Site No. 1 2 3 4 5 6

A soil zoological study of *Pinus pinaster* plantations at Gnangara Western Australia. 1968-1971.

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Summary

1. The history of soil zoology in the world and in Western Australia is briefly reviewed. Australian soil ecosystem studies are handicapped by a lack of information on the identity and life cycles of most soil animals.

2. Six sample sites at Gnangara W.A. were chosen. Site 1 Native vegetation, under, *Eucalypt*, *Banksia* and *Hakea* with some volunteer *Pinus pinaster*. Site 2 *P. pinaster* plantation 30 years old, Site 3 *P. pinaster* plantation 25 years old with a basal area of 160 square feet per acre, Site 4 *P. pinaster* plantation 25 years old with a basal area of 31 square feet per acre, Site 5 *P. pinaster* plantation 17 years old control burnt three years before the beginning of this study, Site 6 as site 5 but unburnt.

3. Microarthropods were extracted from soil cores with a heat funnel extractor. Litter decomposition rates were estimated by measuring the weight loss of leaves enclosed in nylon mesh bags and the loss of tensile strength of cotton strips buried in the soil.

4. The number of infrequently occurring species is reduced under the Pine plantations compared with the number under native vegetation. In the plantations the number of larger predator species reduced.

5. It is suggested that the beginning of the breeding season is linked to the beginning of the rainy season, probably through diapause or aestivation, and that the population density is related to the amount and pattern of winter

rainfall. Early rains followed by further drought conditions having a deleterious effect on the population.

6. Life cycles of Oribatidae. The adults reach prebreeding status, or possibly lay drought resistant eggs, during the summer, the autumn rains trigger off breeding activity and the appearance of the first generation in the soil samples is highly synchronised. One or two non synchronised generations occur before the population as a whole returns to the over summering adult population.

7. Life cycles of other microarthropods. In most cases there were insufficient data to make a model of the life cycles, in general breeding and development took place during the wet winter months. However adult Psocidae and Tuckrellidae (Acarina) increase in numbers during the summer indicating that the immature stadia are actively growing and developing during the summer.

8. Analysis of the feeding groups within the population showed that on all sites approximately half the microarthropods were specialised fungal feeders, with 48 percent on the native vegetation and 60 percent on the youngest _P. pinaster_ stands. The percentages of general feeders were lowest under the youngest pines. The feeding activity of the animal populations, as indicated by the proportion of animals with food in their guts is significantly lower on the burnt stand of _P. pinaster_ than on any other stand.

9. The litter decomposition studies, using leaf litter in mesh bags showed that schlerophyll litter decomposes in 3 to 5 years whether it is under native bush or <u>P. pinaster</u>. Pine litter decomposes in 12 to 15 years in 30 year old pine stands or on native bush and in 25-30 years on 17 year old pine. Burning had the effect of preventing decomposition until five years after the burn. Decomposition studies using cotton strips showed a similar pattern of decomposition rates. Fastest decomposition being on the native bush and slowest on the burnt young pine.

10. The sample sites can be arranged in order of both their decomposition rates and their species content.

    1 2 3 4 6 5.

11. Forest litter decomposition rates in several forest types are discussed, and are classified into four main groups.

    a) The very long periods of litter accumulation of 50 to 300 years in harsh continental climates.

    b) The long periods of 5-15 years which have been measured in most continental forests.

    c) The fairly short periods 1-4 years in moist, temperate oceanic forests.

    d) The very short periods of less than one year in moist tropical forests.

12. The probable changes in the litter content of the forest floor during the life of a plantation are outlined with a graphical model incorporating the predictable changes in litter input and decomposition rates. The effects of weather are not included.

13. The importance of the decomposer system in maintaining soil structure and fertility in Australian forest ecosystems is discussed. It is suggested that classification of the soil microhabitat in terms relevant to biological processes should be developed and combined with total energy flow measurements and autecological studies to prescribe the structure, energy input and species composition necessary for the continuing cropping of a healthy soil.

Soil Zoology

An historical review

The early history of soil zoology is adequately summarised in a twelfth century Latin Bestiary which states that "worms germinate without sexual intercourse out of mean or wood or any earthly thing." Apart from lice, fleas, bugs, ticks and other "flesh worms" it lists "airworms" (caterpillars) "clothesworms" "earthworms - the earth millipede which hides in large numbers under flower pots rolled up in a ball" and "wood worms" or termites which "breed from trees which are felled at the wrong season."

However modern soil zoology did not start until Linnaeus' system of nomenclature, and the microscope came into use in the 1760's. Botany and Zoology blossomed during the Victorian era of gentlemen collectors and unfortunately soil animals were not neglected. The nineteenth century literature is full of valid species names attached to inadequate descriptions and it will take more than the entire twentieth century to clear up the mess. In many groups no attempts at clearing up have yet been made in a few groups the nineteenth century work has been discarded and a fresh start made, but in the majority of groups good and bad descriptions with and without available type specimens occur within the same genus and all have to be carefully sifted before new species can be described old ones identified and taxonomic relationships worked out. Some of the old species descriptions are based on such bizarre characters as whether the animal curled to the left or right when preserved, but on the other hand some nineteen century descriptions are better than descriptions 100 years younger. In many cases species descriptions are good and valid but the characters necessary for generic or family groupings were omitted from the original diagnoses.

Towards the end of the nineteenth century, although the morass of taxonomy was still getting deeper, there were the beginnings of a movement to collect more than lists of specimens; to collect information on the numbers of animals present in the soil and their activities and distribution. Descriptions of extraction funnels for collecting soil animals were published by Ormay in 1890, Berlese in 1908 and Tullgren in 1918, a floatation methods for extracting nematodes was described by Bass in 1906 and Darwin published his "Earthworms and Vegetable Mould" in 1881, but the species list phase did not really give way to the population numbers phase until the late 1920's. A pioneer of the next phase was Bornebusch who in 1930 published his evaluation of the activity of soil fauna in which biomass and respiration and life cycles were the key measurements. However further work in this new direction was not carried out until after a period of technical expansion both in methods of handling the animals and statistical methods of handling data. Much of this later work was brought together in 1958 at the 1st meeting of the Soil Zoology Committee of the International Society of Soil Science and was published in 1962 in Progress in Soil Zoology. By the 2nd meeting of the Soil Zoology Committee in 1962 Macfadyen could review the components of the animal respiration in the soil from the publications of only three workers other than himself. Since the mid 1960's the present phase of soil zoology, i.e. energy flow and systems analysis is getting into its stride although the 3rd and 4th meetings of the Soil Zoology Committee in 1966 and 1970 were dominated by biomass, respiration and life cycle studies.

Meanwhile the taxonomists have been battling with the flotsam and jetsom of the past 200 years. Taxonomy has the biggest work force and is the biggest block to further work in soil zoology. All the animal phylla except sponges, corals and starfish have representatives in the soil. Many groups have no living taxonomic specialists, very few have more than one specialist in the world and a high proportion of these specialists are elderly having started their work on the species list era of the 1930's. I have outlined the main phases of soil zoology and included some of the key workers in Figure 1.

Where does Western Australia fit into this pattern?

The early Dutch explorers in the seventeenth century noted 'anthills' and 'flies' and the abundance of dung on the soil surface and the eighteenth century added records of beautiful beetles and mosquitos. In 1801 Peron recorded a soil mite and some black ants. By 1820 centipedes, scorpions and snails had been added to the species list and by this time some of the animals had acquired latin names. By 1830 W.A. was settled, and after settlement, records became more numerous and confusing. Descriptions were published from time to time, usually in Europe, for example in 1833 the Reverend Hope described six Australian beetles at a meeting of the Entomological Society of London. In spite of Darwin's visit in 1836 when he described Western Australia as "exceedingly dull and uninteresting" there was a steady trickle of species records to the end of the nineteenth century. In 1905 a German expedition to South Western Australia lead by Prof. Michaelsen and Dr. Hartmeyer really began the study of W.A. soil fauna. Michaelsen and Hartmeyer's collections were taken to Germany to be worked up by specialists, and the records of this expedition were published between 1905 and 1914 with a much later paper on the earthworms in 1934. In the 1920's and 1930's seven West Australian authors, Nicholls, Glauert, Barnes, Roewer, Jackson, Bowley and Iredale had published species lists and descriptions of Isopods, Scorpions, Amphipods, Opiliones, Oligochaetes and Snails. There has been less work done since the 1930's, probably partly because of the splitting of the Biology Department at the University and the subsequent concentration on the vertebrate fauna. Dr. George Bornemizza spent some years at the Zoology Department, and made extensive collections of the soil microfauna. Many of Bornemizza's specimens were sent to overseas specialists some of whom have yet to publish descriptions of the new Australian species. Bornemizza also studied carcass and dung fauna and published notes on the recovery of soil microarthropod populations after burning in Kings Park (1969).

At a recent specialist conference in Soil Biology in Adelaide, of 50 reports 11 were concerned with animals and 6, those by Greenslade et al, Stout, Lee and Wood, Greaves, King and Hutchinson, and Springett were concerned with the decomposer fauna. Taxonomists were not represented at the conference. In relation to the general history of soil zoology it can be seen that Australia is trying to step in to the systems era with papers like King and Hutchinson's "Soil microarthropods in grazing systems" without having done more than scratch the surface of the species list phase, and without any information on life cycles, distribution, abundance, and population fluctuations.

The taxonomic gap is most noticeable when publication of results is necessary, but even worse than the taxonomic gap is the gap in the knowledge of the natural history of the species. For example work on northern hemisphere oribatid mites has indicated that they invariably have a life cycle of larva, protonymph, deutonymph, tritonymph and adult. Oribatids are particularly important in the northern Jarrah forests but the few species I have cultured in the laboratory have produced an array of quiescent phases, possible diapauses and paedogensis. Many of the recorded oribatid life cycles are fairly long (3-4 months at 20°C) and it would obviously be an advantage for Australian oribatids to have diapause or quiescent stages for unfavourable periods. Additionally oribatids might be able to shorten their life cycle by omitting the final stadia to take maximum advantage of short favourable periods of weather. It is not possible to interpret field measurements of population numbers, and metabolic activity or to extrapolate laboratory measurements of feeding and respiration to the field without details of life histories.

Introduction

The plant structural polysaccharides form the major energy source for metabolic processes in the soil, including both nitrogen fixation and the reduction of oxides of nitrogen, sulphur, phosphorus and iron. It is assumed that the rate of decomposition of cellulose and lignin is related to the rate of cycling of other nutrients, but this relationship has never been directly measured or even clearly demonstrated. It is possible that litter is robbed of its minerals early in the course of events and it is the rate of humus production and its type and ability to trap nutrients which is more important. Humus production may or may not be related to the rate at which cellulose and lignin disappear from the litter layer.

The Forests Department was more interested in the rate of breakdown of Pinus pinaster litter on the coastal sands than in litter breakdown in the native forest types and experimental plots at Gnangara were used in this study. It was decided to use the plots to study : the species composition, population densities and annual life cycles of the soil microarthropods under P. pinaster as compared with native vegetation; the species composition, population densities and annual life cycles of the soil microarthropods on burnt and unburnt, and on thinned and unthinned Pinus pinaster; the rate of litter breakdown under P. pinaster and native vegetation, and the rate of litter breakdown on burnt and unburnt P. pinaster.

In 1968 and 1969 additional estimates were made of species composition and population densities of soil animals in Gleneagle Forest Pine and Jarrah, and on adjacent broad leaved deciduous fruit orchards. Collections of soil animals were also made in several areas in the south west of the state, Southern Jarrah, Main Karri, eastern Karri and Southern coastal scrub. The reason for this sampling and collection was to obtain a rough estimate of population densities and faunal types in the native bush and to gauge its flexibility and ability to adapt.

Soil Fauna studies in Gnangara.

Pinus pinaster plantations - Field work.

Sample sites

The six experimental plots from which soil samples were taken for estimation of the soil microarthropod populations and on which studies on litter decomposition rates were made were:-

Site 1 South Lane Poole compartment 66, an area of bush which had been cleared and used as a paddock but then allowed to regenerate naturally with banksia, hakea, eucalypts and some pines since 1938.

Site 2 South Lane Poole compartment 2, _Pinus pinaster_ planted in 1938 from Portuguese seed and with present spacing of 6ft by 6ft.

Sites 3 and 4 South Lane Poole compartment 69, Pinus pinaster basal area thinning plots, planted in 1946 and thinned to present levels in 1966. Only two of the treatment plots could be sampled, plot 18 with a basal area of 160 square feet (O.B.) per acre and plot 20 with a basal area of 31 square feet (O.B.) per acre were used (W.P. 20/65).

Sites 5 and 6 North Kendal Compartment 26, Pinus pinaster planted in 1951 pruned but unthinned when given a normal control burn on 28th and 29th July, 1966. Four plots 1, 6, 2, 7 mentioned in W.P. 1/64).

Methods

Animal numbers.

Sampling and extraction.

Because of the sandy texture fairly large sample cores of soil were taken. A circular corer of 100 square centimetres was pressed through the litter into the soil to a depth of 12 cm and the contents of the corer were placed in a polythene bag. The sample was not divided into horizontal layers. Eight samples were taken at monthly intervals from the bush site 1 and the old Pine site 2. Eight samples were taken on alternate months from the two basal area thinning plots and the burnt and unburnt plots. The samples were hand sorted for larger animals, worms, spiders, large insects and larvae which were preserved in alcohol. Large surface active animals were collected during 1970 using pitfall traps, twenty 1 lb jam jars were sunk at four foot intervals on a square grid in sites

1, 2, 5 and 6. The jars contained alcohol as a preservative and were emptied at weekly intervals. The microarthropods were extracted from the soil cores in a heat extractor of the Kempson, Lloyd and Gelhardie 1963 type. The efficiency of the extractor was checked both by adding a known number of animals to sterile soil before extraction and by hand sorting soil cores after extraction. Neither of these methods is very accurate, particularly as juvenile animals are excessively damaged when added to sterile soil and the recovery rate of juvenile and soft bodied small animals by hand sorting heated samples is very low. The results are shown in Table 1.

Table 1

Efficiency of soil extractor.

	Recovered from Sterile soil	Hand sorted from cores after extraction
% Mature oribatids	85	0
% small, immature mites	-	11
% Collemboles	75	5

It is probable that as all the sites were of the same sandy soil the extraction efficiency was similar in all cases.

The extracted animals were counted in a petri dish under a stereomicroscope at a magnification of X20 and classified into the following major groups : mites, collemboles, protura, pseudoscorpions, oligochaetes, myriapods, spiders, insects, endopterygote larvae, and psocids. A sub sample of one sixth (estimated by area using a grid marking one sixth of a disc (in Southwood 1967)), was removed from the total sample and was examined in detail. It was impossible to identify all the animals and each individual in the sub-sample was placed into its major taxonomic group. Additional information on each animal's age and gut contents were also recorded. The percentages of each age and feeding class in the total sample were calculated for each sample date.

Litter decomposition

The decomposition rates of litter on the sample sites were compared using two methods, the first method being the estimation of the dry weight losses of leaf litter enclosed in nylon mesh bags; two sets of nylon mesh bags were buried on sites 1 and 2 one set containing fresh <u>P. pinaster</u> needles and the other containing a mixture of fresh banksia, hakea and eucalypt leaves. Only one set of bags, containing pine needles were put out on sites, 3, 4, 5 and 6. Duplicate sets of leaves were used for initial oven dry weight measurements. The bags were collected after 7, 21, 22, 27 and 30 months in the field and their dry weight loss measured. The second estimate of decomposition rates was made by measuring the loss in tensile strength and the change in nutrient content of strips of cotton cloth buried vertically in the soil. Two series were used, the first was placed in the field in April, 1969 and brought in in November, 1969. The second series were put out into the field at three weekly intervals between November 1970 and June 1971, each set of strips was left in the field for three weeks. Five strips were put out at each site on each date. With the first series of cotton strips sub sample strips were cut and their breaking strength measured at points on the strip corresponding to five different horizons in the litter and soil. In the second series for estimating the decomposition rates throughout the year only one horizon was measured, that which corresponded to the soil/litter interface. In all cases after collection the strips were dried, brushed free of sand and dirt and ten sample strips 5 threads wide were cut across the strip at each horizon. The subsample strips were mounted on hoffmann clips before being stored for two or three days over a saturated solution of sodium bromide prior to strength testing. The strength testing apparatus was very simple in construction, the sample strip was clamped in two places, the upper clamp was fixed to a bar and weights were added directly to the lower clamp. In comparison with the beam balance type of strength tester in use in the International Biological Programme (P.T. Arctic Tundra programme) this tester is much faster to load and use, (one sample taking 1-2 minutes compared with 7-10 minutes); it takes a smaller sample; is no more subject to operator error, and because of the larger number of small samples which can be cut and processed it gives a more reliable and detailed estimate of the decomposition of the whole cloth.

Climate

Meteorological data were not collected at each site and the data for the weather station at Wanneroo are used to assess the impact of climate on the soil fauna. The temperature and rainfall data are shown in Figure 11.

Results

Species composition on six sites at Gnangara.

Identification of animals extracted from Gnangara soil samples is incomplete but those which have been identified to family, genus or species are listed in Appendix 1, which also includes the occurrence of identified and unidentified species on each site. The total number of mites recognised as belonging to different species is greater for site 1 than for the pine sites, 44 species compared with 23, 18, 21, 17 and 19 species on sites 2 to 6. The number of collembolan species is also slightly greater on site 1, nine species being recognised compared with seven on site 2, six on sites 3 and 4 and five on sites 5 and 6. Two species of pseudoscorpion occur on site 1, only one species occurs on the pine sites. The common species tend to be the same on all sites, site 1 having a larger number of infrequently occurring or 'rare' species.

In addition to animals collected in heated funnel extractors, animals were also collected by pitfall trapping on sites 1, 2, 5 and 6 and by hand sorting litter in the field, ants and termites were discarded from the samples. The major differences between the native bush and the pine sites lie in the absence of scorpions in the pitfall traps under the pines, the number of large spiders in the pine traps was also smaller. The pitfall traps on the North Kendal sites, sites 5 and 6, caught only millipedes and earwigs, on these two sites in particular the number of large predators seems to be much reduced.

Total animal populations.

These data are presented as line graphs on a linear scale, the mean population numbers and the standard error of the mean are shown for each date and site and trend lines are plotted on Figure III 1-6. As was expected the tendency on all sites is for the population to have winter maxima and summer minima. However there are two noticeable features in the total population figures, one is the low level of animals at the end of June, 1969, after initial high population levels in the autumn; the other factor is the much lower maximum populations in the winter of 1970 when compared with the previous winter.

Soil zoological studies in the 1950's and 1960's (Weiss-Fogh 1948, Guild 1955, Nielsen 1955, Rapoport et al 1967, Witkamp and van der Drift 1961, Kuhnelt 1961, Murphy 1963, O'Connor 1967, Hale 1966, Graff and Satchel 1967, Springett 1970) have shown that soil animal populations are greatly influenced by weather, either directly by accelerating or retarding metabolic processes or causing death by heat or cold shock or desiccation or indirectly through the food supply. The most salient features of the weather from 1968 to 1971 seem to be the high rainfall in 1968 which extended to November, and the lower rainfall in 1969 which was fairly evenly distributed from the break of season in March until September. The long dry hot summer 1969-1970 was an outstanding feature with the mean October 1969 temperature nearly 7°F above average. In February 1970 there was a false break of season with over 200 points of rain and high mean temperature (5°F above mean average) followed by a hot dry March and early April (seven weeks without rain and mean maximum temperature of 95°F and extreme maxima of 104°F on two days). It is suggested that the higher animal populations in 1969 were the result of cool continuously wet winters in 1968 and 1969. The lower populations in 1970 and 1971 were probably the result of very hot summer of 1969-70 and a false break to the season in both 1969 and 1970.

When the total populations on the six sample sites are compared it is seen that the highest populations occur on the old pine stand, site 2, in August and September, 1969 and the lowest in the thinned pine stand, site 4, in February 1970 and the old pine stand in October, 1970. The mean numbers of animals extracted from the soil samples over the whole sampling period are shown in Table 2, site 4 has the lowest mean value of 670 animals per sample core and site 2 the highest value with 1017 animals per sample core. The means of each of the animal groups and the percentage composition of the fauna over the whole period are also shown. Acarina are the most numerous members of the fauna and of these the Oribatidae are dominant. Oribatids make up about half the total animal population on all the sites with a slightly higher proportion on the North Kendal sites, 56% on site 5 and 60% on site 6, both these sites having a lower proportion of Collembola. For most of the other major groups the six sites are similar except for a higher proportion, 20% of Acaridae on site 3 and higher proportions, 6% and 4%, of Protura on sites 1 and 2.

Life cycles of the major animal groups.

Juvenile and adult individuals were distinguished in the field samples for Oribatidae, Acaridae, Collembola and the Endopterygota Insecta. These data are presented as histograms in Figures IV 1-6. Only total numbers of the remaining groups, Mesostigmatidae, Protura, Psocidae, Tuckerellidae and a final group containing Arachnida, Exopterygota Insecta, Oligochaeta, Pseudoscorpionidae, and Myriapoda are presented as line graphs in Figures V 1-6 to VIII, 1-6.

Oribatidae (Figs. IV 1-7)

A theoretical model of the type of life cycle occurring in the Oribatidae at Gnangara is shown in Figure IV 7. There are at least two generations a year, and the hatching of the first generation, in autumn, is highly synchronised. Larvae of oribatidae were rarely found in the samples, being too delicate to come through the extraction process, so that the first evidence of hatching is the appearance of protonymphs in the samples. The degree of synchronisation implies that the whole oribatid fauna responds at once to the autumn rains, that is, they all attain prebreeding status during the summer and breeding is triggered by the first rain. Such a high degree of synchronisation would produce a period at the end of the first generation when most of the fauna is again in the egg or larval stage and therefore would not appear in the samples. The second and succeeding generations are not synchronised, eggs hatch in the order in which they are laid and do not have to wait for the triggering effect of the rains, therefore a relatively smooth and extended population curve is produced. All the oribatid populations on all the sites at Gnangara fall into this pattern although the timing is slightly different on site 1 to that on the *Pinus pinaster* sites. On sites 2, 3, 4, 5 and 6 in 1969 there is an initial sharp rise in population numbers, the majority of animals being immature, this rise is followed by a drop in population numbers when few of the animals are immature followed by a second rise in population with an increased proportion of immature animals. However, the proportion in the immature stage never reaches the high level shown in the initial population increase. The population then falls to a summer minimum when most of the animals are adult. Sites 3 and 4 and sites 5 and 6 were sampled bi monthly which means that parts of the life cycle are obscure, however the changes in numbers and in the proportions of each life stage are those which would be expected from the theoretical model. The pattern of population changes on site I is of the same type but the first population sampled had a high proportion, 93%, of immature mites. The population level and the proportion of immature mites fell during the next two sample periods before rising to a second maximum. A second trough and peak in the proportion of immature mites indicates distinct second and third generations which overlap sufficiently to cause one second peak in the total population curve.

The picture in 1970 is complicated by the false break in season. In March the population numbers on all sites rose, almost all the population being in the immature stage, indicating a much higher larval population. It is suggested that the succeeding hot dry period of seven weeks caused a very high mortality in the newly hatched larvae and consequently the breeding population at the real start of the season in early May was very low. Sites 1 and 2 show a pattern of rise and fall and second rise in both numbers and proportion of immature animals but at a much lower level and less well defined than in 1969. When sites 5 and 6 are compared, in 1969 there are differences between the burnt and unburnt pine both in the level of population reached and its age class composition. There were more immature animals present at an earlier date on the unburnt site than on the burnt site. On average a much lower proportion of the population was in the immature stage on the burnt site (site 5) and even in March 1970 only 41% of the population was immature compared to 70% on the unburnt site (Site 6) 67% on the old pine site 2 and 74% on the native bush site 1. This implies that the high proportion of adults in the population are either in a state of reduced activity for most of the year or that the adults are producing a large number of larvae which suffer a very high mortality.

Collembola (Fig. IV 1-6)

Studies on laboratory cultures of the common species of collembola found at Gnangara gave information on the size at which breeding could take place. Collembola from field samples were divided into adults which were larger than the average minimum breeding size and "immature" which were smaller than this size. The population densities of total collembola and of immature animals are shown in Figure IV 1-6.

Collembola are numerically, relatively unimportant in the Gnangara sands being 16% of the total population in site 2 and 7% on site 5. The population densities change fairly smoothly over the sampling period without the variation apparent in the Oribatidae. This is as would be expected in animals with a generation time of 2-3 weeks. The population follows a pattern of winter maxima and summer minima on all sites with a reduced population in 1970. There is an indication that in March 1970 some breeding occurred but the populations were very low and there was no marked increase in numbers until May and June 1970. There was little difference in total numbers amongst the sites, the old pine,(site 2) had the highest populations and the North Kendal burnt and unburnt sites the lowest populations. There was a tendency for the proportion of immature animals in the population to be higher in 1970 than in 1969 particularly in site 2.

Acaridae (Acaridiae, Acaridia, Acaroidea) Fig. IV 1-6.

The Acaridae are a group of soft bodied mites which are not numerically important but for which age class data are available and which have been cultured successfully in the laboratory. The total number of Acaridae and the number of immature animals are shown in Figure IV 1-6. The general pattern for 1969 is similar to that shown by the oribatid population. The 1970 population had a simple population curve on the pine sites. Only on sites 5 and 6 was there any evidence of breeding in March 1970, when 62% and 50% of the Acaridae were in an immature stage compared with zero percent on the other two sites sampled on the same date.

Mesostigmata Fig. V 1-6.

The adults and later stadia of the larger predatory mesostigmatid mites were counted in the field sample, the young stages were not distinguished from the other young or small Acarina. The Mesostigmata populations follow the same general pattern as the Oribatidae populations, that is winter maxima and summer minima with subsidiary peaks indicating some degree of synchronisation in the population as whole. The timing of the peaks and troughs in the summer 1969 population tends to lag behind those of the oribatid mites and the acarids. As small young mesostigmated mites were not counted separately, it is not possible to say whether troughs in the numbers of adults coincided with peaks in the number of individuals in the young stages.

Tuckerellidae (Prostigmata Tetranychoidea) Fig. VI 1-6.

The later stadia and adults of these mites were easily distinguishable and were counted separately from the other mites in the one sixth subsamples. The estimated totals in hundreds per square metre are shown in Figure VI 1-6. Unlike any of the other mites the numbers of adult Tuckerellidae increased during the summer reaching a maximum in April 1970. This implies that the young stadia are actively growing and moulting throughout the summer.

Other Acarina Fig. VII 1-6

This group includes all the unidentifiable mites, mainly young stages of all mites and many young and adult small Prostigmata such as Raphignathidae, Cryptognathidae and

Eremaeidae. As might be expected with such a mixed group, there is no clear pattern, but spring and autumn populations are relatively high with lower winter and summer populations.

Insecta and other invertebrates Figs. VIII 1-6.

Population estimates from counts of the whole sample cores, (not the one sixth subsamples) are shown in Figures VIII 1-6 for Protura, Psocidae, Insecta Endopterygote larvae, and the final group which contains adult Insecta, Exopterygote nymphs, Arachnida, Oligochaeta, Myriapoda, Pseudoscorpionidae. All follow the same pattern of winter maxima and summer minima except the Psocidae, which like the adult Tuckerellidae have maximum population densities in the summer. Psocidae and Protura were most common site 2, the proportion of these animals on the native bush site 1 being somewhat higher than the other four pine sites.

Trophic analysis of the soil fauna by feeding groups.

The feeding categories used in this analysis were defined by examining the gut contents of animals from field samples and by observing the animals behaviour in laboratory cultures. Fungal feeders were defined as those animals which had only fungal hyphae or fungal spores in the gut and which were observed to select hyphae or spores in the culture chambers. Most of the adult and later stadia Oribatidae, the Psocidae and some insect larvae were fungal feeders. General feeders were defined as those animals which had plant cells, fungal hyphae and spores, brown amorphous material and mineral particles in the gut. Most of the collembola and the adult Acaridae were general feeders. Predators included the larger trombids, mesostigmatids, pseudoscorpions small spiders and some insect larvae and adults. The last group of which the feeding habits are unknown contains many small and immature mites, Protura and some Collembola and this group includes

Table 3

Percentages of each feeding group over 21 months.

	1	2	3	4	5	6
Fungal feeders	48	49	50	54	56	60
% with full guts	73	72	73	71	62	75
General feeders	22	20	22	20	15	15
% with full guts	91	91	94	92	91	91
Predators	7	6	6	6	3	3
Unknown	23	25	22	20	26	22
Total number of animals	16,095	21,325	9,211	6,737	8,128	8,695

bacterial feeders and those animals which feed by sucking plant, animal or microbial cell contents. On average 22% of the sampled animals fall into the latter category, the maximum recorded proportion being 58% on site 2 in March 1970 and the lowest being 5% on site 4 in October 1969. The overall trophic structure for the six sites over the 21 month sampling period is shown in Table 3. The proportion of fungal feeders increases from site 1 to site 6 the proportion of general feeders is similar (20-21%) on sites 1-4 but lower (15%) on sites 5 and 6. Sites 5 and 6 also differ in having a lower percentage of microarthropod predators.

The seasonal changes in the trophic structure of the population are shown in Figure IX 1-6 and can be related to the life cycles of the predominant animal groups, the proportion of general feeders present in the populations of all sites is very low throughout the summer but increases during the winter. The proportion of micropredators is relatively constant during the period except that there is a decline from 1969 to 1970, particularly noticeable in sites 1 and 2. On site 1 the proportion of fungal feeders is relatively high for most of the year but is low during the period when most of the oribatid fauna is in the early immature stage, May 1969 and June 1970. Many of the oribatid juvenile stadia were classed as of unknown feeding habits and at these times a higher proportion of the population was in the "unknown" category.

The two occasions when fungal feeders formed a very large proportion of the population were caused by two different series of events. In December 1969, the high proportion of fungal feeders was due to changes in the other members of the whole population, there being a 68% reduction in the number of "general feeders" and a 50% reduction in the number of "unknown feeders." However in August 1970, 66% of the population were fungal feeders and this was caused mainly by a 65% increase in the number of large immature oribatids. A similar pattern of events is apparent on site 2 with fungal feeders being numerically important for most of the year with a reduction in importance when the juvenile stadia are too small to graze on fungus; and an increase in importance when the juveniles reach the necessary size and again when the more drought resistant adults survive the early summer droughts longer than most of the other microarthropods.

Feeding Activity

The number of animals in the field population with food in the gut is taken to be an indication of the feeding pressure they are exerting on their habitat. It is necessarily a very rough guide as it makes no allowance for the time necessary between feeds for digestion or for the quality of the food. An active animal may digest and eliminate a meal and immediately take another meal appearing in the sample with a full gut. An inactive animal may take a long time over digestion and also be recorded as full. Only if the population as a whole spends as much time between meals as in digestion would the proportion of full and empty animals accurately indicate the feeding pressure. Animals which take distinct meals with no feeding activities between them, predators and specialised feeders, can be expected to have empty guts for some of the time whereas animals which feed almost continuously, e.g. collembolan general feeders, seldom have empty guts unless they are undergoing ecdysis. An animal with a full gut may be retaining undigested food or it may be digesting one of a rapid succession of meals, but an animal which has an empty gut is clearly an animal which was not feeding at the time of sampling. On sites 1 and 2 over most of the year between 30% and 40% of the fungal feeders have empty guts, (Figure X.) However at the beginning of the breeding season in both 1969 and 1970 and at the beginning of the summer very few, 15% and 0% of the animals were empty suggesting an increase in feeding activity at these times. The other four sites were sampled too infrequently to allow seasonal changes to be detected. When the average percentages of full animals over the whole sampling period are considered it is seen that the burnt pine sites has a lower percentage of full animals, (62%). The proportions of full animals were not high at the beginning or end of the breeding season in 1969, the only high value, (90%), being recorded in June 1970. Compared to the adjacent unburnt site, site 5 has a reduced feeding activity which suggests that the lower proportion of juveniles in the population is due to reduced breeding activity.

In contrast to the fungal feeders the general feeders had high proportions, (92%), with full guts on all the sites throughout the sampling period. This is to be expected in animals which take in large quantities of low quality food rather than smaller quantities of high quality food.

Litter Decomposition Studies at Gnangara.

Litter Bags.

The oven dry weights of leaves in nylon mesh bags are shown on a semi logarithmic scale in Figure XI. It is seen that the weight loss is greatest on site 1 and the weight losses on sites 2, 3 and 4 are less. Both the North Kendal sites have a much lower rate of weight-loss. When scherophyll and conifer leaves are compared it is seen that the weight loss is greater from the scherophyll than from the conifer litter regardless of whether the litter is placed under pines or under scherophylls. If the weight loss curves for pine litter and banksia/eucalypt litter are extrapolated they give approximate periods for approaching 95% decomposition of five years for native vegetation, ten to twelve years for pine on the older sites and twenty five to thirty years for the two North Kendal sites. The burnt site differs from all other sites in failing to lo~~o~~se weight for the first twenty two months, but its eventual rate of weight loss is equal to that of the unburnt site.

Cotton Strips

Cotton strips left in the field for six months,
April 1969 to November, 1969.

Decomposition was far advanced on all sites except the North Kendal burnt and unburnt sites 5 and 6. The percentage loss in strengths at the soil/litter interfaces are tabulated Table 4.

Table 4

The percentage loss in strength of cotton strips after six months in the field.

Site	% Loss	
1	55	no significant difference
2	52	
3	49	
4	53	
5	23	significantly different at the 0.5% level.
6	37	

Sites 1, 2, 3 and 4 differed from sites 5 and 6 during the winter of 1969, sites 5 and 6 having a smaller loss in strength. The burnt site, site 6, also had a significantly smaller strength loss than the unburnt sites.

The decomposition rates, as indicated by the residual strength of the cotton strips are shown in Figure XII for the period November 1970 to June 1971. The rates on site 1 are highly variable and there is no significant pattern over the period. The decomposition rates on sites 2, 5 and 6 show significant differences over the eight month period. Site 2 and site 6 have an increased rate of decomposition in March and April. The burnt site, site 5, is again different from the other sites, and in this case the period of significantly increased decomposition is delayed until June.

The average percentage loss in strength over the eight month period is 42% for sites 1, 2 and 6 and 33% for site 5. This differs from the loss in strength recorded between April and November 1969 when both the North Kendal sites (5 and 6) lost less strength than the other four sites although the loss on the burnt site was much lower than on the unburnt site.

In addition to the residual strength of the cotton strips being measured the nitrogen content of the strips was determined. The results are shown in Figure XIII. It is suggested that the nitrogen content of the cotton strips indicates the amount of microbial protein associated with the cellulose, the microflora using the cotton strip as an energy source. If this is so then in all sites the microbial population is low during the summer months with a minimum in January/February. This is followed by a sharp increase in February/March and subsequent high levels during the winter. The most pronounced rise in nitrogen content occurs in the banksia, hakea, eucalypt site, site 1 and the least pronounced on site 2.

Discussion

Model of litter accumulation

The major changes in litter accumulation and decomposition during the life of a forest can be described, but the sequence of events in the development of the soil biota is less well documented. In the history of a plantation the initial event is often the clearing of the native vegetation. Clearing cuts off most of the energy input to the soil-litter system. However, the soil-litter system will continue to function until it runs out of energy, theoretically until complete decomposition has occurred in both the litter and humus layers and there is a 100% mineral soil. In practice, the role of energy fixation is taken over by the herb layer so that the soil litter system is never without an energy input. If, for example, the only energy fixation allowed on the site is by crop trees (if there are no weeds) then there will be no significant input to the decomposer system for several years after clearing and planting. If the litter and humus decomposition rates can be predicted then it would be theoretically possible to calculate the interval before the trees would be growing in a humus free soil. As the trees increase in size, the input to the litter layer increases slowly with a sudden large input in both leaf and wood litter at canopy closure. Further sudden inputs occur if there is pruning, with a fairly steady low level input from pruning, thinning and cropping. The decomposition rate before the initial clearing is likely to be fairly high and will decrease after clearing (particularly if there is burning) to reach a minimum level which may even be zero if there is no litter or humus in the soil. As the forest grows, the litter decomposition rate increases. It is probable that the decomposition rate changes several times during the life of the forest in response to variations in the litter input and to factors such as weather, burning and fertiliser application.

Litter decomposition and accumulation have been measured in several forest types around the world and the results are summarised in table 5. The data are of two types, from the direct study of the disappearance of marked leaves on the soil (leaves confined in mesh bags, tied to strings, or radioactively tagged), and from the measurement of litter fall and the amount of accumulated litter on the forest floor. Litter accumulation and decomposition are assumed to be exponential and the value 3/k (the time taken to reach 95% of the asymptote) is calculated from both types of data :

for the leaf disappearance studies, from the formula describing exponential decay

$$\frac{\text{leaf remaining}}{\text{initial leaf quantity}} = e^{-k}$$

For the forest floor studies, from the expression describing a steady state

$$k = \frac{\text{input of litter}}{\text{accumulated litter}} \qquad \begin{matrix}\text{(Olson 1963)}\\ \text{(Jenny et al 1949)}\end{matrix}$$

Neither of the assumptions is necessarily true, and it can be seen from the table that there are conflicting estimates of decomposition rates. Perel's estimates of 10 years and 40 years for the accumulation of oak litter are calculated from leaf disappearance rates measured in a dry year and a wet year. Other factors which affect the decomposition rates are : the presence or absence of soil animals (Heath et al 1966), the absence of soil animals from oak litter changing an estimated 3 year accumulation period into one of 48 years; and the age of the stand. Both the litter disappearance studies at Gnangara and the forest floor studies at Tumut N.S.W. (Forrest et al 1970) have a longer estimated accumulation period in the younger stands.

Despite these factors the litter accumulation periods for the forest types can be placed in four main groups:

1. very short periods, frequently of less than one year in moist tropical forests,
2. slightly longer periods of 1 to 4 years in temperate oceanic forests,
3. medium length accumulation periods of 5 to 20 years for the majority of continental forests,
4. very long periods estimated by Jenny (1949) as 25 to 300 years for litter accumulation in the very harsh continental climate of the Sierra Nevada, California.

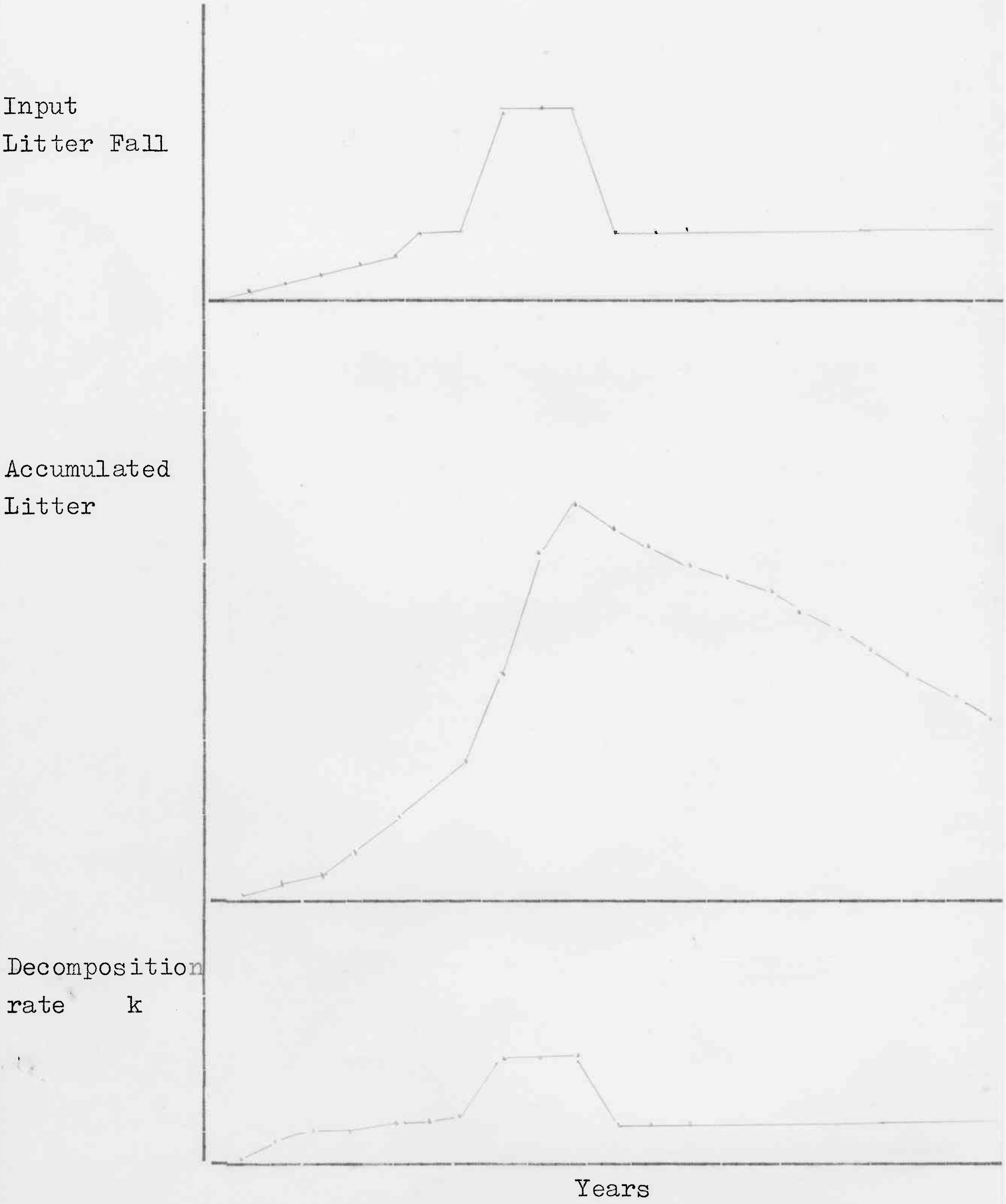
It is instructive to compare the Russian continental oak forest (Perel 1971) with the oceanic temperate oak forest (Heath et al 1966) and the black oak forest in the Sierra Nevada (Jenny 1949). The weather during Perel's experiments ranged from mild temperate to harsh continental in the two years. The two calculated decomposition rates were similar to those recorded by Heath et al (1966) for mild temperate climate forest and by Jenny (1949) for harsh continental climate forest.

Where both conifers and broad leaved species have been examined in the same climatic region, conifer leaf litter has been shown to decompose more slowly than broad leaved litter. However, it is suggested (Healy and Swift 1970) that the woody material in the litter would decompose more rapidly in a soft wood than in a hard wood forest:

A graphical model of litter accumulation based on the changes in litter fall and decomposition rates outlined above has been constructed, Figure XIV. The model shows a litter input which rises slowly to a steady level with additional input at canopy closure and pruning. The decomposition rate is at first high, but falls to a steady level, rising when there is additional input. The curve for litter accumulation in these circumstances does not reach a steady state until after the maximum litter accumulation. The exponential litter accumulation curve shown as a broken line illustrates the differences between the theoretical levels and the levels to be expected in the field.

Figure XIV

Graphical Model of Litter Fall, Litter Accumulation and Decomposition.



The soil fauna.

The importance of the soil fauna in increasing litter decomposition rates has been clearly demonstrated by Heath et al (loc cit), Kircheva 1960, and Witkamp et al 1963. Witkamp's studies also show that the macrofauna is important in determining the rate of physical breakdown of the litter. Main (pers.comm.) suggests that the marsupial fauna of Australian forests may have an impact on the decomposer cycle through their feeding and behaviour. The effect of soil animals on the soil microbial populations has been little studied except by the total energy flow methods mentioned. Feeding preferences of individual animal species have been studied by Hartenstien (1962), Karg (1963), Lebrun (1970) but have not been related to the distribution of either prey or predator in the field. Springett, Latter and Staddon (in press) found that animals usually inhabitating the upper layers of the litter were more attracted to traps containing the microbes involved in initial decomposition of plant litter than to traps containing microbes involved in later stages of decomposition. Springett (1971) showed that in laboratory cultures the fungus *Trichoderma* sp. cannot withstand the feeding and trampling pressure of a collembolan population. It is known that *Trichoderma* sp. can be antagonistic to mycorrhizae but the interrelations of these three groups with the rest of the soil biota, with the plants and with the inorganic fraction of the soil are unknown.

It is becoming increasingly obvious that the major questions arising in the study of the soil fauna and flora are not related to the energy flow concept of "how much and how fast?" but to the natural history concept of "in what way?". Ultimately the two concepts will merge but this will not happen until a great deal more is known about the relative competitive ability of groups of organisms in the soil environment. Techniques for measuring total soil metabolism are available but there is a need for methods whereby energetics can be combined with natural history observations to identify essential elements in the decomposer system. The need for this type of data was stated by Macfadyen (1963) and again by Van der Drift (1970). The greatest need, and particularly in all Australian habitats, is for taxonomic studies and there is little chance that the quantity and quality of manpower considered essential for environmental management by Sailer (1969) and Christensen (1970) will be available in the near future.

In addition to taxonomic studies of the soil organisms, their habitats should be classified. Soils should be classified in terms relevant to the animal life in them, using such characteristics as cavern size, root penetration, the species composition of the microflora in the soil and the structure of the microfloral community, the number of fruiting bodies, rhizomorphs and growing tips. Embedding and sectioning of soil blocks and the use of scanning electron microscopy in biological studies are techniques which, if it were possible to identify the organisms, would make feasible a classification of soil habitats similar to that developed by Kikkawa and Webb (1967) for tropical forests.

In the absence of detailed information on the mechanisms of the natural biological cycles of carbon, nitrogen, phosphorus, oxygen and other nutrients the broad energetics viewpoint is a useful tool, as all these cycles are driven by solar energy. Man's approach to the biological cycle is to channel an increasing proportion of the fixed energy through himself. In any one system the trend has been to increase the energy fixed, but to remove most of it leaving less available to drive the biological cycle in that system. The system usually runs on the reduced energy by having fewer organisms working at their normal rate (Edwards 1970), although the alternative of having the same number of animals working at less than their normal rate may have taken place in the burnt plots at Gnangara.

The changes in the soil community following clearing and reafforestation have been studied by very few workers. Huhta et al (1967, 1969) have studied the effects of silvicultural practices on soil animals in Finland; Dunger (1967, 1968) has studied the development of the soil community on mining tips; van den Berg and Ryke (1967) have studied the development of the mite fauna in exotic pine plantations in South Africa. These studies and the present work show that the number of animal species in the soil is reduced after planting a monoculture, and the larger species, particularly the predators, disappear. Rare species vanish, as might be expected when habitat diversity is reduced. The new habitat is recolonised by those animals which can make a living there; the rate of recolonisation depends on the weather, the microclimate and the habitat diversity within the litter.

The microclimate and the habitat diversity will depend largely on the depth of litter and the age of the stand. Microbial feeders and plant feeders will be able to colonise before predators which may only do so when an adequate food supply is already established. Once predators become part of the community they have an accelerating effect on the total population metabolism, the energy needed for hunting and escape being added to that required for growth and reproduction.

Decomposer systems can probably be classified into two major types:-

1. Opportunistic - Systems with sudden unpredictable litter falls in an erratic climate.
2. Steady - Systems with a predictable input in a predictable climate.

Many Australian decomposer systems, particularly in semi arid areas seem to belong to the opportunistic type. There is a large proportion of standing dead material and decomposition occurs rapidly after relatively small amounts of rainfall (Charley and Cowling 1968). Thus in favourable conditions of energy supply and weather, decomposition is fast but at other times decomposition is very slow and the standing dead material in the ecosystem accumulates.

Clearing of native bush for agriculture usually occurs during a period of wetter-than-average climate, a time when the opportunistic decomposer system would be very active. If this postulate is correct subsequent farming practice results in the very active decomposer system having a much reduced energy input which is used up very rapidly. There are no reserves of standing dead material and annual top dressings of organic material are insufficient to have a permanent effect on the structure and humus content of the soil. The soil in such a system would have a very low humus content for most of the year and any added organic matter would disappear very rapidly, a description which fits many marginal agricultural lands.

A steady decomposer system is not adapted to long irregular periods of inactivity during drought or reduced litter input. Observations in the Darling Ranges near Perth show that, in the jarrah bush, litter accumulates in the soil surface and when decomposition occurs it is almost complete before the litter is incorporated into the soil and the humus content of the soil is therefore fairly low. It may be that this tendency to litter decomposition above ground with little incorporation of humus into the soil is a character of opportunistic systems and that even the better forested areas, and the non-marginal agricultural lands, belong in that category. In contrast, deciduous pome fruit orchards in the Darling Ranges near Perth have little litter accumulation on the soil surface, and decomposition appears to be rapid but incomplete, as much of the litter is mixed into the soil probably by the large populations of lumbricid-worms. Moist temperate and tropical forests and agricultural areas are of this latter type with animals having a long development period and a regular life cycle.

To maintain this type of community, a regular energy input above a certain minimum would seem to be essential and this will probably vary with climate, soil and vegetation. For example, wet tropical forests have a large steady litter input and a very fast decomposition rate, and the time taken for impoverishment after clearing is fairly short. On the other hand, European temperate oceanic forests have withstood clearing and agriculture for many hundreds of years. How much of this difference is due to energy storage or to a relatively lesser reduction in input is unknown but the falling soil humus content and the reduced crop yield on many English farms show that the temperate oceanic system is not immune to soil humus bankruptcy. The cleared Karri forest soils in the Warren area of W.A. are also showing a loss of structure and reduced humus content after a relatively short period under intensive cropping.

Clearing forest for agriculture reduces the number of species of soil animals. If the number and diversity of animal species is related to the ability of the soil to maintain its fertility, it is possible that the initial reduction of species when clearing the highly diverse tropical forest is sufficient to reduce the soil's ability to maintain fertility. In the less diverse temperate forests, early clearing does not reduce the soil animals by a critical amount but modern agricultural practices such as chemical spraying, the use of larger fields, and the use of inorganic fertilisers may have effected the final critical reduction.

If a viable soil decomposer system is essential to the maintenance of soil fertility, humus, soil structure and if maintenance of soil fertility is desirable, then several questions are raised by consideration of the ecosystem basis for agricultural practices:

1. How far can the energy income to the soil and the species diversity in the soil be reduced before soil poverty backlashes and reduces profitability?
2. For how long will the area produce a profitable crop without treatment? (In theory, all crop production could be by sterile hydroponic units, but this is not practical if only because of the vast amounts of energy which would be needed to run artificial recycling units. However, some degree of "hydroponics" is necessary for maximum yield in a non-self-sustaining system).
3. What level of treatment is economic now and will be in the future?
4. Is it possible to use the system for maximum yield, with or without fertiliser treatment, until the soil is exhausted and then to regenerate a self-sustaining system?
5. What would such a self-sustaining system consist of: how long would regeneration take: would it be physically and economically possible?

Measurements of total metabolic activity give an indication of the time it would take to reach a steady state in the decomposer system with a given input. Unfortunately, a detailed prescription of the species of flora and fauna which are essential for a cultivated system to be kept in a self-perpetuating state, a prescription which does not also decrease soil fertility, is well beyond the capability of any soil biologist today.

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Table 2

Mean number of animals extracted from the soil samples in 21 months and the percentage composition of the fauna.

Site No.	1	2	3	4	5	6
Mean Number per Core						
Total animals	771	1017	921	670	903	955
Collemboles	117	157	106	86	67	76
% of total animals	15	16	12	13	7	9
Total Mites	602	793	792	556	787	838
% of total animals	78	78	86	83	87	88
Oribatids	365	488	454	364	504	579
% of total animals	47	48	49	54	58	60
% of total mites	61	62	57	66	64	69
Acarids	100	103	184	68	125	123
% of total animals	13	10	20	10	14	13
% of total mites	17	13	23	12	16	15
Tuckerellids	43	35	34	20	37	30
% of total animals	6	3	4	3	4	3
% of total mites	7	4	4	4	5	4
Mesostigmatids	26	50	39	39	23	28
% of total animals	4	5	4	6	3	3
% of total mites	4	6	5	7	3	3
Other mites	68	115	82	64	98	78
% of total animals	9	12	9	10	11	8
% of total mites	11	15	10	12	12	9
Protura	43	36	13	15	19	18
% of total animals	6	4	1	2	2	2
Others	10	32	11	13	30	14
% of total animals	1	3	1	2	3	2

Heath et al 1966	Oak no animals		24	48	L
	Lime " "		80	2	L
	Birch " "		75	2	L
Witkamp et al 1963	Oak animals alive	11m	59	3	L
	Oak animals killed with naptha	11m	43	6	L
	Pine	1yr	47	6	L
	Oak	1yr	70	3	
	Maple	1yr	71	3	
	Pine	1dy	0.3	ca.1	L
	Maple	1dy	0.6	1	L
Gifford 1967	Scots Pine	20m		2-4	L
Jenny et al 1949	Oak Sierra Nevada	1yr	3-12	25-50	F
	Pine " "	1yr	1-3	50-300	F

Table 5 Time taken for litter to accumulate in forests throught the world. L = leaf disappearance studies
F = forest floor studies.

Author	Forest type of tree species	Time	% Loss	Years 3/K	Type of Study.
Jenny et al 1949	Tropical	1 yr.	39-62	3-6	F
Landelout et al 1954	Tropical	1 dy	0.9	0.75	F
Madge 1965	Tropical	1 yr	90	1.5	L
May 1961	Tropical	1 dy	1.3	0.75	F
Attiwill 1968	Dry Schlerophyll	1 yr	49	5	F
Hatch 1955	Dry schlerophyll			7	F
Hatch 1962 (file 114.3)	Pinus pinaster			50	F
McColl 1966	Dry schlerophyll	1 yr	36	8	F
Forrest et al 1970	Pine five year old			25-50	F
	twelve year old			12	F
	average to twelve years.			20	F
Perel et al 1970	Oak USSR wet summer	8m	25	10	L
	" USSR dry summer	8m	6	40	L
	Linden USSR	8m	28	8	L
	Birch USSR	8m	27	8	L
Springett	Pine, Gnangara 15 years	30m		15	L
	" 30 years	30m		7	L
	Dry schlerophyll	30m		4	L
Wood 1970	Dry schlerophyll Euc. delegntensis	1 yr	41	5	L
	Dry schlerophyll Euc. pauciflora	1 yr	35	7	L
Zlotin 1970	Oak USSR	6m	35	6-11	L
Heath et al 1966	Ash U.K. with animals	1 yr	99	1	L
	Elm		99	1	L
	Beech		64	3	L
	Oak		89	1.5	L
	Lime		99	1	L
	Birch		99	1	L

APPENDIX 1.

Microarthropods found at Gnangara.

	Number of Species recognised.					
Site	1	2	3	4	5	6
Acarina. Oribatidae						
Anellozetes spp.	2	2	2	2	2	2
Incabates sp	1	1	1	1	1	1
Amenioppia sp	1	1	0	0	0	0
Passalozetes sp	1	1	1	1	1	1
Cosmochthonius (Brachipthonus)	1	1	1	1	1	1
Pedrocortesia	1	1	1	1	1	1
Platynothrus	1	1	0	0	0	0
Zygoribatula	1	1	1	1	1	1
Oppia	3	1	1	1	1	1
Galumnidae	2	1	1	1	0	0
Phthiracaridae	1	1	1	1	1	1
Mesostigmata	5	3	3	3	2	2
Prostigmata						
Erythraeidae	3	0	0	0	0	0
Cunaxidae	1	0	0	0	0	0
Raphignathidae	3	2	1	1	1	1
Pseudochylidae	1	0	0	0	0	0
Cryptognathidae	1	0	0	0	0	0
Tuckerellidae	1	1	1	1	1	1
Others not identified beyond Prostigmata	11	4	5	5	3	5
Cryptostigmata						
Acaridae	2	1	1	1	1	1
Protura						
Acerentulus sp	1	1	1	1	1	1
Collembola						
Lepidocyrtus (languinosus?)	1	1	1	1	1	1
Entomobria (marginata?)						
Isotoma sp	1	1	1	1	1	1
Tullbergia krausbaueri	1	1	1	1	0	0

Bourletiella sp (albanica?)	1	1	0	0	0	0
Sminthurus multifasciatus	1	0	0	0	0	0
Hypogasturara (inermis?)	1	1	1	1	1	1
Brachystomella parvula	1	1	1	1	1	1
Pseudoarchorutes (asigillatus?)	1	0	0	0	0	0
Pseudoscorpionidae						
Austrochthonius australis	1	1	1	1	1	1
Xenolpium bornemissza	1	0	0	0	0	0

List of figures.

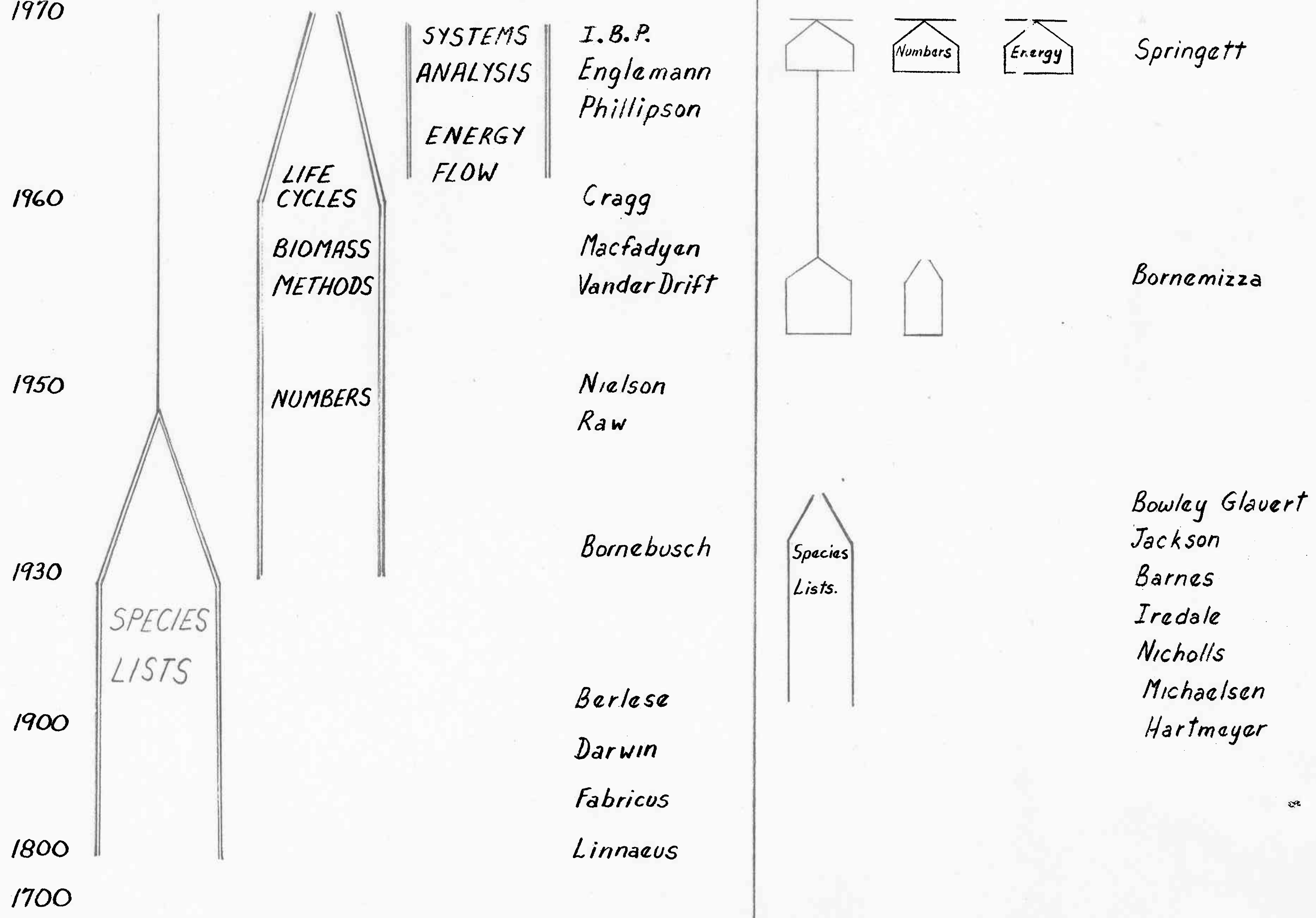

1970
1960
1950
1930
1900
1800
1700
SPECIES LISTS
LIFE CYCLES
BIOMASS
METHODS
NUMBERS
SYSTEMS ANALYSIS
ENERGY FLOW
I.B.P.
Englemann
Phillipson
Cragg
Macfadyen
VanderDrift
Nielson
Raw
Bornebusch
Berlese
Darwin
Fabricus
Linnaeus
Numbers
Energy
Species Lists.
Springett
Bornemizza
Bowley Glauert
Jackson
Barnes
Iredale
Nicholls
Michaelsen
Hartmayer

Fig. I

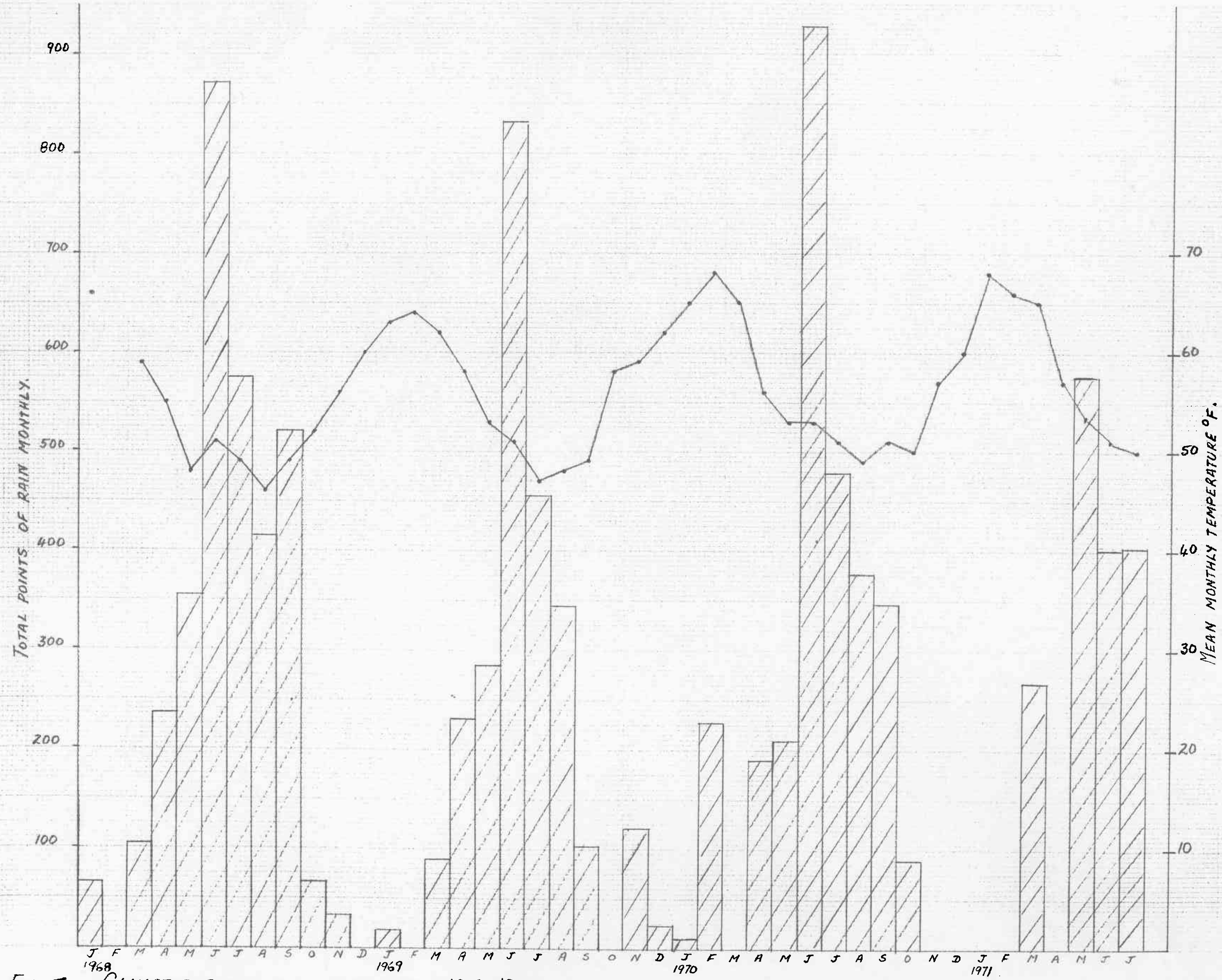


FIG. II : CLIMATIC DATA FOR WANNEROO. 1968-1971.

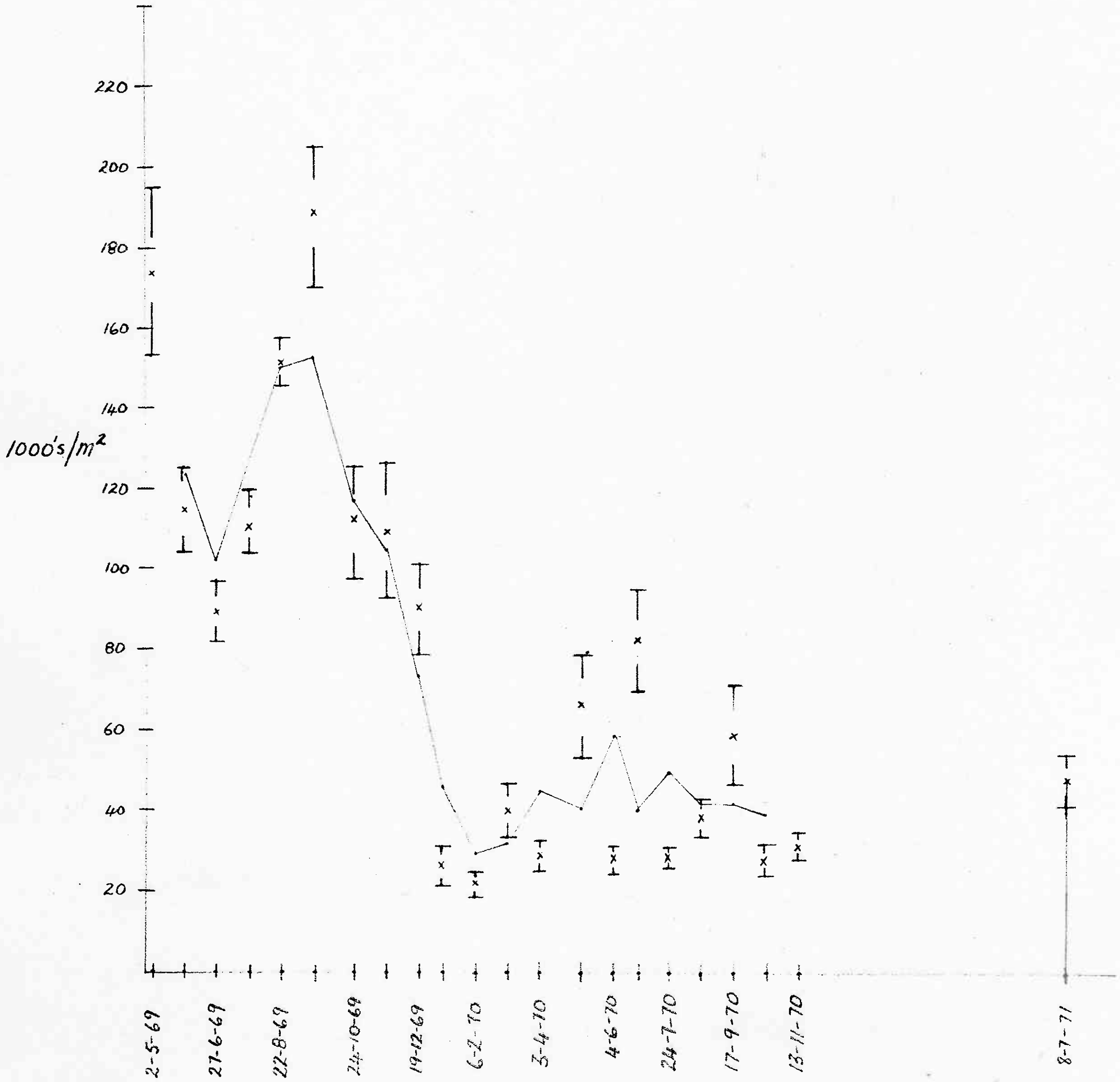


Fig. III$_1$: Total numbers on Site 1.

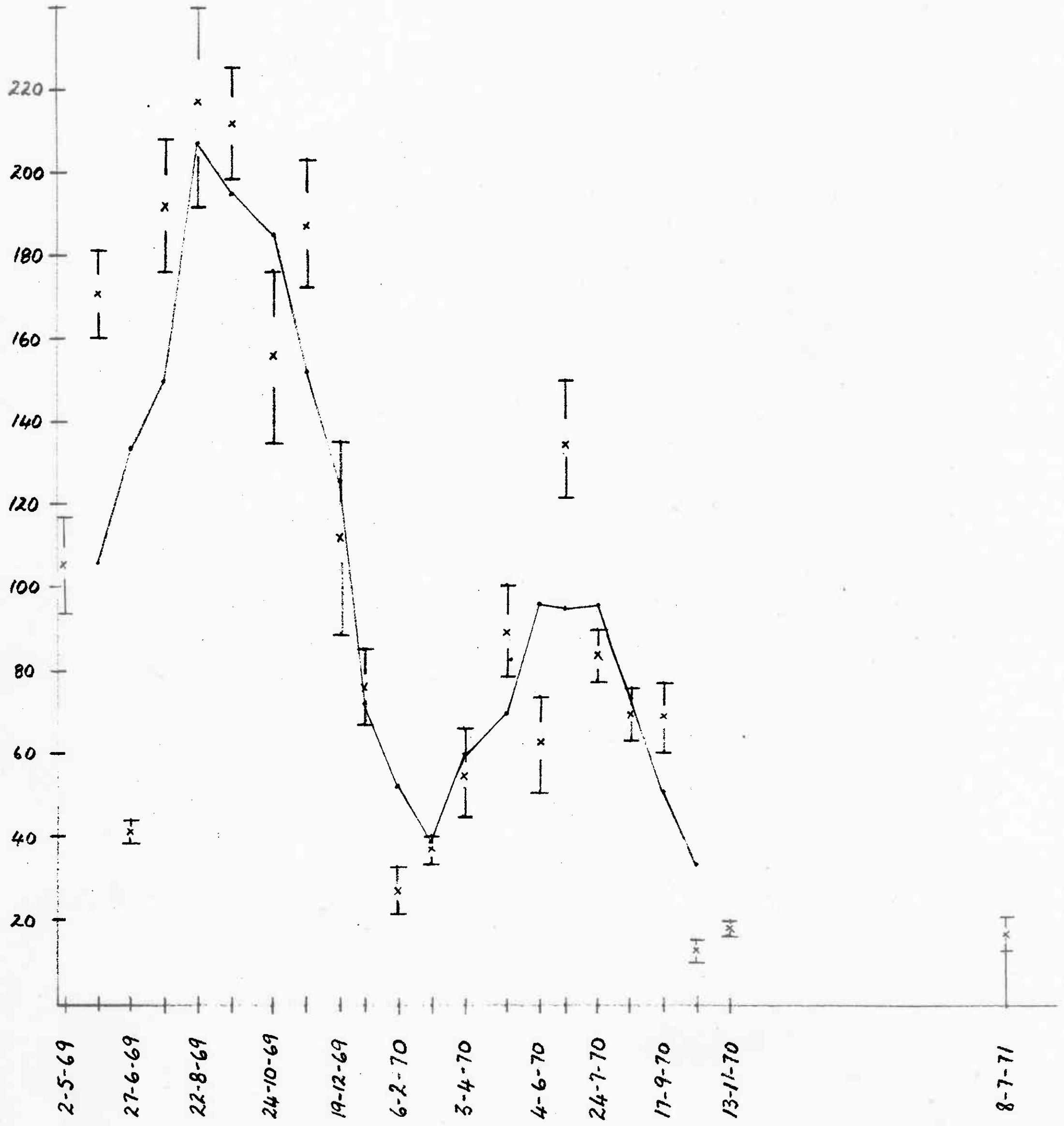


Fig. III$_2$: Total numbers on Site 2.

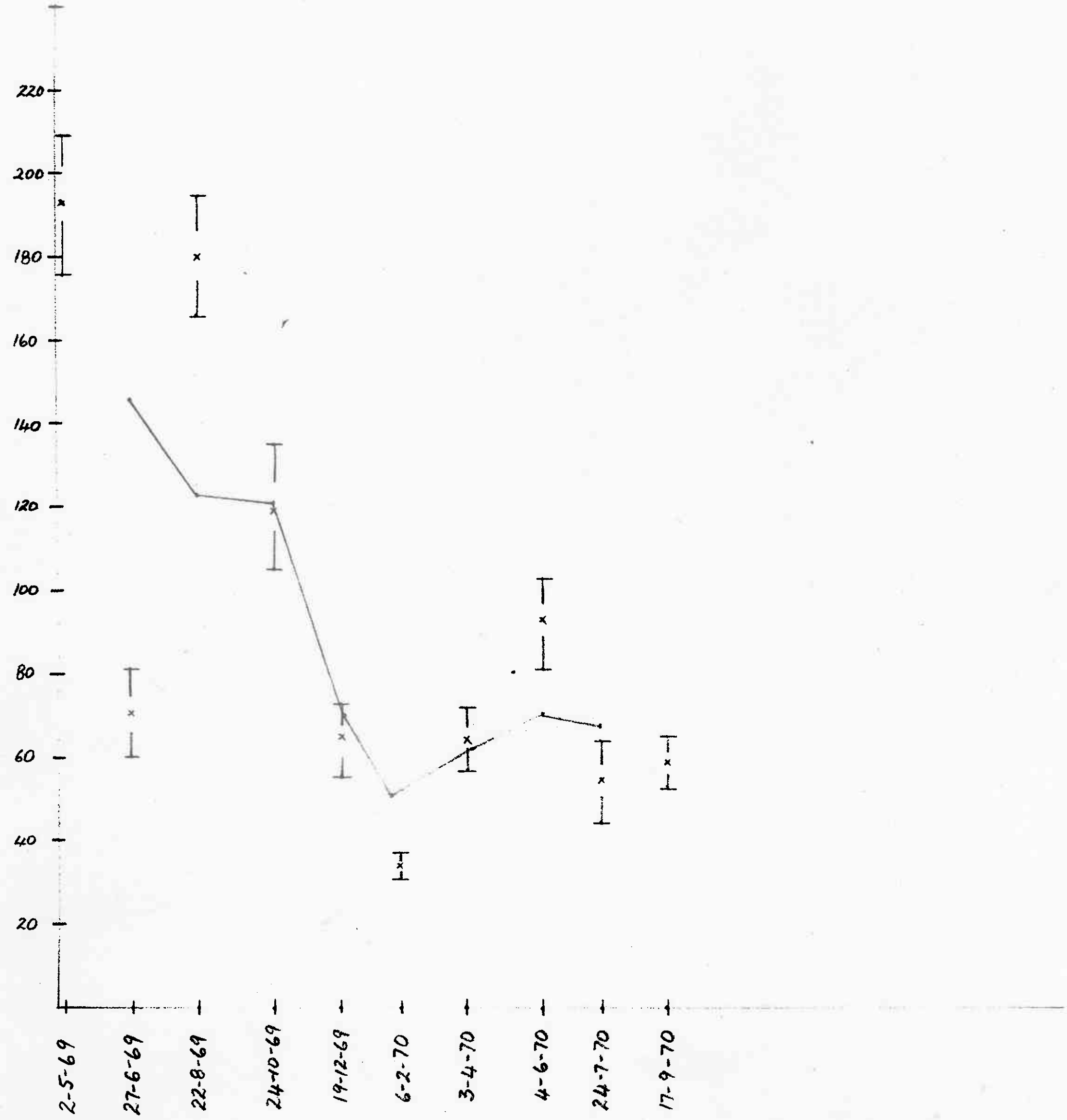


FIG. III$_3$: TOTAL NUMBERS ON SITE 3.

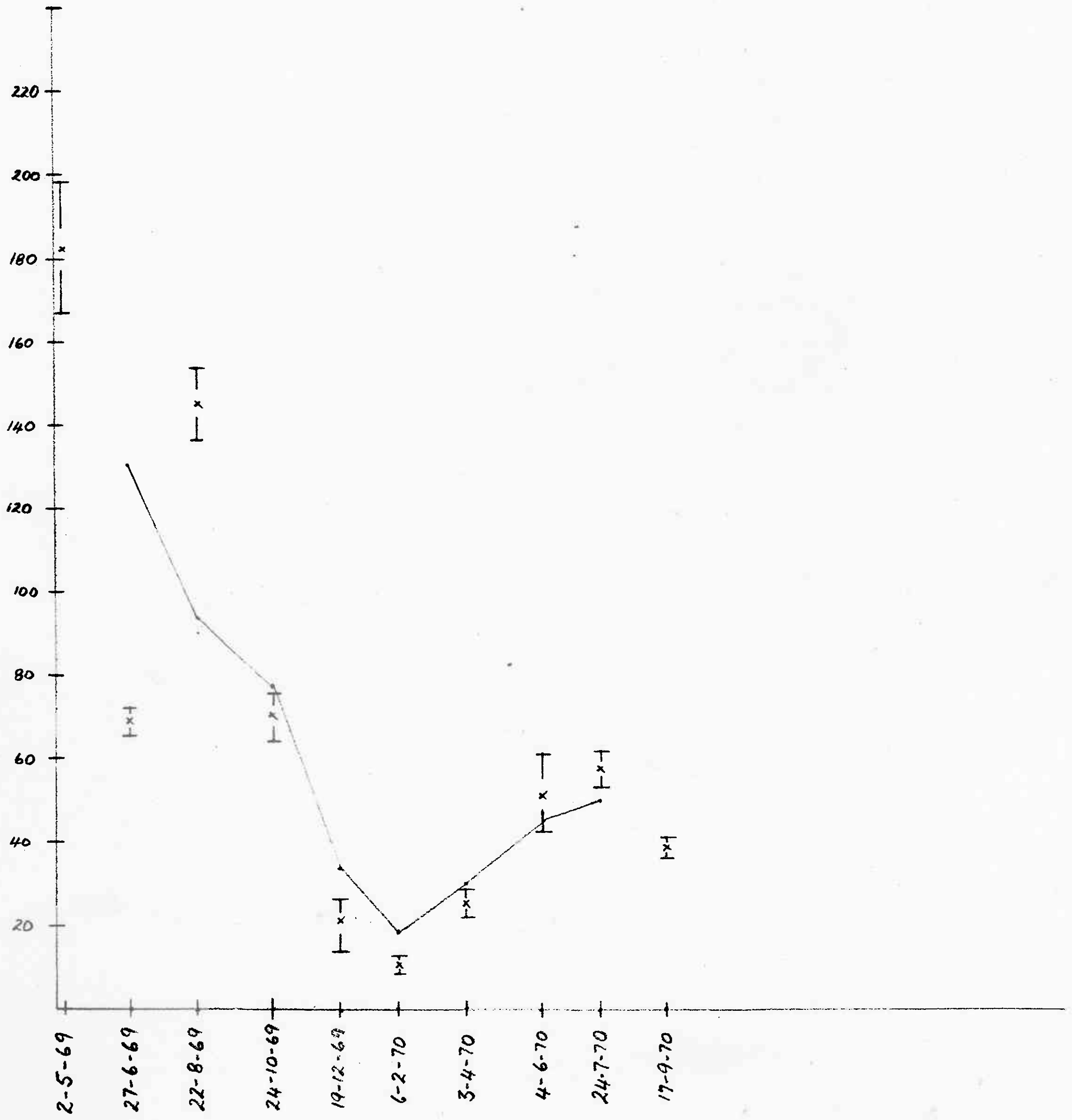


FIG. III$_4$ TOTAL NUMBERS ON SITE 4.

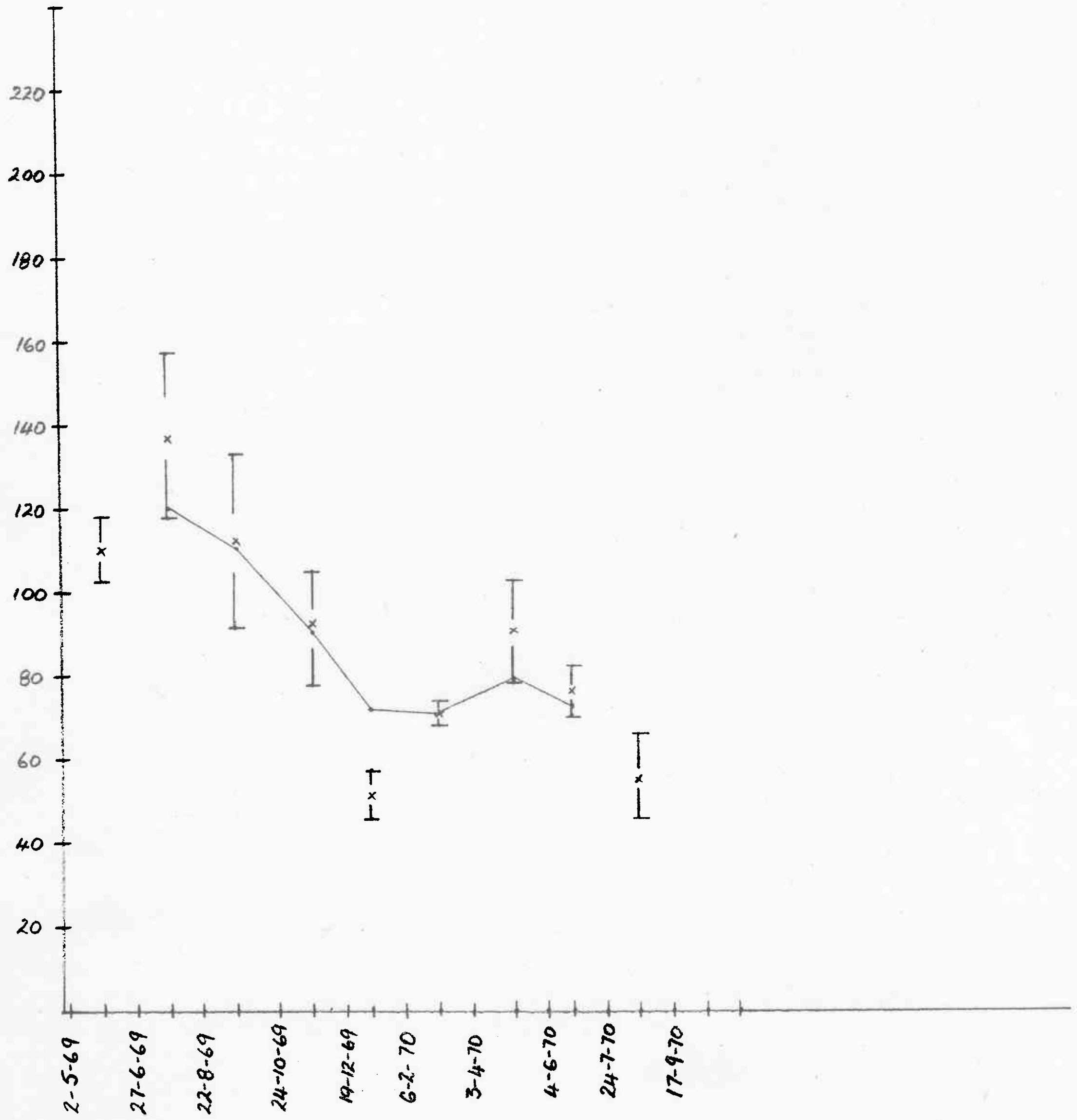


FIG. III_5 : TOTAL NUMBERS ON SITE 5.

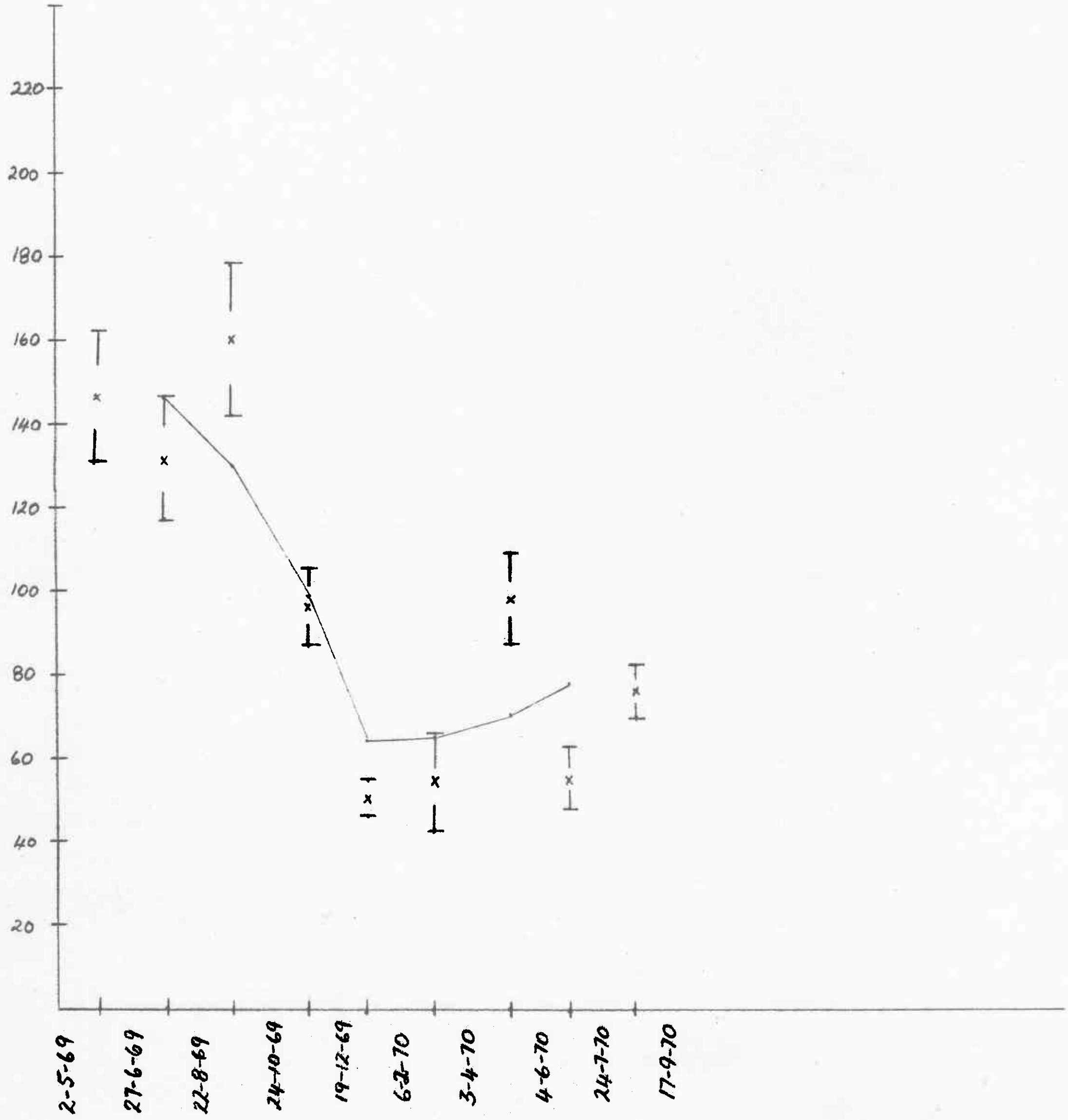
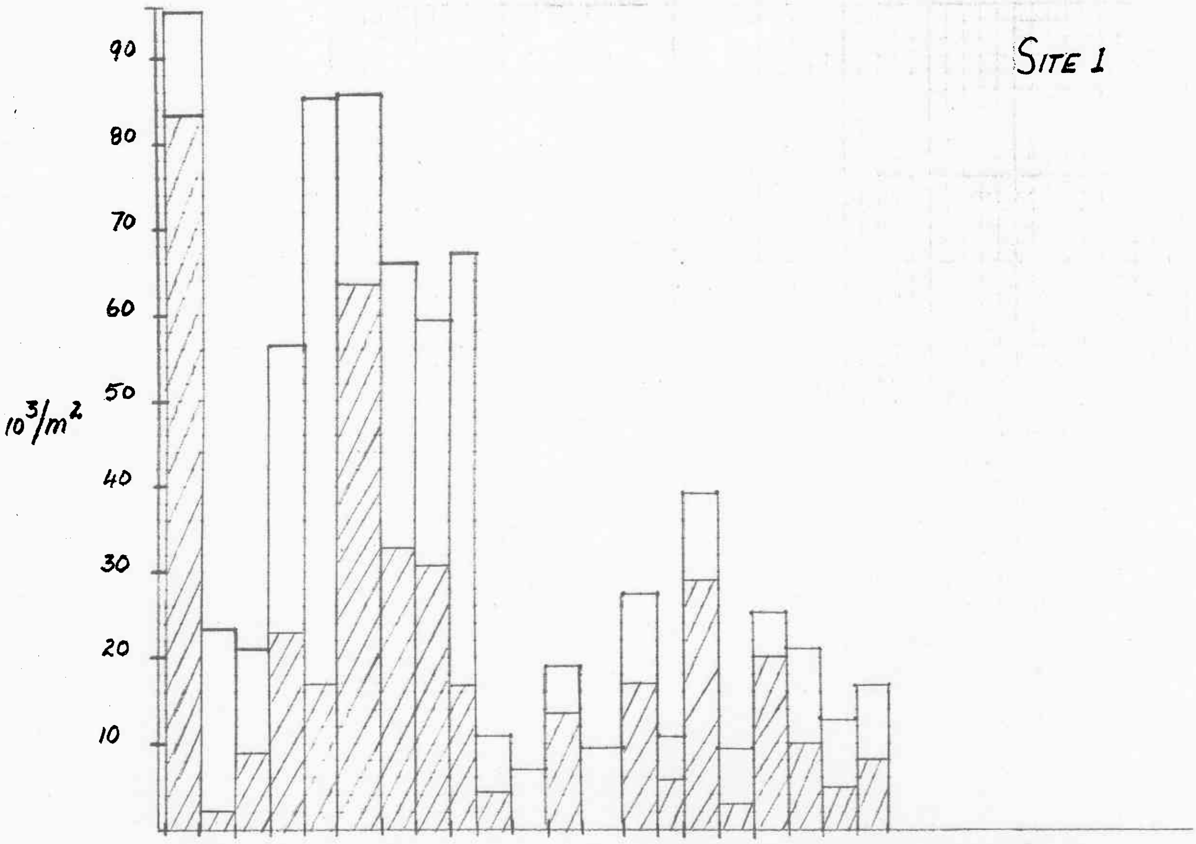
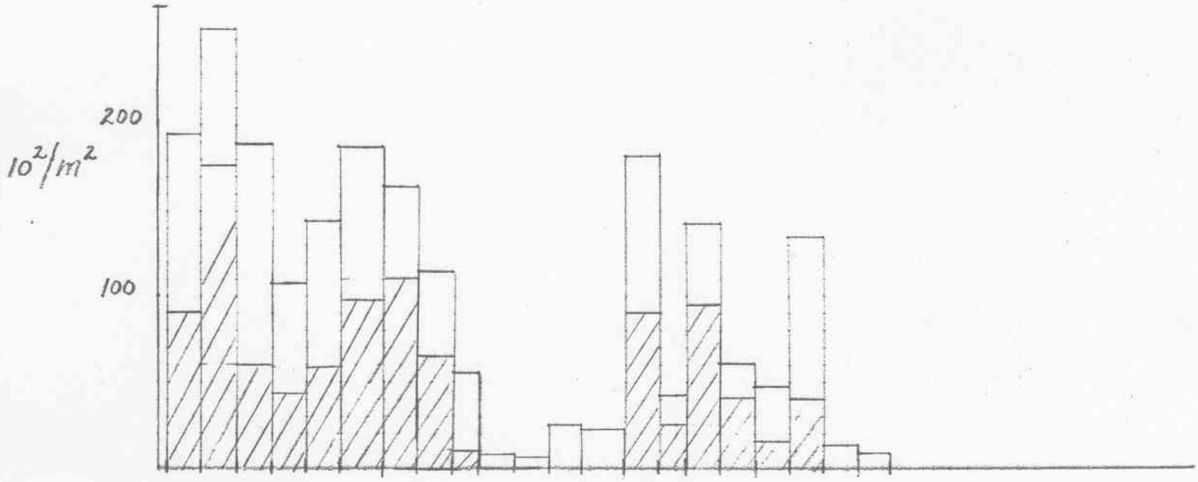


FIG. III_6 : TOTAL NUMBERS ON SITE 6.

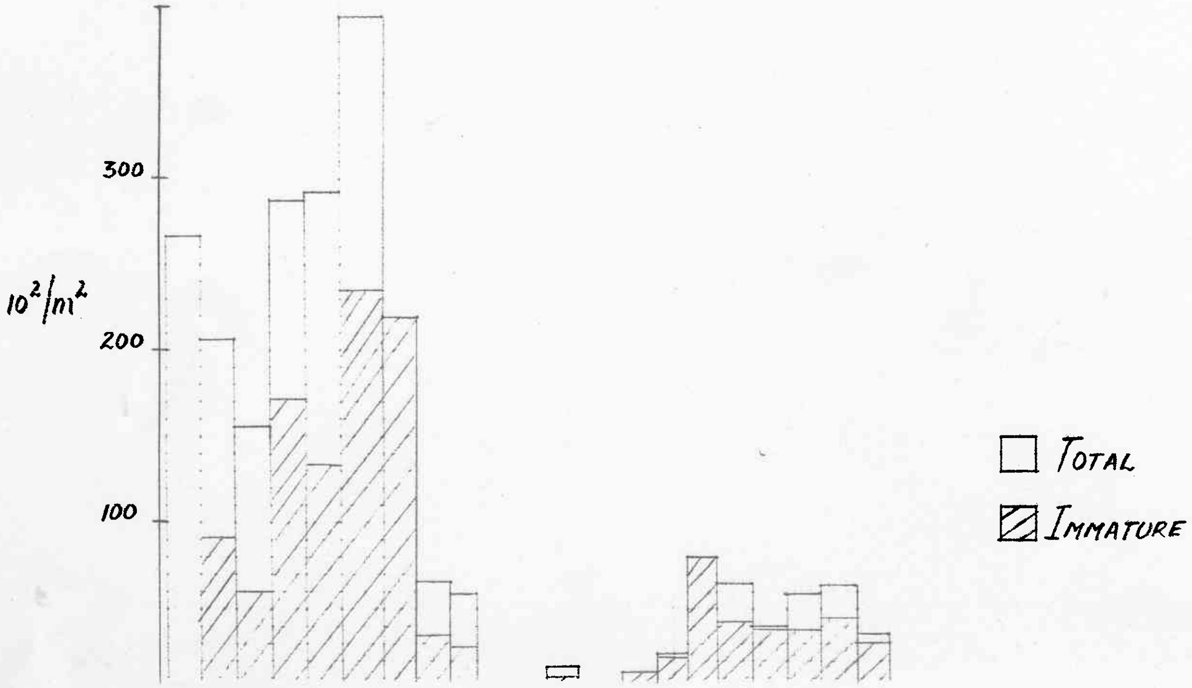
SITE 1



MEAN TOTAL ORIBATIDAE AND THE NUMBER OF JUVENILE ORIBATIDAE.



MEAN TOTAL AND JUVENILE ACARIDAE.



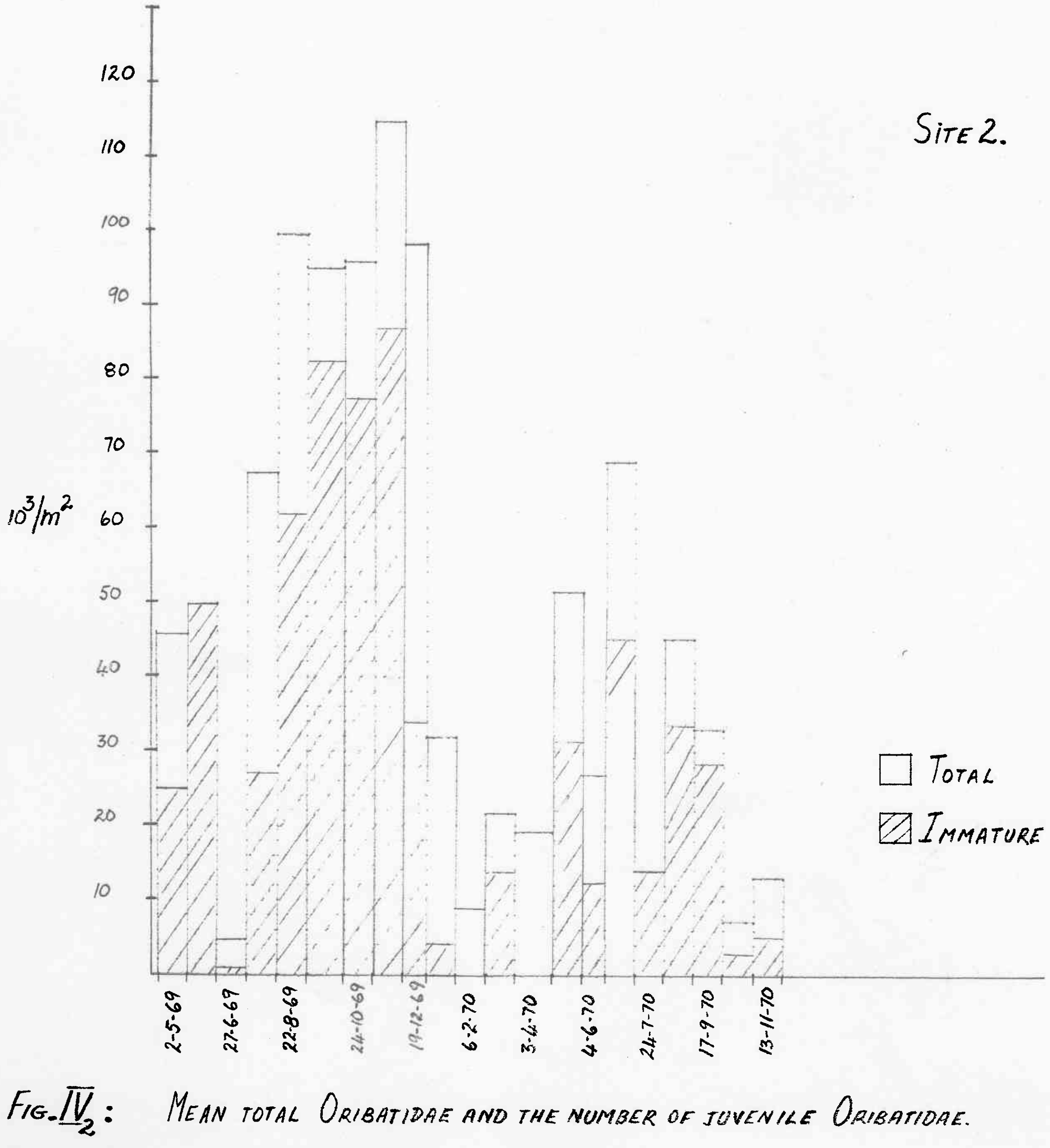
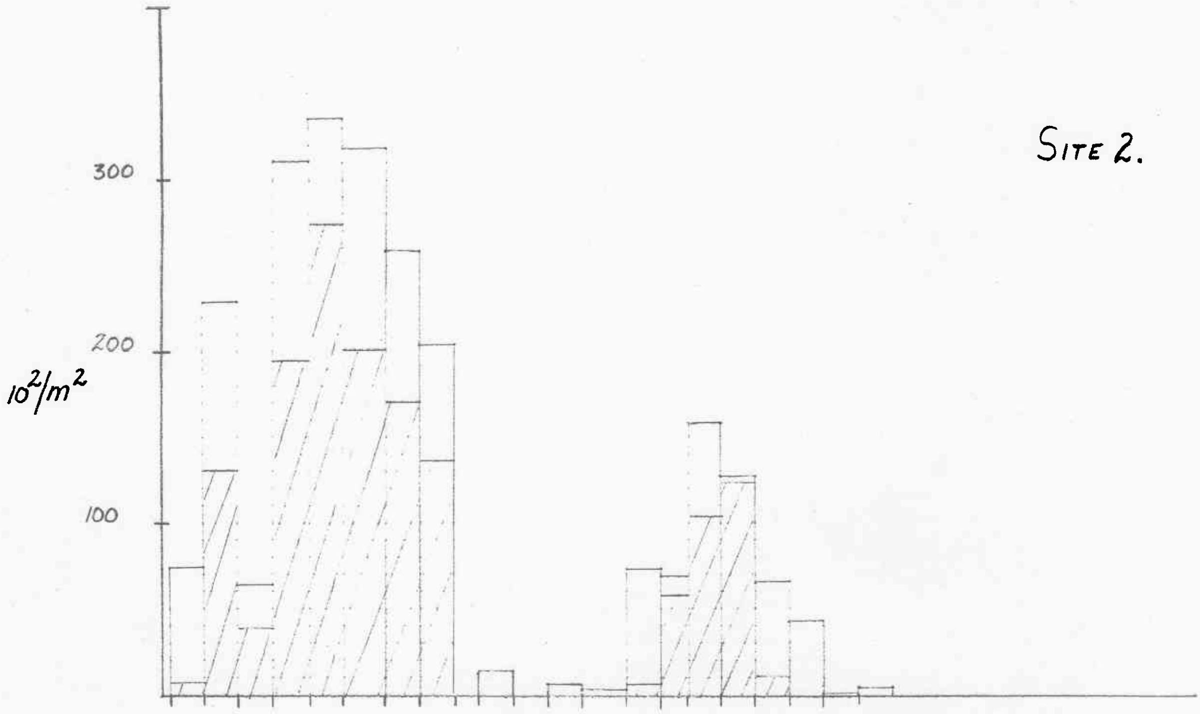
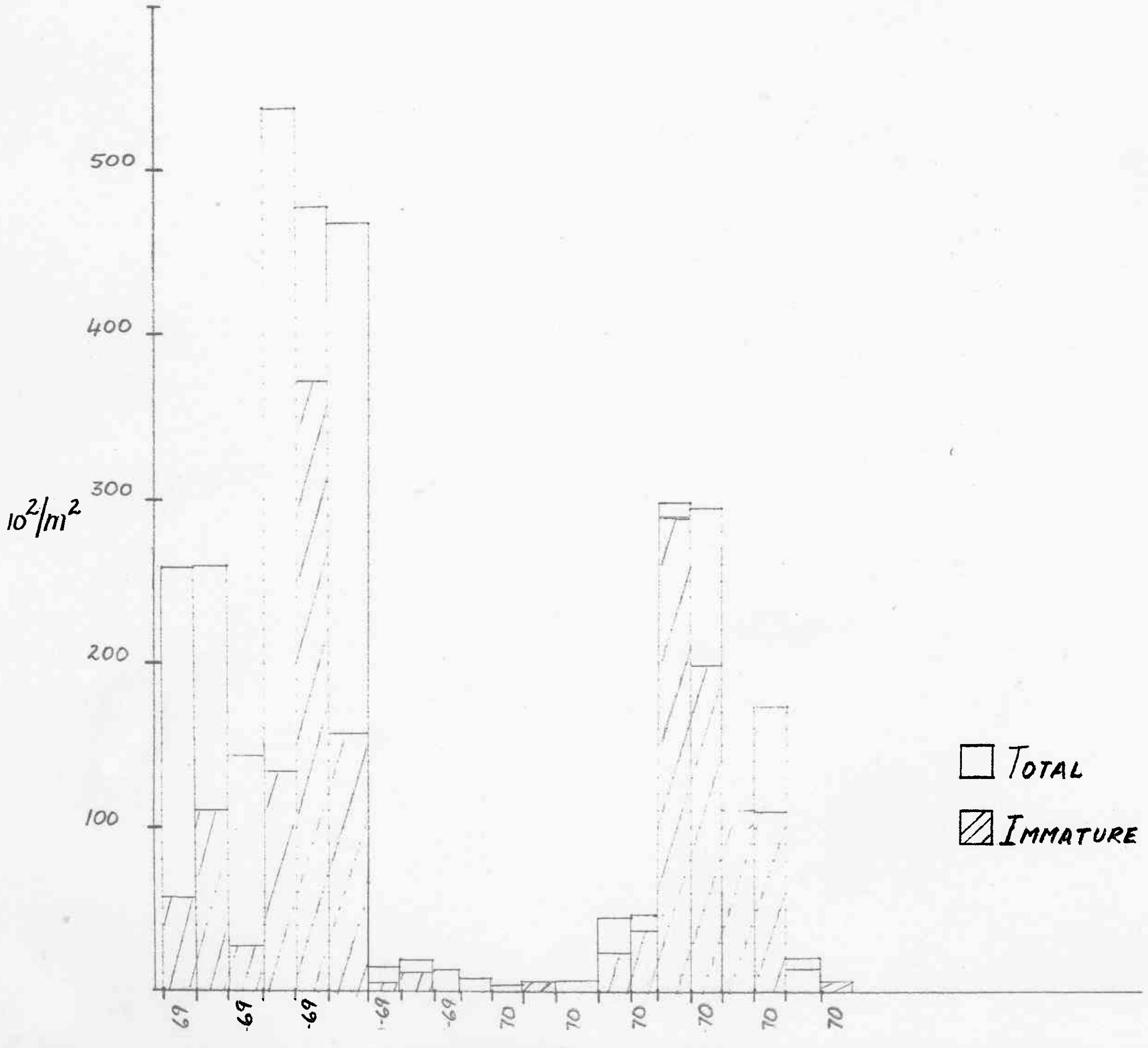
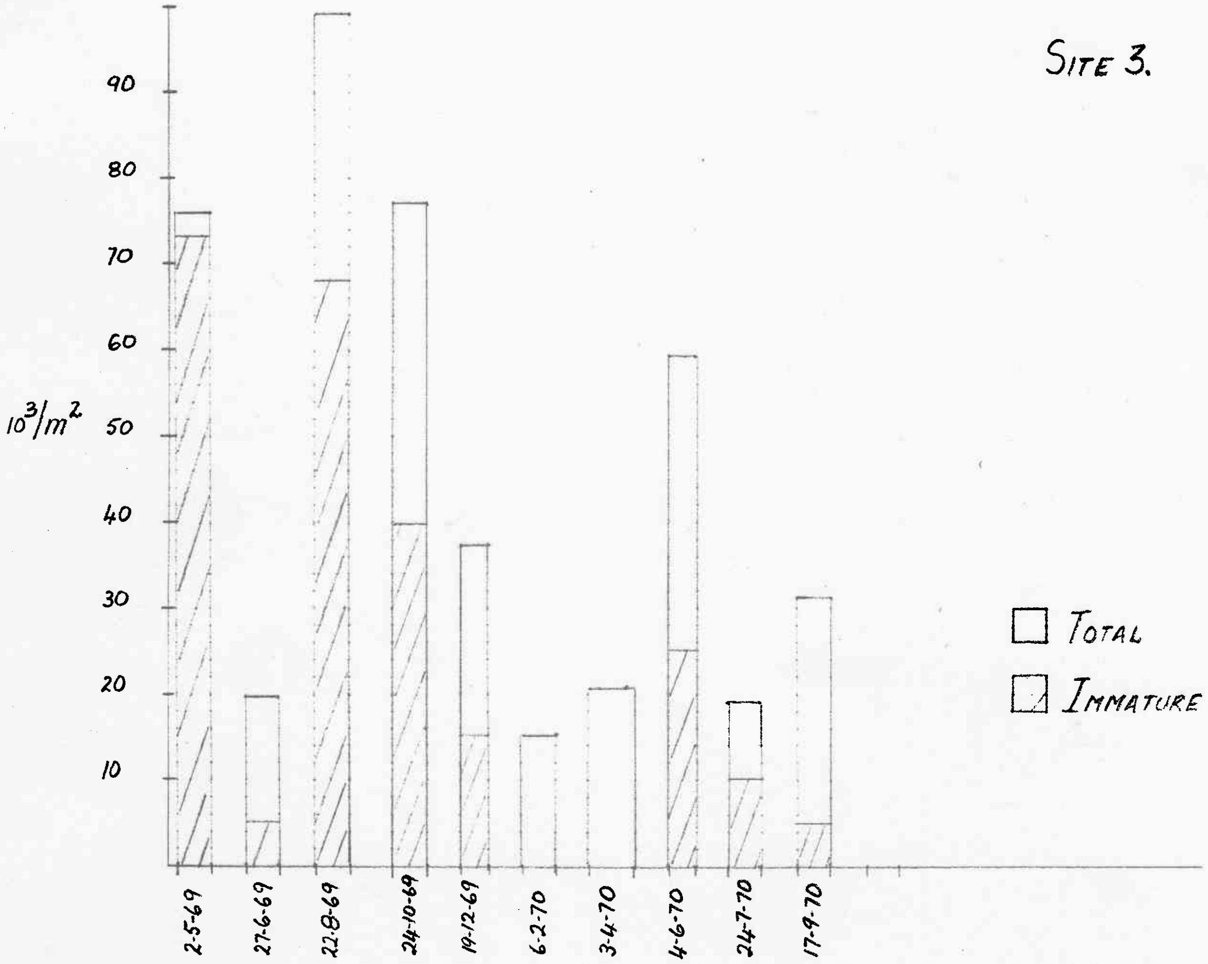


Fig. $\underline{IV}_2$: Mean total Oribatidae and the number of juvenile Oribatidae.

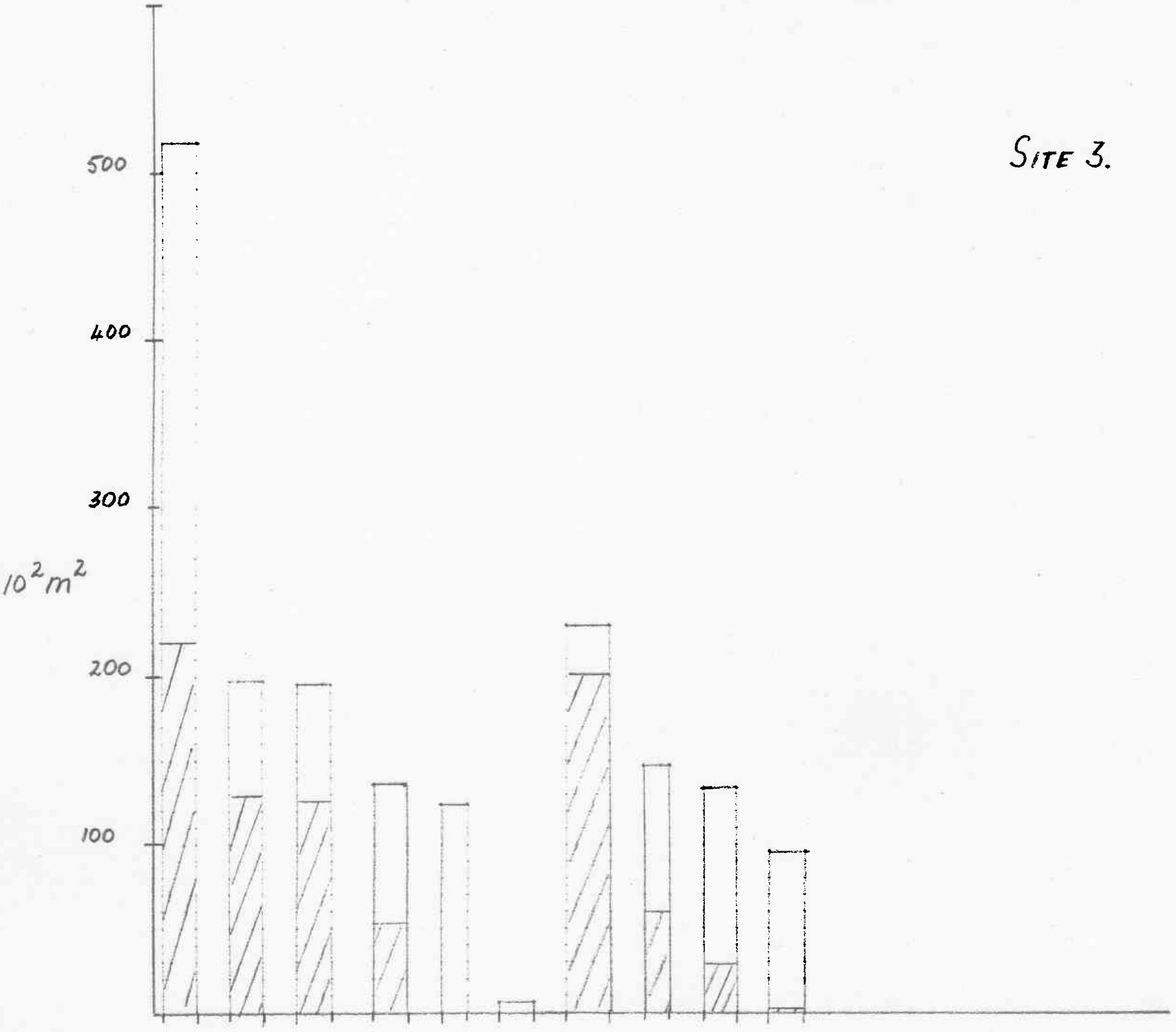


Mean total and juvenile Acaridae.

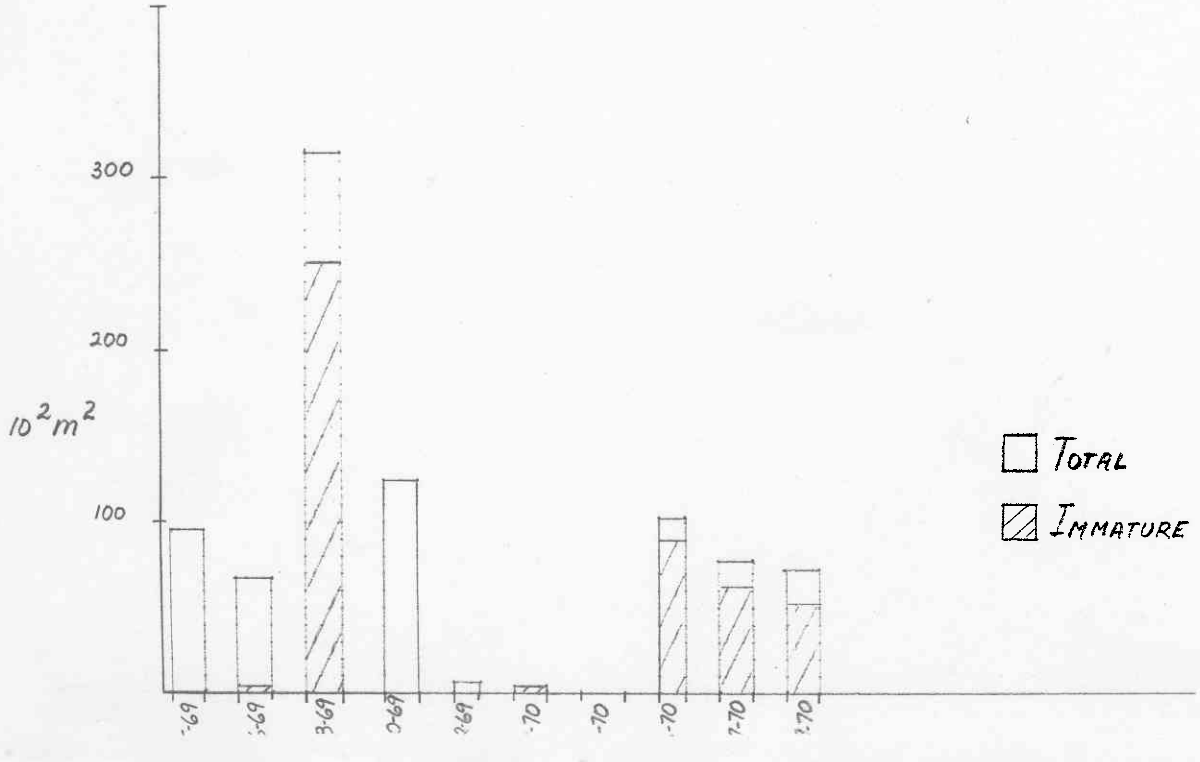



SITE 3.

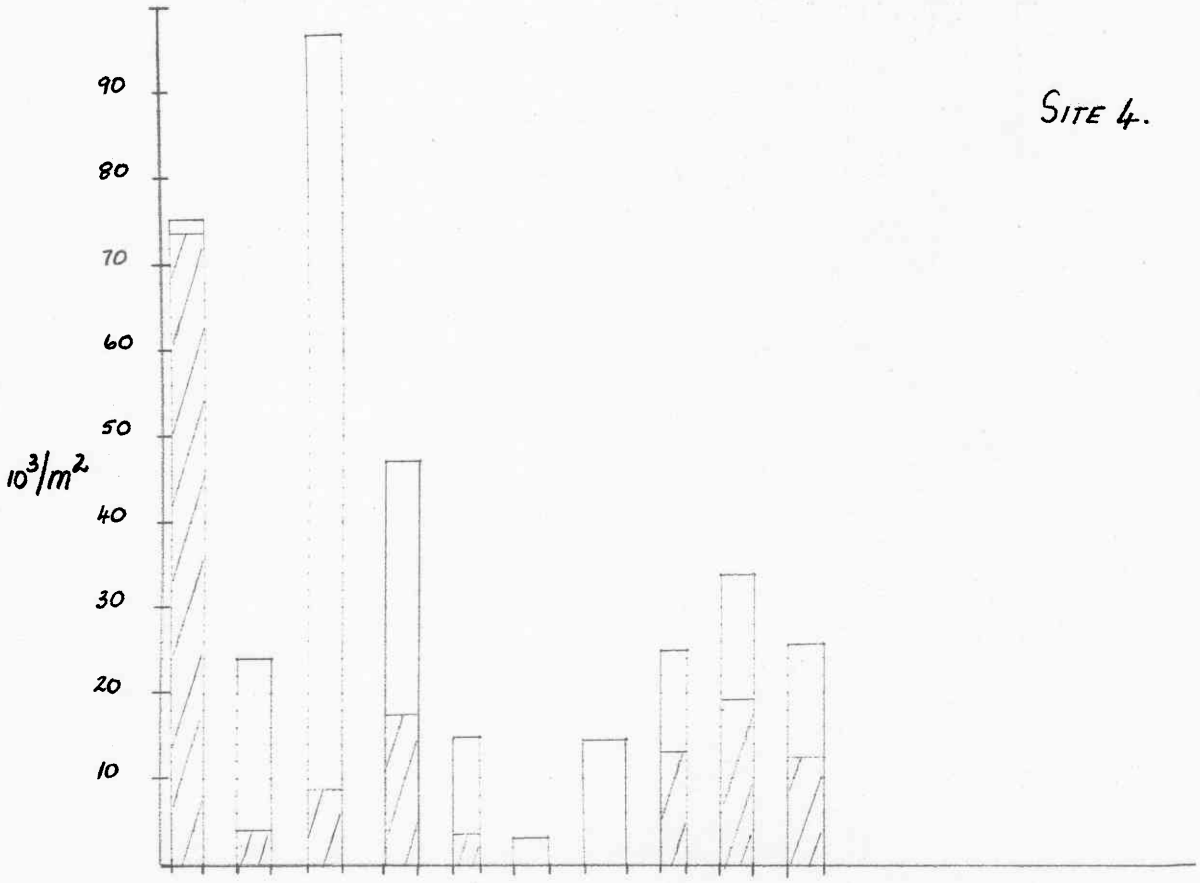
$10^3/m^2$
90
80
70
60
50
40
30
20
10
2-5-69
27-6-69
22-8-69
24-10-69
19-12-69
6-2-70
3-4-70
4-6-70
24-7-70
17-9-70
☐ TOTAL
▨ IMMATURE



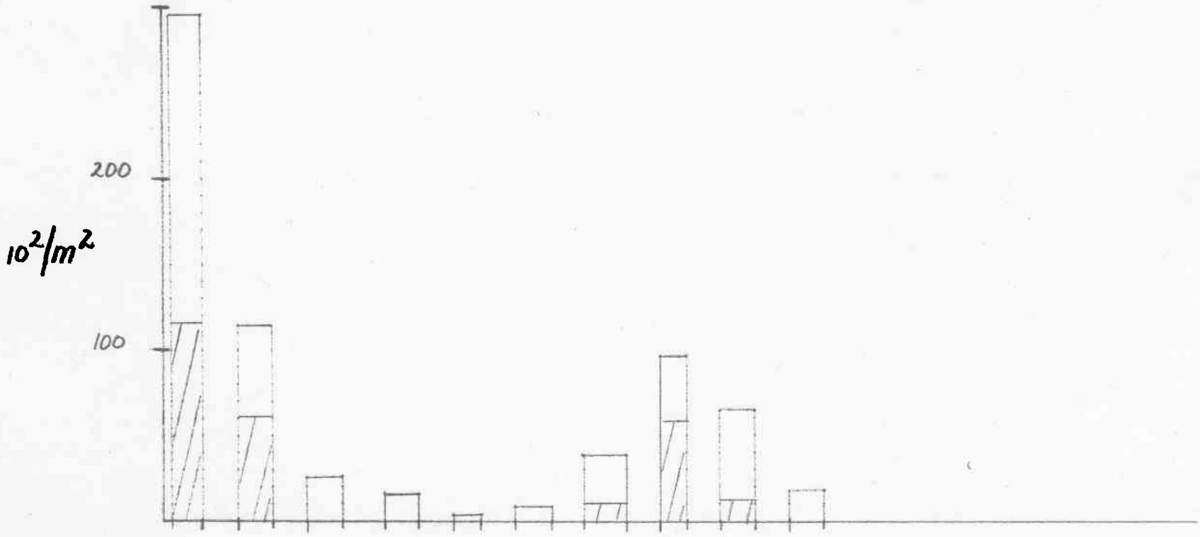
Mean total and juvenile Acaridae.



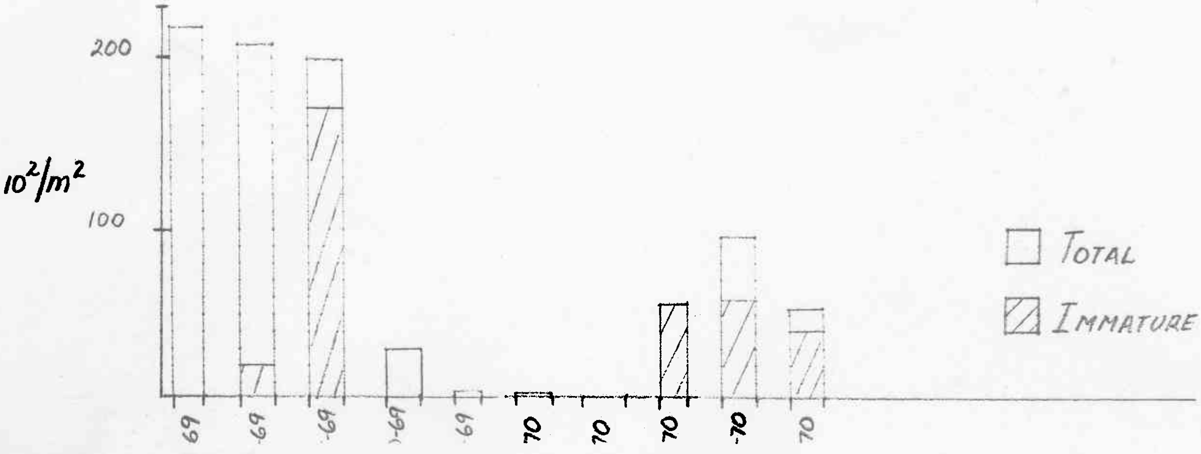
Site 4.



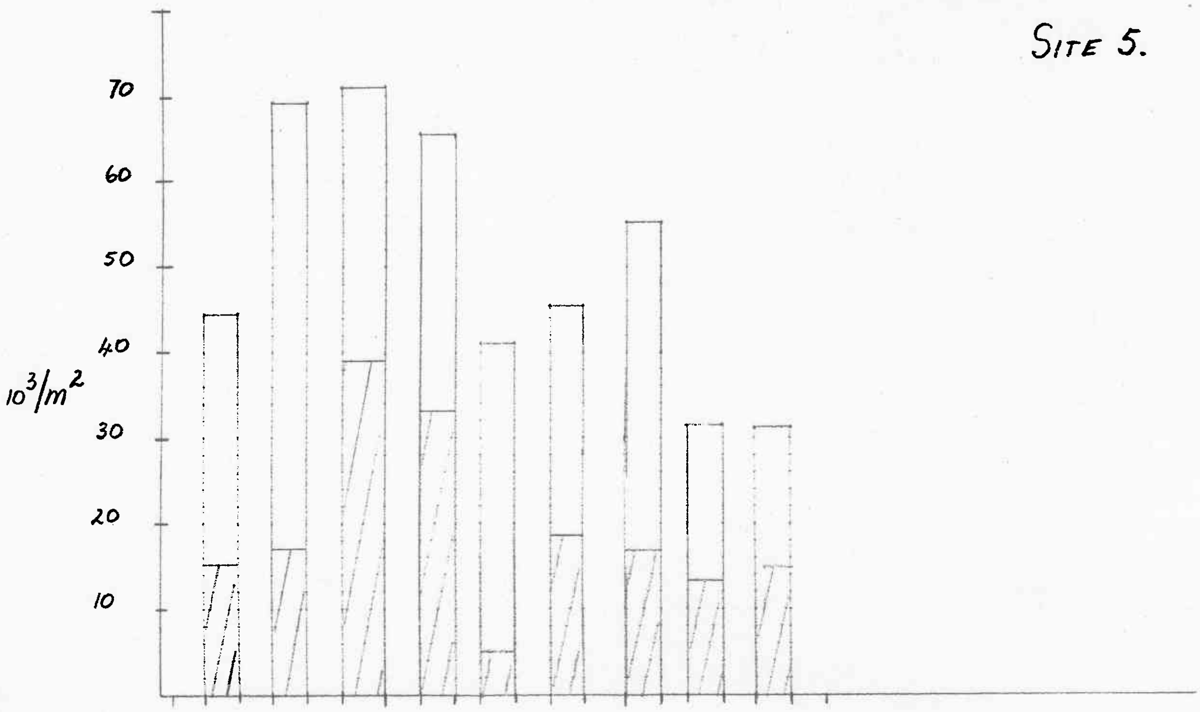
Mean total Oribatidae and the number of juvenile Oribatidae.



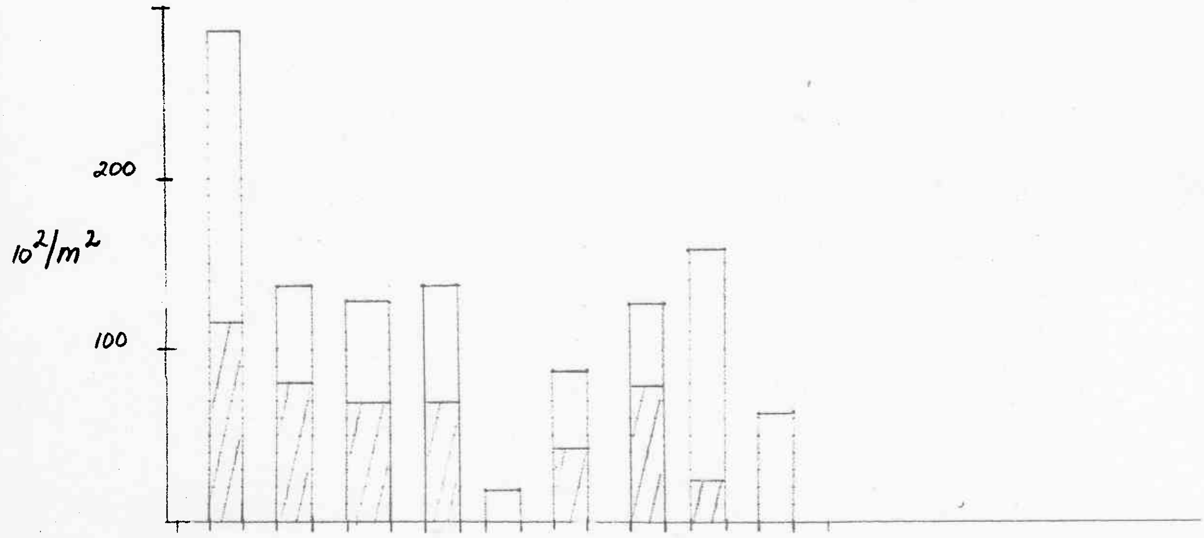
Mean total and juvenile Acaridae.



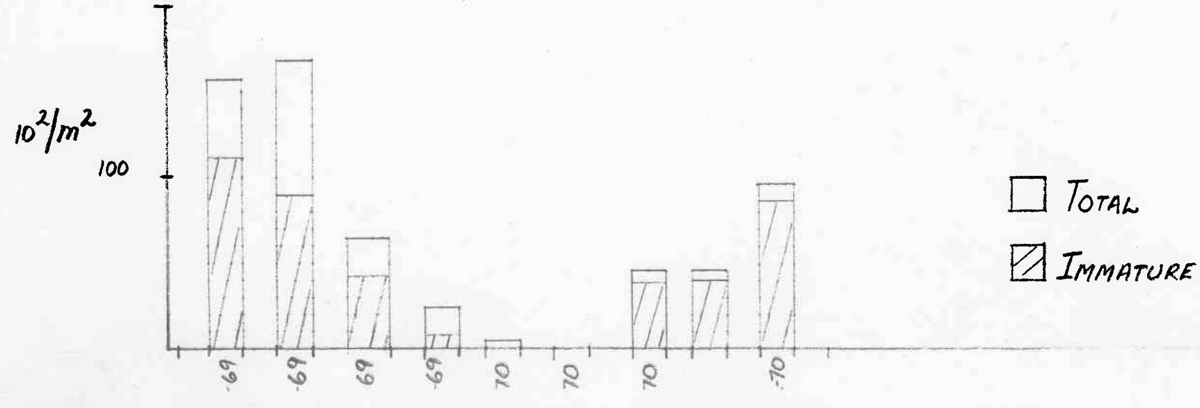
SITE 5.



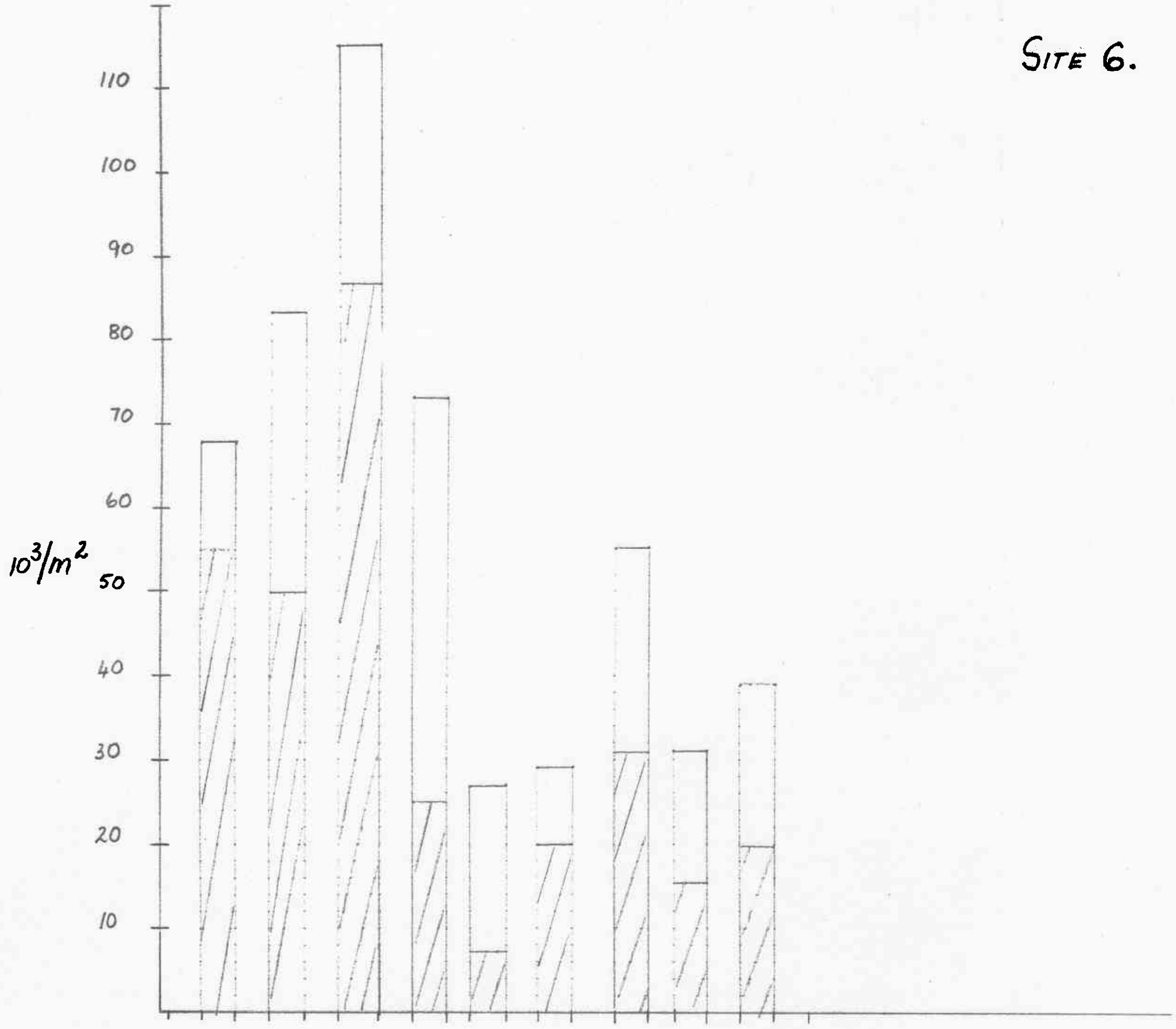
MEAN TOTAL ORIBATIDAE AND THE NUMBER OF JUVENILE ORIBATIDAE.



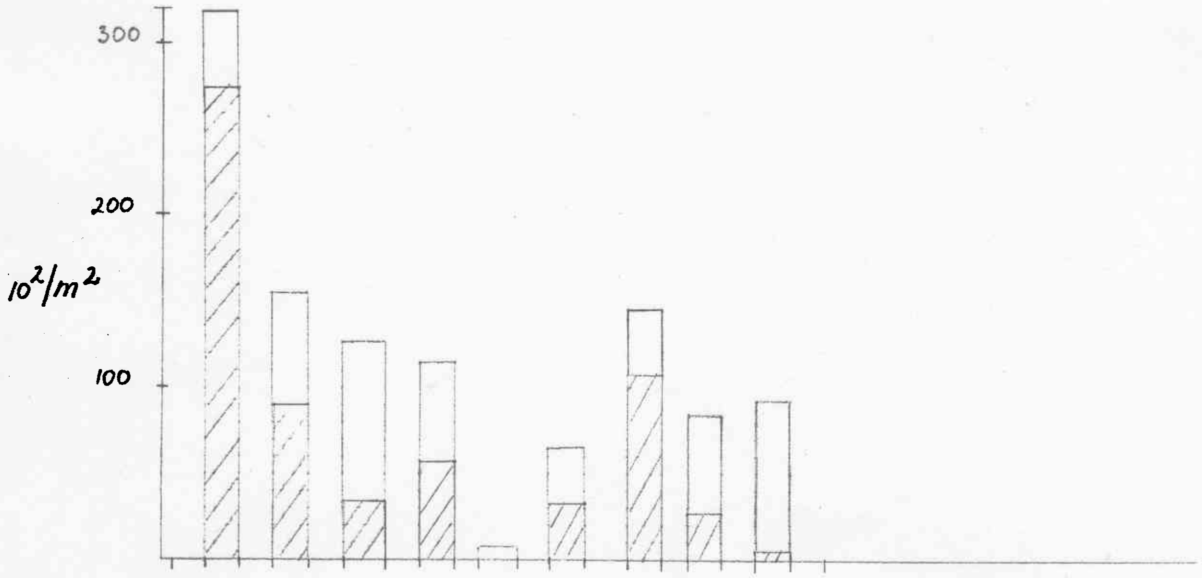
MEAN TOTAL AND JUVENILE ACARINA.



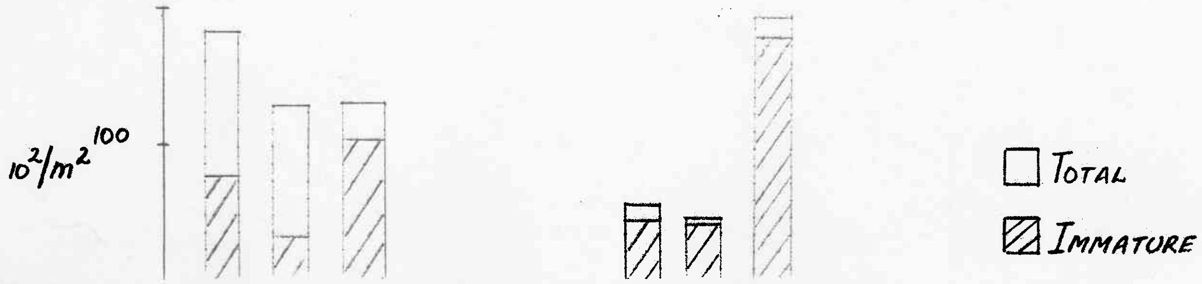
Site 6.



Mean total Oribatidae and the number of juvenile Oribatidae.



Mean total and juvenile Acarina.



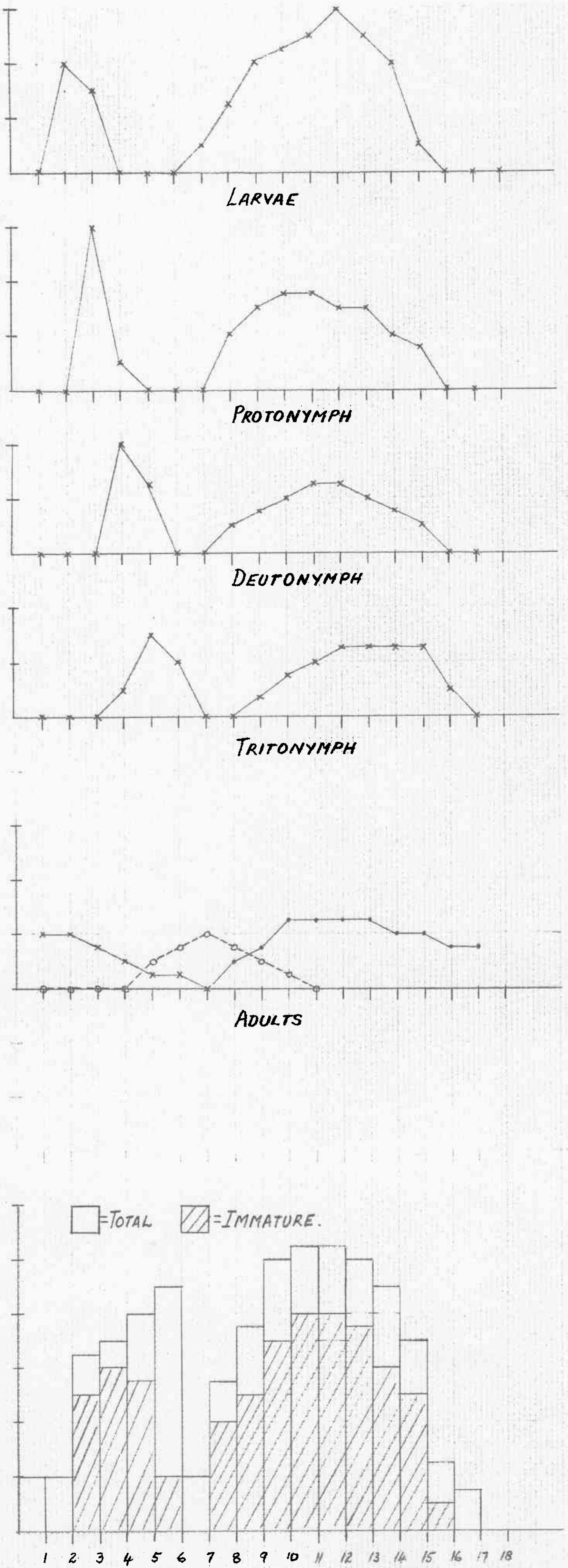


FIG. IV 7 THEORETICAL CURVES FOR ORIBATIDAE LIFE CYCLES.

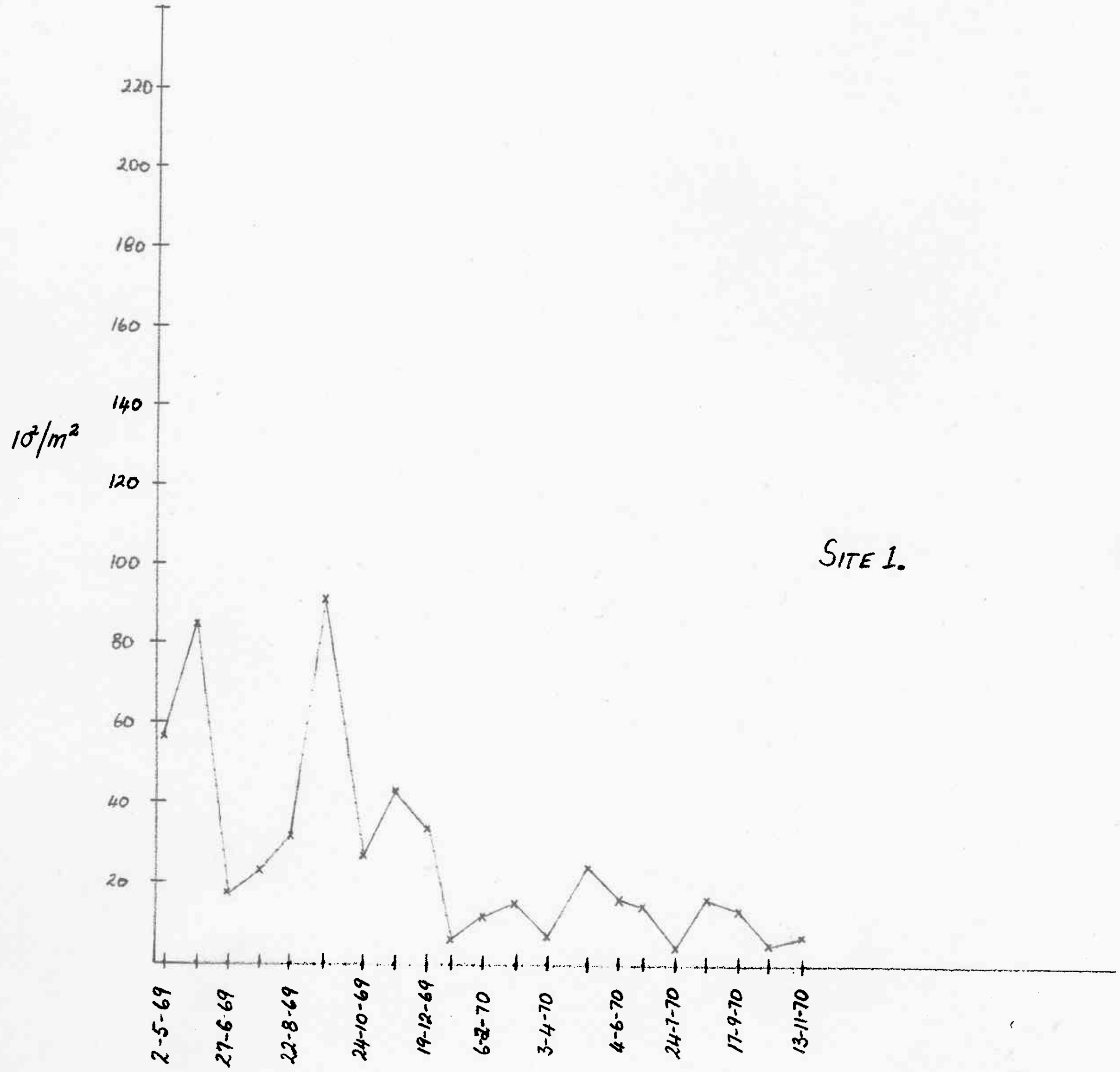


Fig. V₁ : Mean population of adult Mesostigmata (Acarina).

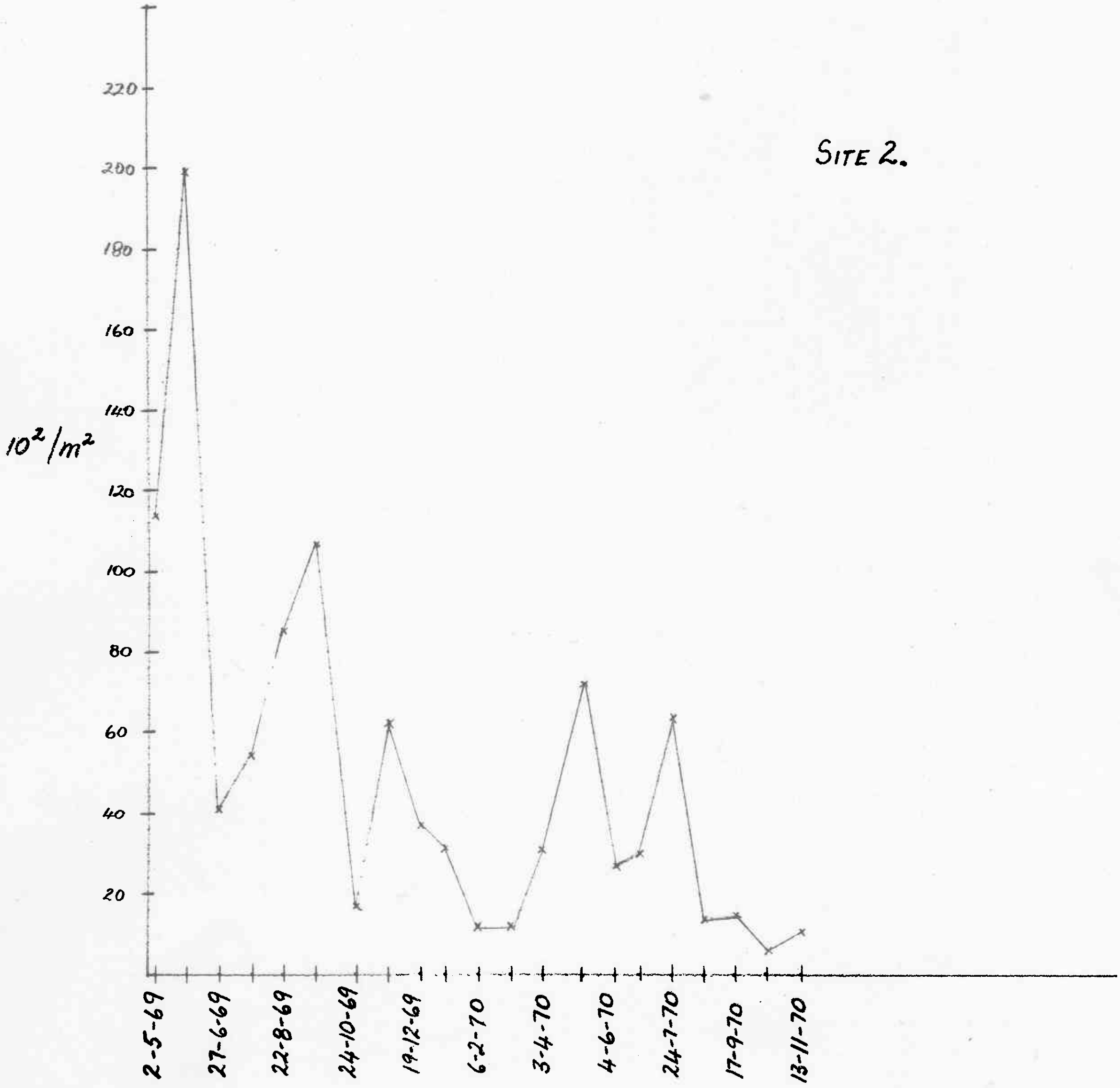


Fig. V₂: Mean population of adult Mesostigmata (Acarina).

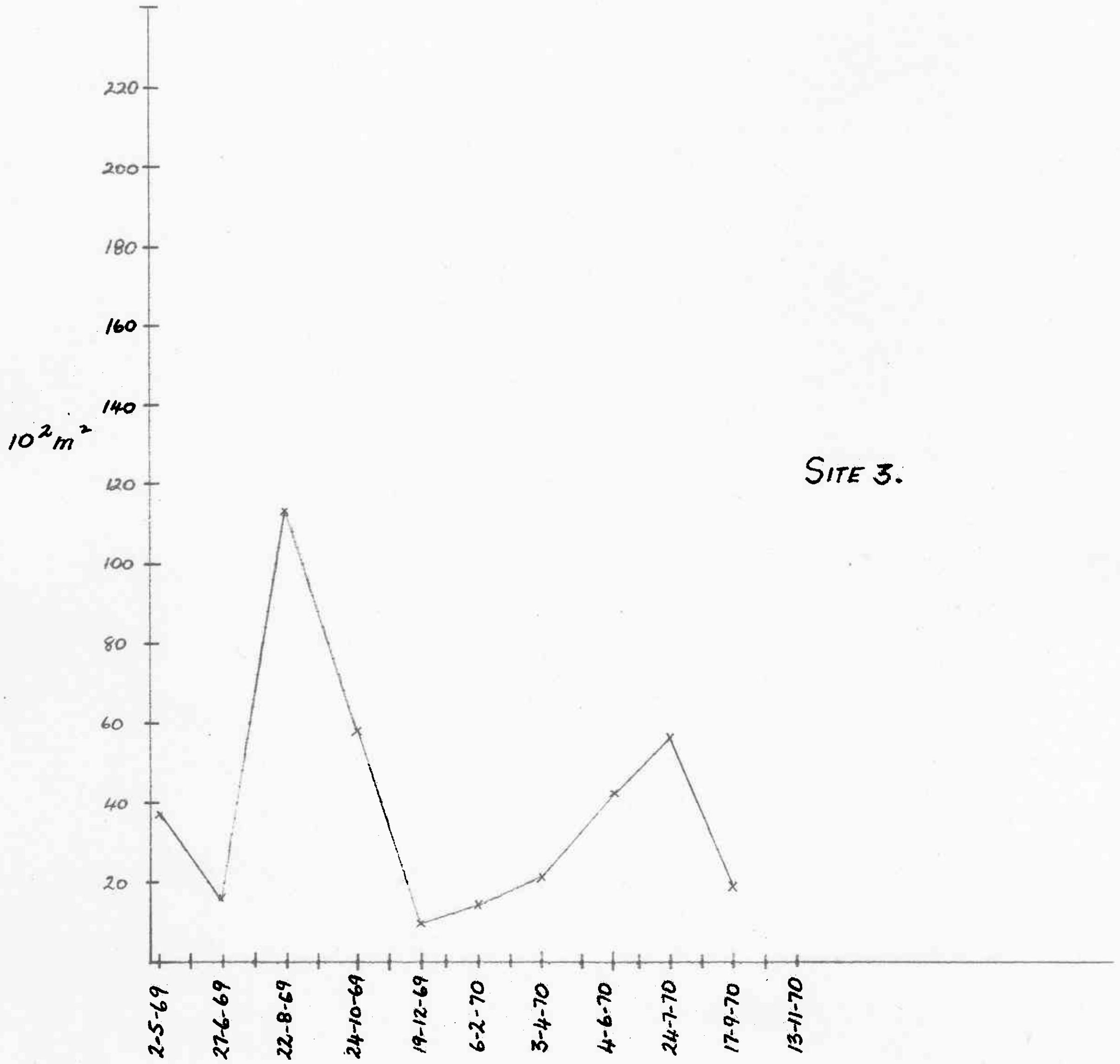


FIG. V_3 : MEAN POPULATION OF ADULT MESOSTIGMATA (ACARINA).

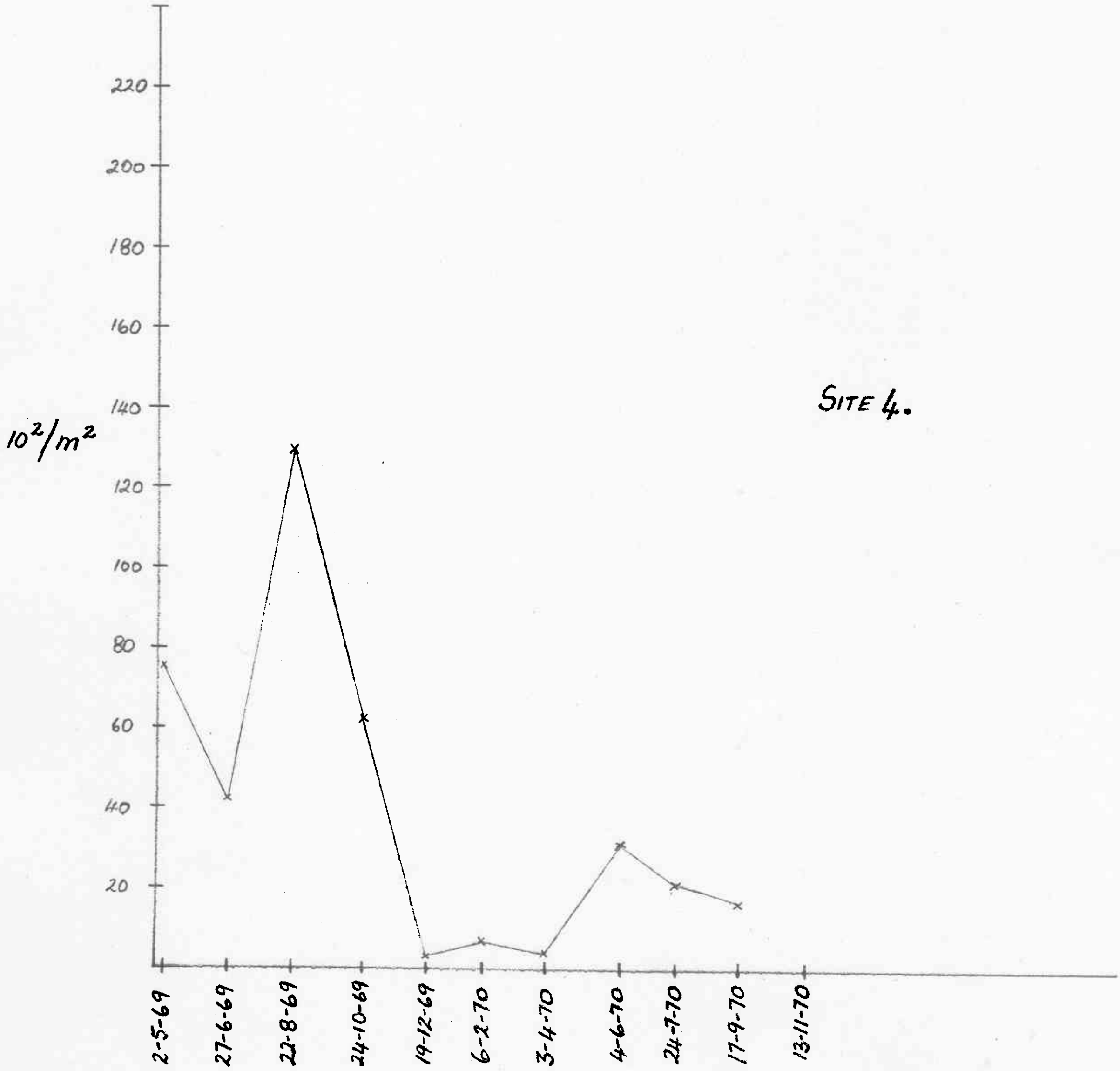


Fig. V_4: Mean population of adult Mesostigmata (Acarina).

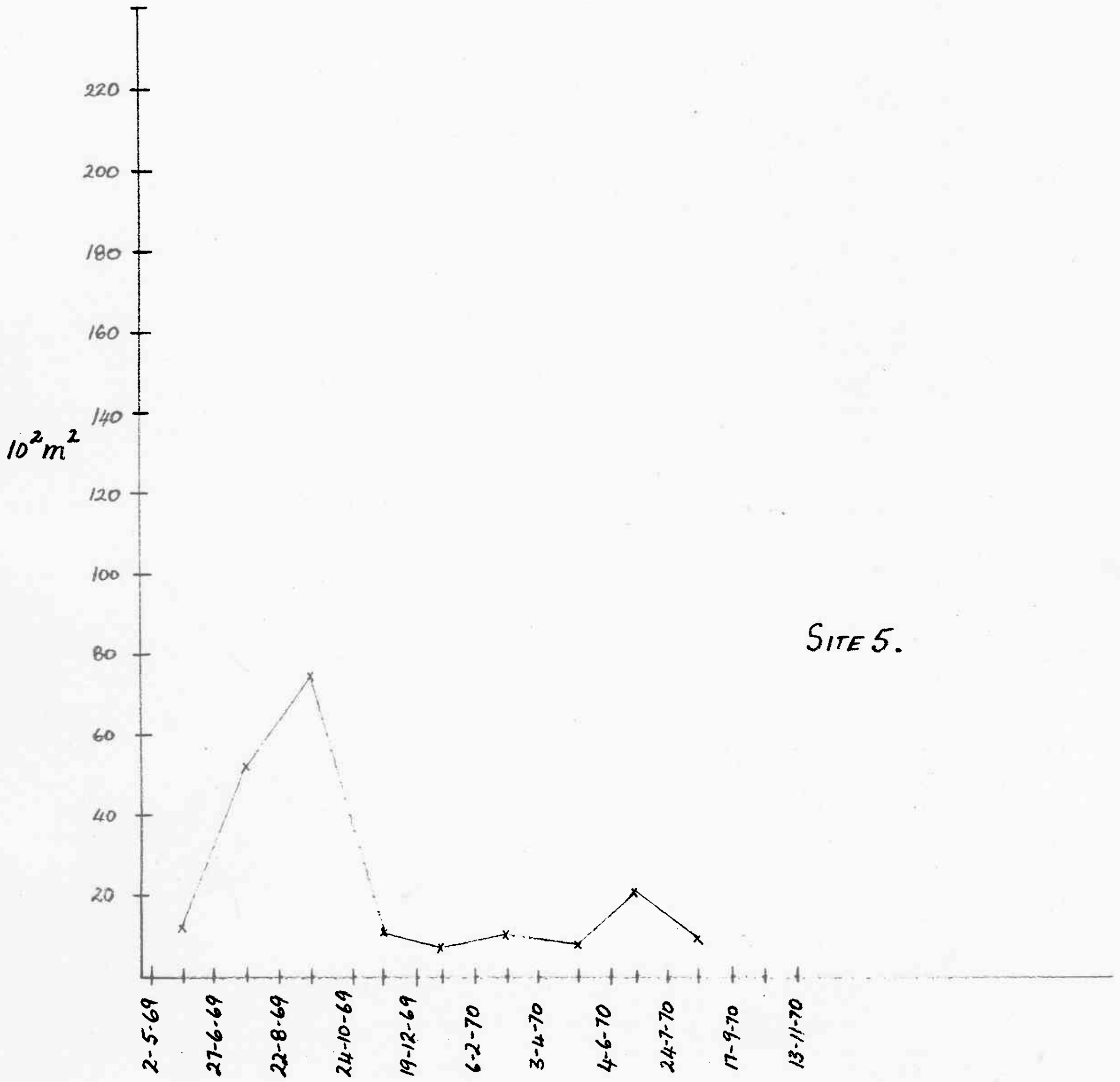


FIG. $\underline{V}_5$: MEAN POPULATION OF ADULT MESOSTIGMATA (ACARINA).

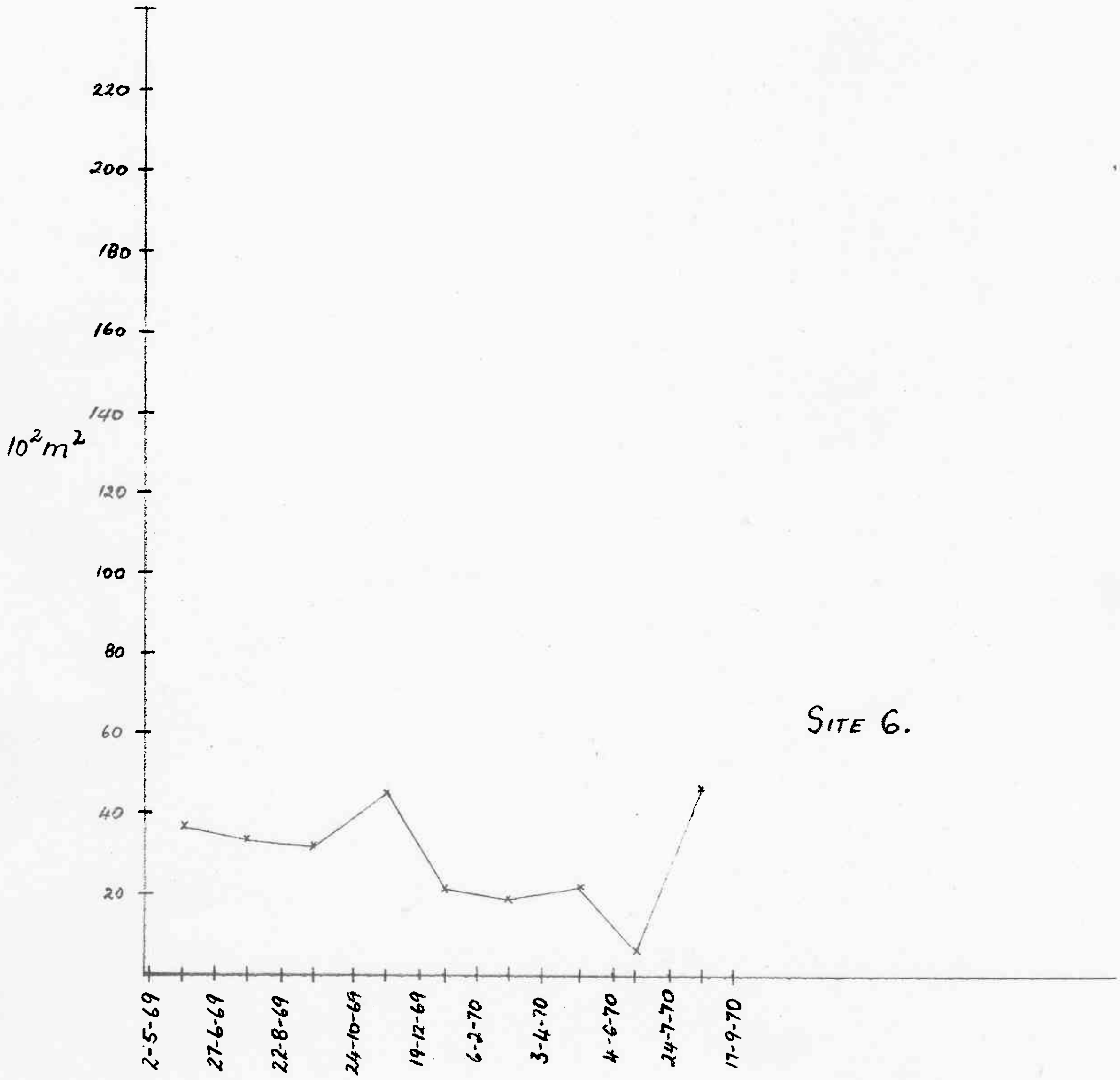


FIG. V_6: MEAN POPULATION OF ADULT MESOSTIGMATA (ACARINA).

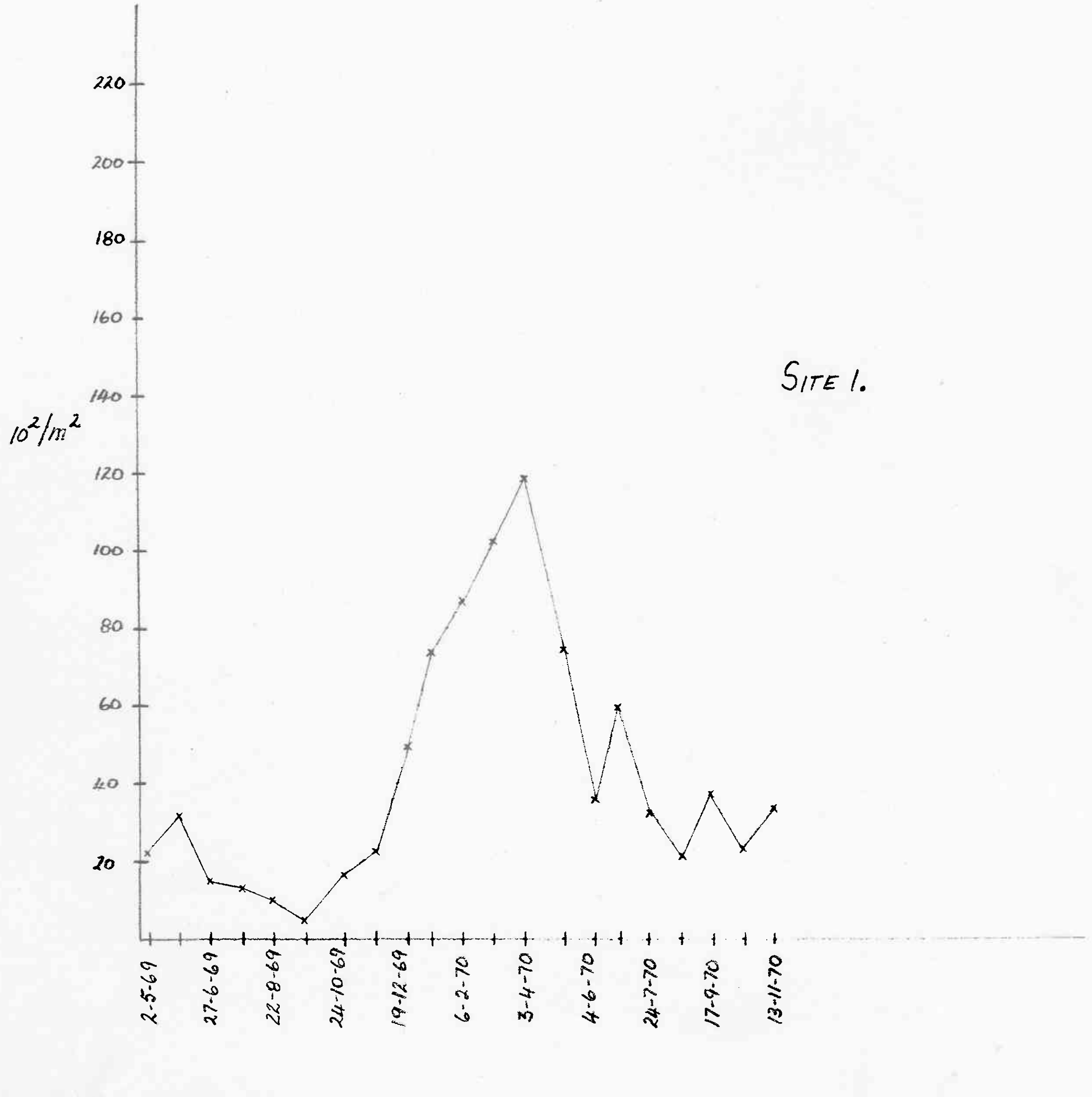


Fig. $\overline{\underline{VI}}_1$: Mean population of adult Tuckerellidae (Acarina).

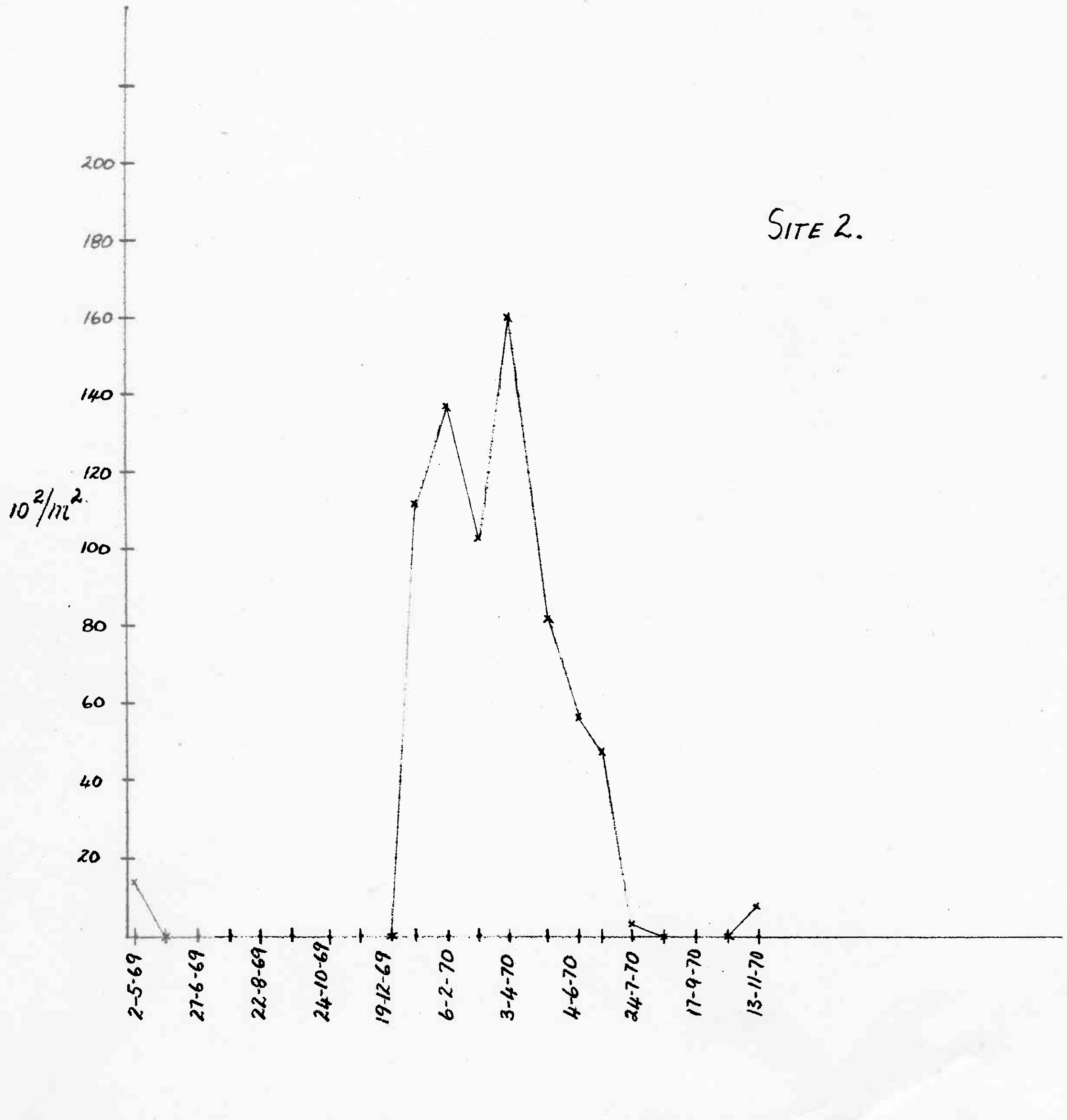


Fig. VI₂: Mean population of adult Tuckerellidae (Acarina).

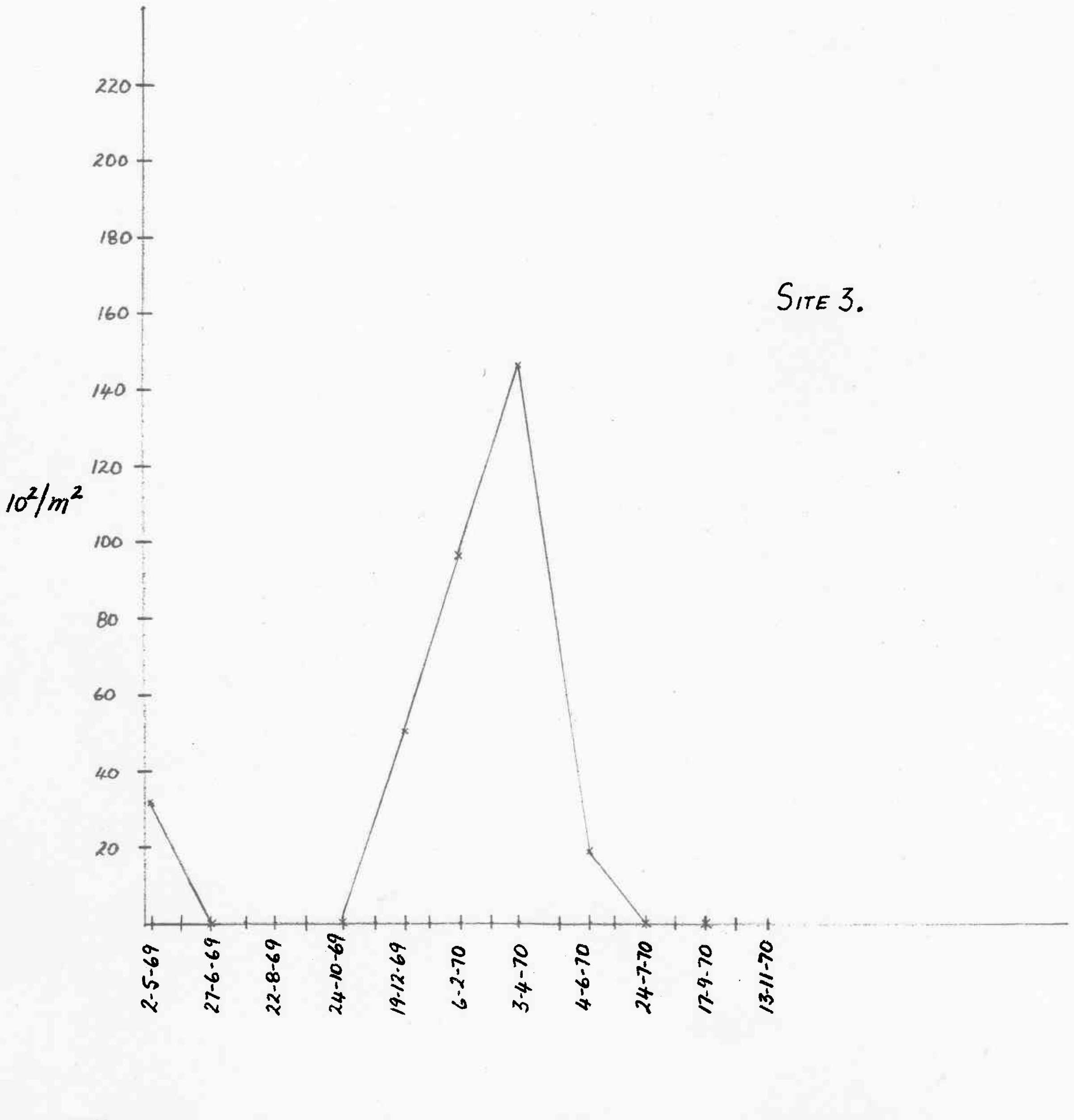


Fig. VI_3: Mean population of adult Tuckerellidae (Acarina).

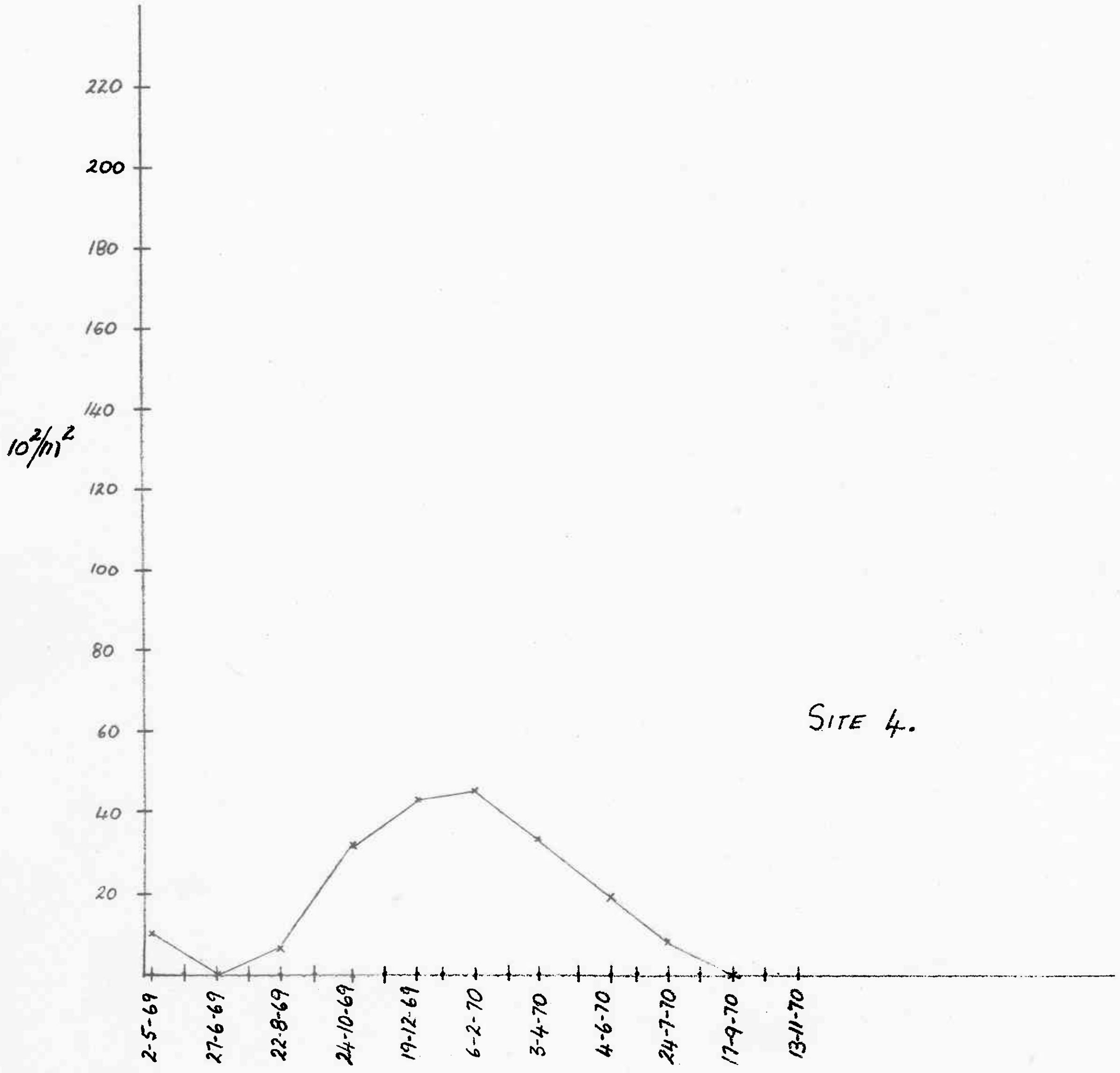
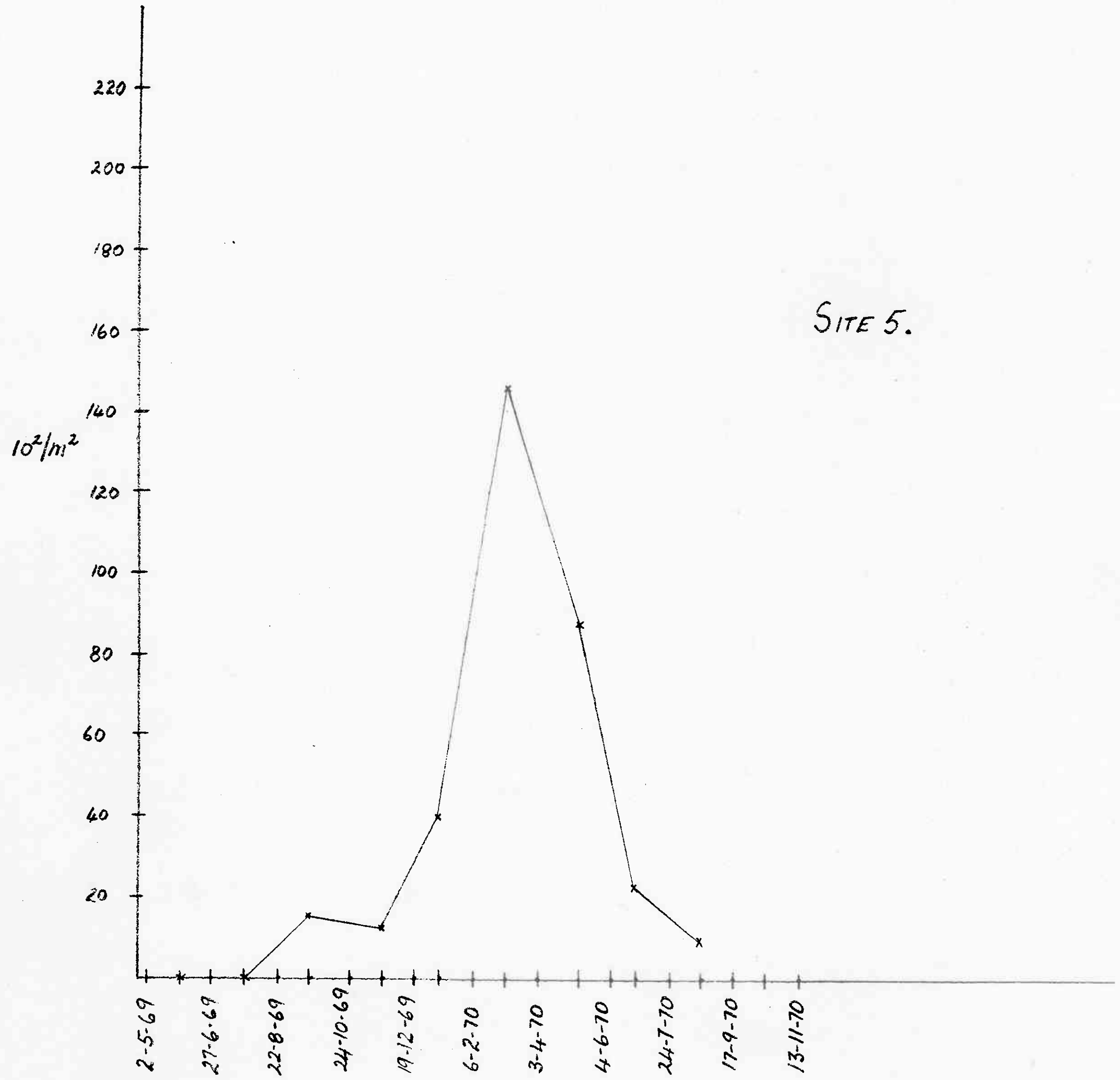


Fig. VI_4: Mean population of adult Tuckerellidae (Acarina).



SITE 5.

FIG. $\underline{VI}_5$: MEAN POPULATION OF ADULT TUCKERELLIDAE (ACARINA).

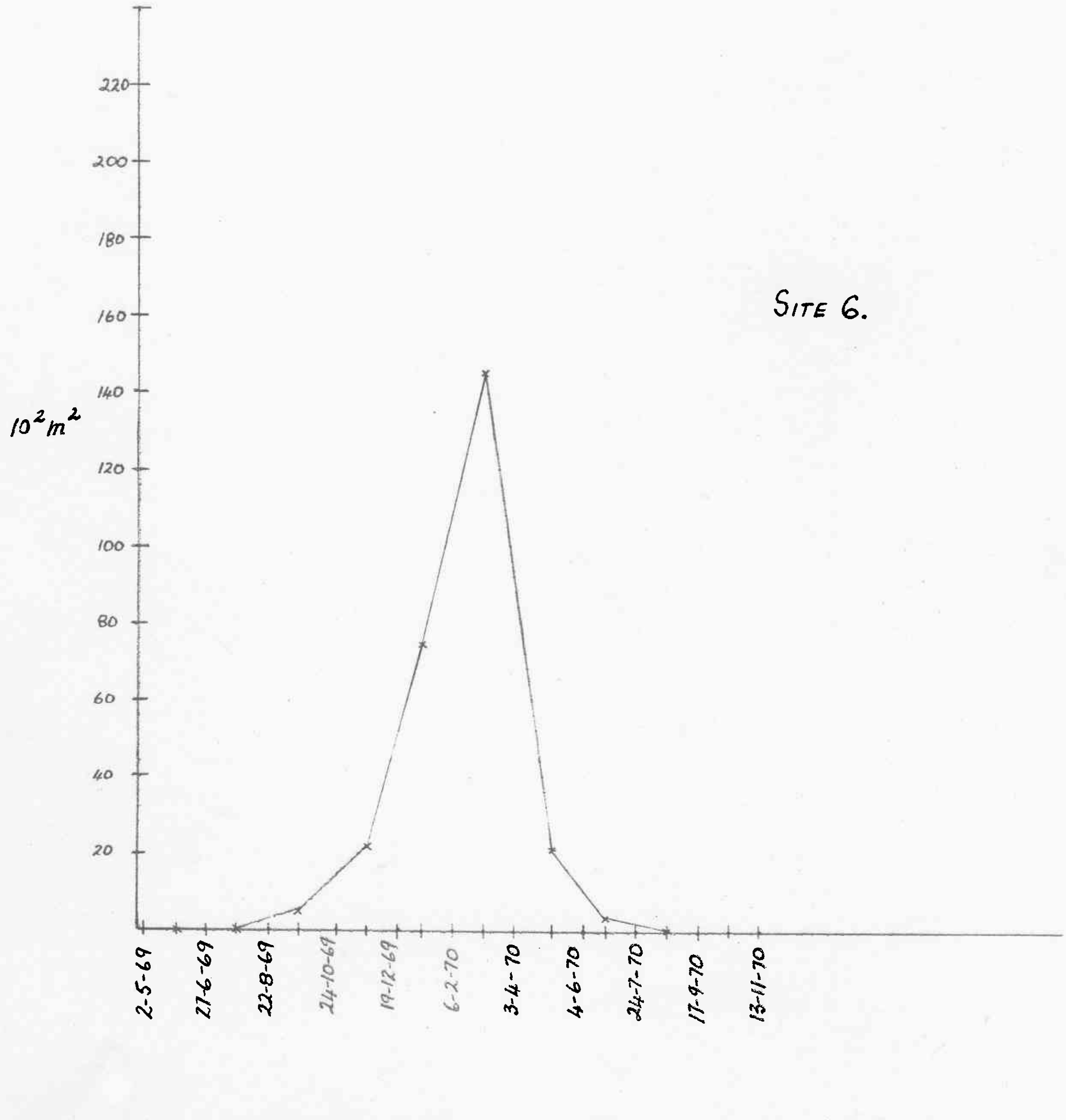


Fig. VI₆ : Mean population of adult Tuckerellidae (Acarina).

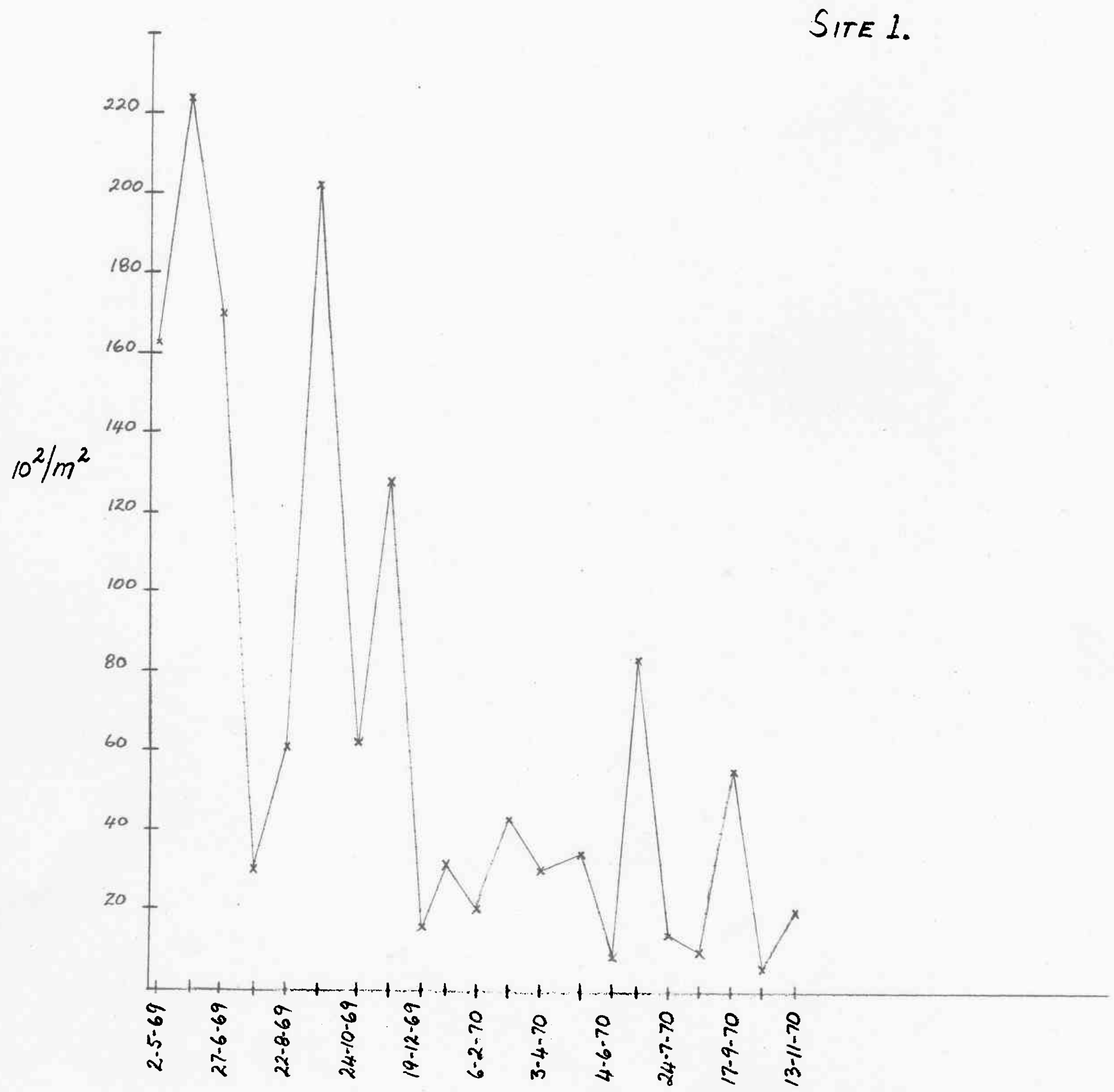
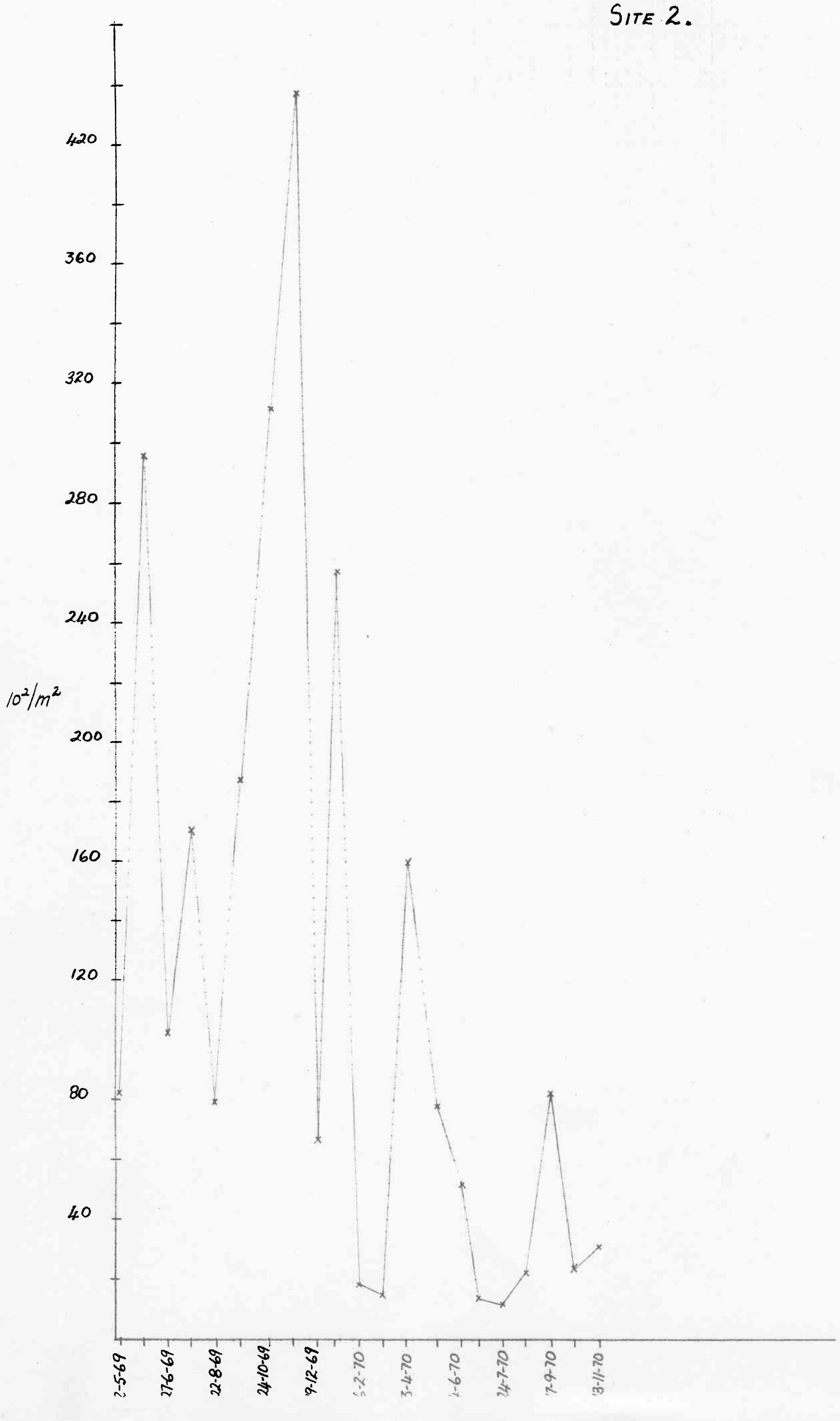


Fig. VII$_1$: Mean population of unidentified Acarina including small trombidiforms and young stadia.

SITE 2.


420
360
320
280
240
200
160
120
80
40
10²/m²
2-5-69
27-6-69
22-8-69
24-10-69
9-12-69
-2-70
3-4-70
-6-70
24-7-70
7-9-70
3-11-70

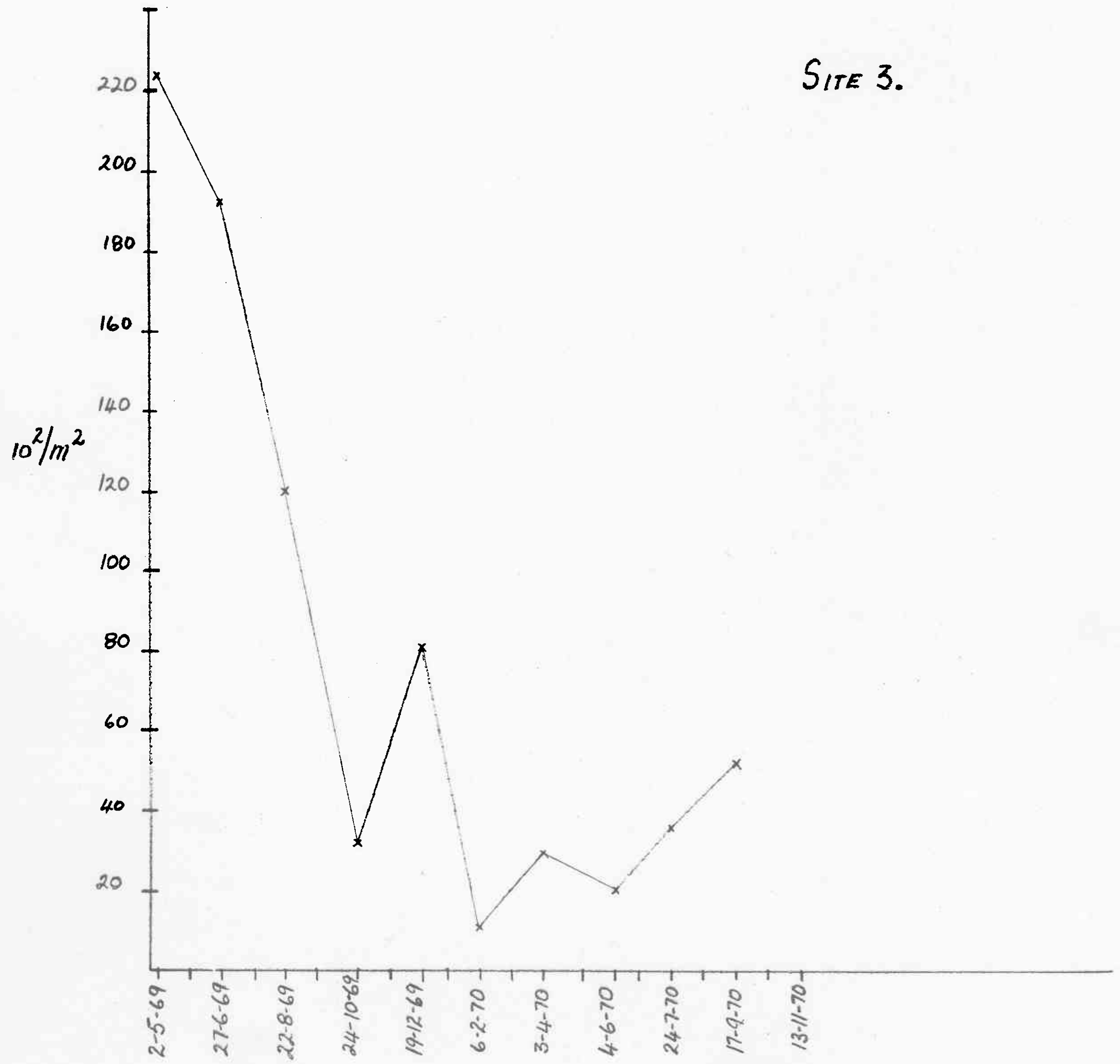


Fig. $\overline{VII}_3$: Mean population of unidentified Acarina including small trombidiforms and young stadia.

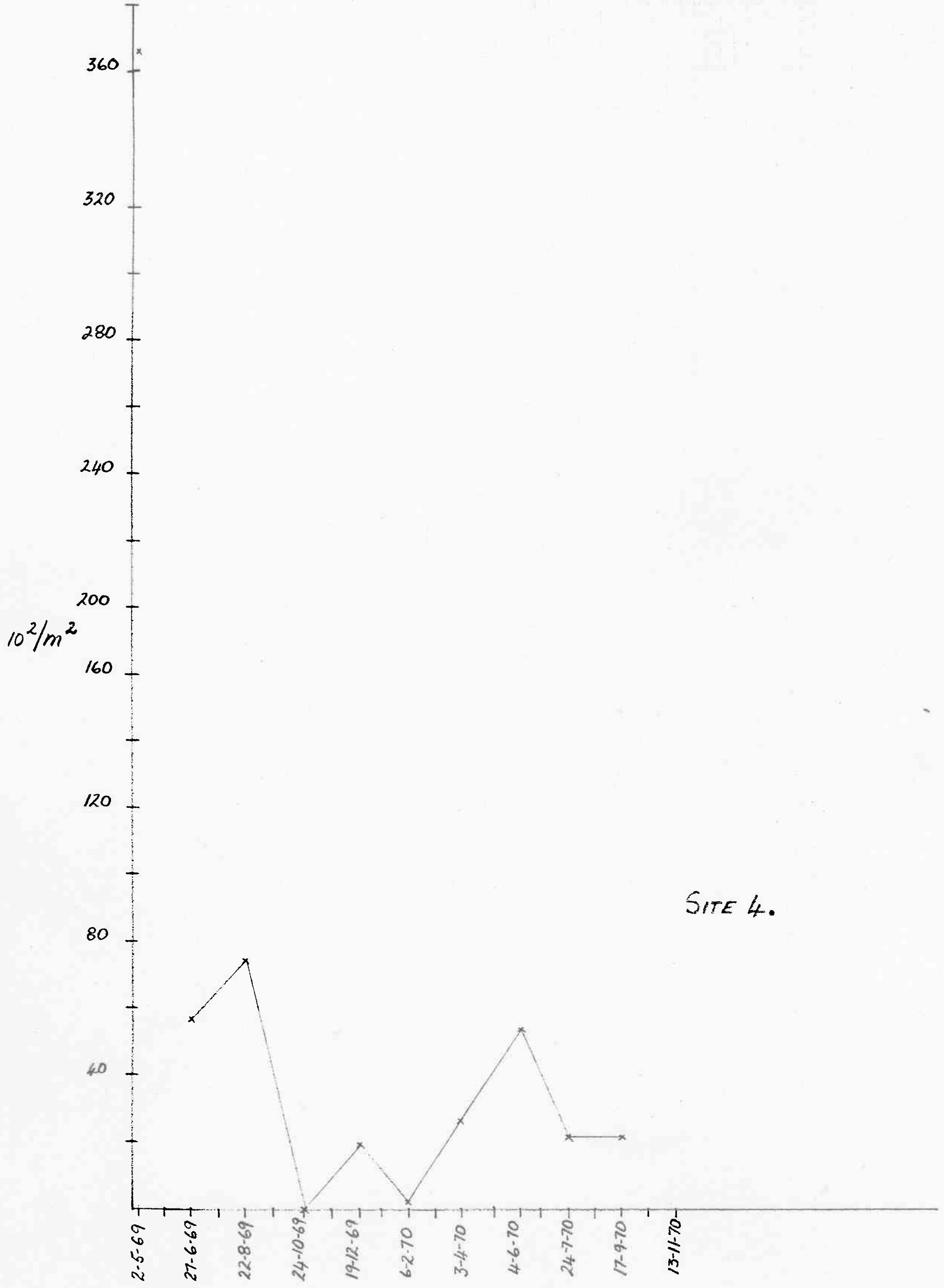


Fig. VII_4: Mean population of unidentified Acarina including small trombidiforms and young stadia.

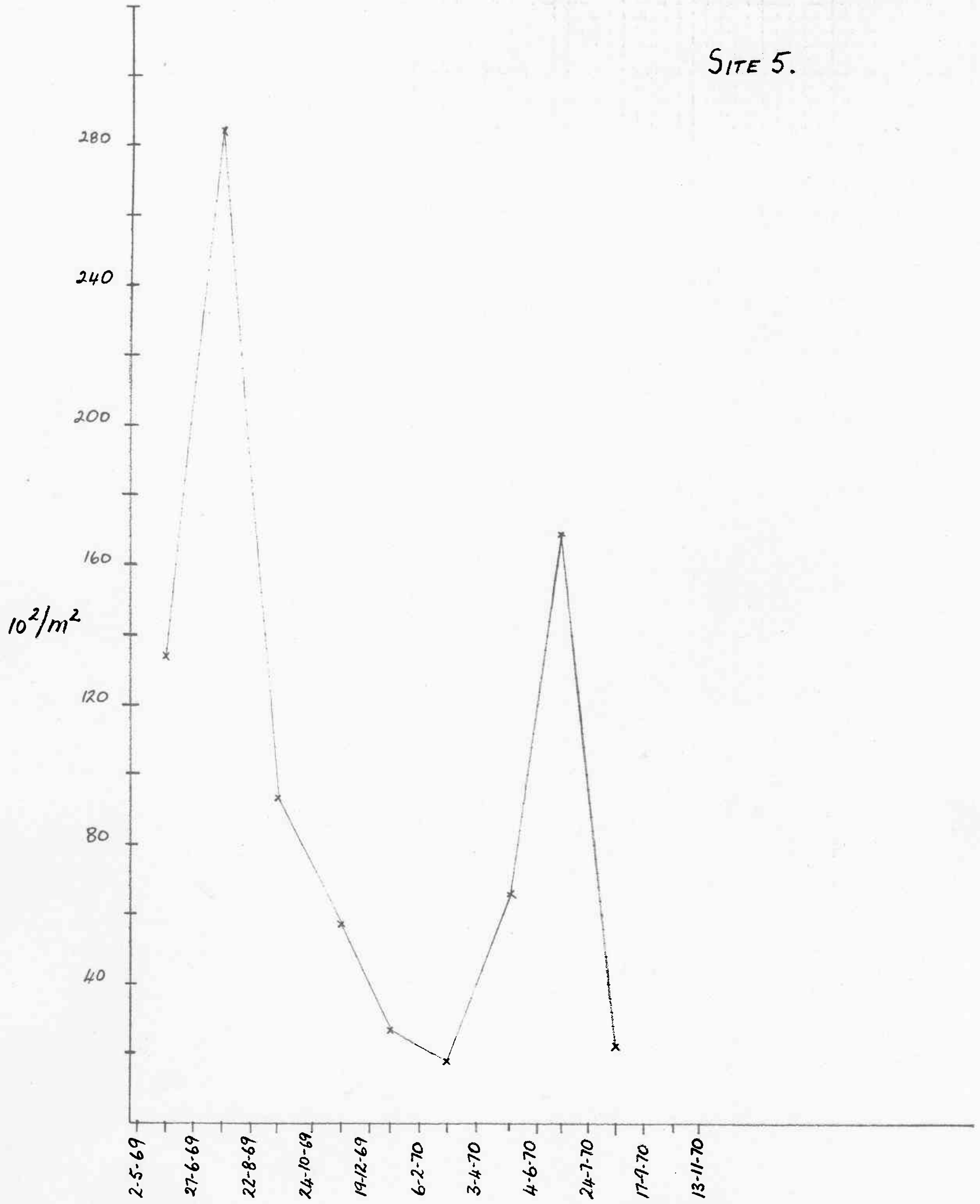


Fig. VII$_5$: Mean population of unidentified Acarina including small trombidiforms and young stadia.

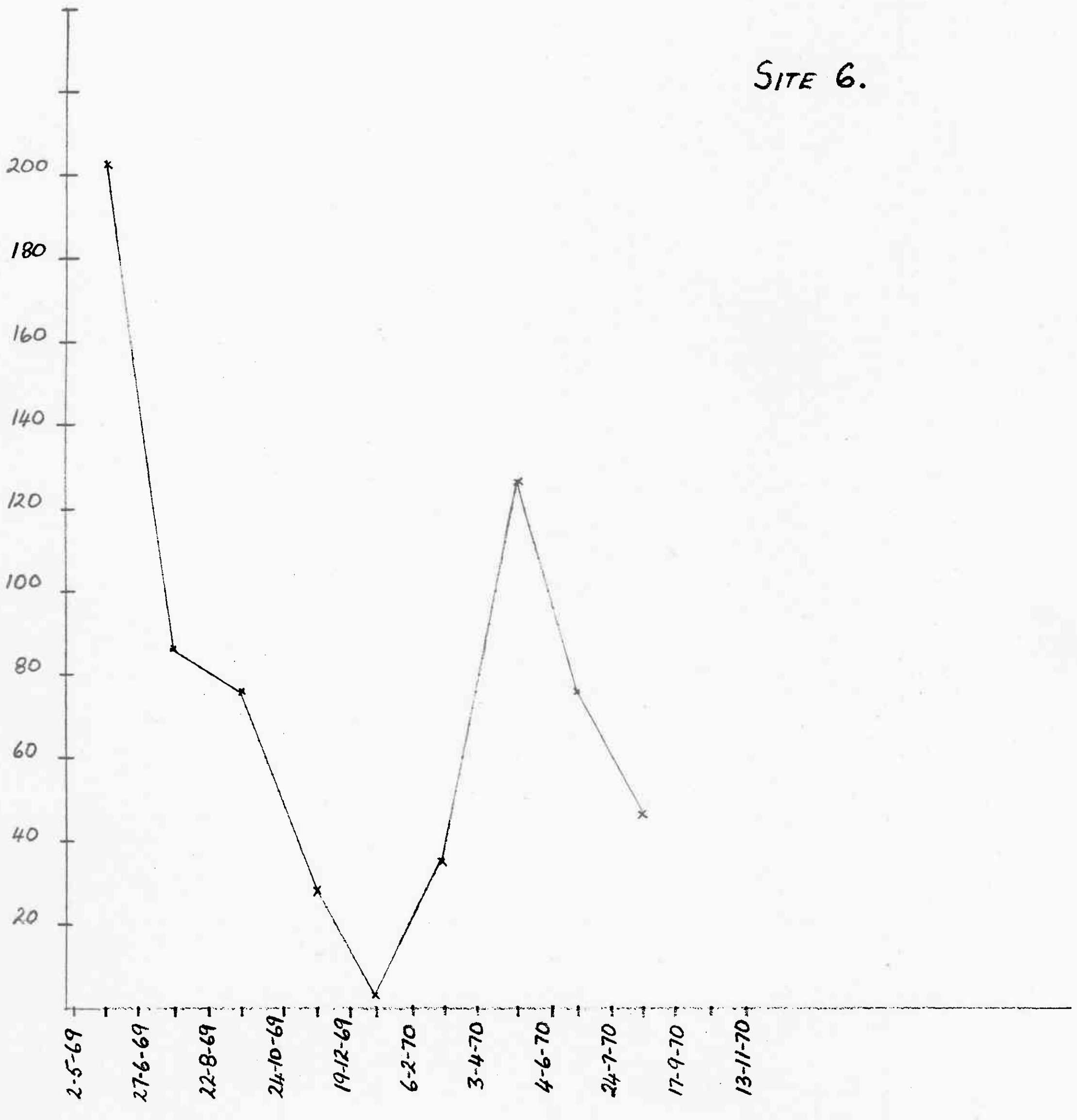
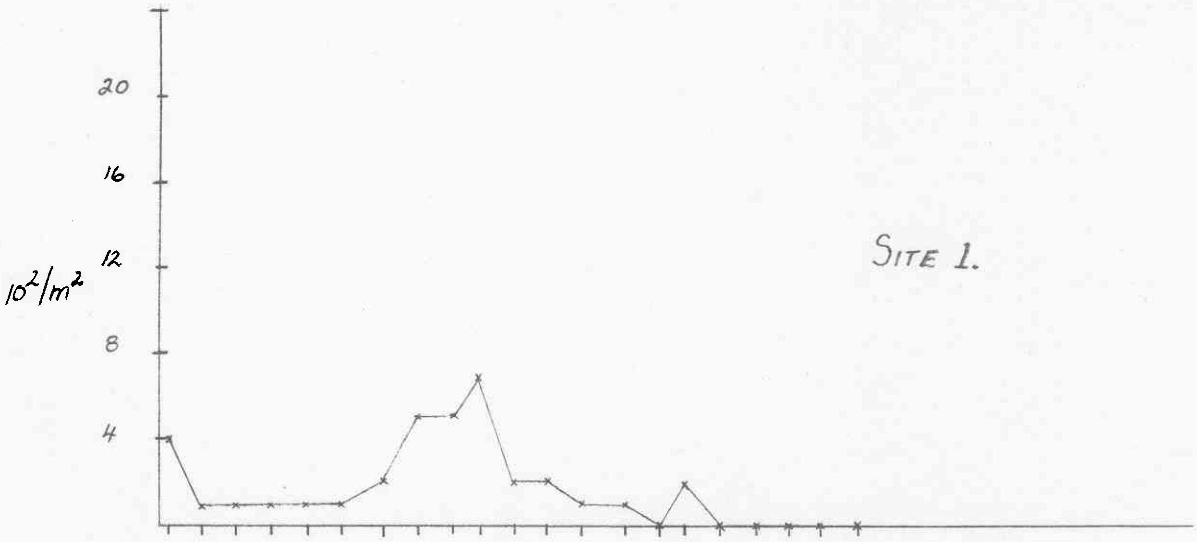


Fig. VII$_6$: Mean population of unidentified Acarina including small trombidiforms and young stadia.



Mean population of Psocoptera (Insecta).

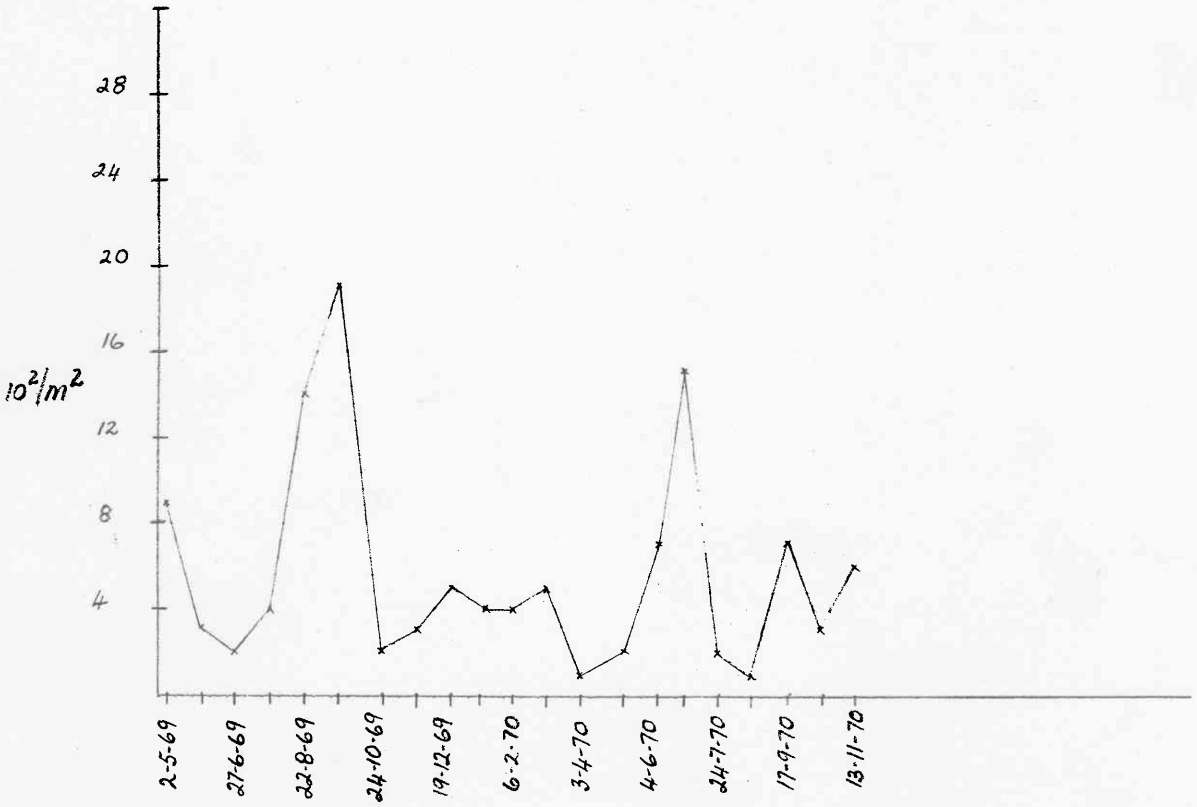
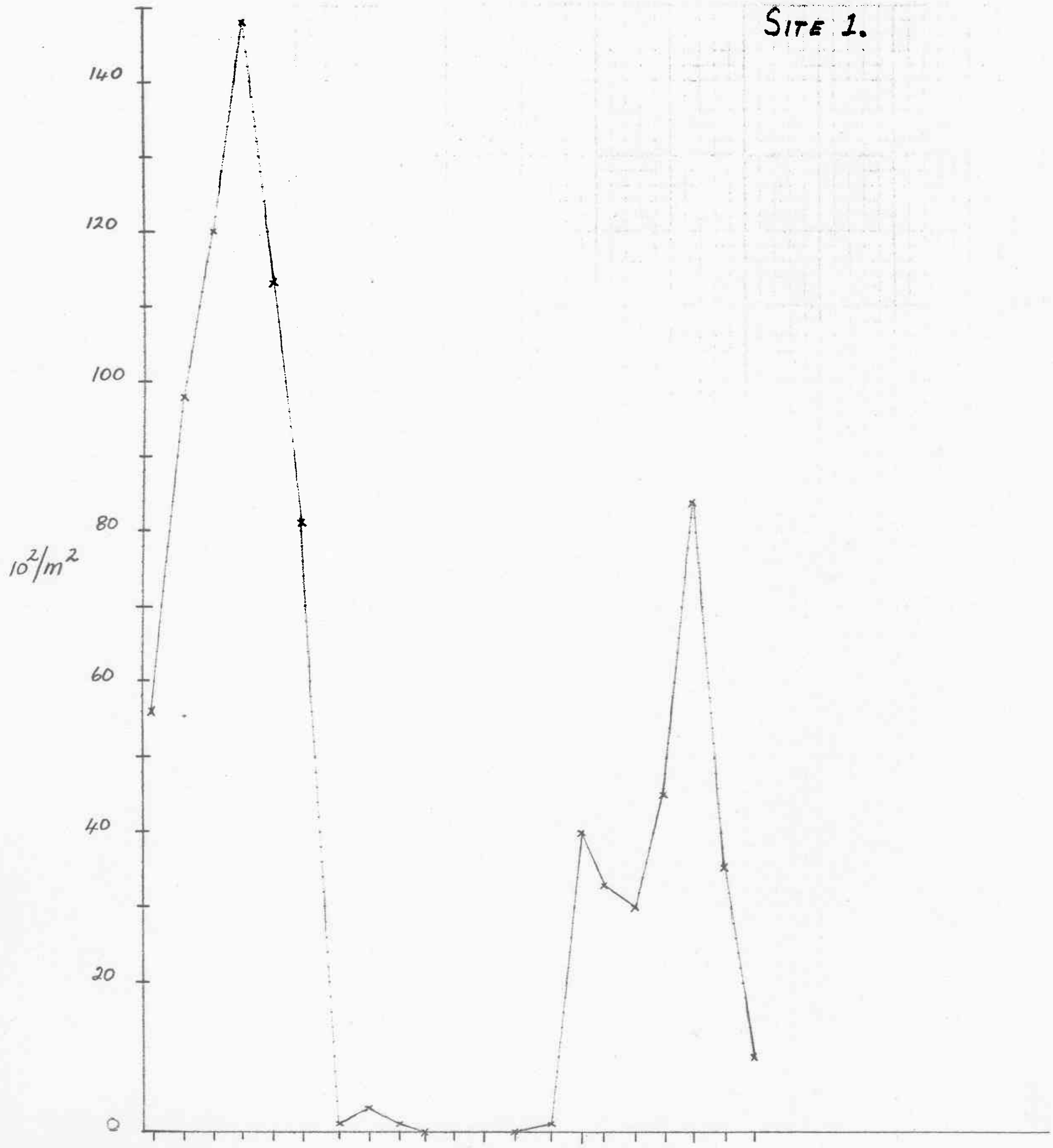
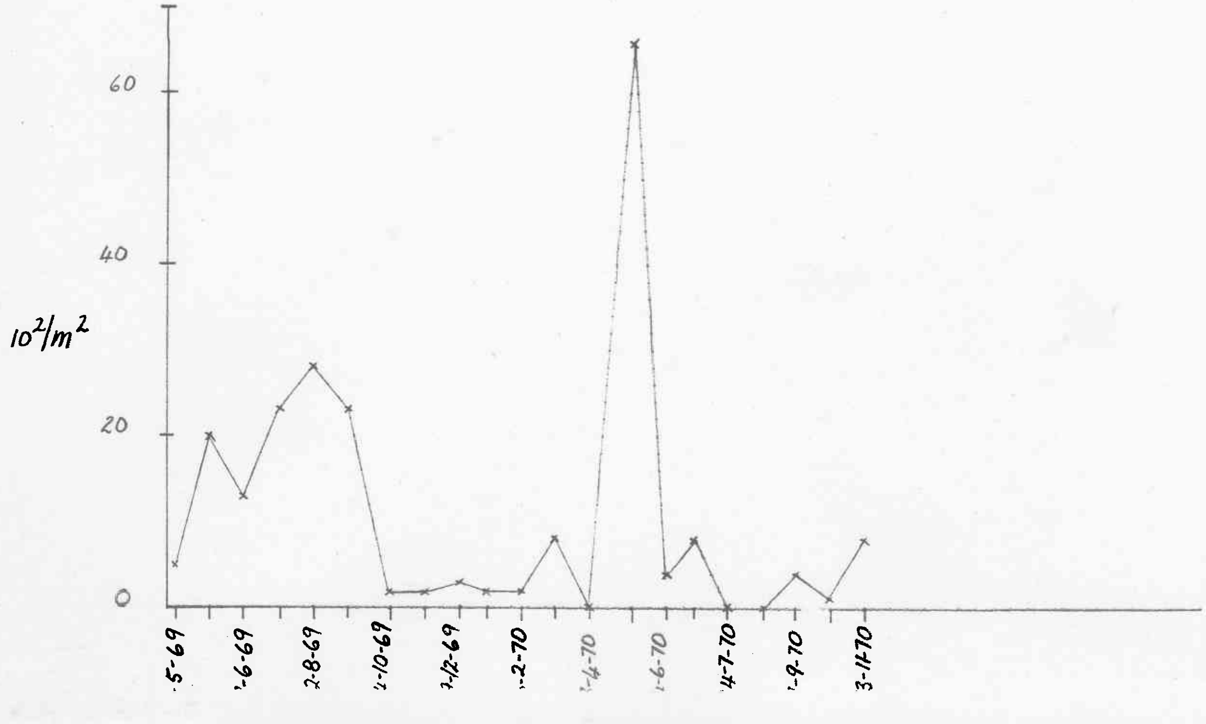


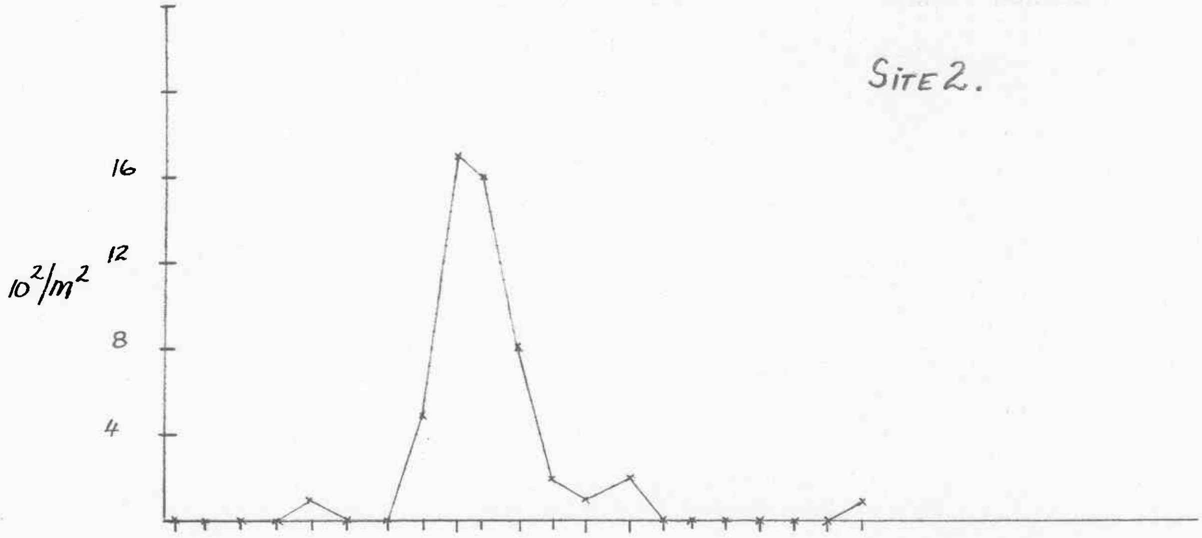
FIG. VIII Mean population of other invertebrates including Pseudoscorpionida

SITE 1.



MEAN POPULATION OF PROTURA (INSECTA).





MEAN POPULATION OF PSOCOPTERA (INSECTA).

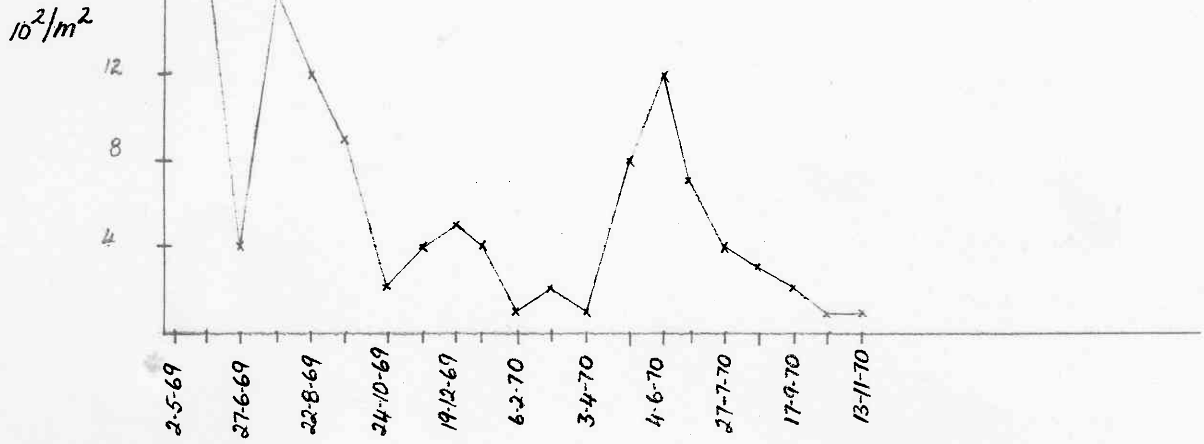
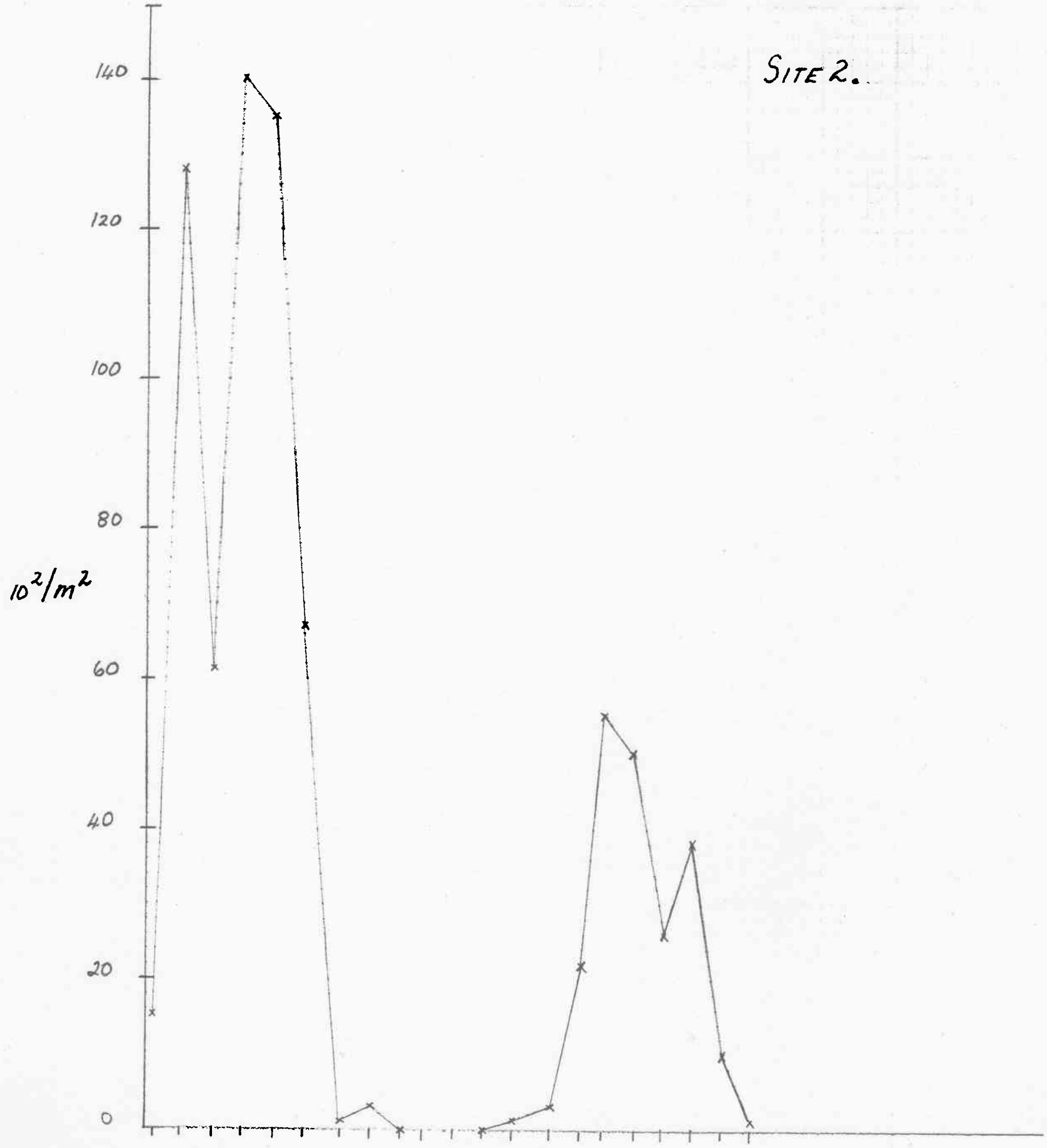
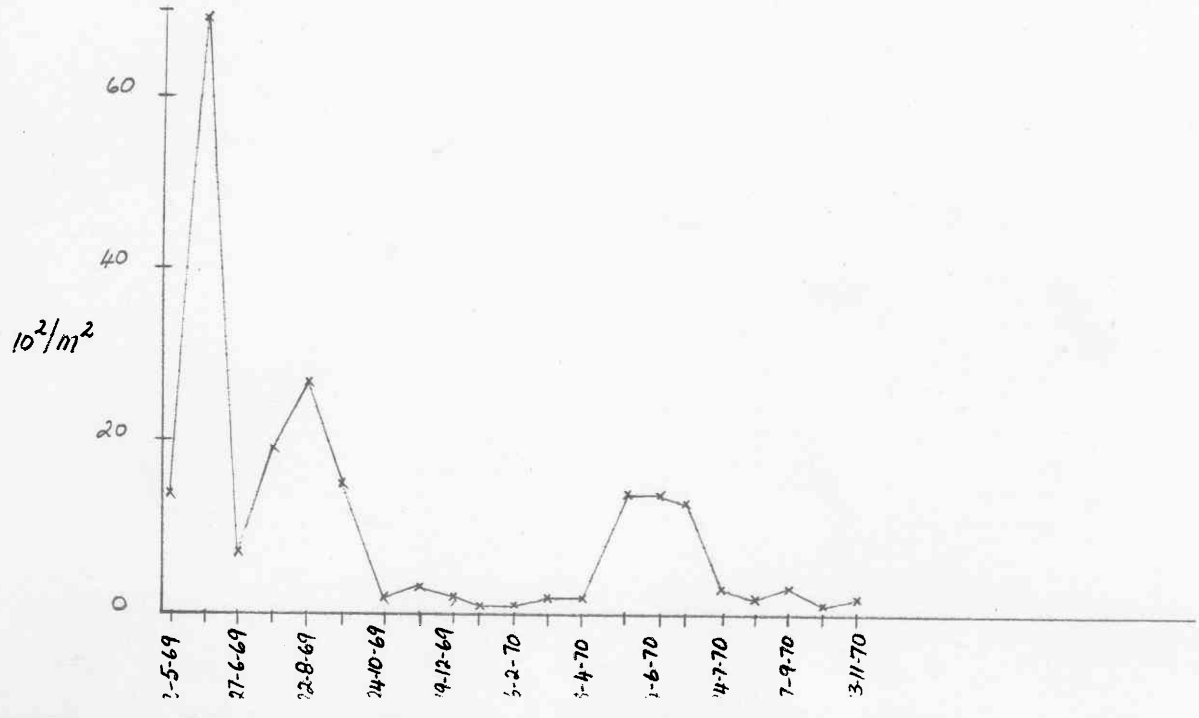
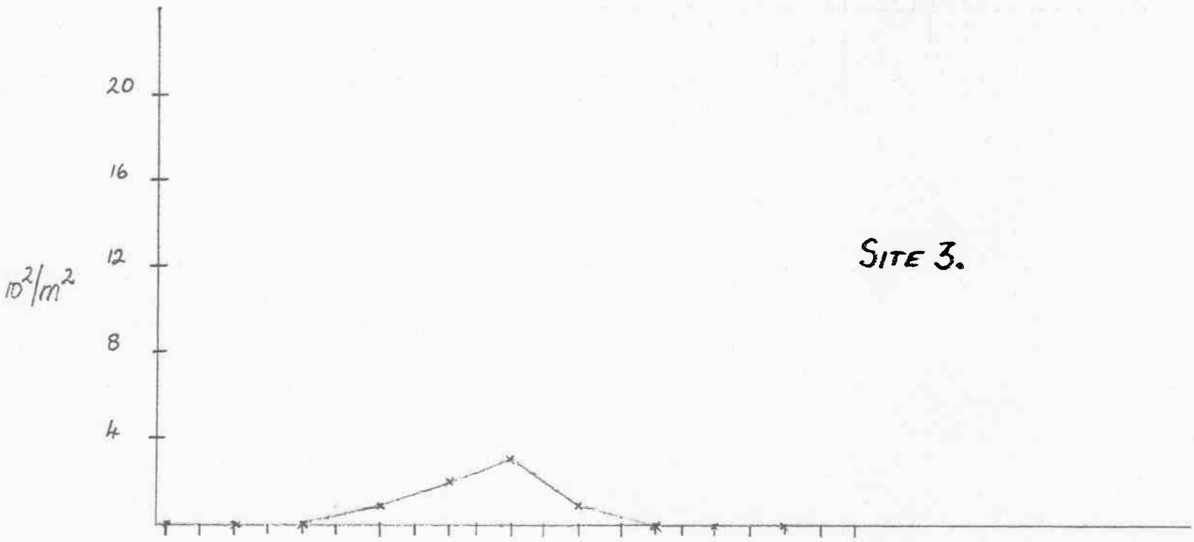


FIG. VIII : MEAN POPULATION OF OTHER INVERTEBRATES INCLUDING PSEUDOSCORPIONIDA



MEAN POPULATION OF PROTURA (INSECTA).





MEAN POPULATION OF PSOCOPTERA (INSECTA).

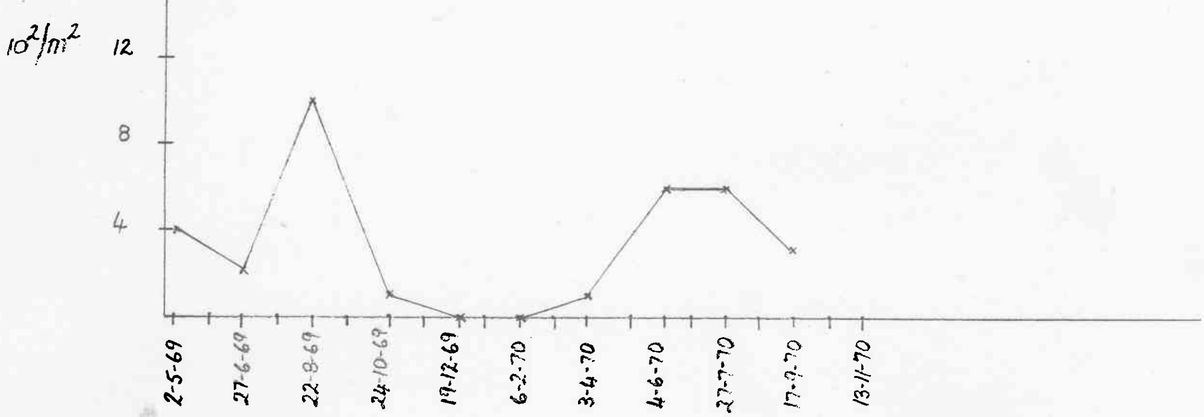
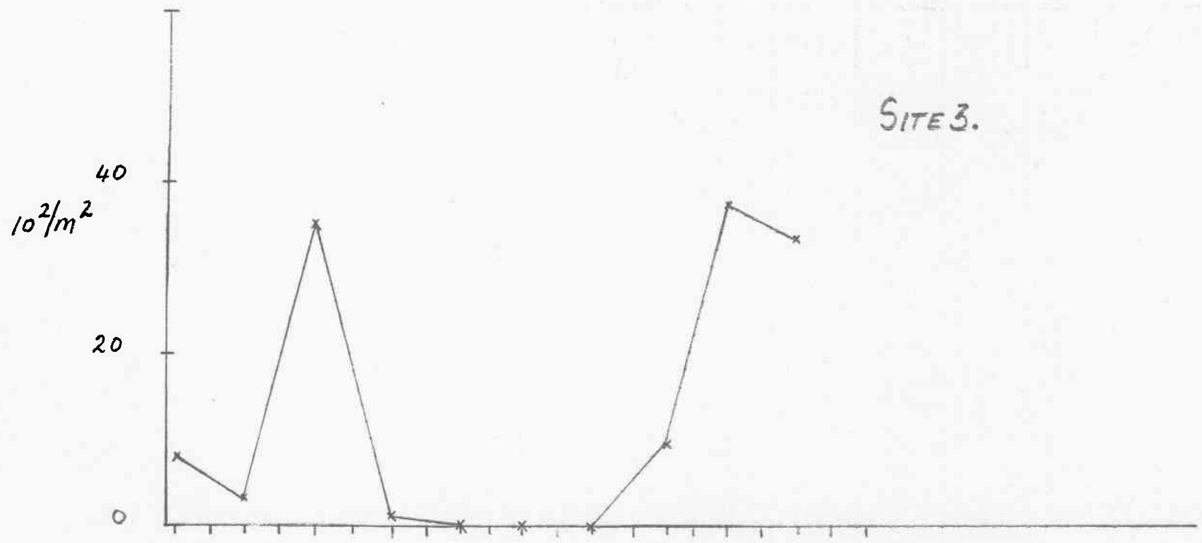


FIG. VIII. MEAN POPULATION OF OTHER INVERTEBRATES INCLUDING PSEUDOSCORPIONIDA



MEAN POPULATION OF PROTURA (INSECTA).

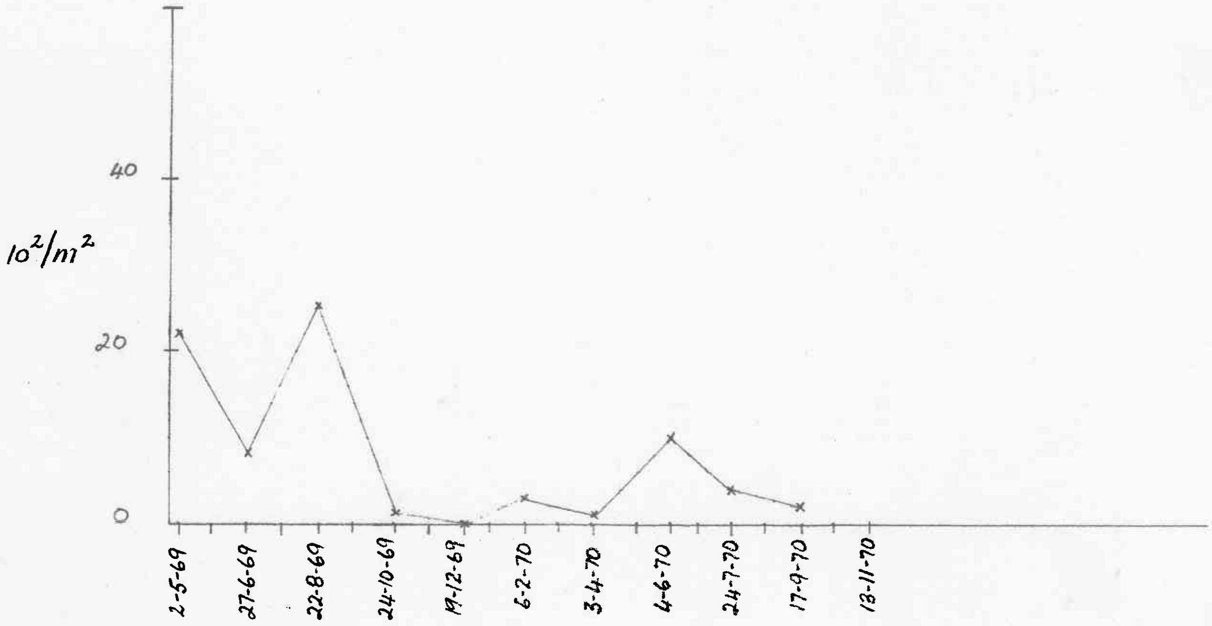
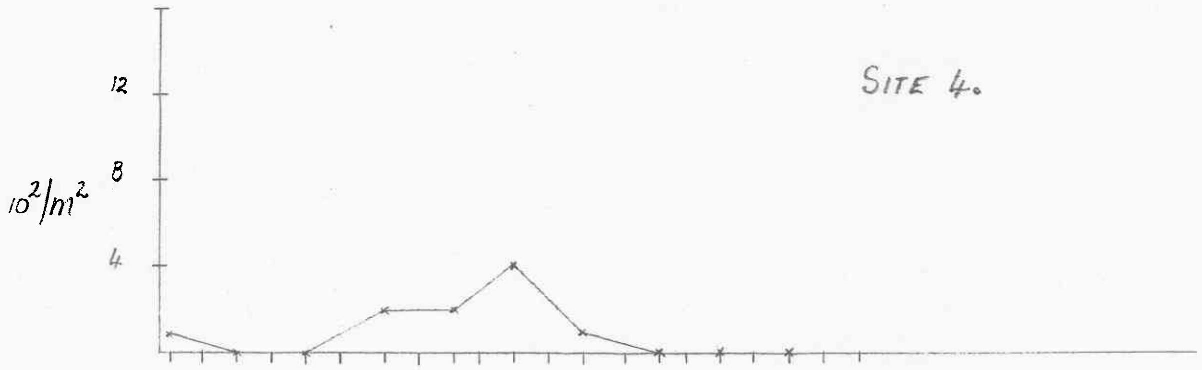


FIG. VIII$_3$ cont^d: MEAN POPULATION OF ENDOPTERYGOTE INSECT LARVA.



Mean population of Psocoptera (Insecta).

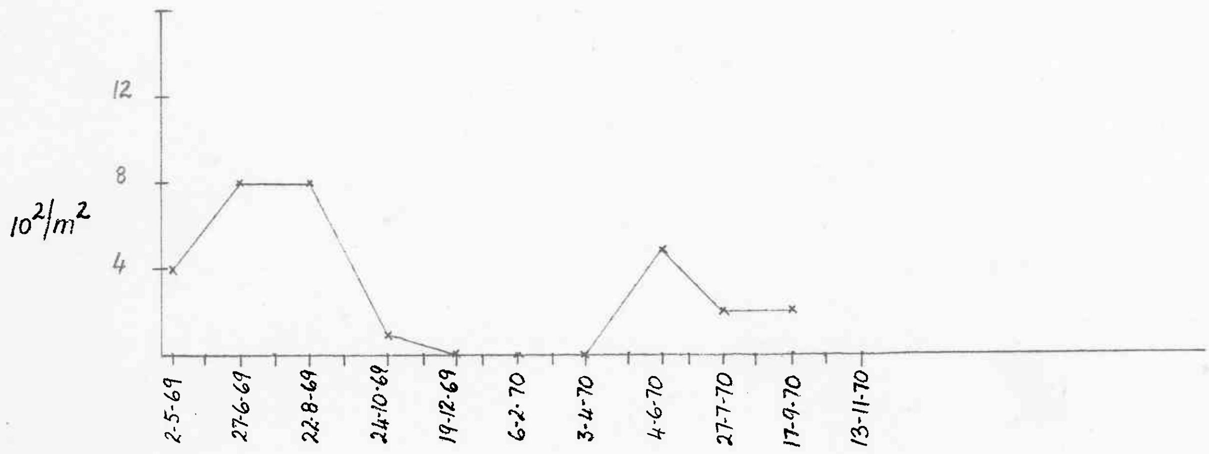
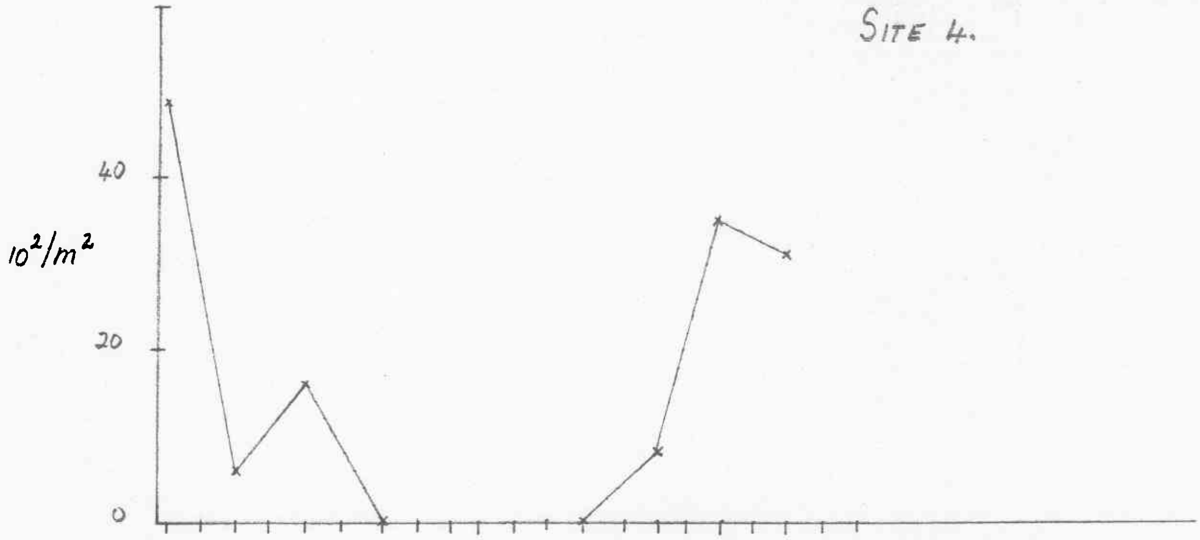


Fig. $\underline{VIII}_4$: Mean population of other invertebrates including Pseudoscorpionida, Arachnida, Oligochaeta, Myriapoda and Insecta.

SITE 4.



MEAN POPULATION OF PROTURA (INSECTA).

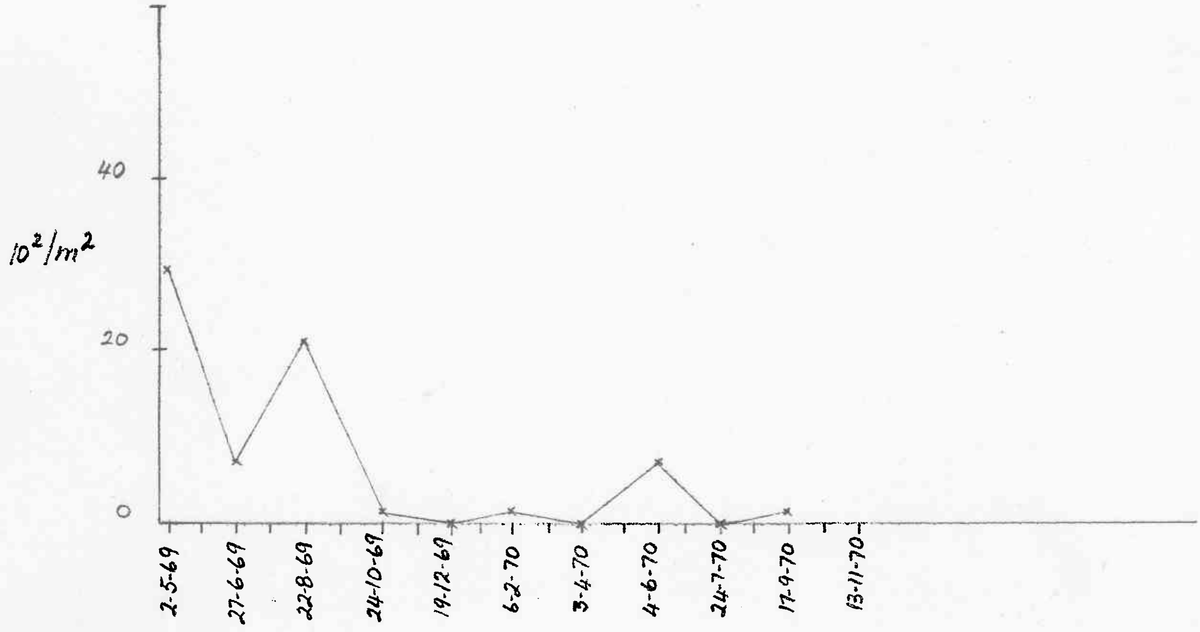
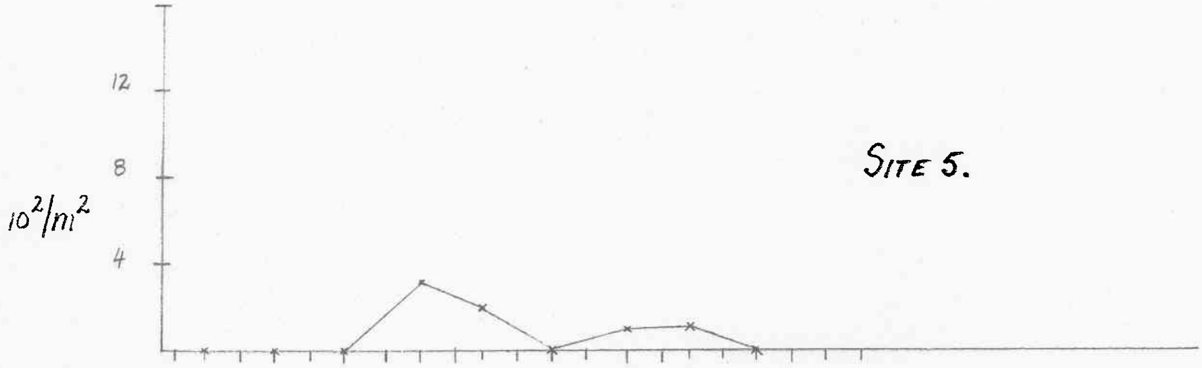


FIG. VIII$_4$ cont^d: MEAN POPULATION OF ENDOPTERYGOTE INSECT LARVA.



Mean population of Psocoptera (Insecta).

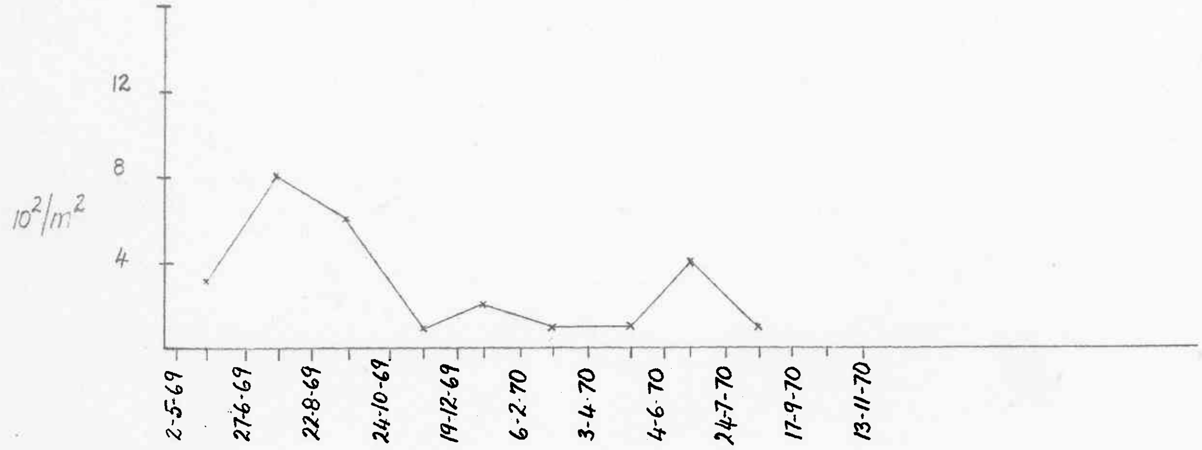
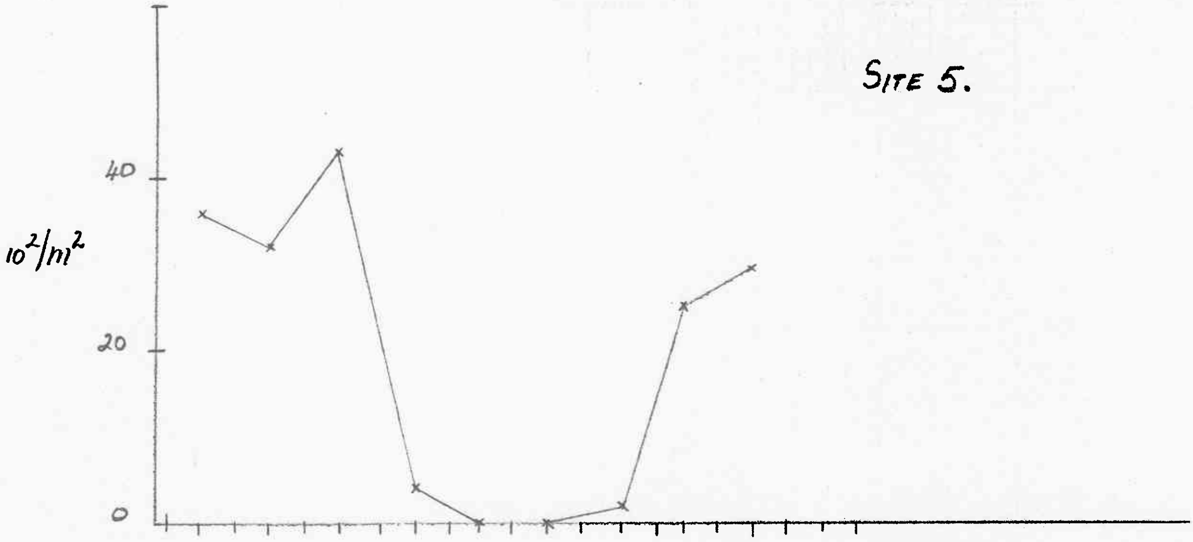


Fig. VIII_5 Mean population of other invertebrates including Pseudoscorpionida, Arachnida, Oligochaeta, Myriapoda and Insecta.



Mean population of Protura (Insecta).

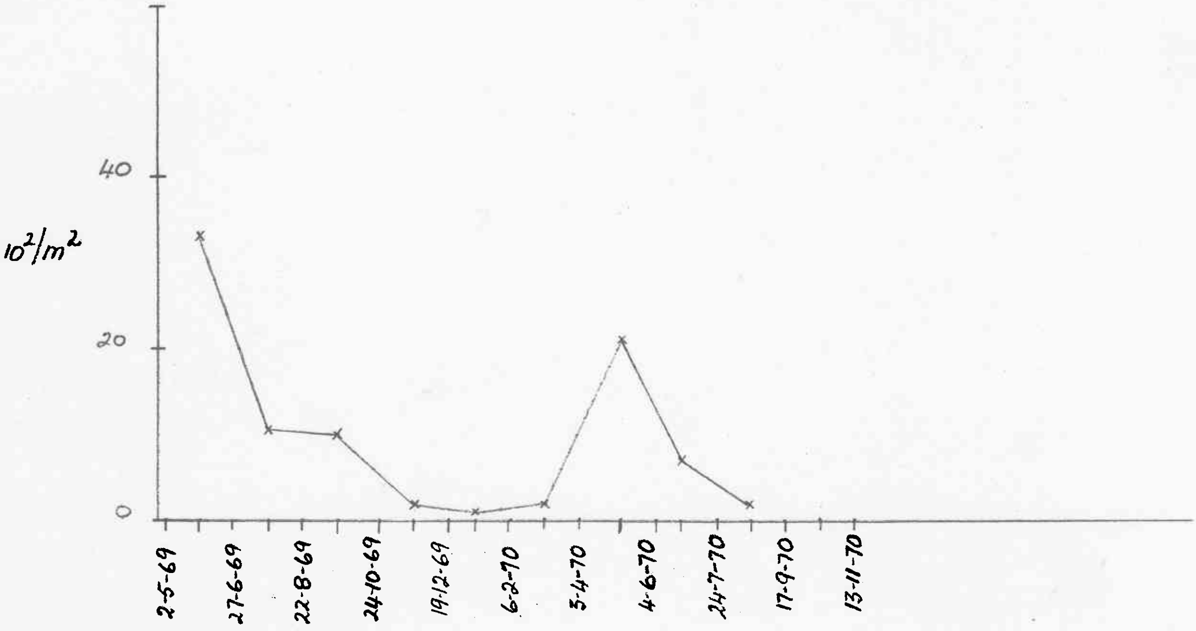
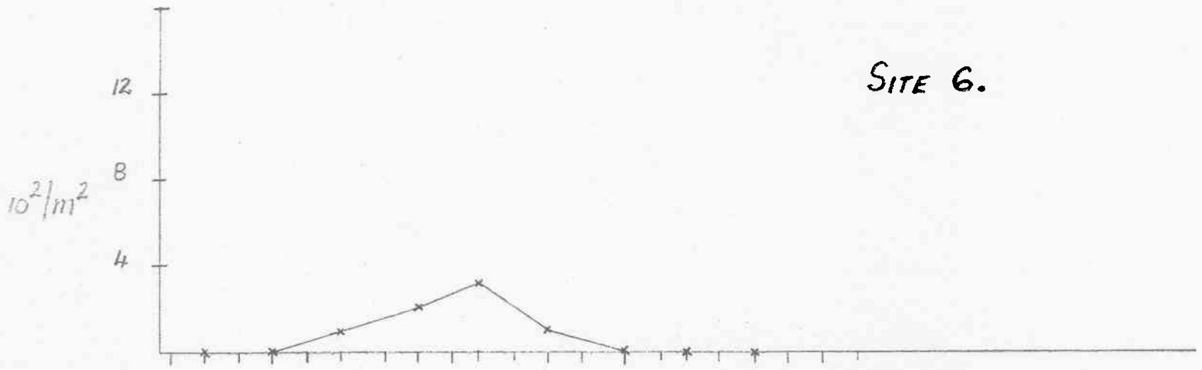


Fig. VIII$_5$ cont^{d}: Mean population of endopterygote insect larva.



Mean population of Psocoptera (Insecta.)

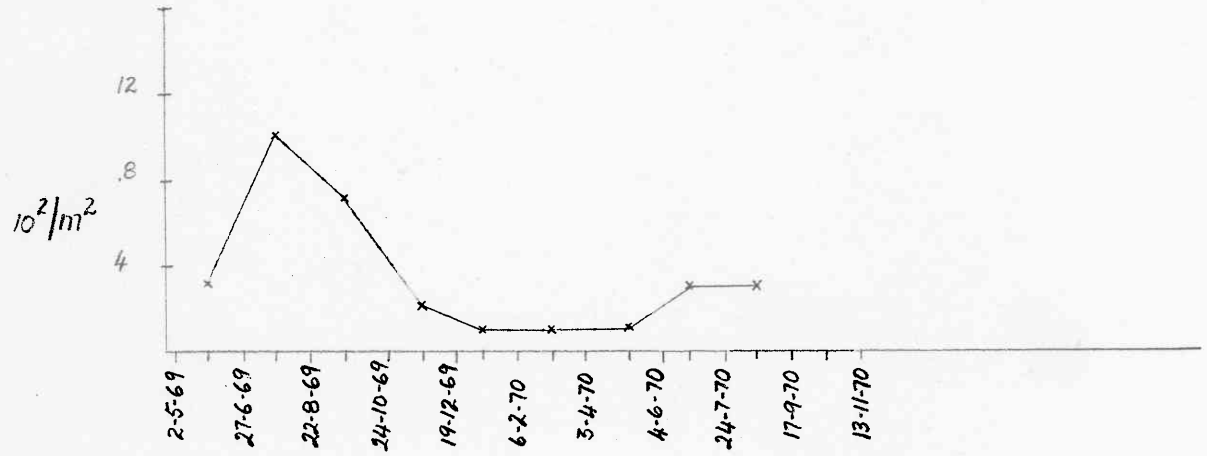


Fig. VIII$_6$: Mean population of other invertebrates including Pseudoscorpionida, Arachnida, Oligochaeta, Myriapoda and Insecta.

SITE 6.

MEAN POPULATION OF PROTURA (INSECTA).

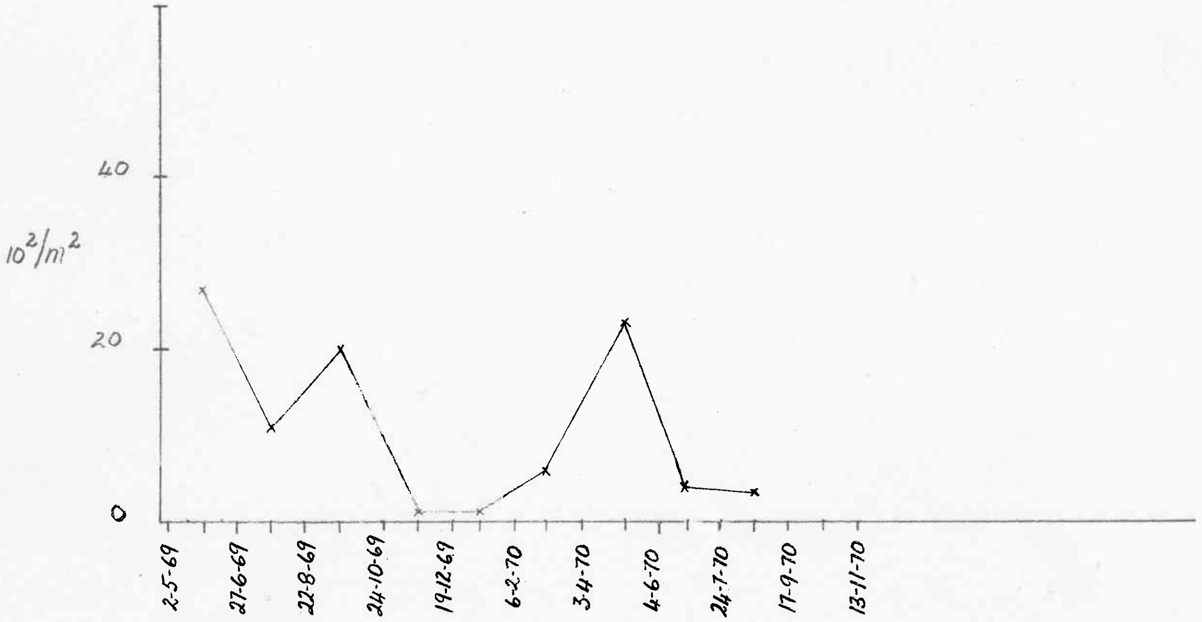


FIG. VIII$_6$ cont^{d}: MEAN POPULATION OF ENDOPTERYGOTE INSECT LARVA.

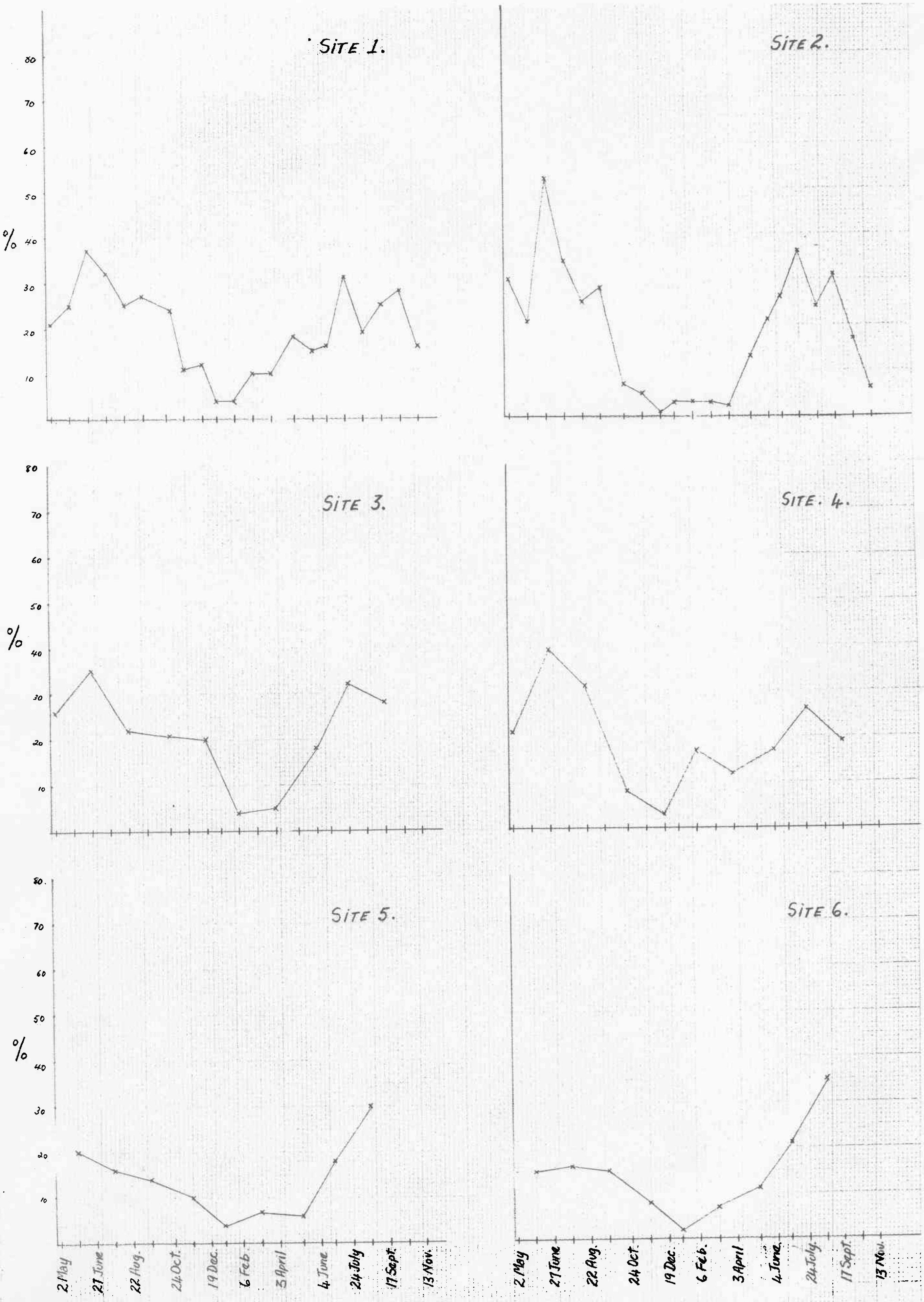


FIG IX, : PERCENTAGE OF GENERAL FEEDERS IN THE TOTAL POPULATION.

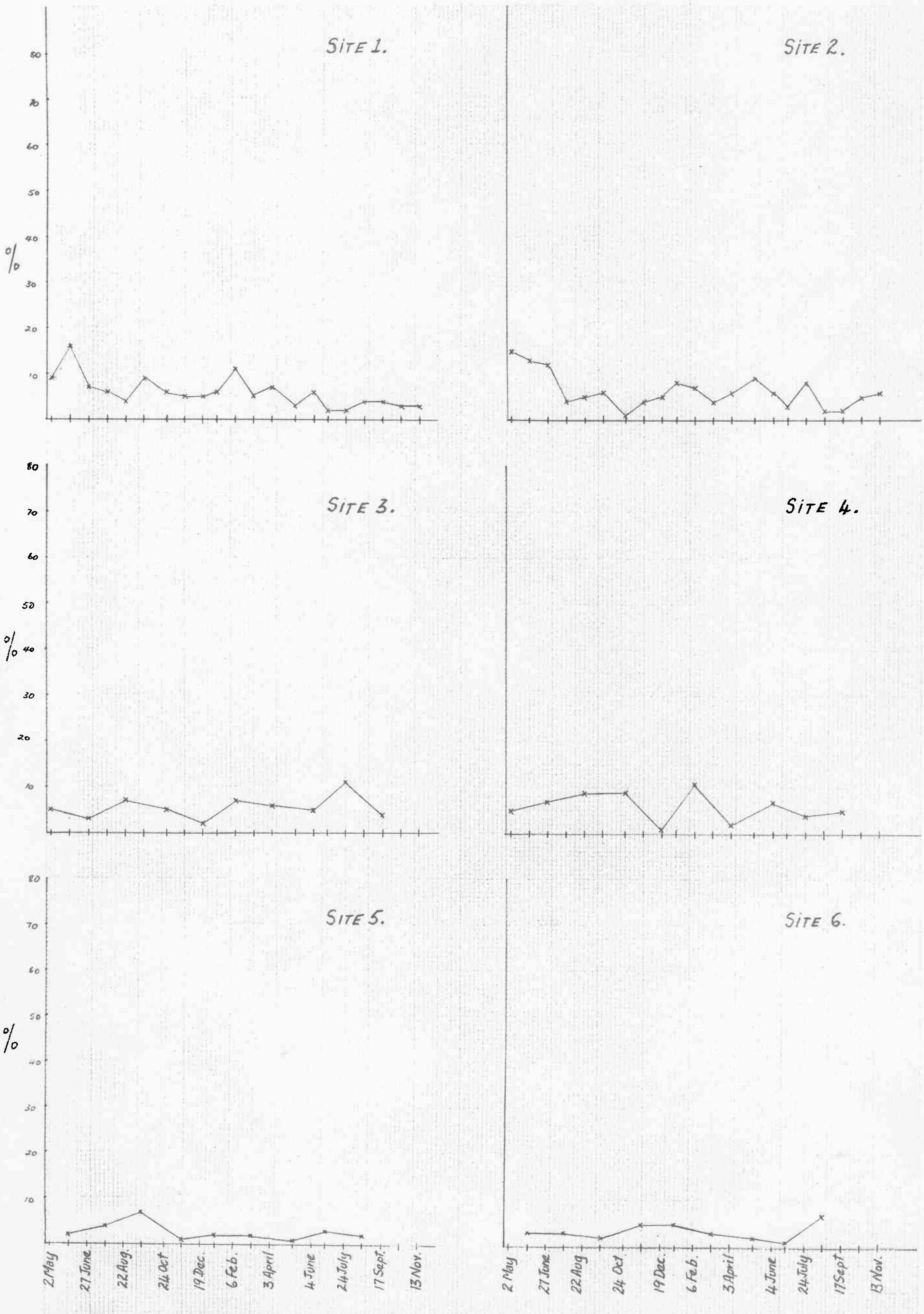


FIG. IX$_2$ PERCENTAGE OF PREDATORS IN THE TOTAL POPULATION.

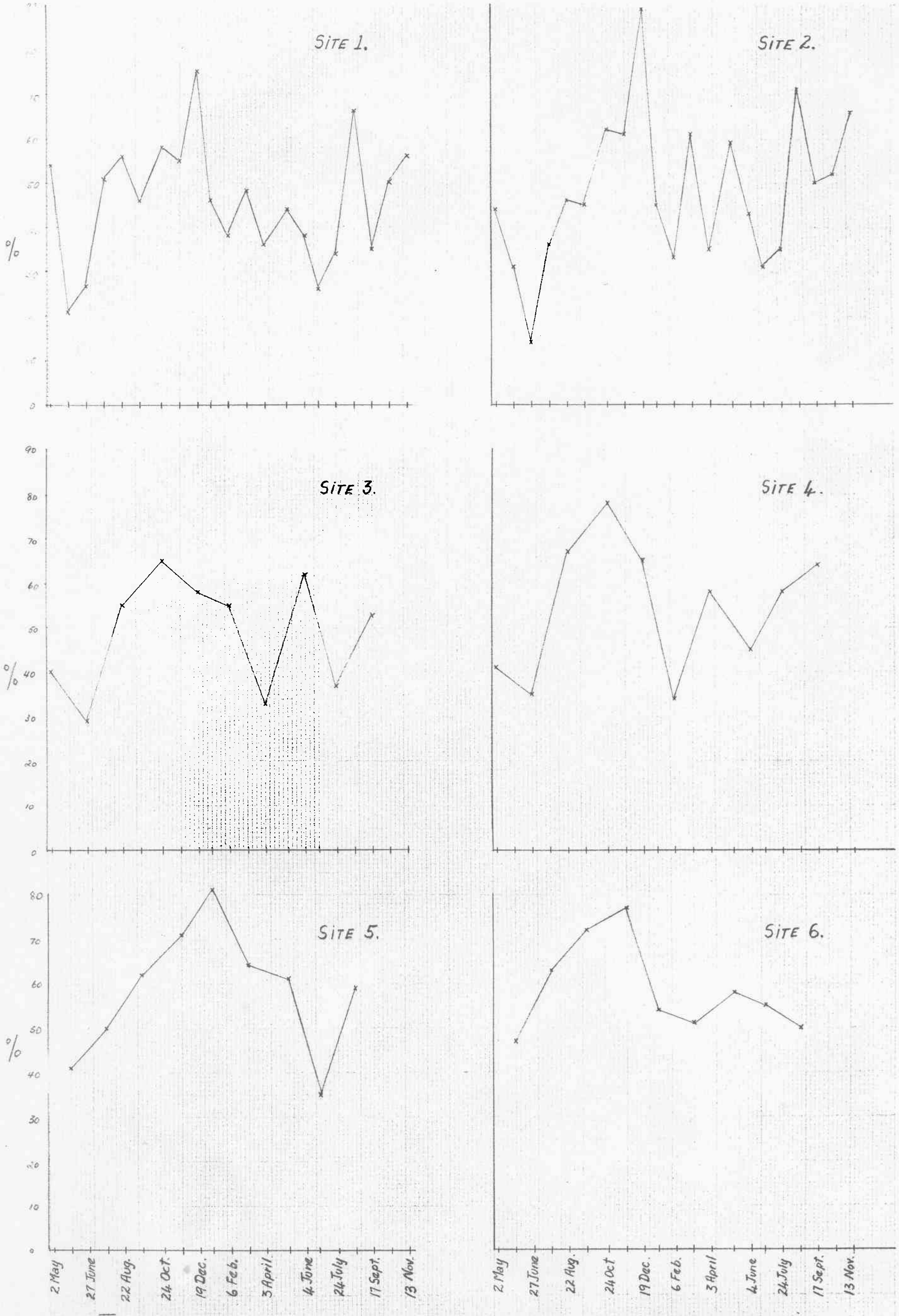


FIG. $\overline{IX}_3$: PERCENTAGE OF FUNGAL FEEDERS IN THE TOTAL POPULATION.

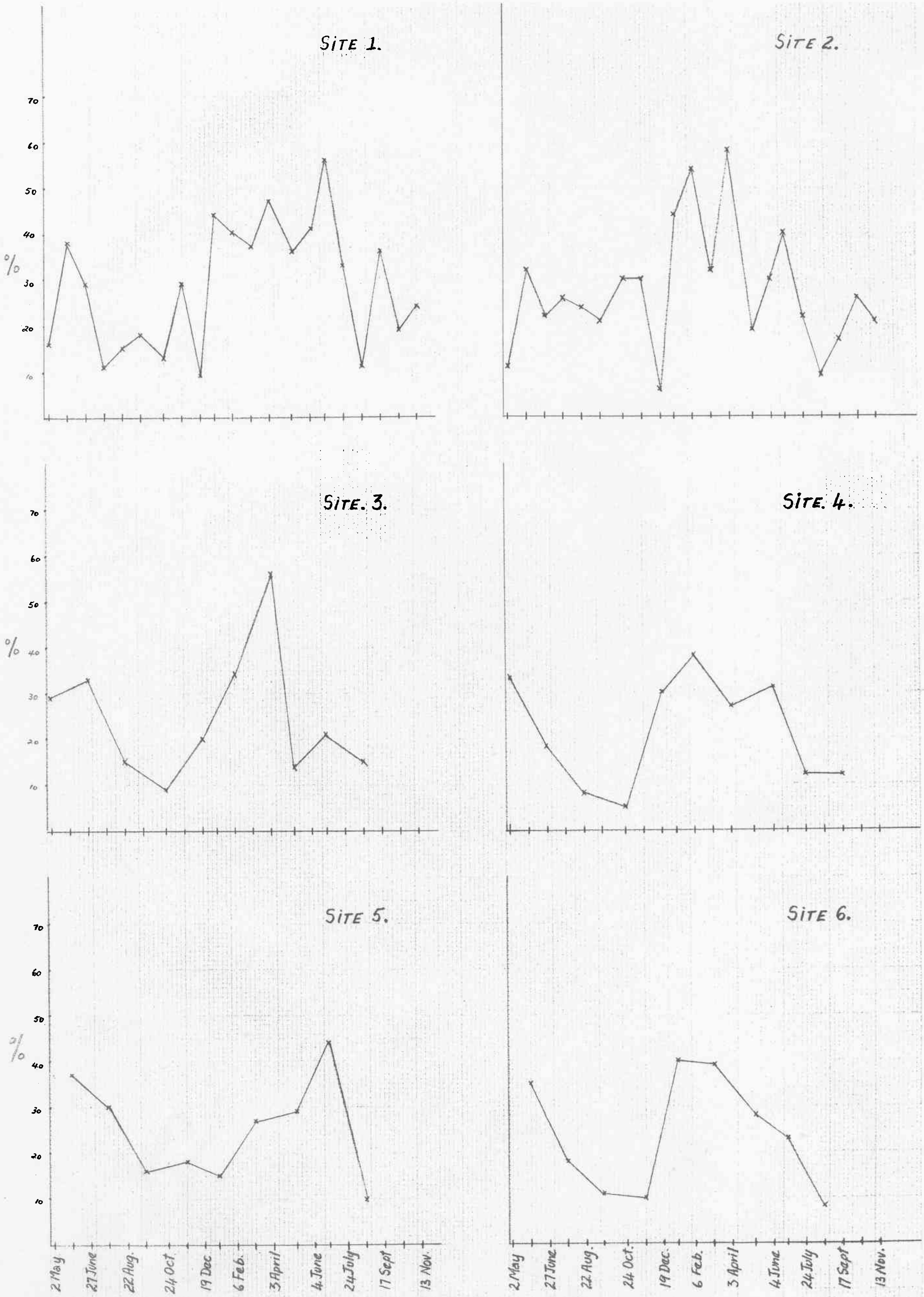


FIG. $\underline{IX}_4$: PERCENTAGE OF UNKNOWN FEEDERS IN THE TOTAL POPULATION.

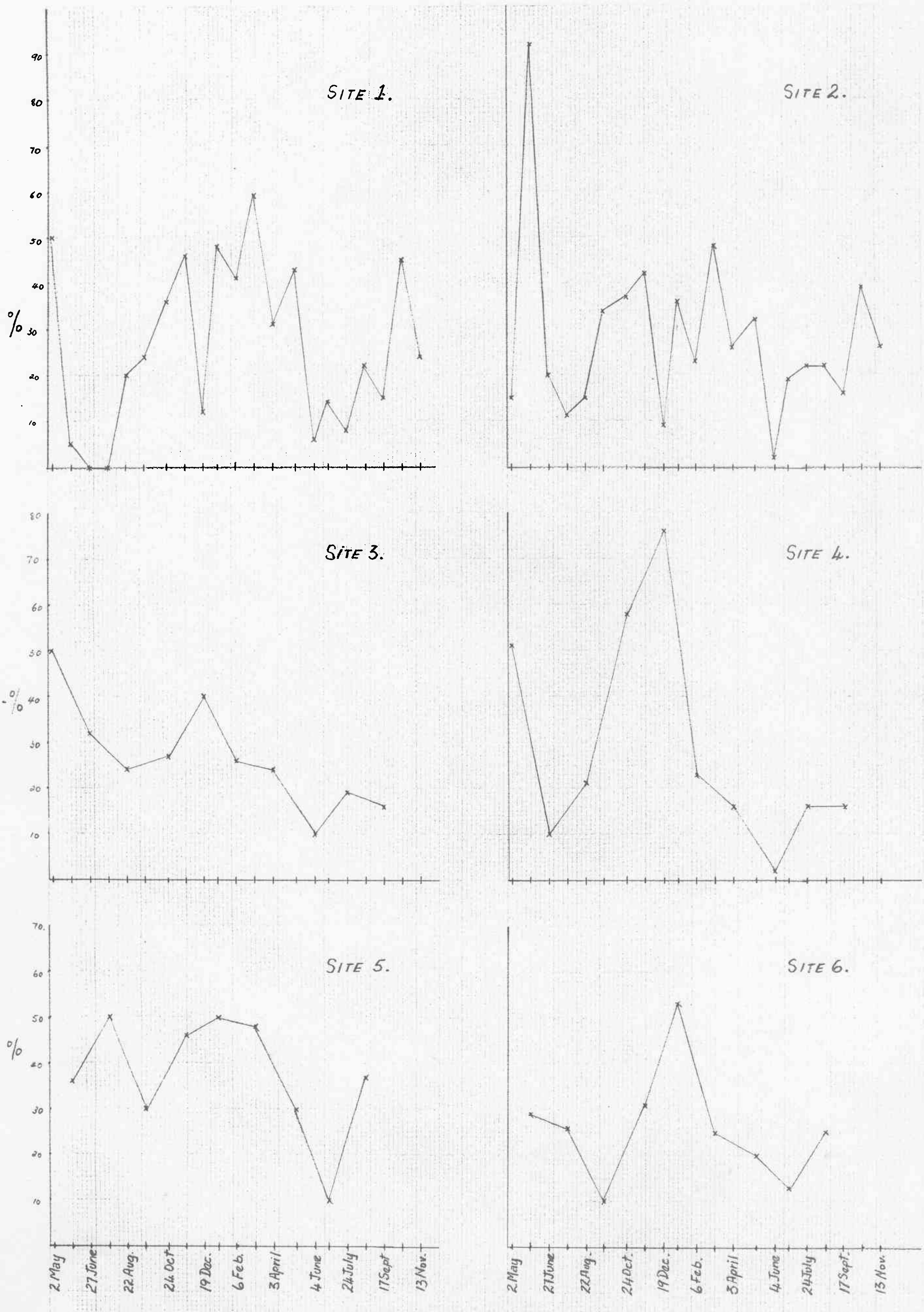


FIG. X: PERCENTAGE OF FUNGAL FEEDERS WITH NO VISIBLE GUT CONTENTS ON EACH SITE.

LITTER DECOMPOSITION RATES SHOWING EXTRAPOLATION TO TIME AT WHICH 95% DECOMPOSITION OCCURS.

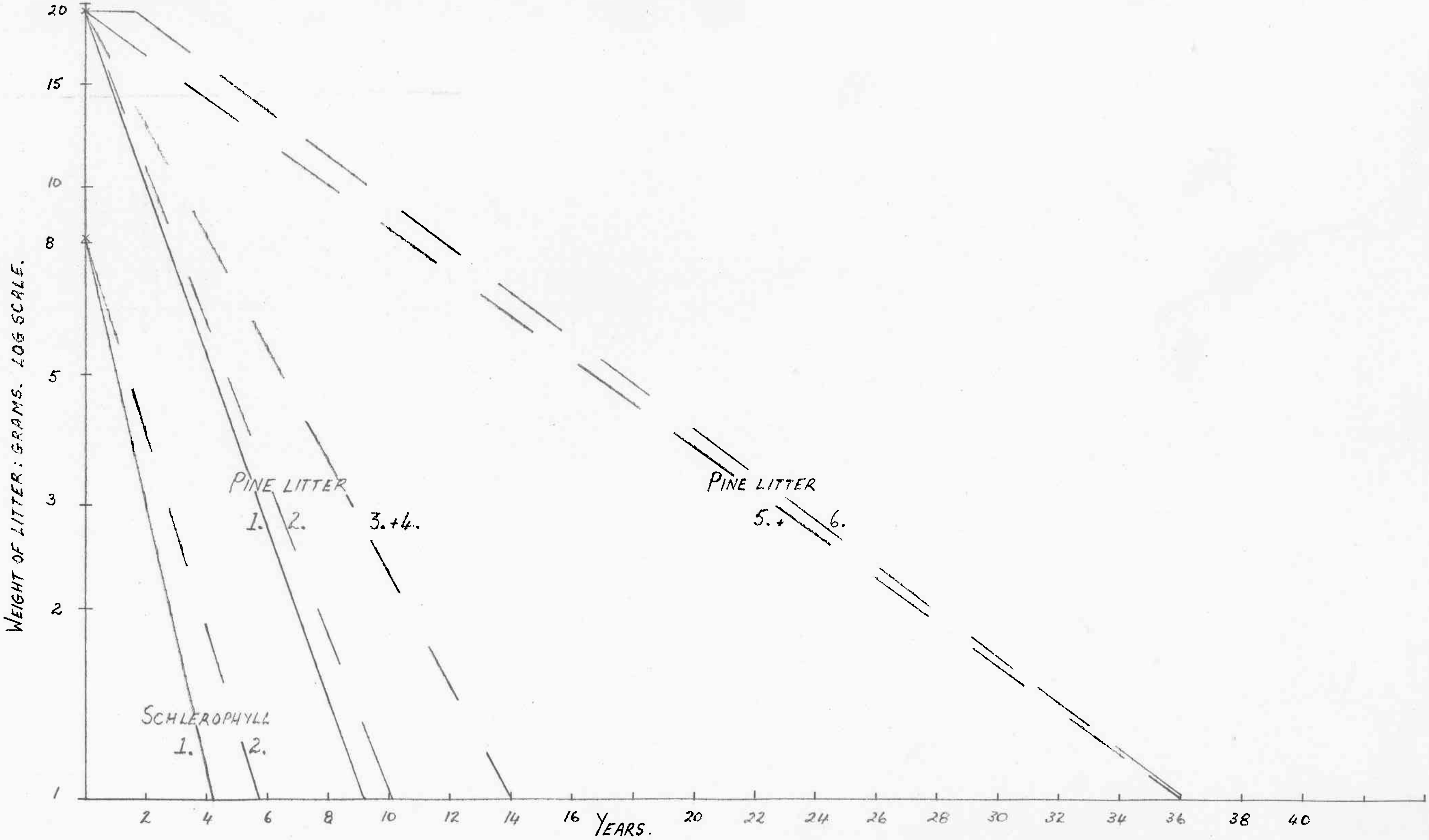


Fig [illegible]

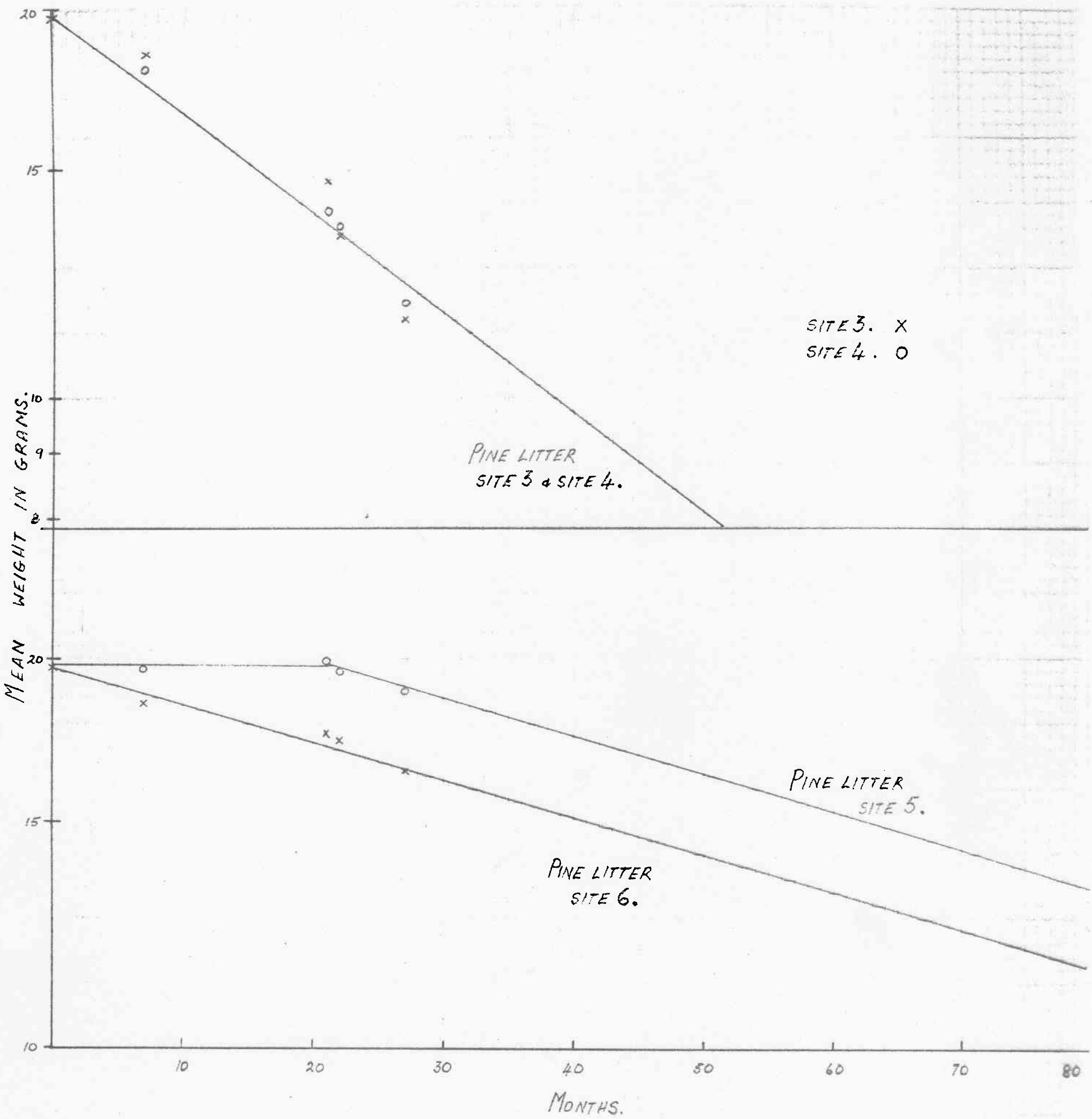
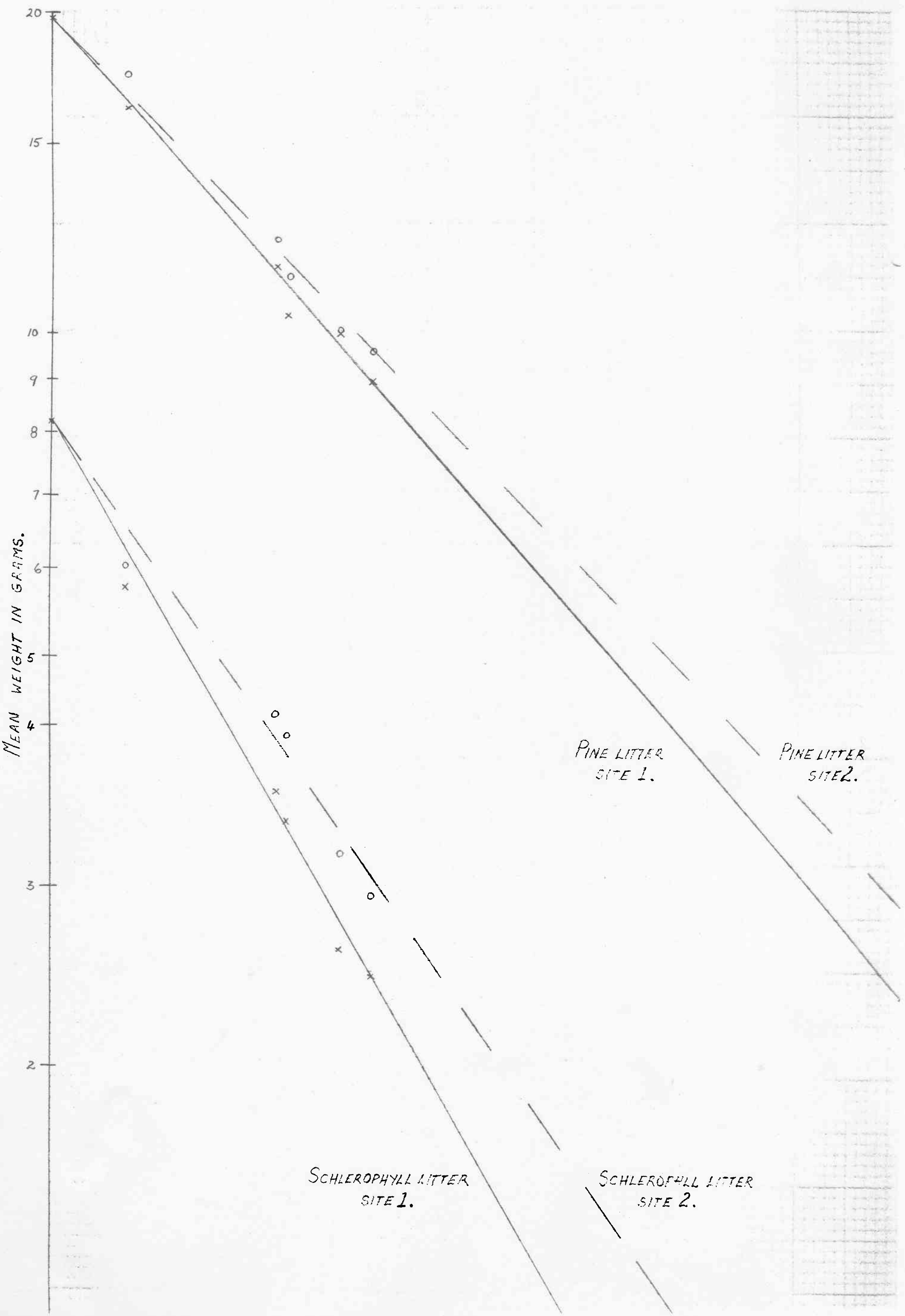

20
15
10
9
8
MEAN WEIGHT IN GRAMS.
SITE 3. X
SITE 4. O
PINE LITTER
SITE 3 & SITE 4.
20
15
10
PINE LITTER
SITE 5.
PINE LITTER
SITE 6.
10
20
30
40
50
60
70
80
MONTHS.

FIG. XI:


MEAN WEIGHT IN GRAMS.
20
15
10
9
8
7
6
5
4
3
2
PINE LITTER SITE 1.
PINE LITTER SITE 2.
SCHLEROPHYLL LITTER SITE 1.
SCHLEROPHYLL LITTER SITE 2.

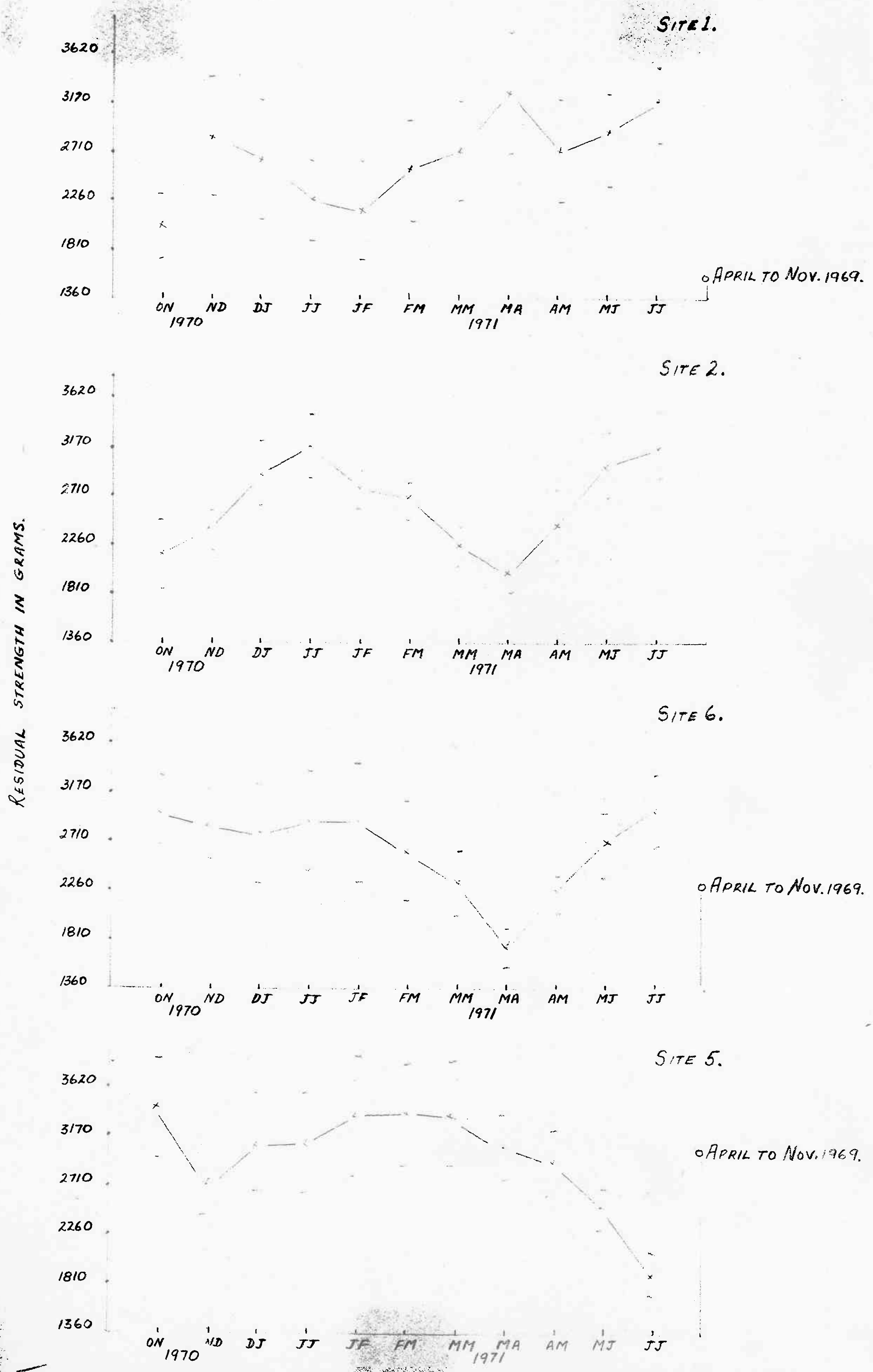


Fig. XII: Residual strength of cotton strips at three-weekly intervals.

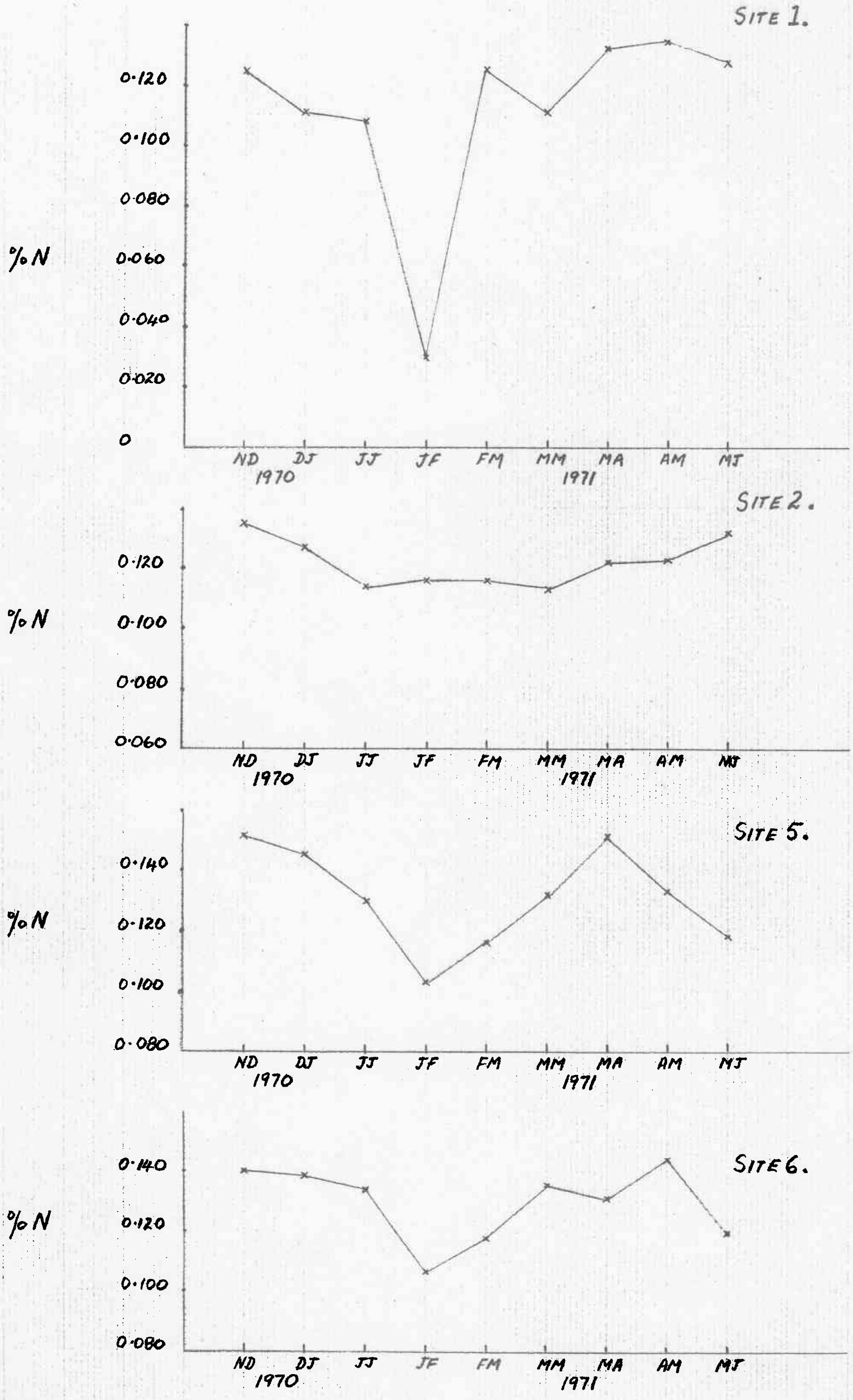


FIG. XIII : NITROGEN CONTENT OF COTTON STRIPS LEFT IN THE FIELD FOR THREE WEEKS.