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DIPLOPODA OF A MICHIGAN BEECH-MAPLE FOREST:

POPULATION ECOLOGY AND SEASONAL ACTIVITY

by

Vivian Mestey-Villamil

A THESIS

Submitted to

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ABSTRACT

DIPLOPODA OF A BEECH-MAPLE FOREST:

POPULATION ECOLOGY AND SEASONAL ACTIVITY

By

Vivian Mestey-Villamil

The present study assessed some aspects of population density, vertical and horizontal distribution, and activity of the dominant diplopod species of Baker woodlot, a beech-maple forest, in Michigan. Field work was focused on quantitative sampling of leaf litter, organic layer and A horizon. Pitfall traps were used to assess seasonal activity during two consecutive years (1984-1985).

Of six diplopod species collected in the study area only three were common enough for quantitative analysis: Ophyiulus pilosus (Newport), Polydesmus inconstans Latzel, and Polyzonium bivirgatum (Wood). Ophyiulus pilosus was the dominant species.

Vertical migration and distribution of the life stages of O. pilosus was affected by climatic parameters such as seasonal temperature and precipitation. Differences in these two parameters among years also affected population density of the species.

Ophyiulus pilosus can overwinter in any stage (small juvenile, juvenile or adult), except probably as eggs, which are laid during spring and summer. Adults were common in spring and were present in every soil layer. Inmature stages were most common, during summer and fall, in O and A horizons.

The horizontal distribution of the dominant species could not be related to the amount of litter or its moisture content.

Data from pitfall traps showed different activity peaks for each species. Ophyiulus pilosus was mainly active in spring, P. inconstans during summer and P. bivirgatum in the fall. Adults were the most active stage in every species, and both sexes were equally active, indicating that activity peaks of each species corresponded to their matting season.

To my husband, family and friends

ACKNOWLEDGEMENTS

I wish to thank the members of my guidance committee: Dr. Richard Snider, Dr. Max Hensley, and Dr. Donald Straney, Department of Zoology, and Dr. Peter Murphy, Department of Botany and Plant Pathology for their assistance in the course of this study.

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I. INTRODUCTION

The Diplopoda, commonly known as millipedes or thousand-leggers, are an entirely terrestrial group of more than 7,500 described species (Barnes, 1980). They are found throughout the world, especially in the warm and humid tropics, but also in all temperate regions except the most arid. Millipedes are found up to the snow line and down to the sea level (Williams and Hefner, 1928). They live underneath stones, bark, logs, among leaves and in the soil, consuming leaf litter and other organic debris and thereby contributing to the formation of humus. A number of species are cave inhabitants, others are tree dwellers, and a few are commensal in ant nests, but most are free living (Barnes, 1980).

Although Diplopoda are very well distributed, not much is known about their natural history, life cycles, and population densities. There are many publications on the millipede fauna of North America and Europe, but most of these papers deal with the taxonomy and morphology of the group. The first scientist to investigate American Diplopoda was Thomas Say (1821) who described 18 species, of which half still stand generically. Bollman (1893) published the first catalogue of North American millipedes. A second was written by Chamberlin (1947). The most recent checklist was made by Chamberlin and Hoffman (1958). Faunistic studies have been published for only four states: Ohio (Williams and Hefner, 1928); Michigan (Johnson, 1952, 1953); New York (Bailey, 1928); and for some areas of North Carolina (Shelley, 1978).

Population studies that attempt to determine density, age structure, and vertical or horizontal distribution are few in number. Early studies were made in Denmark by Bornebusch (1930), who recorded populations of up to 160 millipedes/m^2 in deciduous woodlands. Van der Drift (1951) estimated a density of 80 julids/m^2 (mainly Cylindroiulus punctatus (Leach)) in a beech wood with raw humus in Holland. Blower and Gabbutt (1964) described the population structure of Cylindroiulus latestriatus (Curtis), Cylindroiulus punctatus, Ophyiulus pilosus (Newport, 1842), and Iulus scandinavius Latzel in Devon Oak Wood in England, but could not estimate population density because they only sampled litter. Density and surface-activity of diplopods were also recorded by Blower (1969) in an English woodland where he sampled soil and litter.

Several scientists have investigated the vertical distribution of millipedes. Bocock and Heath (1967) studied the feeding activities in soil of Glomeris marginata (Villers) in relation to its vertical distribution. Dowdy (1944) worked on the influence of temperature on vertical migration of invertebrates inhabiting different soil types. Peitsalmi (1974) investigated the vertical orientation and aggregation of Proteroiulus fuscus (AM Stein). And Davies, Hassall and Sutton (1977) described the vertical distribution of isopods and diplopods in a dune grassland at East Yorkshire, England.

Some European researchers (Miller, 1974; Blower, 1974a; Sakwa, 1974) have shown that diplopod distribution can be related not only to available food, but also, to leaf litter depth, area topography and other factors such as humidity and temperature. Very few reports on vertical distribution are published for North America.

Michigan Diplopoda have been investigated by Johnson (1952, 1953), Kane (1981) and Snider (1980). Johnson recorded 16 species not previously known from the state. The autecology of some of the 31 species reported to occur in Michigan is known (Johnson, 1952). Many of these species are hardwood forest inhabitants and can be found all over the state. Snider (1980) studied the bioecology of Polydesmus inconstans Latzel, 1884, and Kane (1981) worked on the systematics, morphology, and natural history of Polyxenus lagurus (Linne).

The present investigation deals with species composition, vertical distribution, and activity of three Diplopoda species in a maple-beech forest on the Michigan State University campus in East Lansing, Michigan. The studied species were: the julid Ophyiulus pilosus, the polydesmid Polydesmus inconstans and Polyzonium bivirgatum (Wood) 1864, which is the only representative of the colobognath family Polyzoniidae in Michigan (Johnson, 1952).

Ophyiulus pilosus has been studied by Blower and Gabbutt (1964), Blower (1970, 1974a), Miller (1974) and Blower and Miller (1974) in England. These authors found that O. pilosus was one of the most common julids associated with leaf litter, where it contributes to litter degradation. Ophyiulus pilosus is a semelparous species which upon reaching maturity, dies, unlike most British julids which become mature, breed and and survive for several years (Blower, 1969). Compared to other British julids, for example Iulus scandinavius which needs 3 years to mature, O. pilosus reaches maturity in 2 years. It has been suggested (Blower, 1969) that this type of neotenic contraction of the life history has conferred on the species the ability to succeed as a colonist. Ophyiulus pilosus has spread over the world and now dominates exotic faunas (Blower, 1969).

In Europe O. pilosus is found from the British Isles, where it is the second most frequently recorded species (Blower, 1985), to Central Europe, Northern Italy, Yugoslavia and both the European plains and Carpathian regions of the Soviet Union; but it has not been recorded from Finland, France and Belgium (Blower, 1985). It has also been described from New Zealand by Dawson (1958) and Johns (1962, 1967).

In North America O. pilosus has been studied by Johnson (1952, 1953), who described its morphology and distribution with some notes on its autecology and natural history. He reported O. pilosus for the first time in Michigan and recorded it from 41 localities. Johnson (1952) also characterized it as an inhabitant of Ulmus-Acer associations in Ingham County (where the present study took place). The species has also been reported from Ohio (Williams and Hefner, 1928), New Jersey, Pennsylvania, Quebec (Chamberlin, 1947), Nova Scotia, Virginia, Tennessee, and the Appalachians (Chamberlin and Hoffman, 1958). It thus seems that O. pilosus is found in regions characterized by temperate deciduous forests (Miller, 1974).

Polydesmus inconstans, listed by Johnson (1952) as P. coriaceus Porat, is considered a Palearctic species found in most European countries and the Soviet Union (Blower, 1985). It was introduced to the

United States, Canada and Iceland (Blower, 1985) and is widely spread. In the United States it has been reported from New York (Bailey, 1928), Indiana (as *O. testi* by Bollman, 1887), Ohio (Williams and Hefner, 1928), Massachussets, Delaware (Chamberlin, 1947); from Newfoundland to New England, Oregon, British Columbia (Chamberlin and Hefner, 1928) and from 14 localities in Michigan by Johnson (1952, 1953) who described it as an inhabitant of grasslands in Ingham County. *Polydesmus inconstans* was intensely studied by Snider (1980, 1981, 1984a) who described its ecology and life cycle.

Polyzonium bivirgatum an endemic North American species is the least well known of the three studied species. It was first described by Wood (1864) and later by Cook and Loomis (1928). It has been reported from Tennessee (Cook and Loomis, 1928; Bailey, 1928), Ohio (Williams and Hefner, 1928; Dowdy, 1944; Johnson, 1952), and Michigan (Bollman, 1888, 1893; Chamberlin, 1914; Johnson, 1952). Johnson (1952) characterized *P. bivirgatum* as an inhabitant of *Ulmus-Acer* associations in Ingham County.

The primary objectives of the present research were:

1) to study the community structure and dominance relationships of the Diplopoda fauna in a beech-maple forest;
2) to quantify the seasonal population dynamics of the dominant species *Ophyiulus pilosus* in the study site;
3) to study the influence of moisture and temperature on the spatial distribution of the dominant

species' life stages; and

4) to describe the activity patterns of _O. pilosus_, _P. inconstans_ and _P. bivirgatum_ during spring, summer and fall.

To accomplish the above, data were collected in the field from April to October of two consecutive years (1984-1985). Aspects of diplopod biology listed above have been only superficially studied in North America. In particular, no studies of the vertical distribution of millipedes are in existence. The present study assessed those aspects.

II. MATERIALS AND METHODS

1. Description of the study area

The study site was located in Baker woodlot, a beech-maple woodlot in Ingham County on the campus of Michigan State University. The woodlot comprises 30 ha with *Acer saccharum* Marsh. dominant, followed by *Fagus grandifolia* Ehrh. mixed with *Quercus rubra* L. and *Fraxinus americana* L.

Area topography consists of low hills interspersed with pronounced depressions, among which four ponds are found. This study took place around the largest pond, encompasing approximately 1 ha in area.

Different types of soil occurred in Baker woodlot. In depressions the soil consisted of moderately drained loam with pH between 5.7 to 6.5, and approximately 9% organic matter. Hill soils were more variable, well drained sandy loams predominating with pH 6.2 to 6.6, and approximately 6% organic matter (Snider, 1980). Soil was always covered with leaf litter, its thickness varying seasonally. Pond size also varied with the season, being largest during springtime after snowmelt and smallest during August, the dry season.

2. Sampling methods

A total of 14 sampling dates were selected during year 1 (1984) and 13 during year 2 (1985), each set spanning the months from April to October. Collection dates in each year were organized in three groups. These corresponded approximately to the spring, summer and fall seasons. All collection dates between April 1 and June 21 were classified as "spring", between June 22 and August 21 as "summer", and between August 22 and October 31 as "fall".

2.1. Quadrat sampling

Ten general sample locations, approximately 10-15 m apart and surrounding a small pond, were selected (Figure 1); within each a 25cm x 25cm sample of the forest floor was taken randomly at 2 week intervals. Each sample was divided into 3 subsamples:

1) The leaf litter (LL) which was the upper portion of the forest floor most recently deposited including leaves, twigs, branches, etc.

2) The organic layer, or O layer (OL), which consisted of decomposed and partly decomposed organic matter, raw humus, well delimited from the mineral soil.

3) The upper layer of the A horizon (AL) which was the zone of pronounced decomposition and humification, in which only few plant residues are recognizable.

A total of 30 subsamples were obtained per date, consisting of all the leaf litter present in the quadrat, the organic layer, and the A layer. The amount of soil collected in the A horizon varied from quadrat to quadrat depending on its naturally occurring depth at a given sampling point.

Samples were inmediately placed in plastic bags and transported to the laboratory in a foam cooler to avoid over-heating. Even though

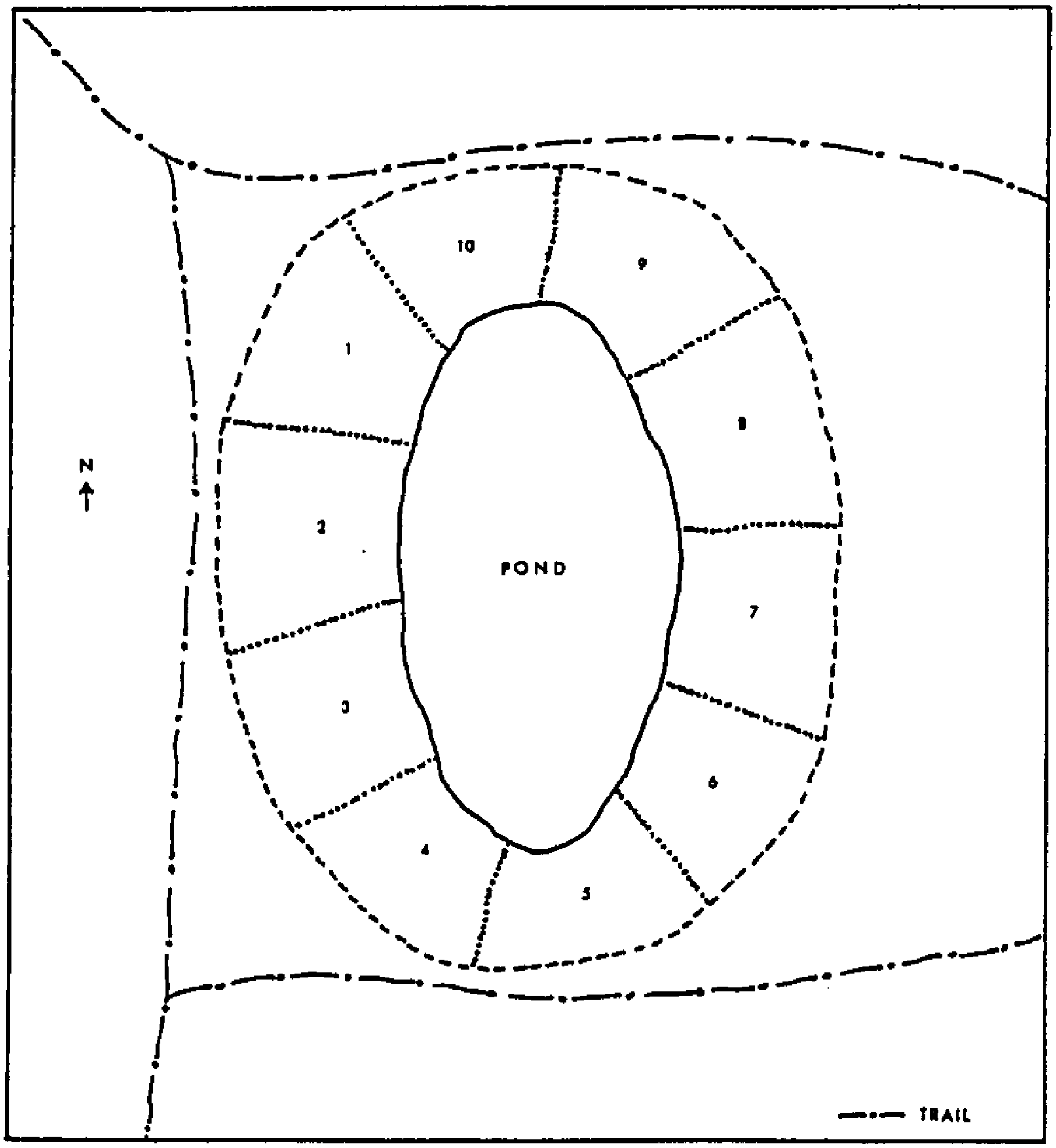


Figure 1. Approximate quadrat sampling locations in Baker woodlot.

Tullgren heat extraction is commonly used to extract organisms from soil and litter samples, it was not used in this study. During preliminary experiments dead millipedes, especially small juveniles, were found inside rolled leaves and seeds after extraction was completed. Moreover, with this method it was impossible to find egg cases. Hand sorting of samples was, therefore, prefered. All seeds, wood and leaves were carefully inspected under a powerful magnifying glass. Millipedes were preserved in 95% ethanol alcohol, with 2% glycerin added, and classified by species, life stage, and sex.

2.2. Pit-trapping

Surface activity of millipedes was determined by the pitfall trap method. Traps consisted of a large, permanently emplaced outer cup, and a snap-in funnel to guide the catch into the inner collecting cup (Figure 2). The rim of the outer cup was flush with the soil surface.

Twenty traps were distributed around the pond at intervals of approximately 10 meters. During the second year seven of the traps were relocated because increased pond size threatened to flood them. Sampling took place every other week from April to October during 1984 and 1985. Traps were activated for a period of 24 hours, and the catch was preserved in 95% ethanol with 2% glycerin. During the first year ethylene glycol was used as trapping medium in the inner cups. In the second year animals were live-trapped and preserved later at the laboratory. The distance between traps at the end of the second year is described in Table 1.

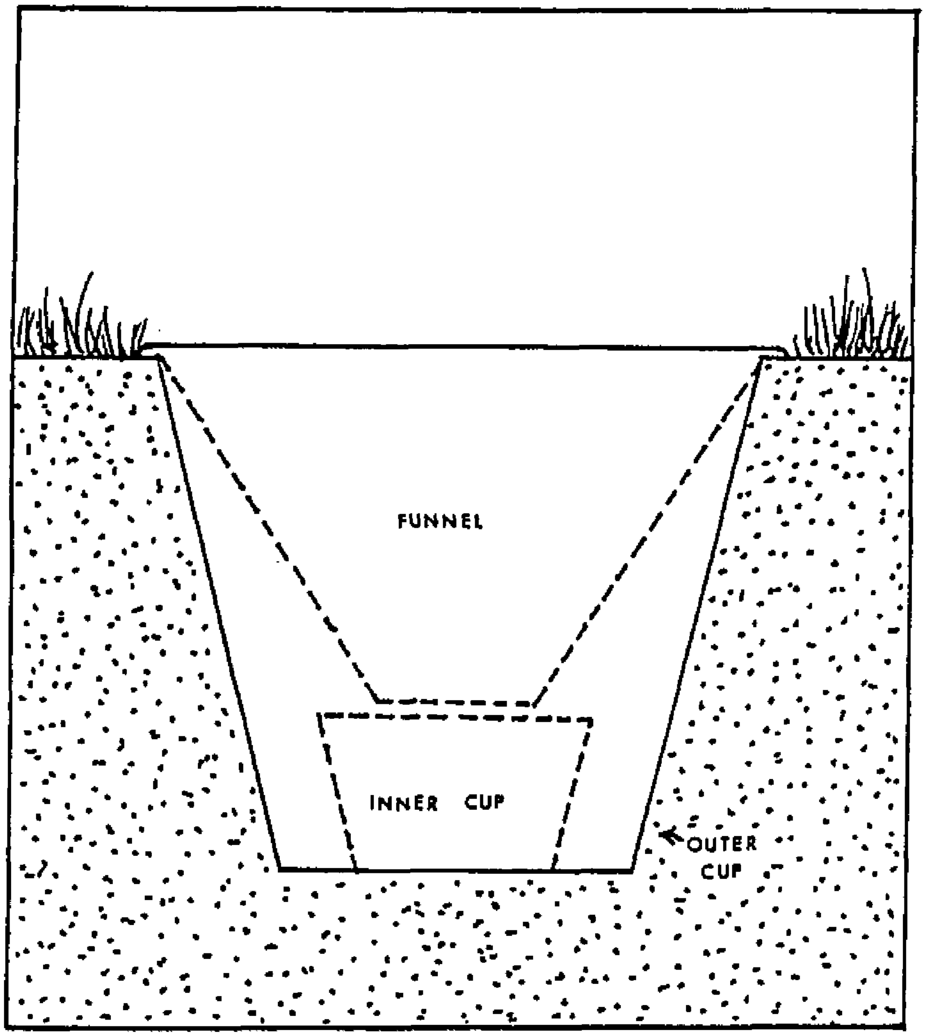


Figure 2. Profile of collecting cups used in pit-trapping.

Table 1. Inter-trap distances.

Traps	Distance (meters)
1-2	9.02 *
2-3	15.27
3-4	16.92 *
4-5	11.31 *
5-6	7.68 *
6-7	10.85
7-8	8.50
8-9	9.45 *
9-10	9.11 *
10-11	9.05
11-12	10.14
12-13	9.26
13-14	7.38 *
14-15	7.77 *
15-16	11.03
16-17	8.20
17-18	12.19
18-19	13.25 *
19-20	11.79 *
20-1	15.24 *

* Traps that were moved from their original position after first year.

Table 2. Characteristics of developmental stages used to classify <u>Ophyiulus</u> <u>pilosus</u>.

Stage	# podous segments	# apodous segments
SJ I	4	2
to V	22,23	7,8
JU VI	29,30	6,7
to IX	44	2,3
AD IX	45,48	(males) 3
		(females) 3,4
to XI	51,54	2

Data taken from Blower and Miller (1974).

2.3. Classification of life stages

Millipede life stages were classified by counting the total number of body segments. Categories established for *O. pilosus* were: small juveniles (SJ), juveniles (JU), and adults (AD). Table 2 shows the range of segment numbers with legs (podous) and without legs (apodous) present in each of these categories.

Polydesmus inconstans were also lumped as small juveniles, juveniles, and adults, encompassing a total of eight developmental stages. Table 3 shows how they were organized for the purpose of this study.

Table 3. Characteristics of developmental stages used to establish categories for *Polydesmus inconstans*.

Category	Instar	Total # of segments
SJ	I *	7
	II	9
	III	12
JU	IV	15
	V	17
	VI	18
	VII	19
AD	VIII	20

* larval stadium

Data taken from Schubart (1934)

Small juveniles of *P. bivirgatum* were rarely found, but when that was the case they were shorter than 2 mm. Juveniles consisted of animals with less than 29 segments. Adults possessed 30 to 60 segments.

2.4. Soil moisture determination

On each date, 10 samples of each layer were placed in tightly covered containers 6.5 cm high by 9 cm diameter. Samples were wet weighed, dried in a 24°C oven for one week or until no further weight loss ocurred, and weighed again. Percent moisture of each layer was obtained by using the following equation:

$$\% \text{ Moisture} = 100 \times (\text{Wet weight} - \text{Dry weight}) / \text{Dry weight}$$

2.5. Leaf litter mass determination

The 10 leaf litter subsamples obtained on each date were used to determine leaf litter mass after all animals, twigs, seeds, and pieces of wood had been removed. The leaves were placed in paper bags, dried in a 24°C oven for one week, and re-weighed.

2.6. Temperature and precipitation

Temperature and precipitation data were obtained from the U.S. Department of Commerce National Weather Service (N.W.S.) in East Lansing.

III - RESULTS AND DISCUSSION

1. Physical parameters

1.1. Daily temperatures

Maximum and minimum temperatures recorded by the National Weather Service during the two years of study are presented in Figures 3, 4. Low temperatures were reported at the beginning of the study during both years. However, warmer temperatures were obtained earlier in April of year 2. In addition many more warmer days were observed in year 2 (e.g. 4 days with temperatures above 20°C in year 1, and 12 days for year 2). During mid-May of year 1, more cold days and temperatures below zero were recorded.

Summer temperatures were warmer in year 1 than in year 2, many more days with temperatures above 26.4°C were reported (e.g., 21 days in June, year 1, and 8 days in year 2). The highest temperatures recorded for both years ocurred in July (33.0°C year 1 and 32.4°C year 2).

The warm period was prolonged until the beginning of September (both years). Fall temperatures were very similar to those obtained in spring.

1.2. Daily precipitation

Daily precipitation recorded by the National Weather Service is presented in Figures 5 and 6. Snow was recorded early in April during both years, however more snowy days were reported for year 2. Only in

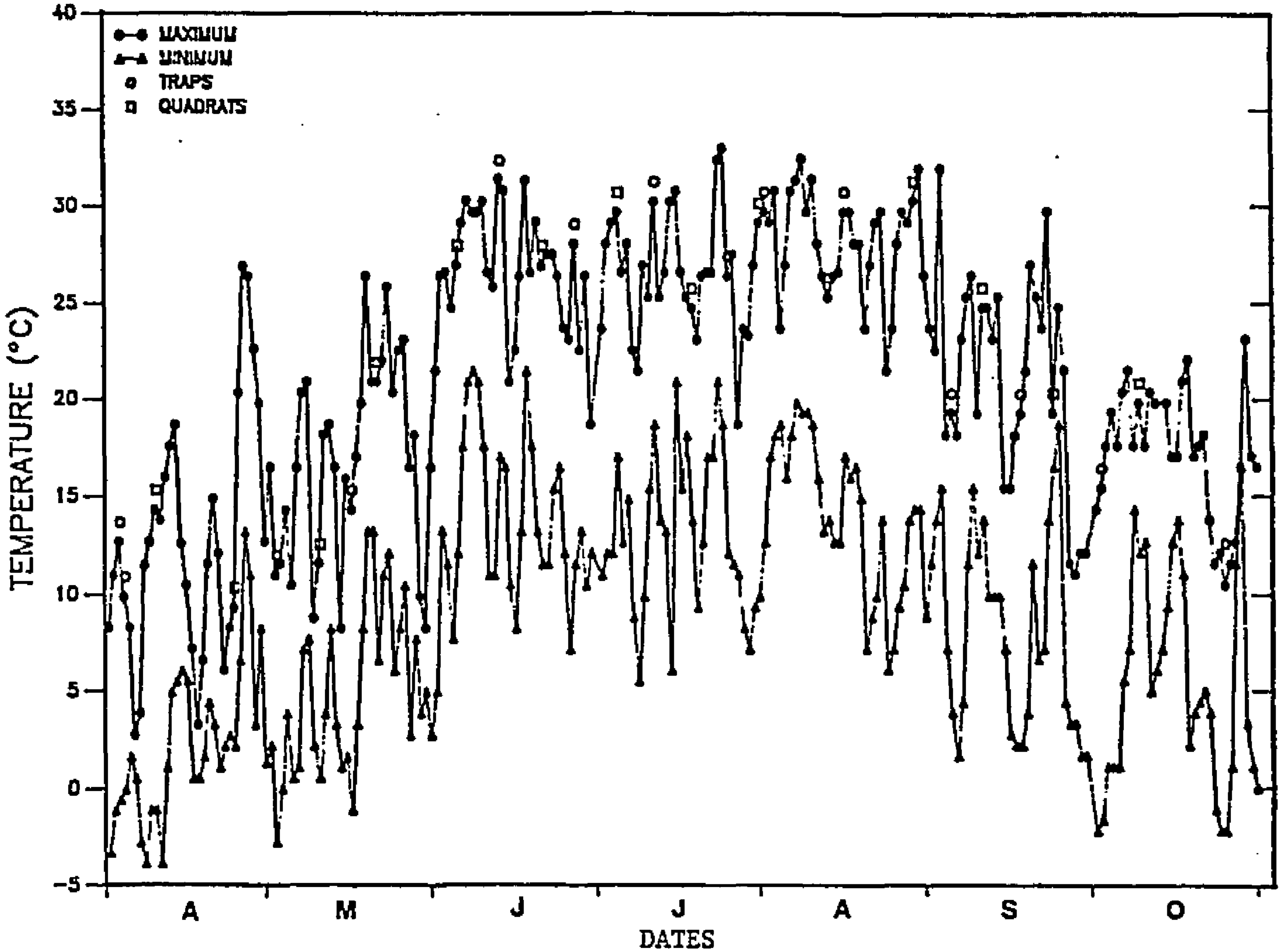


FIGURE 3. DAILY AIR TEMPERATURES, NATIONAL WEATHER SERVICE, EAST LANSING STATION, YEAR 1 (1984).

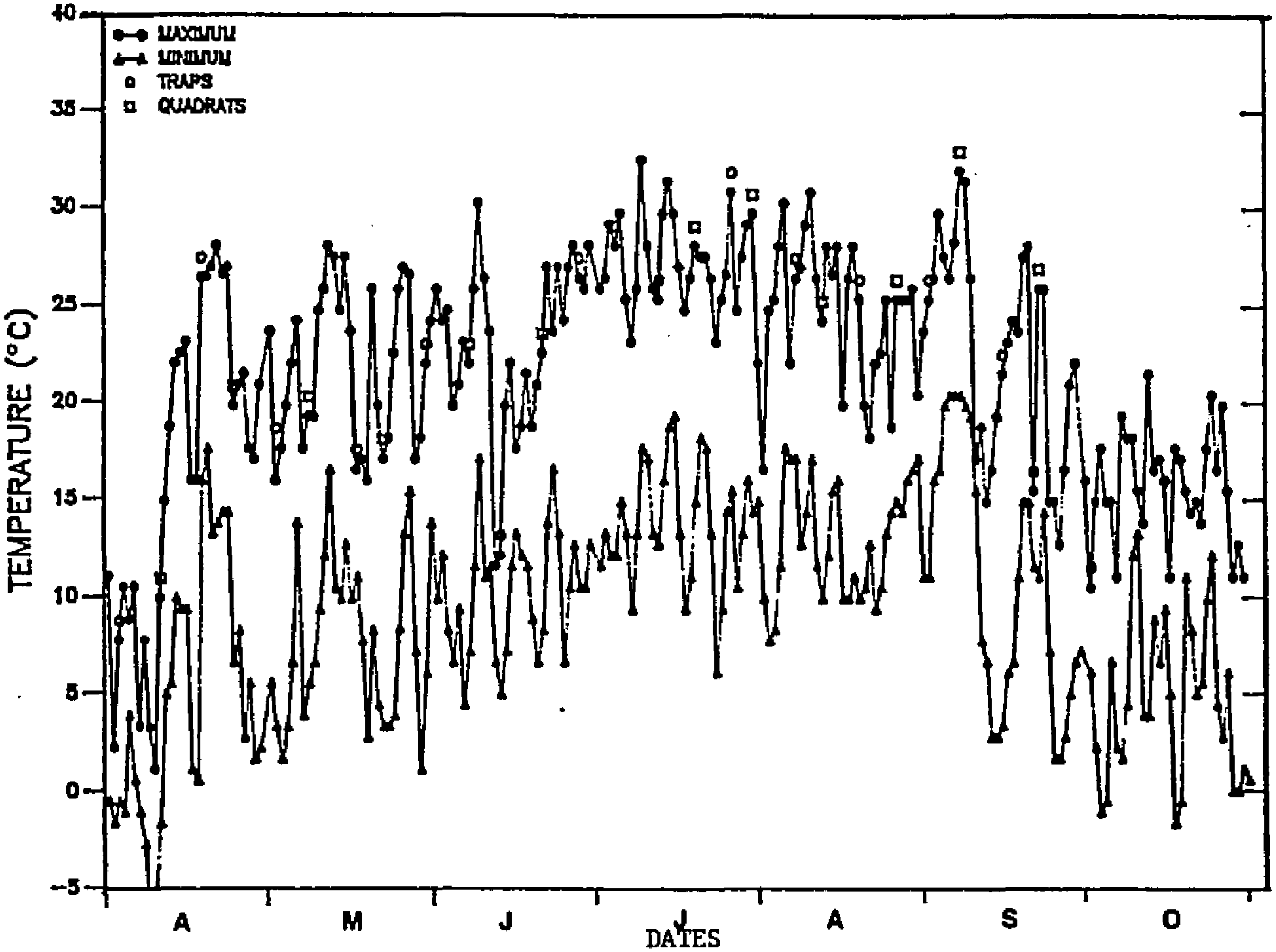


FIGURE 4. DAILY AIR TEMPERATURES, NATIONAL WEATHER SERVICE,
EAST LANSING STATION, YEAR 2 (1985).

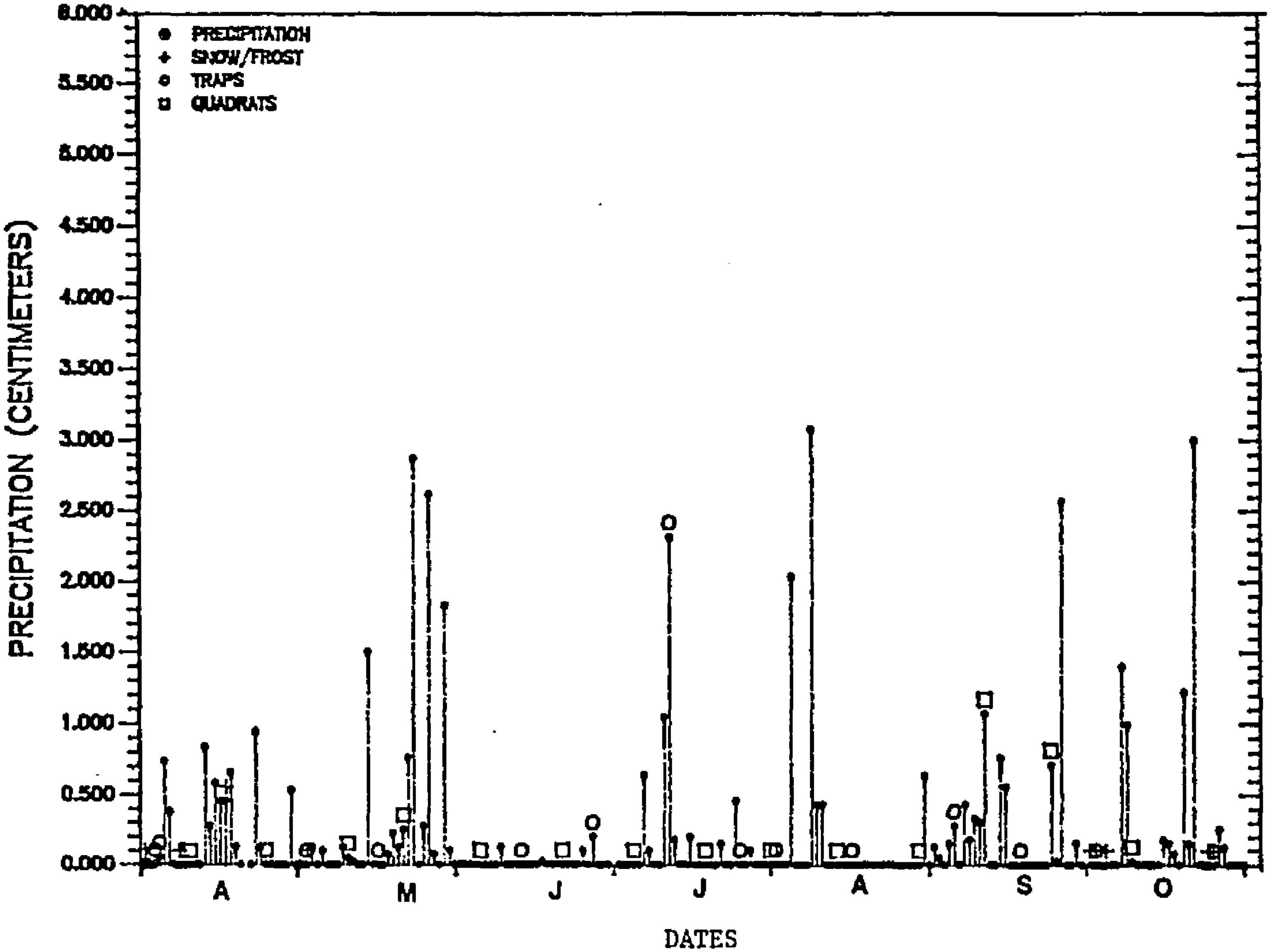


FIGURE 5. DAILY PRECIPITATION, NATIONAL WEATHER STATION, EAST LANSING STATION, YEAR 1 (1984).

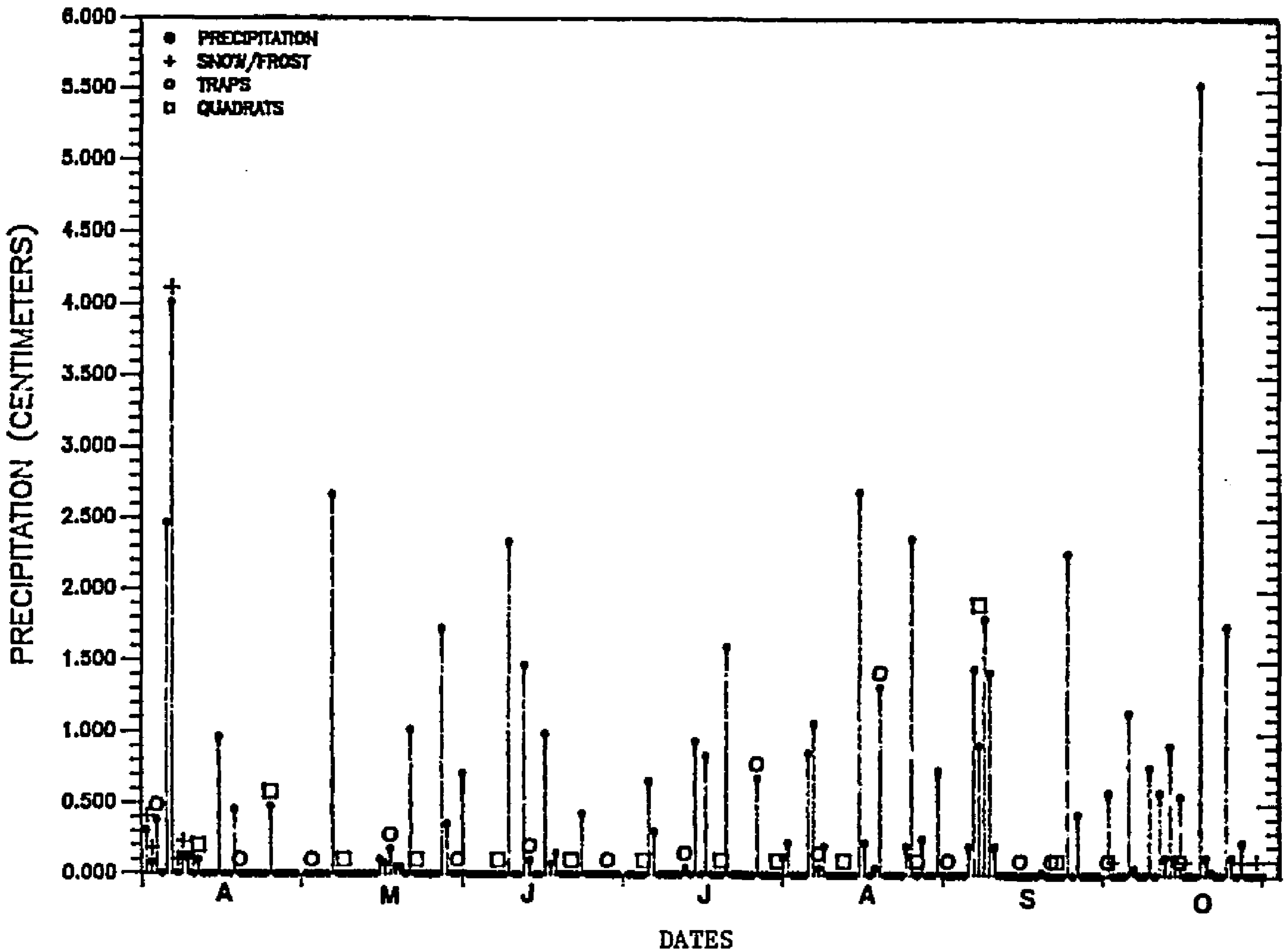


FIGURE 6. DAILY PRECIPITATION, NATIONAL WEATHER STATION, EAST LANSING STATION, YEAR 2, (1985).

year 1 did snowfall occur well into the month of April. In year 2 precipitation in the form of rain was observed earlier in the spring, however, more precipitation days were recorded for year 1.

A total rainfall of 44.42 cm was obtained for the study period of year 1 and 58.83 cm for year 2. As shown in Figure 5 rain was not evenly distributed throughout year 1 as it was in year 2 (Figure 6). The dryest and warmest period was observed during summer of year 1 (12.34 cm of rain), where 4 rainy days were recorded in June, 9 in July, and 5 in August. The highest accumulation occured in June, with a total of 0.4572 cm. In summer of year 2 rain was evenly distributed (Figure 6) and the warmest days were always preceded by rain.

After the warm and dry summer, several rainy days were recorded early in September and in October. During fall of year 1, few more days were reported with a total of 15.27 cm. However, in year 2 the total amount of precipitation in the fall was 21.36 cm.

1.3. Substrate moisture

Average percent moisture of leaf litter, O layer and A layer is presented in Figure 7.

A) Leaf litter:

The leaf litter was the least humid layer in both years except between weeks 11, and 13 of year 1, where many rainy days were recorded after the dryest period of the year.

Moisture peaks of litter shown in Figure 7 correspond to days of

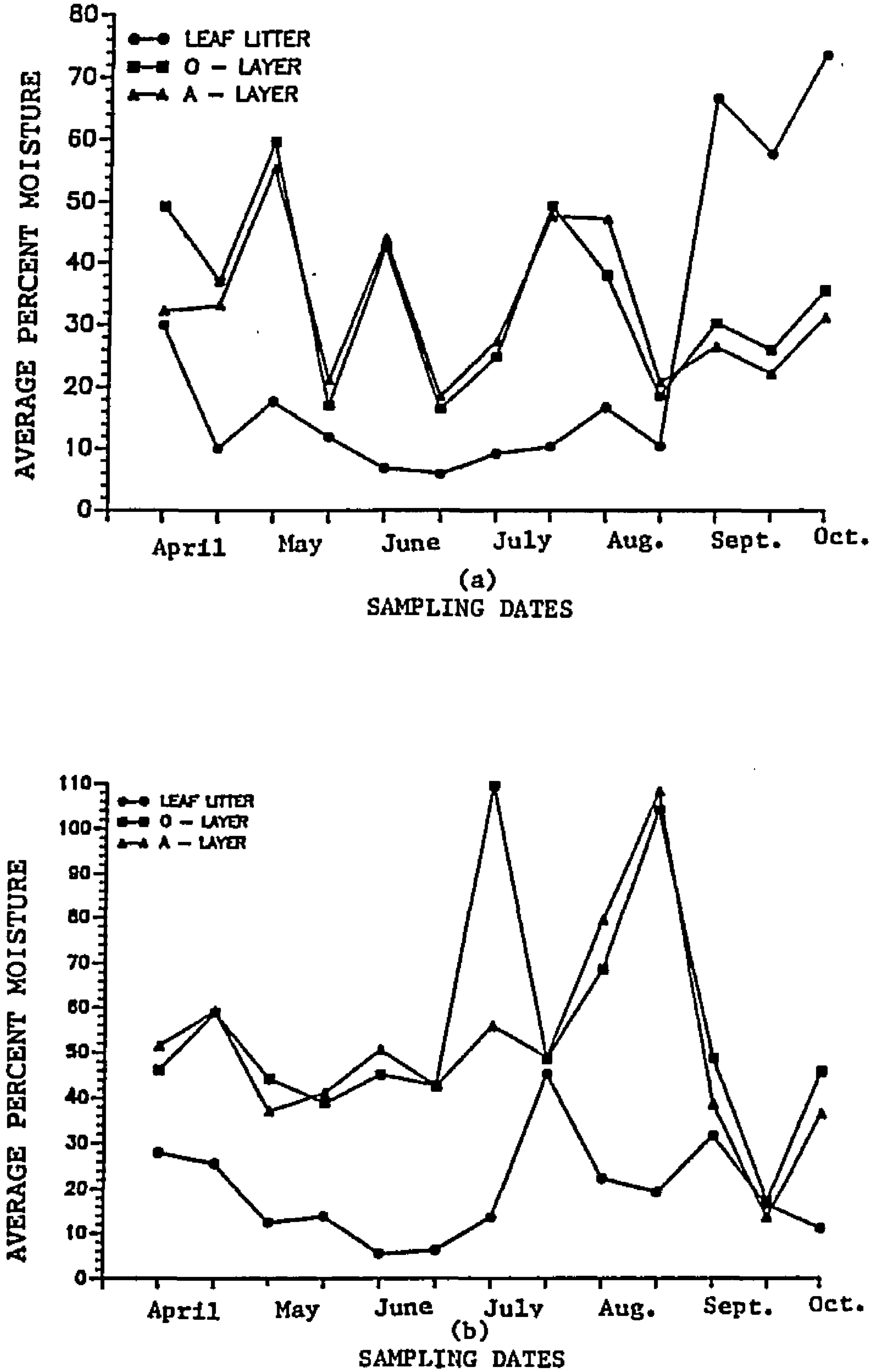


FIGURE 7. MOISTURE IN % OF DRY WEIGHT, OF LITTER, O AND A LAYERS IN BAKER WOODLOT.

high precipitation in both years.

The driest conditions were observed between weeks 4 and 9 of year 1 and weeks 3 to 7 in year 2, these periods corresponds to the dry season of each year. The dryness of the leaf litter ended earlier in year 2 (week 8) than in year 1 (week 11).

B) O layer:

The O layer was the most humid layer during year 1 and in a few weeks of year 2. Average percent moisture was very similar at the beginning of both years, but differed throughout the remaining seasons. In year 1 this parameter oscillated more than in year 2, where precipitation was evenly distributed. Year 2 showed a dramatic increase in average percent moisture during week 7 (108%) and week 10 (105%). In year 2 the O layer was not only more moist in the summer but also during fall.

C) A layer:

The results obtained for the A layer during year 1 were very similar to those for the O layer. This was also the case for year 2 except in week 7, where no increase in the average percentage of moisture was observed.

1.4. Litter cover

Table 4 summarizes average litter mass/m^2 in Baker woodlot for each season. Litter cover diminished considerably during year 2, being

Table 4. Average dry mass of forest floor litter (g/m^2)

SEASON	YEAR 1	YEAR 2
Spring	545.28	328.37
Summer	409.12	258.68
Fall	325.72	256.11

only about 2/3 of the amount recorded for spring or summer of year 1 and about 3/4 the amount in the fall of that same year.

The highest litter mass was recorded in spring, decreasing slowly towards fall. Spring litter mass in year 2 was very similar to the amount obtained in fall of the previous year. The litter mass was smaller in summer and fall of year 1, and almost the same for both seasons in year 2.

2. Species dominance

Six Diplopoda species ocurred in the study site. These were *Pseudopolydesmus serratus* (Say), 1821; *Aniulus venustus* (Wood), 1864; *Diploiulus caeruleocinctus* (Wood), 1864; *O. pilosus*; *P. inconstans*, and *P. bivirgatum*. Only one specimen of *A. venustus* and *D. caeruleocinctus*, and two specimens of *P. serratus* were collected during the two years. Because of the low frequency of occurrence of these three species, species dominance was assessed using only data on *O. pilosus*, *P. inconstans*, and *P. bivirgatum*.

To seasonally assess species dominance, the percent of the total number of individuals collected in Baker woodlot was computed for each species (Table 5 , Figures 8 and 9). *Ophyiulus pilosus* was the most common species during year 1 and in the spring and fall of year 2. During summer of year 2 it was surpassed by *P. inconstans*. The apparent population peak of *P. inconstans*, however, was due to 61 hatchings recovered from a single sample (as evidenced by the large SE) and is thus a somewhat biased estimate.

Table 5. Percent of total number for the three species studied in Baker woodlot each season.

(a) YEAR 1

SPECIES	SPRING	SUMMER	FALL	TOTAL
O. pilosus	93.26%	90.00%	89.51%	91.53%
P. inconstans	3.70%	6.67%	5.59%	4.91%
P. bivirgatum	3.04%	3.33%	4.90%	3.56%

(b) YEAR 2

SPECIES	SPRING	SUMMER	FALL	TOTAL
O. pilosus	91.18%	40.00%	86.26%	75.93%
P. inconstans	4.41%	56.36%	10.99%	20.56%
P. bivirgatum	4.41%	3.64%	2.75%	3.57%

FIGURE 8. SEASONAL FLUCTUATIONS IN PERCENT OF TOTAL NUMBERS FOR THE THREE SPECIES OF DIPLOPODS STUDIED IN BAKER WOODLOT IN YEAR 1.

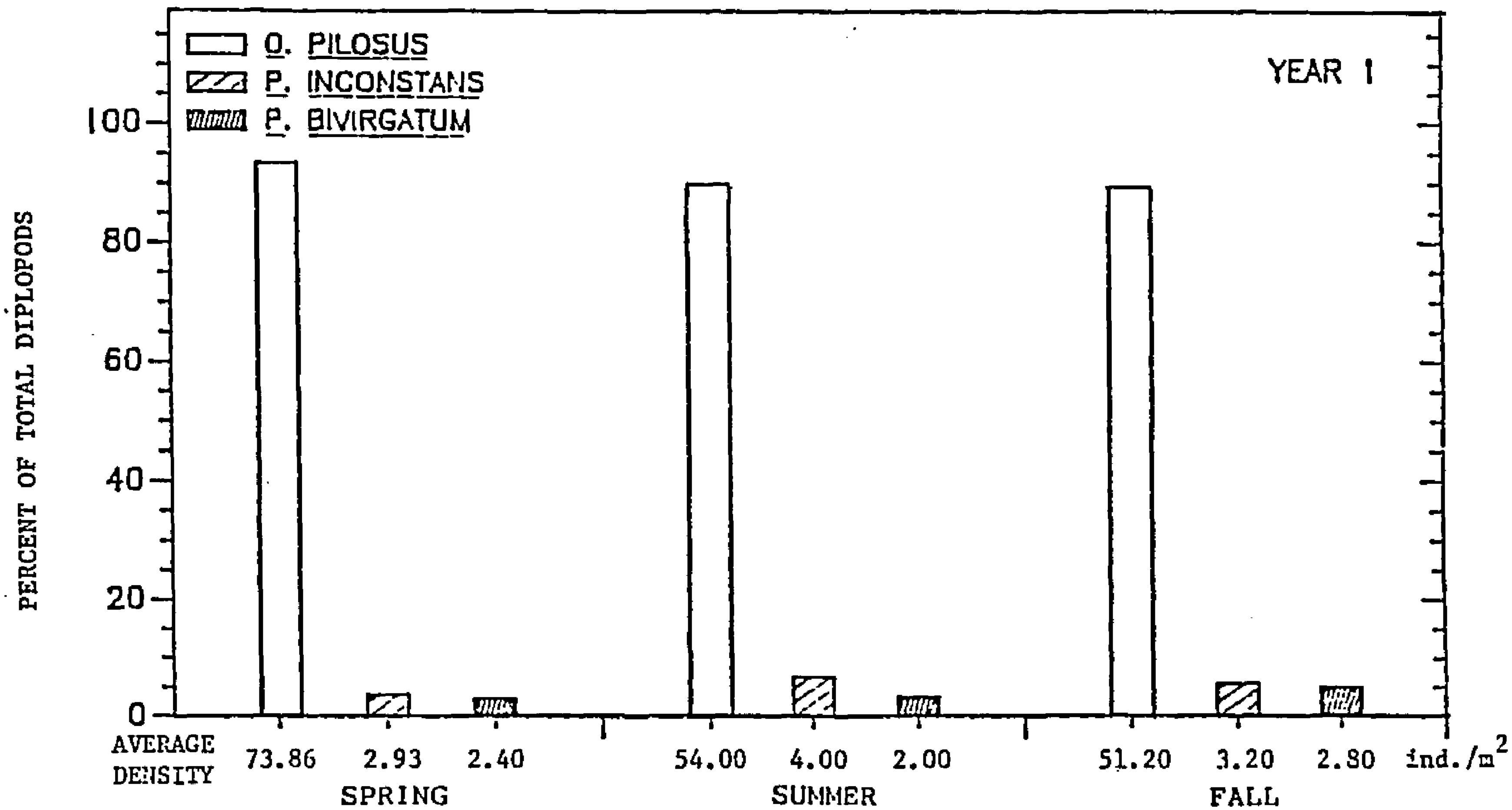
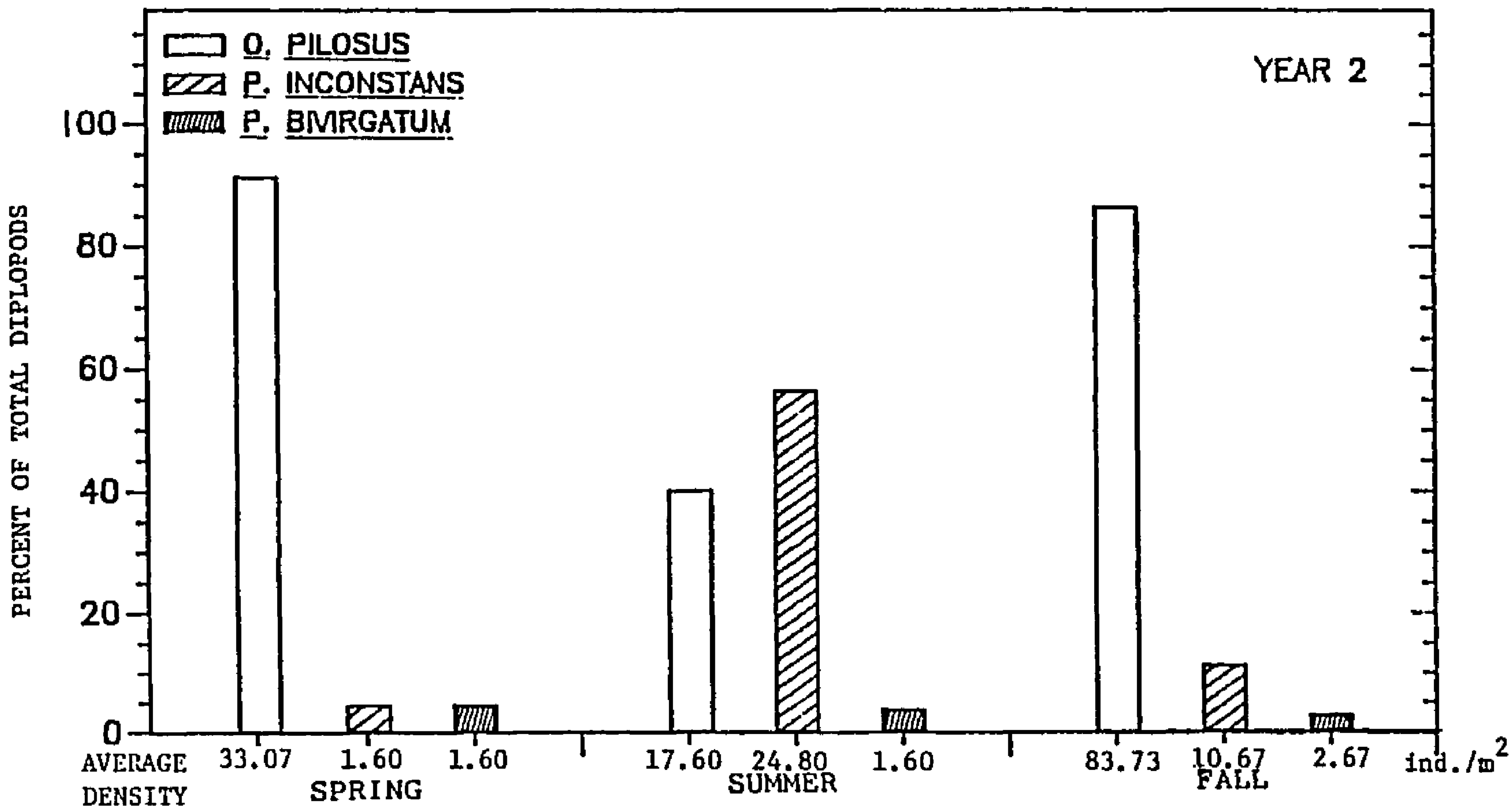


FIGURE 9. SEASONAL FLUCTUATIONS IN PERCENT OF TOTAL NUMBERS FOR THE THREE SPECIES OF DIPLOPODS STUDIED IN BAKER WOODLOT IN YEAR 2.



3. *Population density*

Population densities of the three common species are presented in Table 6 and Figure 8 and 9. Each average represents the expected number of individuals (all stages combined)/m^2 (all layers combined) during a collection date. *Ophyiulus pilosus* showed the highest population density in all seasons of year 1 and in spring and summer of year 2. During year 1 the maximum density was observed during spring (73.86 millipedes/m^2). However, in year 2 the maximum density was obtained in the fall (83.73 millipedes/m^2). *Polydesmus inconstans* was most abundant in summer of year 2, with an estimated 24.80 millipedes/m^2, and occurred in very low numbers throughout year 1. The low density during summer of year 1 was probably due to a hot and dry summer (Section 1). Blower (1969) has suggested that low numbers or complete absence of *Polydesmus* during summer can result from very dry conditions. *Polyzonium bivirgatum* showed the lowest population density in all seasons, especially during year 2. The maximum density obtained for this species was 2.80 millipedes/m^2 in fall of year 1.

Population studies of other julids in Europe show densities similar to those obtained for *O. pilosus* in the present study. Van der Drift (1951) found densities of 80 millipedes/m for *Cylindroiulus punctatus* and *Iulus scandinavius* in a Beech wood with raw humus. However, Blower (1970) reported very high population densities for British forests on limestone, ranging from 350 to 650 millipedes/m^2

Table 6. Seasonal variations in average population density from the three species studied in Baker woodlot (± S.E.).

(a) YEAR 1

SPECIES	SPRING	SUMMER	FALL	TOTAL
<u>O. pilosus</u>	73.86 ± 10.85	54.00 ± 16.15	51.20 ± 9.43	61.71 ± 6.67
<u>P. inconstans</u>	2.93 ± 1.11	4.00 ± 1.64	3.20 ± 1.54	3.31 ± 0.79
<u>P. bivirgatum</u>	2.40 ± 0.83	2.00 ± 1.30	2.80 ± 1.39	2.40 ± 0.65

(b) YEAR 2

SPECIES	SPRING	SUMMER	FALL	TOTAL
<u>O. pilosus</u>	33.07 ± 7.90	17.60 ± 4.09	83.73 ± 24.71	40.00 ± 7.15
<u>P. inconstans</u>	1.60 ± 1.35	24.80 ± 24.39	10.67 ± 4.15	10.83 ± 7.58
<u>P. bivirgatum</u>	1.60 ± 0.98	1.60 ± 0.96	2.67 ± 1.73	1.85 ± 0.67

rising to 800 millipedes/m^2 at times of juvenile emergence. Seventy-five percent of these were julids like O. pilosus and I. scandinavius. Blower and Miller (1974) found that O. pilosus showed four times higher densities than other julids such as I. scandinavius. In addition, when species of different orders were compared, julids always exhibited the highest abundance. Blower (1970), for instance, reported numbers/m^2 of 58 Iulus, 38 Polydesmus and 6 Tachypodoiulus at Ernocroft woods.

Abundance estimates obtained for P. inconstans and P. bivirgatum were much smaller than those reported by Snider (1980, 1984a) and Johnson (1952). Snider (1984a) estimated 450 individuals of P. inconstans/m^2 in April but densities generally did not exceed 200 individuals/m^2 in depressions and 5 to 74 individuals/m^2 in upland areas of Baker woodlot.

Estimated density ranges in upland areas (Snider, 1984a) were similar to those obtained for P. inconstans in the present study (Table 6). Conditions in these areas may have been similar to the hot/dry climate of 1984-85, which could be partly responsible for low densities. The most important causative factor may have been intensive collecting activity prior to 1984. During an experiment in which diplopods were offered as prey to carabid beetles (Snider, 1984b), several thousand individuals of P. inconstans were removed from the Baker woodlot population. Slightly increasing abundance in 1985 (year 2 of the present study) may have represented the beginning of population recovery.

Given the known history of population depletion (Snider, 1984b) prior to this study, dominance relationships within the diplopod community of Baker woodlot (Table 6) may well change in future years; eventually they may return to the "undisturbed" state characteristic of the site, in which P. inconstans becomes dominant (Snider, 1980) or co-dominant with O. pilosus.

Johnson (1952) reported densities for Polyzonium bivirgatum in Southern Michigan forests of 30 to 40 individuals/m^2. According to this author, P. bivirgatum abundance was generally lower in Northern forests, but no numbers were given.

4. Population stage structure

Stage-specific densities were computed for each season only for the dominant species, O. pilosus, in order to study stage-related seasonal fluctuations.

The stage structure of O. pilosus is presented in Table 7 and Figure 10. Ophyiulus pilosus is a semelparous species which lives for two years (Blower and Miller, 1984). Its life cycle starts with small juveniles hatched at the end of spring or summer and ends after they mature and reproduce during their second summer. In the present study, small juveniles showed an increase in numbers from spring (overwintered individuals) to fall in both years. This increase was caused by hatchlings entering the population at the end of spring and summer, this was observed during both years. Small juveniles showed a density

Table 7. Stage-specific average number of *O. pilosus* per square meter for each season (± S.E.).

(a) YEAR 1

STAGE	SPRING	SUMMER	FALL
Small juveniles	2.66 ± 1.91	30.80 ± 11.40	40.80 ± 8.37
Juveniles	36.80 ± 8.15	16.00 ± 4.17	4.00 ± 1.25
Adults	34.40 ± 5.94	7.20 ± 2.43	6.40 ± 1.97
Total	73.86 ± 10.85	54.00 ± 16.15	51.20 ± 9.43

(b) YEAR 2

STAGE	SPRING	SUMMER	FALL
Small juveniles	3.20 ± 1.65	4.40 ± 1.98	20.27 ± 7.89
Juveniles	12.27 ± 4.72	3.20 ± 1.83	58.13 ± 16.76
Adults	17.60 ± 4.11	10.00 ± 2.90	5.33 ± 2.34
Total	33.07 ± 7.90	17.60 ± 4.09	83.73 ± 24.71

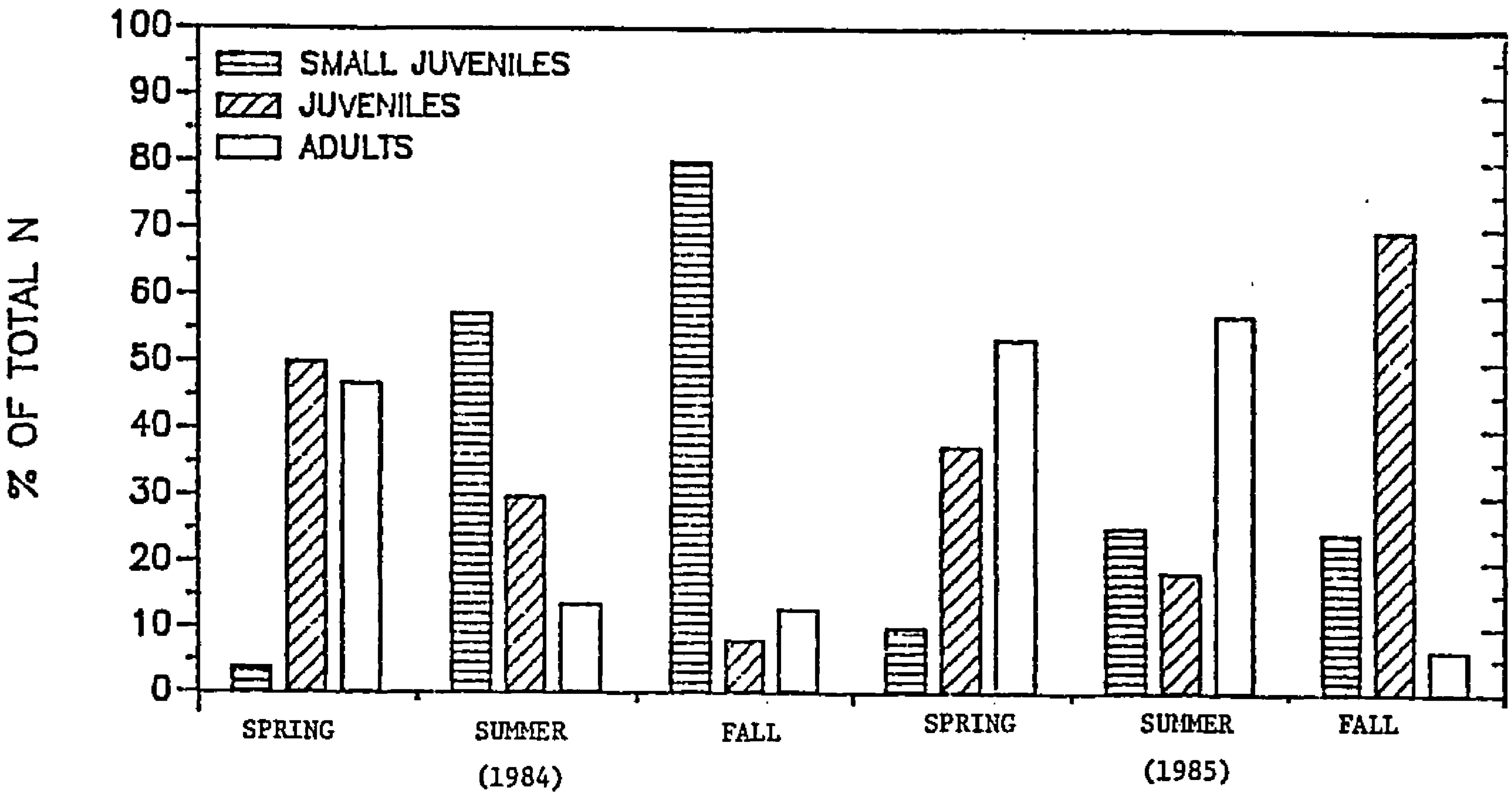


FIGURE 10. SEASONAL DISTRIBUTION OF STAGES IN THE *O. PILOSUS* POPULATION IN 1984-1985.

decrease from fall of year 1 to spring of year 2. This decrease was caused by molting of this category to the juvenile category at the end of fall and in early spring.

The juvenile portion of the population showed a progressive decrease in density from spring to fall of year 1. The juvenile decrease was caused by molting of instars VIII and IX to adult. These new adults replaced the two-year-old adults during that time. In addition, unfavorable weather conditions caused estivation in the prevailing stages and an apparent population decrease.

The population in year 2 showed an increase from the previous fall, again caused by new juveniles entering the population. After the vernal increase of year 2, a decrease was observed in the summer, again attributable to climatic conditions. However, the population showed a large density increase in the fall, probably caused by a higher survivorship of estivating individuals (small juveniles and juveniles) which now re-appear in the upper soil horizon and are now sampled for the first time. In addition some of the small juveniles (instar V) molted to juveniles. The large survivorship was probably caused by moister conditions during this summer. The presence of fewer small juveniles and more juveniles could be indicative of a faster development than in the previous year (Blower (1974a); Blower and Miller (1974)). The effects were subtle, however, most juveniles collected at the end of fall of both years were instars VII, VIII, and IX, overwintering as such. This confirmed data given by Blower and Miller (1974) for the British Isles.

The adult subpopulation was most abundant in spring, decreasing consistently towards fall. All two-year adults apparently died after reproducing during summer. Adults collected in the fall were young adults which would mature the following spring.

5. Spatial distribution of the dominant species

5.1. Seasonal horizontal dispersion

The variance/mean ratio test (Elliot, 1973) was used to evaluate the population dispersion of *O. pilosus* in comparison with a Poisson series. Three sample groups were considered, one per season (years and layers combined), using all quadrat data from a given season. Because the number of samples was large, agreement with the Poisson model was tested with the standard normal variable:

$$d = \sqrt{2\chi^2} - \sqrt{2\nu - 1}$$

where ν represents degrees of freedom and χ^2 is the variance/mean ratio proposed by Elliot (1973).

Results are detailed in Table 8. As all values of d were much larger than 2.58, agreement with a Poisson series was rejected at the 99% probability level. This implies that the population was not distributed randomly. A check with the χ^2 goodness-of-fit confirmed these results.

The extremely high values of d (Table 8) indicate that the dispersion of the population was strongly aggregated. A χ^2 test for goodness-of-fit with the negative binomial distribution gave positive results for spring data. Because of different sample sizes, a

Table 8. Variance/mean ratio test parameters for large samples from the *O. pilosus* population. Data from both years were combined.

SEASON	n	$\bar{X}$/sample	S^2	χ^2	d	DISPERSION
Spring	120	3.34	22.59	804.85	24.73	aggregated
Summer	80	2.24	17.08	602.37	22.18	aggregated
Fall	70	4.07	38.98	660.84	24.65	aggregated

* d is normally distributed N(0,1) and Prob(d > 2.58) $\approx$ 0.0049

comparison of the relative degree of clumping between seasons was not possible. It can be assumed, however, that the distribution of *O. pilosus* generally conformed to the negative binomial.

The aggregated distribution of *O. pilosus*, as well as of other diplopods (Snider, 1980), can be in part related to oviposition habits. Blower and Miller (1974) found that one female of *O. pilosus* can lay an average of more than 72 eggs. Eggs are laid in masses and newly hatched individuals have very low mobility, thus clustering the population.

5.2. Horizontal distribution and litter mass

A possible relationship between the spatial distribution of *O. pilosus* and leaf litter mass was assessed by linear regression for each season. Scatter diagrams of litter mass and number of individuals in each quadrat are presented in Figures 11 to 16 for spring, summer, and fall.

The parameter r^2 was used to validate the linear model. The small values of this parameter (Table 9) indicated lack of fit with that model. In particular, less than 8% of the variability in number of individuals per sample in year 1 and less than 13% in year 2 could be explained by linear regression. Although r^2 was somewhat higher in summer of year 1 and fall of year 2, no significant linear relationship between the amount of leaf litter and the density of *O. pilosus* became apparent.

Figures 11 to 16 illustrate this lack of correlation between densities and litter mass, and no additional regression models were

FIGURE 11. SCATTER DIAGRAMS FOR REGRESSION ANALYSIS BETWEEN LITTER MASS AND NUMBER OF O. PILOSUS DURING SPRING YEAR 1.

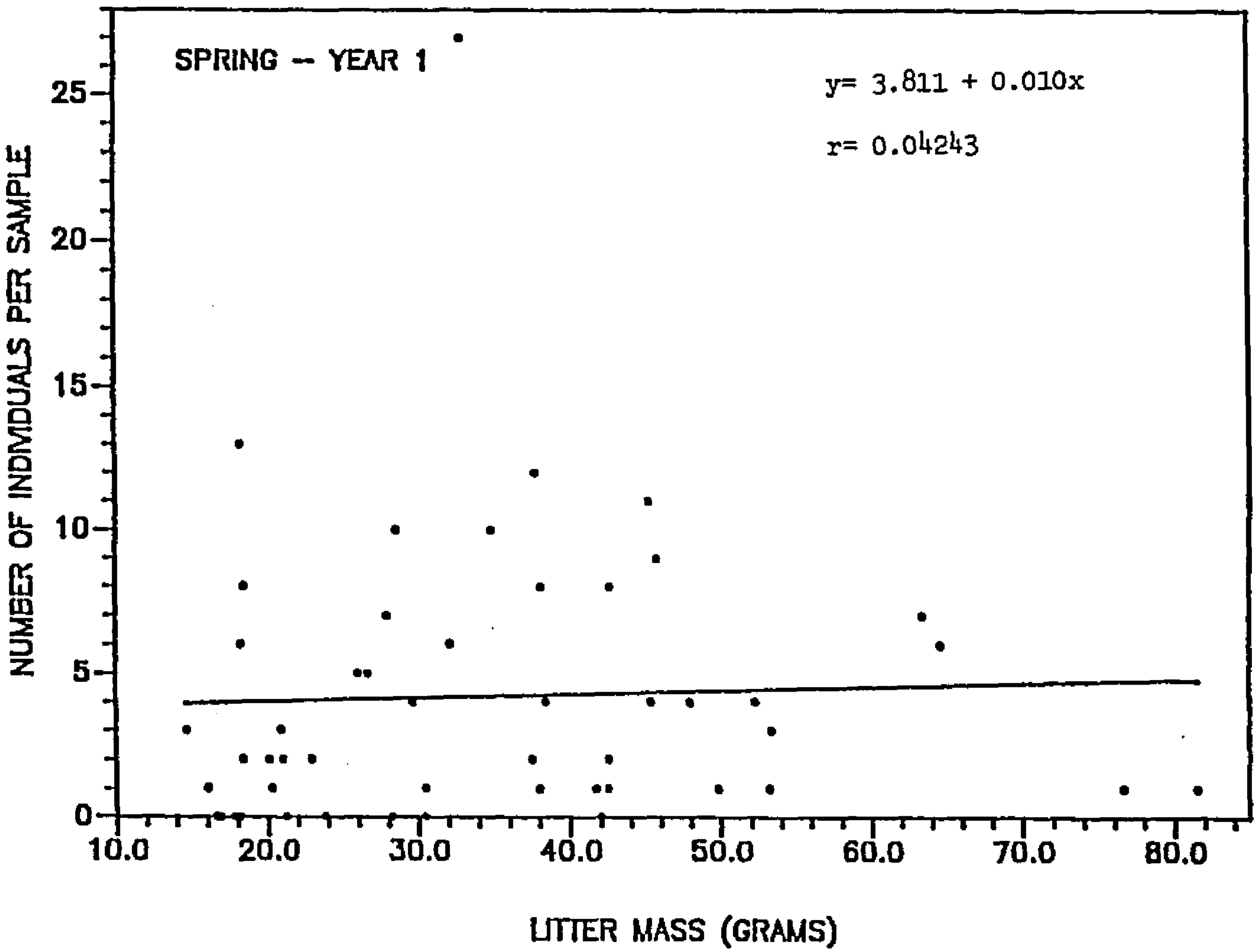


FIGURE 12. SCATTER DIAGRAMS FOR REGRESSION ANALYSIS BETWEEN LITTER MASS AND NUMBER OF O. PILOSUS DURING SPRING YEAR 2.

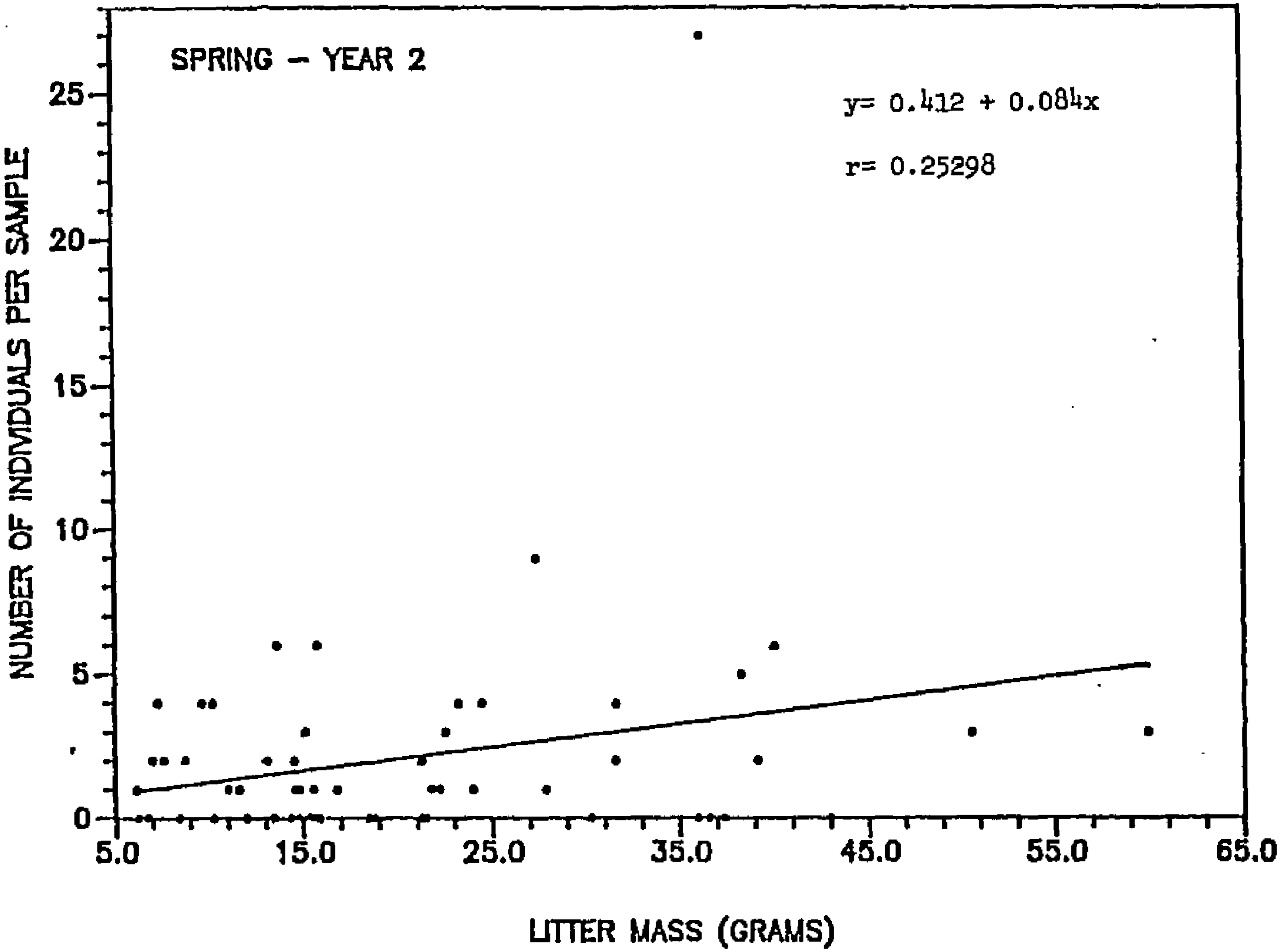


FIGURE 13. SCATTER DIAGRAMS FOR REGRESSION ANALYSIS BETWEEN LITTER MASS AND NUMBER OF <u>O. PILOSUS</u> DURING SUMMER YEAR 1.

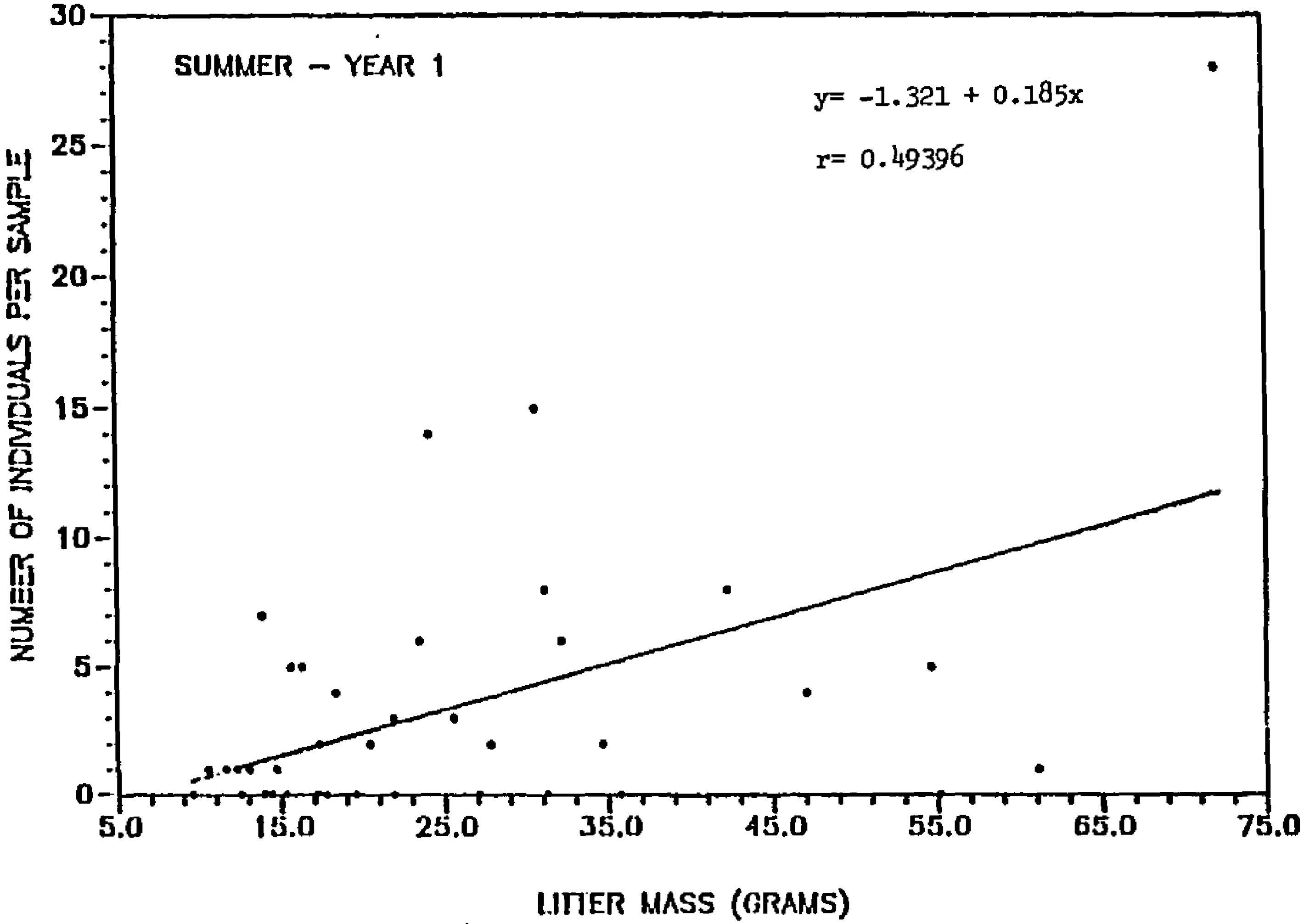


FIGURE 14. SCATTER DIAGRAMS FOR REGRESSION ANALYSIS BETWEEN LITTER MASS AND NUMBER OF O. PILOSUS DURING SUMMER YEAR 2.

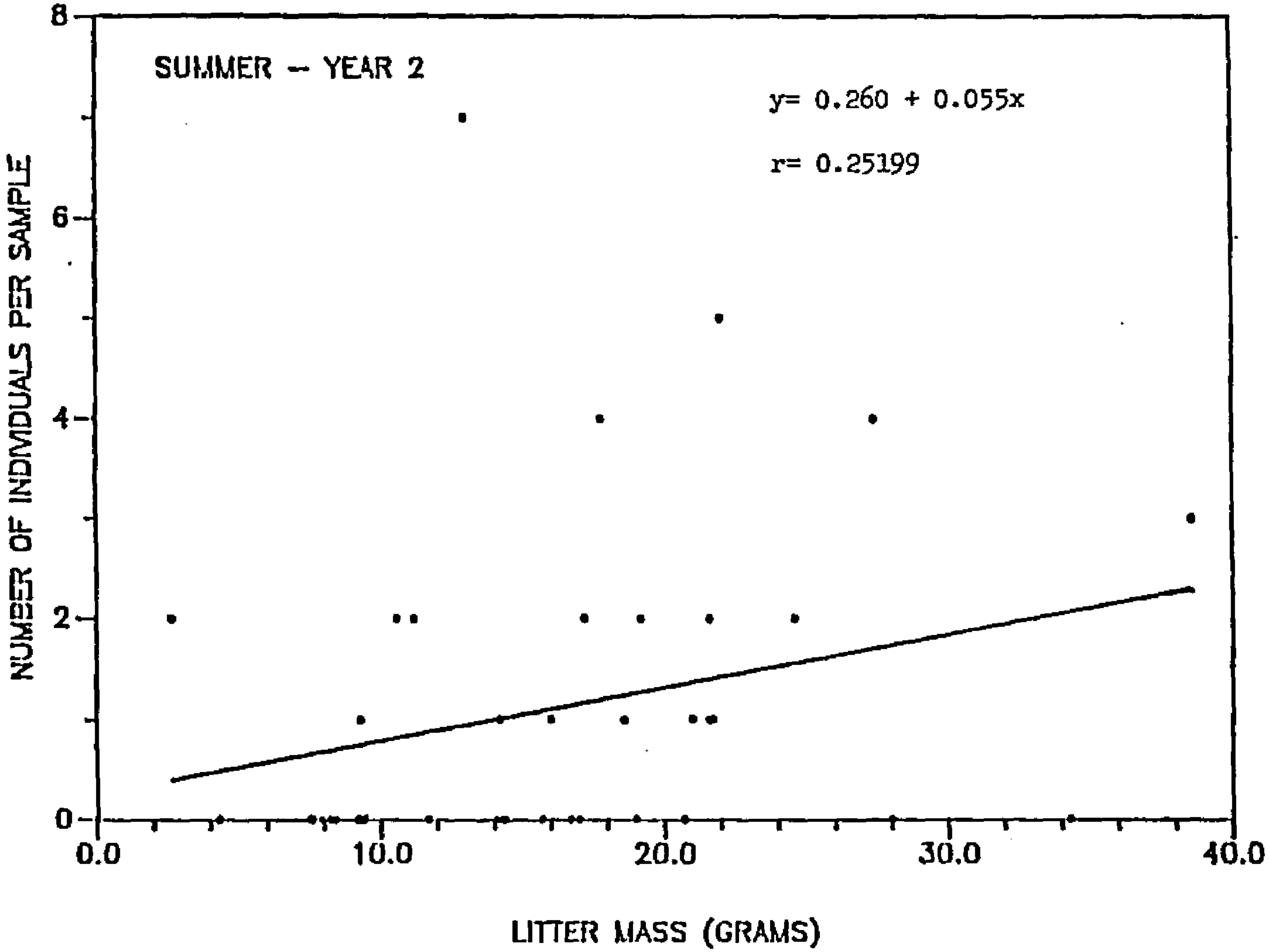


FIGURE 15. SCATTER DIAGRAMS FOR REGRESSION ANALYSIS BETWEEN LITTER MASS AND NUMBER OF O. PILOSUS DURING FALL YEAR 1.

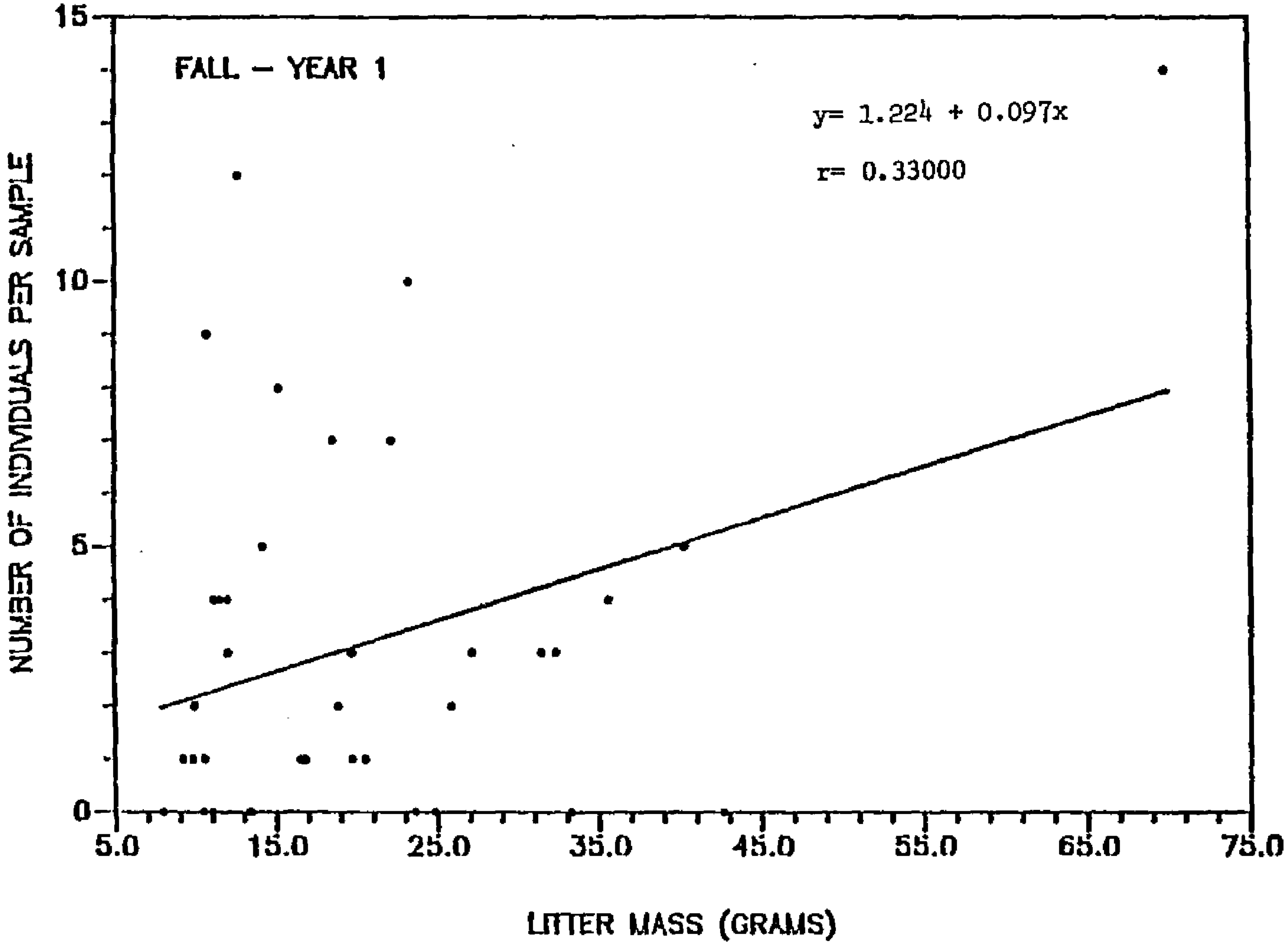


FIGURE 16. SCATTER DIAGRAMS FOR REGRESSION ANALYSIS BETWEEN LITTER MASS AND NUMBER OF <u>O. PILOSUS</u> DURING FALL YEAR 2.

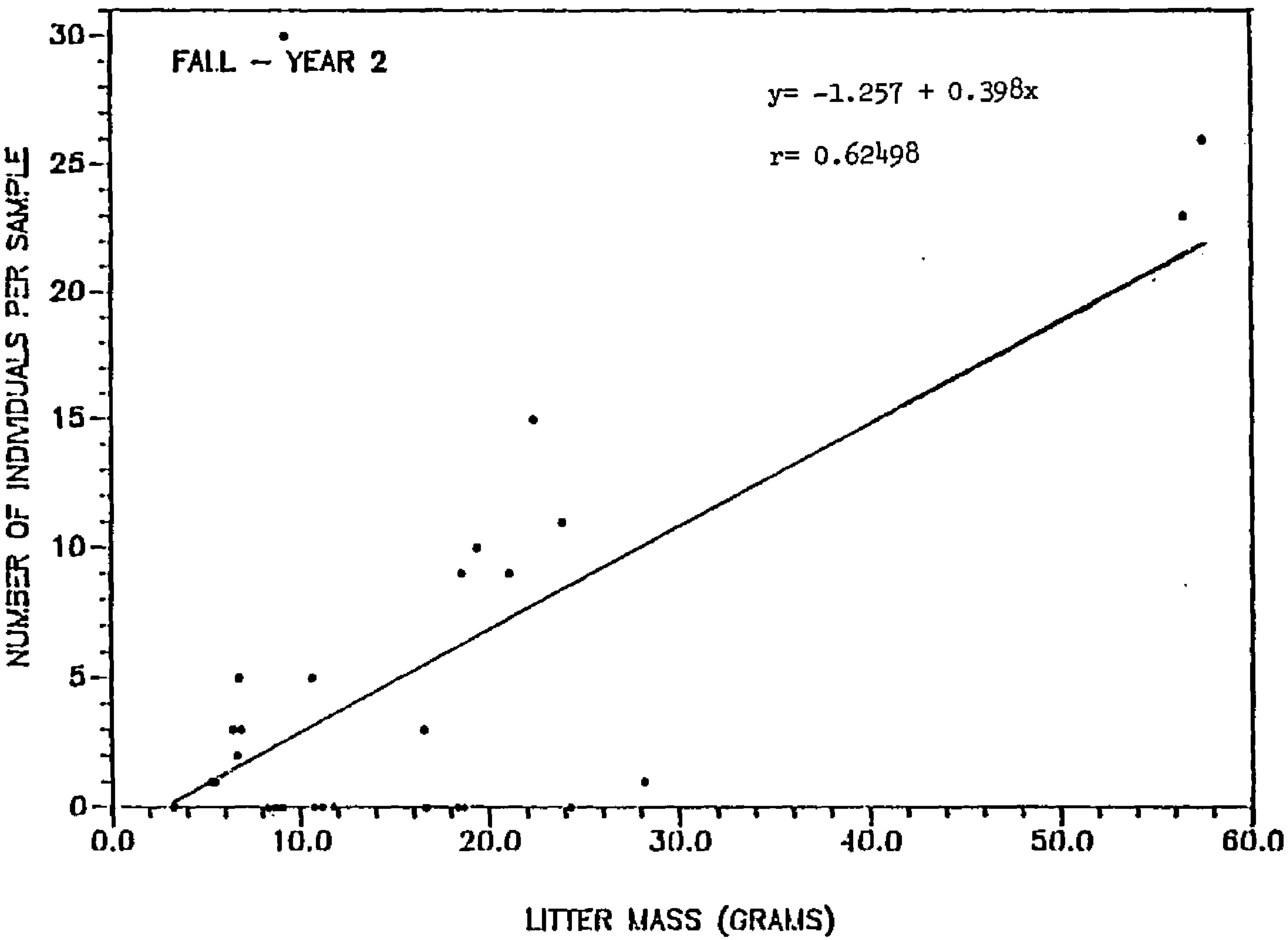


Table 9. Values of r^2 for linear regression test between litter mass and number of *O. pilosus.*

SEASON	YEAR 1	YEAR 2
Spring	0.0018	0.0640
Summer	0.2440	0.0635
Fall	0.1089	0.3906
Annual	0.0800	0.1300

tried on the data. An expected direct proportionality between litter mass and numbers of O. pilosus could not be confirmed. A brief evaluation of potential relationships between litter moisture and population density was equally inconclusive. The distribution of the species appeared to be a function of other, possibly interacting parameters (e.g. temperature, amount of woody debris, or even A horizon characteristics).

6. Vertical distribution of the dominant species

6.1. Seasonal distribution

Data presented in Figure 17 and Table 10 show that leaf litter was consistently the least populated layer during both years, except during fall of year 2. Most of the millipedes were present in the A horizon during spring and fall and in the O layer during summer of year 1 and 2.

6.2. Stage-specific distribution

A.1) Small juveniles

No small juveniles were found during spring (both years) in the leaf litter (Figures 17 and 18 and Table 11). The few small juveniles collected were overwintering forms (stadias IV and V) and were found in the A layer (100%) during year 1 and from the O (66.56%) and A layer (33.44%) in year 2 (Figure 18).

Adverse weather conditions at the beginning of each year (Section 1) may have caused absence of the stage in leaf litter, forcing it to

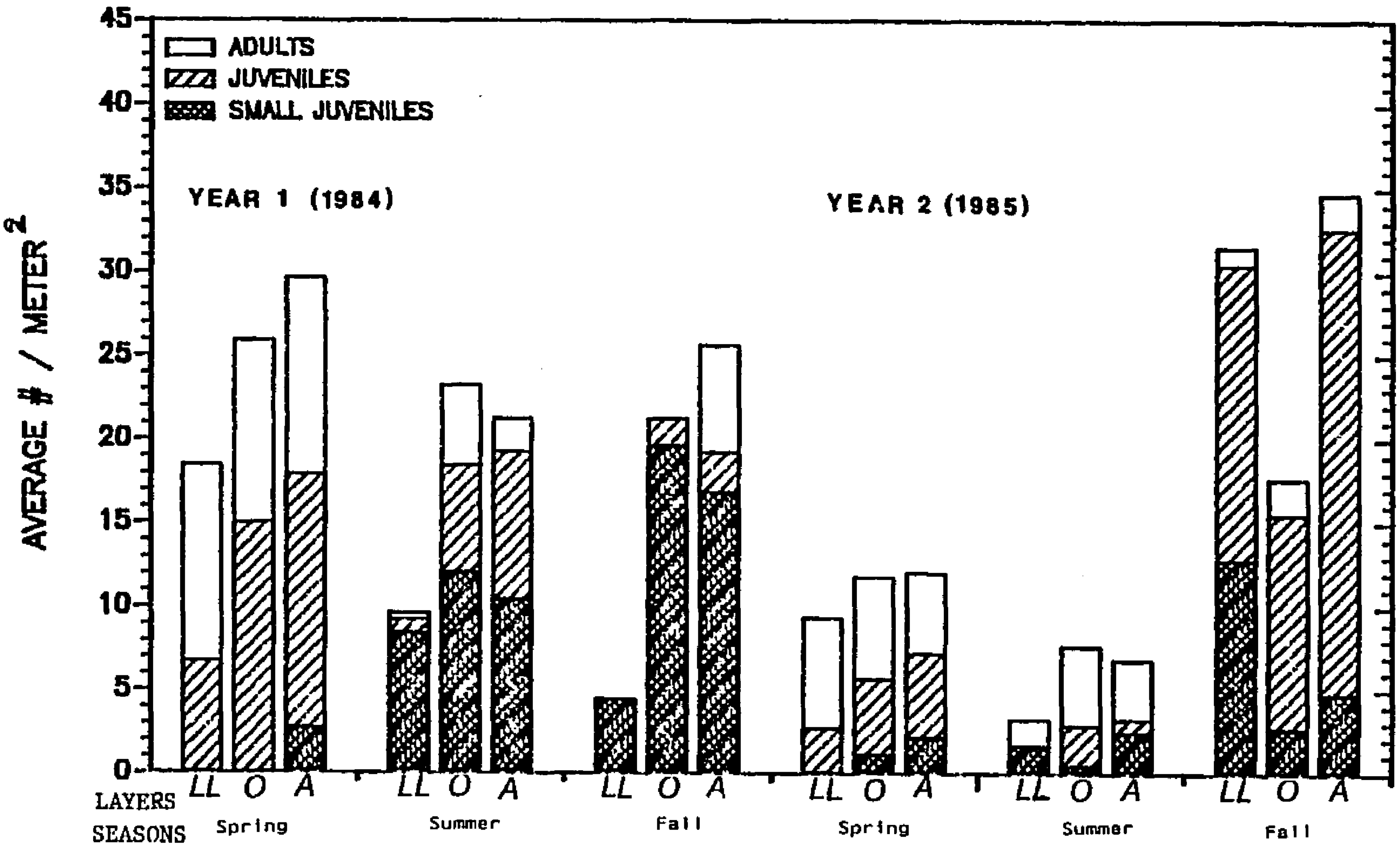


FIGURE 17. SEASONAL VERTICAL DISTRIBUTION OF
<u>O. PILOSUS</u> STAGES (AVERAGE # / METER^2)

Table 10. Seasonal vertical distribution of average number of _O. pilosus_ per square meter ± S.E. (percent of season total).

	LAYER	YEAR 1	%	YEAR 2	%
SPRING	LL	18.40 ± 5.29	(24.93)	9.33 ± 3.51	(28.21)
	OL	25.86 ± 7.71	(35.00)	11.74 ± 2.63	(35.51)
	AL	29.60 ± 5.88	(40.07)	12.00 ± 4.02	(36.28)
	TOTAL	73.86 ± 10.85		33.07 ± 7.90	
SUMMER	LL	9.60 ± 8.02	(17.78)	3.20 ± 1.64	(18.18)
	OL	23.20 ± 6.30	(42.96)	7.60 ± 2.56	(43.18)
	AL	21.20 ± 5.74	(39.26)	6.80 ± 2.49	(38.64)
	TOTAL	54.00 ± 16.15		17.60 ± 4.09	
FALL	LL	4.40 ± 2.43	(8.59)	31.47 ± 15.20	(37.59)
	OL	21.20 ± 5.45	(41.41)	17.60 ± 6.29	(21.02)
	AL	25.60 + 5.92	(50.00)	34.66 ± 9.55	(41.39)
	TOTAL	51.20 ± 9.43		83.73 ± 24.71	

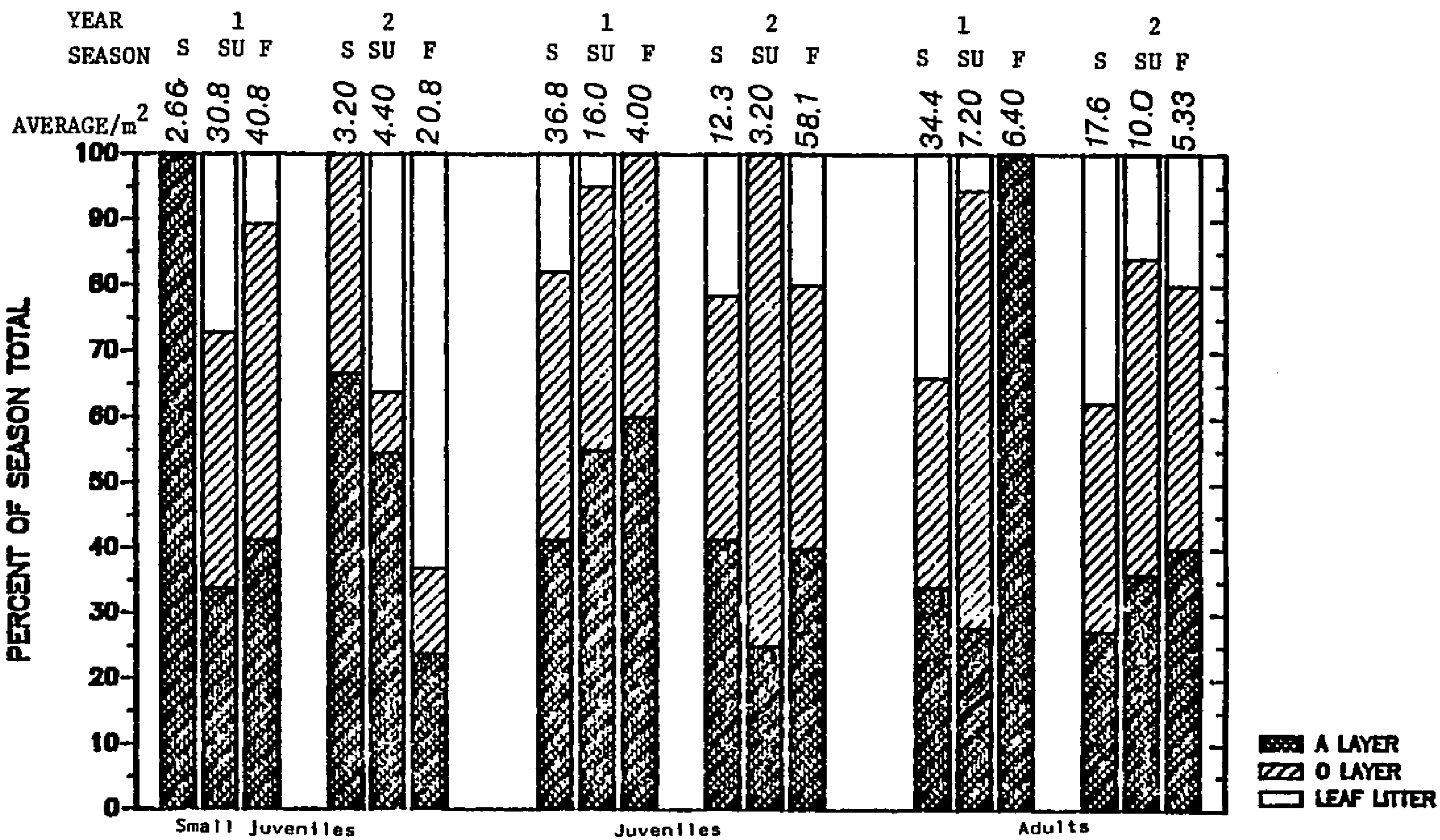


FIGURE 18. VERTICAL DISTRIBUTION OF *O. PILOSUS* STAGES IN PERCENT OF TOTAL FOR EACH SEASON.

Table 11. Spring vertical distribution of average number of *O. pilosus* per square meter by stages ± S.E. (percent of season total).

	LAYER	YEAR 1	%	YEAR 2	%
SJ					
	LL	0.00 ± 0.00	(0.00)	0.00 ± 0.00	(0.00)
	OL	0.00 ± 0.00	(0.00)	1.07 ± 0.75	(33.44)
	AL	2.66 ± 1.91	(100.0)	2.13 ± 1.49	(66.56)
	Total	2.66 ± 1.91		3.20 ± 1.65	
JU					
	LL	6.67 ± 2.47	(18.13)	2.66 ± 1.71	(21.68)
	OL	14.93 ± 6.65	(40.57)	4.54 ± 1.32	(37.00)
	AL	15.20 ± 3.85	(41.30)	5.07 ± 2.30	(41.32)
	Total	36.80 ± 8.15		12.27 ± 4.72	
AD					
	LL	11.73 ± 3.38	(34.10)	6.67 ± 2.19	(37.90)
	OL	10.94 ± 2.03	(31.80)	6.13 ± 2.32	(34.83)
	AL	11.73 ± 2.97	(34.10)	4.80 ± 1.71	(27.27)
	Total	34.40 ± 5.94		17.60 ± 4.11	

remain in the soil. Several authors (Davis et al, 1977; Dowdy, 1944 and Bocock and Heath, 1967) found that diplopods remain deep in the soil during unfavorable weather conditions (winter and summer) and their vertical migration is activated by temperature.

Warm early summer temperatures probably triggered migration of overwintering individuals (instars IV and V) and of newly hatched individuals (instars II and III) from the A layer to the upper soil and leaf litter (Figure 18 and Table 12). Warmer surface temperatures (Section 1.3) and more available food created favorable conditions that were not present before.

Blower and Miller (1974) reported that at least one month was necessary for the first individuals of stadium III to appear in the field. Individuals collected from soil samples (A layer) must have emerged from eggs laid during April, May and the beginning of June. In a preliminary study, 32 small juveniles and several eggs were found inside an acorn in the leaf litter. This may indicate that the species laid its eggs not only in the soil but that it used other resources as well. The presence of eggs and instars III in all layers also indicated that summer was the hatching season for O. pilosus.

Small juveniles were distributed over all horizons during fall. In year 1 most were found in the O and A layer but in year 2 they preferred the leaf litter (Figure 18 and Table 13).

Early onset of cold temperatures during fall of year 1 (Figure 3) may have caused migratory movements to lower soil layers. During this season 48.04% of the small juveniles (instars IV and V) were in the O

Table 12. Summer vertical distribution of average number of *O. pilosus* per square meter by stages ± S.E. (percent of season total).

	LAYER	YEAR 1	%	YEAR 2	%
SJ					
	LL	8.40 ± 7.62	(27.27)	1.60 ± 1.12	(36.36)
	OL	12.00 ± 4.92	(38.96)	0.40 ± 0.40	(9.09)
	AL	10.40 ± 3.69	(33.77)	2.40 ± 1.67	(54.55)
	Total	30.80 ± 11.40		4.40 ± 1.98	
JU					
	LL	0.80 ± 0.56	(5.00)	0.00 ± 0.00	(0.00)
	OL	6.40 ± 1.88	(40.00)	2.40 ± 1.77	(75.00)
	AL	8.80 ± 2.86	(55.00)	0.80 ± 0.56	(25.00)
	Total	16.00 ± 4.17		3.20 ± 1.83	
AD					
	LL	0.40 ± 0.40	(5.56)	1.60 ± 0.96	(16.00)
	OL	4.80 ± 2.23	(66.67)	4.80 ± 2.00	(48.00)
	AL	2.00 ± 1.02	(27.77)	3.60 ± 1.67	(36.00)
	Total	7.20 ± 2.43		10.00 ± 2.90	

Table 13. Fall vertical distribution of average number of *O. pilosus* per square meter by stages ± S.E. (percent of season total).

	LAYER	YEAR 1	%	YEAR 2	%
SJ					
	LL	4.40 ± 2.43	(10.78)	12.80 ± 6.25	(63.15)
	OL	19.60 ± 5.23	(48.04)	2.67 ± 1.55	(13.17)
	AL	16.80 ± 4.21	(41.18)	4.80 ± 2.56	(23.68)
	Total	40.80 ± 8.37		20.27 ± 7.89	
JU					
	LL	0.00 ± 0.00	(0.00)	17.60 ± 8.69	(30.28)
	OL	1.60 ± 0.77	(40.00)	12.80 ± 5.11	(22.02)
	AL	2.40 ± 1.08	(60.00)	27.73 ± 8.12	(47.70)
	Total	4.00 ± 1.25		58.13 ± 16.76	
AD					
	LL	0.00 ± 0.00	(0.00)	1.07 ± 1.07	(20.08)
	OL	0.00 ± 0.00	(0.00)	2.13 ± 1.67	(39.96)
	AL	6.40 ± 1.97	(100.0)	2.13 ± 1.27	(39.96)
	Total	6.40 ± 1.97		5.33 ± 2.34	

layer and 41.18% were in the A layer. This migratory movement probably continued until the end of fall when the animals started hibernating.

During fall of year 2 most small juveniles were collected from leaf litter (63.15%), indicating that the stimuli causing vertical migration in year 1 were not yet present at the time. Downward migration probably occurred later in the season.

Some researchers (Dowdy, 1944; Davies et al, 1977) have found that many invertebrates move downward when the temperature falls below a critical level, the threshold being around 4-7°C (Dowdy, 1944, and Bocock and Heath, 1967) or 4-9°C (Davies et.al.,1977). In the present study similar temperatures were reported early in fall of year 1 (Section 1.1).

A.2) <u>Juveniles</u>

Juveniles were found in all horizons in the spring of both years (Figures 17 and 18 and Table 11). The majority of individuals ocurred in the A horizon (41.30% in year 1 and 41.32% in year 2) and in the O layer (40.57% in year 1 and 37% in year 2). It is not known why this stage was present in all layers during April (both years), regardless of cold temperatures or the presence of snow. It is possible that juveniles respond to different temperature stimuli than small juveniles. Following a subzero winter, temperatures above 5.5 °C were recorded in March and early April (Section 1.1), this may have triggering upward mobility. Dowdy (1944) found that temperatures between 3.3 °C and 7.15 °C influenced upward movements in soil invertebrates during spring.

During summer of both years fewer juveniles were collected mainly from the O layer (40% in year 1 and 75% in year 2), and A horizons (55% in year 1 and 25% in year 2) (Figure 18 and Table 12). Presence of juveniles in soil during summer of both years may be indicative of unfavorable conditions in the leaf litter. Dryness and summer heat (Section 1) could have triggered downward migration and estivation of juveniles in order to survive temperature stress. The number of survivors would depend on the intensity of these climatic conditions (Levings and Windsor, 1985).

It has been known (O'Neill, 1969; Lewis, 1971a, 1971b, 1974) that the annual molt in some millipedes corresponded to the period when the forest floor became dry. At this time millipedes burrowed into logs (O'Neill,1969) or migrated down into the soil, building thick walled molting chambers and entering diapause through the dry season (Lewis, 1974). These are mechanisms which protect the population during climatic stress, particularly in tropical regions (Lewis, 1974). Dessiccation is one of the most important forms of stress to which millipedes are subject in their natural habitat (O'Neill, 1969).

After an unfavorable summer, juveniles remained in the A horizon (60%) and O layer (40%) during fall of year 1, but ocurred in all soil horizons (47.70% in the A horizon, 30.28% in the leaf litter, and 22.02% in the O layer) during fall of year 2 (Table 13). The behavior of juveniles in the fall of both years was thus very similar to that exhibited by small juveniles during the same season.

A.3) Adults

Adults were found in all horizons during spring of both years (Figures 17 and 18 and Table 11). This suggested that adults started their post-hibernation activity very early in the spring. Small juveniles densities (Figures 17 and 18) and presence of eggs in dissected females early in the summer indicated that spring was the reproductive season for the species.

A subtle preference for leaf litter in both years (34.1% in year 1 and 37.9% in year 2) suggested that surface-activity is beneficial to the species. It gives the advantage of a two-dimensional rather than a three-dimensional habitat to search for a mate and also offers a richer source of food than the soil (Lewis, 1974). Figures 17 and 18 also show, however, that adults were common in the soil (34.1% in A horizon and 31.8% in O layer during year 1, and 27.27% in A horizon and 34.83% in the O layer during year 2).

After the spring reproductive season, extended into the beginning of summer, surviving adults (Section 4) migrated into the soil. In year 1, 66.67% were found in the O layer, 27.77% in the A horizon and 5.56% in leaf litter (Table 12). In year 2, 48% were present in the O layer, 36% in the A horizon and 16% in the leaf litter. The dry, warm summer of year 1 may have caused more pronounced vertical migration in order to survive the dry season. The large body size of adults allows them to survive dessication better than smaller stages (Lewis, 1974). However, they can not survive extreme conditions, because they lack the ability to construct protective molting chambers (Lewis 1971a, 1971b, 1974). Even in the temperate conditions of Baker woodlot, many dead adults were found during hand collecting. Adults collected at the end of summer were probably young adults, having molted from juvenile to adult at that time (Section 4).

The few adults which survived the summer were present in the A layer (100%) during fall of year 1 and in every horizon (39.96% in A horizon, 39.96 in the O layer and 20.08 in the leaf litter) during fall year 2 (Table 13). Fall vertical distribution patterns were thus similar for all life stages. Young adults would overwinter in the A horizon, migrating to the upper soil and leaf litter to reproduce the following spring.

7. Surface activity

7.1. Total number of individuals captured

Catches from all 20 traps were added to obtain frequencies for each sampling date, because considering individual traps did not give additional information. The most abundant species was *O. pilosus*. The other two species were scarce, accounting for about 1/5 of the total. A total of 472 individuals were captured in year 1. Among these, 78% (368) were *O. pilosus*, 17% (83) were *P. inconstans* and 5% (21) *P. bivirgatum*. In year 2, 206 individuals were captured. *Ophyiulus pilosus* accounted for 87% (179) of the total, *P. inconstans* for 6% (13) and *P. bivirgatum* for 7% (14). The high percentages obtained for *O. pilosus* indicated that this species was the most active, and confirmed its dominant position in the community (Section 2.1). A similar distribution has been reported for the British Isles (Blower, 1979) where O. pilosus was the dominant species in several forests studied.

The number of individuals of all species trapped in year 1 was double the total number for year 2. This decrease in year 2 may have been the result of a reduction in population density caused by summer drought, year 1 sampling activities (e.g., trapping and hand collecting) and possibly by predation. Quantitative population data also showed a marked reduction in population density from year 1 to year 2.

Similar reduced catches were described by Fairhurst (1979) who documented a decrease in the number of individuals trapped after the first year. He pointed out that this was related to a decrease in population size due to over-trapping and not to periodic population outbreaks as reported by Barlow (1957).

The effect of predators on millipede activity and density has not been taken into consideration by many authors, but an effective predator can potentially influence population density. Snider (1984b) found that carabid and staphylinid beetles could live on a millipede diet in laboratory experiments, and were capable of consuming large numbers of diplopods per day. Snider (1984b) reported that all stages of P. inconstans were suceptible to several species of predaceous beetles. Adult Ophyiulus pilosus were also offered as prey by Snider (1984b), but there is no doubt that they can eat juveniles and small juveniles as well (personal observations). These inmature stages tend to cluster so that, one beetle could decimate a whole cluster in a short period of time.

7.2. Stage-specific activity

Stage-specific catches are shown in Table 14. Catches of small juveniles were infrequent, representing only 1% of all individuals collected in years 1 and 2, and attributable to low mobility of the stage. Pit-trapping is not a good method to collect small juveniles, not even during summer and fall when they are more abundant. Adults were most active, constituting 89% of the total in year 1 and 83% in year 2.

Other authors have found that small juveniles are indeed relatively inactive. Snider (1981) reported that first instars of *P. inconstans* showed a tendency to aggregate near the empty egg chamber. In the present study, small juveniles near empty chambers were found in leaf litter (see Section 6.2). Blower and Miller (1974) reported that instar II of *O. pilosus* could walk out from the egg capsule but were relatively inactive. Instar III, which is the normal stage for this species to leave the nest, were also not very active. The four small juveniles trapped in year 1 and the two in year 2 were all third instars.

High frequency of adults is probably related to the fact that millipedes actively search for mates and oviposition sites (Lewis, 1971b, 1974; Barlow, 1958; Banerjee, 1967a). It appears that adults

Table 14. Distribution among stages of pit-fall trapped individuals (all species combined).

STAGE	YEAR 1	YEAR 2
Small juvenles	4	2
Juveniles	47	32
Adults	421	172

move to the surface in search of mates, giving them the advantage of searching in a two- dimensional rather than a three-dimensional habitat. Also the soil surface provides a richer source of food than the soil but has the potential disadvantage of allowing increased predation (Lewis, 1971b).

7.3. Seasonal activity patterns

A) At species level:

Data for both years (Figures 19 to 21) showed an activity peak for each species. In *O. pilosus* it ocurred in April-May with the highest numbers captured early in May; *P. inconstans* was most active in June-July, with a distinct peak in June; *P. bivirgatum* activity peaked in September-October. It is significant that none of these peaks overlapped, indicating seasonality of reproductive behavior (activated by temperature or precipitation) and the possibility of specialization to avoid interspecific competition for resources during a given season. Blower (1979) reported that when two species (*O. pilosus* and *Microchordeuma scutellare* (Ribaut)) were at their highest biomass simultaneously, they would need most of their food at the same time and presumably concentrated on different food items. If the same resource was used by two or more species the maximum biomass of each species would be reached at different times, thereby avoiding competition temporally.

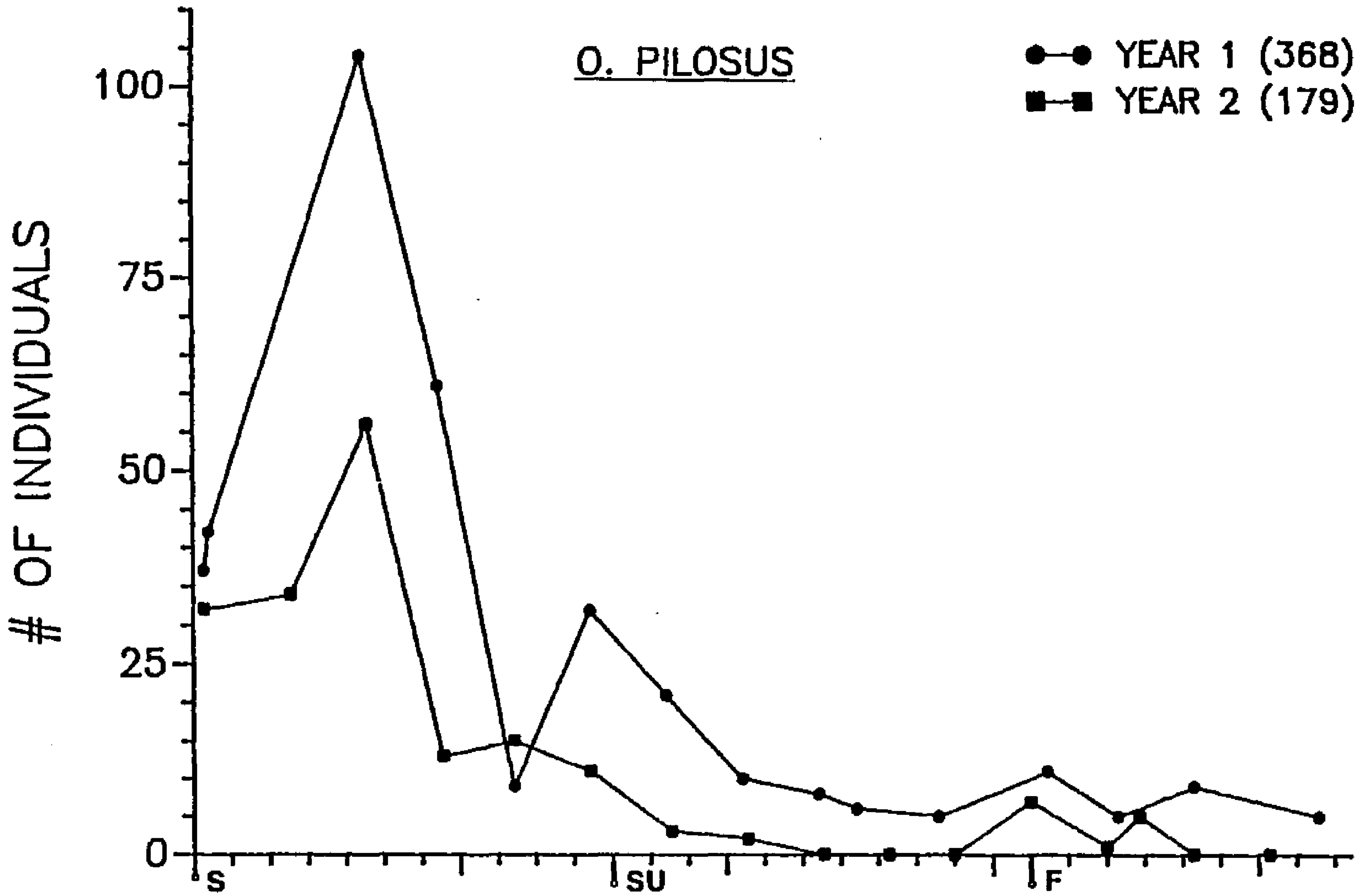


FIGURE 19. SEASONAL FLUCTUATIONS IN O. PILOSUS ACTIVITY.
S = SPRING SU = SUMMER F = FALL

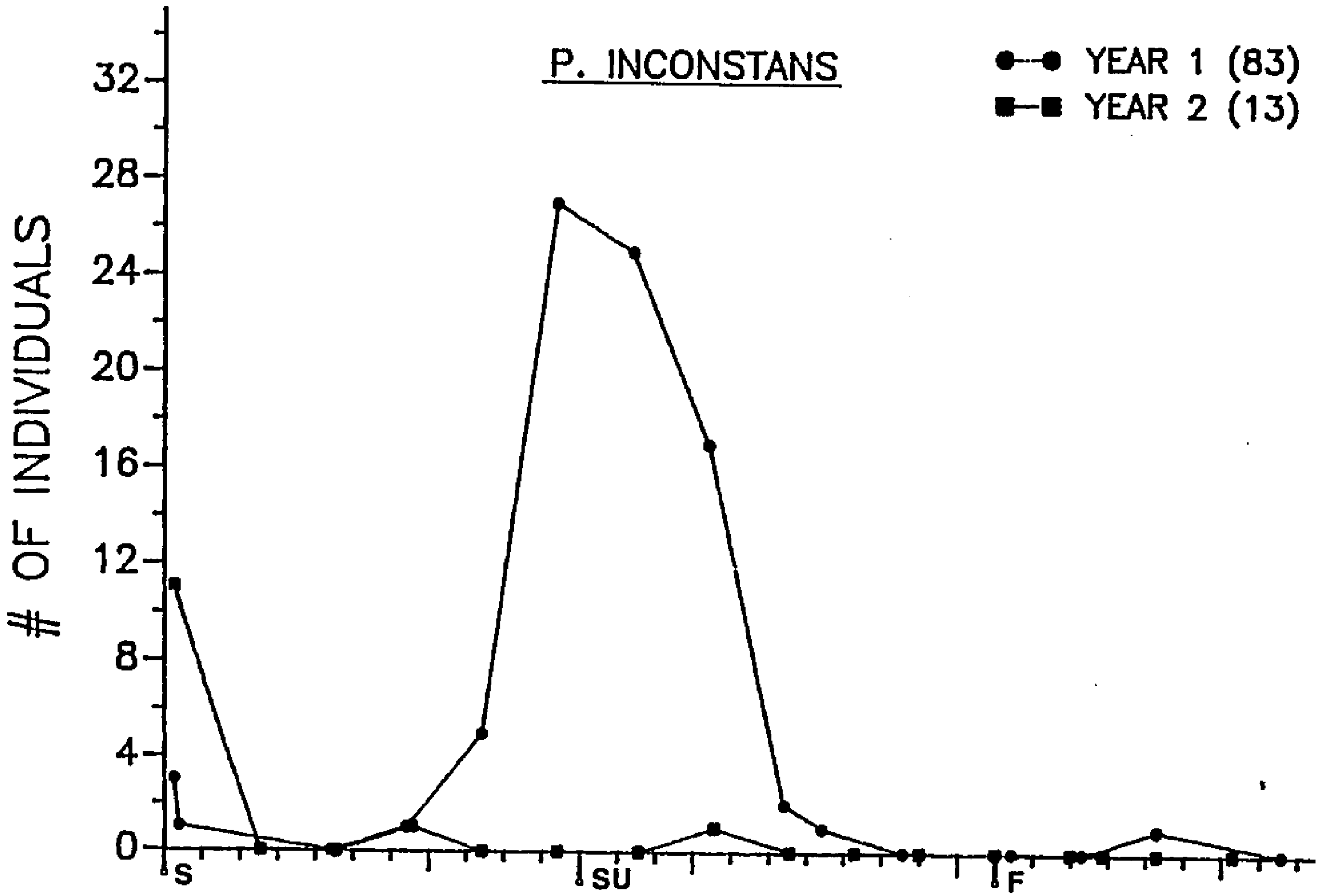


FIGURE 20. SEASONAL FLUCTUATIONS IN P. INCONSTANS ACTIVITY.
S = SPRING SU = SUMMER F = FALL

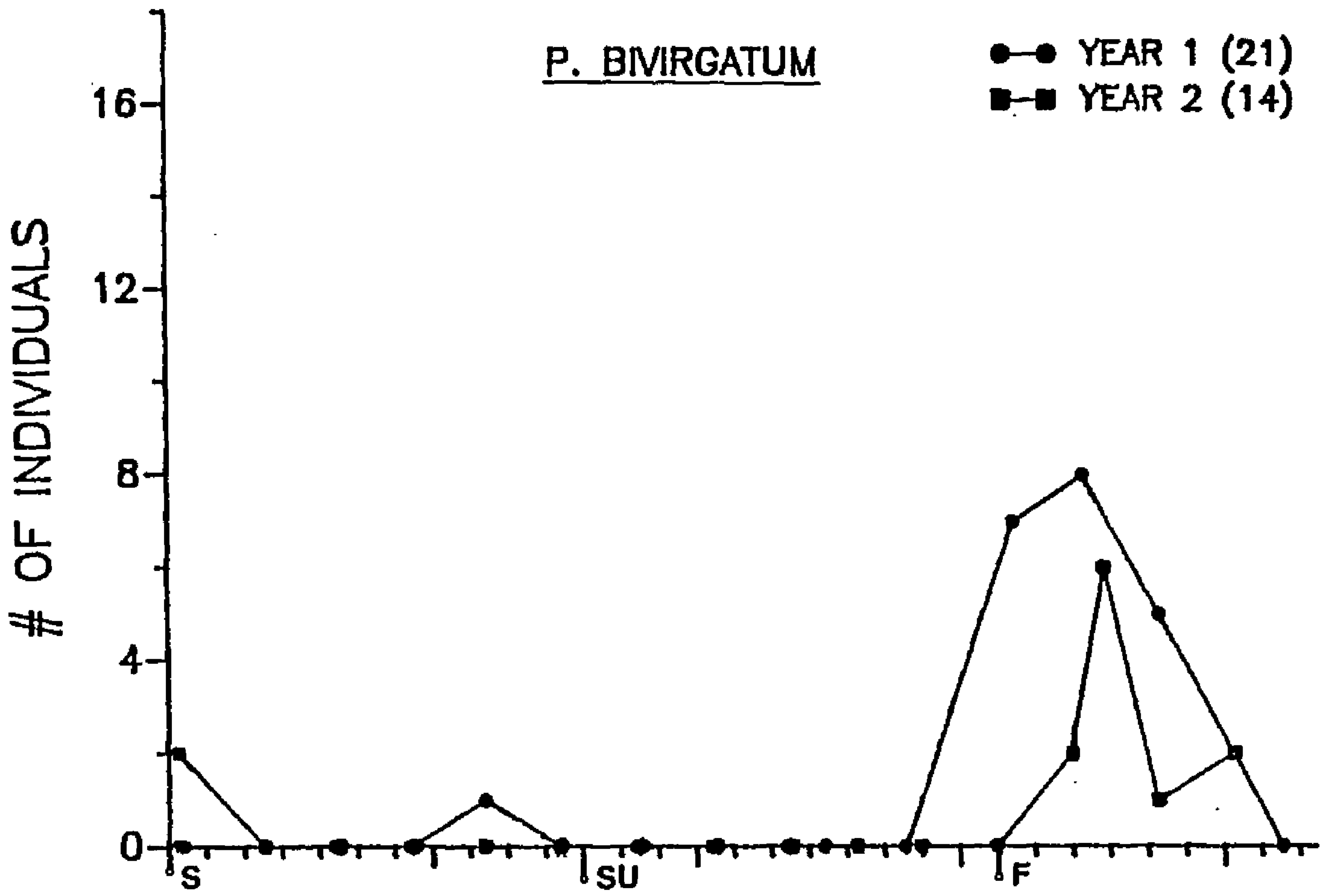


FIGURE 21. SEASONAL FLUCTUATIONS IN P. BIVIRGATUM ACTIVITY.
S = SPRING SU = SUMMER F = FALL

Relationship with temperature and precipitation:

Barlow (1958) maintained that temperature and precipitation initiated spring activity and governed its termination later in the year. According to this author temperature was apparently more influential in changing activity. In the present study, this relationship was investigated by analyzing data from the two collection days which yielded the highest numbers. The temperature range for these days is presented in Figures 22, and 23. Data for both years illustrate the marked preference of *O. pilosus* for cool early spring temperatures and of *P. bivirgatum* for moderate early fall temperatures. Temperatures during the periods of maximum activity for both species were somewhat similar, but there was no overlap in the activity patterns (Figures 19 and 21).

The relation between temperature and activity of *P. inconstans* was less clear. During year 1 the species was more active when the temperatures ranged from 11.55 °C to 31.35 °C (Figure 22). In year 1 a small activity peak was also observed at the beginning of the trapping period (Figure 20), but this may have been triggered by the freshly digging-in of the new traps. In year 2, traps from year 1 were reused, eliminating diggin-in effects. The only activity peak recorded in year 2 ocurred at the beginning of the trapping period (Figure 20). This was probably caused by my activities in the area. No other peak was observed, possibly due to the small number of individuals trapped during year 2.

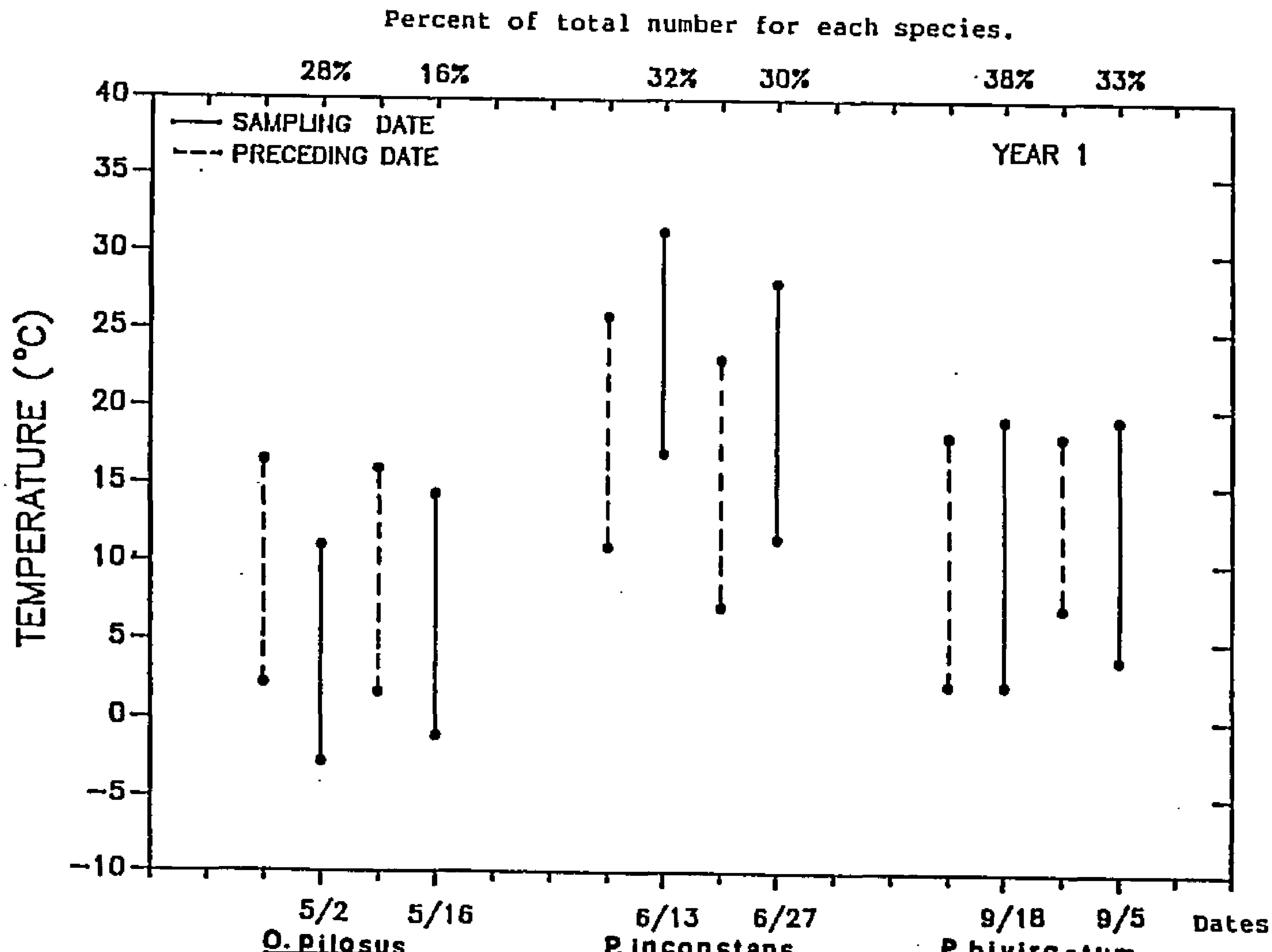


FIGURE 22. MAXIMUM AND MINIMUM TEMPERATURES ON TRAPPING DAYS WITH MAXIMUM DIPLOPOD ACTIVITY AND ON DAYS PRECEDING THEM, YEAR 1 (1984).

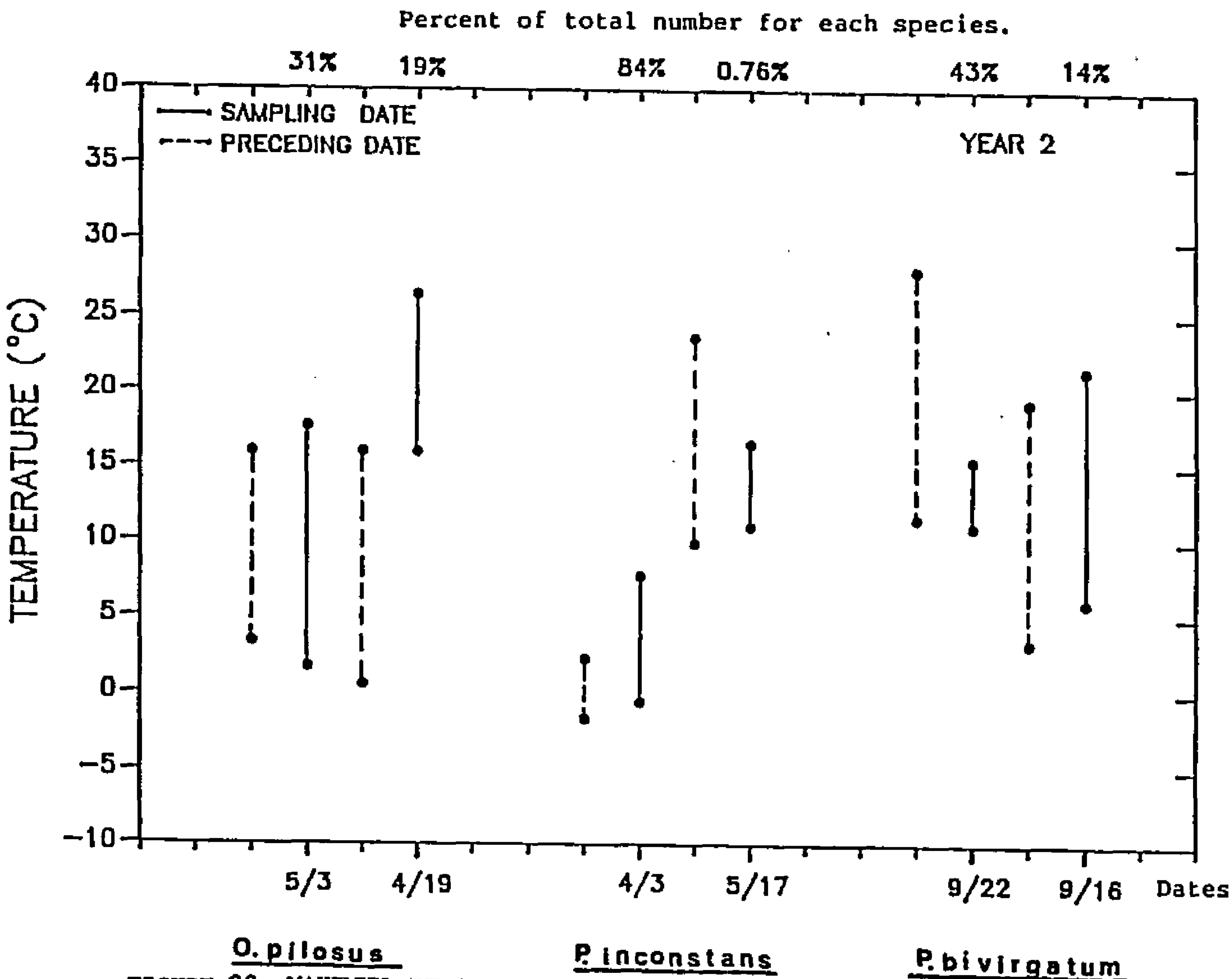


FIGURE 23. MAXIMUN AND MINIMUM TEMPERATURES ON TRAPPING DAYS WITH MAXIMUM DIPLOPOD ACTIVITY AND ON DAYS PRECEDING THEM, YEAR 2 (1985).

B) At stage level:

Stage-specific activity for all species is summarized in Table 15. The few small juveniles trapped in years 1 and 2 were found during fall and were all *O. pilosus*. No small juveniles of *P. inconstans* or *P. bivirgatum* were collected.

Fairhurst (1979), in his study of *P. inconstans*, only trapped four small juveniles during the entire study and was unable to deduce the species' life history by these means. Blower (1969) found that small juveniles of other polydesmids also rarely fell into traps.

Polyzonium bivirgatum is the least known of the three species. No small juveniles were trapped during the study; the adult stage was the most active (Table 15). It was found that *P. bivirgatum* preferred decaying wood and areas of abundant, humid leaf litter, confirming observations by Johnson (1952).

Among juveniles, 59% (28) of the total in year 1 and 19% (19) of the total in year 2 were collected in the spring; 35% (16) of year 1 and 19% (6) of year 2 totals were collected in the summer and 6% (3) of year 1 and 22% (12) of year 2 were collected in the fall.

Ophyiulus pilosus juveniles active in the spring represented individuals hatched the previous year. All individuals trapped were instars VII, VIII and IX and became sexually mature during spring and early summer. Quantitative data also showed a high frequency of juveniles in spring and a decrease towards summer.

According to Blower and Miller (1974) *O. pilosus* juveniles overwinter as instars VI, VII and VIII. Laboratory studies by these

Table 15. Total numbers captured of each species.

DATE	O. PILOSUS SJ	JU	AD	P. INCONSTANS SJ	JU	AD	P. BIVIRGATUM SJ	JU	AD	TOTAL SJ	JU	AD
APR 3	0	4	33	0	3	0	0	0	0	0	7	33
APR 4	0	2	40	0	0	1	0	0	0	0	2	41
MAY 2	0	13	91	0	0	0	0	0	0	0	13	91
MAY 16	0	2	59	0	1	0	0	0	0	0	3	59
MAY 30	0	1	8	0	0	5	0	0	1	0	1	14
JUN 13	0	2	30	0	0	27	0	0	0	0	2	57
JUN 27	0	3	19	0	2	23	0	0	0	0	5	42
JUL 11	0	0	10	0	0	17	0	0	0	0	0	27
JUL 25	0	4	4	0	0	2	0	0	0	0	4	6
AUG 1	0	2	6	0	0	1	0	0	0	0	2	7
AUG 16	0	0	5	0	0	0	0	0	0	0	0	5
SEP 5	3	5	3	0	0	0	0	0	7	3	5	10
SEP 18	0	0	5	0	0	0	0	0	8	0	0	13
OCT 2	1	1	7	0	1	0	0	1	4	1	3	11
OCT 25	0	0	5	0	0	0	0	0	0	0	0	5
TOTAL	4	39	325	0	7	76	0	1	20	4	47	421

(a) Year 1

DATE	O. PILOSUS SJ	JU	AD	P. INCONSTANS SJ	JU	AD	P. BIVIRGATUM SJ	JU	AD	TOTAL SJ	JU	AD
APR 3	0	3	29	0	7	4	0	0	2	0	10	35
APR 19	0	0	34	0	0	0	0	0	0	0	0	34
MAY 3	0	1	55	0	0	0	0	0	0	0	1	55
MAY 17	0	1	12	0	0	1	0	0	0	0	1	13
MAY 30	0	0	15	0	0	0	0	0	0	0	0	15
JUN 13	0	7	4	0	0	0	0	0	0	0	7	4
JUN 28	0	0	3	0	0	0	0	1	0	0	1	3
JUL 12	0	0	2	0	0	1	0	0	0	0	0	3
JUL 26	0	0	0	0	0	0	0	0	0	0	0	0
AUG 7	0	0	0	0	0	0	0	0	0	0	0	0
AUG 19	0	0	0	0	0	0	0	0	0	0	0	0
SEP 2	2	5	0	0	0	0	0	0	0	2	5	0
SEP 16	0	1	0	0	0	0	0	0	2	0	1	2
SEP 22	0	5	0	0	0	0	0	1	5	0	6	5
OCT 2	0	0	0	0	0	0	0	0	1	0	0	1
OCT 16	0	0	0	0	0	0	0	0	2	0	0	2
TOTAL	2	23	154	0	7	6	0	2	12	2	32	172

(b) Year 2

authors showed that males could reach sexual maturity at instar IX (two months after the presence of instar VII). However, males which reached sexual maturity at instar X spent a large amount of time in moulting chambers. They appeared at the same time as the females, which could reach sexual maturity only at instar X (10-13 months were needed to reach that instar).

Overwintered juveniles of P. inconstans found in spring were instars V, VI and VII, and would become sexually mature by the end of spring and through summer. Quantitative data showed a larger number of P. inconstans juveniles in the spring than in summer.

Little is known about P. bivirgatum and the extremely low frequency of juveniles trapped during this study (Table 15) made it impossible to draw conclusions. The adult stage was the most active in all species studied during all seasons, and therefore was the determinant of the activity patterns of all species shown in Figures 19 to 21.

C) Sex-related differences in adult activity:

Sex-specific activity frequencies for each species are presented in Table 16, and Figures 24 to 26. Both sexes were equally active in all species. In year 1, 52% (220) of all adults were males and 48% (201) females. In year 2, 44% (76) of the total were males and 56% (96) were females. The pronounced activity peaks of each species ocurred in both sexes (Figures 24-26) and were directly related to reproductive periods.

Table 16. Total numbers of males and females captured.

DATE	O. PILOSUS ♂	O. PILOSUS ♀	P. INCONSTANS ♂	P. INCONSTANS ♀	P. BIVIRGATUM ♂	P. BIVIRGATUM ♀	TOTAL ♂	TOTAL ♀
APR 3	14	19	0	0	0	0	14	19
APR 4	28	12	0	1	0	0	28	13
MAY 2	53	38	0	0	0	0	53	38
MAY 16	41	18	0	0	0	0	41	18
MAY 30	4	4	4	1	0	1	8	6
JUN 13	12	18	9	18	0	0	21	36
JUN 27	7	12	14	9	0	0	21	21
JUL 11	4	6	7	10	0	0	11	16
JUL 25	1	3	0	2	0	0	1	5
AUG 1	1	5	1	0	0	0	2	5
AUG 16	4	1	0	0	0	0	4	1
SEP 5	0	3	0	0	2	5	2	8
SEP 18	2	3	0	0	5	3	7	6
OCT 2	5	2	0	0	1	3	6	5
OCT 25	1	4	0	0	0	0	1	4
TOTAL	177	148	35	41	8	12	220	201

(a) Year 1

DATE	O. PILOSUS ♂	O. PILOSUS ♀	P. INCONSTANS ♂	P. INCONSTANS ♀	P. BIVIRGATUM ♂	P. BIVIRGATUM ♀	TOTAL ♂	TOTAL ♀
APR 3	7	22	0	4	1	1	8	27
APR 19	19	15	0	0	0	0	19	15
MAY 3	22	33	0	0	0	0	22	33
MAY 17	11	1	0	1	0	0	11	2
MAY 30	6	9	0	0	0	0	6	9
JUN 13	0	4	0	0	0	0	0	4
JUN 28	3	0	0	0	0	0	3	0
JUL 12	0	2	1	0	0	0	1	2
JUL 26	0	0	0	0	0	0	0	0
AUG 7	0	0	0	0	0	0	0	0
AUG 19	0	0	0	0	0	0	0	0
SEP 2	0	0	0	0	0	0	0	0
SEP 16	0	0	0	0	0	2	0	2
SEP 22	0	0	0	0	3	2	3	2
OCT 2	0	0	0	0	1	0	1	0
OCT 16	0	0	0	0	2	0	2	0
TOTAL	68	86	1	5	7	5	76	96

(b) Year 2

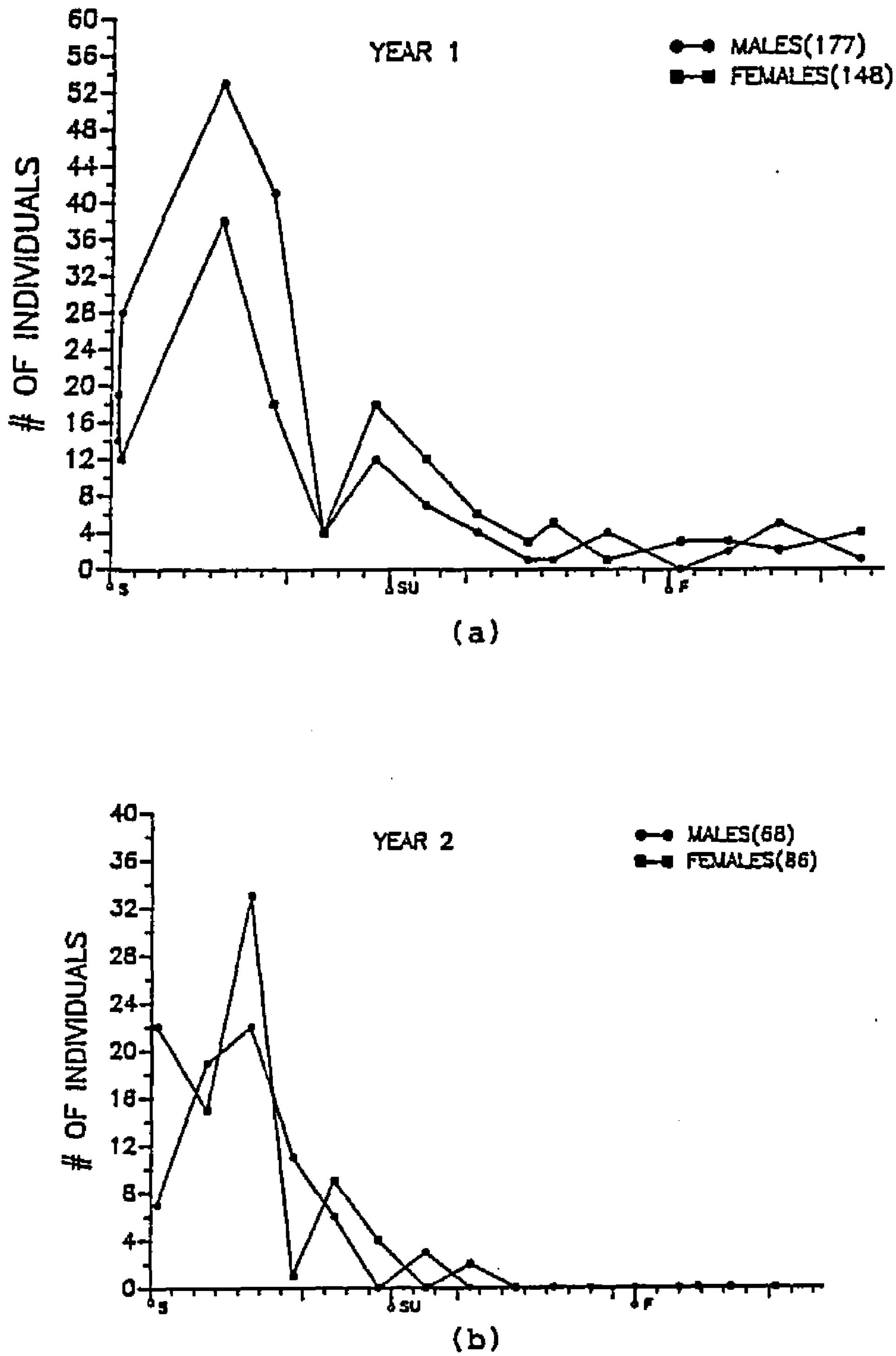


FIGURE 24. SEASONAL FLUCTUATIONS IN THE ACTIVITY OF O. PILOSUS ADULTS (BY SEXES).

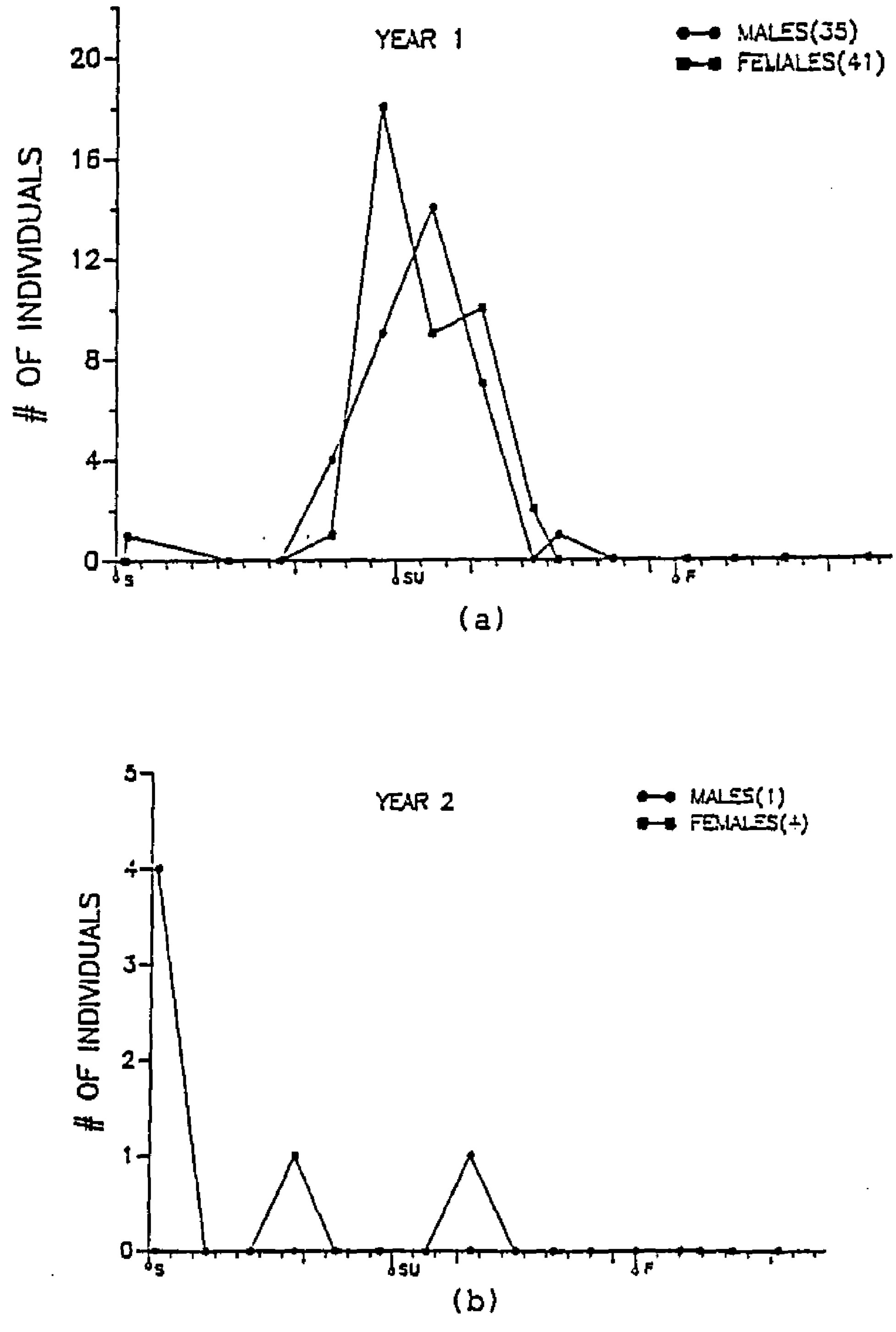


FIGURE 25. SEASONAL FLUCTUATIONS IN THE ACTIVITY OF <u>P. INCONSTANS</u> ADULTS (BY SEXES).

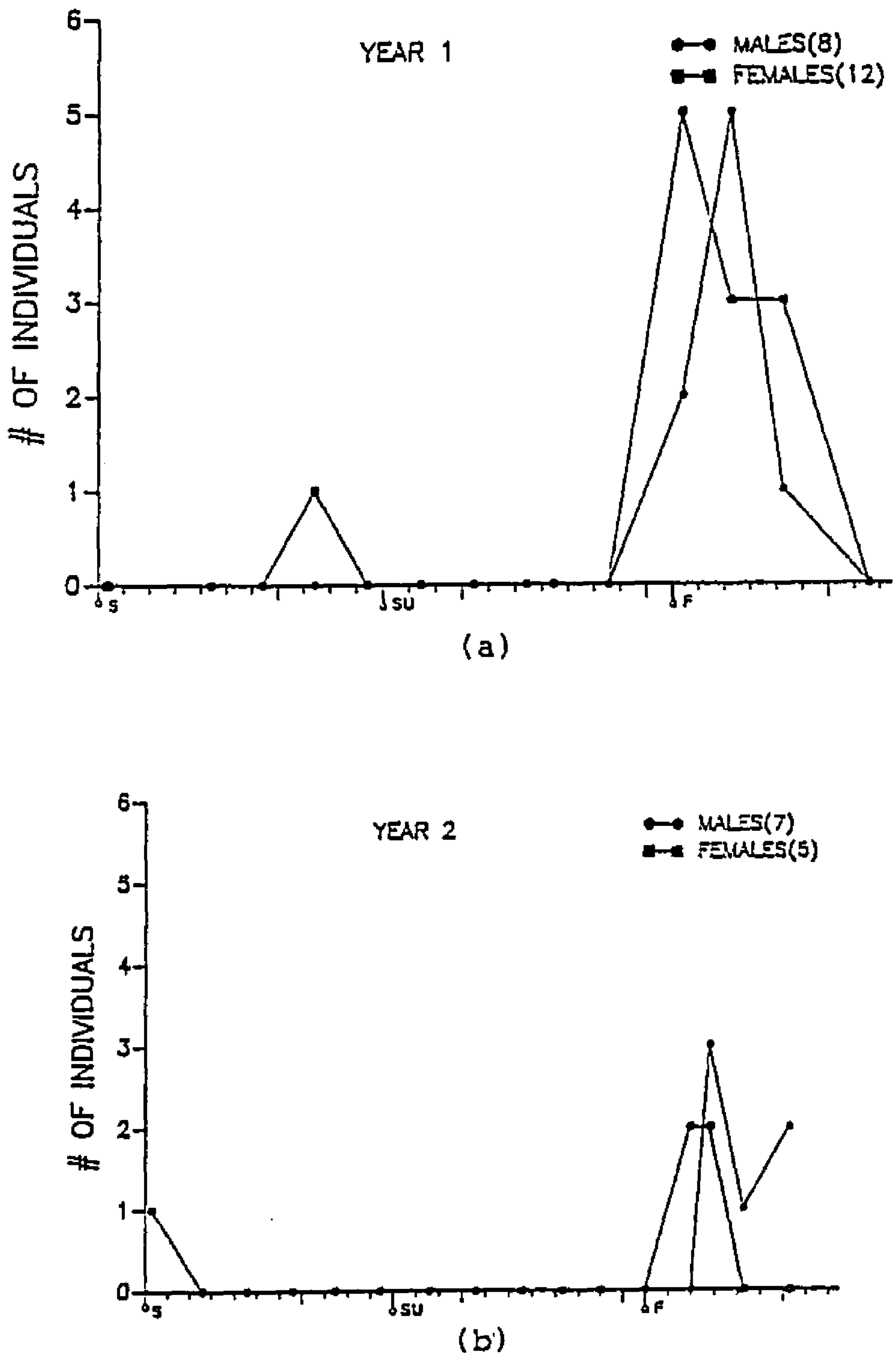


FIGURE 26. SEASONAL FLUCTUATIONS IN THE ACTIVITY OF <u>P. BIVIRGATUM</u> ADULTS (BY SEXES).

Banerjee (1967a) reported that the time when the largest number of diplopods were collected in pitfall traps coincided with their breeding period, when adults became active in search for mates and suitable sites for oviposition.

C.1) Ophyiulus pilosus

More males (159) than females (109) of O. pilosus were captured during the spring of year 1, but more females (26) were captured in the summer (males = 3). In spite of the fewer captures of year 2 more females (84) than males (65) were found in the spring of that year.

Both sexes showed a peak of activity during spring (Figure 24) which is the reproductive season for this species. Blower and Miller (1974) reported that O. pilosus eggs were laid between April and June. The relative sizes of each peak can be related to the relative densities of each sex. This was indeed the case in year 2 when quantitative data showed a 1:1.8 male:female ratio in the spring (trap data showed a 1:1.3 ratio). Relative dominance of males trapped in the spring of year 1 (1.4:1 ratio) was not in correspondence with the quantitative data ratio (1:1.2) but the difference is negligeable when standard errors are considered. Blower and Miller (1974) also found sex ratios of approximately 1:1 in overwintering O. pilosus, but did not assess activity sex ratios. In the present study, these ratios differed slightly from the density standards.

A decline in activity of O. pilosus adults at the end of summer is evident from Figure 24. Blower and Miller (1974) found that this species suffered a high mortality of older stadia in their second year, finishing the species' life cycle. The few active adults during fall (Table 16 and Figure 24) were probably young adults (see section 6.2).

C.2) Polydesmus inconstans

The highest activity of P. inconstans adults in year 1 occurred between late May and late July (Figure 25). Both sexes were active at the same time. The numbers obtained during year 2 were very small (Table 16), but most of the trapped individuals were females. No activity trend could be observed in that year.

The main peak obtained for P. inconstans during year 1 corresponded to the reproductive season of the species. This was supported by the presence of eggs in females dissected during this study and by Snider (1984a) who reported eggs laid in May and June (with a peak of egg production probably in June).

An approximate 1:1 sex ratio in trapped adults was characteristic of year 1 (year 2 data were inconclusive), similar to sex ratios of field-collected individuals reported by Snider (1984a).

A drop in activity of P. inconstans adults was observed at the end of July (Figure 25). This can be related to the fact that P. inconstans is a semelparous species in which no individuals survive beyond the summer breeding season (Snider 1980, 1981).

C.3) Polyzonium bivirgatum

Highest activity of adults occurred during September and early

October, simultaneously in both sexes (Figure 26). Approximate 1:1 sex ratios were obtained during this period.

Johnson (1952) observed males and females in copulation during May, which suggests that spring is the reproductive season for *P. bivirgatum*. Unlike the other species discussed previously, there appeared to be no correlation between high activity and reproductive behavior in this species.

IV. SUMMARY AND CONCLUSIONS

The physical parameters of temperature, precipitation, soil moisture, and litter cover were different in each study year. Year 1 was characterized by a cooler springtime, a drier and warmer summer, and a slightly more humid fall when compared to year 2. In year 2 the effect of warm temperatures was probably buffered by precipitation. Furthermore, litter cover was greater in year 1.

These parameters, together with the impact of sampling activities in this and previous studies, may have affected the seasonal population densities each year. Year 1 densities for _O. pilosus_, _P. inconstans_ and _P. bivirgatum_ were higher than year 2. _Ophyiulus pilosus_ showed the highest density during year 1 and in spring and fall of year 2. _Polydesmus inconstans_ outnumbered _O. pilosus_ in summer of year 2. The densities reported for _P. inconstans_ and _P. bivirgatum_ in this study were the lowest ever recorded in Michigan.

Dominance analysis demonstrated that _O. pilosus_ was the dominant species in Baker woodlot. Stage structure assessment of _O. pilosus_ showed that its small juvenile subpopulation increased consistently from spring to fall during both years. This increase was caused by newly hatched individuals entering the population at the end of spring and summer. The juvenile stage was most abundant in spring of year 1 (overwintered individuals) and fall of year 2. In year 1 the juvenile subpopulation decreased from late spring to fall, but in year 2 a decrease was observed only from spring to summer. In both years the decrease was caused by metamorphic changes in instars VIII and IX and by unfavorable weather conditions that induced estivation and thus an apparent decrease of the population. The large increase of the juvenile subpopulation during fall of year 2 was probably caused by higher survivorship during summer due to favorable weather conditions. The adult population reached its maximum density during spring (both years), diminishing consistently towards fall. This decrease was caused by death of most two-year adults at the end of their reproductive period in the summer. The few adults collected during fall were probably young adults.

It was found that O. pilosus stages followed a seasonal pattern in their vertical distribution. Horizon preferences of the species were influenced by temperature and precipitation. The leaf litter was least populated, indicating the species's stronger preference for the soil layers.

The few small juveniles collected in the spring were found in the A layer in year 1 and in the O and A layer in year 2. During the summer this stage was found in every layer but more predominantly in the O and A layer in year 1 and in the A and leaf litter in year 2. Fall preferences were very similar to the summer during year 1, but in year 2 most of the small juveniles were in the leaf litter. The presence of small juveniles in the leaf litter during summer and fall of year 2 could be an indication of adequate moisture conditions due to higher and more evenly distributed precipitation.

Juveniles were present in the leaf litter, O layer and A layer during the spring of both years, however, most individuals were found in the A layer. During summer of year 1 most juveniles were in the A layer followed by the O layer but the reverse situation was observed in year 2. During fall of both years this stage also showed a stronger preference for the A layer.

Adults were present in all strata, with a stronger preference for the A layer in year 1 and for the O in year 2. They were also present in every strata during the summer showing a stronger preference for the O layer followed by the A. During fall of year 1 adults showed a stronger preference for the A layer, while they were present in all strata during year 2.

The variance/mean ratio test for the horizontal distribution of the dominant species showed that the O. pilosus population was aggregated. This clustering tendency is typical of the Diplopoda and can be related to their oviposition habits.

A regression analysis revealed no direct relationship between litter mass and the number of O. pilosus in a sample. Similar results were obtained when analyzing the relationship between soil moisture and density. The spatial distribution of O. pilosus was probably affected by the joint effects of various parameters such as temperature, precipitation, type of substrate, moisture and litter cover.

Pitfall trap data showed that O. pilosus was the most surface-active species in Baker woodlot. A characteristic peak of high surface-activity was documented for each species. These peaks occured in spring for O. pilosus, summer for P. inconstans and fall for P.

bivirgatum. The presence of eggs in dissected females of O. pilosus and P. inconstans and of small juveniles in the following season may indicate that these activity peaks were related to reproduction.

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