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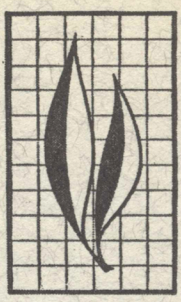

Vertical distribution patterns and seasonal changes in abundance of the microarthropod fauna of a ponderosa pine forest soil are described. The study area, located near Grass Valley, California, is marked by an abundant rainfall from October to May, and near-drought conditions from June to September. Microarthropods in the study area, estimated at about 220,739 per square meter, were characterized by considerable diversity. The Acarina (130 species) were the most abundantly represented—with densities of about 146,107 per square meter; the Prostigmata were dominant. The Collembola ranked next (44,039) per square meter. Smaller proportions of other arthropod groups were found—including the Psocoptera, Protura, and Pauropoda. Abundance of these groups and of various subcategories of Acarina and Collembola are presented. Substantial proportions of the microarthropod fauna occurred and remained fairly constant in the mineral subsoil all year. Greater densities in the humus and litter layers during the wet season was due mostly to upward shifts of the fauna. Psocoptera, Bdelloidea, and Raphignathoidea, however, remained primarily in the litter and humus all year becoming more abundant during the dry season. Other surface-dwelling forms showed little seasonal change in abundance.

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Abundance and Vertical Distribution of Microarthropods in the Surface Layers of a California Pine Forest Soil[1]

INTRODUCTION

THE ARTHROPOD FAUNA of the soil and overlying layer of organic debris normally includes a variety of mites, collembolans, insect larvae, psocids, small beetles, proturans, symphylans, pauropods, centipedes, millipedes, and various other groups. Most of these animals are less than 2 or 3 millimeters in length, and are usually referred to collectively as the soil microarthropod fauna. Some are restricted to the litter and upper layers of the humus and never penetrate to any extent into the soil proper. Others are more truly soil-inhabitants and remain hidden below the surface during their entire life histories. Vertical distribution patterns of most components of the soil fauna, however, are poorly known.

The species composition and abundance of the soil fauna are influenced by the geographical location, climate, physical and chemical properties of the soil, type of vegetative cover, nature and depth of the litter and humus, and a variety of other environmental factors. Thus, the fauna of the soil may vary considerably from one locality to another. In addition, seasonal changes in soil moisture and temperature, food supplies, biotic pressures from other components of the fauna and microflora, and inherent factors in the life cycle of each species result in cyclical fluctuations and spatial movements within the soil community.

Superimposed on these natural factors, there may be an array of potentially disruptive influences attributable to man. Growing concern about possible long-term harmful effects of various types of habitat disturbances and chemical pollutants on the soil fauna has resulted from recent studies which confirm that soil microarthropods play a significant role in processes of organic decomposition, the maintenance of soil structure, and nutrient recycling (Karg, 1962; Kühnelt, 1962; Ghilarov, 1963; Macfadyen, 1963; Crossley, Jr., and Witkamp, 1964; and Edwards, Reichle, and Crossley, Jr., 1970). Several workers have also suggested that soil microarthropods may serve as excellent indicators of soil quality (Ghilarov, 1956, 1965; Balogh, 1963; Karg, 1968). The increasing demands being placed on our soil resources make it imperative to understand more completely the nature and function of soil animal populations, and to assess the impact of forest management and agricultural practices on soil biological systems.

Research on the ecology and dynamics of soil microarthropod populations is made difficult by the complex and highly variable nature of the soil habitat, the small size, delicate nature,

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and secretive habits of these animals, taxonomic problems, and problems of sampling and experimental design. Because of these difficulties, basic information concerning the microarthropod fauna in the area chosen for study is needed before experimental or comparative studies can be initiated. In particular, there is a need for data concerning (1) the composition of the fauna; (2) population densities and the relative abundance of the various faunal components; (3) horizontal and vertical distribution patterns, and (4) the influences of seasonal and other environmental changes on the above factors.

Prior to the study reported here, only Snell (1933) in southern California has attempted to describe the general characteristics of soil microarthropod populations in western North America. Thus, the nature of the soil fauna under the varied climatic, edaphic, and cultural conditions in California remains virtually unknown. Of particular interest in this study was the influence of the extended dry season, which is typical of much of California, on the vertical distribution of the soil fauna. The information presented should facilitate future studies at the study site or at similar locations in this region. Observations were made on microarthropod groups representing all major components of the soil fauna. The study period was between October, 1964, and March, 1966.

THE STUDY AREA

The study area was located in a ponderosa pine forest habitat (*Pinus ponderosa* Dougl.) at the Boyce Thompson Institute Forest Research Station, about 5 miles south of Grass Valley, Nevada County, California. The elevation of the area is approximately 2,400 feet. Drainage is to the west into the Sacramento Valley of northern California. The soil and vegetation at the study area are representative of an extensive ponderosa pine forest occurring at lower elevations along the western slope of the Sierra Nevada.

Other trees present in this habitat are California black oak, *Quercus kelloggii* Newb., sugar pine, *Pinus lambertiana* Dougl., and incense cedar, *Libocedrus decurrens* Torr. The forest floor supports a sparse growth of manzanita, *Arctostaphylos* spp., poison oak, *Rhus diversiloba* T. and G., and seedling oak and pine trees (fig. 1). A variety of herbaceous annuals and grasses appear during the spring, but do not persist through the dry summer months. The study area comprised about half an acre in the pine forest, within which samples were taken from five adjacent plots.

The soil at the study site belongs to the Red Podzolic Group and the Sierra Clay Loam Series (Watson and Hammon, 1921). It is a reddish, acidic soil derived from underlying granitic parent material. Red podzolic soils of this general type occur over extensive timbered, high-rainfall, upland areas of the Sierra Nevada and northern Coast Ranges of California. The pH of the humus layer averaged 4.65, while that of the upper 2 inches of the mineral subsoil averaged 5.15.

The surface litter layer (L) in the study area varied in depth from about ½ to 2 inches. Below the litter layer, a shallow layer of humus measuring about 1 inch in thickness was present. The "fermentation" or F layer and the true humus or H layer could not be separated and are therefore considered together as the "humus layer" (H) in this paper. As is characteristic of most acidic, well-drained, podzolic soils of coniferous forests, a fairly distinct

Figure 1. View of the study area in a ponderosa pine forest habitat at the Boyce Thompson Institute Forest Research Station, 5 miles south of Grass Valley, California.

boundary occurred between the humus layer (A horizon) and the underlying mineral subsoil (B horizon). This permitted stratification of soil corings for separate treatment of the two layers.

The Forest Research Laboratory is located in a region which was the scene of intensive mining activities following the California gold rush of 1849. The larger trees present in the area were about 100 years old indicating that the study area was partly deforested during the mining period. During the past 75 to 100 years, the area has been relatively undisturbed.

The Grass Valley area receives about 55 inches of precipitation annually. This occurs largely during the period from October through May, an eight-month period normally receiving about 53.6 inches. The period of heaviest precipitation is from December through March, a four-month period with an average of 38.2 inches. A small amount of this falls as snow. In marked contrast, the summer dry season extends from June through September, a four-month period which normally receives only 1.4 inches of rainfall. Of particular importance to the soil-moisture regime is the fact that the dry season is also the warmest part of the year. The average low and high temperatures in July, the hottest month, are 60° and 92°F., respectively.

During this investigation, rainfall patterns deviated to some extent from the normal. The dry season lasted from early May to early November 1965, a six-month period having only 2.35 inches of rainfall. The preceding six months, November, 1964, to April, 1965, received 67.8 inches, while the following six-month period, mid-November, 1965 to April, 1966, received 38.5 inches, The monthly rainfall, departures from normal, and average minimum and maximum temperatures at Grass Valley

TABLE 1

PRECIPITATION AND TEMPERATURE DATA FOR GRASS VALLEY, CALIFORNIA, OCTOBER 1, 1964, TO MAY 31, 1966 (UNITED STATES WEATHER BUREAU)

Month	Precipitation		Temperature	
	Total	Departure from norm	Av. Min.	Av. Max.
1964	*Inches*	*Inches*	°F	°F
October	1.76	−1.03	49.9	80.0
November	11.17	+5.72	35.1	55.4
December	28.15	+18.54	36.4	49.9
1965				
January	14.87	+4.24	34.6	52.6
February	1.79	−7.78	34.5	61.5
March	3.24	−5.14	36.3	59.5
April	8.56	+3.86	40.8	60.9
May	0.31	−2.17	45.3	72.9
June	0.20	−0.40	48.9	77.6
July	0.00	−0.03	57.5	91.4
August	0.96	+0.94	57.6	89.3
September	0.36	−0.13	47.5	79.9
October	0.52	−2.27	48.9	80.6
November	11.04	+5.59	38.6	58.3
December	8.26	−1.35	31.2	52.6
1966				
January	8.07	−2.56	30.8	50.8
February	5.41	−4.16	30.4	51.6
March	3.12	−5.26	36.7	60.7
April	2.58	−2.12	45.3	73.4
May	0.64	−1.84	48.1	77.5

TABLE 2

SOIL MOISTURE LEVELS OF THE HUMUS AND UPPER 2 INCHES OF MINERAL SUBSOIL AND SOIL TEMPERATURES AT THE HUMUS-MINERAL SOIL INTERFACE AT 1 P.M. ON 19 SAMPLING DATES. MARCH 9, 1965, AND MARCH 30, 1966

Date*	Soil moisture (per cent of dry sample weight)		Soil temperature (°F)
	Humus	Subsoil	
I. Wet period:			
March 9	55.5	27.3	45
April 1	44.6	29.2	49
April 17	55.9	27.2	49
April 29	32.7	23.0	49
May 7	31.1	21.7	48
May 25	21.4	19.6	58
II. Dry period:			
June 5	12.5	23.5	60
June 15	10.2	12.3	60
July 2	8.7	8.7	71
July 26	6.1	6.7	67
Aug. 21	8.5	8.8	65
Sept. 25	9.1	7.2	65
Oct. 9	9.1	7.3	64
Oct. 24	8.6	9.5	60
Nov. 6	6.1	6.5	56
III. Wet period:			
Nov. 30	67.7	27.0	43
Dec. 22	65.8	27.2	40
Feb. 20	62.7	31.1	45
March 30	42.5	33.3	47

* Wet and dry periods refer to sampling periods shown in tables 4, 7, 8, and 9.

during the study period are given in table 1. Moisture levels of the humus layer and upper 2 inches of the mineral subsoil, and temperature readings taken in the shade at 1 p.m. at the humus-mineral soil interface are shown in table

The dry condition of the soil during the summer and fall months of 1965 is apparent from data in table 2. Soil moisture levels during July, August, September, and October averaged 8 per cent for both the humus and upper two inches of the subsoil. These were also the warmest months of the year with an average maximum air temperature of 85.3°F. A heavy rainfall in mid-November (11.04 in.) resulted in a marked increase in soil moisture levels (table 2).

METHODS

Five small plots, situated in close proximity to each other, were selected for their uniformity of appearance. For our purposes, a single larger plot would have served equally well, but one could not be found with a comparable degree of homogeneity. Small plots permitted the exclusion of trees, logs, and other features which would have an obvious modifying effect on the soil fauna. The habitat studied, therefore, can be defined as the more-or-less open forest floor as shown in figure 2.

Sampling

The plots were large enough so that the sampling operation did not seriously disturb the habitat within their

Figure 2. Plot 1 of the study area.

boundaries. Plots 1 to 4 were rectangular in shape, 6×30 feet, and could be sampled from the sides with a minimum amount of entry by the person taking the corings (fig. 2). Plot 5 was a square, 20×20 feet. Plots 1, 2, 3, and 5 were always sampled to a depth of 2 inches in the mineral subsoil (M-2). Since the humus layer was about 1 inch in thickness, the total depth of the coring was about 3 inches. The overlying leaf litter was always included in the sample.

Plot 4 was used for both the 3-inch and the deeper corings. The latter extended from 6 to 10 inches below the humus-mineral soil interface (M-6 to M-10). These deep corings were stratified into the litter plus humus layer (A horizon) and each two inches of the mineral subsoil (B horizon). The plane of separation between the humus and mineral layers was slightly below the interface so that the animals living on the surface of the mineral soil would be included in the counts from the humus layer. As nearly as possible, therefore, the 0–2 inch, mineral-soil layer was free of humus. The deeper corings were restricted to plot 4, since their removal caused some disturbance to the surrounding soil.

Plots 1 to 4 were considered to be subdivided into 180 square-foot areas. These were arranged for sampling purposes into six rows of 30 squares each. The method of determining the coring site was to select the row (1 to 6) and the square within the row (1–30) by random selection. The squares thus determined were divided among the four plots. As a rule, four corings were taken from each of plots 1, 2, and 3, and two corings from plot 4. Thus, plots 1 to 4 were considered as a unit with most samples comprised of 14 corings. Within each square-foot area selected, the investigator exercised discretion with regard to the actual point of coring. Sites

TABLE 3

NUMBER OF SPECIMENS COLLECTED ON EACH OF 13 SAMPLING DATES BETWEEN MARCH 9 and DECEMBER 22, 1965

Specimen	Mar. 9	Apr. 1	Apr. 17	May 7	May 25	June 15	July 2	July 26	Sept. 25	Oct. 24	Nov. 6	Nov. 30	Dec. 22
Symphyla	2	0	0	8	5	2	0	0	1	3	1	9	4
Geophilidae	15	15	12	16	3	4	2	1	2	7	2	17	18
Cunaxa snowi	12	4	3	7	18	12	10	14	18	9	8	10	6
Bdella longicornis	1	0	1	0	9	6	3	7	6	3	1	0	0
Neognathus terrestris	8	11	15	2	21	8	19	25	27	51	32	20	12
Ledermuelleria segnis	7	0	4	4	8	5	14	20	34	31	42	17	7
Pomerantziidae	0	0	0	0	6	16	23	3	5	1	0	1	0
Belba sp.	25	24	50	29	34	18	16	34	16	15	19	38	16
Ceratoppia bipilis	3	4	5	23	27	14	13	7	16	4	2	9	6
Plesiodamaeus sp.	3	16	16	13	13	8	22	24	5	31	5	94	14

TABLE 4

VERTICAL DISTRIBUTION OF TOTAL MICROARTHROPODS AND SEVEN MAJOR TAXA BASED ON 16 CORINGS 8 TO 10 INCHES DEEP IN THE SUBSOIL FROM PLOT 4 JUNE 5, 1965, TO MARCH 30, 1966

Category and weather period*	Per cent of total microarthropod distribution in:					Total no. microarthropods
	Litter humus	Subsoil depth (inches)				
		0–2	2–4	4–6	6–10	
Collembola						
Dry period	8.5	23.1	31.7	22.0	14.8	824
Wet period	46.3	18.2	16.4	12.6	6.6	1449
Dry & wet per.	32.6	19.9	21.9	16.0	9.6	2273
Protura						
Dry period	7.7	28.6	31.9	13.2	18.7	91
Wet period	25.4	19.0	17.5	19.0	19.0	126
Dry & wet per.	18.0	23.0	23.5	16.6	18.9	217
Pauropoda						
Dry period	0.4	4.3	12.2	36.2	46.8	483
Wet period	38.4	12.7	15.7	19.8	13.4	440
Dry & wet per.	18.5	8.3	13.9	28.4	30.9	923
Mesostigmata						
Dry period	14.7	23.6	20.1	22.8	18.9	259
Wet period	17.5	17.2	22.5	22.5	20.4	506
Dry & wet per.	16.5	19.3	21.7	22.6	19.9	765
Prostigmata						
Dry period	39.0	27.5	14.4	13.2	5.9	1496
Wet period	55.8	13.3	10.5	9.0	11.4	2374
Dry & wet per.	49.3	18.8	12.0	10.6	9.3	3870
Cryptostigmata						
Dry period	40.6	17.8	18.3	16.4	6.9	979
Wet period	46.3	16.4	15.3	10.3	11.7	1927
Dry & wet per.	44.3	16.9	16.3	12.4	10.1	2906
Acarina						
Dry period	37.3	23.6	16.3	15.3	7.5	2734
Wet period	47.9	15.0	13.7	11.0	12.4	4807
Dry & wet per.	44.1	18.1	14.7	12.5	10.6	7541
Microarthropoda						
Dry period	27.2	20.9	19.0	19.0	13.9	4292
Wet period	45.8	15.7	14.7	12.2	11.6	7101
Dry & wet per.	38.8	17.7	16.3	14.8	12.4	11393

* "Dry-period" samples were taken on June 5, August 21, and October 24; "wet-period" samples were taken on November 30, December 22, February 20, and March 30.

of previous corings, rocks, and other objects were avoided.

Samples consisting of shallow corings (to M-2) were taken from plots 1 to 4 on 13 dates between March 9 and December 22, 1965 (table 3). Deeper corings were taken from plot 4 on 7 dates between June 5, 1965, and March 30, 1966 (table 4). Plot 5 was used only for a comparison of the "wet" and "dry"

TABLE 5
ABUNDANCE OF 13 SELECTED CATEGORIES OF ACARINA IN SAMPLES TAKEN FROM PLOT 5 ON APRIL 29, AND OCTOBER 9, 1965

Category	April 29 (n = 60)			October 9 (n = 60)		
	Total	Mean	±†	Total	Mean	±†
Mesostigmata						
Zerconidae*	156	2.60	1.32	34	0.57	0.32
Cyrtolaelaptidae*	178	2.97	0.80	20	0.33	0.22
Total Gamasina*	436	7.27	1.14	116	1.93	0.76
Prostigmata						
*Cunaxoides snowi**	42	0.70	0.25	154	2.55	0.72
Total Bdelloidea*	73	1.22	0.38	259	4.32	0.95
*Ledermuelleria segnis**	23	0.38	0.24	224	3.73	1.86
*Neognathus terrestris**	78	1.30	0.48	206	3.43	1.09
Total Raphignathoidea*	154	2.57	0.71	661	11.02	3.49
Paratydeidae	151	2.52	0.64	203	3.38	1.16
*Lasiotydaeus krantzi**	11	0.18	0.17	1020	17.00	7.23
Cryptostigmata						
Trichoribates sp.	254	4.23	0.80	190	3.17	0.77
Belba sp.*	105	1.75	0.38	44	0.73	0.49
Plesiodamaeus sp.	86	1.43	0.37	117	1.95	0.95

* Differences between means significant at $P \leq 0.05$.
† .95 confidence limits of the mean.

TABLE 6
ABUNDANCE OF 19 SELECTED CATEGORIES OF MICROARTHROPODS IN SAMPLES TAKEN FROM THE STUDY AREA ON OCTOBER 3 AND NOVEMBER 17, 1964

Category	October 3 (n = 20)			November 17 (n = 16)†		
	Total	Mean	±†	Total	Mean	±†
Psocoptera*	866	43.30	±11.11	50	3.13	± 1.59
Collembola:						
Poduridae*	0	0.00	....	998	62.38	21.24
Entomobryidae*	31	1.55	1.21	404	25.25	13.93
Sminthuridae*	0	0.00	....	144	9.00	3.42
Protura*	0	0.00	....	116	7.25	4.34
Pauropoda*	0	0.00	....	283	17.69	8.23
Mesostigmata:						
Rhodacarus spp.*	0	0.00	....	115	7.19	3.16
Gamasina (total)*	1	0.05	....	305	19.06	4.58
Prostigmata:						
Cunaxa snowi	74	3.70	2.90	24	1.50	2.00
*Spinibdella cronini**	74	3.70	1.41	4	0.25	....
Bdelloidea (total)*	190	9.50	3.53	40	2.50	2.08
Ledermuelleria segnis	47	2.35	2.30	38	2.38	3.55
Neognathus terrestris	116	5.80	2.81	41	2.56	1.63
Raphignathoidea (total)	211	10.55	4.97	116	7.25	5.51
Paratydeidae	89	4.45	2.01	67	4.19	2.44
Lasiotydaeus krantzi	176	8.80	9.51	104	6.50	11.05
Cryptostigmata:						
Trichoribates sp.	101	5.05	1.95	133	8.31	5.64
Belba sp.*	3	0.15	....	36	2.25	1.54
Plesiodamaeus sp.	49	2.45	1.32	58	3.63	3.76

* Differences between means significant at $P \leq 0.05$.
† .95 confidence limits of the mean.

periods. Samples consisting of 60 corings each were taken from arbitrarily selected points within this plot on April 29 and October 9, 1965 (table 5). The samples of October 3 and November 17, 1964, were taken from within the study area before the plots were established (table 6). All sampling, sorting, and counting of the fauna were done by the writer. Also, with the exception of four species of Cryptostigmata which were examined by Dr. T. A. Woolley of Col-

Figure 3. Twelve-inch coring tool.

orado State University, all specimens collected were identified by the writer.

Two similar soil-coring tools were used. These were rectangular in cross section, measuring $2 \times 2\frac{1}{2}$ inches across (fig. 3). One was 6 inches long, the other 12 inches. Each coring, therefore, included 5 square inches of the soil surface. Each tool consisted of two U-shaped pieces of $\frac{1}{16}$ inch steel plate, one of which fit tightly over the other to form the complete tool. The two halves were held in place by two bolts which passed through the overlapping sides.

The sampling tools could be opened to expose the core in place within one-half of the tool (fig. 4). The core could thus be removed intact or stratified into layers with a minimum amount of disturbance and compression. The tool was forced into the soil by gently tapping the upper end with a sledgehammer. A block of wood was placed over the end to prevent damage to the tool.

Extraction

Upon removal from the coring tool, soil samples (if dry) were placed in sealed polyethylene bags or (if wet) in paper containers and returned to the laboratory for processing. Care was exercised to keep the samples cool and without moisture loss during transport. If storage of samples was necessary prior to extraction of the fauna, this was done at 40°F. Tests indicated that storage at this temperature for periods up to 17 days had no apparent detrimental effect on survival of the fauna (Price, 1967). In this study, however, sample storage never exceeded four days.

The microarthropod fauna was extracted from the soil by means of a modified Berlese funnel or Tullgren apparatus (fig. 5). In studies of the type reported which involve many different categories of small arthropods, no single extraction procedure is best suited or equally efficient for all groups. As a result, the data presented only provide minimal estimates of the density of certain categories, and are biased in favor of those species and life stages which are extracted most readily by the technique employed. To keep this bias as constant as possible during the course of the investigation, the operational procedure was rigidly standardized.

The Berlese-funnel cabinet shown in figure 5 is open as it would be when loading or removing samples. When ready for operation, a piece of plywood

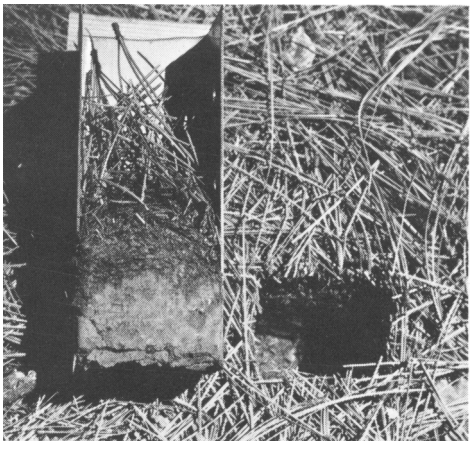

Figure 4. Six-inch coring tool opened to expose soil sample; coring site at right.

Figure 5. Open Berlese funnel cabinet showing six extraction units.

was placed in front of the cabinet and the top was lowered. This resulted in a closed cabinet with a 75-watt incandescent light bulb positioned directly above each sample container. By controlling the voltage to the light bulbs, the temperature in the top section of the cabinet could be regulated. In this study, the temperature in the upper section of the cabinets was held between 95 and 100°F for the first 24 hours. Thereafter, the temperature was raised about 10 degrees for each subsequent 24-hour period. The time required for complete extraction of the fauna was approximately three days (Price, 1967).

Separate samples were taken for soil moisture determinations. Soil moisture levels were determined by measuring weight loss of samples after complete drying in a vacuum oven at 160 to 170°F at –21 pounds pressure for three days. Soil moisture is expressed as per cent of dry sample weight.

CHARACTERISTICS OF THE FAUNA

The term "microarthropod" is used here to designate all small arthropods which were extracted from the soil samples. These ranged in size from less than 0.5 mm for many of the Acarina to 5 or 6 mm in the case of the Japygidae (Diplura) and Geophilidae (Chilopoda). A wide range of microarthropod taxa were encountered. With the exception of certain Cryptostigmata and Prostigmata (Acarina), the fauna was sorted and counted at family or higher taxonomic levels. In several of the tables herein, only certain "selected categories" are included. These represent microarthropod groups which were either most abundant in the samples or most appropriate to the observations being presented.

The most abundant major compo-

nents of the fauna were the Acarina, Collembola, Pauropoda, Psocoptera, and Protura. Other groups less commonly encountered were the Symphyla, geophilid centipedes, polyxenid millipedes, pseudoscorpions, spiders, japygids, thrips, ants, micro-Coleoptera, and various other larval and adult insects. The Collembola were counted as three family groups, sometimes considered superfamilies, *i.e.*, the Poduridae, Entomobryidae, and Sminthuridae. The Acarina were divided into the Mesostigmata, Prostigmata, and Cryptostigmata. Members of the acarine suborder Astigmata were rarely encountered.

The Mesostigmata encountered were predominantly members of the cohort Gamasina and superfamily Parasitoidea. Approximately 35 species were found. Two subgroups of the Gamasina were treated separately, *i.e.*, the genus *Rhodacarus* of the family Rhodacaridae, and the family Zerconidae. Five species of *Rhodacarus* were present and included both *R.* (*Rhodacarus*) spp. and *R.* (*Rhodacarellus*) spp. Three unidentified species of Zerconidae representing three genera *i.e., Parazercon, Prozercon,* and *Zercon,* were encountered. Other members of the Gamasina included five species of Ascidae, seven species of Hypoaspidae, two species of Pachylaelaptidae, two species of Parasitidae, four species of Phytoseiidae, three species of Rhodacaridae excluding *Rhodacarus* spp., and four species of Cyrtolaelaptidae. It is believed that many of the species of Gamasina in the study area are undescribed. The four species of Phytoseiidae were *Amblyseius brevispinus* (Kennett), *A. neomexicanus* (Chant), *A. inornatus* Schuster and Pritchard, and *A. floridanus* (Muma). One species of Rhodacaridae present was *Antennoseius magniscutum* (Weis-Fogh). One species of Ascidae appeared to be closely related to *Zerconopsis decemremiger* Evans and Hyatt. Two species of Cyrtolaelaptidae were closely related to *Cyrtolaelaps* (*Gamasellus*) *legetti* Ryke, and *C.* (*Gamasellus*) *falciger* (G. and R. Canestrini). In addition to the Gamasina, two species of Uropodina in the genus *Urodiaspis* were encountered, although infrequently.

Approximately 33 species of Cryptostigmata were collected. Of these, individual counts were made on only four species. These were examined by Dr. T. A. Woolley of Colorado State University, who noted that only one, *Ceratoppia bipilis* (Hermann) of the family Ceratoppidae, had been described. The other species represent the family Belbidae (*Belba* sp.) Ceratozetidae (*Trichoribates* sp.), and Gymnodamaeidae (*Plesiodamaeus* sp.).

The Prostigmata were the most abundant group of mites, as well as the most diverse in species composition. An estimated 60 species were collected. The bulk of the population of Prostigmata was composed of relatively small mites in the families Nanorchestidae, Pachygnathidae, Tarsonemidae, Pyemotidae, Scutacaridae, Tydeidae, and Eupodidae. Other members of the Prostigmata represented the families Rhagidiidae, Tetranychidae (especially *Bryobia praetiosa* Koch, *Petrobia latens* Müller, and *Oligonychus* spp.), Linotetranidae (*Linotetranus achrous* Baker and Pritchard), Caeculidae, Labidostommidae, Trombiculidae (especially chiggers), Anystidae, Erythraeidae, and Cheyletidae (*Hypopicheyla elongata* Volgin), and *Cunliffella panamensis* (Baker).

Because of the particular interest and taxonomic competence of the writer, emphasis among the Acarina was placed on predatory Prostigmata belonging to the Bdellidae and Cunaxidae (Bdelloidea), and the Caligonellidae, Cryptognathidae, Raphignathidae, and Stigmaeidae (Raphignathoidea). The most common species of Bdelloidea were

Bdella longicornis (Linn.), *Spinibdella cronini* (Baker and Balock), *Cunaxa snowi* Baker and Hoffmann, and *Cunaxoides whartoni* Baker and Hoffmann. Other Bdelloidea present included *Bdellodes longirostris* (Hermann), *Cyta coerulipes* (Dugès), *Cyta latirostris* (Hermann), *Spinibdella tenuirostris* (Ewing), *Cunaxa capreolus* (Berl.), *Cunaxa setirostris* (Hermann), and *Cunaxa womersleyi* Baker and Hoffmann. The most common species of Raphignathoidea were *Cryptognathus aureatus* Summers and Chaudri, *Raphignathus gracilis* (Rach), *Neognathus terrestris* (Summers and Schlinger), and *Ledermuelleria segnis* (Koch). Other Raphignathoidea present included *Caligonella humilis* (Koch), *Raphignathus collegiatus* Atyeo, Baker, and Crossley, *Ledermuelleria pectinata* (Ewing), and *Ledermuelleriopsis plumosa* Willmann.

Pomerantzia prolata Price, a member of the rare Raphignathoid family Pomerantziidae, was treated separately due to its peculiar vertical distribution pattern. One species of Tydeidae (*Lasiotydaeus krantzi* Baker), and the only species of Paratydeidae (*Neotydeus* sp.), were counted separately.

VERTICAL DISTRIBUTION OF THE FAUNA

As previously noted, the standard subsampling unit, or coring, used in this study included the leaf litter, humus layer, and the upper 2 inches of the mineral subsoil. In view of results published by other workers on the microarthropod faunas of woodland or coniferous forest habitats (Murphy, 1953; Bellinger, 1954; van der Drift, 1962; Poole, 1961), it was expected that corings extending to this depth would include the majority of individuals in most categories, and that periodic sampling to this depth would provide data indicating seasonal changes in population densities. In order to determine which, if any, groups were present in significant proportions at soil depths below those included in this standard sample, a limited number of deeper corings were taken at intervals in plot 4. These corings extended in depth from 6 to as much as 10 inches in the mineral subsoil. The depth varied due to sampling difficulties. In some cases, the soil at the bottom fell from the coring tool upon withdrawal and was lost. More commonly, the sampling tool struck rocks or large roots below the soil surface which prevented deeper penetration.

Examination of the fauna extracted from the various strata of these deeper corings revealed that a substantial proportion of some taxonomic categories occurred below the level selected for the standard samples. This fact has an important bearing on the interpretation of data pertaining to seasonal changes in abundance.

Information on vertical distribution is presented in tables 4 and 7. Table 4 gives the percentages of the total fauna in seven major taxa, as well as the total microarthropod fauna which were collected from the litter and humus, and from each 2-inch layer of the subsoil. These data are based only on those corings which extended either to 8 or to 10 inches in the subsoil. In order to determine if vertical distribution patterns were related to soil moisture levels, the sampling period was divided into a dry and a wet period. Although the point of division is arbitrary, the data presented in table 2 indicate that the two periods were distinct with regard to soil moisture levels. The data for the entire

TABLE 7

DISTRIBUTION OF SPECIMENS (SELECTED CATEGORIES) FROM 39 PLOT-4 CORINGS 6 TO 10 INCHES DEEP IN THE SUBSOIL, FOR BOTH DRY AND WET PERIODS OF YEAR

Taxa	Microarthropods found during:					
	Dry period*			Wet period*		
	Total	Per cent of total in:†		Total	Per cent of total in:†	
		L&H	L,H,MO–2		L&H	L,H,MO–2
	No.	*Per cent*		*No.*	*Per cent*	
Psocoptera	199	78.4	88.9	14	78.6	78.6
Protura	213	3.3	20.7	132	24.2	41.7
Collembola						
Poduridae	1774	2.9	19.2	1062	34.0	50.7
Entomobryidae	572	10.7	28.5	426	73.2	83.8
Sminthuridae	0	...	...	31	90.3	90.3
Total	2346	4.8	21.4	1519	46.1	64.7
Symphyla	35	0.0	20.0	41	12.2	24.4
Chilopoda						
Geophilidae	13	23.1	38.5	40	15.0	32.5
Diplura						
Japygidae	52	0.0	1.9	29	0.0	3.4
Gamasina						
Zerconidae	47	25.5	59.6	37	43.2	73.0
Rhodacarus spp	299	3.7	26.8	257	3.1	20.6
Other Gamasina	70	28.6	51.4	141	15.6	34.0
Total	416	10.5	34.1	435	12.2	29.4
Prostigmata						
Bdelloidea	57	96.5	98.3	29	100.0	100.0
Raphignathoidea	131	87.0	93.9	41	97.6	97.6
Pomerantziidae	96	2.1	12.5	73	0.0	0.0
Paratydeidae	181	27.6	80.7	109	20.2	64.2
L. krantzi	52	90.4	100.0	8	100.0	100.0
Cryptostigmata						
Belba sp	40	22.5	80.0	23	100.0	100.0
Trichoribates sp	29	86.2	100.0	16	100.0	100.0
C. bipilis	47	93.6	100.0	13	100.0	100.0
Plesiodamaeus sp	58	84.5	100.0	17	99.0	100.0

* Data for dry period (June 5 to October 24) based on 28 corings, for wet period (November 30 to March 30) based on 11 corings.
† L = Litter; H = humus; MO–2 = upper 2 inches of subsoil.

sampling period is included to indicate the general vertical distribution of these major taxa.

In table 7 vertical distribution patterns are presented for 17 subcategories of microarthropods. These data are based on all coring taken during the sampling period which extended to depths of between 6 inches and the maximum coring depth of 10 inches in the subsoil. The per cent of the total numbers collected, which were found in the litter and humus only, and in the litter, humus, and upper 2 inches of the subsoil are given. These data are divided into a dry and wet period, as in table 4.

POPULATION DENSITIES

It is evident from data presented in tables 4 and 7 that estimates of population densities of most major taxa must be based on corings which extend relatively deep into the mineral subsoil. For this reason, population estimates of the total microarthropod fauna and seven major taxa given in table 8 are based on corings which extended either to 8 or 10 inches in the subsoil. The totals obtained

TABLE 8

ESTIMATED POPULATION DENSITIES OF TOTAL MICROARTHROPODS AND SEVEN MAJOR TAXA BASED ON 16 CORINGS EXTENDING 8- TO 10-INCHES DEEP IN THE SUBSOIL TAKEN DURING THE PERIOD FROM JUNE 5, 1965, TO MARCH 30, 1966

Category	Estimated number:			
	Per square foot			Per square meter
	Dry period	Wet period	Dry & wet periods	Dry & wet periods
Collembola	3,850	4,403	4,091	44,039
Protura	419	403	391	4,204
Pauropoda	2,493	1,313	1,661	17,883
Mesostigmata	1,299	1,372	1,377	14,822
Prostigmata	7,363	6,923	6,966	74,981
Cryptostigmata	4,389	5,567	5,231	56,304
Acarina	13,053	13,862	13,574	146,107
Microarthropoda	20,526	20,807	20,507	220,739

TABLE 9

ESTIMATES OF POPULATION DENSITIES OF 23 SELECTED CATEGORIES OF MICROARTHROPODS BASED ON DATA PRESENTED IN TABLE 7

Category of microarthropod	Dry period		Wet period	
	No./ft²	No./m²	No./ft²	No./m²
Psocoptera	205	2203	37	395
Protura	219	2358	346	3720
Poduridae	1825	19641	2781	29929
Entomobryidae	588	6333	1115	12006
Sminthuridae	0	0	81	874
Total Collembola	2413	25974	3977	42809
Pauropoda	969	10429	1257	13527
Symphyla	36	388	107	1156
Geophilidae	13	144	105	1127
Japygidae	54	576	76	817
Zerconidae	48	520	97	1043
Rhodacarus spp.	308	3310	673	7243
Other Gamasina	72	775	369	3974
Total Gamasina	428	4605	1139	12260
Bdelloidea	59	631	76	817
Raphignathoidea	135	1450	107	1156
Pomerantziidae	99	1063	191	2057
Paratydeidae	186	2004	285	3072
Lasiotydaeus krantzi	54	576	21	226
Belba sp.	41	443	60	648
Trichoribates sp.	30	321	42	451
Cerattopia bipilis	48	520	34	366
Plesiodamaeus sp.	60	642	254	2734

from these corings are given in table 4. In addition, estimates of populations of several major taxa and a number of lesser categories are presented in table 9. These are based on total numbers collected from all corings which extended to depths of at least 6 inches in the subsoil. These totals are presented in table 7. In the text, population densities are expressed as numbers per square meter.[2]

[2] To facilitate comparison with the results of other workers and to more easily visualize abundance, estimates of density given in tables 8 and 9 are presented as numbers per square foot, as well as numbers per square meter.

SEASONAL CHANGES IN ABUNDANCE

Three sets of samples were taken to determine if seasonal changes in soil moisture had a noticeable impact on the abundance and composition of the soil fauna. The first set consisted of two samples. The first was taken on October 3 and the second on November 17, 1964. The first sampling date was near the end of the summer-fall dry period. Soil moisture levels of the humus and top 1 inch of the subsoil analyzed together was only 3.7 per cent. The sample of November 17 followed a rainy period (October 28 to November 13) with 11.60 inches of precipitation. The moisture level of the humus and top 1 inch of the subsoil increased to 37.8 per cent. Table 6 gives the mean number of individuals collected on each sampling date in 19 selected categories. The 95 per cent confidence limits of the mean are included for those categories with mean counts exceeding 1.0. The samples included the litter, humus, and upper 1 inch of subsoil.

The second set of two samples each consisted of 60 corings taken from plot 5 on April 29 and October 9, 1965. The sample of April 29 was taken during the moist spring period. Soil moisture was 32.7 per cent for the humus and 23.0 per cent for the upper 2 inches of the subsoil. By October 9, soil moisture levels had dropped to 9.1 per cent for the humus and 7.3 per cent for the subsoil. Soil temperatures at the humus-mineral soil interface at 1 p.m. rose from 49°F on April 29 to 64°F or October 9 (table 2). Counts were made only for selected categories of Acarina. The total and mean counts and 95 per cent confidence limits of the mean for each of the categories of Acarina are given in table 5.

The third set consisted of a sequence of 13 samples taken from plots 1 through 4 during the period between March 9 and December 22, 1965. Most samples consisted of 14 corings, each of which covered an area of 5 square inches and penetrated to a depth of 2 inches into the mineral subsoil. Soil moisture levels and soil temperatures on each sampling date are given in table 2. On the basis of these measurements, this 10-month interval was divided into three periods.

In the first period (I), soil moisture levels initially were high and soil temperatures were low. During this period, however, soil moisture dropped, while temperatures rose. In the second period (II), soil moisture remained low, and soil temperatures were high. This represents the warm, dry summer and early fall period. In the third (III), soil temperatures were low, and soil moisture was high. The increase in soil moisture in the third period followed the first rainfall of the season in mid-November (table 2).

Seasonal changes in the abundance of 16 selected categories of microarthropods are presented in figs. 6, 7, and 8. The estimated numbers per square foot are plotted together with the mean and 0.95 per cent confidence interval of the mean for each of the three periods indicated in table 2. Confidence intervals of the means for each sampling date are given by Price (1967). Analysis of variance/mean ratios indicated a high degree of aggregation of the various components of the fauna. Appropriate tests revealed that for almost every category the probability of random distribution in the soil was considerably less than 5 per cent. The high variance of the data remains evident in figs. 6, 7, and 8, even though the confidence intervals are based on a large number of subsampling units, i.e., 70 corings for period I, 76 for period II, and 26 for period III. Grouping of the data in this manner, however, permitted the recording of seasonal changes in abundance rela-

tive to these three periods. More extensive data on changes in the abundance of a number of family and species groups during this 10-month interval have been presented by Price (1967). In most cases, the total numbers obtained on each sampling date were too low to establish any significant seasonal change in abundance. Some examples are given in table 3.

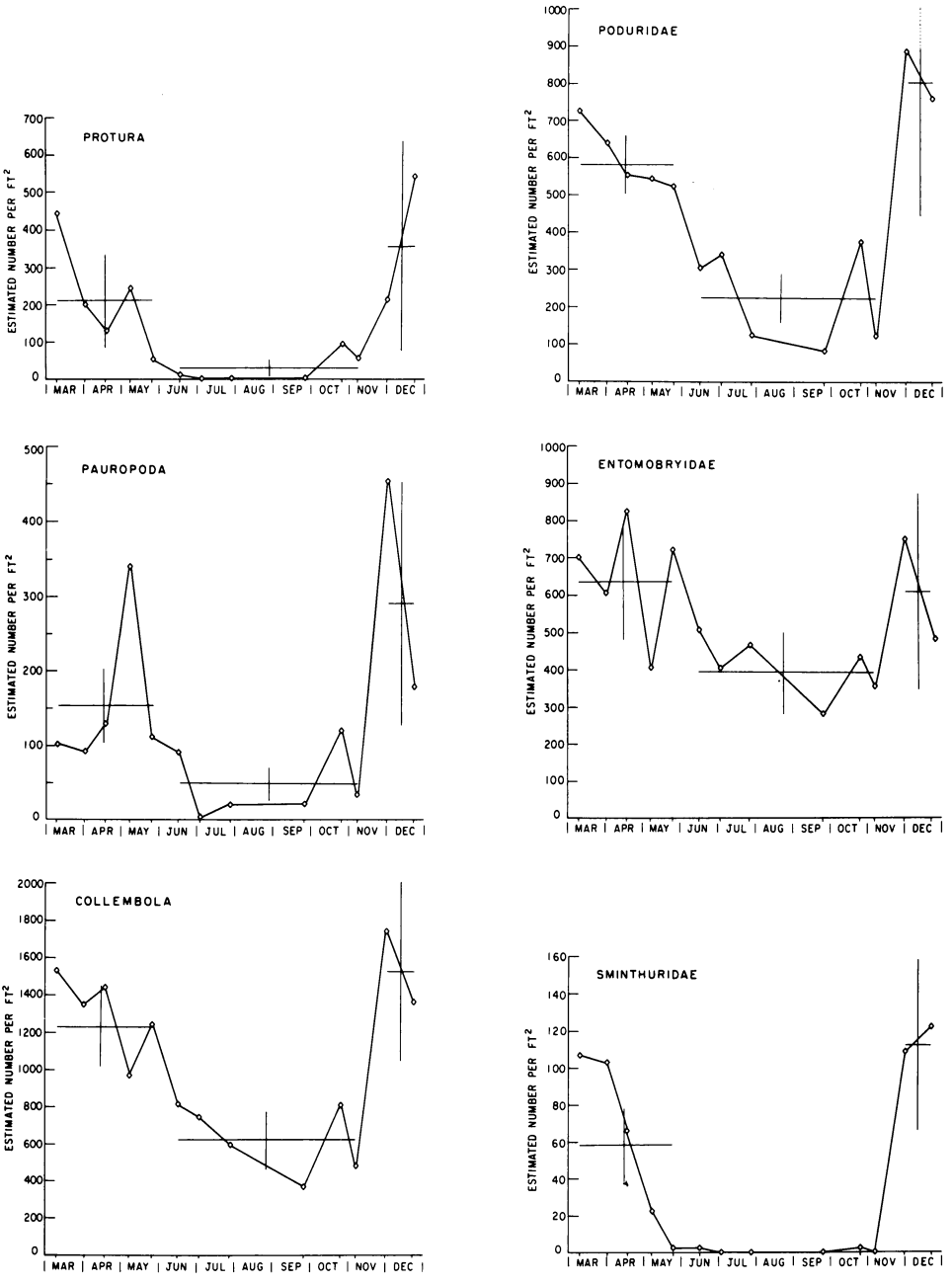

Figure 6. Abundance of Protura, Pauropoda, and Collembola in the litter, humus, and upper 2 inches of the subsoil during the period from March 9 to December 22, 1965. Average numbers per square foot and 95% confidence intervals are included for each of three periods of the years as indicated in table 2.

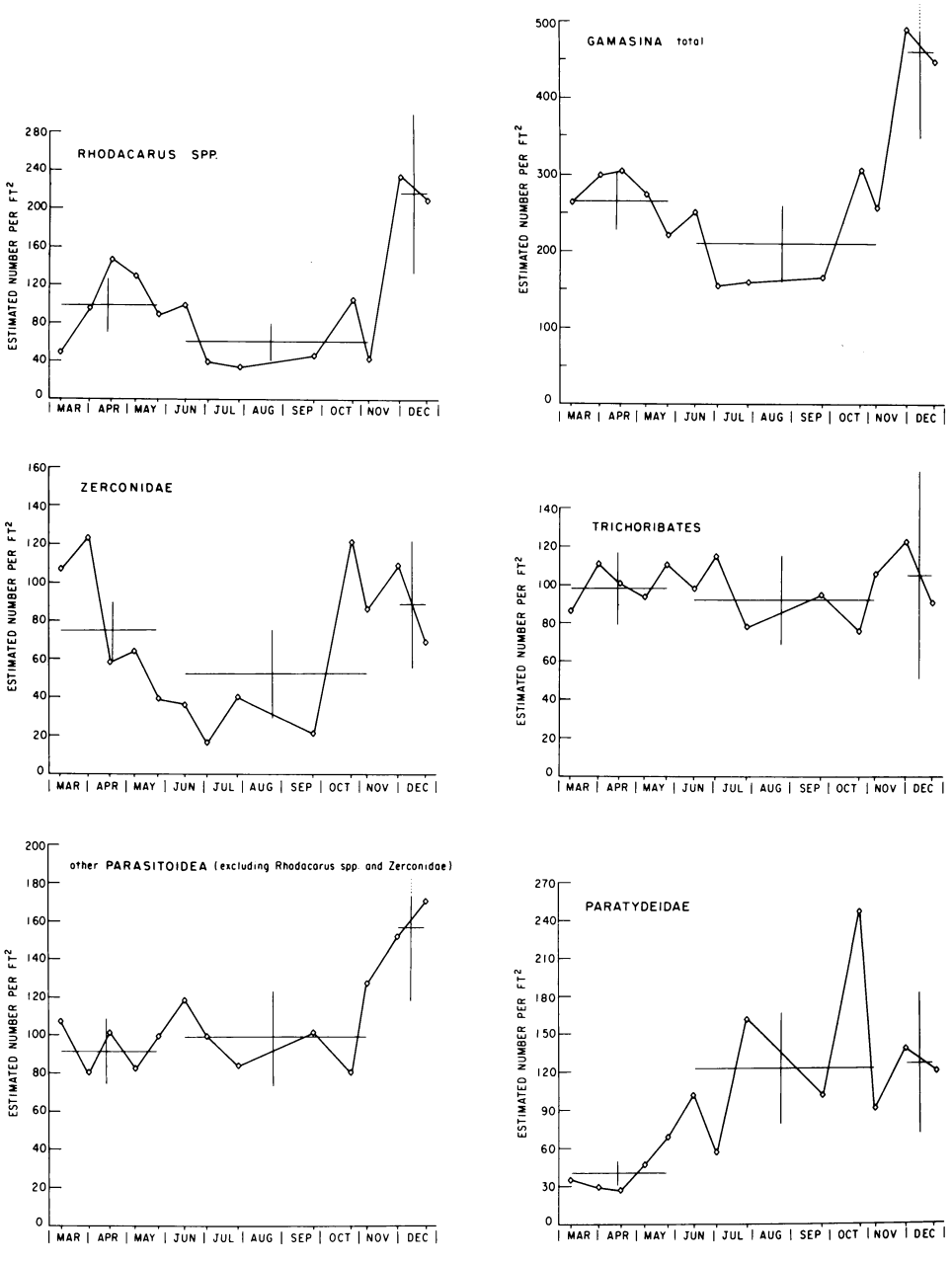

Figure 7. Abundance of six selected categories of Acarina in the litter, humus, and upper 2 inches of the subsoil during the period from March 9 to December 22, 1965. Average numbers per square foot and .95 confidence intervals are included for each of three periods of the year as indicated in table 2.

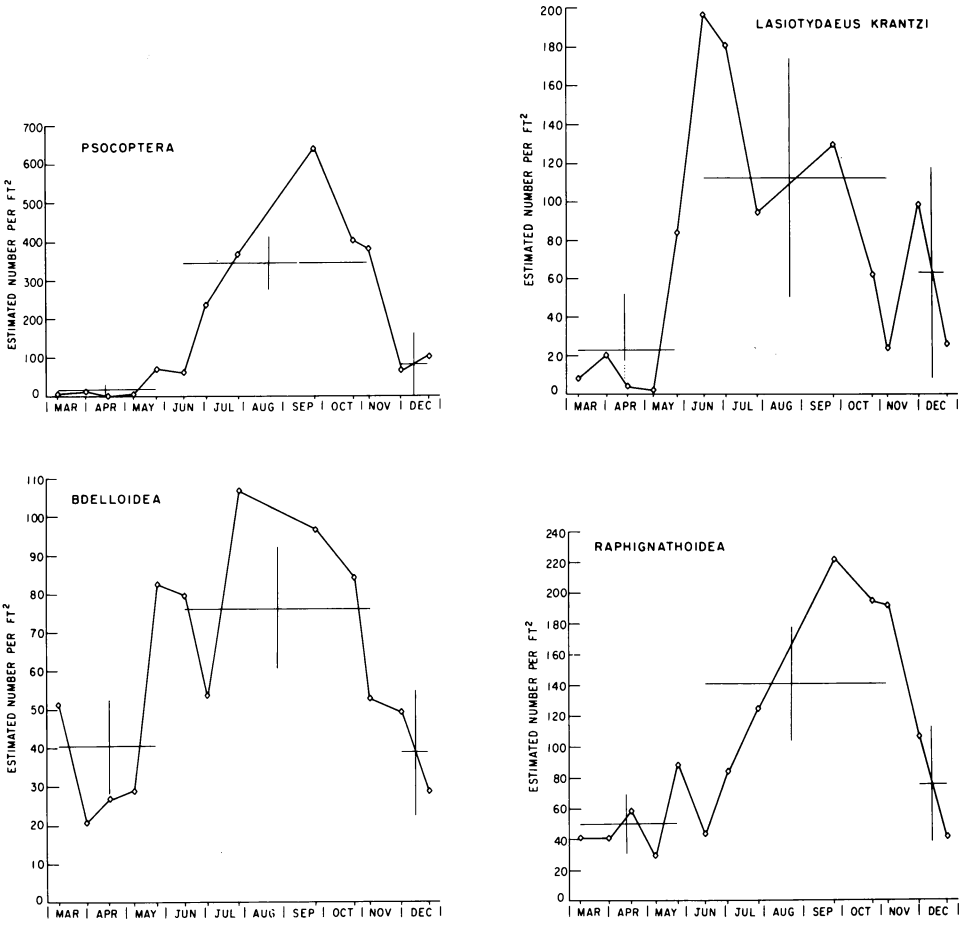

Figure 8. Abundance of Psocoptera and three selected categories of Acarina in the litter, humus, and upper 2 inches of the subsoil during the period from March 9 to December 22, 1965. Average numbers per square foot and 95 per cent confidence intervals are included for each of three periods of the year as indicated in table 2.

DISCUSSION

Vertical distribution

During the sampling period as a whole, only about 39 per cent of the total microarthropod fauna was found in the litter and humus layers (table 4). During the wet period, less than one-half of the fauna occurred in these layers, whereas during the dry period, the proportion dropped to about one-fourth of the total (table 4). Of the seven major categories considered, more than 50 per cent of the fauna in every group except the Prostigmata occurred in the mineral subsoil in both the dry and wet periods of the year. Only 39 per cent of the Prostigmata occurred in the litter and humus during the dry season, and 56 per cent occurred in the wet season (table 4).

Data in table 4 indicate that substantial proportions of the fauna occurred below depths of two inches in the mineral subsoil. For example, during the wet period, only about 65 per cent of

the Collembola, 63 per cent of the Acarina, and 62 per cent of the total fauna occurred above this level. Members of the Protura, Pauropoda, Poduridae, Symphyla, Geophilidae, Japygidae, *Rhodacarus* spp., Gamasina, and Pomerantziidae were found to occur in large part below 2 inches in the subsoil during both the dry and wet periods of the year (tables 4 and 7). The numbers of Collembola, Protura, Pauropoda, and Prostigmata in the litter and humus were greater during the wet than during the dry part of the year. This suggests an upward movement of these groups in response to increased soil moisture in the surface layers. Other groups, however, tended to remain deep in the soil and showed little or no increase in the surface layers during the wet season. These included the Mesostigmata, Cryptostigmata, Geophilidae, Japygidae, Gamasina (except Zerconidae), Pomerantziidae, and Paratydeidae (tables 4 and 7). The Psocoptera, Bdelloidea, Raphignathoidea, and certain species of Cryptostigmata remained in the surface layers throughout the year (table 7).

Data in table 4 also indicate that some part of the population of every major category extends to depths below 10 inches in the subsoil. Thus, the percentages given in tables 4 and 7 are higher than would be obtained if the corings had extended deeper into the soil.

The occurrence of substantial proportions of the fauna below the humus layer in the study area is unusual. Workers in the eastern North America, Great Britain, and northern Europe have usually noticed a marked concentration of the fauna in the uppermost levels of the soil (Kevan, 1962; Wallwork, 1970). This surface concentration is particularly true of most of the Acarina and Collembola (Evans, Sheals and Macfarlane, 1961; Hale, 1967; Wallwork, 1967). Certain components of the fauna, however, such as the Pauropoda, Protura, Symphyla, *Rhodacarus* spp. (Gamasina), and *Onychiurus* spp. (Collembola) have been shown to be more subterranean in habits (Glasgow, 1939; Salt *et al.* 1948, Edwards, 1959; Poole, 1961; Sheals, 1957; and Raw, 1967). Murphy (1953), for example, took corings 12 inches deep in natural heathland in England and found 96 per cent of the total fauna in the upper 2¼ inches. Dhillon and Gibson (1962) found 92.6 per cent of the collembolan fauna in grassland soil in England in the upper 1½ inches. Haarløv (1950) in Denmark found 86 per cent of the total fauna in a hawthorn thicket in the upper 5 cm. Wood (1967*b*) in a study of four grassland sites in England found over 76 per cent of the Collembola and Acarina in the upper 4 cm and 90 per cent or more of the total fauna in the upper 6 cm. Similar results for other non-wooded habitats are reported by Ford (1935), Weis-Fogh (1948), Salt *et al.* (1948), Macfadyen (1952), and Block (1966).

According to Murphy (1953, 1955), a concentration of the fauna in the uppermost soil layers is most apparent in wooded habitats and particularly in coniferous forest. In the latter case, this is attributed to the discrete and relatively shallow litter and humus layers overlying more-or-less impoverished mineral subsoil. Evans, Sheals, and Macfarlane (1961) suggest that in English forests, the Acarina are largely confined in or above the humus-mineral soil interface, and that Mesostigmata, with certain exceptions, are rarely encountered below 2–3 cm. Van der Drift (1962) in a study of three woodland sites in Holland found 80 per cent or more of the common arthropod species restricted to the upper 5 cm. Bellinger (1954) in a study of three coniferous forest sites in Connecticut found the Collembola confined largely to the organic horizon. Poole (1961) found

more than 75 per cent of the total Collembolan fauna within the litter and humus in a forest plantation in Wales. Frenzel (1936) and Strenzke (1952) both report a surface concentration of oribatid mites in woodland habitats in Germany. Starling (1944) in North Carolina found the Pauropoda in a woodland habitat to be most abundant in the upper 1–2 inches of the soil.

In the foregoing areas, a certain amount of precipitation occurs during almost every month of the year. As a result, the soil surface never becomes excessively dry, and the relative humidity within the litter and humus layers remains near saturation. If moisture conditions remain favorable, high surface densities may be attributed to the greater abundance and variety of food resources, greater amount of living space, and better aeration.

In regions with distinct seasonal changes in precipitation, workers have described deeper vertical distribution patterns, e.g., Strickland (1947) in Trinidad, Lawrence (1953) in South Africa, and Belfield (1956) in Ghana (Gold Coast). Hairston and Byers (1954) in a study of a sandy, mull soil of an abandoned field in southern Michigan found a relatively deep penetration of the fauna. In four samples taken during four seasons of the year and extending to depths of 48 inches, these workers found approximately one-half of the fauna below 5 inches, one-third below 8.5 inches, and one-fifth below 12 inches. Seasonal changes in vertical distribution were observed and attributed to a wide annual range of temperatures in the surface soil and to a distinct summer dry period. Snell (1933) in southern California noticed an increase in populations in the humus following the first winter rains. She suggested that these additional components may have come from deeper levels in the soil where they resided during the hot and dry California summers. This hypothesis is supported by the data presented here.

Abundance and composition of the fauna

A population density of 220,739 microarthropods/m² (table 8) is comparable to estimates reported by other workers investigating similar habitats. For example, van der Drift (1951) estimated 336,500 arthropods/m² in a beech forest soil in Holland. Crossley and Bohnsack (1960) estimated 102,000/m² in a pine forest soil in Tennessee, and Harding (1969) reported 215,000/m² in an oak woodland in England.

The use of population estimates from various authors for making comparisons between differing types of habitats is difficult. One problem arises from variations in the depth of samples upon which the estimates are based. Using standardized procedures, however, workers are beginning to make such comparisons. The work of Krivolutsky (1969) with the Oribatei in tundra, taiga, steppe, and other soils of the U.S.S.R. is an example.

The Acarina constituted the most numerous component of the fauna in the study area, with an average density estimated at 146,107/m² (table 8). These forms comprised 66.2 per cent of the arthropod fauna. The Collembola were somewhat less than a third as abundant as the Acarina, with an estimated density of 44,039/m². The Myriapoda were composed primarily of Pauropoda, which had an estimated density of 17,883/m² or 8.1 per cent of the fauna. The remainder of the Myriapoda consisted of about equal numbers of Symphyla and Geophilidae (Chilopoda), estimated at about 1,000 each/m² (table 9).

The density of Pauropoda far exceeds the numbers reported by Starling (1944) of 413 and 538/m² in oak and pine forest respectively, and of Salt *et al.* (1948) of 629/m² in pasture soil. Population levels of Protura of 4,204/

m^2 exceed that reported by Salt *et al.* (1948) of 1,363 in pasture soil but are below those noted by Raw (1956) of about 8,000/m^2 in permanent grassland. The abundance of Collembola in the study area is very close to the figures of Poole (1961) of 46,700/m^2 in a Douglas fir plantation, Ford (1935) of 59,277/m^2 in meadow soil, and Salt *et al.* (1948) of 61,269/m^2 in pasture soil. These estimates, however, are only about half of the 120,000/m^2 reported by Trägårdh (1933) in a spruce forest soil in Sweden. Acarine populations in the study area compare with those reported by other workers; *e.g.*, Salt *et al.* (1948) found 164,363 mites/m^2 in pasture soil, while Harding (1969) estimated 178,450/m^2 in oak woodland soil. Wood (1967*a*) found a range of densities of Acarina and Collembola combined of 167,000 to 281,000/m^2 in four grassland and two moss habitats in England.

Mites in the suborder Prostigmata were the most numerous of the Acarina with an estimated density of 74,981/m^2. This group comprised 51.3 per cent of the mite fauna. The Cryptostigmata (Oribatei) with 56,304/m^2 comprised 38.5 per cent, and the Mesostigmata with 14,882/m^2 comprised 10.2 per cent of the Acarina. The Mesostigmata was composed almost entirely of mites in the cohort Gamasina. Virtually no members of the Astigmata were encountered. The relative numbers of Prostigmata and Cryptostigmata stand in marked contrast to those reported by other workers. Madge (1965), for example, found that in four different habitats in England the Prostigmata averaged only 3 per cent of the Acarina, while the Oribatei averaged 90 per cent and the Mesostigmata 7 per cent. Similarly, Block (1965), in a study of 6 habitats in England, found the Prostigmata to range from 0.2 to 15 per cent of the Acarina, with five of the six habitats yielding 3.0 per cent or less of Prostigmata. In this same study (Block, 1965) the Cryptostigmata ranged from 62 to 94 per cent of the Acarina. Block (1966), in a study of five other habitats, found the Prostigmata to comprise only 0.4, 1.5, 9.0, 0.4, and 0.9 per cent of the Acarina. These figures are typical of most studies of soil mites. Wallwork (1967) states that the Cryptostigmata occur in greatest numbers in coniferous forest soils where they may represent as much as 75 per cent of the total acarine fauna. In contrast, Gill (1969), in a study of an old-field habitat in southern Michigan, found that the total microarthropod population in his control plots, estimated at 492,000/m^2, contained about equal numbers of Cryptostigmata and Prostigmata. He notes that the Eleutherengona Oudemans, a part of the Prostigmata, numbered about 171,000/m^2 or 35 per cent of the total microarthropod fauna.

The reason for the relatively large numbers of Prostigmata in the study area is not known. It may be explained by the fact that the Prostigmata are mostly small, delicate mites which are more easily overlooked than the Cryptostigmata; or they may not be as readily obtained by the Tullgren or flotation methods often employed, as suggested by Gill (1969). The dominance of the Prostigmata in the study area might also be due to some physiological or behavioral adaptation which makes them, as a group, more tolerant of dry environmental conditions, as suggested by Ryke and Loots (1967).

Estimates of the numbers of species of mites in the study area were: Prostigmata, 60; Mesostigmata, 37; and Cryptostigmata, 33. Thus, there were almost twice as many species of Prostigmata as Cryptostigmata. This ratio is very different from figures of most other workers. Block (1965), for example, in four grassland habitats found a total of 55 species of Cryptostigmata, 46 species of Mesostigmata, and only four species of Prostigmata. Sheals (1957), also in a

grassland habitat, found 12 species of Cryptostigmata, 18 species of Mesostigmata, and only a single species of Prostigmata. Numerically, the latter constituted only 1.1 per cent of the Acarina. Sheals suggests that the low yield of the Prostigmata in his samples was probably due to the inefficiency of the flotation technique employed. In contrast, however, Wood (1967*a*) found 58 species of Cryptostigmata, 50 species of Prostigmata, and 33 species of Mesostigmata in four grassland and two moss sites in England. Ryke and Loots (1967), in a study of 11 South African soils, found the Prostigmata to be the dominant form in the majority of cases. Marshall and Kevan (1964), in an account only of Mesostigmata and Trombidiformes (Prostigmata), found a total of 29 species of Mesostigmata compared to 67 species of Trombidiformes in three woodland habitats in Quebec.

Published studies in soil zoology reveal considerable variation in the descriptions of microarthropod populations. It is often difficult to assess whether or not these discrepancies are due to intrinsic differences between the many kinds of habitats studied, or to differences in emphasis of individual workers and in the techniques employed. The need to develop standardized methods so that results can be compared with greater confidence is obvious. The variety of the fauna collected in the study area and the relatively dense populations observed suggest that the extraction techniques employed were efficient, at least as much so as those used by other workers. It is felt that the abundance of small and delicate microarthropods, such as many of the Prostigmata, the Protura, and Pauropoda, also attest to the efficiency of the extraction procedure used here.

Seasonal changes in abundance

In this study, changes in abundance of certain groups of microarthropods during the sampling period were the result, at least in part, of vertical movements of populations within the soil. Migrations of such groups as the Protura, Pauropoda, Entomobryidae, Poduridae, Zerconidae, and *Rhodacarus* spp. to soil levels below the sampling zone resulted in apparent but not actual decreases in population densities during the dry part of the year (figs. 6 and 7, tables 5 and 6). Data presented in tables 8 and 9 confirm that these categories are about equally abundant during the wet and dry season. The influence of vertical migrations on estimates of seasonal changes in abundance was noted also by Hairston and Byers (1954) in their study in southern Michigan.

Observed seasonal changes in abundance indicated in figs. 6, 7, and 8, and tables 5 and 6 reflect actual changes in density in those groups which remained primarily within the sampling zone throughout the sampling period, that is, above 2 inches in the subsoil. These groups include the Psocoptera, Sminthuridae, Bdelloidea, Raphignathoidea, *Lasiotydaeus krantzi,* and the four selected species of Cryptostigmata. It is interesting to note that all of these groups, except the Sminthuridae, either showed little change in density during the sampling period, or became more abundant during the dry period of the year. The Sminthuridae disappeared almost entirely during the dry season (fig. 6). Since these forms do not penetrate into the soil during this period (table 7), they probably pass through the dry season in a quiescent, drought-resistant egg stage (Davies, 1928).

Although occurring primarily below the standard sampling zone, the various species of Gamasina other than the Zerconidae and *Rhodacarus* spp. showed little change in abundance during most of the sampling period (fig. 7). This group increased in numbers, however, in November and December, apparently

by moving into the surface layers following the first rains of the season. The four selected species of Cryptostigmata showed little change in abundance during the sampling period (fig. 7, table 3). Of these, however, *Ceratoppia bipilis* appeared to become more numerous during the dry season (table 9). The very stable population densities of *Trichoribates* sp. (fig. 7) and *Belba* sp. (table 3) reveal that these species have considerable tolerance to changes in soil moisture levels and soil temperatures.

The period between April 17 and July 26 was one of gradually decreasing moisture levels in the humus layer (table 2). Changes in populations of the categories shown in figs. 6, 7, and 8 apparently reflect responses to soil moisture levels, primarily, although environmental or intrinsic factors other than soil moisture may also have been involved. Also of interest in figs. 6, 7, and 8 is the representation of changes in abundance occurring between November 6 and November 30. As noted, these two sampling dates were separated by a period of heavy rainfall which marked the end of the dry season (table 1). Moisture levels in the humus layer jumped from 6.1 per cent on November 6 to 67.7 per cent on November 30 (table 2). Marked increases in populations between these two dates no doubt reflect movements into the sampling zone rather than true population growth. The increase in numbers of Sminthuridae probably reflects the reappearance of active stages.

Population trends shown in figs. 6, 7, and 8 are supported by data given in tables 5 and 6. For example, significant increases in numbers of Collembola, Protura, Pauropoda and Gamasina were observed in the sample taken on November 17, after the initial rainfall of 1964 (table 6). This same sample also showed a significant decrease in abundance of Psocoptera and Bdelloidea. A decrease in abundance also was noted for all other categories of Prostigmata included in table 6. The reason for the decrease of these groups was not determined, although some may have moved onto tree trunks or other aboveground vegetation. Mortality factors may have reduced populations of certain groups. Similar trends were found in the set of samples taken on April 29 and October 9 (table 5). A significant decrease in abundance was observed on October 9 for Zerconidae, Cyrtolaelaptidae, and total Gamasina. An opposite trend was noted for all categories of Prostigmata considered, that is, these groups were more abundant in the dry period sample.

Because of widely differing climatic and pedological conditions, seasonal changes in population densities observed in this study are difficult to compare directly with those reported by other workers (Ford, 1935; Strickland, 1947; Weis-Fogh, 1948; Evans, 1951; Belfield, 1956; Sheals, 1957; Poole, 1961; Madge, 1965; and Harding, 1969). Varied sampling techniques and differences in emphasis on particular components of the fauna also make such comparisons difficult to interpret. As noted, many workers have taken relatively shallow corings, and some may not have considered the extent of possible vertical movements in the soil or the effects of such movements on the data obtained. Data from the study reported here show that such considerations are essential in assessing seasonal changes in soil populations under California conditions.

In a general way, seasonal changes in abundance and vertical distribution in the study area compare more closely with those reported from Ghana by Belfield (1956) than with those from north temperate regions. There appear to be no studies of this type from the Mediterranean basin, an area very similar climatically to California.

Poole (1961), in a detailed study of

Collembola in a forest habitat in Wales, noted that "The whole collembolan community is in a constant state of flux with first one species increasing and then another, depending on the varied environmental factors favouring different species." Poole concludes, "So little is known of the factors influencing the lives of Collembola that it is difficult to account for population changes based on a single year's data." These comments of Pool are pertinent and can be extended to all other members of the soil community. Each component no doubt responds to environmental changes in a unique manner. Also, many species doubtless respond to inherent reproductive cycles and other life-history factors, and undergo population fluctuations irrespective of prevailing environmental conditions. Biotic pressures exerted by other members of the community are also responsible for this "constant state of flux."

CONCLUSIONS

More than 100 species of Acarina were found in the study area. These occurred in association with many species of Collembola and a variety of other small insects and myriapods, a clear demonstration of the complexity of the soil ecosystem. A conservative estimate of the diversity of the microarthropod fauna would be about 150 species, with the relatively open parts of the forest floor supporting a population of at least 200,000 individuals per square meter.

The fauna can be divided into two general groups: those taxa that are primarily resident in the mineral subsoil and those that primarily occur in the litter and humus. The first group includes most of the Collembola and Acarina and all of the Protura, Pauropoda, Symphyla, and Geophilidae, which together form the bulk of the total population. Those forms which are largely subsoil inhabitants migrate to some extent into the humus and litter layers at the onset of the wet season. However, even during the wet part of the year, the majority of individuals in this group remain in the subsoil. In the study area a substantial part of the fauna is adapted to a more-or-less permanent subterranean life, and apparently this is due to the very low moisture levels and warm temperatures which prevail in the litter and humus during an extended period of the year. The data indicate that members of this group maintain relatively stable population levels throughout the year.

The second group, the litter and humus inhabitants, includes the Psocoptera, Sminthuridae, Bdelloidea, Raphignathoidea, and certain species of Cryptostigmata. The Cryptostigmata, in general, however, belong to the first group. With one exception, the Sminthuridae, these categories either maintained a stable population density throughout the year or showed a distinct increase in abundance during the dry season.

Periodic sampling of the litter, humus, and upper 2 inches of the subsoil revealed for the categories in the first group, i.e., the subsoil inhabitants, low populations in the summer-fall dry period and high populations during the wet periods. It is shown, however, that these apparent seasonal changes are due to vertical movements of parts of the populations into and out of the sampling zone.

Noteworthy were high population densities of the Pauropoda, and the dominance of the Prostigmata both in population densities and species diversity. These attributes of the fauna may be characteristic of regions subject to seasonal drought.

The fauna was characterized by a great variety of forms, with no one

species, genus, or family being numerically dominant. The variability of the data resulting from highly aggregative distribution patterns indicates that large numbers of replicates per sample are advisable. In studies of a comparative or experimental nature, one investigator probably should restrict himself to only a few components of the total fauna. Large numbers of replicates would also provide more useful data at the species level, particularly for species which are present in low densities or which are highly aggregated in their distribution.

Studies of soil populations in regions with a predominantly subterranean fauna present greater difficulties than do those in areas with high surface densities. Deep corings are difficult to obtain, particularly in hard or rocky soils; and because large volumes of soil are obtained, greater demands are made on the extraction apparatus. The depth at which target organisms occur can limit the scope of research projects, such as those involving experimental manipulations or habitat comparisons. It is obvious that data pertaining to surface-dwelling forms such as Psocoptera or Raphignathoid mites are more easily obtained than comparable data on subterranean forms such as the Protura or Pauropoda. The depth of occurrence of a species also will determine whether or not it will be affected directly by a particular treatment, such as a pesticide application. Under California conditions, a chemical applied to the soil surface in early summer might remain in the litter and humus for months before any substantial part of the fauna moves into contact with it. Surface-dwelling forms are more likely to yield useful indicator species since habitat disturbances and chemical contaminants are more apt to affect the fauna of the litter and humus than the fauna from deeper zones. Under California conditions, predatory groups such as the Bdelloidea and Raphignathoidea may be of greatest importance in this respect.

The soil has great importance as a basic natural resource and as a habitat for a great variety of organisms, many of which contribute to essential processes of organic decomposition and nutrient recycling. Nonetheless, the soil remains a largely unexplored segment of the biosphere. Research on soil microarthropods in California has been negligible. The importance of our soil resources makes this neglect difficult to explain. The unique attributes of the soil fauna under California climatic conditions indicate that information of the type presented here can serve to facilitate future studies in soil zoology in this region.

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