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A STUDY OF SOIL AND LITTER INVERTEBRATES IN SEMI-ARID KWONGAN VEGETATION WITH SPECIAL REFERENCE TO FIRE AGE.

by

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This thesis is presented in partial fulfillment of the requirements for Honours in Biology and represents 85% of the formal course requirements for one academic year.

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ABSTRACT

Soil and litter invertebrates were studied in three different sites of semi-arid kwongan vegetation, each with a different fire history and identified by the year they were last burnt. Twenty-nine taxonomic groups (predominantly orders) of invertebrates, and 125 species of Araneae (spiders) were identified. Invertebrate abundances peaked during spring, and were greatest in the oldest (1932) site. The spider fauna showed similar trends. Higher spider and invertebrate abundances in the 1932 site were attributed to an abundance of leaf and woody litter, though the proximity of this site to a neighbouring stand of _Allocasuarina huegeliana_ also appeared to influence the spider and invertebrate communities. The most-recently burnt (1965) site showed a depletion of desiccation-prone fauna, particularly detritus feeders. This was attributed to a decrease in litter cover resulting from the last burn. The implications of this study in relation to existing fire management policies are discussed.

CHAPTER 1

INTRODUCTION

INTRODUCTION

Fire has formed an integral part of ecological communities in the south-west of Western Australia. Lightning induced fires have occurred frequently in the south-west for at least the past 5000 years (Churchill 1968), and Aboriginal firing of the bush appears to date from around 20,000 years ago (Hallam 1975). Such a prevalence of fire in the south-west environment has resulted in a mosaic of vegetation associations and structural stages reflecting past fire histories (CALM 1987). It is also quite likely that such a prevalence of fire has influenced the composition of faunal communities, with certain susceptible species becoming extinct when unable to tolerate fire regimes with a high fire frequency (Hallam 1975).

To date most studies on fire effects have been conducted on vegetative aspects. Studies of Australian plant communities have found that many plant species have evolved adaptive strategies for coping with fire (Bell, Hopkins and Pate 1984; Gill and Groves 1981). However, according to Main (1981), only behavioural strategies for fire avoidance are shown by animals.

Studies of fire effects on animal communities have been relatively few compared to the numerous vegetation studies. Suckling and Macfarlane (1984) note that relatively little attention has been paid to the effects of fire upon the richness, composition, and successional aspects of animal communities.

With regard to invertebrate studies, most work has been conducted in moist forest areas where fire, in the form of prescribed burning, is used as a silvicultural tool to reduce the fuel (litter and shrub layer) available for combustion (e.g. Abbot, Van Heurck, and Wong ----; Campbell 1973; Campbell and Tanton 1981; Christensen and Kimber 1975; Majer 1978; Springett 1976). Both eastern states and Western Australian studies have found profound, and often controversial, effects of burning on invertebrate populations (e.g. Abbott 1984; Campbell 1973; Campbell and Tanton 1981; Springett 1976). However, consistent with the majority of studies is the finding that there is a strong association between litter density and soil and litter invertebrate abundance (e.g. Campbell and Tanton 1981; Hutson and Veitch 1985; Majer 1985; Postle 1989; Raison, Woods and Khanna 1986). In fact, Springett's (1976) study on fire effects on invertebrates, has been extensively criticised by Campbell and Tanton (1981) for not taking into account litter structure and distribution.

The importance of the litter layer is emphasised by Di Castri and Vitali-Di Castri (1981) who note that this layer represents the centre of the soil subsystem, and largely determines the pattern of distribution of soil animals. Thinning or removal of the humus layer, as occurs during fire, causes a reduction habitat, a change in microenvironmental conditions, and a decline in the food supply of the soil and litter fauna litter fauna (Raison et. al. 1986, Springett 1979).

Fire can also have significant effects on litter decomposition (Springett 1976; Springett 1979). From her study of litter decomposition in jarrah (<u>Eucalyptus marginata</u>) and karri (<u>Eucalyptus diversicolor</u>), Springett (1976) found that decomposition ceased for four years following fire. This decline in litter decomposition was associated with a reduction in soil microfauna populations following burning. Further studies by Springett (1979) confirmed this association. From these studies, Springett postulated that burning caused profound changes in the microbial ecology resulting in a decrease in decomposition and a decline in food supply for microarthropods, particularly fungal feeders (Springett 1979).

O'Connell, Grove, and Dimmock (1979), studying in jarrah forest, found that major changes in the nutrient cycle only occurred when fires were severe enough to scorch and defoliate the crowns of trees. As Springett (1979) notes, <u>Eucalyptus</u> species have a well developed nutrient translocation mechanism, so that by the time leaves are ready to fall from a tree, they have a low nutrient content. In the case of severe fire which scorches the crowns of trees, the majority of leaves still contain high levels of nutrients. Hence, the litter and ash remaining after fire, have a higher than normal amount of phosphorous and nitrogen (O'Connell et. al. 1979). It is possible that such changes in nutrient composition of the soil and litter layers may influence the rate of fauna return to the burnt area, though to date no work has examined this possibility.

Not usually discussed in invertebrate studies, is the effect of fire on the soil chemistry and physical properties. Fire can cause changes in the soil organic chemistry by altering or destroying the nature of certain phytotoxic compounds (Christensen 1985), though the effect of this upon invertebrate populations remains largely unknown. Humphreys and Craig (1981) note that high intensity burning can cause an agglomeration of soil particles thus altering the nature of the surface soil fabric. This can lead to an intensification of hydrophobic, or water repellent properties, and may adversely affect infiltration, thus producing harsher microenvironmental conditions for the soil fauna to live.

The effect of fire on invertebrate populations also needs to be examined in light of fire chacteristics. Studying prescribed burning in shrub and woodland communities, Hobbs and Atkins (1988) found that there was a great degree of spatial variation in fire intensity during low intensity burning. This was attributed to differences in fuel distribution and type. They also found that uniform fire treatment was only apparent in very intense fire caused by heavy fuel loads. From studies such as this, it has been hypothesised that the response of invertebrate populations to burning, very much depends on the intensity of the fire in question.

From work conducted in the south-west of Western Australia, where rotational burning is implemented as a management tool, it has been found that invertebrate communities show a wide range of responses to burning. Springett (1976) found that invertebrates populations in jarrah and karri do not recover from burning within a normal five to seven year rotation. Sawle (1979) also found that invertebrate abundance was lower in a nine-year-old burnt karri site compared to a forty-year-old site. Koch and Majer (1980) compared the invertebrate fauna of three jarrah sites with different fire histories. From this study they found that invertebrate species richness is reduced for at least three years following fire. Majer (1984) also studying jarrah, found that invertebrate abundance had still not recovered from burning effects, thirteen months following fire.

In contrast to these studies, Whelan, Langedyk, and Pashby (1980) found that a two-week-old burn site in jarrah-Banksia woodland contained a greater abundance of invertebrates than compared to adjacent unburnt areas with similar vegetation. Abbott (1984), studying jarrah forest, found that the majority of soil and litter fauna recovered within three years of burning, with many taxa occurring in greater numbers in the burnt area.

The reasons for these different findings may well be attributed to variances in experimental design, intensity of fire studied, and the level of taxonomic treatment used (Majer 1984). Gill and Groves (1981) and Majer (1985) further suggest that such differences in findings may be a response to the season of burn.

In comparison to the numerous studies conducted in the forest areas of the south-west, very little work has examined invertebrates in the semi-arid areas of Western Australia. Hutson (1985), Majer (1985) and Hopkins (1985) have all postulated that the invertebrate fauna becomes less resilient as aridity increases. However only few studies, notably Majer (1985) and Hutson and Veitch (1983) have examined the influence of fire on invertebrate communities over a changing climatic gradient.

Comparing burning in dry wandoo (Eucalyptus wandoo) at Dryandra to burning in moist jarrah (Eucalyptus marginata) at Karragullen, Majer (1985) found that invertebrates in the jarrah recovered more quickly following fire. He attributed this to differences in annual rainfall. Similarly, from their studies of Eucalyptus forest in south-eastern Australia, Hutson and Veitch (1983) found that both collembolan and mite densities increased with rainfall. These findings have important implications for possible invertebrate responses to fire. Lower rainfall and associated drier conditions, may cause slower plant regeneration following fire. Hence, harsher, more arid conditions, are likely to be prevalent in the soil and litter for a longer time period following fire, thus reducing the rate at which invertebrates are able to recolonise the burnt site (Majer 1985). Cowling and Lamont (1985) have found that growth rates for several Banksia species deteriorates as rainfall declines. It thus appears quite plausible that fire effects on arthropod communities are more long-lasting in semi-arid areas than in the moister forest areas, due to the slower regeneration of the vegetation and subsequent harsher microenvironmental conditions.

From studies in South Australian indigenous forest, Hutson (1985) found that the half-life of litter for three forest types (annual rainfall of 1050, 690, and 635 mm) increased with aridity. This change in litter decomposition was also positively associated with the decomposer organisims whose density also declined as aridity increased (Hutson and Veitch 1985). Given the lower density of decomposer organisms and the slower rate of litter decomposition, it is quite possible that burning would have a significant deleterious effect on nutrient recycling in more arid and semi-arid environments.

The areas of native vegetation remaining in the semi-arid wheatbelt area of Western Australia are charcaterised by woodlands and shrublands (Brown and Hopkins 1983). Within the wheatbelt, the woodlands tend to occur on sandy loams and clays on lower slopes whereas the shrublands are predominantly confined to sands and gravels derived from residual areas of laterite (Mulcahy 1973, Nyagba 1976). Such shrublands are termed "kwongan" (Beard 1976), and this vegetation type has been extensively studied in terms of its floristic composition (Brown 1989) (Brown and Hopkins 1983), modes of nutrition (Lamont 1984), and its adaptive responses to fire (Bell et. al. 1984). However, no reported invertebrate surveys have yet been conducted in this vegetation type. Subsequently, the effects of fire upon invertebrate communities in kwongan are as yet unknown.

Fire policy in Western Australia falls under the jurisdiction of the Department of Conservation and Land Management (CALM). This department presently designates the majority of its lands in the semi-arid wheatbelt areas as falling under a "No Fire Regime" classification (Underwood 1988). This prohibits the use of prescribed burning for any purpose, except for possibly habitat management, wildlife research, or fire protection (CALM 1988). In most cases a "No Fire Regime" policy is applied to special management areas (where species sensitive to fire exist), research reference areas, areas where a lack of information neccessitates such a policy, and areas which are required to be left unburnt so as to provide a diversity of fire ages within a reserve (Underwood 1988). The kwongan sites examined in this study lie within Tutanning Nature Reserve which has such a "No Fire Regime" policy.

The purpose of this study is two-fold. Firstly, it aims to examine the invertebrate communities of three different fire-age, semi-arid kwongan sites for possible signs of long-term fire effects. Litter cover, plant floristics and structure are assessed and possible relationships between these parameters and the invertebrate populations are addressed. Secondly, it is intended that the findings of this study will be used as baseline data for a long-term study, examining the effects of a prescribed burn in the youngest the kwongan site, planned for autumn 1990.

CHAPTER 2

STUDY SITE - THE TUTANNING NATURE RESERVE

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2.1. Location, Climate and History

Tutanning Nature Reserve is located at 32°^31°S, 117°23°E, and lies approximately 150km SE of Perth (see Fig. 1). It covers an area of 2194 ha. The closest town is Pingelly, located 18km to the north-west of the reserve.

The area has a mediterranean-type climate with the majority of rainfall occurring during winter between the months of April and August. Figures 2 and 3 show the mean monthly temperature and average annual rainfall for Narrogin, located 40km south-south-west of the reserve.

Tutanning was declared a nature reserve in 1960 (G. Friend pers. comm.). The numerous natural vegetation communities contained within the reserve serve to provide baseline habitat information necessary to study the effects of adjacent agriculture on the soils and geomorphology of the area.

2.2. Geology, Topography and Soils

The soils and landforms and their relation to the geology of Tutanning, have been extensively described by Nyagba (1976). The elevation of Tutanning varies from 320 to 430m above sea level. The area is fairly rugged, characterised by numerous residual lateritic caps, usually separated by steep scarps, concave pediment slopes or by incipiently stripped zones (Nyagba 1976). These residual sites are situated about 30-35 metres above the main drainage lines which are principally first order streams (Nyagba 1976). An idealised three dimensional view of Tutanning is presented in Fig. 4 (A. Hopkins pers. comm.).

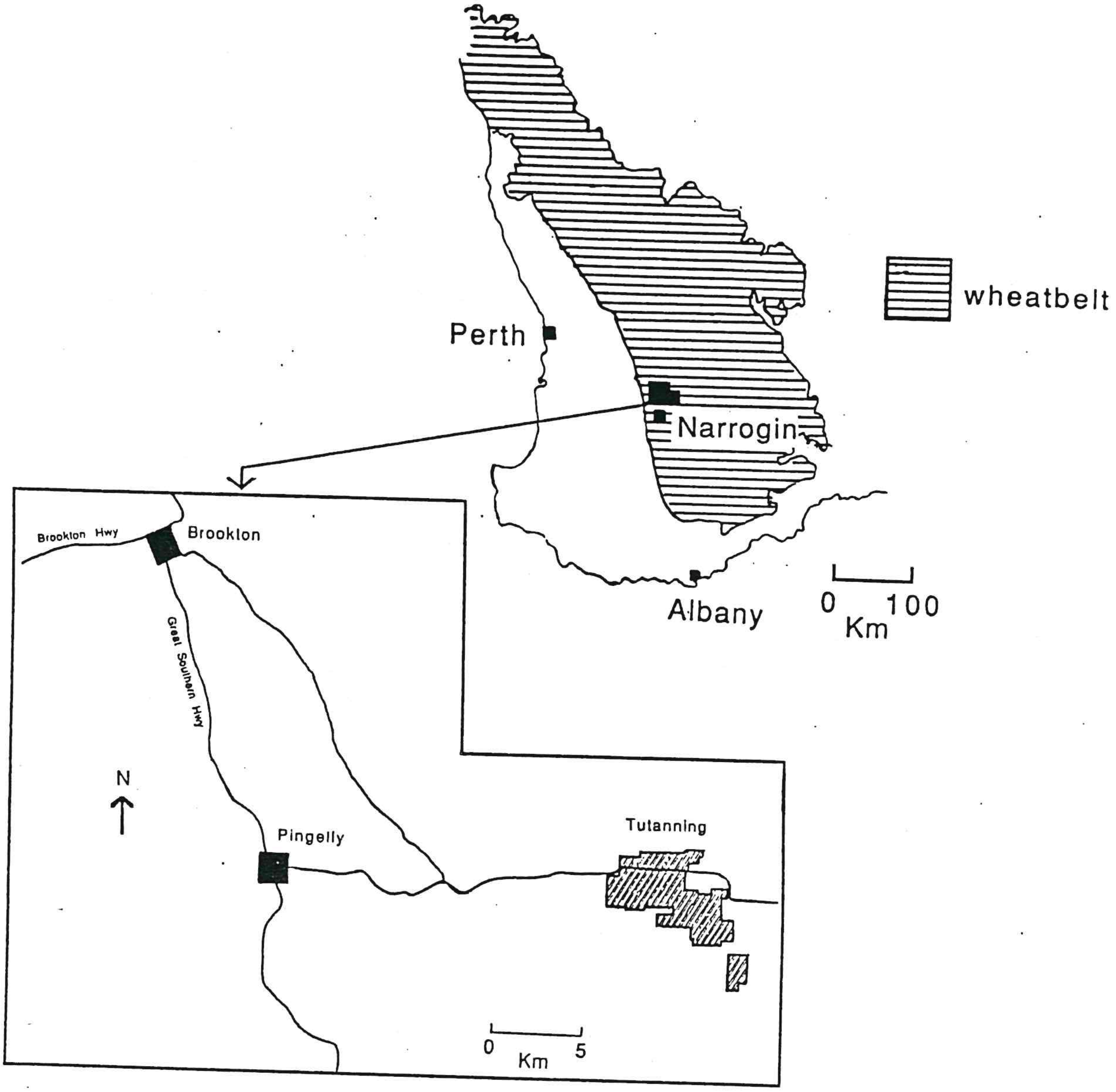

FIG. 1. Map of south-west Western Australia showing the location of Tutanning Nature Reserve.

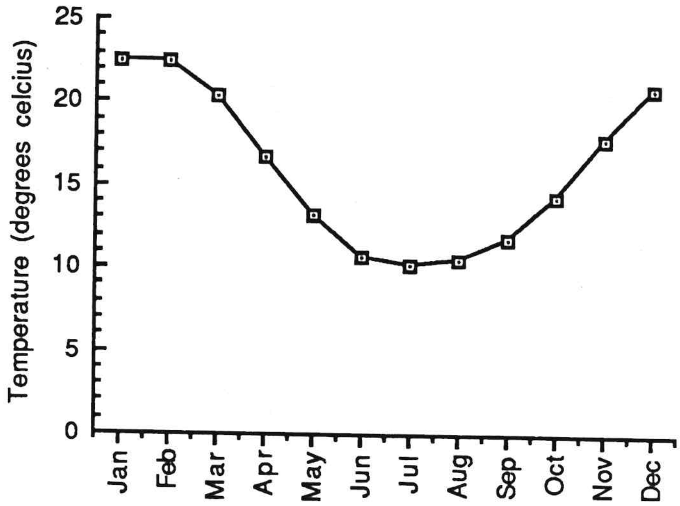

FIG. 2. Mean monthly temperature for Narrogin, located 40km SE of Tutanning.

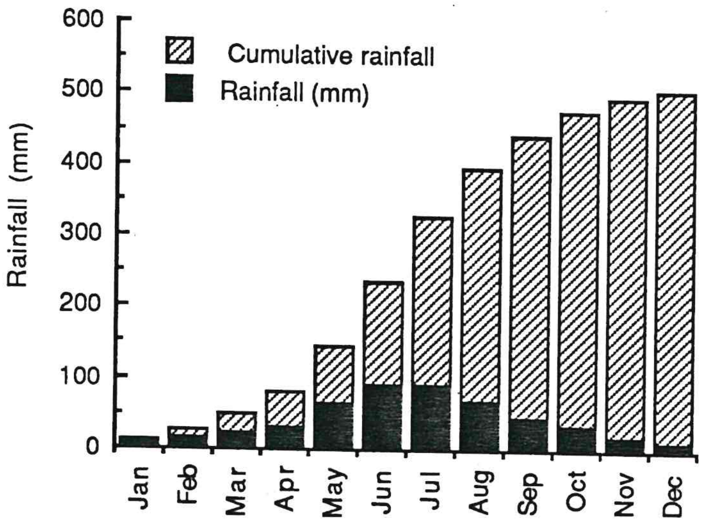

FIG. 3. Average monthly rainfall for Narrogin, located 40km SE of Tutanning.

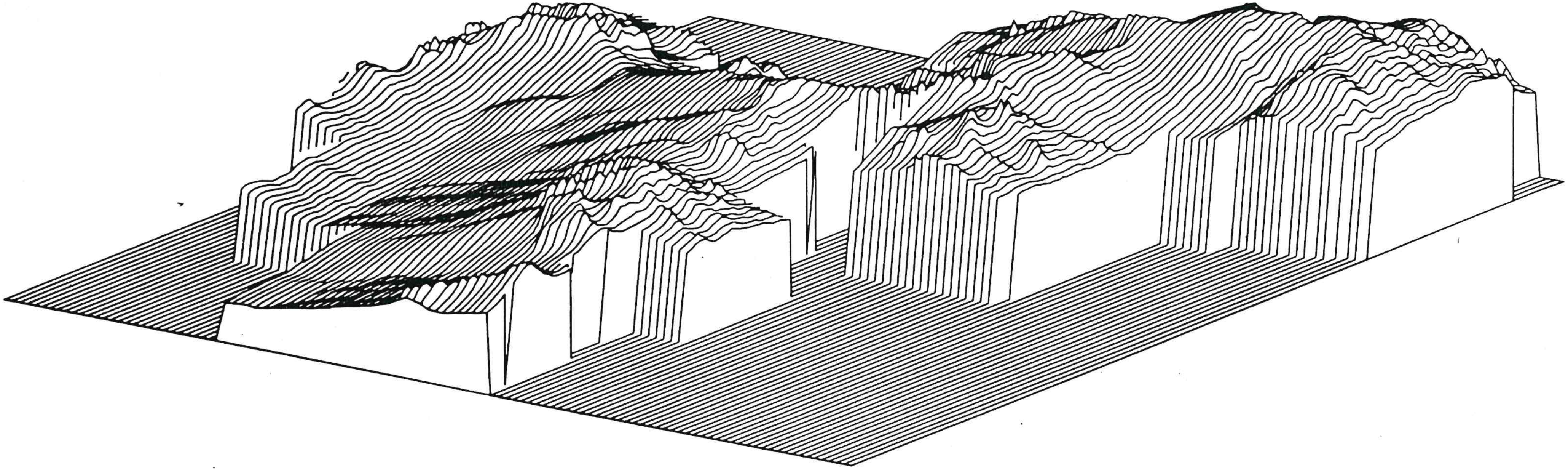

FIG. 4. An idealised three dimensional view of Tutanning showing the landform features (slopes are exaggerated) (A. Hopkins pers. comm.).

The three sites of kwongan vegetation examined lie on the midslope position and conform with the Magpie soil mapping unit as described by Nyagba (1976), and the Norrine landform unit as described by Brown and Hopkins (1983). This soil shows a duplex profile with the surface A horizon being brown or grey sand, usually characterised by an abundance of ironstone gravels (2-15mm diameter). This horizon passes through a sharp boundary 10 - 25 cm below the surface, to what Nyagba describes as a sandy clay loam. Nyagba's classification of this lower B horizon as a loam is questionable, considering that this layer is massive and compact with low porousity and poor internal drainage. This B horizon is almost impenetrable during summer, and I would tend to class this layer as a sandy clay according to Northcote (1979) (Fig.5).

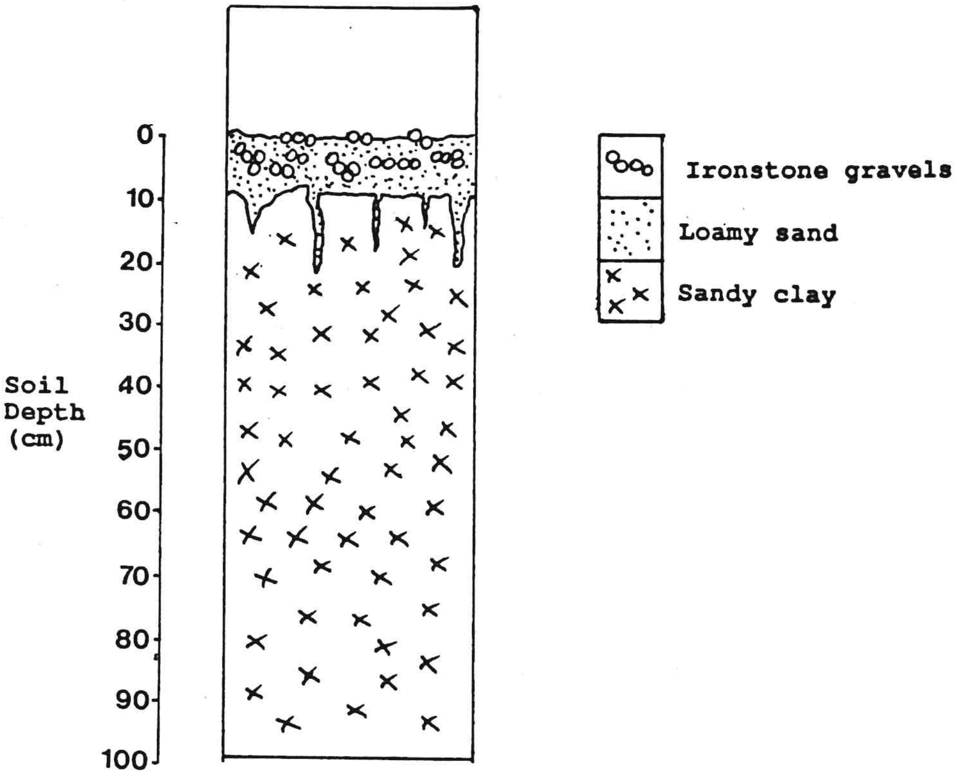

FIG. 5. Soil profile of the study sites (based on Nyagba's (1976) Magpie Soil Mapping Unit).

2.3. Vegetation

The vegetation communities at Tutanning are closely related to soil type and topography, though Nyagba (1976) notes that several soil boundaries transgress vegetation boundaries. The lateritic and granitic uplands are characterised by Dryandra and Petrophile shrublands with open woodlands of powderbark wandoo (Eucalyptus accedens). The breakaway faces containing sandy loams and loams support brown mallet (Eucalyptus astringens) or powderbark wandoo (Eucalyptus accedens). Lower gravel slopes support communities of wandoo (Eucalyptus wandoo). Stands of sheoak (Allocasuarina huegeliana) are related to granite outcrops and gritty sand deposits (Nyagba 1976), (CALM 1988).

The floristic composition of the kwongan communities in Tuttaning has been documented by Brown and Hopkins (1983). The kwongan vegetation is extremely species rich, containing over half the species in the entire reserve (Brown and Hopkins 1983).

2.4. Fire History

Fire has formed an integral part of Tutanning's history. Figure 6 shows the reserve in terms of its most recent fires, and the location of the three study sites. For the purpose of this thesis, the three kwongan study sites are identified and referred to by the year they were last burnt, i.e. 1932, 1940, and 1965. All three sites were burnt by wildfire, but the intensities of these fires are unknown.

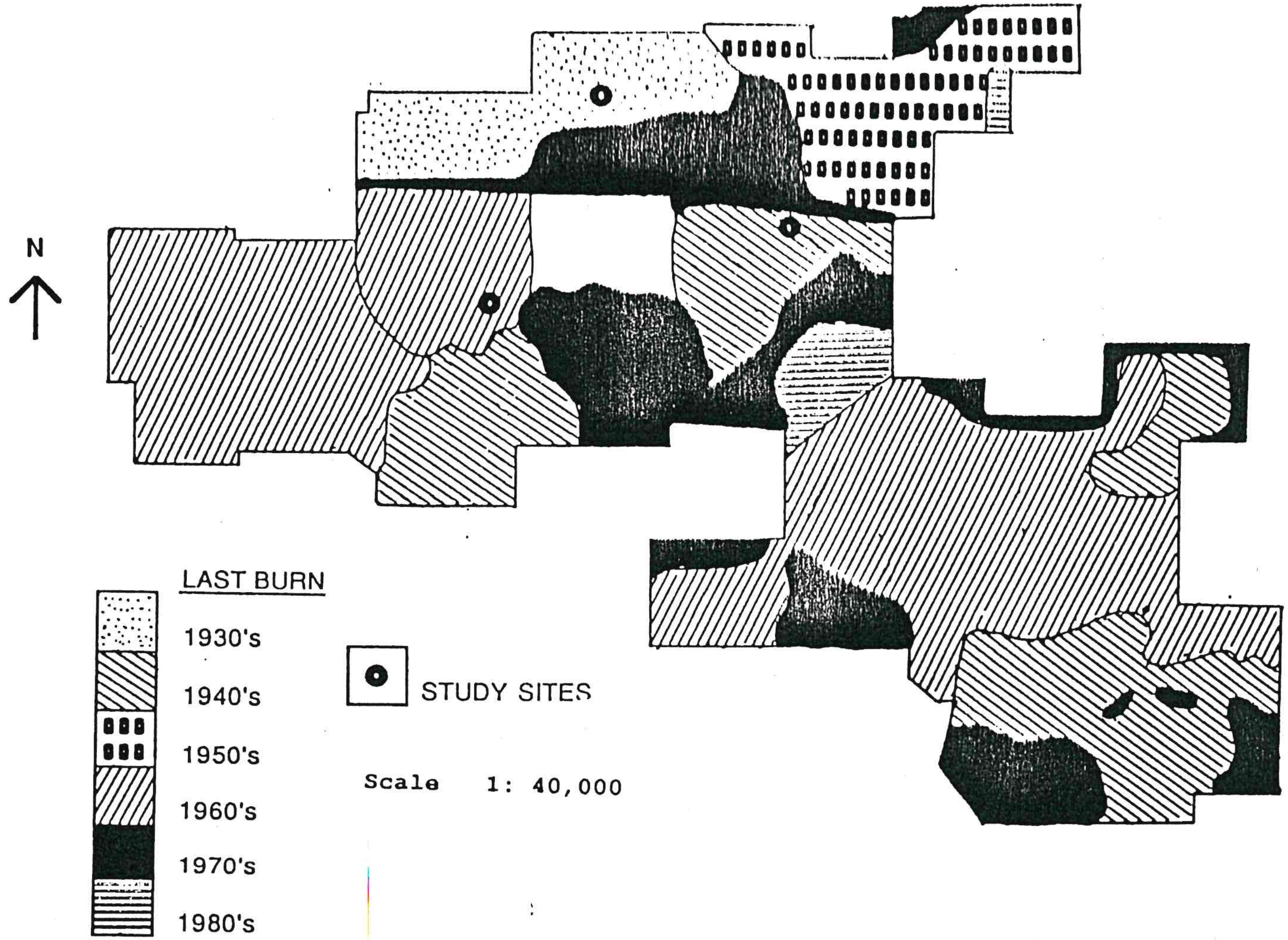

FIG. 6. Tutanning Nature Reserve - Fire History.

CHAPTER 3

METHODOLOGY

METHODOLOGY

3.1. Invertebrate Sampling

Pitfall traps were used to sample the invertebrate fauna. The limitation of this sampling technique is outlined by Southwood (1966) and Adis (1979). Although limited in its efficiency for comparing different community types and estimating absolute invertebrate populations, Southwood (1966) notes that this method can be used to assess the relative abundance of invertebrate populations of similar habitat types. Pitfall trapping was also selected because of its ease of operation. The method is also consistent with the invertebrate sampling being conducted by G. Friend and D. Mitchell (CALM), who are examining the invertebrates in other community types at Tutanning, Kellerberrin, and in the Stirling Range National Park.

Two grids were placed on each site so that within-site variation of invertebrate abundances and diversity could be examined in relation to the between-site variation. Each grid consisted of four replicates. A numbered stake at each corner of the grid enabled the replicates to be identified according to their position on the grid: 1 or 5 = SW, 2 or 6 = NW, 3 or 7 = NE, 4 or 8 = SE (numbers 1 - 4 correspond to the first grid, numbers 5 - 8 correspond to the second grid). Grids were identified by the year of burn and the number alloted to the staked south-western corner of the grid (i.e. 1 or 5) (Figures 7-12).

Sixteen pitfalls spaced at 5m intervals, were placed in each grid. This created a 4 X 4 matrix of pitfall traps covering an area of 15m X 15m per grid (see Fig. 13). Each pitfall trap consisted of a plastic cup (90mm diameter, 110mm deep). This was placed inside a sleeve of PVC piping, enabling pitfall traps to be set and removed with minimum disturbance to the surrounding soil and litter. This design of trap is described by Majer (1978).

FIG 7. Grid 1932/1

FIG. 8. Grid 1932/5

FIG. 9. Grid 1940/1

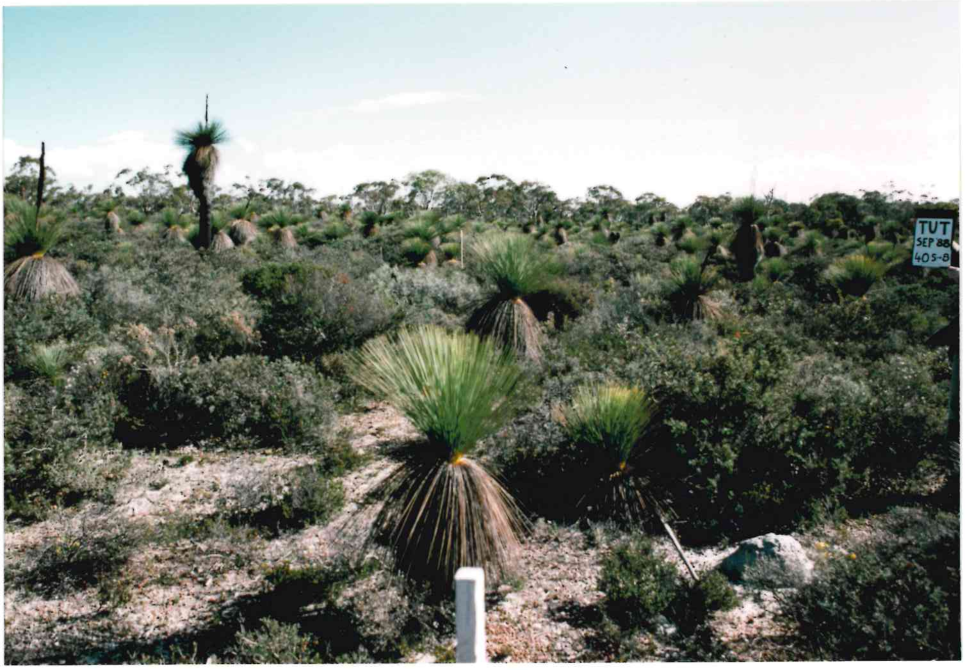

FIG. 10. Grid 1940/5

FIG. 11. Grid 1965/1

FIG.12. Grid 1965/5

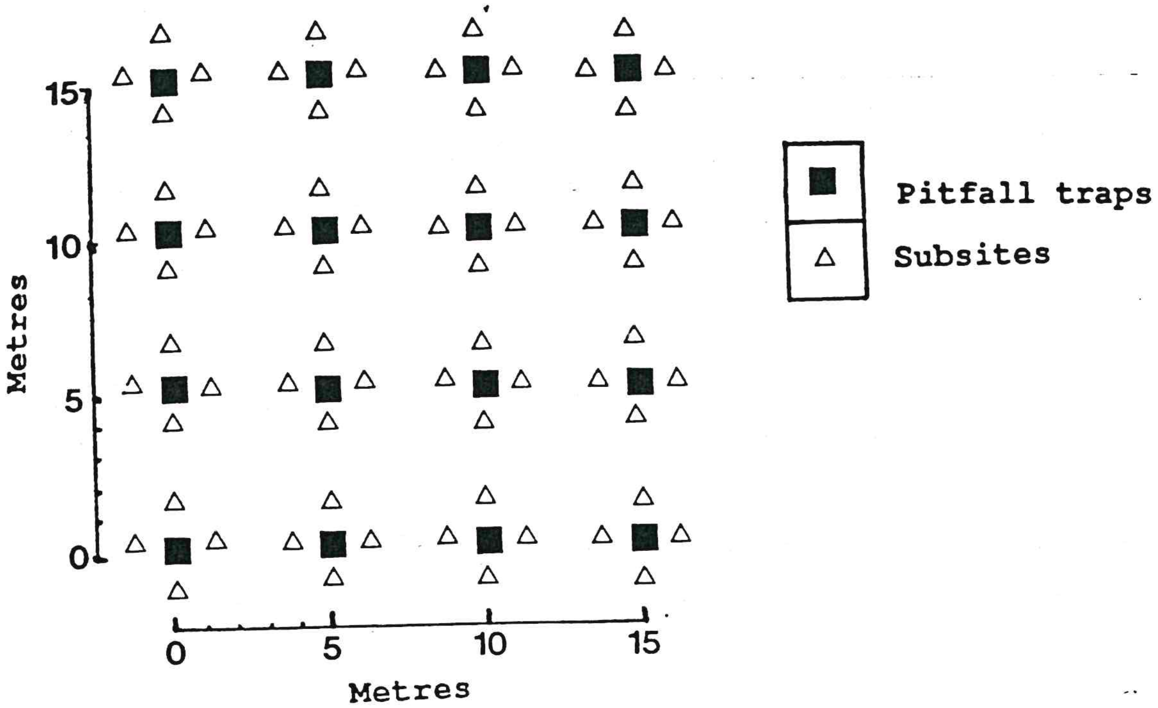

FIG. 13. Layout of an invertebrate sampling grid.

When in use, each pitfall was filled with Galt's solution (see Appendix 1). Greenslade and Greenslade (1971) have noted that certain preservatives can influence invertebrate catches, however invertebrates do not appear to be attracted by Galt's solution (G. Friend pers. comm.). At the end of each sampling period the pitfall traps were collected, and the four pitfall traps about each corner of the grid bulked to form four replicate samples from each grid (see Fig. 14). These replicate samples were marked according to their date set and date collected, site (1932, 1940, or 1965), and position on the grid (i.e. 1-4 or 5-8, depending on the grid) (Fig. 14). Samples were then transferred from Galt's solution to 70% ethanol. Sand-filled cups were then placed in the PVC sleeves to close the pits until the next sampling period.

Pitfall traps were installed in March 1988. Sampling was started in May 1988 to minimise digging-in effects as found by Greenslade (1973), with pits being opened and run for ten days every second month. It should be noted here that sampling periods are identified by the month the pitfall traps were set, not collected. Although sampling is still continuing, this study examines only six sampling periods concluding with the February 1989 sample. In most instances there was a six-week break between sampling periods. However, between the January 1989 and February 1989 samples there was only a four-week break due to a scheduled prescribed burn planned for March 1989. It should be noted that this prescribed burn did not eventuate and has been rescheduled for March-April 1990.

FIG. 14. Collecting the Pitfall Traps.

Laboratory analysis was conducted using a stereo microscope. Many of the samples were heavily contaminated with bark, soil, and gravel which made sorting of Collembola (size range) particularly difficult. Collembola were present for all samples, but due to the reasons mentioned they were omitted from the taxonomic sorting.

Invertebrates were initially sorted to class level. Arachnids and insects were subsequently identified to order level, the latter with the aid of the keys in C.S.I.R.O. (1970). The abundance of each taxonomic unit was then recorded for each sample. Hymenoptera Formicidae (ants), Coleoptera adults (beetles), and Araneae (spiders) were placed in separate vials, the latter being taxon identified to family and species levels using the classification keys of Main (1980) and Mascord (1980).

3.2. Habitat Assessment

Habitat assessment was conducted using methods devised by G. Friend and D. Mitchell (pers comm.) at CALM, Woodvale. Measurements were taken at four subsites, located at 1m intervals (N,S,E,W) from each pitfall trap (see Fig 13). Therefore there were a total of 16 subsites per replicate, or 64 subsites per grid. Selected subsites were permanently marked by a metal square (40mm X 40mm). Structure was also assessed over the entire quadrat.

3.2.1. Subsite Measurements

The following attributes were recorded at each subsite:

1. Presence/absence of lichen or moss. The number of occurrences was tallied for each replicate, and converted to a percent. This was subjected to a log transformation. General Linear Modelling procedure (GLM) was then used on this transformed data to assess site differences (Ott 1984).

2. Leaf litter cover (%) in a 30cm X 30cm area. This was scored as 0=absent, 1=1-25%, 2=25-50%, 3=50-99%, and 4=100%.

At each site, litter cover was recorded from 128 subsite locations. These were scored into one of five categories as described above. The frequency of each of these five categories was totalled per site. No further statistical analysis was conducted.

3. Number of units of woody litter - "trash" (dead/down branches or logs >5mm diameter) bisected by a plane 50cm each side of the subsite. Woody litter diameter categories were as follows: 1=5-10mm, 2=10-25mm, 3=>25mm.

Three categories of woody litter were assessed, and the frequency of occurrence of woody litter in each of these categories was noted for each subsite. The frequency of occurrence was then totalled for each replicate. From these data, means and standard errors of the frequencies were calculated for each of the woody litter classes in each site. Since the raw data conformed to a normal distribution, log transformation was not conducted. GLM was used on the raw data to examine site differences, grid within site differences, and a possible interaction effect between the woody litter categories and sites. Scheffe's (1953) test was then carried out to identify sites with similar and dissimilar means.

4. Number of touches of vegetation on 11 intervals of a vertically held levy rod. Height intervals (cm) used were as follows: 1=0-12.5, 2=12.5-25, 3=25-50, 4=50-75, 5=75-100, 6=100-125, 7=125-150, 8=150-175, 9=175-200, 10=200-250, 11=250-300, 12=>300.

These data were used to calculate horizontal and vertical distribution of plant foliage.

The horizontal distribution of plant foliage was calculated by dividing the number of subsites within each replicate which had a recorded "touch" by the number of subsites within each replicate (n=16). This was then converted to a percentage. The mean percent foliage cover for each site was calculated from the eight replicate samples of each site. The percent foliage cover for the replicate samples was then transformed to natural logs since it was based on count data and showed a skewed distribution. GLM was subsequently performed on the transformed data to identify any significant differences between sites and between grids within sites.

The vertical distribution of plant foliage was obtained by calculating the plant cover density (a measure of thickness of vegetation where it occurred). Plant cover density was obtained for each site by dividing the total number of plant contacts per levy rod interval by the number of rods which touched any vegetation. This was then used to create a vertical profile of plant cover density.

The levy rod data did not conform with a normal distribution. Statistical analysis of the levy rod data was thus performed by transforming the data to natural logs, with zero values being replaced by a value of 1.0. This last point needs to be justified. There were numerous zero values in the higher levy rod intervals, thus causing a skewing of the data. Replacement of these zero values with a value less than 1.0 resulted in negative log values being attained, again highly distorting the distribution of the data. Merging the various upper height intervals resulted in a loss of information. It was thus decided to replace zero values by a value of 1.0, the natural log of which gave a reading of zero. However, the statistical validity of the levy rod results must be questioned.

5. Majority of touching vegetation in intervals 1 - 11 alive or dead.

For each subsite with a recorded vegetation "touch", the majority of vegetation touching the levy rod was assessed as being alive, and given a value of 1, or dead, achieving a value of 0. The percentage of live standing vegetation per site was then calculated by tallying the number of "alive" recordings per site, and dividing this by the number of subsites which had a recorded "touch". The data were then transformed to natural logs since they did not conform to a normal distribution, and GLM used to assess site differences and grid differences within sites.

3.2.2. Grid Measurements

The following site characteristics were measured over the entire grid:

1. Percent of total foliage in each of five layers. i.e. 1 - 0.5m, 0.5 - 1.0m, 1.0-2.0m, 2.0-5.0m, and >5m.

2. Percent canopy cover (>2m) derived from four readings (N,E,S,W) of a canopy densiometer taken over the centre of each quadrat.

3. Projected foliage cover (percent) of understorey vegetation (<2m).

4. Percent of soil surface which is sand <2mm; gravel 2-4mm; gravel 5-10mm; and gravel >10mm.

5. Slope in degrees, measured North to South, and East to West.

Measurements of these site characteristics were then averaged for each site and standard errors calculated.

3.3. Floristics

The plant floristics survey was conducted by A. Hopkins and J. Harvey in early November 1988. A 5.64 metre radius circle, encompassing an area of 100 square metres, was centred on each grid. The plant species falling within the radius of the circle were recorded and given a rank based on an 8-point foliar abundance (percentage cover) scale. For the purpose of this study, however, only presence/absence was considered. Recordings of species' presence/absence for each grid is given in Appendix 2.

Hierarchical Classification Analysis (HCA) was conducted on the presence/absence data using the average-linkage method and squared Euclidean distance as the distance measure (Gauch 1982).

Similarity of the plant species composition of the six grids was also examined by using using Sorensen's (1948) "quotient of similarity" (QS). This is calculated by the following formula:

$$QS= \frac{2c}{a + b}$$, where

a=number of species in sample A
b=number of species in sample B
c=number of species common to samples A and B.

HCA was also performed on Sorensen's similarity index to examine if these groupings differed from those identified by HCA on the presence/absence data.

3.4. Statistical Analysis of Invertebrate Data

Computer analysis of the invertebrate abundance data was conducted using the SAS package on the VAX 3 and VAX 7 computers at Curtin University.

Normality of the abundance data could not be assumed, hence non-parametric tests were initially employed on the data. A chi-square analysis was used on the unsorted abundance data to test the independence of sites (1932, 1940, and 1965) vs. seasonality (months) (May '88, July '88, September '88, November '88, January '89, February '89) using the total number of invertebrates. This analysis was then carried out on the individual taxa.

A categorical modelling procedure using log-linear models (CATMOD) (Fienberg 1980, SAS 1985) was then used to test the significance of sites, months, grids nested within sites, and the interaction effect between sites and months, by using the individual invertebrate taxa as the response variable. It should be noted that zero abundance values were replaced by a very low positive value (0.0001) so that the log-linear modelling procedure could work.

Analysis of variance was then conducted on the taxa using log-linear modelling in order to examine how site preferences, time of sampling (months), and grid within-site differences, affected the populations of the invertebrate taxa. Log linear modelling was selected because it minimises the influence of "accidental" fluctuations in the populations of the common taxa on the number of observations of the less common ones. Simultaneously, this procedure also allows the dominant species to influence the statistical index more than a rare one (Huhta 1979). Log linear modelling also aligns the data so it more closely resembles a normal distribution (S. Ganeshanandam pers. comm.).

Scheffe's pairwise comparison tests were performed on those groups showing a significant differences between months. These tests grouped months with similar means together. Similarly, Scheffe's tests were performed on those taxa showing a significant difference between sites, grouping sites with similar means together.

3.5. Statistical Analysis of Spider Data

A species reference collection was created from the spiders captured. This collection is currently kept at Curtin University, School of Biology. Spiders were identified by using the keys of Main (1980) and Mascord (1980). Dr. Louis Koch helped in distinguishing between males, females, and juvenile spiders, and assisted in identifying these species according to family. Classification of the spiders proved to be difficult since many of the species had not previously been recorded (L. Koch pers. comm.). Although positive identification of some of the spiders to family level may be questionable, the author is confident that the reference collection correctly represents a species level classification.

A table of total spider abundance for each site at each sample period is provided in Appendix 3. Community parameters calculated from the spider abundance data include total number of individuals, species richness, and the evenness of species distribution. Total spider abundance was obtained by summing individuals of all species occurring in each of the eighteen site/month samples. Spider species richness (S) was obtained by summing the number of species collected in a particular month and site. The community diversity was estimated using Shannon's (1948) H index which attempts to give a measure of species richness and evenness (Majer 1981). Shannon's (1948) H index is calculated by the following formula:

$$H = -\Sigma n_i \log_e n_i$$

where H is the information content of a sample, S is the number of species, and n_i is the importance value of the ith species. This formula can also be used to derive the evenness index (J'). The evenness index if calculated from the following formula:

$$J' = \frac{H}{\log_e S}$$

The higher the value of J', then the greater degree of evenness in the relative abundance of individuals of each species.

Similarity of spider fauna in terms of species composition and abundance was examined using Hierarchical Classification Analysis (HCA). This utilised the average-linkage method to cluster groups using squared Euclidean distance as the distance measure (Gauch 1982). This analysis procedure used the spider totals for each of the eighteen month/site combinations, and then clustered these combinations so that similar communities were grouped together.

CHAPTER 3

RESULTS

RESULTS

4.1. Climate Data

The mean monthly temperature and monthly rainfall for the duration of the study, are provided in figures 15 and 16.

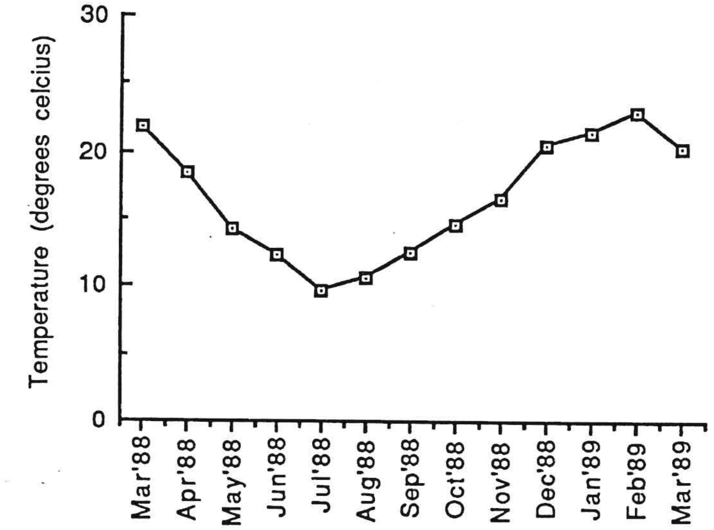

FIG. 15. Mean monthly temperature (Narrogin), March 1988 - March 1989.

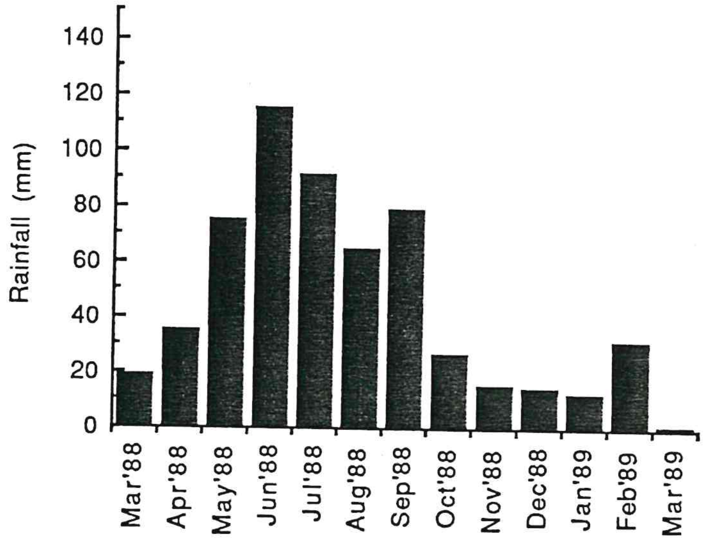

FIG 16. Monthly rainfall (Narrogin), March 1988 - March 1989.

4.2. Habitat Results

4.2.1. Subsite Measurements

GLM revealed no significant difference in lichen cover between sites.

Figure 17 shows the frequency of occurrence of the five leaf litter classes surveyed at each site. Note that this figure shows the frequency of predetermined leaf litter distribution classes. As such this figure only gives insight into the horizontal distribution of litter and not vertical density, though the latter is inferred from this diagram. Hence, for the purpose of this study reference to leaf litter distribution (leaf litter cover) is supported by the findings presented in this diagram, whereas reference to leaf litter density will be based on the assumption that there is a positive correlation between density and distribution.

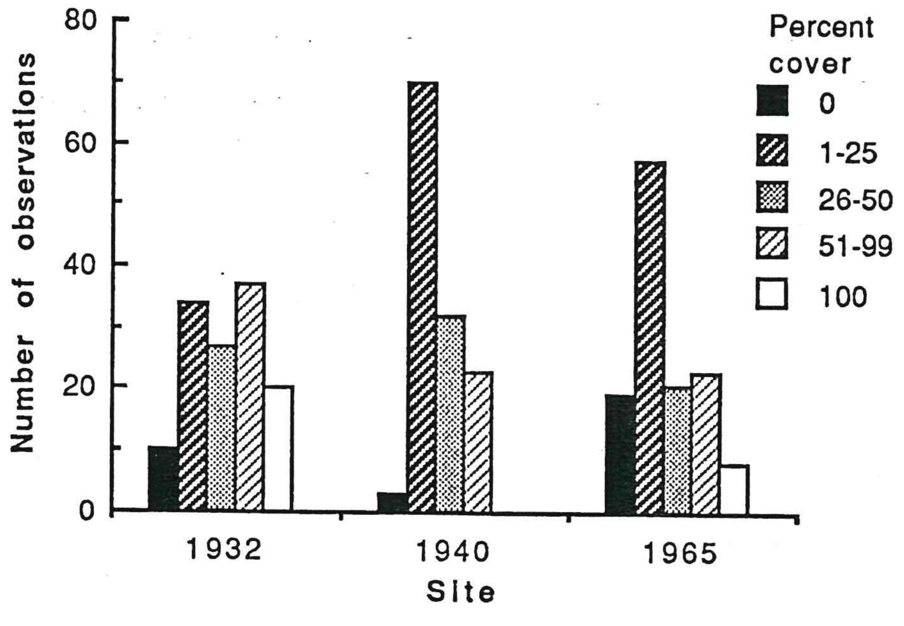

FIG 17. Frequency of occurrence of the five leaf litter classes for each of the three burn sites.

Although no statistical analysis was conducted on the leaf litter cover data collected, differences in litter distribution between the three sites are apparent. Litter is more abundant in the 1932 site with numerous subsites containing 100% litter cover. A lighter litter load characterises the 1940 site and this appears to be evenly distributed throughout the site. In contrast the 1965 site is more barren than the other two sites, as shown by the high number of observations of the 0% litter class, and litter seems to be concentrated in pockets, as inferred from the frequency of the 100% cover values.

GLM revealed no significant difference in woody litter abundance between the grids within each site. However, GLM did reveal a significant difference between sites in terms of the abundance of woody litter (F=6.65, P>0.01). Scheffe's groupings revealed that the 1932 burn site had a higher mean frequency (26.5) of occurrence of woody litter than the other two sites. This can be seen in figure 18. GLM also revealed a significant site difference for the individual woody litter categories (F=3.79, P>0.01). From figure 18, it can be seen that the 1932 site has the greatest abundance of woody litter with a diameter of 5-10mm, while the 1940 site has the least woody litter in the 10-25mm diameter category.

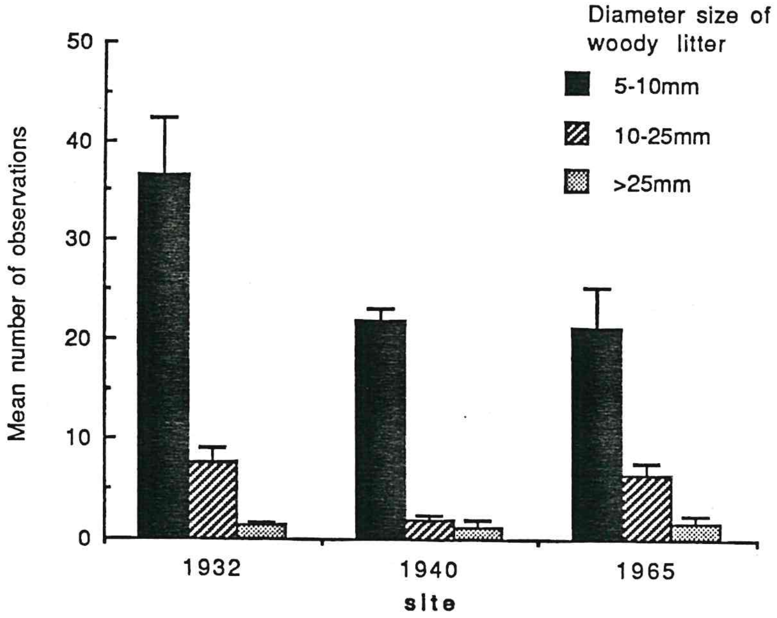

FIG. 18. Site differences in the mean frequency of the three woody litter categories (n=8). Standard error shown as bars above the means.

Analysis of the levy rod data revealed no significant differences in canopy cover between sites or between the grids of each site.

Analysis of the vertical structure (levy rod height interval data) revealed no significant difference between grids within sites. However, GLM showed that there was a significant difference between sites in terms of the frequency of vegetation "touches" ($F=4.89$, $P>0.01$). From Scheffe's groupings it was found that the 1932 and 1940 site were not vastly different from the 1965 site, but the 1932 and 1940 site were very different from each other. The 1932 site had the highest number of "touches", while the 1940 site had the lowest. The interaction effect between site and levy rod interval fell just outside the 0.05 level of significance indicating that the number of recordings in each interval was not significantly different between sites. However, from the plant cover density profiles provided in figure 19, it is apparent that the 1940 and 1965 burn sites were characterised by very dense vegetation up to 1.0m, with a negligible vegetation cover above 1.4m. The 1932 site, however, showed the presence of emergents in the upper canopy.

GLM found no difference between sites in terms of the percent of live standing standing vegetation.

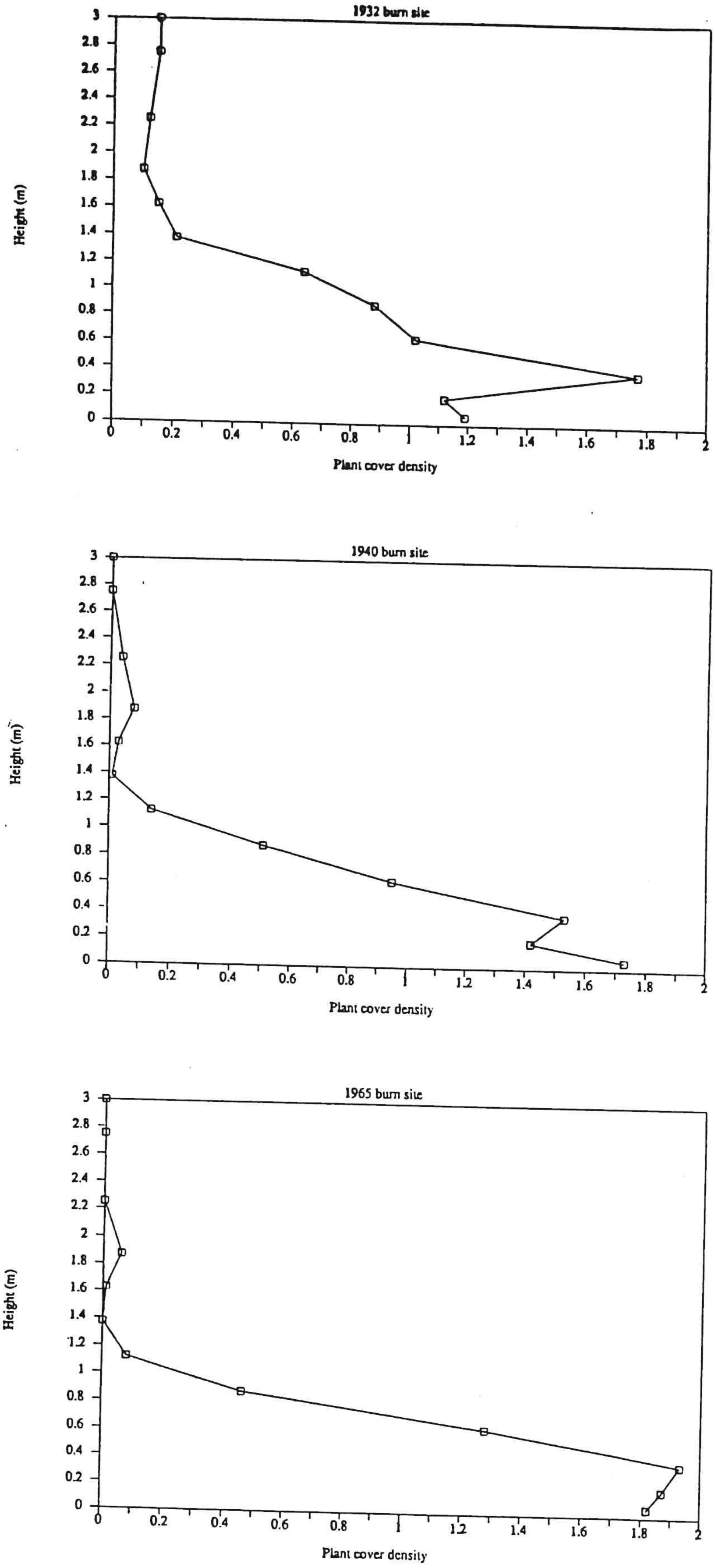

FIG 19. Plant cover density profiles for the three burn sites.

4.2.2. Grid Measurements

Proportion (%) of total foliage in each of five layers (1 - 0.5m, 0.5 - 1.0m, 1.0 - 2.0m, 2.0 - 5.0m, and >5m) as measured over the entire grid, was consistent with the results of the levy rod data. The percentage canopy cover (>2m), and projected foliage cover (%) of understorey vegetation (<2m), revealed trends that were consistent with the information gained by vertical structure measurements for each subsite. Hence, these results are not discussed further.

Figure 20 shows the coarse soil fabric composition of each of the three study sites. There were no significant differences between sites in terms of coarse soil fabric.

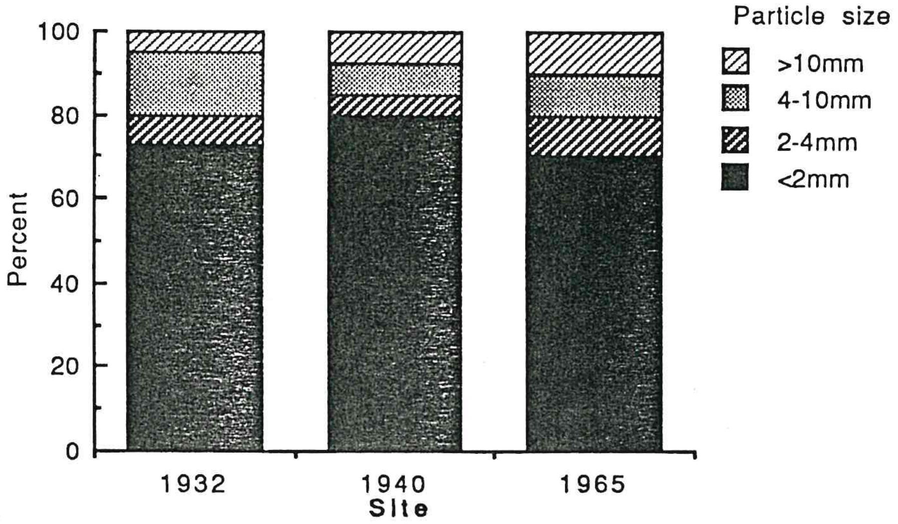

FIG. 20. Coarse soil fabric composition of the three burn sites (n=2).

Table 1 lists the mean slopes of the three sites based on grid measurements. Note that the 1940 site has a steeper EW slope than the other two sites.

TABLE 1. MEAN SLOPES OF THE STUDY SITES (n=2).

Site	Slope (degrees) N-S	E-W
1932	-0.75	-1.25
1940	-0.50	-3.00
1965	-0.5	-1.50

4.3. Plant Floristics

Plant species richness (S) for the three sites was 83, 88, and 76 for the 1932, 1940, and 1965 sites, respectively.

The dendogram of the grid groupings identified by HCA on the presence/absence floristic data is provided in figure 21. It may be seen that clustering initially joined the grids from the same sites. The second level of clustering grouped the 1965 and 1932 site together, identifying the the 1940 site as having a different floristic composition from the other sites. It should be noted however that grouping coefficients were low, varing from 35 to 64, indicating that the three sites were not vastly different from one another.

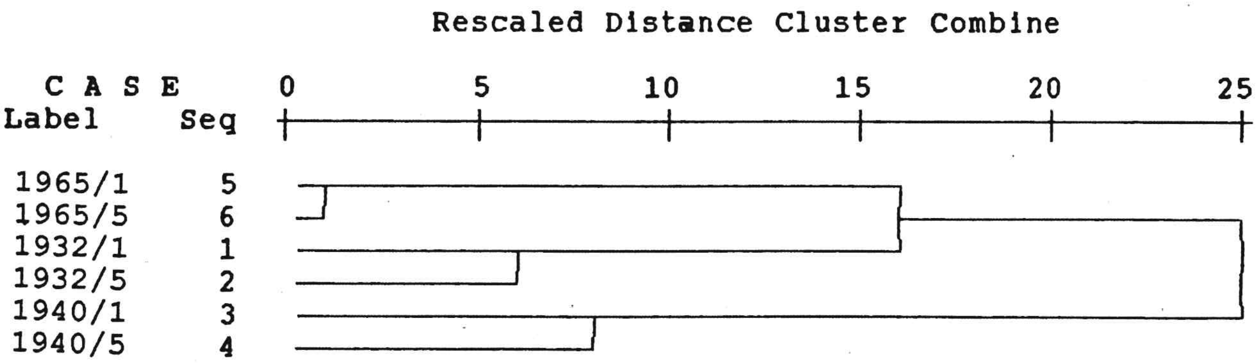

FIG. 21. Dendogram of grid groupings using Hierachical Cluster Analysis on floristic presence/absence data.

A matrix of the calculated Sorensen's (1948) "quotient of similarity" (QS) index for each of the six grids is provided in Appendix 4. The dendogram produced from HCA on this matrix is provided in figure 22. HCA revealed that the grids within each site were initially grouped together, the 1965 site having the least disparity in terms of species composition between its two grids (QS=0.701). The second clustering grouped the 1932 and 1965 site together, identifying the 1940 site as the most dissimilar site in terms of floristic composition. Thus, grouping of the grids on the basis of Sorensen's similarity index confirmed the trend revealed by the groupings of the presence/absence data.

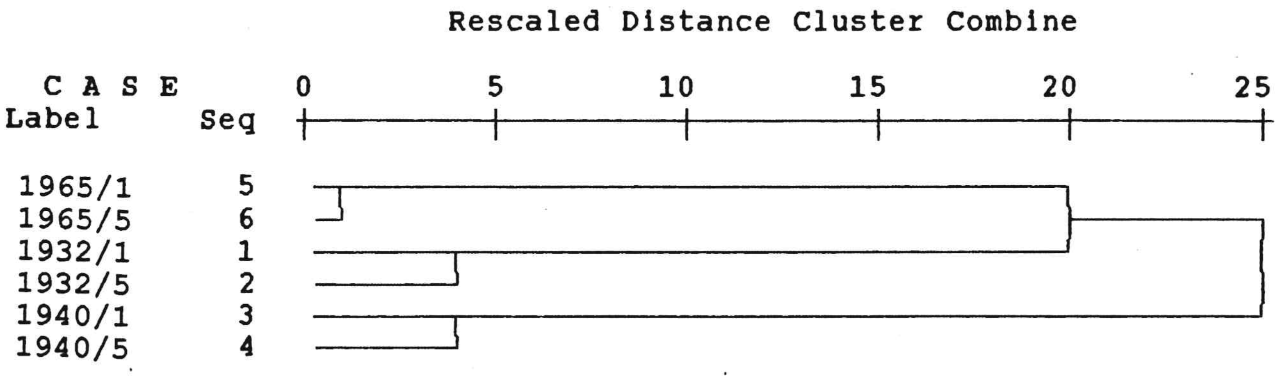

FIG. 22. Dendogram of grid groupings using Hierachical Cluster Analysis on Sorensen's (1948) similarity index.

4.4. Invertebrates

A total of 29 broad taxonomic invertebrate groups (class and order) were sampled: Annelida (worms); Arachnida: Scorpionida (scorpions), Pseudoscorpionida (pseudoscorpions), Opiliones (harvestmen), Araneae (spiders), Acarina (mites); Crustacea Isopoda (woodlice); Diplopoda (millipedes); Chilopoda (centipedes); Insecta: Thysanura (bristle-tails), Blattodea (roaches), Mantodea (mantids), Isoptera (termites), Dermaptera (earwigs), Orthoptera (locusts), Phasmatodea (stick-insects), Psocoptera (bark-lice), Hemiptera (bugs), Thysanoptera (thrips), Neuroptera adults (lacewings), Neuroptera larvae (antlions), Coleoptera adults (beetles), Coleoptera larvae (beetle larvae), Diptera adults (flies), Diptera larvae (fly larvae), Lepidoptera adults (moths), Lepidoptera larvae (moth larvae) Hymenoptera Formicidae (ants), and Hymenoptera others (wasps).

Annelida, Pseudoscorpionida, Mantodea, Phasmatodea, Psocoptera, Neuroptera adults, and Neuroptera larvae all had less than 20 total recorded observations and hence no statistical analyses were performed on these individual taxa. Diptera larvae have also been excluded from analysis analyses since 70 of a total of 113 recorded observations occurred in one replicate.

Chi-square analysis on total invertebrate abundance data revealed that months (seasonality) and sites were not independent (chi-sq value 11399.384, $P>0.001$). Chi-square analysis on the individual taxa showed that only eight invertebrate taxa (Acarina, Araneae, Orthoptera, Hemiptera, Coleoptera - adults, Diptera - adults, Hymenoptera Formicidae, and Hymenoptera (excluding Formicidae) were abundant enough to validate the use of chi-square analysis. Of these eight taxa, all but Orthoptera were strongly influenced by months and sites ($P>0.001$).

Using invertebrate abundances as the response variable, CATMOD yielded a significant difference between the three sites (chi-sq. 2 689 809.02, P>0.001), between the months of sampling (chi-sq. 80 046 190.04, P>0.001), between the grids nested within sites (chi-sq. 8 831.58, P>0.001) and the interaction effect between month and sites (chi-sq. 4 959 643.14, P>0.001).

Analysis of variance on the transformed log abundance data was conducted for total invertebrates (excluding Formicidae) since Formicidae accounted for 60% of total invertebrate captures and thus strongly influenced total invertebrate numbers. From this analysis of variance, it was found that total invertebrates (excluding Formicidae) showed distinct seasonality effects (F=80.20, P>0.001) with abundances peaking in the spring (September and November samples). Site differences were also significant (F=11.23, P>0.001) for total invertebrates (excluding Formicidae) with Scheffe's test on the transformed log data revealing that the 1965 site was characterised by a much lower invertebrate abundance when compared to the 1932 and 1940 sites. A significant interaction effect between sites and months was also found (F=3.01, P>0.001), with the 1932 site showing a peak in abundance in September while the 1940 and 1965 sites peaked in abundance in November. Figures 23 and 24 show site and seasonal variation in the mean number of observations per replicate for total invertebrates and total invertebrates (excluding Formicidae), respectively.

The abundance of Scorpionida was affected by season (F=8.11, P>0.001) with numbers peaking in January (Fig. 25). No site preferences found for this taxa, and there was no significant difference between the grids within each site.

Opiliones were also strongly influenced by seasonal changes (F=37.67, P>0.001) with numbers peaking in July and declining to zero during late spring and summer. A strong site preference was also apparent for this taxon (F=5.41, P>0.01), recorded observations being lowest in the 1965 site. There was also a strong interaction effect between months and sites (F=8.68, P>0.001). From figure 26 it may be seen that Opiliones abundance in the 1940 site peaks sharply in July and then rapidly declines, whereas in the 1932 site captures are consistent over July and September.

Seasonality effects were apparent for Acarina (F=110.84, P>0.001) which peaked in January and were least abundant during May and July (Fig. 27). No site preference was shown for this taxa though the interaction effect proved to be significant (F=2.79, P>0.01). Acarina abundance in the 1932 site rises sharply in September to peak in November, whereas abundance in the 1940 and 1965 sites rises more gradually to peak in January.

Araneae occurred least frequently (F=24.06, P>0.001) in July and peaked sharply in September. Site differences were also apparent for this taxon (F=17.11, P>0.001), the 1932 site having the greatest abundance, and the 1940 site having the least (Fig. 28). There was also a significant interaction effect between months and sites (F=5.23, P>0.001), the 1965 site showing the highest abundance in the May sample, and the 1932 site showing the highest abundance for the other five sampling times.

Crustacea Isopoda were also significantly influenced by season (F=19.75, P>0.001) with numbers being low until January, then rising sharply to peak in February. There is also a significant difference between sites (F=22.54, P>0.001), with numbers in the 1965 site being much lower than the other two sites (Fig. 29). The interaction effect between months and sites was also significant for this taxon (F=5.14, P>0.001). The highest numbers were recorded from the 1932 site between May and November and from the 1940 site, between January and February.

Diplopoda showed strong seasonal effects (F=11.20, P>0.001) with the majority of captures occurring between May and September. This group was absent from the November sample, but low numbers were recorded during the January and February sample periods (Fig. 30). Site differences were also apparent (F=15.61, P>0.001). This taxon occurred least frequently on the 1965 site, with this taxon being present in only two of the six sampling periods. The interaction effect between sites and months was also significant (F=6.82, P>0.001), the 1932 site peaking in abundance in September, the 1940 site in May, and the 1965 site in January.

Only 25 Chilopoda were recorded and these showed no seasonality trends or site differences.

Abundance of Thysanura was influenced by season (F=14.00, P>0.001). This taxon was absent from the May and July samples, but peaked in abundance in November and January (Fig. 31). Site differences were also apparent (F=3.61, P>0.05) with the 1965 site having the highest abundance figures. There was a significant interaction between months and sites (F=4.51, P>0.01). In the 1932 site Thysanura peaked in abundance in November, and in the 1965 and 1940 sites, January.

Populations of Blattodea differed significantly between seasons (F=10.19, P>0.001). This taxon was absent from the September sample, but then peaked in abundance in the January and February samples (Fig. 32). Blattodea also showed significant site preference (F=3.15, P>0.05), occurring most frequently in the 1932 site. However, the interaction effect between sites and months did not prove to be significant.

Strong seasonality effects were apparent for Isoptera (F=41.05, P>0.001). This taxon was absent during May and July but numbers rose sharply in November and peaked in abundance in February (Fig. 33). Site differences and the interaction effect between month and sites both proved to be not significant.

No seasonality effects were apparent for Dermaptera, though site effects proved significant (F=3.48, P>0.05). They were recorded most frequently from the 1932 site and were least abundant on the 1940 site. There was also a significant difference for grids nested within sites (F=3.23, P>0.05), revealing that differences in Dermaptera numbers tends to be very localised. Dermaptera abundance is presented in figure 34.

Orthoptera abundance revealed no significant seasonality trends, though from figure 35 it appears that there could be a possible peak in numbers during spring. Site differences were found to be highly significant (F=8.70, P>0.001), the abundance of Orthoptera on the 1940 site being consistently higher than on the other two sites (Fig. 35). However, grid within-site differences were also significant (F=4.31, P>0.01), indicating that more localised (within-site) influences tend to affect Orthoptera numbers.

There was a significant difference in the seasonality of Hemiptera abundance (F=40.46, P>0.001), with numbers peaking in September (Fig. 36). No site differences were found for this taxon, though the interaction effect between months and sites proved to be highly significant (F=4.32, P>0.001). From figure 36, it may be seen that for the May sample, the 1940 site had the highest number of observations, whereas in the July sample the 1932 site had the highest number. For the remaining four sample periods, the 1965 site had a consistently higher level of abundance.

Thysanoptera abundance was strongly affected by seasonal changes (F=81.38, P>0.001) with numbers being extremely low throughout the duration of the study except for a peak in November (Fig. 37). Site differences also proved to be significant (3.34, P>0.05), the 1940 site being apparently less favourable than the other two sites. There was also a significant interaction between sites and months (F=4.51, P>0.001). The 1940 site returned the highest figures from the September sample period, the 1965 site from the November and February periods, and the 1932 site from the January sample period.

Seasonality effects very significantly influenced the abundance of Coleoptera adults (F=73.43, P>0.001). At all three sites abundance peaked in September (Fig. 38). Numbers were at their lowest during January and February. Site differences were not significant for this taxon, however there was a significant interaction effect between months and sites (F=5.86, P>0.001). The 1940 site had the highest numbers of Coleoptera in May, the 1965 site in July and September, and the 1932 site in the November, January, and February sample periods.

Seasonal changes were found to affect Coleoptera larvae (F=17.20, P>0.001). Abundances peaked from May to July and declined over the spring and summer period (Fig. 39). Site differences were also significant (F=11.99, P>0.001), the 1965 site having much lower numbers than the other two sites. There was also a significant interaction effect between months and sites (F=3.04, P>0.01). It may be seen on figure 40 that the 1940 site declined in abundance from May through to February while the 1932 site peaked in May and September. The 1965 site peaked in abundance in July.

The abundance of Diptera adults showed a strong seasonal influence (F=37.06, P>0.001). Abundance was greatest during the spring (September and November sample), and was lowest during late autumn and winter (May and July) (Fig. 40). The 1940 site appeared unfavourable for this taxon (F=13.35, P>0.001) with numbers being much lower than the 1932 and 1965 sites. A significant interaction effect between months and sites was also apparent (F=4.80, P>0.001). The 1932 site peaked in abundance in September whereas the 1940 and 1965 sites peaked in November.

Populations of Lepidoptera adults were also influenced by seasonal effects (F=7.57, P>0.001). Numbers were highest during spring and lowest during late autumn and winter (Fig. 41). Site differences were also apparent (F=3.41, P>0.001), the number of Lepidoptera adults being higher in the 1940 site. There was also a significant interaction effect between sites and months (F=10.24, P>0.001). The 1932 site peaked in numbers in February whereas the 1940 and 1965 sites peaked in November.

A total of 46 observations were recorded for Lepidoptera larvae and no significant seasonality trends or site differences were found for this taxon.

Hymenoptera Formicidae accounted for over 60% of the total invertebrates trapped. This taxon showed a strong seasonal trend (F=147.42, P>0.001). Numbers were greatest during summer and lowest during late autumn and winter (Fig. 42). Strong site preferences were also shown by the taxon (F=45.95, P>0.001) with the 1940 site containing higher abundances. Grid within-site differences were apparent (F=4.25, P>0.01), indicating that localised effects within each site were influencing captures. The interaction effect between sites and months was also significant (F=3.07, P>0.01). From figure 42 it may be seen that apart from the February sample, the 1965 site was consistently lower in abundance than the other two sites. Whereas abundance showed a steady incline from September to February for the 1932 and 1940 sites, the 1965 site showed a drammatic peak in abundance in February.

Seasonality effects were apparent for Hymenoptera (excluding Formicidae) (F=24.68, P>0.001). Note that two peaks occurred in the abundance of this taxon, one in November the other in February (Fig. 43). There was no significant differences in abundance between sites. However, the months and sites interaction effect was significant (F=4.38, P>0.001). The 1940 and 1965 sites peaked in numbers in November whereas the 1932 site peaked in February.

A summary of the seasonality and site trends revealed by analysis of variance on the transformed log data, is shown in tables 2 and 3. Table 4 provides a list of the principal invertebrate groups trapped, their main food source, the season they peaked in abundance, and any site preference shown.

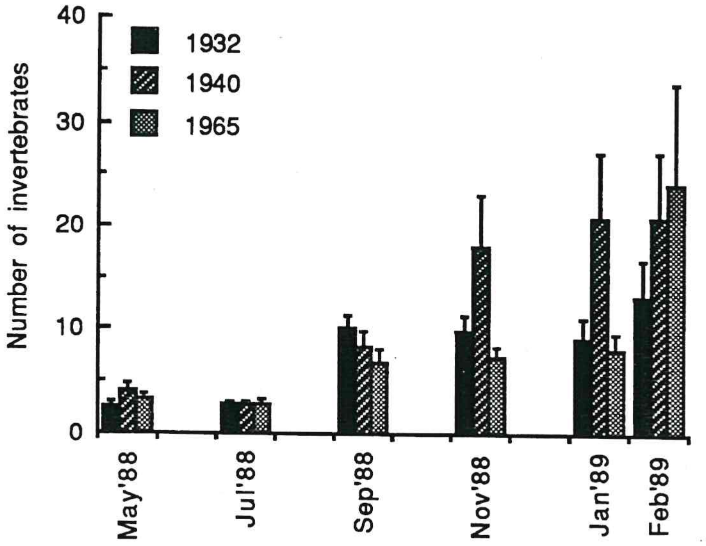

FIG. 23. Ten-day means per replicate (n=8) for Total Invertebrates in the three study sites. Standard error shown as bars above the means.

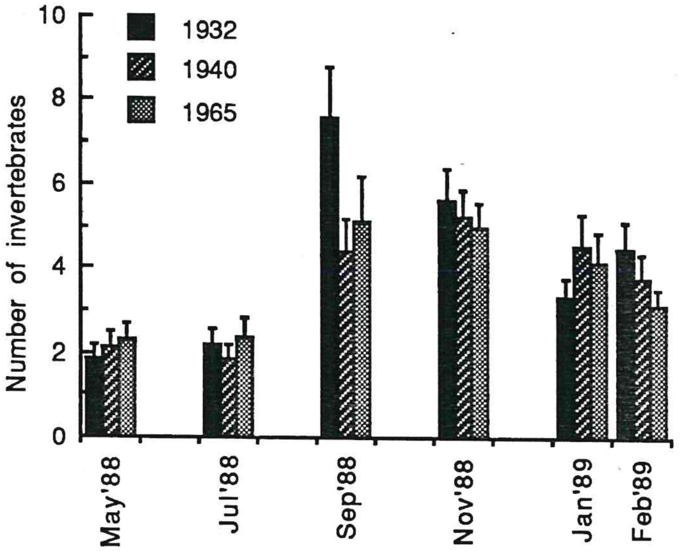

FIG. 24. Ten-day means per replicate (n=8) for Total Invertebrates (excluding Formicidae) in the three study sites. Standard error shown as bars above the means.

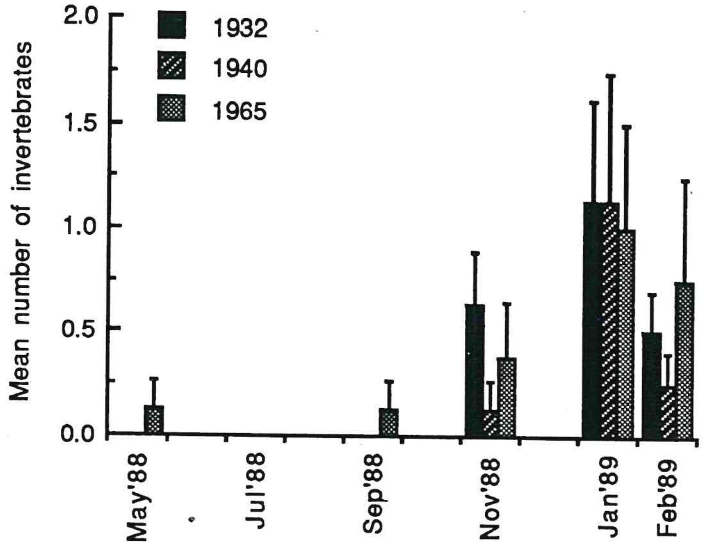

FIG. 25. Ten-day means per replicate (n=8) for Scorpionida in the three study sites. Standard error shown as bars above the means.

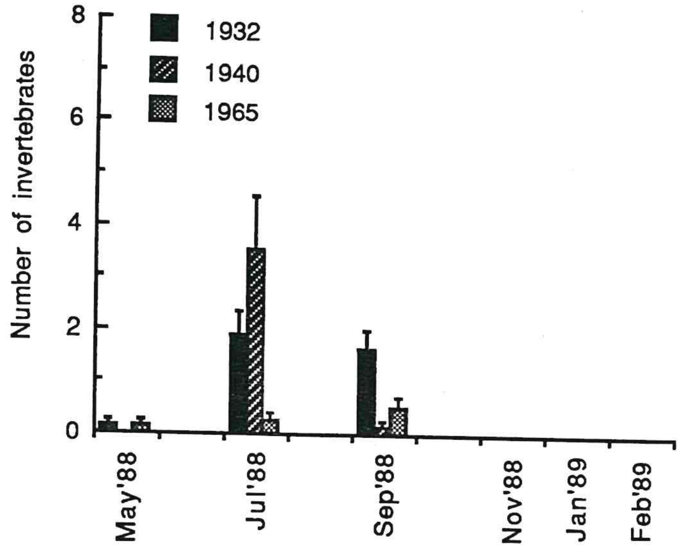

FIG. 26. Ten-day means per replicate (n=8) for Opiliones in the three study sites. Standard error shown as bars above the means.

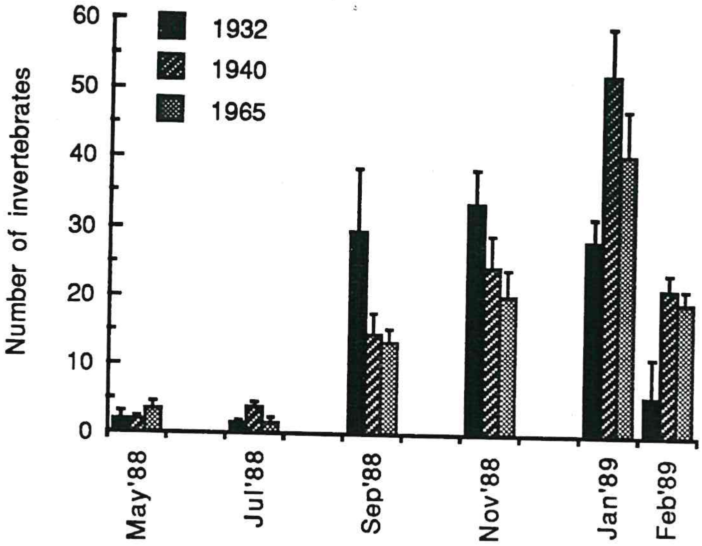

FIG. 27. Ten-day means per replicate (n=8) for Acarina in the three study sites. Standard error shown as bars above the means.

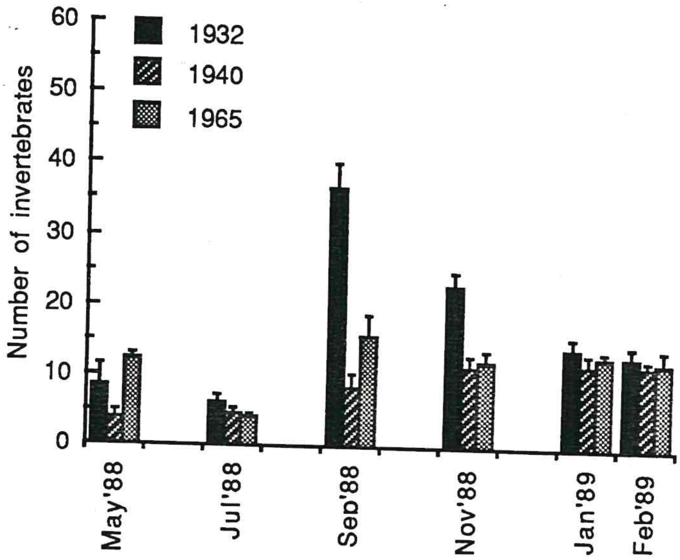

FIG. 28. Ten-day means per replicate (n=8) for Araneae in the three study sites. Standard error shown as bars above the means.

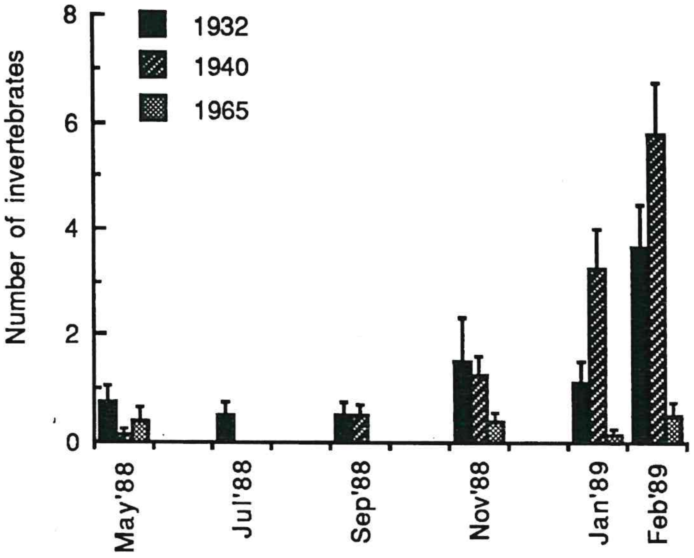

FIG. 29. Ten-day means per replicate (n=8) for Isopoda in the three study sites. Standard error shown as bars above the means.

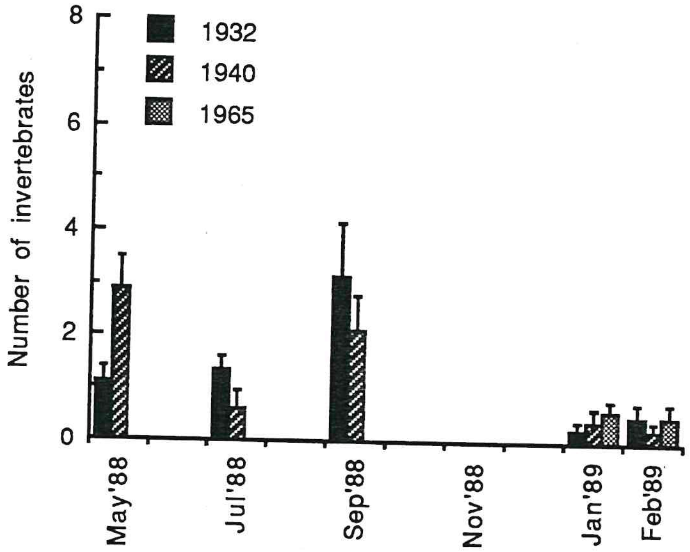

FIG. 30. Ten-day means per replicate (n=8) for Diplopoda in the three study sites. Standard error shown as bars above the means.

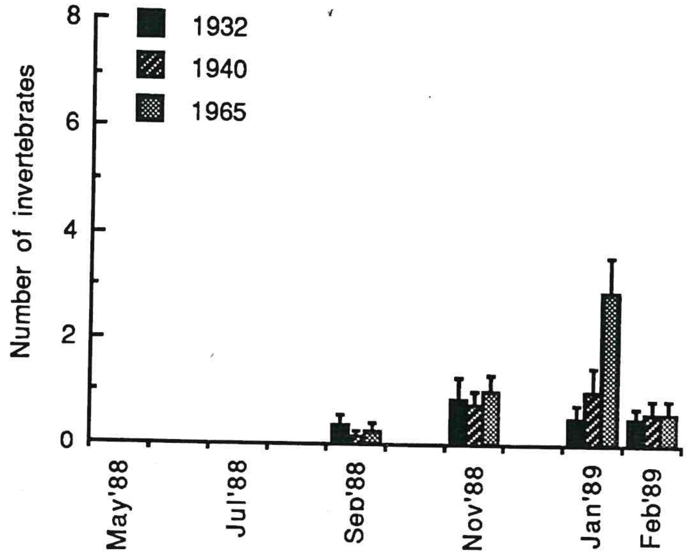

FIG. 31. Ten-day means per replicate (n=8) for Thysanura in the three study sites. Standard error shown as bars above the means.

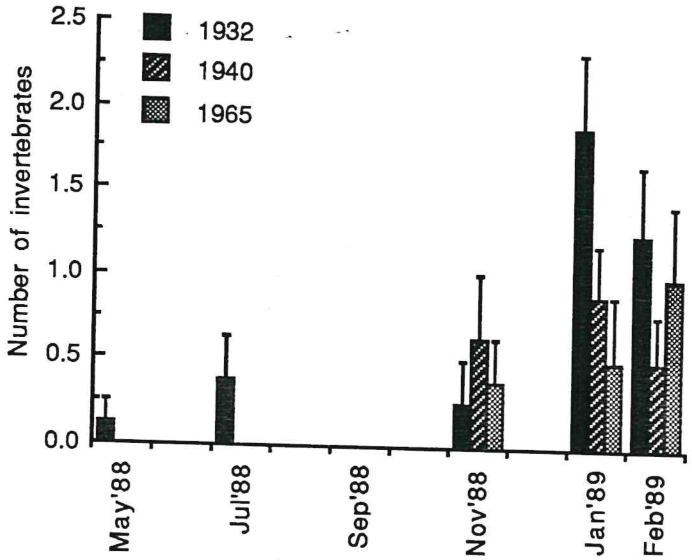

FIG. 32. Ten-day means per replicate (n=8) for Blattodea in the three study sites. Standard error shown as bars above the means.

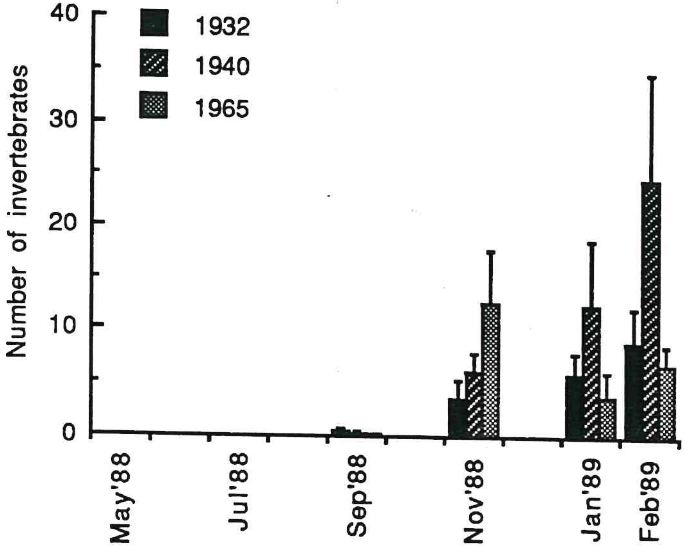

FIG. 33. Ten-day means per replicate (n=8) for Isoptera in the three study sites. Standard error shown as bars above the means.

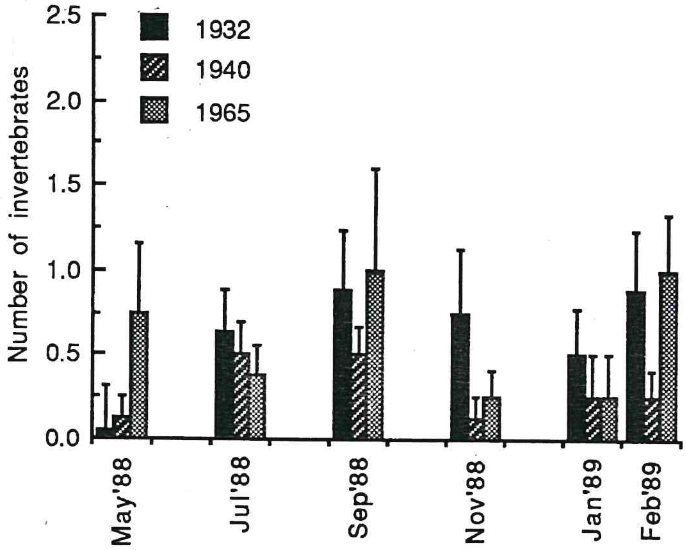

FIG. 34. Ten-day means per replicate (n=8) for Dermaptera in the three study sites. Standard error shown as bars above the means.

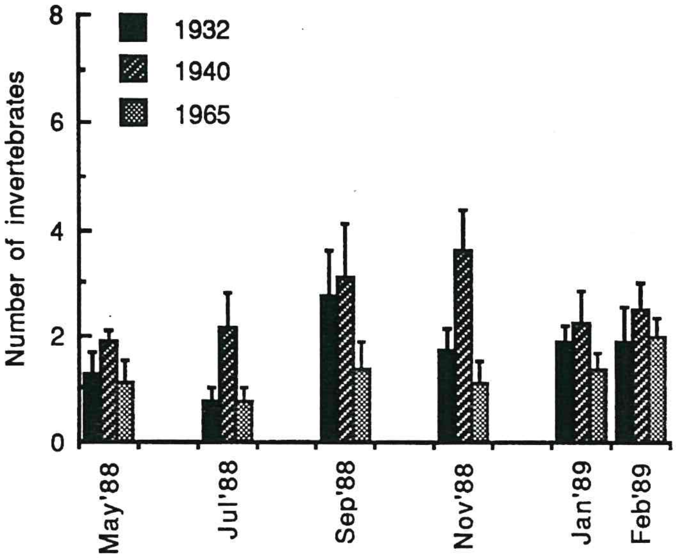

FIG. 35. Ten-day means per replicate (n=8) for Orthoptera in the three study sites. Standard error shown as bars above the means.

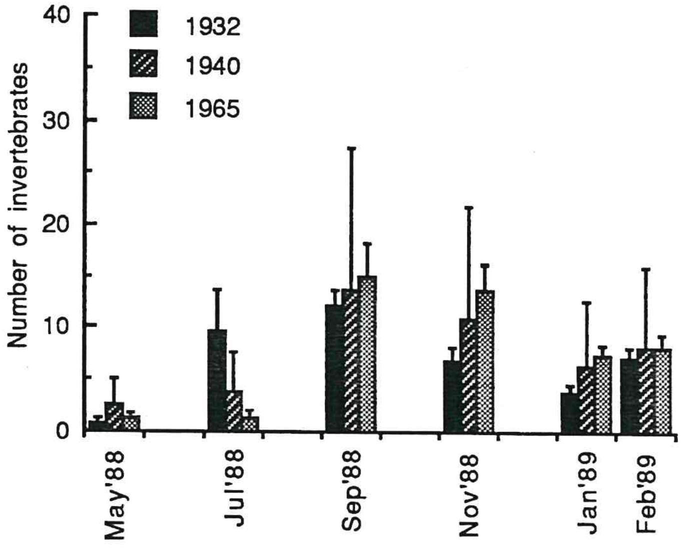

FIG. 36. Ten-day means per replicate (n=8) for Hemiptera in the three study sites. Standard error shown as bars above the means.

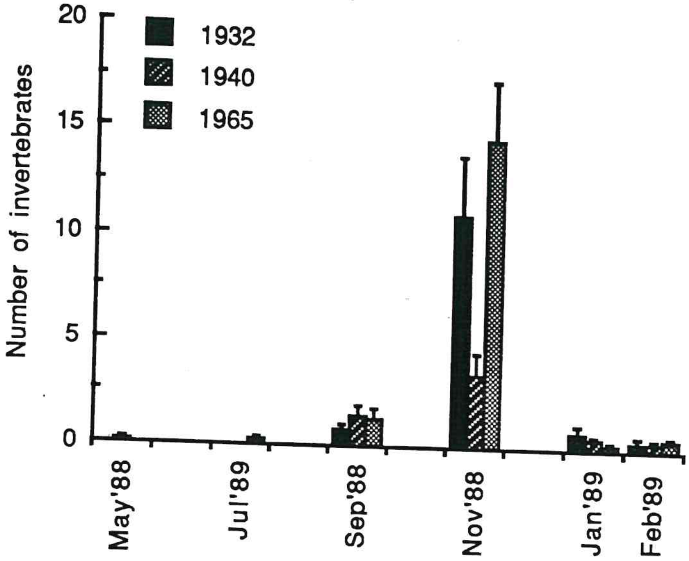

FIG. 37. Ten-day means per replicate (n=8) for Thysanoptera in the three study sites. Standard error shown as bars above the means.

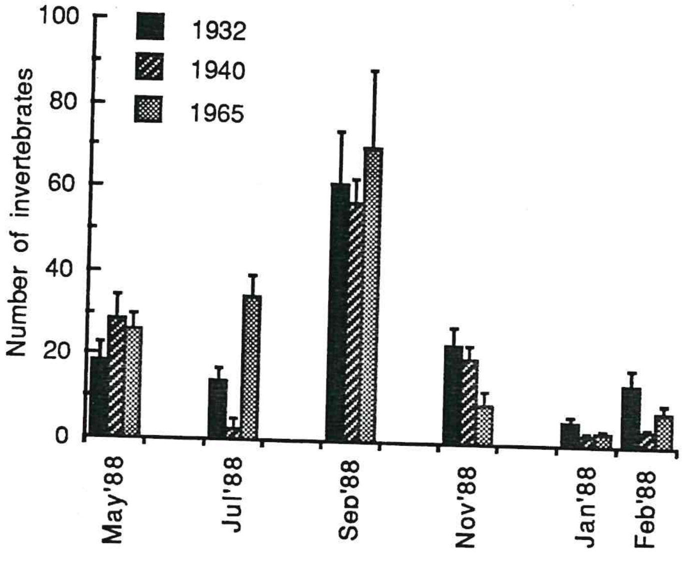

FIG. 38. Ten-day means per replicate (n=8) for Coleoptera - adults in the three study sites. Standard error shown as bars above the means.

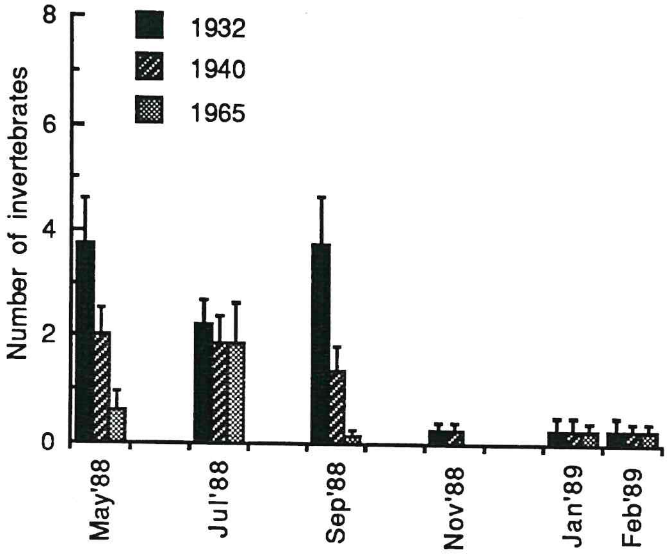

FIG. 39. Ten-day means per replicate (n=8) for Coleoptera - lavae in the three study sites. Standard error shown as bars above the means.

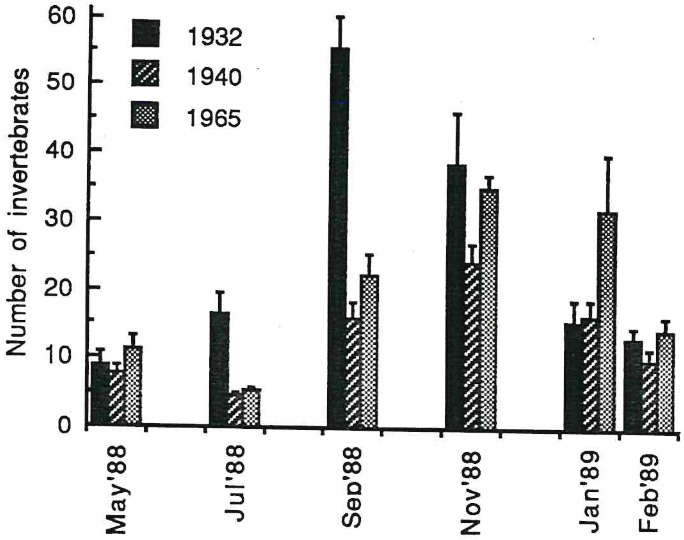

FIG. 40. Ten-day means per replicate (n=8) for Diptera - adults in the three study sites. Standard error shown as bars above the means.

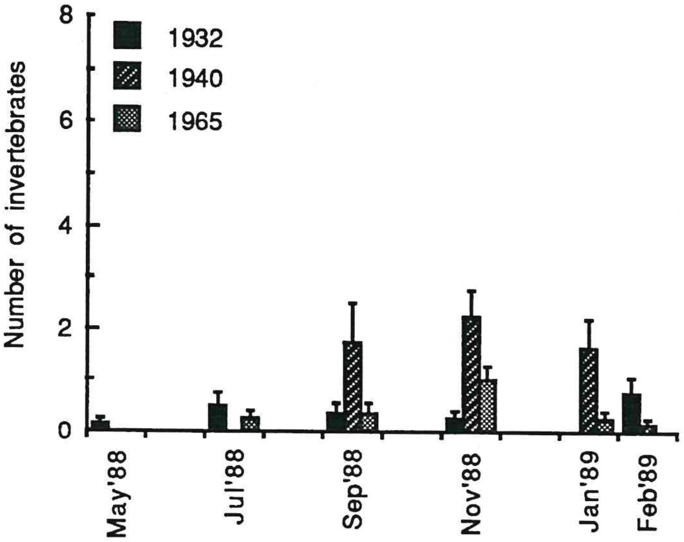

FIG. 41. Ten-day means per replicate (n=8) for Lepidoptera - adults in the three study sites. Standard error shown as bars above the means.

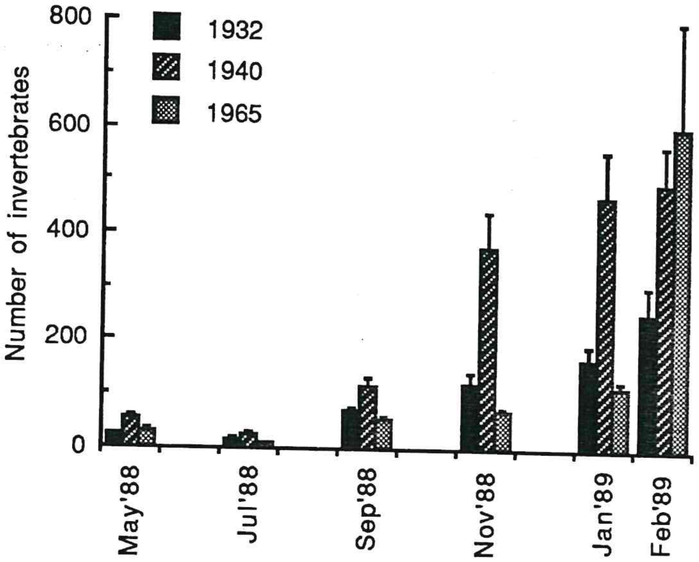

FIG. 42. Ten-day means per replicate (n=8) for Hymenoptera Formicidae in the three study sites. Standard error shown as bars above the means.

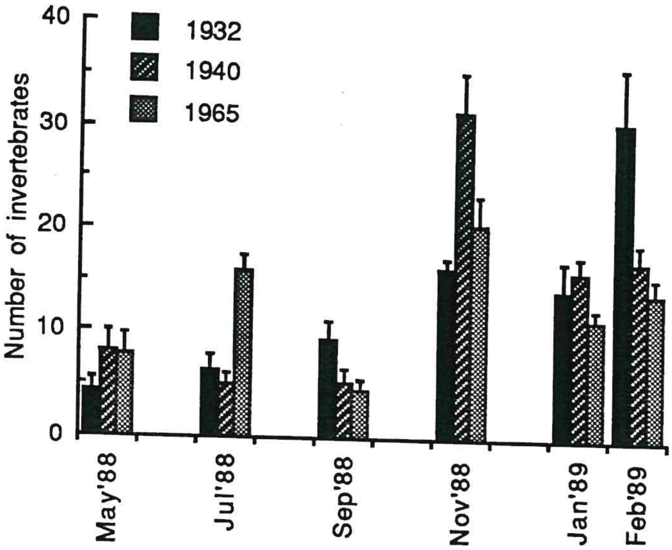

FIG. 43. Ten-day means per replicate (n=8) for Hymenoptera (excluding Formicidae) in the three study sites. Standard error shown as bars above the means.

TABLE 2. MEANS AND STANDARD ERRORS OF INVERTEBRATE ABUNDANCES PER REPLICATE ACCORDING TO MONTH. The data are compared using log linear analysis of variance; *P<0.05; **P<0.01; ***P<0.001; NS, not significant; NA, not analysed.

Taxon	Month												
	May'88		Jul'88		Sep'88		Nov'88		Jan'89		Feb'89		
	$\bar{x}$	s.e.	$\bar{x}$	s.e.	$\bar{x}$	s.e.	$\bar{x}$	s.e.	$\bar{x}$	s.e.	$\bar{x}$	s.e.	
Annelida	0.00	(0.00)	0.42	(0.18)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	NA
Arachnida													
Scorpionida	0.04	(0.04)	0.00	(0.00)	0.04	(0.04)	0.38	(0.13)	1.08	(0.29)	0.50	(0.18)	***
Pseudoscorpionida	0.00	(0.00)	0.00	(0.00)	0.04	(0.04)	0.04	(0.04)	0.00	(0.00)	0.00	(0.00)	NA
Opiliones	0.08	(0.06)	1.88	(0.45)	0.42	(0.15)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	***
Acarina	2.46	(0.52)	2.29	(0.46)	19.08	(3.52)	26.21	(2.66)	40.46	(3.78)	23.67	(2.32)	***
Araneae	8.13	(1.27)	5.00	(0.47)	20.21	(2.96)	15.54	(1.46)	12.96	(0.79)	12.46	(0.80)	***
Crustacea Isopoda	0.42	(0.15)	0.17	(0.10)	0.33	(0.12)	1.04	(0.31)	1.50	(0.39)	3.29	(0.62)	***
Diplopoda	1.33	(0.33)	0.67	(0.18)	1.75	(0.47)	0.00	(0.00)	0.42	(0.12)	0.42	(0.13)	***
Chilopoda	0.17	(0.10)	0.04	(0.04)	0.29	(0.14)	0.21	(0.10)	0.17	(0.08)	0.17	(0.08)	NS
Insecta													
Thysanura	0.00	(0.00)	0.00	(0.00)	0.25	(0.09)	0.88	(0.18)	1.46	(0.36)	0.58	(0.13)	***
Blattodea	0.04	(0.04)	0.13	(0.09)	0.00	(0.00)	0.42	(0.17)	1.08	(0.24)	0.92	(0.22)	***
Mantodea	0.00	(0.00)	0.00	(0.00)	0.04	(0.04)	0.00	(0.00)	0.04	(0.04)	0.13	(0.07)	NA
Isoptera	0.00	(0.00)	0.00	(0.00)	0.29	(0.11)	7.46	(1.95)	7.38	(2.32)	13.42	(3.79)	***
Dermaptera	0.46	(0.17)	0.50	(0.12)	0.79	(0.23)	0.38	(0.15)	0.33	(0.14)	0.71	(0.18)	NS
Orthoptera	1.42	(0.21)	1.21	(0.28)	2.42	(0.48)	2.17	(0.37)	1.83	(0.25)	2.13	(0.30)	NS
Phasmatodea	0.13	(0.07)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.04	(0.04)	0.04	(0.04)	NA
Psocoptera	0.08	(0.08)	0.00	(0.00)	0.17	(0.10)	0.08	(0.06)	0.38	(0.20)	0.04	(0.04)	NA
Hemiptera	1.58	(0.28)	4.88	(1.56)	13.58	(1.25)	10.46	(1.27)	5.79	(0.64)	7.75	(0.61)	***
Thysanoptera	0.04	(0.04)	0.08	(0.06)	1.13	(0.26)	9.63	(1.64)	0.50	(0.15)	0.42	(0.12)	***
Neuroptera adults	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	0.04	(0.04)	0.17	(0.10)	0.00	(0.00)	NA
Neuroptera larvae	0.04	(0.04)	0.00	(0.00)	0.08	(0.06)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)	NA
Coleoptera adults	24.42	(2.63)	23.50	(2.77)	62.88	(7.47)	17.75	(2.31)	3.83	(0.54)	8.92	(1.59)	***
Coleoptera larvae	2.13	(0.44)	1.75	(0.45)	1.75	(0.45)	0.17	(0.08)	0.25	(0.12)	0.25	(0.11)	***
Diptera adults	9.21	(1.04)	8.71	(1.53)	31.29	(4.08)	32.50	(3.04)	21.17	(3.30)	12.54	(1.03)	***
Diptera larvae	0.83	(0.25)	0.25	(0.12)	0.29	(0.13)	2.92	(2.92)	0.00	(0.00)	0.42	(0.18)	NA
Lepidoptera adults	0.04	(0.04)	0.25	(0.11)	0.83	(0.29)	1.17	(0.25)	0.63	(0.24)	0.29	(0.13)	***
Lepidoptera larvae	0.54	(0.15)	0.54	(0.19)	0.38	(0.16)	0.21	(0.08)	0.08	(0.08)	0.17	(0.10)	NS
Hymenoptera ants	35.92	(4.16)	16.83	(2.51)	80.08	(8.18)	188.88	(35.00)	250.96	(43.20)	450.88	(74.58)	***
Hymenoptera others	6.79	(1.00)	9.08	(1.29)	6.38	(0.88)	22.71	(2.00)	13.88	(1.13)	20.50	(2.32)	***
Total invertebrates	3.22	(0.34)	2.62	(0.25)	8.18	(0.81)	11.37	(1.72)	12.23	(2.20)	18.69	(3.87)	***
Total invertebrates (excluding ants)	2.08	(0.22)	2.12	(0.22)	5.68	(0.60)	5.25	(0.41)	3.98	(0.38)	3.78	(0.31)	***

TABLE 3. MEANS AND STANDARD ERRORS OF INVERTEBRATE ABUNDANCES PER REPLICATE ACCORDING TO SITE. The data are compared using log linear analysis of variance; *P<0.05; **P<0.01; ***P<0.001; NS, not significant; NA, not analysed; # denotes significant differences between grids nested within sites, P<0.05; ## denotes significant differences between grids nested within sites, P<0.01.

Taxon	Site							
	1932		1940		1965			
	$\bar{x}$	s.e.	$\bar{x}$	s.e.	$\bar{x}$	s.e.		
Annelida	0.04	(0.03)	0.02	(0.02)	0.15	(0.09)	NA	
Arachnida								
Scorpionida	0.38	(0.11)	0.25	(0.12)	0.40	(0.13)	NS	
Pseudoscorpionida	0.00	(0.00)	0.01	(0.01)	0.00	(0.00)	NA	
Opiliones	0.44	(0.14)	0.60	(0.25)	0.15	(0.05)	**	
Acarina	20.85	(2.79)	19.69	(2.84)	19.03	(1.53)	NS	
Araneae	16.88	(1.74)	8.69	(0.72)	11.58	(0.83)	***	
Crustacea Isopoda	1.33	(0.26)	1.81	(0.37)	0.23	(0.07)	***	
Diplopoda	1.06	(0.24)	1.04	(0.22)	0.19	(0.06)	***	
Chilopoda	0.27	(0.09)	0.10	(0.04)	0.15	(0.05)	NS	
Insecta								
Thysanura	0.38	(0.10)	0.42	(0.11)	0.79	(0.20)	*	
Blattodea	0.65	(0.15)	0.33	(0.10)	0.31	(0.11)	*	
Mantodea	0.02	(0.02)	0.04	(0.03)	0.04	(0.03)	NA	
Isoptera	3.10	(0.84)	7.25	(2.29)	3.92	(1.13)	NS	
Dermaptera	0.69	(0.12)	0.29	(0.07)	0.60	(0.15)	* #	
Orthoptera	1.71	(0.22)	2.58	(0.28)	1.29	(0.15)	***	##
Phasmatodea	0.04	(0.03)	0.04	(0.03)	0.02	(0.02)	NA	
Psocoptera	0.06	(0.05)	0.25	(0.11)	0.06	(0.05)	NA	
Hemiptera	6.69	(0.92)	7.52	(0.78)	7.81	(1.04)	NS	
Thysanoptera	2.15	(0.73)	0.96	(0.26)	2.79	(0.90)	*	
Neuroptera adults	0.00	(0.00)	0.10	(0.05)	0.00	(0.00)	NA	
Neuroptera larvae	0.02	(0.02)	0.02	(0.02)	0.02	(0.02)	NA	
Coleoptera adults	22.85	(3.51)	22.50	(3.00)	22.29	(4.59)	NS	
Coleoptera larvae	1.75	(0.32)	1.00	(0.18)	0.52	(0.16)	***	
Diptera adults	24.67	(2.96)	13.10	(1.20)	19.94	(2.16)	***	
Diptera larvae	0.60	(0.16)	1.58	(1.46)	0.17	(0.06)	NA	
Lepidoptera adults	0.33	(0.09)	0.96	(0.22)	0.31	(0.08)	***	
Lepidoptera larvae	0.25	(0.08)	0.38	(0.12)	0.33	(0.09)	NS	
Hymenoptera ants	108.40	(15.68)	255.75	(35.11)	147.63	(43.04)	***	##
Hymenoptera others	13.46	(1.63)	13.79	(1.56)	12.42	(1.00)	NS	
Total invertebrates	7.65	(0.77)	12.04	(1.68)	8.47	(1.60)	***	
Total invertebrates (excluding ants)	4.16	(0.29)	3.63	(0.25)	3.66	(0.27)	***	

TABLE 4. PRINCIPAL GROUPS OF INVERTEBRATES COLLECTED AT TUTANNING SHOWING FEEDING HABITS, MAIN PEAK IN OCCURRENCE, SITE PREFERENCES, AND FIGURE NUMBER IN TEXT. [1]O. = Order, F. = Family; [2]N.P. = No Preference.

Class	Taxon[1]	Feeding Habits	Main Peak in Occurrence[2]	Site Characteristics[2]	Figure No.
Arachnida	O.Scorpionida	Predators	Summer	N.P.	25
Arachnida	O.Opiliones	Predators	Winter, early spring	Low in 1965 site	26
Arachnida	O.Acarina	Predators, herbivores, scavengers, parasites and detritus feeders	Late spring, summer	N.P.	27
Arachnida	O.Araneae	Predators	Spring	Low in 1940 site	28
Crustacea	O.Isopoda	Dead plant material and detritus	Summer	Low in 1965 site	29
Diplopoda		Dead plant material and detritus	Late autumn - spring	Low in 1965 site	30
Insecta	O.Thysanura	Plant debris and fungi	Late spring, summer	High in 1965 site	31
Insecta	O.Blattodea	Omnivorous Scavengers	Summer	High in 1932 site	32
Insecta	O.Isoptera	Wood and grass feeders	Late spring, summer	N.P.	33
Insecta	O.Dermaptera	Scavengers and detritus feeders	N.P.	Low in 1940 site	34
Insecta	O.Orthoptera	Omnivores, predators, detritus, and plant feeders	N.P.	High in 1940 site	35
Insecta	O.Hemiptera	Sap suckers	Spring	N.P.	36
Insecta	O.Thysanoptera	Fungal hyphae, nectar	Spring	High 1965, Low 1940	37
Insecta	O.Coleoptera (adults)	Various	Spring	N.P.	38
Insecta	O.Coleoptera (larvae)	Various	Late autumn, winter	Low in 1965 site	39
Insecta	O.Diptera (adults)	Various	Spring	Low in 1940 site	40
Insecta	O.Lepidoptera (adults)	Nectar feeders	Spring, summer	High in 1940	41
Insecta	O.Hymenoptera F.Formicidae	Predators, nectar and seed feeders	Summer	High in 1940	42
Insecta	O.Hymenoptera (excluding Formicidae)	Nectar feeders	Late spring, summer	N.P.	43

4.5. Spiders

Figure 44 shows the dendogram created from HCA using the average-linkage method. Note that the September sample from the 1932 site has not been included because it was vastly different to the other month/site combinations and caused a compaction of the clusters to accomodate it.

From figure 44 it can be seen that at value 7 on the rescaled distance measure, two predominant community groups emerged from this analysis. Group 1 is comprised of all the sites from the May and July sampling periods, and Group 2 is comprised of the sites from the November sampling period plus the February 1932 sample. The communities remaining had either not been grouped or had only undergone a single grouping. At value 8 on the rescaled distance measure, Groups 1 and 2 were joined. All subsequent clustering showed a stringing effect joining all other samples which had either not been grouped or had only undergone one grouping, to this main cluster. This stringing effect has obscured similarities between the spider fauna of the January 1940, January 1965, February 1932, and February 1965 samples, linking the two January samples to the main cluster which then, and only after this linking, showed enough similarity to encorporate the two February samples.

The dendogram presented in figure 44 identifies the November 1932 sample as being very different from the others. Recall that the September 1932 sample, excluded from this dendogram, was also extremely different in terms of its spider fauna. Thus it can be concluded that the spider fauna in the 1932 site shows a vastly different community structure during spring.

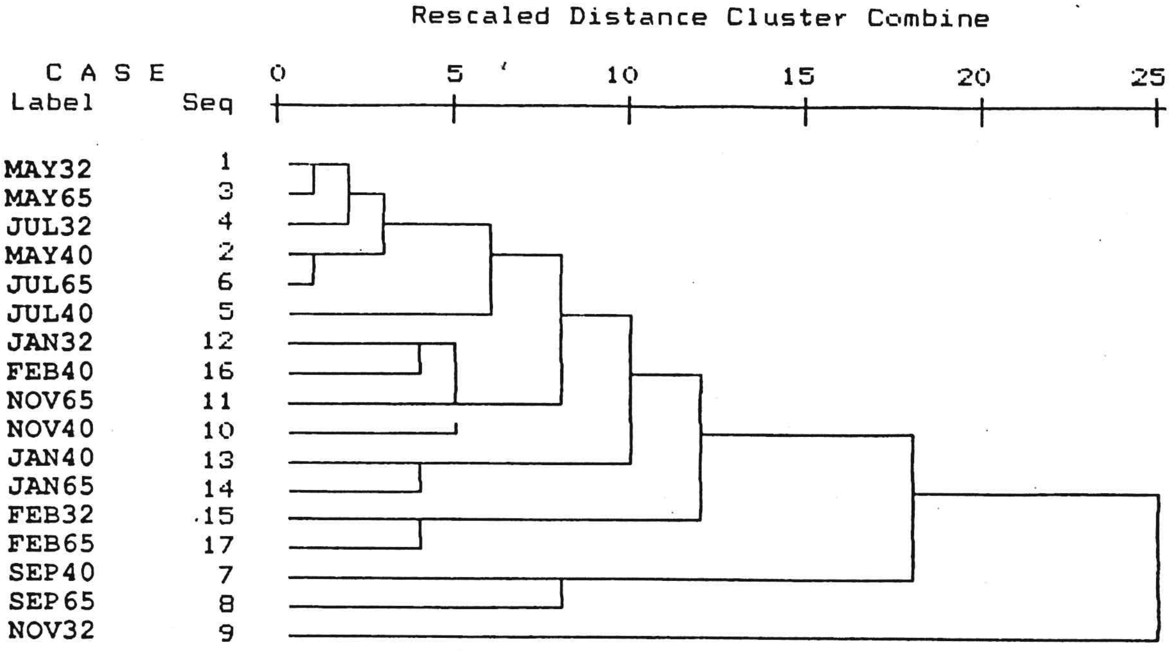

FIG. 44. Dendogram produced by HCA showing clustering of similar samples according to spider fauna characteristics.

Table 5 provides a summary of the spider fauna parameters measured during the study. Total individuals are lower in the 1940 site and peak in spring. This information has been presented in figure 28. Species richness is highest for the 1932 site for all months except May and July. Diversity is variable between sites but is generally higher in spring. Spider diversity in the 1965 site shows the least fluctuation between nmonths. The 1932 and 1940 sites retain a high spider diversity throughout summer, whereas the diversity of the 1965 site decreases after peaking in November. High values of evenness correspond to samples with a low number of individuals yet which retain a relatively high species richness, indicating that total individuals increases disproportionately to species richness. Total spiders, species richness, and diveristy is greatest in the 1932 site during the September and November samples.

TABLE 5. SPIDER FAUNA PARAMETERS FOR THE THREE KWONGAN SITES FOR EACH SAMPLE PERIOD.

	Month					
Parameter	May'88	Jul'88	Sep'88	Nov'88	Jan'89	Feb'89
Total Individuals						
1932	67	50	294	182	112	105
1940	91	37	67	92	94	96
1965	37	33	124	99	105	98
Species Richness (S)						
1932	12	12	37	32	31	31
1940	17	14	15	23	26	25
1965	22	14	27	26	25	22
Diversity (H)						
1932	2.092	2.027	2.718	2.832	2.977	2.853
1940	2.586	2.059	2.044	2.586	2.582	2.874
1965	2.249	2.391	2.653	2.762	2.560	2.369
Evenness (J')						
1932	0.842	0.816	0.753	0.817	0.867	0.831
1940	0.913	0.780	0.755	0.824	0.792	0.893
1965	0.728	0.906	0.805	0.848	0.795	0.767

Table 6 provides the total number of individual spiders according to family, caught at each site for the each of the the sampling periods. No statistical analysis was conducted on this data. However, the more abundant families notably the Clubionidae, Gnaphosidae, Salticidae, and Theridiidae do show site and seasonal preferences.

Clubionidae show a spring peak in abundance, but the 1940 site is lower in numbers than the other two sites. Gnaphosidae also show a spring peak, the high numbers in the 1932 site during spring probably contributing significantly to the identification of the September and November 1932 samples as outliers in the HCA (Fig. 44). Salticidae have a higher abundance in the 1932 site, and peak in numbers during spring and early summer. Unlike the other families, Theridiidae peak in abundance during late autumn, but numbers being less in the 1940 site.

TABLE 6. TOTAL NUMBER OF SPIDER INDIVIDUALS TRAPPED ACCORDING TO FAMILY FOR THE THREE KWONGAN SITES FOR EACH SAMPLE PERIOD.

	Month					
Family	May'88	Jul'88	Sep'88	Nov'88	Jan'89	Feb'89
Araneidae						
1932	2	0	28	7	3	3
1940	3	2	18	2	3	9
1965	6	0	15	10	6	4
Clubionidae						
1932	22	23	95	25	21	24
1940	3	4	18	19	18	5
1965	28	12	41	18	27	9
Ctenizidae						
1932	8	9	3	1	0	0
1940	10	12	0	0	0	4
1965	9	6	0	0	2	0
Dinopidae						
1932	0	0	1	0	0	0
1940	0	0	0	2	0	0
1965	0	0	1	1	0	1
Gnaphosidae						
1932	9	4	114	119	57	59
1940	3	16	26	59	47	57
1965	8	9	61	62	59	73
Hersiliidae						
1932	0	0	0	0	3	0
1940	0	0	0	0	2	0
1965	0	0	0	0	0	0
Lycosidae						
1932	0	0	0	0	0	0
1940	2	0	0	0	0	0
1965	0	0	0	0	0	0
Mimetidae						
1932	0	0	0	0	0	0
1940	0	1	0	0	0	0
1965	0	0	0	0	0	0
Miturgidae						
1932	0	0	0	1	0	0
1940	0	0	0	0	0	0
1965	0	0	0	0	0	0
Oxyopidae						
1932	0	0	0	0	0	0
1940	0	0	0	0	2	0
1965	0	0	0	0	1	0
Pholcidae						
1932	0	0	0	0	1	0
1940	0	1	0	0	0	0
1965	2	0	0	0	0	0
Salticidae						
1932	0	1	30	18	18	11
1940	2	0	4	3	13	10
1965	0	1	3	7	8	8
Theridiidae						
1932	22	13	10	0	0	0
1940	7	1	1	0	1	0
1965	42	4	1	1	1	1
Thomisidae						
1932	1	0	2	1	5	2
1940	1	1	0	1	1	0
1965	2	0	0	0	0	0
Zodariidae						
1932	0	0	2	8	4	5
1940	0	0	0	5	7	9
1965	0	0	0	0	2	1
Damaged						
1932	3	0	2	2	0	1
1940	0	0	0	1	0	2
1965	0	1	2	0	0	1

CHAPTER 5

DISCUSSION

DISCUSSION

5.1. Scope of the Study

Space-for-time substitution (SFT) has come under considerable criticism recently and the limitations of this type of study need to be outlined. Too often, SFT is used by ecologists as a substitute for for long-term studies under the belief that there is a homology between sequences of spatial zones and temporal sequences (Picket 1989). However, as Picket (1989) notes, space should not be treated as a substitute for time, and SFT should ideally be used in conjunction with long-term studies.

This study utilised SFT to examine the possible influence of fire history on invertebrate populations. It is anticipated that this study will ultimately be used in conjunction with, and as a baseline study for, a future long-term survey examining the effects of prescribed burning on invertebrate communities in Tutanning. It is planned that this long-term survey will utilise a prescribed burn planned for the 1965 site in autumn 1990.

By using differences in spatial patterns to represent the influence of fire history, an attempt was made to keep climate, soils, and vegetation type constant between sites. These controls may appear very coarse, but the proximity of sites to one another minimised the influence of all but extremely localised environmental factors. By taking into consideration such environmental controls it was anticipated that greater insight into long-term fire effects on invertebrate community characteristics would be achieved. To this end, the study has been considered successful, although many of the findings are conjecture until supported by long-term studies.

Limitations in the sampling technique also need to be outlined. It should be stressed that pitfall traps sample epigaeic invertebrates only, and that traps show a bias toward more mobile taxa (Majer 1981). A more complete census of the invertebrate fauna should incorporate soil cores to obtain a sample of the subsoil invertebrate fauna, and should include a sample of invertebrates directly associated with the vegetation. However, the scope of this study was not to obtain a complete census of the invertebrate fauna inhabiting the kwongan vegetation at Tutanning, but to use the invertebrates collected as bio-indicators of site differences. To this end, pitfall trapping has proven a successful sampling method.

The other limitation in drawing inference from this study, is that for each of the sites, the season of burn and fire intensity is unknown. With regards to the former, the possible repurcussions of seasonal differences in burning, are outlined in Majer (1985). As regards to the latter, all three sites were burnt by wildfire and as Hobbs and Atkins (1988) note, most woodland and shrub communities vary greatly in their array of standing vegetation and litter composition, and hence there is a high degree of spatial variation in the fire intensity during burning. However, if each site had a similar degree of spatial variance in fire intensity, then fire intensity may not be such an imperative factor in influencing the invertebrate communities of the three sites.

The areas selected for this study represent a long-term fire regime. There was no compatible area of kwongan in Tutanning which had a fire history of less than 24 years. To my knowledge, no studies have examined possible long-term repurcussions of fire on soil and litter invertebrates and their association with surrounding vegetation, as was addressed in this study. It is possible that a comparable site with a more recent fire history than what was examined here, would given greater insight into the recovery of invertebrate populations following fire in semi-arid climatic regimes. Future studies on fire effects in semi-arid vegetation types would do well to compare sites with a more recent fire history, e.g. 5-10 years, 10-20 years, and 20-30 years.

A critical examination of the results of this study in light of other research, is limited. To date, studies of invertebrate populations in the drier areas of Australia have been minimal, with the exception of Greenslade (1979) and (1981). There has also been no reported invertebrate studies conducted in kwongan (G. Friend pers. comm.). Comparison of this study to those in the moist forest areas is also hampered by the fact that many of the control areas used by researcher have had fire ages of less than twenty-four years (e.g. Majer 1984, Majer and Koch 1982, Springett 1976). Given the limitations in comparing this research to other studies, this paper should be viewed as identifying areas where a considerable amount of research is still required, rather than drawing possible unfounded parallels between this and equivalent surveys in different ecosystems.

5.2. Influence of Site

In general, invertebrate populations were higher in the 1932 site. Two explanations are given for this occurrence. This site is the oldest and contains a greater distribution and density of leaf litter and a greater abundance of woody litter than the other two sites. This litter composition provides a plentiful array of microhabitats while also providing a major food source for detritus-feeders such as Isopoda, Diplopoda, and the omnivorous scavenger, Blattodea which all showed preferences to this site. However, the influence of site aspects, such as size and proximity to neighbouring ecotypes, on these invertebrate populations, also needs to be examined.

The 1932 site is only about 4 ha (approx.) and is surrounded from all sides by a sheoak (Allocasuarina huegeliana) dominant woodland, which is encroaching onto this site. The 1940 and 1965 sites are comparitively larger, each comprising of 10 ha (approx.) and are both bordered by a community of wandoo (Eucalyptus wandoo) on one side, and sheoak on the other. The possible influence of these site characteristics on the invertebrate communities needs to be examined in light of island biogeographical theory.

The principals of island biogeographical theory are detailed in Krebs (1985), and Lunney and Recher (1986) have applied its principals to design the optimum size for national parks. More recently Majer (1989) has used its principals to explain long-term fauna colonization of reclaimed lands. Here it is used to explain possible differences in invertebrate species richness between sites using spiders as a representative taxon. It is assumed that the responses shown by this taxon are fairly indicative of the total invertebrate population.

The principals of island biogeographic are based on the view that species richness is a product of area and isolation (Majer 1989). Since the kwongan vegetation differs in floristic and botanitical structure from the surrounding area, it is not unreasonable to assume that the three kwongan sites may function as "islands" for many invertebrate species. The 1940 and 1965 sites contain the greatest area, but are also the most isolated from the different neighbouring ecotypes. There would therefore be a minimum influx of woodland and sheoak invertebrate species into these kwongan communities. In comparison, the 1932 site is comprised of a smaller area and with all sides bordered by sheoak which appears to be encroaching onto the kwongan. It should be stressed that this apparent succession is most likely to be attributed to proximity of the 1932 kwongan site to the neighbouring sheoak woodland rather than being indicative of a climax stage in natural succession.

Given that the spider fauna was generally richer in the 1932 area in terms odf species composition, and given that the two spring samples in this site were identified by Hierarchical Classification Analysis as being extremely different from all the other samples in terms of their spider fauna composition, it appears very likely that the adjacent sheoak woodland is influencing the spider community composition of the 1932 site. It thus appears that spider species, and most likely the invertebrate species in general, are migrating from the woodland into the kwongan, resulting in a higher species richness, abundance, and diversity, than what would normally occur given the location characteristics of the other two sites. The extent to which these site factors are influencing invertebrate and spider abundance is unknown, though the spider fauna does show a positive relationship between species richness and abundance.

5.3. Invertebrates, Vegetation and Fire

From their study of kwongan vegetation at Tutanning, Brown and Hopkins (1984) found that only a very small percent of floristic variability could be related to fire age. Brown and Hopkins (1984) attributed floristic differences in kwongan vegetation types to differences in soil type. In this study the 1932 and 1965 sites had the most similar floristic composition, supporting the findings of Brown and Hopkins (1984) that fire age has little influence upon the floristic composition of kwongan. The greater plant species richness in the 1940 site maybe a response to localised environmental differences, possibly related to soil nutrient composition.

In the case of this study, Orthoptera, Lepidoptera adults, and Hymenoptera Formicidae occurred in higher abundances in the 1940 site. This could be related to the greater plant species richness contained in this site. The relationship between floristic richness and Lepidoptera adults seems particularly apparent given that these nectar feeders peaked in abundance in spring, co-inciding with the main flowering period of many kwongan species (Bell and Stephens 1984). Orthoptera, which feed on living plant material as part of their diet, might also be attracted to this site because of its floristic richness.

Hymenoptera Formicidae which are predators, nectar and seed feeders, are also more abundant in the 1940 site. They may also attracted to the 1940 site because of its floristic richness. However microclimate may also be influencing abundance of this taxon. Koch and Majer (1980) note a positive correlation between Formicidae abundance and temperature. Given that the 1940 site, like the 1965 site, is relatively open, it is very likely that ground temperatures are hotter in this site, stimulating activity. However, it should also be noted site preference may be related to one or two numerically dominant species and that a high abundance does not necessarily infer a high species richness. Thus, given that Formicidae accounted for 60% of the invertebrates trapped, site preference should be examined at a species level classification.

Moving from floristic influences to structural and environmental influences on the invertebrate populations, one of the major finding of this study was that the 1965 site contained a deficiency in the abundance of the detritus-feeders, Isopoda and Diplopoda, and the predator, Opiliones. All three of these taxa are prone to desiccation (Wallwork 1970). Although soil moisture was not measured during the course of this study, it was found that the 1965 site contained a lower leaf cover than the other two sites. This defiency in leaf litter cover infers a lower abundance of microhabitats, a harsher microclimate with less moisture, and quite possibly less food stock for the detritus feeders.

Considering the detritus feeders in more detail, the importance of Diplopoda and Isopoda as decomposers has been noted by Howard (1975), Springett (1979), and more recently, Postle (1989). It is quite possible that the defiency in litter cover and the lack of detritivores in the 1965 site, is inferring a lower rate of biomass accumulation. Bell et al. (1984) note that Western Australian heath vegetation communities are characterised by low rates of biomass accumulation and low ceiling biomass values. Since there is a lower number of detritus feeders in the 1965 site, it is not unreasonable to assume that the rate of litter turnover and nutrient cycling may also be lower compared with the other two sites.

In her study of burning in jarrah (Eucalyptus marginata) and karri (Eucalyptus diversicolor), Springett (1976) found that litter decomposition ceased until four years after burning. Raison et al. (1986) found that following fire in sub-alpine eucalypt forests, the rates of decomposition varied inversely with aridity. Changes in the microenvironment, through the removal of the shading understorey and the reduction in depth of the litter layer, were attributed as causes to this lower rate of decomposition. Although no studies have focused on fire effects on litter decomposition in kwongan vegetation, Pate and Dell (1984) have noted significant losses of soil nutrients directly following fire. However, eighteen months following the fire Pate and Dell (1984) found that the quantity of nutrients contained in the resprouting kwongan was greater than what had initially been deposited as ash following the fire, signifying that fire does not deplete kwongan of available nutrients.

Placing these findings in the context of the 1965 site at Tutanning, the deficiency in leaf litter cover and associated detritivores in the 1965 site may be attributed to a lower nutrient regime, when compared with the other two sites. Such a regime may be inherant in the soil, or it may have possibly resulted from ash and litter removal by wind or surface water run-off following the last burn. Humphreys and Craig (1981) detail such occurrences. Alternatively, the leaf litter in 1965 site may still not have accumulated a density great enough to sustain "normal" (as expressed by the 1940 and 1932 sites) detritivore populations. Given that that soil types are constant for all three sites, it seems that fire has been the major contributing factor to the lack of leaf litter cover and associated low detritivore populations characteristic of the 1965 site.

5.4. Implications for Prescribed burning

From invertebrate studies in the Australian Capital Territory (A.C.T.), Campbell and Tanton (1981) found that prescribed burning in winter was more detrimental to the soil and litter fauna than a spring burn. However, based upon studies in Western Australia, Majer (1985) found a spring burn to have greater deleterious effects. Two explanations have been posed for the difference in burning effects (Moulton 1982), the first based upon climatic differences between the two states, the second based upon direct effects on the soil fauna.

In the temperate latitudes of the east coast, rainfall is more evenly distributed throughout the year whereas in the south-west of W.A., characterised by its mediterranean-type climate, rainfall predominates throughout winter and summer is characterised by drought. Moulton (1982) notes that in the areas of the east coast where he and Campbell and Tanton worked, there is a greater probability of rain in spring resulting in plant growth and litter production, thus providing the soil with favourable microenvironmental conditions during summer. Thus they argue that a winter burn is more detrimental because the fauna is more sessile and less reproductively active than during spring.

In Western Australia, however, plant growth and litter accumulation is greatest after the winter rains co-inciding with a peak in invertebrate activity as found in this study and Majer's (1985) study. However, during the summer months, such plant growth and litter accumulation is minimal creating a harsh microenvironment for soil and litter arthropods. Consequently, it is argued that for W.A., prescribed burning in spring would have a greater detrimental effect upon invertebrate populations given that conditions in summer are deleterious for the invertebrate populations.

Campbell and Tanton (1981) give a different reasoning as to the rationale behind the effects of prescribed burning on soil and litter arthropods. They consider that the soil and litter fauna is more susceptible to fire in winter because it is sessile or shows low mobility, and thus less able to avoid fires. Spring fires correspond with the greatest level of activity and when the majority of animals are in a reproductive stage. Fire avoidance by active invertebrate fauna has been studied by Main (1981) and Whelan et. al. (1980). It is in of this avoidance strategy that Campbell and Tanton (1981) argue that the effects of spring fire upon invertebrate populations, are soon overcome.

It has also been noted by Main (1981) that life history cycles may represent a method of fire tolerance. Many invertebrates reside in the soil itself rather than in the litter, and some of those taxa which are surface active in their adult stage are soil dwellers in their egg and larval stage of development (C.S.I.R.O. 1970). Hutson and Veitch (1983) examined the density of mites and Collembola in a duplex soil with a sandy loam A horizon, which is comparible to the soil type examined in this study. From examination off the A horizon, they found that the density of both mites and Collembola was greatest in the upper 0-4 cm of the soil profile.

This activity in the upper soil surface layers has important consequences for control burning. Temperatures experienced in the soil during burning depend upon ground heat fluxes, thermal conductivities of the soil, fuel load and distribution, ambient wind speed, ambient humidity and temperature conditions, and soil and litter moisture content (Gill and Groves 1981, Humphreys and Craig 1981). However, Humphreys and Craig (1981) note it takes very severe fire to heat the soil below 2.5 cm. Hence, Specht (1981) postulates that there is usually a sufficient number of organisms in the ash and dust above the ground (principally protozoa, nematodes, and rotifers) and in the deeper soil layers to recolonise the soil/litter interface.

One possible disadvantage of burning, not usually mentioned in the invertebrate literature, is that burning can alter the physical nature of the soil surface so that it repels moisture (P. Mitchell pers. comm., Humphreys and Craig 1981). This has direct implications for the surface ash layer remaining after the burn since such a repellence would increase water run-off, thus depleting the ecosystem of nutrients that would normally be recycled. Such an effect is also probably worse in sandy soils (P. Mitchell pers. comm.).

The consequences of this moisture repellence for autumn burning needs to be discussed.

Following an autumn burn, winter rains would probably have less effective infiltration into the soil, and hence run-off would be increased. Nutrients (remaining as ash) that would normally be returned to the burnt ecosystem ash would probably be removed by this increase in surface run-off, reducing the capabilities of the ecosystem to recover following the burn. A spring burn, however, would have a relatively less deleterious effect given that there is less chance of rain and subsequent nutrient removal by run-off following the burn. The effect on invertebrate populations from moisture depletion is likely to be less, given that soil moisture is likely to be depleted over summer despite burning. However, clearly these possible effects upon the environment and the invertebrate populations depend upon how effective the surface soil repels moisture and how long such repellence lasts. As Humphreys and Craig (1981) note there have been few quantitative studies conducted in the Australian environment on these aspects, and subsequently the duration of the moisture reppellence and its relationship with fire, is still relatively unknown in this country.

From the point of view of invertebrate activity, the findings of this study support Majer's (1985) view, that burning should be conducted in autumn. Following autumn burning, winter rains would promote the vigorous resprouting from root stocks of fire-resistant species which predominate kwongan vegetation (Bell et al. 1984), providing an immediate food and litter source for invertebrates. Winter rains would be followed by the spring peak in arthropod activity characterised by migration into the burnt area from those areas not burnt, and by reproduction of the invertebrate fauna in the burnt site. In contrast a spring burn is likely to be followed by summer drought, minimal plant regrowth, and a resulting harsher microclimate inhibiting soil and litter fauna return. Clearly if this theory is to be proven or disproven, soil and invertebrate studies will have to encorporate soil core samples, identify arthropods to a species or trophic level, note the life stages of development, and ultimately compare long term studies on autumn- and spring-burnt environmentally-similar sites.

CHAPTER 6

CONCLUSION

CONCLUSION

The soil and litter inverebrate populations of the three sites appear to be closely associated with leaf litter density and woody litter abundance. Floristics seems only important for those taxa which feed on predominantly live plant material.

Plant floristics does not appear to be determined by fire, though there does appear to be a positive association between litter accumulation and fire age.

The spider fauna, both in terms of species richness and abundance, shows a positive association with woody litter abundance and leaf litter cover, showing a preference to the 1932 burn site. Invertebrate abundance in general also tends to favour this site. However, the extent to which the proximity of neighbouring ecotypes influences the population parameters of spiders and the abundance of the invertebrates as a whole, remains unknown.

Allowing for possible site effects, the invertebrate populations do not appear to be considerably different between the three sites. However the 1965 site does contain a deficiency in detritivore populations. This appears to be associated with a deficiency in leaf litter cover and a subsequent harsher microclimate which in turn appears to be a result of long-term fire effects. Hence, it seems that fire effects are still influencing, albeit indirectly, detritivore populations 24 years after burning.

Invertebrate populations peak during spring, and are lowest during late autumn and early winter. Based upon invertebrate activity, it would seem that prescribed burning in spring would be more detrimental to the invertebrate fauna of kwongan than autumn burning. However, this is not conclusive and further research studying long-term fire effects on invertebrates, and an examination of the arthropods at a species or trophic level, is required. An examination of invertebrates from soil samples, noting the phenology of the animals concerned, their stage of development, and their depth of occurrence, would immensely benefit such research.

The findings of this study support the present "No Fire Regime" policy designated for Tutanning Nature Reserve, since the 1965 site still seems to be deficient in detritus feeding invertebrates even after 24 years without burning.

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APPENDIX 1 - GALT'S SOLUTION COMPOSITION

Chemicals used in the preparation of Galt's solution are provided below. Note that the quantities given should, with the addition of water, make five litres of the solution. Note also that the quantities given vary according to season.

Summer: - [400 ml per trap]

125g NaCl
25g Pottassium Nitrate
25g Chloral Hydrate
10g Glycerine
Add water to make 5 litres.

Autumn and Spring: - [150-200 ml per trap]

250g Sodium Chloride
50g Potassium Nitrate
50g Chloral Hydrate
5g Glycerine
Add water to make 5 litres.

Winter: - [100 - 150ml per trap]

500g Sodium Chloride
100g Potassium Nitrate
100g Chloral Hydrate
2g Glycerine
Add water to make 5 litres.

APPENDIX 2 - FLORISTIC COMPOSITION

Site	Species present (according to code)
1932K1	2,6,7,8,10,13,14,15,16,17,18,20,22,23,25,26,27,29,30,31,33,34,35,36,37,38,39,40,41,42,45,47,48,49,50,51,55,57,59,63,67,68,73,76,77,79,85,88,90,94,97,98,100,02,103,110,111,113,114,115,116,117,118,119,124,126,129,130,131,133,134,136.
1932K5	8,9,10,14,16,18,21,22,27,29,31,33,34,35,36,40,41,42,43,47,50,51,,55,57,58,61,65,68,76,77,79,94,97,99,101,102,105,107,109,110,111,114,116,117,124,126,129,130,131,133,134,136.
1940K1	1,4,5,6,7,8,10,11,16,19,22,23,,28,33,34,38,39,40,42,43,45,46,47,48,50,53,54,55,57,59,60,62,66,67,68,69,70,72,73,74,75,79,80,87,90,91,92,102,108,110,111,112,114,115,117,118,119,123,125,126,130,131,133,134,135,136.
1940K5	1,2,3,6,7,8,10,13,15,16,20,22,24,27,28,34,36,40,42,43,45,47,48,51,53,54,55,57,58,62,68,69,70,71,73,74,79,82,83,84,87,90,91,92,98,101,104,110,111,114,115,117,118,120,121,122,123,125,126,127,131,132,133,134,135,136.
1965K1	8,11,12,16,21,22,27,28,31,32,34,35,36,38,39,40,41,44,45,46,47,48,49,50,52,53,54,55,56,59,61,64,68,70,72,73,76,78,79,80,81,85,89,93,94,95,101,102,110,111,114,115,117,128,129,130,131,133,134,136.
1965K5	2,4,11,14,16,21,22,24,27,28,32,34,36,38,40,41,42,46,47,49,50,52,54,56,59,61,65,68,70,72,73,76,77,78,79,82,85,86,93,94,96,98,101,102,106,109,110,113,115,117,118,126,130,131,133,134,136.

APPENDIX 2 (con't)

Species Code	Species Name
1.	poaceae,poa,neurachne,or amphipogon species (?)
2.	Borya sphaerocephala
3.	Caesia micrantha
4.	Caesia occidentalis
5.	Chamaescilla corymbosa
6.	Chamaescilla spiralis
7.	Laxmannia paleacea
8.	Thysanotus patersonii
9.	Tricoryne humilis
10.	Hydrocotyle callicarpa
11.	Hydrocotyle pilifera
12.	Platysace teres
13.	Trachymene ornata
14.	Trachymene pilosa
15.	Arctotheca calendula
16.	Blennospora drummondii
17.	Brachycome bellidioides
18.	Ceratogyne obionoides
19.	Chrysocoryne drummondii
20.	Helipterum demissium
21.	Helipterum laeve
22.	Hypocheris glabra
23.	Millotia tenuifolia
24.	Podotheca augustifolia
25.	Podolepis canescens
26.	Ursinia anthemoides
27.	Waitzia citrina
28.	Waitzia paniculata
29.	Wahlenbergia gracilenta
30.	Wahlenbergia campestris
31.	Allocasuarina huegeliana
32.	Allocasuarina microstachya
33.	Centrolepis aristata
34.	Centrolepis humillima
35.	Crassula pedicellosa
36.	Caustis dioica
37.	Isolepis marginata
38.	Lepidosperma gracile
39.	Lepidosperma leptostachyum
40.	Lepidosperma tenue
41.	Schoenus armeria
42.	Schoenus subflavus
43.	Chamaexeros serra

APPENDIX 2 (con't)

Species Code	Species Name
44.	Lomandra suaveolens
45.	Hibertia exasperata
46.	Hibertia microphylla
47.	Drosera leucoblaster
48.	Drosera subhirtella
49.	Astroloma serratifolium
50.	Leucopogon dielsianus
51.	Leucopogon fimbriatus
52.	Lysinema ciliatum
53.	Poranthera microphylla
54.	Dampiera lindleyi
55.	Goodenia caerulea
56.	Conostylis petrophiloides
57.	Conostylis setigera
58.	Haemodorum paniculatum
59.	Glischrocaryon aureum
60.	Patersonia juncea
61.	Hemigenia incana
62.	Microcorys ericifolia
63.	Cassyntha melantha (?)
64.	Cassyntha pomiformis
65.	Mitrasacme paradoxa
66.	Acaicia acuminata
67.	Acacia pulchella
68.	Acacia stenoptera
69.	Acacia sulcata
70.	Baeckea crispiflora
71.	Baeckea floribunda
72.	Baeckea preissiana
73.	Beaufortia bracteosa
74.	Calytrix empetriodes
75.	Calytrix flavescens
76.	Calytrix leschenaultii
77.	Calothamnus planifolius
78.	Hypocalymma augustifolium
79.	Melalueca subtrigona
80.	Verticordia grandiflora
81.	Verticordia huegelii
82.	Verticordia picta
83.	Caladenia flava
84.	Caladenia roei
85.	Caladenia saccharata
86.	Diuris longiflora

APPENDIX 2 (con't)

Species Code	Species Name
87.	Elythranthera brunonis
88.	Pterostylis nana
89.	Pterostylis sargentii
90.	Gastrolobium hookerii
91.	Gompholobium marginatum
92.	Jacksonia alata
93.	Jacksonia capitata
94.	Jacksonia restiodes
95.	Oxylobium parviflorum
96.	Trifolium subterraneum
97.	Aira caryophyllea
98.	Amphipogon turbinatus
99.	Briza maxima
100.	Briza minor
101.	Danthonia pilosa
102.	Neurachne alopecuroidea
103.	Pentaschistis airoides
104.	Stipa trichophylla
105.	Vulpia myuros
106.	Comesperma calymega
107.	Comesperma sp_indet.
108.	Comesperma volubile
109.	Anagallis arvensis
110.	Banksia sphaerocarpa
111.	Dryandra armata
112.	Dryandra nivea
113.	Hakea gilbertii
114.	Hakea sp_indet.
115.	Hakea lehmanniana
116.	Hakea trifurcata
117.	Isopogan teretifolius
118.	Persoonia quinquinervis
119.	Petrophile media
120.	Petrophile spuamata
121.	Synaphea petiolaris
122.	Lepidobolus chaetocephalus (?)
123.	Loxocarya fasciculata
124.	Lyginea barbata
125.	Cryptendra glabiflora
126.	Opercularia vaginata
127.	Tripterococcus brunonis
128.	Levenhookia dubia
129.	Levenhookia pusilla

APPENDIX 2 (con't)

Species Code	Species Name
130.	Levenhookia stipitata
131.	Levenhookia breviscapum
132.	Stylidium hirsutum
133.	Stylidium luteum
134.	Stylidium repens
135.	(a goodeniaceae, probably a vellia species)
136.	Xanthorrhoea drummondii

APPENDIX 3 - SPIDER SPECIES ABUNDANCE

Sample

Sp. Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1	0	1	3	0	0	0	25	16	13	0	0	0	0	0	0	0	0	0
2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	1	0	0	0	0	0	0	2	0	0	7	0	0	0	0	0	0
4	2	1	2	0	2	0	2	2	0	2	0	0	2	0	0	1	0	0
5	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0
6	0	0	0	0	0	0	0	0	0	1	2	1	0	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	3	0	2	0	1	0	0	1	0
8	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0
10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	1
11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
16	12	1	13	15	1	6	11	0	6	0	0	0	1	0	0	6	0	5
17	7	0	7	2	0	1	23	2	1	0	12	0	0	1	1	1	0	0
18	0	0	1	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
19	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	1	0	2	0	0	0	7	0	1	0	0	2	3	0	1	0	0	0
21	0	0	2	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0
22	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
23	1	1	1	0	0	0	0	0	0	0	0	0	4	0	1	0	0	0
24	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
25	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	0	5	3	5	54	15	24	3	5	2	4	16	21	3	5	2
27	0	0	0	1	0	0	0	0	0	0	0	2	0	1	2	0	0	0
28	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	4	0	0	2	0	0	1	0	0
30	0	0	0	0	0	0	1	1	1	1	1	1	0	0	0	1	0	2
31	0	0	0	0	0	0	1	0	0	0	1	2	1	0	1	1	0	0
32	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	3	0	0	1	0	0	6	0	0	10	0	0
34	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0
35	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
36	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
37	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
39	5	3	5	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
40	0	3	1	4	11	1	0	0	0	0	0	0	0	0	0	0	0	0
41	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
42	3	3	3	4	0	3	3	0	0	1	0	0	0	0	2	0	4	0

APPENDIX 3 (con't)

Sample Sp. Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
43	3	0	0	0	0	1	2	0	2	2	1	0	0	0	0	1	2	1
44	0	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0	1
45	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
46	6	0	5	0	1	0	14	3	5	7	1	3	7	6	18	19	6	17
47	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
49	0	1	0	0	0	0	0	0	0	1	2	0	0	0	1	1	3	0
50	3	0	0	0	1	0	59	17	20	14	10	6	6	0	2	12	7	22
51	0	0	0	3	11	3	4	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	1	4	0	0	1	0	0	0	0	0	0	0	0	0
54	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	2	2	0
55	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
56	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
57	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
58	0	0	0	1	0	0	8	0	1	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	1	1	17	0	0	0	0	0	0	0	0	1
61	0	0	0	0	0	0	5	0	3	0	0	0	0	0	0	1	1	0
62	0	0	0	0	0	0	3	1	6	22	5	6	3	1	1	0	0	1
63	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
64	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0
65	0	0	0	0	0	0	1	1	1	19	0	2	1	0	0	0	0	0
66	0	0	0	0	0	0	0	0	1	2	1	1	0	0	0	0	0	0
67	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
68	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
69	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	3	4	5
70	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	5	0	0	3	0	0	0	0	0	0	0	0
72	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
73	0	0	0	0	0	0	3	0	0	14	0	0	4	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	3	1	4	0	1	4	3	3	0
75	0	0	0	0	0	0	0	0	0	1	10	15	4	4	2	3	11	4
76	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
78	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
79	0	0	0	0	0	0	0	0	0	0	3	1	0	0	1	1	2	1
80	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0	0
81	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
82	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	1	0	0
83	0	0	0	0	0	0	0	0	0	0	0	0	7	5	8	0	1	1

APPENDIX 3 (con't)

Sample Sp. Code	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
84	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	1	1	1
85	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
86	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
87	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0
88	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
89	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
90	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
91	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
92	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
93	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0
94	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
95	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
96	0	0	0	0	0	1	6	1	3	31	22	20	18	23	17	11	14	20
97	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	0	0	0
98	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
99	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
100	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
101	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0
102	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
103	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
104	0	2	0	1	0	1	30	4	3	16	3	7	18	13	8	10	10	8
105	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
106	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
107	22	7	40	1	1	0	2	0	1	0	0	0	0	1	0	0	0	0
108	0	0	2	12	0	4	8	1	0	0	0	0	0	0	0	0	0	0
109	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
110	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
111	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
112	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
113	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
114	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
115	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
116	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
117	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	1	0	0
118	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
119	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	0
120	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
121	0	0	0	0	0	0	1	0	0	0	4	0	1	3	0	0	4	0
122	0	0	0	0	0	0	0	0	0	8	1	0	0	2	1	0	0	0
123	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
124	0	0	0	0	0	0	0	0	0	0	0	0	3	2	0	4	5	1
125	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

APPENDIX 3 (cont.)

Sample Code	Month	Site
1	May	1932
2	May	1940
3	May	1965
4	Jul	1932
5	Jul	1940
6	Jul	1965
7	Sep	1932
8	Sep	1940
9	Sep	1965
10	Nov	1932
11	Nov	1940
12	Nov	1965
13	Jan	1932
14	Jan	1940
15	Jan	1965
16	Feb	1932
17	Feb	1940
18	Feb	1965

APPENDIX 3 (cont.)

Spider Species Code	Family	Sp.No.	Reference Collection No.
1	Araneidae	1	5
2	Araneidae	2	12
3	Araneidae	3	16
4	Araneidae	4	19,25,36,38
5	Araneidae	5	85
6	Araneidae	6	95
7	Araneidae	7	96,113
8	Araneidae	8	105
9	Araneidae	9	123
10	Araneidae	10	124
11	Araneidae	11	147
12	Araneidae	12	149
13	Araneidae	13	150
14	Araneidae	14	156
15	Araneidae	15	158
16	Clubionidae	1	2
17	Clubionidae	2	3
18	Clubionidae	3	13
19	Clubionidae	4	14
20	Clubionidae	5	20
21	Clubionidae	6	22
22	Clubionidae	7	23,65
23	Clubionidae	8	26
24	Clubionidae	9	34
25	Clubionidae	10	37
26	Clubionidae	11	39,51
27	Clubionidae	12	56
28	Clubionidae	13	60
29	Clubionidae	14	64
30	Clubionidae	15	67,84
31	Clubionidae	16	76
32	Clubionidae	17	77
33	Clubionidae	18	78
34	Clubionidae	19	93
35	Clubionidae	20	102
36	Clubionidae	21	107
37	Clubionidae	22	115
38	Clubionidae	23	160
39	Ctenizidae	1	7
40	Ctenizidae	2	15,28,30,54
41	Ctenizidae	3	18
42	Ctenizidae	4	24,53,126

APPENDIX 3 (cont.)

Spider Species Code		Family	Sp.No.	Reference Collection No.
*	43	**Damaged**	1	35,50,80,112,122
	44	Dinopidae	1	86
	45	Dinopidae	2	121
	46	Gnaphosidae	1	8,42,66,104,151,154
	47	Gnaphosidae	2	10
	48	Gnaphosidae	3	11
	49	Gnaphosidae	4	33,118
	50	Gnaphosidae	5	40,43,62
	51	Gnaphosidae	6	41
	52	Gnaphosidae	7	45
	53	Gnaphosidae	8	46
	54	Gnaphosidae	9	47
	55	Gnaphosidae	10	48
	56	Gnaphosidae	11	49
	57	Gnaphosidae	12	52
	58	Gnaphosidae	13	55
	59	Gnaphosidae	14	57
	60	Gnaphosidae	15	58
	61	Gnaphosidae	16	59
	62	Gnaphosidae	17	61,87
	63	Gnaphosidae	18	68
	64	Gnaphosidae	19	69
	65	Gnaphosidae	20	70
	66	Gnaphosidae	21	71
	67	Gnaphosidae	22	72
	68	Gnaphosidae	23	73
	69	Gnaphosidae	24	74
	70	Gnaphosidae	25	75
	71	Gnaphosidae	26	81
	72	Gnaphosidae	27	83
	73	Gnaphosidae	28	90
	74	Gnaphosidae	29	91
	75	Gnaphosidae	30	94
	76	Gnaphosidae	31	97
	77	Gnaphosidae	32	99
	78	Gnaphosidae	33	100
	79	Gnaphosidae	34	101
	80	Gnaphosidae	35	110
	81	Gnaphosidae	36	117
	82	Gnaphosidae	37	119
	83	Gnaphosidae	38	125
	84	Gnaphosidae	39	127,152,157
	85	Gnaphosidae	40	128

APPENDIX 3 (cont.)

Spider Species Code	Family	Sp.No.	Reference Collection No.
86	Gnaphosidae	41	135
87	Gnaphosidae	42	137
88	Gnaphosidae	43	141
89	Gnaphosidae	44	142
90	Gnaphosidae	45	143
91	Gnaphosidae	46	144
92	Gnaphosidae	47	145
93	Gnaphosidae	48	146
94	Gnaphosidae	49	155
95	Gnaphosidae	50	161
96	Gnaphosidae	51	27,63,92,136,153
97	Hersiliidae	1	138
98	Lycosidae	1	31
99	Mimetidae	1	44
100	Miturgidae	1	106
101	Oxyopidae	1	129
102	Pholcidae	1	6
103	Pholcidae	2	139
104	Salticidae	1	29,32,133,134
105	Salticidae	2	108
106	Salticiae	3	159
107	Theridiidae	1	1
108	Theridiidae	2	9
109	Theridiidae	3	98
110	Theridiidae	4	148
111	Thomisidae	1	4
112	Thomisidae	2	17
113	Thomisidae	3	82
114	Thomisidae	4	88
115	Thomisidae	5	111
116	Thomisidae	6	114
117	Thomisidae	7	120
118	Thomisidae	8	131
119	Thomisidae	9	132
120	Zodariidae	1	79
121	Zodariidae	2	89,116
122	Zodariidae	3	103,109
123	Zodariidae	4	130
124	Zodariidae	5	140
125	Zodariidae	6	162

* Denotes the presence of a spider but due to damage the species of the spider could not be determined.

APPENDIX 4 - FLORISTIC SIMILARITY MATRIX USING SORENSEN'S INDEX

Grid Similarity Matrix [using Sorensen's (1948) "quotient of similarity"].

		GRID					
		1	2	3	4	5	6
	1	1.000	0.672	0.561	0.532	0.541	0.538
	2		1.000	0.441	0.424	0.536	0.514
GRID	3			1.000	0.667	0.540	0.472
	4				1.000	0.429	0.439
	5					1.000	0.701
	6						1.000

Site Code:

1=1932K1
2=1932K5
3=1940K1
4=1940K5
5=1965K1
6=1965K5