumbens* Rose is dominant in the former sites and the grass *M. quadridentata* is dominant in the latter. Plant density and cover have been estimated in a grazed area of 100 by 25 m with three 20-m Canfield lines in three different periods of the year (July, November, and February) (Obieta and Sarukhán 1981). Mean plant density fluctuated between 85 and 180 individuals per line and mean plant cover ranged between 50 and 65%.

Sampling. The sampling site was a 1-ha (100 by 100 m) plot located within the pine forest and with an understory dominated by *Muhlenbergia* and *Festuca*. It was located on a NNE-facing slope at an altitude of 3200 m above sea level. The area is lightly grazed by cows all year around. The root-feeding macroarthropod community was sampled during 14 months, from August 1991 to October 1992. Each month we randomly took 10 samples, each one consisting of a soil cube, 30 cm^3. Cubes were divided into three depths: 0–10, 10–20, and 20–30 cm. Root-feeding macroarthropods were manually separated from each depth and the species and number of individuals were registered. Specimens collected were fixed in a Pampel solution for at least 24 h (Morón and Terrón 1988), dried with a paper

TABLE 1. Biomass (B), density (D), percentage of total biomass (%B), and percentage of total density (%D) of the species of root-feeding macroarthropods. Data are means ± 1SE, n = 132

Taxa	B, g/m^2	%B	D, individuals/m^2	%D
Coleoptera				
Melolonthidae	2.5 ± 0.5	84	42 ± 5.43	40.8
Phyllophaga sp. 1*	2 ± 0.48	67	15 ± 1.75	14.5
sp. 2	0.5 ± 0.13	17	27 ± 4.35	26.8
Curculionidae				
Trachyploeomimus aff. *spurcus*	0.20 ± 0.04	6.8	36 ± 4.2	34.6
Chrysomelidae	0.04 ± 0.012	1.42	10 ± 1.92	9.3
Elateridae	0.14 ± 0.036	4.7	11 ± 2.54	10.5
Hemicrepidius sp.	0.11 ± 0.031	3.7	9 ± 2.27	8.4
Agriotes sp.	0.03 ± 0.011		2 ± 0.85	2.1
Tenebrionidae				
Helopini	0.085 ± 0.025	2.9	3 ± 0.44	2.6
Diptera				
Bibionidae	0.013 ± 0.008	0.44	1 ± 0.58	1.1

*Both species belong to subgenus *Phytallus* and "macrophylla" group.

towel, and weighed. The specimens were preserved in 70% ETOH. Last-instar larvae of all species were kept alive to obtain adults for precise identification. Larvae were transported to the laboratory in Petri dishes or plastic containers with soil and humus. They were maintained in total darkness at 18–20°C and were checked every 15 or 20 days for pupae or adults.

The horizontal distribution pattern for the dominant species was evaluated with the Standardized Morisita Index of Dispersion (I_p) (Krebs 1989). This index ranges from −1.0 to +1.0, with 95% confidence limits at +0.5 and −0.5. Random patterns result in an I_p of zero, clumped patterns in an I_p above zero, and uniform patterns in an I_p below zero. This index was used because it is independent of population density and sample size (Krebs 1989). The association between dominant taxa was assessed with the Jaccard Index (JI) and the Pearson correlation coefficient (r) (Ludwig and Reynolds 1988).

Density and Biomass. During the 14-month study period we collected a total of 1268 individuals belonging to eight species of the orders Coleoptera and Diptera. Coleoptera was the more abundant and diverse group with five families and seven species. Diptera was represented by only one species. Mean density of this fauna was 101 individuals per square metre with a biomass of 3 g per square metre. The greatest density and biomass were recorded for species of Coleoptera (Table 1). The species with the highest density was *Trachyploeomimus* aff. *spurcus* Champion, but *Phyllophaga* sp.1 (subgenus *Phytallus*, "macrophylla" group) (sensu Morón 1986) had the greatest biomass (Table 1).

Species community composition was constant during the year. Monthly density oscillated between 50 (May) and 162 (September) individuals per square metre (Fig. 1). Density of *Trachyploeomimus*, *Phyllophaga* sp.2, and *Hemicrepidius* sp. was highest between August and October and lowest between March and June. This pattern was different from that observed for biomass (Fig. 2), which was generally low with its highest value in November 1991 (1.22 g/m^2) and the lowest in March 1992 (0.07 g/m^2) (Fig. 2).

Vertical and Horizontal Distribution. Eighty-five percent (1027 individuals) of the total number of individuals collected were found in the 0- to 10-cm depth of the soil profile and

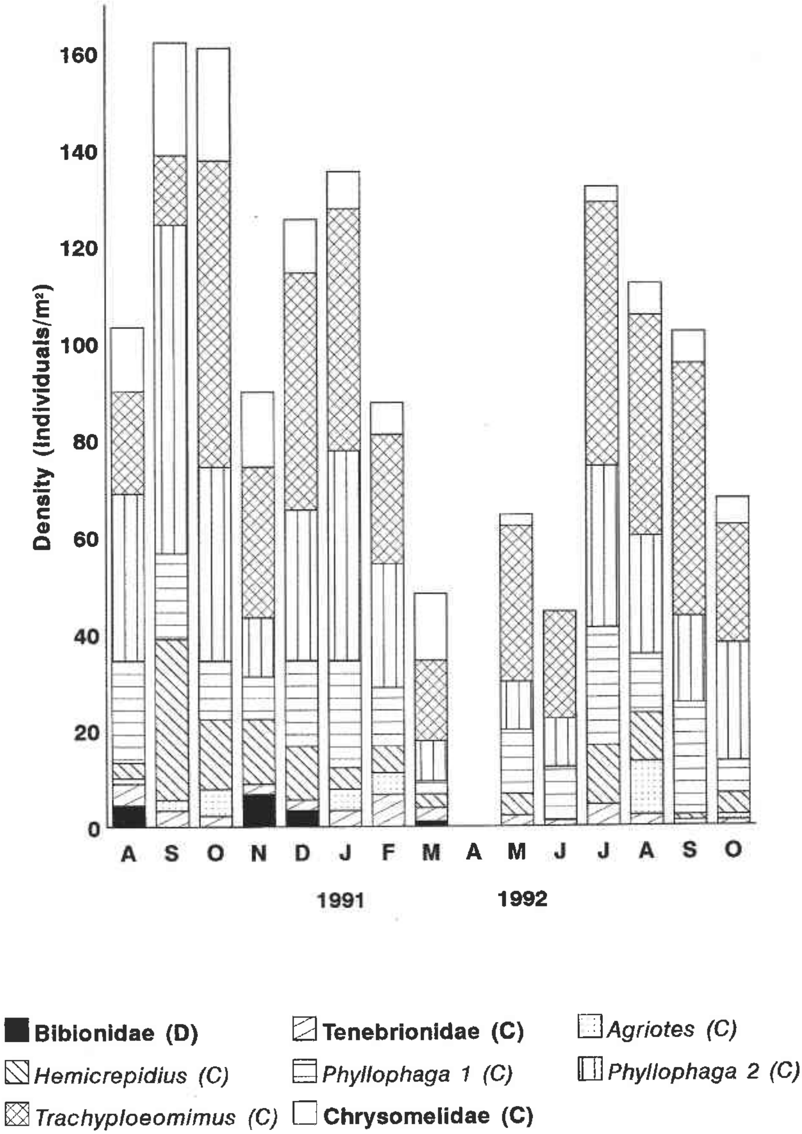

FIG. 1. Monthly variation in density of the community of root-feeding macroarthropods at Zoquiapan, Mex. (C) Coleoptera; (D) Diptera. Values for each group represent the total of 10 replicate samples per month.

this pattern did not change during the year (Fig. 3). During the sampling period, the percentage of individuals located at the 20- to 30-cm depth was lower than 6% (73 individuals) and no specimens were recorded in this stratum in March 1991 and August 1992. The dominant families (Melolonthidae and Curculionidae) showed a clumped horizontal distribution for the major part of the year (Fig. 4). Curculionidae had a more contagious distribution than did Melolonthidae (sensu Endrodi 1966), which showed a distribution statistically indistinguishable from random in May and June. The monthly estimation of *JI*

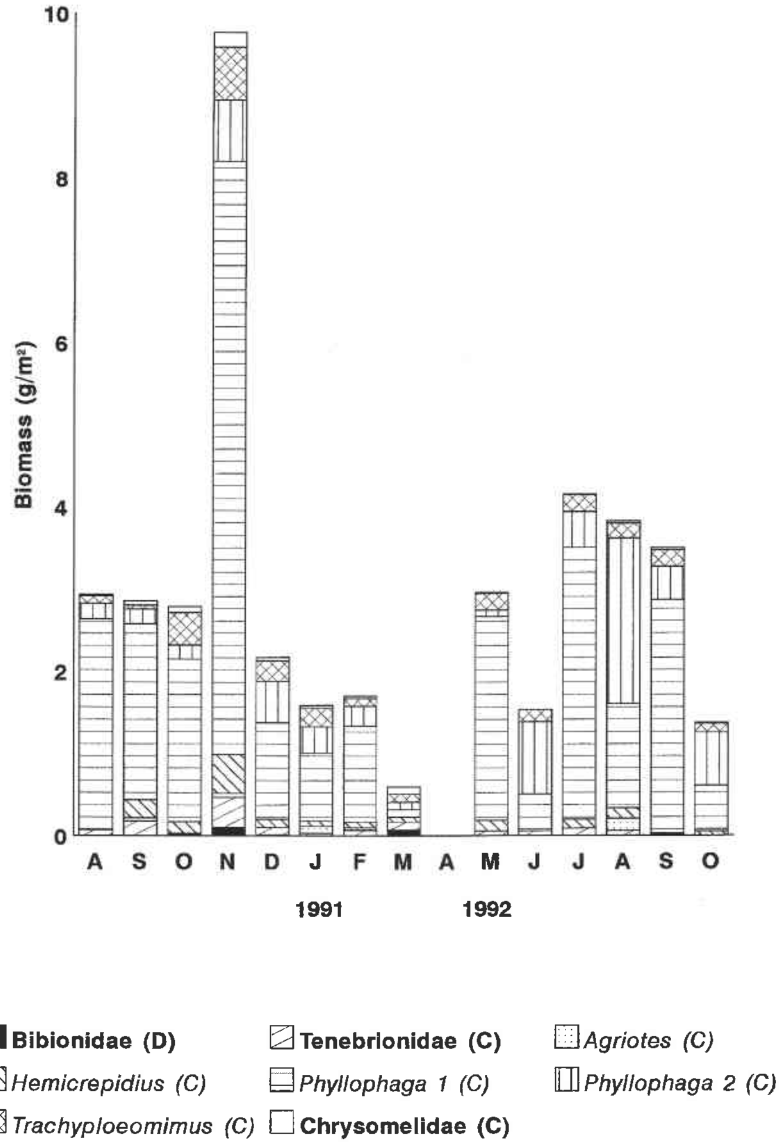

FIG. 2. Monthly variation in biomass of the community of root-feeding macroarthropods at Zoquiapan, Mex. (C) Coleoptera; (D) Diptera. Values for each group represent the total of 10 replicate samples per month.

and the Pearson *r* did not show association between these taxa (chi-square estimations of all cases had $P > 0.07$ for *JI* and $P > 0.38$ for the Pearson *r* coefficient).

Discussion

Comparison of the density and biomass of the Zoquiapan root-feeding Coleoptera with communities from different localities is difficult because the number and size of the samples and the length of the study periods are variable. Nevertheless, our data indicate that density and biomass are relatively low at our study site (Table 2).

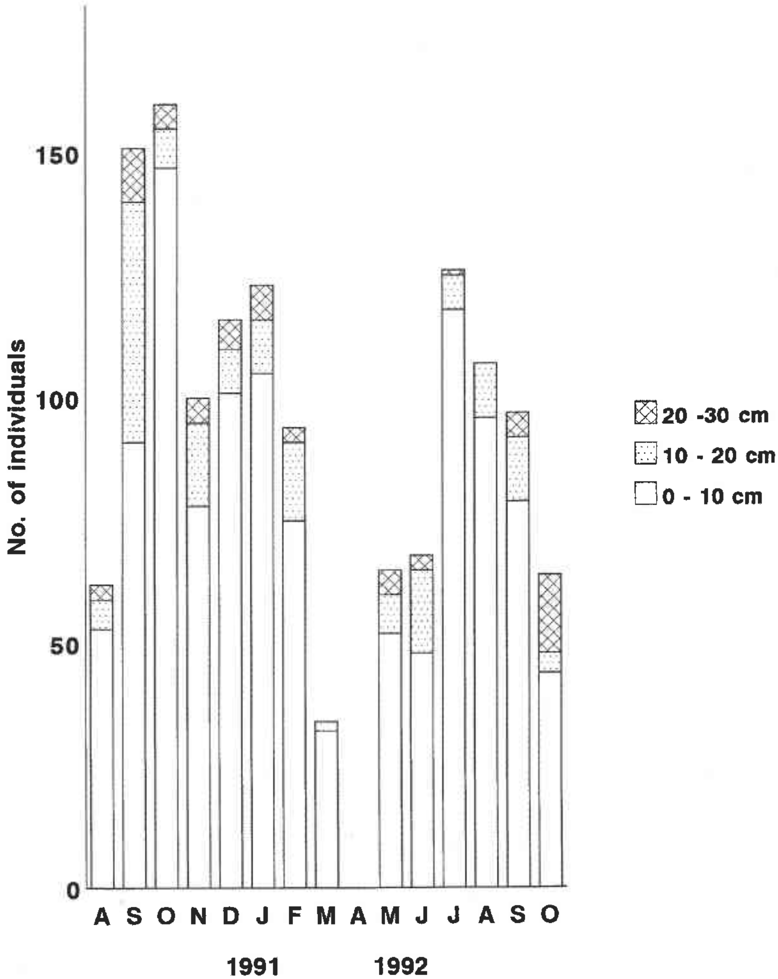

FIG. 3. Vertical distribution of the community of root-feeding macroarthropods in the first 30 cm of the soil profile at Zoquiapan, Mex.

TABLE 2. Density and biomass of root-feeding macroarthropods in tropical and temperate ecosystems. TDF = tropical deciduous forest

Site	Vegetation	Density of Coleoptera, individuals/m^2	Biomass of Coleoptera, g/m^2	Study period
Cambridge, England[1]	Grassland	2 882	Not reported	May/Nov.
Oxford, England[2]	Grassland	334	Not reported	Winter/Spring
Laguna Verde, Mex.[3]	Grassland	175	17	1 year
Laguna Verde, Mex.[4]	TDF	122	2.4	Wet season
Zoquiapan, Mex.	Pine forest	101	3	1 year

References: [1] Salt et al. (1948); [2] Ford (1935); [3] Villalobos and Lavelle (1990); [4] Lavelle et al. (1981).

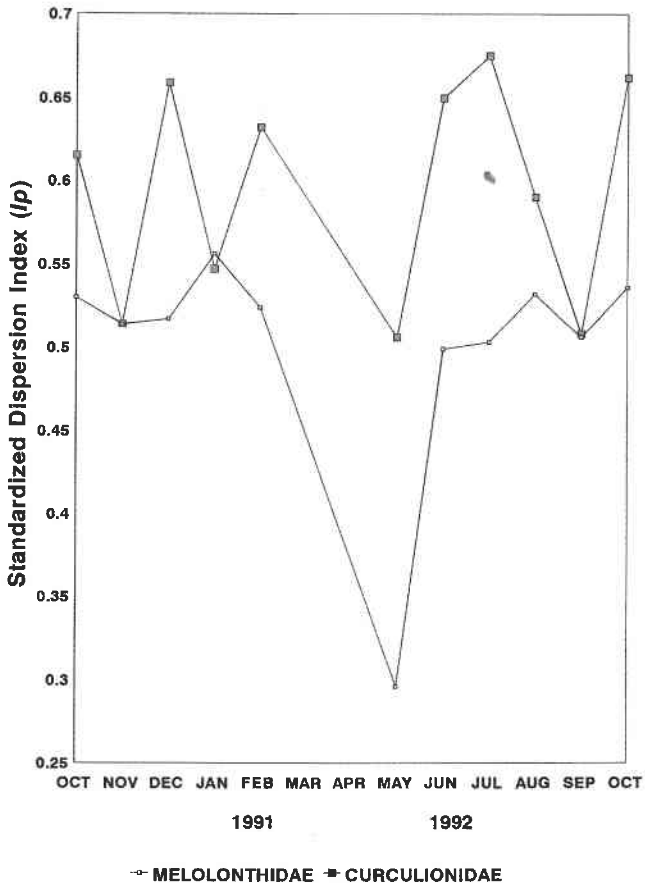

FIG. 4. Morisita's Standardized Dispersion Index (I_p) for the dominant taxa. Values greater than 0.5 indicate significant (95% confidence) aggregation, values less than 0.5 indicate random distribution.

When we compare the density of the families of root-feeding Coleoptera recorded at Zoquiapan with those reported in other studies (Table 3), it is clear that Melolonthidae (also reported as Scarabeidae), Elateridae, and Chrysomelidae are the major groups of root-feeding macroarthropods in these localities. Thus they may be the most important below-ground herbivores in these environments and may represent an important pathway for energy flow in the ecosystem (Hutchinson and King 1979).

Several of the studies in grass-dominated communities (Ford 1935; Salt et al. 1948; Hutchinson and King 1979; Villalobos and Lavelle 1990) have been conducted in cultivated pastures sown with one or two forage species. This extremely low diversity could explain the high densities of some below-ground herbivores reported in these studies. Similar density responses have been observed with above-ground insect herbivores in analogous situations (Root 1973). The plant community at Zoquiapan, on the other hand, has higher plant diversity (64 species; Obieta and Sarukhán 1981), there have been no introductions of forage species, and no cultural practices have been performed to increase primary productivity, although the area is used for grazing cattle.

The vertical distribution of the root-feeding species did not change during the year, in contrast to what has been reported for environments with marked seasonality. In the latter

TABLE 3. Mean densities (individuals per square metre) of Coleoptera reported for different ecosystems

Ecosystem	Melolonthidae	Curculionidae	Elateridae	Chrysomelidae	Tenebrionidae
Tallgrass prairie[1]	8	—	7	—	—
Tropical pasture[2]	64	1	48	58	1
Fagus–Abies forest[3]*	—	3	13	1	—
Tropical deciduous forest[4]	32	1	39	31	1
Pine forest (this study)	42	36	11	10	3

References: [1] Seastedt (1984); [2] Villalobos and Lavelle (1990); [3] Ghilarov (1979); [4] Lavelle et al. (1981).
* Means calculated from original data.

sites, the root-feeding fauna migrates toward deeper soil layers during the dry or cold seasons (Belfield 1956; Lim et al. 1980; Villalobos and Lavelle 1990). It is likely that, at Zoquiapan, the high ambient humidity prevents excessive soil moisture loss, which allows larvae to stay in the top 10 cm of soil all year around.

In general, root-feeders have a clumped distribution, a pattern determined by a complex interaction among soil type, humidity, temperature, and population density (Andersen 1987; Brown and Gange 1990). The aggregated horizontal distribution found for the dominant taxa in this study could be explained by these interactions, as well as by the availability of fine roots, whose distribution in space is heterogeneous (Caldwell 1994). The presence of fine roots is necessary for the survival of first-instar larvae, as has been observed with different species of *Phyllophaga* (Fluke et al. 1932; Chamberlain and Callenbach 1943) and with *Popillia japonica* (Régnière 1983). Despite the clumped distribution, none of the dominant taxa (Melolonthidae and Curculionidae) showed a positive or negative association. This indicates that, at least at the family level, root-feeders may respond independently to resource availability and environmental cues.

The activity of above-ground herbivores may also promote heterogeneity in the distribution of the root-feeding community. Their selective grazing and other grazer activities (e.g. urine deposition) may generate structural and functional heterogeneity in the ecosystem (Harper 1977; Jaramillo and Detling 1992). However, very few studies (e.g. Seastedt et al. 1988) have attempted to explore such interactions and there is a need to do further research in this direction.

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