Fire and Invertebrate Conservation in Mallee-Heath Remnants

Final Report

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Gordon Friend and Matthew Williams

Department of Conservation and Land Management
Western Australia

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SUMMARY AND RECOMMENDATIONS

A three-year study (1989-1992) of the responses of invertebrates to fire was carried out in mallee-heath shrublands in the Stirling Range National Park, Western Australia. Changes in invertebrate abundance were measured at the Order level for major groups, and at the species level for Coleoptera. Changes in floristics and vegetation structure were monitored over the same period.

Responses were highly variable, with no consistent patterns between different intensities or seasons of burn. At the Order level, variation in abundances were attributable more to seasonal and year-to-year effects than to fire. Responses of beetles at the morphospecies level, however, reflected changes due to fire as well those attributable to season and year.

Space-for-time comparisons of seral stages showed varying results for different Orders which were not entirely consistent between sampling years. Coleoptera and Diptera were most abundant 40 years after fire, Hymenoptera and Orthoptera peaked in earlier seral stages, while Hemiptera and Araneae were largely invariant. Most groups showed distinct locality and year-to year effects which outweighed any changes attributable to fire.

Coleoptera and Diptera best reflected changes due to season, year and fire, and together with some Araneae such as Mygalomorph spiders, would most likely be the best groups to consider in future studies. However, results from multivariate analyses indicated that classification to morphospecies level is essential to elucidate changes due to fire. These analyses also indicated that changes in invertebrate abundance and composition did not accord with changes in floristics or vegetation structure. Each set of data therefore represents different facets of change over time, including those due to fire.

Our data and that of Main and Gaull (1993) indicate that there is a clear dichotomy in the fire sensitivity of species inhabiting the wet gullies and thickets of the uplands in the Stirling Range and those occupying the seasonally dry lowland mallee-heaths. Fire management stategies need to take account of this dichotomy by protecting relictual fire sensitive species and habitats. This can be achieved through a combined system of low fuel zones along boundaries and a mosaic of different-aged areas, which vary both spatially and temporally, in the more resilient lowland habitats. As season of burn does not appear to be of major significance to invertebrate communities it is recommended that most protective burning be carried out in spring when weather patterns are more stable and predictable.

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CONTENTS

INTRODUCTION

The role of prescribed burning in the management of remnant vegetation throughout temperate Australia is a complex and sometimes contentious issue. Ironically, fire is one of the most accessible and convenient tools available for habitat management, but also one of the least understood.

Currently, most fire management decisions are based on a reasonably detailed knowledge of weather, fuel and other site parameters and their influence on fire behaviour. This knowledge forms the main rationale for the prescribed burning of forested areas of south-western and south-eastern Australia to reduce fuel loads and wildfire hazard (Shea *et al.* 1981; Cheney 1985; McCaw and Burrows 1989). Increasingly, fire is also being used to change vegetation structure and reduce fuel loads for wildfire protection purposes in many National Parks and conservation reserves throughout the drier mallee woodlands and heathlands of Australia (eg. see Burrows *et al.* 1989; Gill 1990; McCaw and Smith 1992).

In the context of ecosystem management, however, most decisions must be made against a background of little or no research data on the effects of fire (or a fire regime) on the biota. Incorrect decisions could jeopardize the long-term survival of many species (eg. malleefowl; Priddel 1989; Benshmesh 1990). There is thus a serious dichotomy in our levels of understanding of the principles of fire physics and prescibed burning technology on the one hand, and the impacts of fire and its role in ecosystem management on the other. This points to an urgent need to obtain reliable data on the effects of fires of varying intensities and season of burn on the biota, in conjunction with studies on the behaviour of these fires and the management planning processes involved.

Most studies of fire effects have concentrated on vegetational aspects, perhaps because plants are the organisms perceived as being most directly affected by fire. Until the last decade, relatively little fire effects work had been carried out relating to fauna, and there is still a dearth of knowledge with respect to herpetofauna and invertebrates (see reviews by Suckling and Macfarlane 1984; Christensen and Abbott 1989; Friend 1993). Furthermore, the majority of these faunal studies have focussed on the taller hardwood forests and the effects of prescibed burning for fuel reduction (Christensen and Kimber 1975; Catling 1991), but few have been carried out in semi-arid woodlands and shrublands. The majority of fire effects studies in these latter habitat types have considered small mammals, and to a lesser extent reptiles (Friend 1993), but there remains a paucity of information on invertebrates (Key 1978; Majer 1987a; Hill and Michaelis 1988).

Invertebrates as bio-indicators

There is a considerable and growing body of evidence that invertebrates are more important in the maintenance of ecosystems than are vertebrates. Most of the biological diversity we are dealing with in nature conservation is contributed by invertebrates (Greenslade and Greenslade 1984; New 1984, 1987; CONCOM 1989), yet they are usually ignored in ecological research (Majer 1987a). Furthermore, certain guilds of invertebrates are proving excellent bio-indicators of environmental conditions, including pyric status. Suitable groups include ants (Majer 1983; Andersen 1987), spiders (Clausen

1986; Main 1987) and probably also beetles, given their wide diversity of species and life history strategies (Lawrence and Britton 1991). Through analysis of insects comprising small vertebrate diets (e.g. of dasyurids, lizards, frogs) and insect/plant interactions (especially herbivory rates), invertebrate studies can also contribute to an understanding of the processes involved in pyric disturbance ecology.

Invertebrates and fire

The research carried out to date on the impact of fire on invertebrates has frequently produced conflicting results (see Abbott 1984; Tap and Whelan 1984; Majer 1985a). In the Western Australian jarrah (*Eucalyptus marginata*) forest early studies by McNamara (1955) and Springett (1976, 1979) suggested that fire had a significant long-term effect on the litter fauna, with recovery taking longer than the normal prescribed fire interval of 5-7 years. By contrast Bornemissza (1969), Whelan *et al.* (1980), Majer (1980, 1984) and Abbott (1984) found significant short-term effects (both increases and decreases in selected taxa), but found (or predicted) recovery of the invertebrate communities within 2-3 years. Similarly, Abbott *et al.* (1984) found few differences in the litter and soil fauna of regularly burned and long-unburned jarrah forest, and concluded that periodic low intensity fires in these forest types have few permanent effects on such components of the fauna.

In studies in the dry sclerophyll forests of eastern Australia, Linsdell (1969) found greater abundances of Acarina and Collembola three years after a fuel reduction burn than in adjacent unburnt forest, and also concluded that wildfires caused greater reductions in litter-dwelling invertebrates than did prescribed burns. Leonard (1972) recorded a 50 per cent reduction in species richness and a 50 to 90 per cent decline in abundances immediately following a low intensity fuel reduction burn in Victoria, but these values had increased to 80 per cent of those in unburnt forest within 12 months of the fire. In their studies on the impacts of spring and winter burns on invertebrates near Canberra, A.C.T., Campbell and Tanton (1981) concluded that after burning, invertebrate communities remained within the range of variation recorded over a variety of unburnt areas. Furthermore, these authors suggested that the high spatial and temporal variability in the invertebrate fauna, and variability in the nature of the climate, habitat and fires makes it almost impossible to predict the outcome after any particular fire.

Recent work by Neumann and Tolhurst (1991) over four years in mixed eucalypt forest near Daylesford, Victoria, compared the impacts of low-intensity spring and autumn burns on soil and litter invertebrates. The spring burn caused short-term reductions in the common major taxa (Collembola and Diptera) and some minor taxa (eg Opiliones and Lepidoptera) for up to a year, while earthworms declined significantly for three years. The autumn burn reduced Collembola and some minor taxa (eg. Blattodea, Thysanura and Tettigoniidae) for up to ten months, but had no effect on earthworms. These authors concluded that the spring burn, and to a lesser extent the autumn burn, had caused a short-term disruption to the decomposer cycle, but that the soil/litter fauna of dry sclerophyll forest appears to be relatively resilient to occasional low-intensity fire.

In the Brindabella Ranges, A.C.T., O'Dowd and Gill (1985) recorded a dramatic decline in the abundance and species richness of all invertebrates except ants immediately after a planned high intensity summer fire. Ant foraging activity increased markedly (six-fold) after the fire, and species richness also increased. Ants showed a similar response to a low intensity autumn fire at Belair, South Australia (O'Dowd 1985), but the abundance of other macroinvertebrates was not greatly affected. In New South Wales coastal forest ant species richness declined with time since fire, but also declined with an increase in fire frequency, reflecting a close link between habitat structure and ant community composition (York 1991). By contrast, Acarina and Collembola showed no consistent response to a high intensity wildfire in a South Australian forest reserve (Hutson and Kirkby 1985), with some groups increasing and others decreasing.

In the drier woodland and heathland areas preliminary and short-term studies by Tap and Whelan (1984) and Majer (1985b) also showed no consistent post-fire response patterns amongst the invertebrate fauna. Invertebrate abundances increased significantly after fire in Tap and Whelan's (1984) heathland study site, while Majer (1985b) considered the composition and abundance of the ground invertebrate fauna was influenced as much by site factors, such as moisture availability, as by time since fire. Similarly, Little and Friend (1993) concluded that fire did not exert a long-term influence on the composition of invertebrate communities in semi-arid heathland in the Western Australian wheatbelt. Majer (1985a), however, postulated that the invertebrate fauna would be less resilient to fire in the drier, inland areas than in the more mesic forest areas, and that a different and longer-rotation burning regime should be practiced in areas of lower rainfall.

Bamford (1986) recorded lower abundances of invertebrates for up to two years after experimental fires in Western Australian *Banksia* woodland, and found that abundances increased with increasing time since fire. Ants showed responses similar to those recorded by O'Dowd (1985) and O'Dowd and Gill (1985). Seasonal abundance patterns were disrupted for 12 months following a spring fire, but patterns had returned to normal within six months of an autumn burn.

The above brief review of the literature on invertebrates and fire indicates that a wide variety of response patterns may occur. In general, it appears that most impacts are relatively short-term (eg less than 2-3 years), that high intensity wildfires have much greater impacts than lower-intensity prescribed burns, and that spring prescribed burns may have a greater impact than those carried out in autumn.

The impact of spring versus autumn fires has been a long-standing and much-debated question with respect to invertebrates, particularly in forest areas. Majer (1985a, 1992) argued that spring fires are likely to have the greater impact because invertebrates increase in activity during this season and immediate post-fire conditions are becoming increasingly hot and dry. Campbell and Tanton (1981), however, contended that because most invertebrate populations are in an active and reproductive state in spring, the effects of fire at this time are soon overcome. Koch and Majer (1980) and Majer (1985a) also predicted that decomposers are the only component of the fauna which may not be adversely affected by spring fires because such burns occur well in advance of the period of decomposer activity. Available evidence supports Majer's (1985a) prediction regarding season of burn, but the data of Neumann and Tolhurst (1991) do not support the predictions regarding relative impacts on decomposer organisms.

Many of the conflicting conclusions from studies on the impact of fire on invertebrates have arisen because of variations or shortcomings in experimental design, taxonomic treatment and length of study (see also Abbott 1984; Majer 1985a). Few studies have any prefire data (see review by Majer 1985c for Western Australian studies), or any long-term post-fire data (Abbott 1984; Tap and Whelan 1984; Majer 1980, 1985a, 1985c). In the majority of cases invertebrates have been identified only to ordinal level, thus potentially masking important changes in species and family composition following fire. In addition, most workers have contemporaneously sampled areas of different fire histories and ascribed faunal differences to the effect of these fires. Given the inherent within-site variability of invertebrate populations (Campbell and Tanton 1981) this assumption of pre-fire homogeneity between control and treatment plots is tenuous. Furthermore, the effects of intensity and season of burning are likely to be profound, but have frequently been ignored. It is not surprising, therefore, that conflicting results have been obtained, and it is impossible to determine whether the variation in outcomes is real or largely due to differences in experimental design and techniques.

Objectives

Against the above background of information, the present study was developed with the general objective of examining the consequences of instigating deliberate burning for ecological management in remnant mallee shrubland vegetation by studying components of the fauna which are likely to show a range of responses to fire. The specific aims of the project were:

(a) To investigate the effects of a range of prescribed burns of varying intensities and season of burn on invertebrate communities (with particular emphasis on beetles) inhabiting remnant mallee-heath shrublands.

(b) To document invertebrate communities in mallee-heath shrublands of different ages.

(c) To use these data (and those from integrated vertebrate and vegetation studies in the same area) to develop general principles and policies for predictive fire management in these habitat types.

MATERIALS AND METHODS

The objectives were met by adopting two approaches to the work. Firstly, an experimental approach, whereby two 20ha areas (each 400 m x 500 m) and a 400ha area were subjected to fires of different intensities, scale and seasons of burn. Samples of invertebrates were obtained for 12- 18 months before and after these burns, along with data on vegetation and habitat structure. Data on small vertebrates were also obtained from these areas as part of a wider study.

The second approach adopted was a space-for-time sustitution (SFT; Pickett 1989), whereby a variety of mallee-heath shrublands of different ages were contemporaneously sampled for invertebrates, vegetation, habitat structure (and small vertebrates). Ages of vegetation available for sampling included 4, 8, 20, 40 and c. 50-year-old stands (ages as at 1990). The 20 and 40-year-old areas were burned in the experimental approach outlined above. The SFT approach enabled longer-term successional aspects to be examined in a relatively short-term project.

Study area and site layout

Studies were carried out in mallee-heath shrubland vegetation within the 115,000ha Stirling Range National Park, 80km north of Albany in the south-west of Western Australia (Fig 1). This region experiences a mediterranean climate with warm, dry summers and cool, moist winters. Daily maximum and minimum temperatures vary from 26.2°C and 12.8°C respectively in the hottest months (January/February) to 14.2°C and 5.8°C respectively in the coldest month (July), with a mean annual rainfall of 746mm (data for Mt Barker, 50km south-west of the Park, Western Australian Yearbook 1990). Rainfall declines rapidly further inland, and averages 461mm for Kojaneerup, immediately to the south of the Park (Bureau of Meteorology, Perth).

Grid-based sampling commenced in June 1989, and was centred on two areas near the southern boundary of the Park (Fig 1).

(a) Approximately 18 km east of Chester Pass Road near Two Mile Lake (34° 29' S; 118° 15' E). This area comprised two distinct vegetation alliances which were treated separately in the design of the study. The first site was located on deep sandy soils immediately west of Two Mile Lake, with an upperstorey dominated by *Lambertia inermis*, *Eucalyptus tetragona* and *Eucalyptus decipiens*. The dense understorey was rich in Proteaceous and Myrtaceaous species, the more common including *Beaufortia elegans*, *Banksia nutans*, *Conothamnus neglectus*, *Petrophile ericifolia* and *Melaleuca thymoides*. The date of the last burn at this site is uncertain, but examination of aerial photographs indicate that it was at least pre 1956, so that the vegetation is probably about 40 years old. Three sampling grids were established in this vegetation-type. Grids 1 and 2 (Fig. 1) were located in a 400ha area that was experimentally burnt on 17 April 1991. The fire was line-ignited along the western side of the block commencing at about 1100hr when the air temperature was 31°C, the relative humidity 25% and the wind WSW at ~10 km/hr. Flame heights reached 4-6m and the Byram fireline intensity was calculated as 3000-5000 kW/m, categorizing the fire as high intensity (Cheney 1981). However the fire was very patchy in the western portion of the block, and both Grids 1 and 2 were only partially burnt. Grid 3 (Fig. 1) was located within an existing buffer and remained unburnt (control).

The second site near Two Mile Lake featured more variable soils with low elevated ridges of duplex laterite, and broad swales of deeper sands. These deeper sands supported similar vegetation to that descibed above, but the lateritic ridges were dominated by *Eucalyptus pachyloma, E. tetragona* and *Hakea crassifolia* with a dense understorey of *Hakea trifurcata, Petrophile squamata, P. ericifolia* and *Kunzea preissiana*. The vegetation was 20 years old, having been burnt by a wildfire in 1969. Eight sampling grids (4x2 replicates of each) were established in this vegetation. Grids 4A and 4B were located in a 20ha plot which was burnt on 27 March 1991. This fire was ignited along the western and northern sides when the air temperature was 28°C, the relative humidity 27%, and the wind NW at 10-15 km/hr. Flame heights reached 3-4m and the Byram fireline intensity was calculated as 2000-3000 kW/m, categorizing the fire as moderate intensity (Cheney 1981). All understorey vegetation in and around Grid 4B was consumed by the fire and the overstorey completely scorched, but Grid 4A was only partially burnt. Grids 5A and 5B were located in deeper sands within an adjacent 20ha plot which was burnt under moderate intensity (1500-2000 kW/m) on 24 November 1990. This fire was ignited in lines at 50m intervals when the air temperature was 26°C, the relative humidity 40%, the wind ESE at 10-15 km/hr and the fuel moisture content (shallow litter) was 5%. Although flame heights reached 1-3m, there was considerable variability in fire behaviour with some substantial patches remaining unburnt. Grid 5B was completely burnt, but some unburnt patches remained on Grid 5A. Grids 6A and 6B, located to the west of the two 20ha plots, remained unburnt as controls to the spring and autumn burnt plots. Grids 7A and 7B were located in an area on the southern boundary which was burnt in 1986, allowing a comparison with Grids 4,5 and 6 (see Fig 1).

A further two grids (Grids 10 and 11) were established in October 1991 near the South Isongerup Track (approximately 5 km north-east of Grids 4,5 and 6; Fig 1), following a large scale, very high intensity fire which affected the north-east section of the Park in the first week of April 1991. This fire consumed all vegetation and leaf litter in its path, and left few unburnt patches in the area affected. It was thus a marked contrast to the small scale lower intensity experimental fires deployed on Grids 1,2, 4 and 5, and presented a valuable opportunity to gather some short-term data on the impacts of a wildfire on invertebrates. Grids could not be established immediately after the fire because of the need to comply with restrictions on wet weather activity to reduce the risk of spreading dieback disease (eg. *Phytophthora cinnamomi*). Vegetation and soils in this area were similar to those on Grids 4,5 and 6, and the latter grid was again used as an unburnt control for comparison with Grids 10 and 11.

(b) Approximately 5 km west of Chester Pass Road (34° 28' S; 118° 02' E), where two areas of markedly different ages were sampled each side of a boundary fire break (Fig 1). In both areas the soils comprised deep grey/white sands and the vegetation composition was generally quite similar to that on Grids 1,2 and 3 near Two Mile Lake (see above). Grid 8 was located within the 200m wide boundary buffer, and was last burnt in 1982. Low regrowth vegetation characterised the area, the dominant species being *Eucalyptus marginata, E. pachyloma, L. inermis* and *Melaleuca striata*. Grid 9 was characterised by very dense vegetation estimated to be at least 50 years old (the date of the last burn is uncertain, but certainly well prior to 1950), with *E. marginata*, *Eucalyptus staeri* and *L. inermis* dominating as overstorey to about 5m, and *B. elegans*, *B. nutans*, *P. ericifolia*, and *M. thymoides* representing the major understorey species. These two areas were selected as part of the space-for-time approach to compare two adjacent areas differing only with respect to fire age.

Invertebrate sampling

Sampling commenced in June 1989 on Grids 1-7, and in October 1989 on Grids 8 and 9. Grids 10 and 11 were sampled only four times following establishment in October 1991 (see above). Over the whole period of the study (June 1989 to May 1992) sampling was conducted in June, August, October and December 1989; February, April, June, September and December 1990; April, May, October and December 1991; and March and May 1992. Sampling was mainly confined to the spring and autumn periods to reduce the risk of spreading dieback disease (see above), and because these periods provided maximal captures of invertebrates.

Invertebrates were sampled using three techniques: pitfall trapping, sweeping and intercept traps.

Pitfall trapping

This was the main method used for sampling invertebrates, and the majority of data amenable to statistical analyses were derived from this source. The limitations of this technique have been discussed by Southwood (1978), Adis (1979) and Topping and Sunderland (1992). Although limited in its efficiency for comparing different community types and estimating absolute invertebrate abundances, Southwood (1978) notes that this method can be used to assess the relative abundance of invertebrate populations in similar habitat types. Topping and Sunderland (1992) point out that few ecologists fully appreciate the limitations of this technique; in particular that considerable caution must be exercised in the interpretation of results from pitfall traps where there are large differences in vegetation density and structure between areas being compared.

In this study each pitfall trap consisted of a plastic cup (90mm diameter, 110mm deep), placed inside a sleeve of PVC piping, enabling traps to be set and removed with minimum disturbance to the surrounding soil and litter. This design of trap is similar to that described by Majer (1978). Traps were layed out at 5m intervals in a 4 x 4 matrix, creating a 15m x 15m grid of 16 pitfall traps (Fig. 2). Each grid was layed out with the aid of a compass on a north/south x east/west orientation for columns and rows respectively. Such grids formed the basic sampling unit for both the invertebrate and the vegetation and habitat structure studies.

When in use, each pitfall was half-filled with Galt's solution which consisted of 5% sodium chloride, 1% potassium nitrate, 1% chloral hydrate, a trace of glycerine, and 93% water. Traps were operated for ten days in each sampling session, after which the contents of the four pitfall traps about each corner of a grid were bulked to form four replicate samples. Replicates were numbered 1-4 in a clockwise direction from the south-west corner. Each sample was labelled according to the sample time, site, and position on the grid. Samples were fine-sieved in the field and transferred from Galt's solution to 70% ethanol. Sandfilled cups were placed in the PVC sleeves to close the pits.

Sweeping

During each sampling session a sweep-net sample of invertebrates inhabiting the shrub strata (<2m) within each pitfall-trap grid was taken using a 45cm diameter calico bag hoop-net. A sample comprised fifty sweeps within each 15 x 15m grid with the collector walking slowly in a figure-of-eight over the grid area. Invertebrates were collected from the bag using an aspirator, then immediately labelled and stored in 70% ethanol for later sorting.

Intercept traps

To supplement pitfall trapping, intercept traps were run for the same 10-day sample periods as the grids. Intercept traps were set up at the north-west corner of all grids except the replicate (B) grids at sites 4 to 7. Each trap consisted of a 80 x 100 cm sheet of clear perspex mounted on steel pickets above a 160 mm diameter PVC trough. All traps were orientated in a north/south direction with the 100 cm long trough approximately 60 cm above the ground. When in use the trough was three-quarter filled with Galt's solution. At the end of each sample period the solution was emptied through a hole in the trough and the invertebrates collected in a fine sieve and stored in 70% ethanol for later sorting.

Sorting and identification of invertebrates

Invertebrates were sorted and counted with the aid of a stereo microscope. Animals belonging to the major orders Coleoptera, Araneae, Hymenoptera, Diptera, Hemiptera and Orthoptera were identified with the aid of keys in CSIRO (1970, 1991) and Davies (1986) and their abundance recorded. These were stored in separate vials to enable the possibility of further detailed identification and analyses (see below). Ants were separated from other Hymenoptera, and many have been forwarded to Dr Alan Anderson (CSIRO, Darwin) for further work. The abundance of invertebrates from the less common Orders was also recorded from the September 1990 samples onwards, but these data have not been included in the present analyses.

Coleoptera were identified to species level using the keys of Matthews (1980, 1982, 1984, 1985, 1987), and with the assistance of Drs E.B. Britton and T.A. Weir from the CSIRO Division of Entomology, Canberra, and Mr A. Szito from the Entomology Branch, W.A. Department of Agriculture. For the majority of specimens no specific name could be found, and in some instances a generic name also could not be assigned. Most species were therefore delimited by either a family name plus species number, or by a genus name plus species number. To facilitate analyses each species was assigned a three digit code number. Voucher specimens of all species are currently held at the Wildlife Research Centre, Woodvale, and will be transferred to the W. A. Museum and/or the Australian National Insect Collection in Canberra upon completion of our studies.

Habitat assessment

Vegetation structure was measured at four permanently-marked habitat points located one metre north, south, east and west of each pitfall trap (see Fig. 2). There were thus 64 habitat points per grid. The following attributes were recorded at each habitat point:

1. Leaf litter cover (%) in a 30cm X 30cm area scored as 0=absent, 1=1-25%, 2=26-50%, 3=51-99%, and 4=100%. The midpoint value of each percentage cover value was then used to calculate the percentage cover value per grid using the following formula:

$$C = \frac{\Sigma fm}{64}$$

where: C = percentage cover value
f = frequency of observations
m = midpoint of percentage cover category

2. Number of units of woody litter (dead/down branches or logs >5mm diameter) bisected by a plane 50cm each side of the habitat point. Woody litter diameter categories were 1=5-10mm, 2=10-25mm, and 3= >25mm. Mean trash diameter was calculated for each grid using the midpoints of the litter diameter categories.

3. Number of touches of vegetation on 12 intervals of a vertically held levy rod. Height intervals (cm) used were: 1=0-12.5, 2=12.6-25, 3=26-50, 4=51-75, 5=76-100, 6=101-125, 7=126-150, 8=151-175, 9=176-200, 10=201-250, 11=251-300, 12= >300.

4. Majority of touching vegetation in intervals 1-12 alive (1) or dead (0).

5. Maximum height (cm) of living understorey vegetation (<3m) within 20cm of the levy rod.

Floristics

Plant species falling within a radius of 5.64m (100m^2) of the centre of each grid were recorded (presence/absence and estimated cover/abundance on a modified Domin-Krajina scale; Mueller-Dombois and Ellenberg 1974) by M. Langley during the spring (October-November) before and after each of the experimental burns. Species determinations were made by M. Langley and G. Keighery (CALM Wildlife Research Centre), and entered onto a data-base (dBXL; WordTech Systems Inc.) according to species, grid number, cover/abundance and sample time.

Data analyses

Invertebrates

The numbers of invertebrates belonging to the six major orders were entered onto a data-base (dBXL) according to taxon (order), grid number, replicate number (within-grid), trap type and sample time (month/year). Abundances of beetle species were entered onto a separate data-base with species code number recorded in addition to the above variables. A beetle species master list was also prepared showing species code, family, subfamily, genus and species as well as synonym descriptors and comments fields.

Owing to the relatively low capture rates of invertebrates in the sweeps and intercept traps, all analyses were confined to the pitfall trap data for the purposes of the present report.

(a) Univariate analyses

To determine if fire had any impact on invertebrate abundance and beetle species richness, the abundances of invertebrates (total and separately for the six major orders) and beetle species richness in experimentally burnt grids (viz. 1 and 2, and 4 and 5) were compared with the numbers for the same grids before the fire and the numbers in the unburnt control grids (3 and 6 respectively) using analysis of variance (ANOVA). Abundance data were log transformed ($\ln(x + 1)$) to normalize the distribution of residuals, and to make variances homogeneous. Data were analyzed using the Before and After Control-Impact (BACI) method of Green (1979; cf. Underwood 1991), which uses the repeated sampling occasions before and after the fire at one site as replicates. Analysis of variance was performed separately on each group of invertebrate abundance data (viz. the six orders and beetle species richness), with effects fitted for grid, before/after fire, sampling occasion within before/after, and the interaction between grid and before/after. This interaction term is a test of the null hypothesis that any differences in abundance between the control and burnt grids before the fire is equal to the differences after the fire. The possible impact of fire is assessed by comparison of any post-fire change in the burnt grid with contemporaneous change in the control grid (see Underwood 1991). Similar comparisons using ANOVA assessed differences between grids in areas of different fire-ages (ie. Grids 7 versus 6; 8 versus 9; and 10 and 11 versus 6). Data from the replicate grids A and B for Grids 4-6, and for Grids 10 and 11 were combined to enable balanced comparisons.

These ANOVA comparisons were carried out for the total period of the study for the above grid combinations, and also for the burnt versus unburnt comparisons using only the first post-fire sample versus all pre-fire (acute impact tests), and all except the first post-fire sample versus all pre-fire (chronic impact tests).

Invertebrate abundances were also plotted for the various ages of vegetation using data from all sites for the common pre-fire period June 1989 - June 1990, and for the common post-fire period May 1991 - May 1992. The data were examined in these two time periods because all invertebrates were considerably more abundant in the final year of the study, so that comparisons between older sites (using all data combined) and experimentally burnt sites would have been biassed. Since not all grids were sampled for the same total period, or on every sampling occasion, abundances were calculated as the mean number captured per sample for grids of the same age (including the replicates for Grids 4-7). Post-fire data for the burnt grids were plotted separately as age 0.5 years for the spring (Grids 5A and 5B) and autumn (Grids 1 and 2, and 4A and 4B) experimental burns, and for the autumn (Grids 10 and 11) wildfire.

(b) Multivariate analyses

The univariate analyses outlined above provided means of assessing changes in each individual order and in beetle species richness. It is also germane to consider changes in the overall patterns of abundances of the six major orders, and of beetles at the species level. Two methods of assessing patterns of change in the absolute and relative abundances of invertebrates were used.

First, Bray-Curtis dissimilarity of grids was calculated for each relevant pair of burnt and unburnt grids for each sampling occasion throughout the study. Pairwise comparisons between simultaneously burnt grids (eg. Grids 1 and 2) and between controls (eg. Grids 6 and 7) provide additional information on levels of dissimilarity between grids receiving the same treatments. The null hypothesis underlying such comparisons is that dissimilarity between grids is constant, with alternate hypotheses that burnt grids would increase in dissimilarity from their associated controls, whilst differences between grids receiving the same treatments could either increase or decrease.

In a comparison of similarity indices using aquatic invertebrate abundance data from an impact study similar to the present (Faith *et al.* 1991), the Bray-Curtis metric (Bray and Curtis 1957) was shown to have desirable properties. Although Faith *et al.* (1991) found that the Bray-Curtis metric was equally powerful when based on either raw or logarithmically transformed abundances, the present data were transformed to $\ln(x+1)$ prior to calculation of dissimilarity values to reduce the effect of outliers on the data. Digby and Kempton (1987) have demonstrated that the Bray-Curtis metric is sensitive to such values, and recommend that logarithmic transformation be routinely applied to abundance data prior to calculation of Bray-Curtis dissimilarity to minimise this effect.

Second, multivariate changes in community structure from pre- to post-fire were assessed using principal components analysis (PCA, Pielou 1984). This technique operates on an environment by taxon matrix and summarises data structure in, typically, few dimensions. As before, data were transformed to $\ln(x+1)$ prior to analysis.

Analyses were conducted using two levels of sampling to represent different "environments" in the PCA. Firstly, for the order-level invertebrate abundances, each sampling occasion at each grid was considered to represent a single "environment". This enabled multivariate changes at both the year-to-year and season-within-year level to be assessed on burnt and unburnt grids. The low abundances of individual beetle species at this level (typically zero for all but one species at most sampling times) precluded the use of the beetle data for this analysis. Secondly, data were pooled into two complete years for the periods June 1989 - June 1990 and May 1991 - May 1992, as was done for the successional data for the univariate analyses (see above). Thus each represented before and after fire samples respectively, but precluded the assessment of seasonal effects.

Data at this level were available for both the six major orders and beetle species. Data were centred but not standardized prior to analysis. Centreing reduces all variables to a common mean of zero, while standardizing reduces centred variables to a common standard deviation of one. Data were not standardized because this transformation reduces all variables, both highly variable and invariant, to the same level of variation (Digby and

Kempton 1987). Thus principal components were extracted from the covariance rather than the correlation matrix in order to preserve the inherent variablity of the data. The number of principal components retained in the final analysis was determined by examination of scree plots of eigenvalues associated with each principal component. A flattening of this curve indicates that subsequent principal components are uninformative, and only components prior to the levelling of the curve were retained for subsequent ordinations.

To simplify interpretation of the principal components ordinations and the presentation of the results, biplots were constructed which combine the information of the ordinations with the associated eigenvectors for each principal component (see Digby and Kempton 1987). This presents both ordinations of taxa and environments simultaneously, and obviates the need to rotate the final PCA solution by graphically representing the loading of each variable on each principal component. The dimensionless eigenvectors were appropriately scaled so that sites and taxa could be more easily related.

Vegetation structure

Structure data were reduced to nineteen summary variables prior to analysis. These were: (1) Litter cover, calculated from the midpoints of the cover categories; (2) Mean trash diameter, calculated from the midpoints of the trash diameter categories; (3) Mean trash height; (4) Trash cover, the proportion of levy rod points which had one or more contacts with trash, representing the proportion of the ground covered with any thickness of trash; (5-16) Vegetation density, the number of vegetation contacts for each of the twelve levy rod intervals, reflecting the vertical density of the vegetation present; (17) Horizontal distribution of vegetation, being the proportion of levy rod points with one or more contacts with vegetation and thus indicating the amount of ground with vegetation cover; (18) Mean vegetation height; and (19) Percentage live vegetation calculated by tallying the number of "alive" recordings per grid and dividing this by the number of habitat points which had a recorded contact. These derived variables represented different scales of measurement, and hence PCA was based on the correlation rather than the covariance matrix to avoid the ordination being dominated by those variables with greater variances.

Floristics

The cover of 291 species of plants on the seven grids sampled before and after fire were ordinated using principal components analysis. In ordinating vegetation data, PCA has been criticised because it deals with only linear relationships in the data, and tends to distort vegetational gradients. However, more sophisticated methods of ordination which have been lauded as superior to PCA, such as Correspondence Analysis (CA), Detrended Correspondence Analysis (DCA or Decorana) (Gauch *et al.* 1977) and non-metric methods (Gauch *et al.* 1981; Kenkel and Orloci 1986) have recently also been subject to criticism (Jackson and Somers 1991; Digby and Kempton 1987). Hence, although PCA is known to produce possibly biased ordination results, the nature of these biases is well known (e.g. the "horseshoe effect" often produced by PCA when ordinating vegetation gradients). As the simplest of the ordination techniques, it was therefore felt that PCA would be a suitable choice in an area of uncertainty.

As the cover values were recorded on a geometrical scale, no data transformation other than the usual centreing was conducted.

Comparison of ordinations

Procrustes analysis (Gower 1971) was used to compare ordinations, and Gower's m^2 statistic provided a relative measure of the similarity of ordinations. Procrustes analysis applies a linear transformation to a particular ordination (equivalent to a rotation and/or reflection as appropriate), in order to minimise the euclidean distance between the rotated points and a location defined by some other target ordination. The m^2 statistic is the total (squared) distance of the rotated from the target ordination, and hence provides a measure of how closely two ordinations correspond.

Prior to Procrustes analysis ordinations were standardized (i.e. reduced to a common scale) to obtain comparable distance values for each pairwise comparison of ordinations. The resultant matrix of distance values was then used as a basis for principal coordinates analysis (PCO) of the ordinations (see e.g. Digby and Kempton 1987, Pielou 1984). PCO is a technique akin to PCA, which resolves the structure of a data matrix in typically few dimensions, thus permitting ordination. However, where PCA operates on a correlation or covariance matrix, PCO operates on a matrix of distance values. Like PCA, PCO usually summarizes the bulk of important variation in few dimensions. Grids 10 and 11 were present for only some of the PCA ordinations; thus in constructing the PCO ordination these points have necessarily been excluded from the analysis.

RESULTS

IMPACT OF FIRE ON MAJOR INVERTEBRATE GROUPS

Coleoptera

Total abundance

Trends in the abundance of Coleoptera on Grids 1,2 and 3 were extremely consistent between grids (Fig 3), with distinct seasonal peaks occurring in December. These peaks were largely attributable to one species of the family Cleridae, the larvae and adults of which prey upon insects associated with bark and wood (Lawrence and Britton 1991). The largest peak occurred in the December following the autumn burn, but was not confined to the burnt grids. Accordingly, there was a relative increase in abundance after the fire but this was not significant (Table 1). Similar trends with December peaks in abundance also occurred on Grids 4-6 (Fig 4), but there was a marked increase in numbers immediately following the spring fire on Grid 5. This increase was ephemeral, giving rise to a significant short-term effect (Table 3), and again was attributable to the same species belonging to the family Cleridae. Overall, however, there was no significant change in beetle numbers following the spring and autumn experimental burns (Tables 1 and 4). The four-year-old area (Grid 7) had relatively fewer beetles than the control (Grid 6), but this difference was not significant (Table 1). Trends in Coleoptera abundance over time on Grids 8 and 9 (Fig 5) showed some differences in the time of peak abundances on the two grids, and no consistent December peak as on Grids 1-6. Overall, however, there was no significant difference in coleoptera abundance between these two grids (Table 1). Similarly, no significant difference in beetle abundance was found when comparing Grids 10 and 11 (combined) and the unburnt control Grid 6 (6A and 6B; Fig 6; Table 1).

The mean abundances of Coleoptera (per sample) for the various ages of vegetation are shown in Fig 7 for the common pre-fire period June 1989 - June 1990, and for the common post-fire period May 1991 - May 1992. In the pre-fire period abundances were greatest in the 40-year-old vegetation and declined again in the oldest stand. Abundances were much higher but also considerably more variable on all areas in the post-fire year, but again mean abundance was highest in the 40-year-old area. Abundances in the immediate post-fire period (0.5 years) varied greatly, with the lowest values recorded in the area burnt by the autumn wildfire (Grids 10 and 11), and the highest in the area experimentally burnt near Two Mile Lake (Grids 1 and 2). Much of this variability may be attributable to the low number of samples in the post-fire year comparisons where most data points represent single grids.

Abundance of major families

Of the 405 species of beetles recorded in this study (total from all methods), more than half (219 species; 54%) belong to only three families: Scarabaeidae (94 species; 23.2%), Curculionidae (87 species; 21.5%), and Carabidae (38 species; 9.4%). Furthermore, within the Scarabaeidae the majority of species belonged to the subfamily Melolonthinae and the genera *Heteronyx* and *Liparetrus*, whose larvae live in the soil and hatch into adults which emerge and disperse when rain softens the soil (Lawrence and Britton 1991). Abundances of these three families were plotted against time for the various grid combinations (Figs 8-15), though in many cases sample sizes were too small to allow detailed or valid comparisons.

Carabidae were generally in low abundance on Grids 1,2 and 3 (Fig 8) and sample sizes were too small for any post-fire trends to be evident. However relatively large fluctuations were evident on Grids 4,5 and 6 (Fig 9). Numbers peaked on Grid 5 in October 1989 (mainly *Pogonus* sp1 and *Lecanomerus* sp1), and on the unburnt control in December 1991, mainly due to *Cerotalis* sp 2. Grid 4 showed some increase in Carab abundance in the six month period after the fire, but both burnt grids supported lower numbers of Carabidae than the unburnt control in the October 1991 - March 1992 period. This was also the pattern on Grids 10 and 11 following the high intensity autumn burn ((Fig 11). On Grids 8 and 9 (Fig 10) no clear trends related to vegetation age could be discerned.

Numbers of Scarabaeidae were quite low and consistent between comparative grids (Figs 12-14), but again few fire-related responses were apparent. The local patchiness in species abundance trends, not necessarily related to fire, is illustrated by the marked increase in abundance of Scarabaeidae caused by the melolonthine *Neophyllotochus* sp 4 on both Grids 2 and 9 in October 1991 (Figs 12 and 14). This species, however, did not contribute to the peaks in Scarabaeidae abundances on Grids 5 and 6 in October-December 1991 (Fig 13).

Similarly, the abundances of Curculionidae were mostly too low for comparisons to be made, particularly for Grids 1-3 and 8 and 9. On Grids 4-6 some trends were discernable but did not appear to be related to fire (Fig 15). Grids 4, 10 and 11 showed an increase in Curculionidae in the last two samples (March and May 1992), possibly related to post-fire conditions.

Thus, most of the abundance patterns observed for the three major families of beetles showed little relationship to fire, but related instead to locality and especially season. An examination of the data for other families and species of beetles, however, indicates that some groups do show marked post-fire responses. Two species of "click beetles" (*Agrypnus* sp1 and Elateridae sp. 3) showed marked post-fire peaks on Grids 2 and 4, while two species of the family Mordellidae (*Tomoxioda* sp. on Grids 4 and 11, and *Mordellistena* sp.2 on Grid 11) appeared in numbers only in December 1991 after the respective fires. Similarly, *Pselaphaulax* sp. (Pselaphidae) and Aleocharinae sp. 14 (Staphylinidae) increased markedly after the fire on Grid 5.

Species richness

The patterns of beetle species richness on Grids 1, 2 and 3 were similar both in total numbers and in seasonal trends (Fig 16), and there was no significant change in species numbers after the fire (Table 2). This was also the case for the comparisons of Grids 4, 5 and 6 (Fig 17 and Table 2) and Grids 10, 11 and 6 (Table 2), the fires again having no significant influence on the numbers of species. Grids 8 and 9 also supported very similar numbers of beetle species, and exhibited similar seasonal patterns with peaks generally occurring in late spring (Fig 18 and Table 2).

Beetle species richness showed no clear relationship with age of stand (Fig 19), although mean values were generally greatest in the 20-year-old area, and least in the 8 and 50-year-old areas. The trends on these last two grids, however, may be attributable more to locality than time since fire, since both grids were situated West of Chester Pass Road some 23 km from the Two Mile Lake grids (Fig 2). As with the abundance data, richness increased across all areas in the last year of the study and there was considerable variation between the 0.5-year-old grids. Grids 10 and 11 had the lowest numbers of species in this stand age, but this may reflect the small number of samples (only three sessions) obtained from these grids as much as any fire-related impacts.

Diptera

As with the Coleoptera data, trends in the abundance of Diptera were extremely consistent between grids and showed marked seasonal peaks in spring. On Grids 1 , 2 and 3 (Fig 20) abundance of Diptera increased markedly over the final 12 months of the study (post-fire), and there were significantly more ($p < 0.01$) recorded on the unburnt Grid 3 than on either of the two burnt grids for the overall and the chronic impact comparisons (Tables 1 and 4). Diptera also showed a general increase over the study period on Grids 4-6 (Fig 21), peaking abruptly immediately after the spring fire on Grid 5 to produce a (marginally) significant acute impact ($p < 0.10$), whilst the autumn burnt Grid 4 showed a significant opposite trend ($p < 0.01$) at the acute stage (Table 3). Dipteran abundances were generally lower on Grids 8 and 9 than on the other grids (Fig 22), and there were no significant differences between the two fire ages (Table 1). This was also true for Grids 6 versus 7 (Table 1). By contrast, Diptera were significantly more abundant ($p < 0.05$) 12 months after the fire on Grids 10 and 11 (combined) than on the unburnt Grids 6A and 6B (Fig 23, Table 1).

When plotted against age of stand (Fig 24) Dipteran abundance showed a distinct peak at 40 years for both the pre and post-fire comparisons. This peak was very significant in the post-fire comparison, and abundances were much higher (6-10-fold increase) across all ages at this time. Although fairly variable, immediate post-fire abundances (0.5 years) were within the range for the other older stands (except the 40-year-old area), being greatest on the grids burnt under higher intensities (Grids 1, 2, 10 and 11) than those more patchily burnt at lower intensities (Grids 4 and 5).

Hemiptera

Patterns of abundance of the Hemiptera displayed somewhat more variability between grids than the Coleoptera and Diptera, but distinct spring peaks were again apparent (Figs 25-28). Although Hemiptera numbers increased markedly on Grids 1 and 2 and on Grids 4 and 5 in the spring following the respective fires (Figs 25, 26) BACI analysis indicated that overall post-fire differences were significant only on Grid 4 (marginally) for the chronic impact comparisons (Tables 1, 3 and 4). Comparisons of the different-aged areas (Grids 6 v 7 and 8 v 9) showed no significant differences (Table 1; Fig 27) but the grids burnt in the autumn wildfire (Grids 10 and 11) supported significantly more Hemiptera ($p < 0.05$) than the unburnt control grids (Fig 28 and Table 1).

Hemiptera abundance showed little relationship with time since fire except that mean values and variability were higher in the post-fire comparison year, and in the earlier successional stages up to four years (Fig 29).

Hymenoptera (excluding ants)

Like the preceding groups, Hymenoptera (bees and wasps) showed clear peaks in abundance in late spring/early summer and a general increase in abundance over the period of the study (Figs 30-33). No fire-related differences were detected between grids 1 and 2 versus 3 (Fig 30, Tables 1, 3 and 4), but on Grid 5 there was an abrupt but temporary (non-significant) increase in Hymenoptera after the fire (Fig 31; Table 3), while Grid 4 supported fewer Hymenoptera (marginally significant; $p < 0.10$) than the control grid in the post-fire period (Tables 1, 3 and 4). Although seasonal trends in Hymenoptera were very similar on the different-aged areas compared on Grids 8 and 9 (Fig 32), overall abundances were significantly higher ($p < 0.05$) on the more recently burnt area (Grid 8; Table 1). However there were no consistent or significant differences between the unburnt grids (6A and 6B) and those burnt under high intensity wildfire (Grids 10 and 11; Fig 33, Table 1).

Mean abundances of Hymenoptera varied more between pre and post-fire years than between different-aged stands, although values were greatest in the 8-year-old area (Grid 8) in both years (Fig 34). Values were also high in the 50-year-old area (Grid 9) in the pre-fire year suggesting a distinct locality effect. Immediate post-fire abundances were lowest on Grids 10 and 11, but values for the other recently burnt sites were within the range observed for the older stands.

Orthoptera

Orthoptera also displayed clear seasonal trends in abundance and a general increase over most sites during the final year of the study (Figs 35-38). Abundances were significantly higher ($p < 0.05$ and < 0.01) on Grids 1 and 2 than on Grid 3 after the fire for the overall and chronic comparisons (Tables 1 and 4) but this was not the case in the acute phase (Table 3 and Fig 35). On Grids 4 and 5 overall post-fire abundances of Orthoptera were lower than on Grid 6, but this trend was significant ($p < 0.05$) only on Grid 4 in the acute impact stage (Table 3; Fig 36). No significant differences were apparent between Grids 6 and 7 or between Grids 10 and 11 (combined) and Grids 6A and 6B (Fig 38; Table 1), but there were significantly more ($p < 0.05$) Orthoptera recorded on Grid 8 than on Grid 9 (Fig 37; Table 1).

In both pre and post-fire comparisons of Orthopteran abundances with time since fire (Fig 39) there is a trend of declining numbers with increasing age, and generally high abundances in the youngest (0.5 year) stands. Some inconsistencies in this pattern are apparent in the pre-fire comparison for the oldest stand, but this may reflect locality effects in addition to any attributable to fire.

Araneae

As with the other groups, Araneae showed clear seasonal trends with peaks in spring and a general though small increase in numbers in the final 12 months (Figs 40-43). Differences between burnt and unburnt areas were not significant at any of the stages tested (Tables 1, 3 and 4). Indeed, this was true of all comparisons except that between Grids 8 and 9 (Fig

42; Table 1), where significantly greater numbers ($p < 0.01$) were recorded in the younger area. Abundances of Araneae also showed no consistent relationship with time since fire for the pre- and post-fire year comparisons (Fig 44) with year-to-year variations generally outweighing those related to age of stand. Again, the low values for the 8 and 50-year-old sites in the post-fire year data probably reflect locality effects rather than those attributable to fire.

Multivariate patterns

Dissimilarity measures

Dissimilarity values for the pairwise comparisons between grids 1,2 and 3 (Fig. 45) and between grids 4, 5 and 6 (Fig. 46) showed no consistent change over time. Although dissimilarities between treatment and control grids generally increased after the respective fires, these changes were only temporary and were within the range of variability recorded before the fires.

Ordination of sampling occasions by orders

The first three principal components explained 87% of the variance and thus provide an excellent summary of the original data structure. The first principal component alone accounted for 64% of the variance and clearly separates sampling occasions in 1989/90 from those of 1991/92, both for burnt and unburnt sites (Fig 47). The eigenvectors show that the data are dominated by increases over time in the abundance of all six orders, but primarily by increases in Diptera and to a lesser extent in Hymenoptera and Hemiptera. This first axis corresponds to a size component, showing that total abundances increased from 1989/90 to 1991/92.

Coleoptera, Orthoptera and Araneae dominated the second principal component axis, which separates December 1989 and December 1991 samples before and after the fire on both burnt and unburnt grids from the remaining samples. This component therefore corresponds in part to the seasonal increase in beetles (especially Cleridae) recorded at this time in both 1989 and 1991. Interestingly, samples on the grids subjected to wildfire (10 and 11) did not differ in any marked respect from other 1991/92 samples.

The dominant first principal component thus reflected overall increases in abundance, a common feature of PCA. Correlation between the sum of log abundances for each order and the principal component scores on the first axis for each sampling occasion was 0.99. Whilst the change in absolute abundance from year to year is of interest, two approaches were adopted to reveal further patterns beyond this gross level. Firstly, the second and third axes of this ordination were examined. Secondly, to remove the effects of changes in absolute abundance the data matrix was doubly centred by subtracting from each datum its row and column mean values, and then adding to the result the grand mean of all abundance values in the data matrix. This linear transformation is the equivalent of converting absolute abundances to relative values and then centreing. A new PCA was then applied to this data, and the results compared with the minor axes of the original ordination.

Comparison of axes 2 and 3 from the first PCA with axes 1 and 2 from the PCA of doubly centred data indicated that these axes were essentially the same: the correlation between scores on each pair of axes was -0.78 and -0.86 respectively. Subjective examination of the two ordinations indicated that the ordination of doubly centred data, although clearly very similar to the original ordination, was more readily interpretable. Hence the first two axes of this ordination were retained (Fig 48).

After removal of the effect of absolute abundances, the first two axes accounted for 75% of the remaining variance and hence provide a good summary of the data structure. The first axis corresponds to increasing predominance of Diptera and to a lesser extent Hemiptera in the 1991/92 samples relative to 1989/90 samples, both in control and burnt plots. There was a corresponding decline in the relative proportion of Orthoptera, Araneae and Coleoptera in the samples, except in December 1991 when Coleoptera dominated a number of samples in both burnt and unburnt plots.

Ordination of grids before and after fire by orders

Pooling of sampling occasions for the years before and after the fires effectively produced a summary of the results obtained for individual sampling occasions. The first two axes from this ordination accounted for 90% of the variance, again providing an excellent summary of the data structure. Increases in Diptera and to a lesser extent Hemiptera from 1989/90 to 1990/91 dominated the first principal component axis, although this effect was least apparent in Grids 8 and 9 (Fig. 49). The first axis again corresponded closely with the sum of log abundances ($r=0.99$), and for the same reasons outlined above the data were doubly centred to produce the ordination of Figure 50. In this ordination the first two axes explained 79% of the variation, providing a good summary of the data. Again, the first axis corresponds to increases in the relative abundance of Diptera, and to a lesser extent corresponding decreases in Araneae. Changes in other orders were site specific, with Grid 3 maintaining a notably high relative abundance of Coleoptera and Hymenoptera at the expense of Orthoptera and Hemiptera, whilst Grids 4, 5, 6 and 7 showed the reverse trend. Grids 8 and 9, whilst atypical in terms of absolute abundance, were very similar to the burnt Grids 1 and 2 in relative abundances of the major orders.

Ordination of grids before and after fire by common beetle species

The ten beetle species which were enountered in more than 75% of the pooled yearly samples were used to ordinate sites in the same manner as for invertebrate orders. It was felt that the most frequent beetle species should reflect major patterns of change with less "noise" than rarer species. The first two dominant principal components explained only 59% of the variance, but effectively reproduced the patterns observed in the ordination by orders. Changes from 1989/90 to 1990/91 in both burnt and unburnt sites dominate both axes, and correspond to a decline in the abundance of *Celibe* sp. (Tenebrionidae), and to a lesser extent *Anotylus* sp. 1 and Aleocharinae sp. 10 (both Staphylinidae), with increases in the abundances of *Notagonum* sp. 2 (Carabidae) and Curculionidae sp. 31. Again Grids 8 and 9 appear to be atypical of the the other grids sampled in 1990/91.

Ordination of the doubly centred beetle data matrix was dominated by two principal components together accounting for 56% of the variance. This again produced clear separation of 1989/90 and 1990/91 samples, with 1990/91 samples showing a decline in the relative abundance of *Celibe* sp. concomitant with increases in Curculionidae sp. 31 and Cleridae sp. 7. Grids 8 and 9 were atypical in having high proportions of *Notagonum* sp. 2 and low proportions of *Anotylus* sp. 1 and Aleocharinae sp. 10.

Ordination of grids before and after fire by all beetle species

A total of 280 beetle species was recorded from pitfall traps on Grids 1-9. The first three axes of the principal components ordination of the log-transformed abundances accounted for 71% of the overall variance, with the first principal component again dominated by species abundance effects, although some separation of burnt and unburnt grids, and 1989/90 and 1990/91 samples, is apparent (Fig 51). Ordination of the doubly centred matrix resulted in two dominant principal components, which together accounted for 41% and 51% of the variance. The third principal component axis showed no apparent pattern relevant to the differences between grids, and is not presented here. Despite the low figure for explained variance, the first two principal components clearly separate the three major types of grids: 1989/90 pre-fire grids, 1990/91 control grids and 1990/91 burnt grids (Fig 52). The ten major eigenvectors are indicated on the biplot, and show both year-to-year changes and changes due to fire in abundances of a number of beetle species.

Pre-fire grids were characterized by high relative abundances of *Celibe* sp. (species 112) and Aleocharinae sp. 10 (species 168), but both of these species declined in 1990/91, particularly on burnt grids. The pre-fire grids form a consistent group on axes 1 and 2, although grid 5 is perhaps slightly atypical. Grids 8 and 9 in 1990/91 had high relative abundances of *Notogonum* sp. 3 (species 368), and unburnt control grids in general showed low relative abundances of Aleocharinae sp. 10, *Pogonus* sp. 1 and *Anotylus* sp. 1 (species 168, 80, and 121 respectively). Both control and burnt grids in 1990/91 had increased relative abundance of the melolonthine *Neophyllotochus* sp. 4 (species 341). However, grids subjected to prescribed burns had a markedly different overall pattern of beetle abundances, having high relative abundances of a number of species, the dominant ones being *Tomoxioda* sp., *Agrypnus* sp. 1, Elateridae sp.3, *Mordellistena* sp.4, Aleocharinae sp.7 and Aleocharinae sp. 14 (species 332, 115, 142, 422, 118 and 335 respectively). Grid 5, although showing the same general pattern as the other burnt grids, showed an atypical or extreme response.

FLORISTIC AND VEGETATION STRUCTURE PATTERNS

Ordination of grids before and after fire by floristic data

The first two axes of the PCA of floristic data explained only 54% of the variance, but the ordination produced clear patterns and clearly separated burnt from unburnt grids (Fig. 53). Pre-fire grids were widely spread in the ordination space, although Grids 1-3 and 5, and Grids 4 and 6, represent loosely similar groups. The 11 largest eigenvectors indicated on the biplot show that grids 4 and 6 were characterized by high cover values for *E. tetragona*, *E. decipiens* and *Eucalyptus incrassata*, while grids 1-3 and 5 shared high abundances of a number of species including *B. elegans*, *M. thymoides* and *Isopogon tripartitus*. Grid 9 was atypical of the unburnt grids, with high abundances of *Melaleuca striata* and *E. pachyloma* which occurred at much lower abundances on other grids.

Burnt grids, including Grids 7 (burnt 1986) and 8 (burnt 1982), formed a tight group characterized by reduced cover values for those species which were common on unburnt grids. Interestingly, Grids 1, 2, 4 and 5 show similar relationships both before and after fire, although the unstandardized PCA, by placing much weight on cover values, has contracted this relationship post-fire. Thus, although these grids have apparently maintained at least some differences in species composition, the large reduction in cover values after fire has resulted in greater similarity between these grids.

Ordination of grids before and after fire by structure data

Vegetation structure was effectively summarized by the first three principal components, together accounting for 79% of variance. The first is the usual size dominated component, which clearly separates burnt from unburnt grids (Fig. 54a). As expected, burnt grids were lower in values of all variables. Of the unburnt grids, 7 and 8 had unusually high levels of trash variables, and are distinct from other unburnt grids on the second axis. Similarly, grids 1,3 and 9 represent another extreme, with high levels of vegetation touches in the 30-110cm range, although touches in the 60-70cm range are atypical of this pattern. The greatest change in the grids subject to prescribed burns were in trash and litter components, and in vegetation between 0-20cm. Grids burnt by wildfire showed greater reductions in vegetation contacts.

The second and third principal component axes are dominated by the contrast between vegetation touches in the 0-20cm range (V1-V2) together with litter and trash components, and vegetation touches in the 30-110cm range (V3-V11), although the 60-70cm (V7) interval is atypical of this pattern (Fig. 54b). Separation between burnt and unburnt grids is mainly confined to axis 2, where the patterns discussed above are apparent. When axes 1-3 of the PCA are considered together, grids 3 and 9 have unusual features: in terms of trash and litter components they are typical of unburnt sites, but have vegetation distributions characteristic of burnt sites, i.e. low numbers of contacts in the 0-20cm range, high numbers of contacts in the 40-110cm range and high levels of litter and trash components. Grids 10 and 11 contrast with other grids in having a high proportion of the ground with (low) vegetation cover, while other burnt grids have typically lower values on this component than unburnt grids. These data reflect a sampling artefact in that vegetation structure was measured six months after the fire on Grids 10 and 11 (following some regrowth), but immediately (<1 month) after the fires on the other grids.

RELATIONSHIPS BETWEEN INVERTEBRATES, FLORISTICS AND VEGETATION STRUCTURE

Comparison of ordinations

Procrustes analysis (Fig. 55) confirmed the general conclusion obtained from each of the individual PCA ordinations; viz. that each data set showed different patterns of response. The second and third axes of the structure data were similar, as were the doubly centered ordinations in each case, a result to be expected since each has a common axis. The vegetation structure results were distinct from all other ordinations. Ordination of common beetle species was intermediate between order level invertebrate data and ordinations based on the full complement of beetle species. The only similarity of responses between different data sets was in the doubly centred ordination of invertebrate orders and floristic data. Clearly, each set of data represents different facets of change over time, including those due to fire, and few patterns of change in invertebrates, floristics and structure are comparable.

DISCUSSION

Impact of fire on invertebrates in mallee-heath remnants

The results obtained during this study serve to indicate the complexity of factors which influence the post-fire response patterns of invertebrates. While some groups increased in abundance after fire, others declined, and these trends may be both inconsistent for a particular taxon between different experimentally burnt areas and quite ephemeral. Amongst the Diptera, for example, numbers increased significantly after the experimental spring fire and the autumn wildfire, but declined significantly after both experimental autumn fires. Some of these trends were apparent only at the acute stage, while others were more chronic and still apparent 12 months after fire. The greatest changes in Dipteran numbers, however, simply reflected year-to-year variation.

Within the Coleoptera large fluctuations in numbers occurred on a seasonal basis, primarily due to only a few species such as Cleridae sp. 7 (which peaked in December each year), *Notagonum* sp. 2, *Pogonus* sp. 1 and *Neophyllotochus* sp.4, but these fluctuations were independent of fire. No significant changes in beetle abundance or species richness occurred following either spring or autumn control burns, and none were apparent within six months of a high intensity wildfire. Of the major beetle families examined in detail, only the Carabidae exhibited a consistent response, with numbers generally declining in the short term after fire. Although abundance as a whole was greatest in the 40-year-old area, year-to-year changes and locality effects tended to outweigh any fire-related trends.

Hymenoptera and Araneae showed significant fire-related trends only in one area, there being higher abundances of both groups in the 8-year-old area than in the adjacent long-unburnt area. Neither group showed any distinct and consistent relationship with time since fire. Similarly, although Hemiptera generally increased after fire, this trend was significant only in the wildfire area and may be related to the flush of new growth which had occurred by the time sampling commenced. Such young growth probably represents a significant food resource for this group. New vegetative growth also may explain the higher abundances of Orthoptera in the chronic and longer-term phases following fire, while lack of plant food resources in the acute phase correlates with the significant decline in abundance observed after the experimental autumn fire (Grid 4).

Multivariate analysis using Principal Components Analysis supported the general conclusions reached from the univariate analyses. In all cases these ordinations reflected changes in absolute and relative abundance of orders from one year to the next, and to a lesser extent seasonal changes, all probably tied to climate. Any effects of either prescribed burns or wildfire were not apparent at the order level in the context of these changes.

Multivariate analyses also indicated a lack of correlation between changes in invertebrate abundance and composition, and changes in floristics or vegetation structure. Although direct relationships no doubt exist between individual species of invertebrates and plants which may also reflect differences in vegetation structure due to fire, these patterns are at a much finer level of resolution than is addressed in this or any previous study. Indeed, most studies of invertebrates and fire have not considered any habitat variables to help explain the patterns observed. Yen (1987), however, examined correlations between plants, vertebrates and Coleoptera and found that Coleoptera were very habitat specific and that their distribution and abundance patterns bore little relationship to those of vertebrates. The lack of correlation between invertebrates, floristics and vegetation structure found in the present study further emphasizes Yen's (1987) point that categorizing and protecting areas on the basis of high vertebrate species richness does not ensure that large numbers of invertebrate species are also conserved.

Thus, in this study, as in the majority of others which have examined this topic (eg. Bornemizza 1969; Leonard 1972; Whelan *et al.* 1980; Majer 1980, 1984, 1985a; Abbott 1984; Tap and Whelan 1984 and Neumann and Tolhurst 1991), there are few clear-cut trends in the patterns of abundance and composition of invertebrates, assessed at the Order level, which can be directly related to fire, floristics or vegetation structure. Indeed, as suggested by Campbell and Tanton (1981), the high spatial and temporal variability in invertebrate populations generally overides any changes which may be attributable to fire, and makes prediction of responses to fire almost impossible. It must be emphasized, however, that these conclusions may not necessarily apply to data collected at the family or species level. This would be a worthwhile approach in future studies.

PCA analyses, through examination of the magnitude and direction of the eigenvectors associated with each of the six orders, provided indications of which orders were most important in assessing changes over time. The consistently most useful orders in this respect were Diptera and Coleoptera, which appeared to correspond to different features of the data structure. Diptera reflected year to year variation most clearly whilst Coleoptera reflected (at least some) seasonal changes. Variation in Hymenoptera and Hemiptera provided little additional information to that provided by Diptera, while Araneae were highly correlated with Orthoptera.

Diptera were also considered to have good potential as indicators of disturbance or conservation value by Disney (1986) and Majer (1987b) because of their abundance, and the diversity of species and life history strategies. Coleoptera could also be considered good environmental indicators for the same reasons, but many invertebrate ecologists argue that ants (Hymenoptera) and spiders (Araneae) are also excellent groups (Majer 1983; Clausen 1986; Andersen 1987; Main 1987). In essence, several groups are probably worthy indicators, and this may differ depending on the phenomenon under study and the ecosystem or area of concern. In particular, certain species or functional groups such as Mygalomorph spiders (Main 1987) which have long life spans, low dispersal and reproductive capabilities and specialized habitat requirements, are proving extremely sensitive to fire in these seasonal shrublands. Since they represent an extreme on the invertebrate response spectrum it is clear that they should be included in any future studies of fauna and fire regimes.

However, if causal relationships are to be defined there is a need to examine abundance patterns of invertebrate communities at a finer level of taxonomic resolution. In the present study, patterns clearly related to fire only emerged when Coleoptera were examined at the morphospecies level. Then, three major groups were obvious: pre-fire grids, post-fire control (unburnt) grids and burnt grids. Further examination of the data indicates which species and/or families of beetles show relationships with fire, and thus signify which groups are worthy of more detailed study. These key species belong to five families, none of which include the three numerically dominant families examined in more detail

(Scarabaeidae, Curculionidae and Carabidae). The families and species were:

- Elateridae (*Agrypnus* sp.1 and Elateridae sp.3), the soil-inhabiting larvae of which are primarily phytophagous and liquid-feeding with extraoral digestion (Lawrence and Britton 1991).

- Mordellidae (*Tomoxioda* sp. and *Mordellistena* spp. 2 and 4) whose larvae usually bore through rotten wood or the stems of herbs, whilst adults are found mainly on flowers and foliage (Lawrence and Britton 1991).

- Tenebrionidae (*Celibe* sp.) the subterranean larvae (false wireworms) of which feed on the roots of plants (Lawrence and Britton 1991).

- Staphylinidae (Aleocharinae spp. 7 and 14), which are free-living predators, many parasitizing Dipteran pupae, and some having a symbiotic relationship with ants (Lawrence and Britton 1991).

- Pselaphidae (*Pselaphaulax* sp.), being abundant in rotting wood and leaf litter, feeding on minute organisms (Lawrence and Britton 1991).

There is a wide range of life histories represented amongst these groups, and a considerable amount of detailed study would be required to elucidate causal relationships between their abundance patterns and fire. Work at this level of detail is required, however, if fire response prediction systems are to be developed for invertebrates, and the above may be viewed as a list of potential indicator groups amongst the Coleoptera which may clarify some of the principles underpinning fire/invertebrate relationships.

Results of this study are relevant to the controversial issues of spring versus autumn burning, and the resilience of invertebrate communities to fire in different habitat types. In the seasonally wet/dry mallee-heath vegetation of the Stirling Range National Park, no clear differences in impact were apparent for the spring and autumn burns. Although some groups responded differently to the two types of burns (eg. Diptera, and to a lesser extent Hymenoptera, increasing immediately after the spring burn and declining after the autumn burn), these trends were only temporary and in most cases not significant. It must be emphasized, however, that these prescribed burns were quite patchy and of only small scale. Under these circumstances survival of most species is probably quite high and recolonization from surrounding areas relatively rapid (Matthews and Kitching 1984). Large scale high intensity fires, like the one which affected the north-eastern section of the Park, would be expected to have a severe impact on many invertebrates, perhaps irrespective of season. From our data, however, it appears that abundance levels of the six major Orders, and species richness of Coleoptera, had returned to pre-fire levels within six months of the fire. No data are available from a comparable spring burn in these habitats, but it is unlikely that intensity and scale would be of a similar magnitude to the autumn burn studied here.

Clearly, the invertebrate fauna of these shrublands is quite resilient even to large scale high intensity fires as single events, but it is not known how they may respond to repeated burns imposed in a particular fire regime. Contrasting this data with that from more mesic areas where recovery takes 2-3 years (eg. Majer 1980, 1984; Abbott 1984) or longer

(McNamara 1955; Springett 1976, 1979) suggests that resilience (or more specifically elasticity, *sensu* Westman 1986) may in fact be greater in the seasonally dry mallee-heath habitats than in the wetter, less seasonal habitats (cf. Majer 1985a). As a corollary, the season of burn may be less important in these dry habitats than those which are more seasonally benign. This suggests that the invertebrate fauna of the mallee-heath shrublands has evolved in and adapted to a regime of fairly frequent disturbance. In particular, their adaptations to survive seasonal aridity may also impart considerable resilience to fire, but this does not necessarily imply that the invertebrate fauna will not change greatly under a high frequency fire regime (ie.exhibit low malleability *sensu* Westman 1986).

Studies by Main and Gaull (1993) of the fate of relictual species of trapdoor spiders (Mygalomorphs) on Bluff Knoll following the autumn 1991 wildfire further indicate the relative sensitivities of species occupying markedly different but adjacent habitat types, and also illustrate the importance of single species studies as opposed to those at higher taxonomic levels. These spiders, which occupy cool, shaded gullies on the mountain ranges of the Park where there is a high incidence of fog and rainfall, were severely affected by this fire, whilst Araneae as a group showed no significant response to any of the fires conducted in the lowland mallee-heaths. Detailed studies of Mygalomorph species in the latter habitat may well have revealed some significant changes, and clarified the impact of fire for this one specific group. In view of the seasonal harshness and relatively high incidence of fire in the lowlands (even under a "natural" pre-European regime; Hallam 1975, 1985; McCaw and Gillen 1993) it seems unlikely, however, that the overall effect would have been as great as in the upland habitats.

Implications for conservation and management

Examination of the results from this and other studies of invertebrates in remnant shrublands indicates there is a need for careful and sensitive management of fire if conservation values are to be maintained. While it appears, broadly speaking, that the invertebrate fauna of these highly seasonal environments is relatively resilient to fire, there are some caveats which must be borne in mind when developing a fire management system.

- Firstly, the remnant nature of these habitats means that recolonization from adjacent areas is limited in the event of a fire which affects an entire Reserve or Park. These impacts will be greatly lessened if fires are patchy and of relatively low intensity.

- Secondly, there are no data available on the long-term impacts of a fire regime, and it is better to err on the side of conservatism in developing a fire management regime, especially in deciding frequency and scale of burning. Our data are inconclusive on these two issues, since there were few strong relationships between fire age or scale and invertebrate abundance or (Coleoptera) species richness. It is likely that overall recovery takes longer after a large scale fire, but this may only be a difference of between one and six months, while a mosaic of different ages of vegetation within a particular habitat type probably enhances diversity and provides some flexibility in fire management.

- Thirdly, there is a clear dichotomy in the fire sensitivity of species inhabiting the wet gullies and thickets of the uplands in the Stirling Range and those occupying the seasonally dry lowland mallee-heaths. While an average fire frequency of around 20 years may be appropriate in many parts of the lowlands, this is unlikely to be the case for the mountains. Indeed, the Bluff Knoll area has been burnt under high intensity conditions at this frequency since the turn of the century (late 1930's and 50's, 1972 and 1991; McCaw and Gillen 1993; Main and Gaull 1993), and it is important that these uplands are afforded protection from further similar fires for many decades.

Given the above, some recommendations can be made for an appropriate strategy for managing fire in remnant mallee-heath habitats, and specifically the Stirling Range National Park, with respect to invertebrate conservation:

- An internal and external (boundary) system of firebreaks and low fuel zones should be maintained to reduce the risk of large, high intensity wildfires entering or spreading throughout the reserve or park. Such zones should also exist along major internal access tracks or through-roads, and would need to be frequently disturbed (eg. every 5-10 years) to maintain low fuel loads.

- Small reserves (eg < 500ha) should not be subjected to block burning but rather have an internal (linear) system of low fuel zones in place to reduce the risk of the whole area being affected by wildfire. The objective should be to maintain heterogeneity of habitat. Low intensity burning under mild conditions in spring every 5-10 years should be used to maintain such zones; this in itself adds some heterogeneity to the habitat.

- In larger reserves (and the Stirling Range in particular), small-scale mosaic burning of strategic areas of lowland country should be carried out to protect fire sensitive areas (eg upland country). Results of this and the ongoing vertebrate studies in the Stirling Range suggest that any particular area should not be burnt any more frequently than every 15 to 20+ years. Intensity and scale should be varied as much as possible to produce a mosaic of different-aged areas which may provide a range of resources for a wide variety of species. Burning should be done under mild controlled conditions, mainly in spring when weather patterns are most stable and predictable.

- Mosaic burning operations should be carried out only over discrete areas and should avoid any fire-sensitive habitats such as swamps, gullies and uplands.

- As a general rule larger-scale block burning should not be carried out except in special circumstances (eg for specific regeneration purposes or experimental research). This should ensure that many long-unburnt areas remain within a mosaic of more frequently burnt patches.

These principles are essentially already in place in the majority of fire management plans for these habitat types, but it is the logistics and execution of them which presents problems. The single most important element is the protection of relictual fire sensitive species and habitats. This can only be achieved through a combined system of low fuel zones along boundaries and a mosaic of different-aged areas, which vary both spatially and temporally, in the more resilient lowland habitats. As season of burn does not appear to be of major significance to invertebrate communities it is recommended that most protective burning be carried out in spring when weather patterns are more stable and predictable.

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TABLE 1

Relative perventage change in abundance for each order after fire on various grids compared with changes in the associated unburnt control grid. Significant differences are indicated as: @ $p < 0.10$; * $p < 0.05$; ** $p < 0.01$.

ORDER	GRID COMPARISON					
	1,2 v 3	4 v 6	5 v 6	7 v 6	8 v 9	10,11 v 6
Coleoptera	+13.6	+4.4	+30.8	-16.2	+9.6	-29.0
Diptera	-63.2**	-17.7	+3.5	+3.7	+2.6	+56.5*
Hemiptera	-1.4	+46.6	+47.6	+3.6	+36.8	+115.8*
Hymenoptera	-27.8	-31.2@	-22.0	-7.5	+30.1*	-24.4
Orthoptera	+119.1*	-38.1	-14.0	+1.2	+79.2*	-5.4
Araneae	-15.7	-2.8	+3.7	-1.9	+38.0**	-33.4

TABLE 2

Absolute change in number of species of beetles (calculated as mean per sample) after fire on various grids, corrected for changes in the associated control grid.

GRID COMPARISONS					
1,2 v 3	4 v 6	5 v 6	7 v 6	8 v 9	10,11 v 6
+1.9	+4.7	-0.2	-1.5	-1.2	-0.3

TABLE 3

Relative percentage change in abundance for each order based on comparisons of the first post-fire sample with all pre-fire samples (acute impact tests) for various grids and the associated control. Significant differences are indicated as: @ $p < 0.10$; * $p < 0.05$; ** $p < 0.01$.

ORDER	GRID COMPARISON		
	1,2 v 3	4 v 6	5 v 6
Coleoptera	-3.1	-46.1	+831.8**
Diptera	-65.4	-76.2**	+625.7@
Hemiptera	-14.5	-39.3	+52.3
Hymenoptera	-38.4	-40.7	+133.3
Orthoptera	-40.1	-69.5*	+6.1
Araneae	-39.3	+5.2	+56.2

TABLE 4

Relative percentage change in abundance for each order based on comparisons of all except the first post-fire sample with all pre-fire samples (chronic impact tests) for various grids and the associated control. Significant differences are indicated as: @ $p < 0.10$; ** $p < 0.01$.

ORDER	GRID COMPARISONS		
	1,2 v 3	4 v 6	5 v 6
Coleoptera	+18.2	+19.1	-5.6
Diptera	-62.7**	+5.5	-25.3
Hemiptera	+2.1	+74.7@	+46.8
Hymenoptera	-13.3	-29.2	-35.1
Orthoptera	+203.0**	-28.7	-17.0
Araneae	-5.6	-4.3	-3.2

LIST OF FIGURES

Figure 44: Abundance of Araneae versus age of stand. Means per sample and standard errors are shown (see text).

Figure 45: Bray-Curtis dissimilarity values versus time for pairwise combinations of Grids 1-3.

Figure 46: Bray-Curtis dissimilarity values versus time for pairwise combinations of Grids 4-6.

Figure 47: Principal Components (PCA) ordination (and associated eigenvectors) of sampling occasions by orders. Open squares = all pre-fire samples; open stars = unburnt controls, post-fire; closed stars = burnt samples.

Figure 48: Principal Components (PCA) ordination (and associated eigenvectors) of sampling occasions by orders using doubly centred data matrices. Open squares = all pre-fire samples; open stars = unburnt controls, post-fire; closed stars = burnt samples.

Figure 49: Principal Components (PCA) ordination (and associated eigenvectors) of grids before and after fire by orders. Open squares = all pre-fire samples; open stars = unburnt controls, post-fire; closed stars = burnt samples.

Figure 50: Principal Components (PCA) ordination (and associated eigenvectors) of grids before and after fire by orders using doubly centred data matrices. Open squares = all pre-fire samples; open stars = unburnt controls, post-fire; closed stars = burnt samples.

Figure 51: Principal Components (PCA) ordination (and associated eigenvectors) of grids before and after fire by all Coleoptera species. See text for species names. Open squares = all pre-fire samples; open stars = unburnt controls, post-fire; closed stars = burnt samples.

Figure 52: Principal Components (PCA) ordination (and associated eigenvectors) of grids before and after fire by all Coleoptera species using doubly centred data matrices. See text for species names. Open squares = all pre-fire samples; open stars = unburnt controls, post-fire; closed stars = burnt samples.

Figure 53: Principal Components (PCA) ordination (and associated eigenvectors) of grids before and after fire by floristic data. Open squares = all pre-fire samples; closed stars = burnt samples.

Figure 54a: Principal Components (PCA) ordination (showing first two principal components and associated eigenvectors) of grids before and after fire by structure data. Open squares = all pre-fire samples; closed stars = burnt samples. LC = litter cover; V1-V12 = vegetation density, intervals 1-12 (vertical); HD = horizontal distribution of vegetation; TD = mean trash diameter; TH = mean trash height; Ht = mean vegetation height; TC = trash cover; LV = percentage of live vegetation.

Figure 54b: Principal Components (PCA) ordination (showing second and third principal components and associated eigenvectors) of grids before and after fire by structure data. Open squares = all pre-fire samples; closed stars = burnt samples. LC = litter cover; V1-V12 = vegetation density, intervals 1-12 (vertical); HD = horizontal distribution of vegetation; TD = mean trash diameter; TH = mean trash height; Ht = mean vegetation height; TC = trash cover; LV = percentage of live vegetation.

Figure 55: Procrustes analysis showing comparison of ordinations. ST = structure; FL = floristics; OR = orders; ORC = orders centred; CB = common beetles; CBC = common beetles centred; AB = all beetles; ABC = all beetles centred.

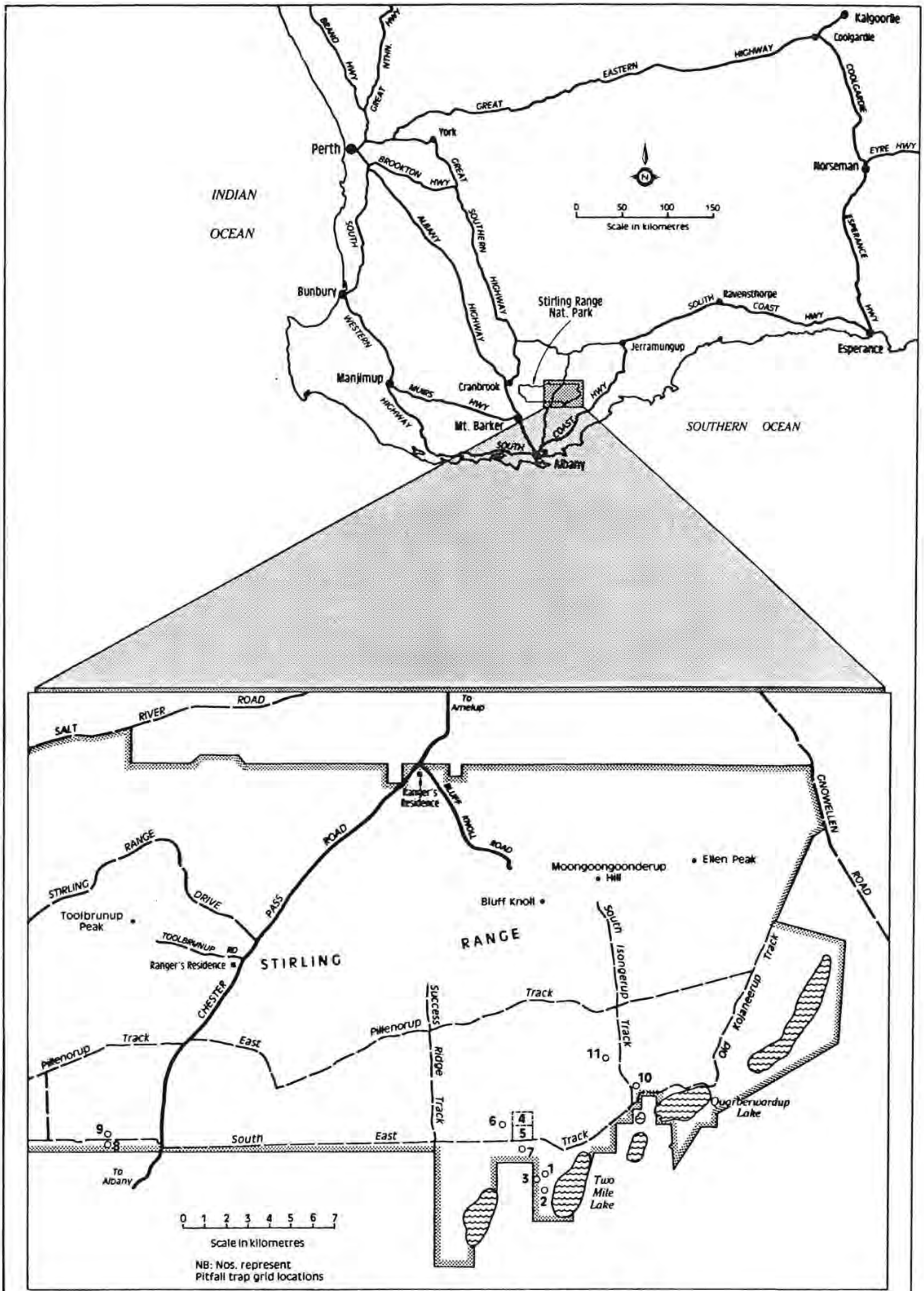

Fig. 1. Location of Stirling Range Nat. Park & Study Sites.

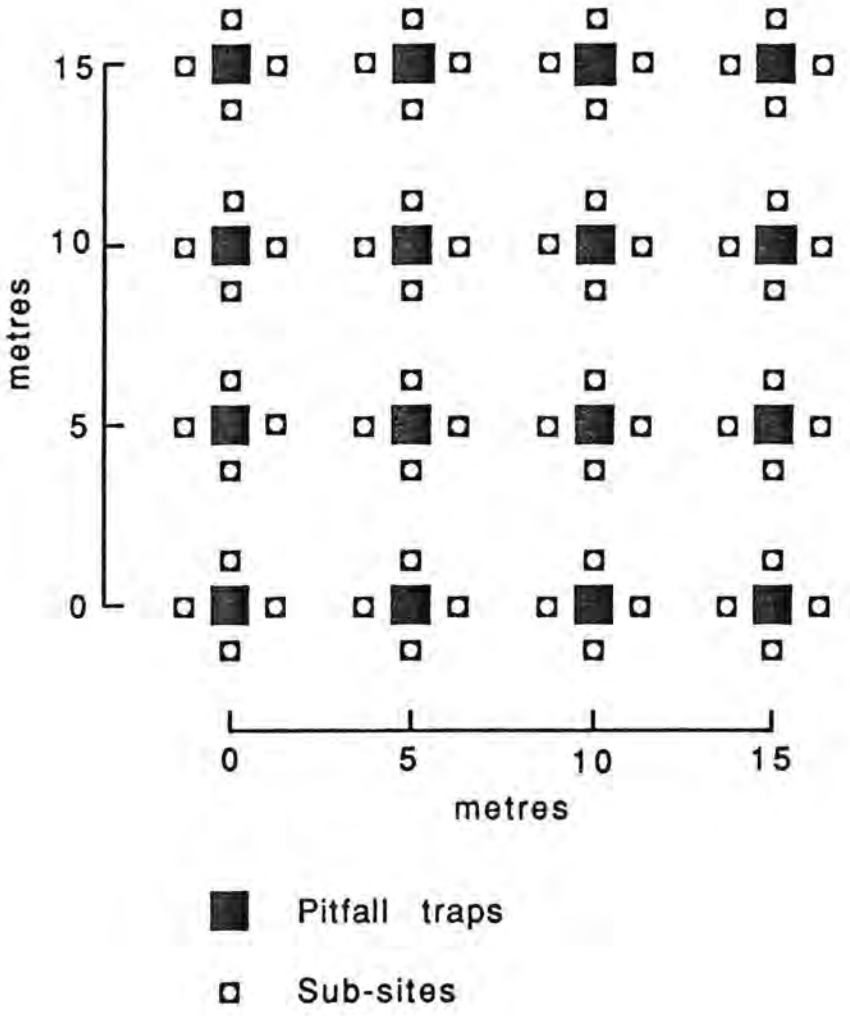

FIG. 2 LAYOUT OF AN INVERTEBRATE SAMPLING GRID

FIG.3 - ABUNDANCE VS TIME

COLEOPTERA

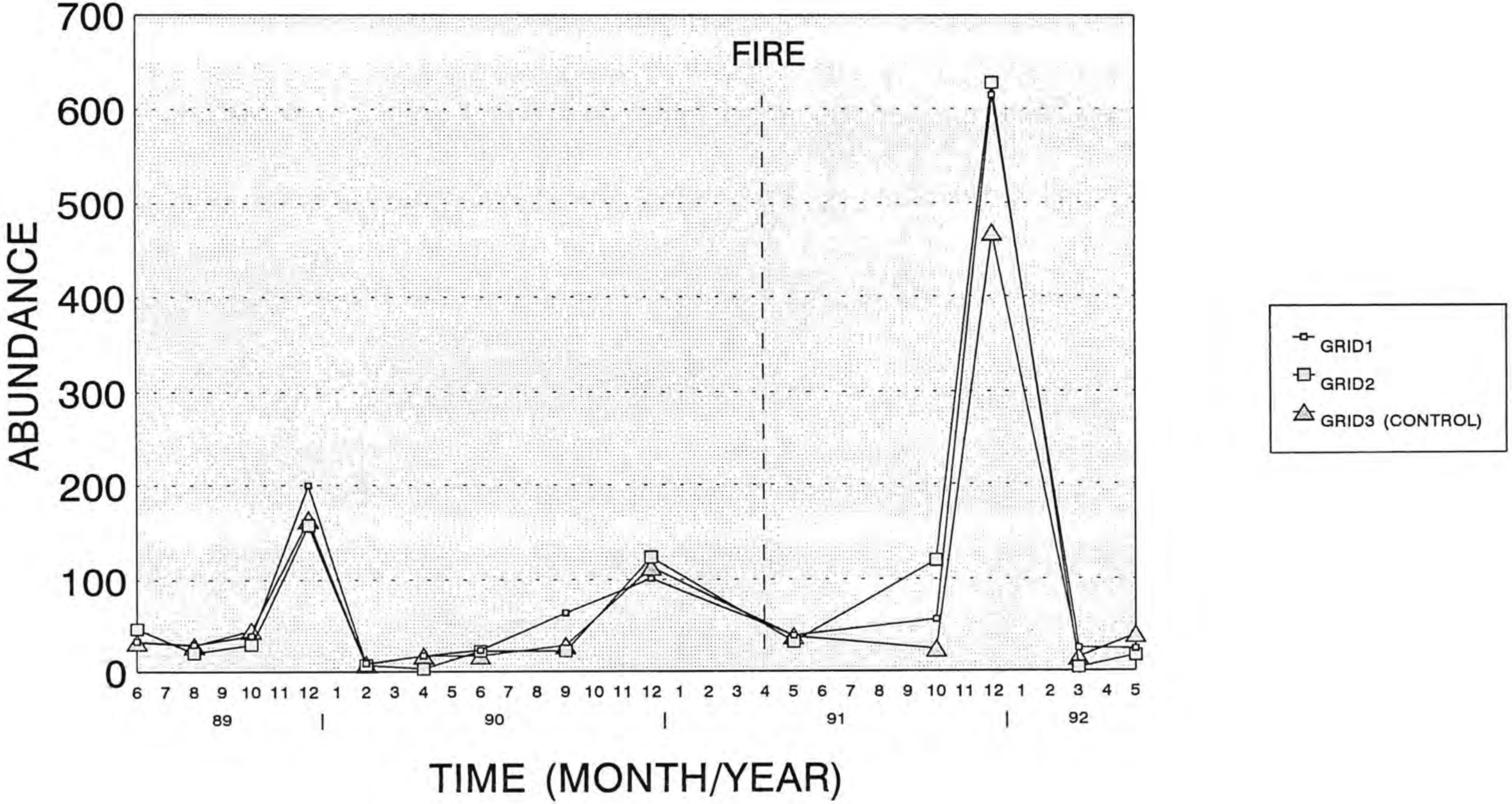

FIG.4 - ABUNDANCE VS TIME
COLEOPTERA

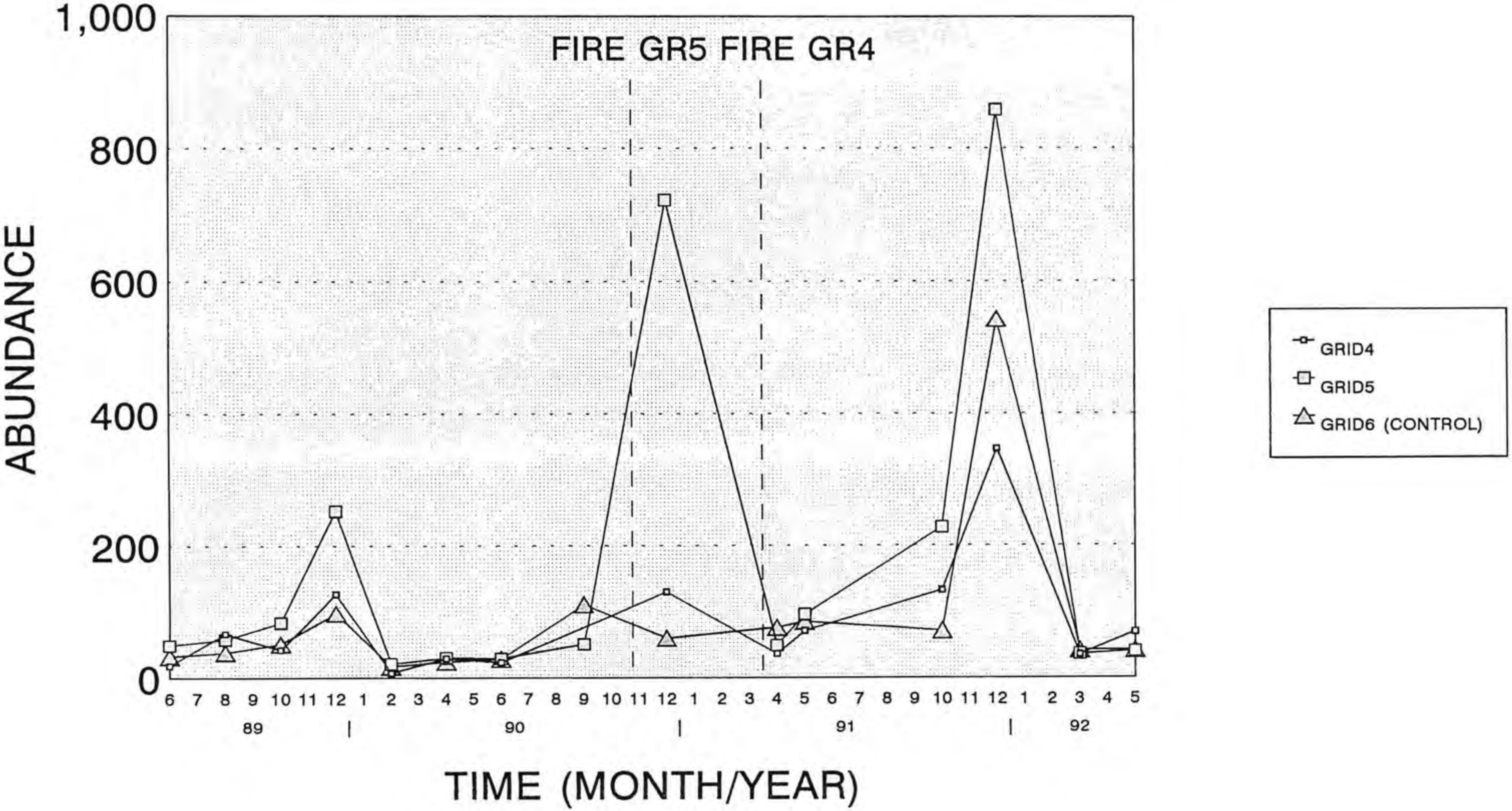

FIG.5 - ABUNDANCE VS TIME

COLEOPTERA

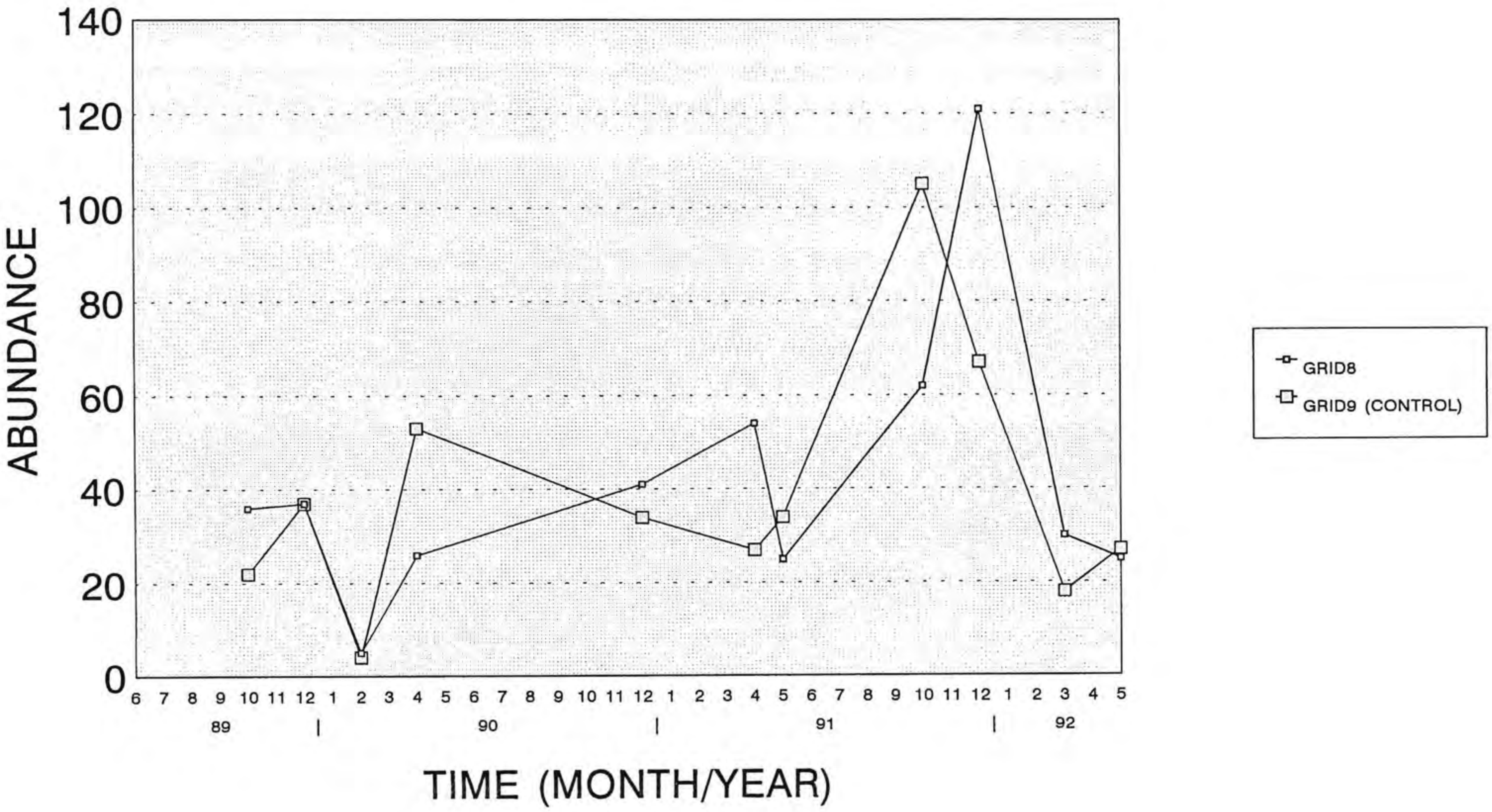

FIG.6 - ABUNDANCE VS TIME

COLEOPTERA

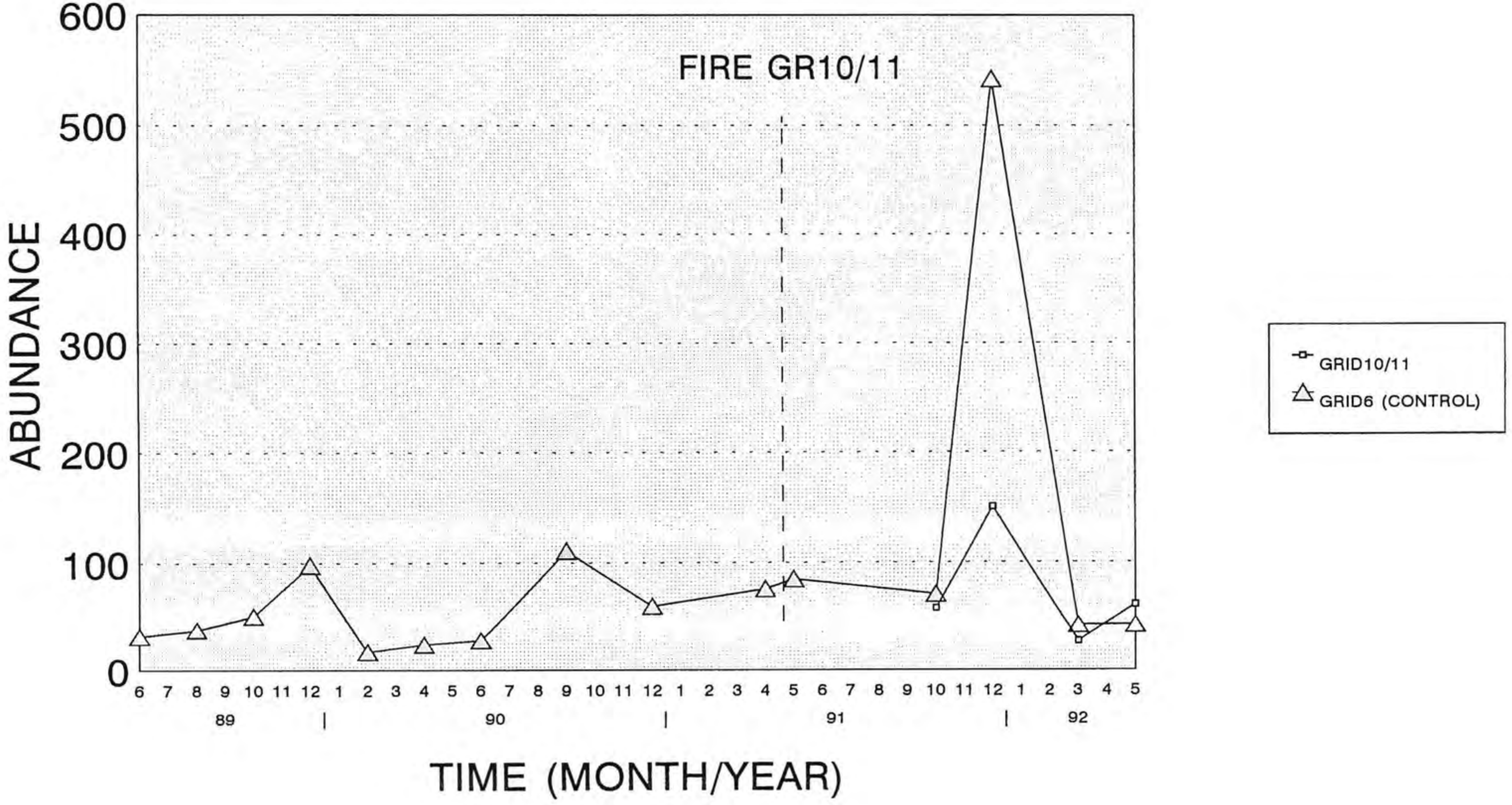

FIG. 7 - MEAN ABUNDANCE v AGE OF STAND

COLEOPTERA

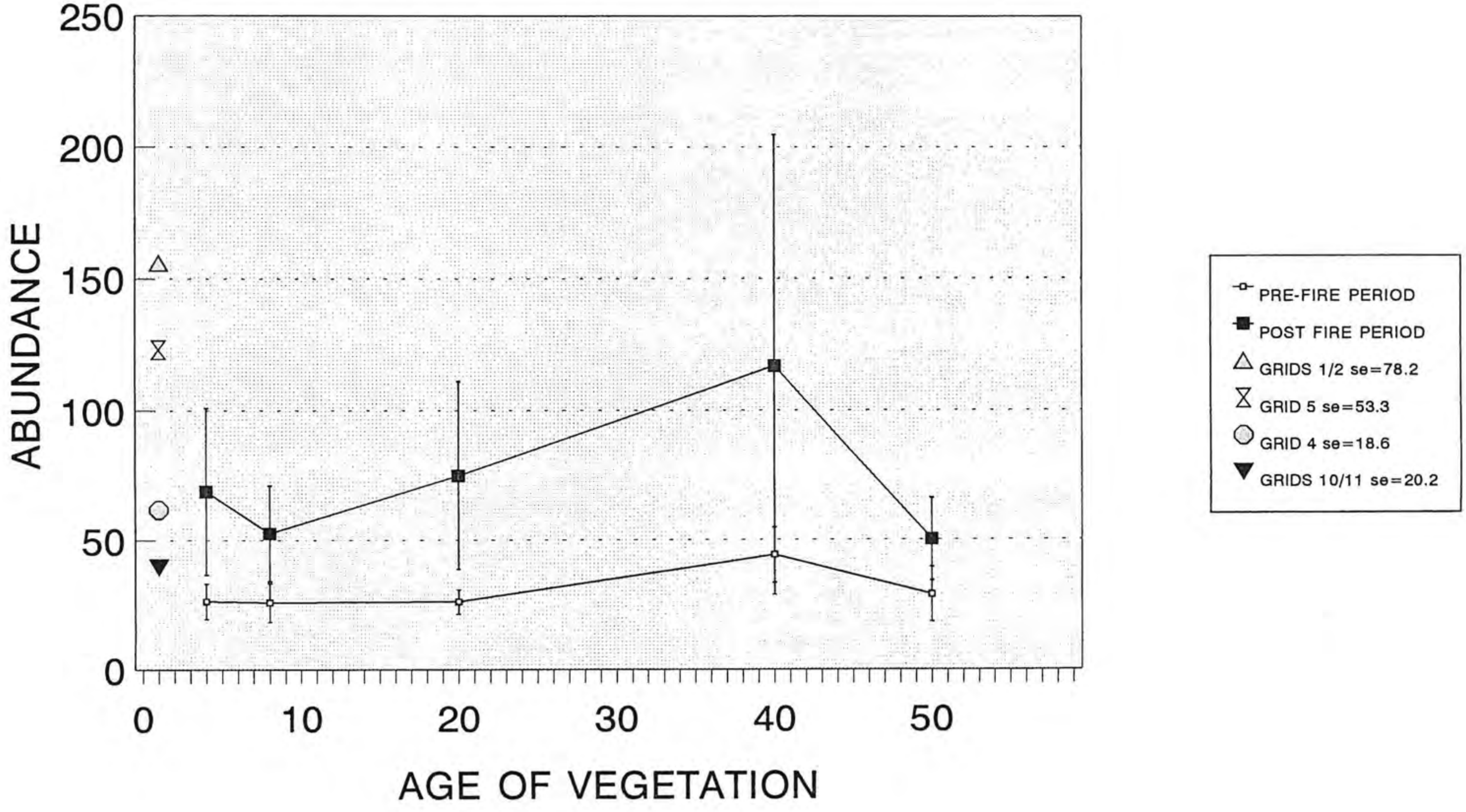

FIG.8 - ABUNDANCE VS TIME

CARABIDAE

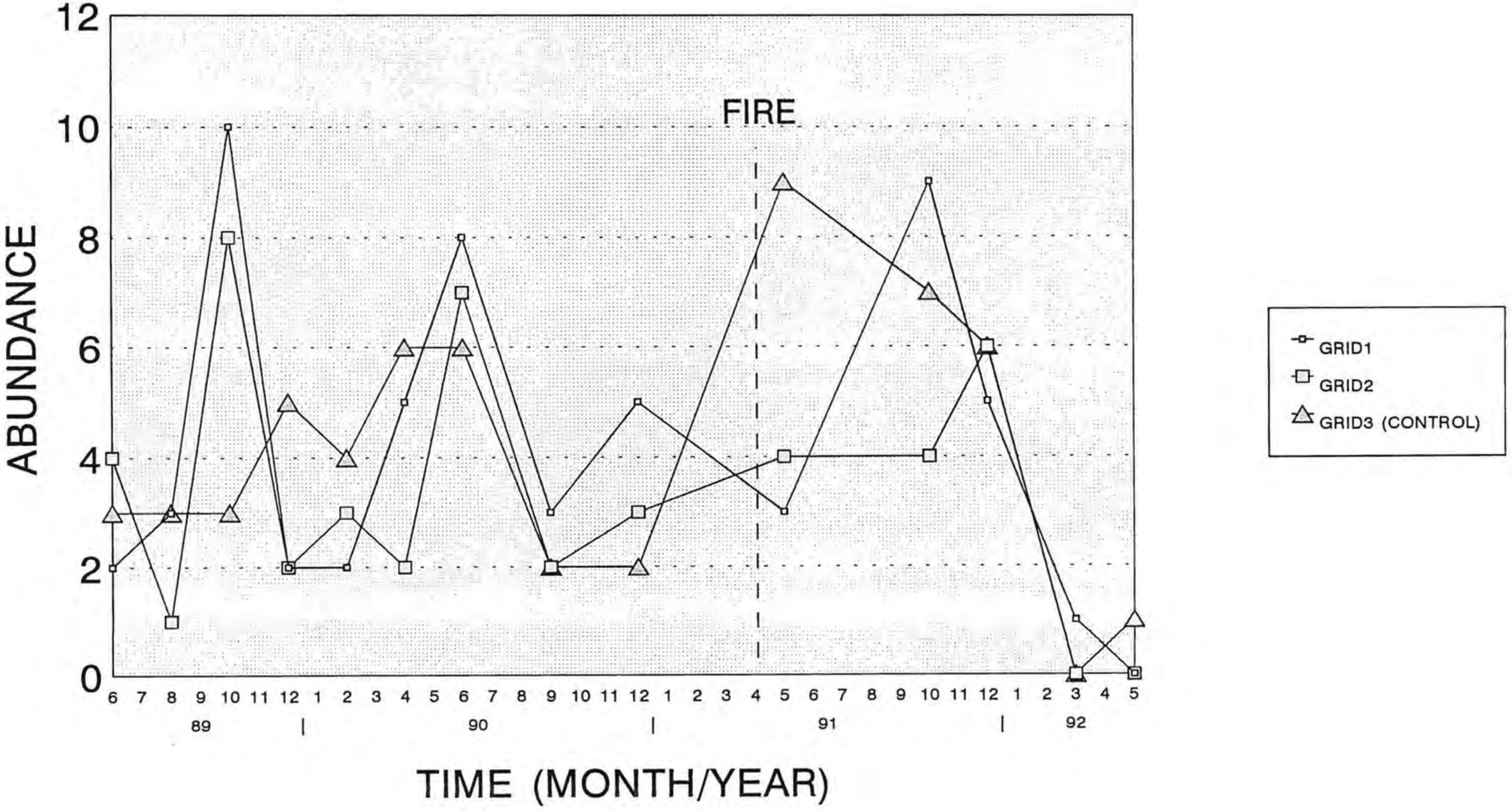

FIG.9 - ABUNDANCE VS TIME

CARABIDAE

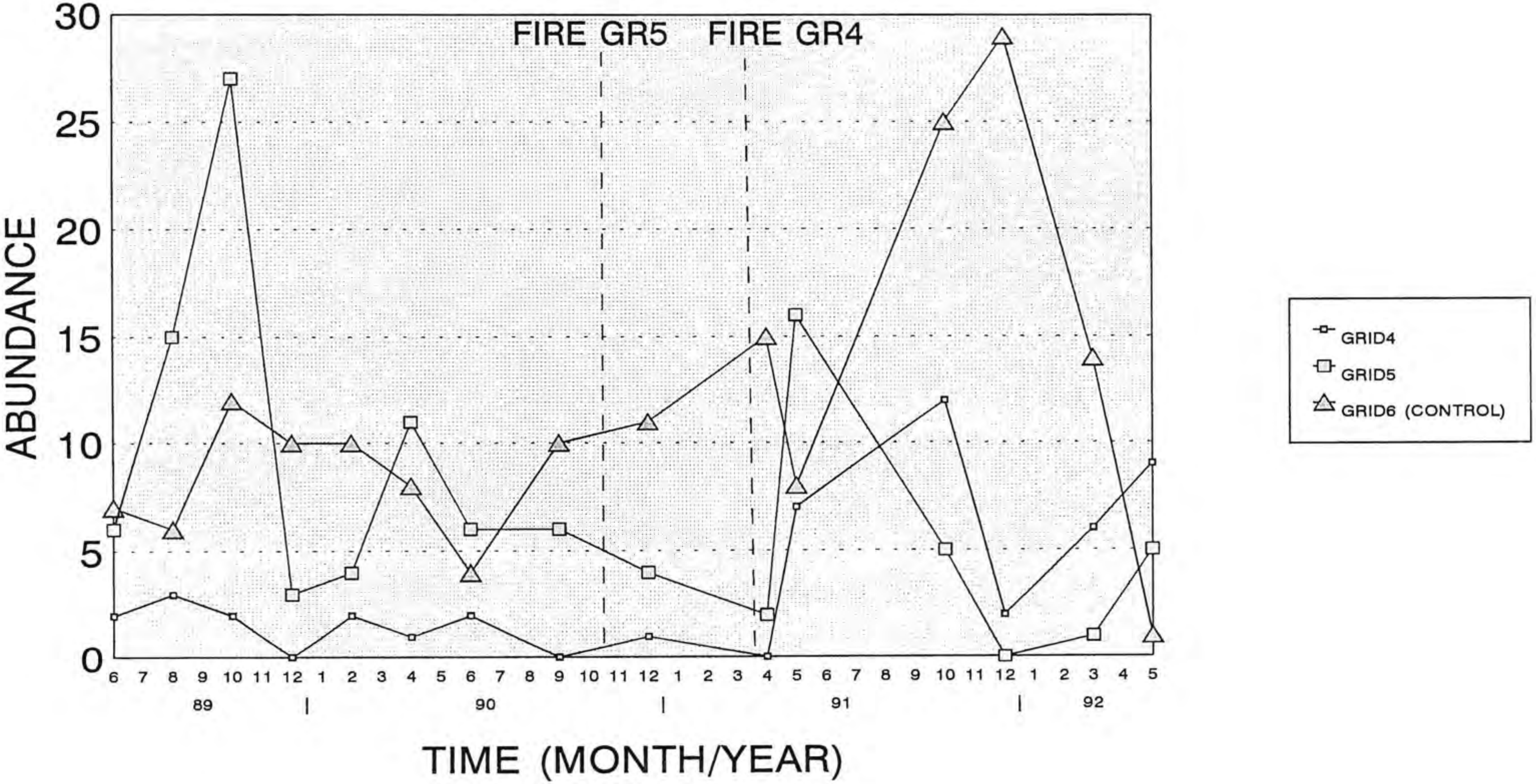

FIG.10 - ABUNDANCE VS TIME

CARABIDAE

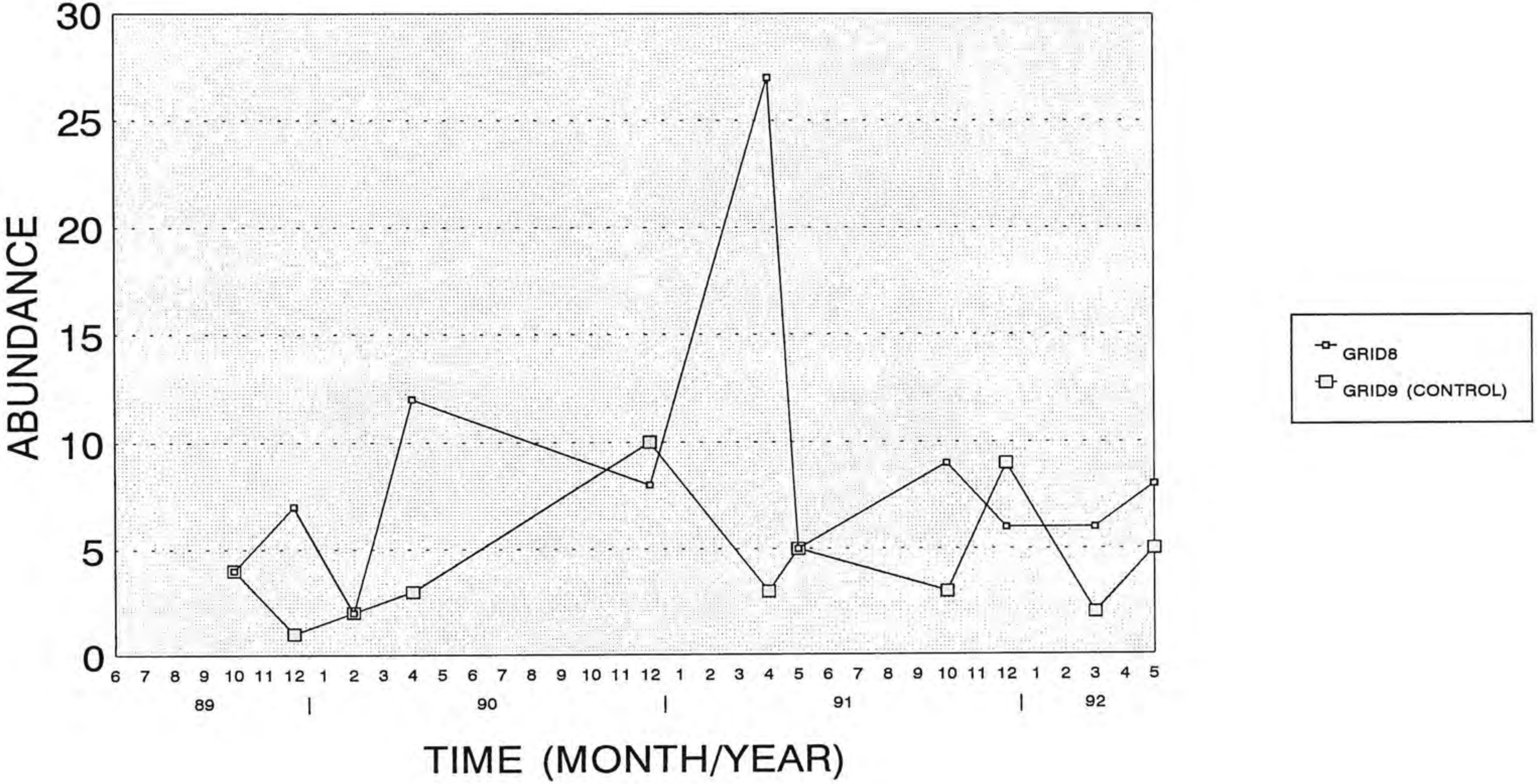

FIG.11 - ABUNDANCE VS TIME
CARABIDAE

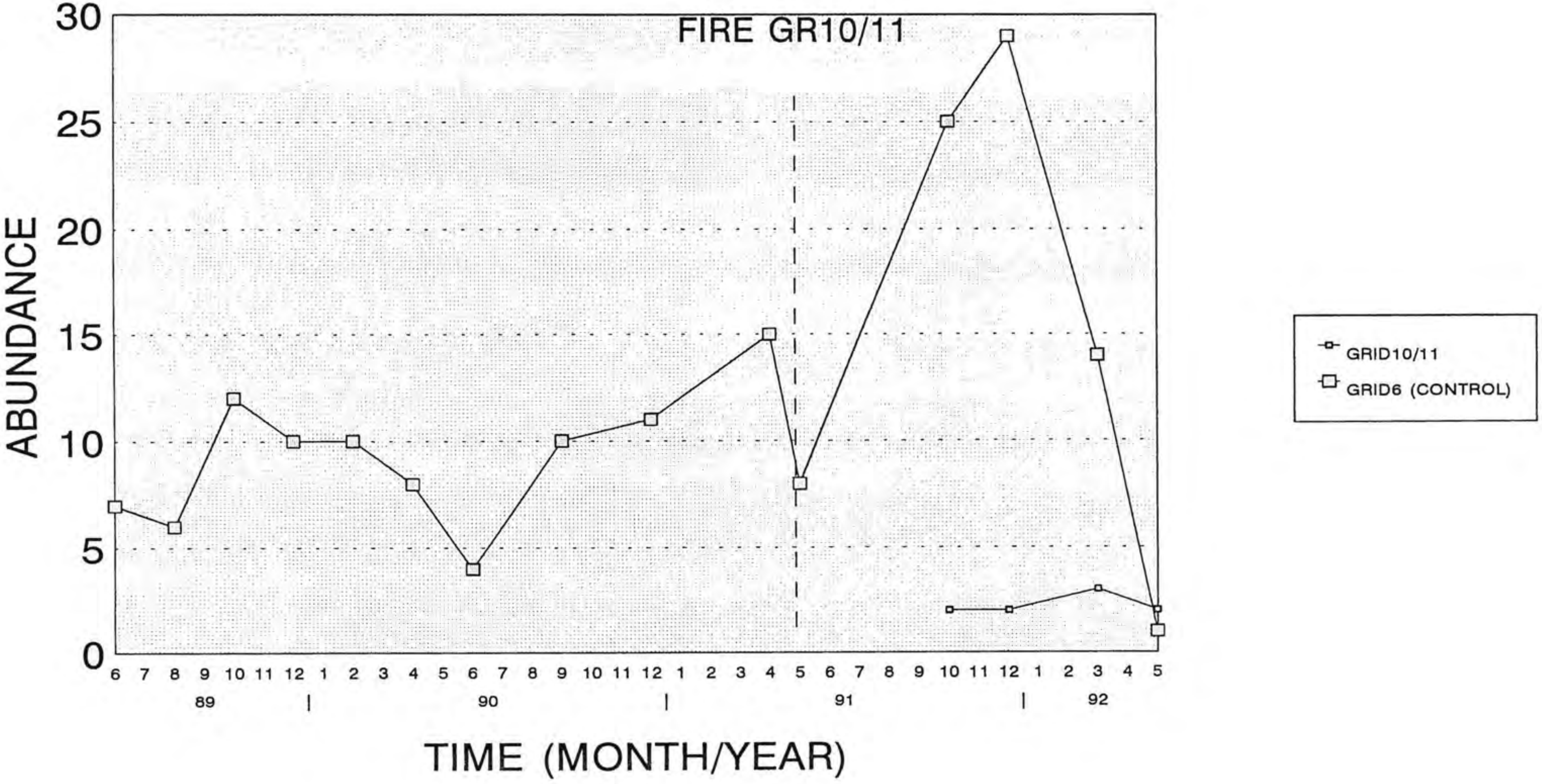

FIG.12 - ABUNDANCE VS TIME

SCARABAEIDAE

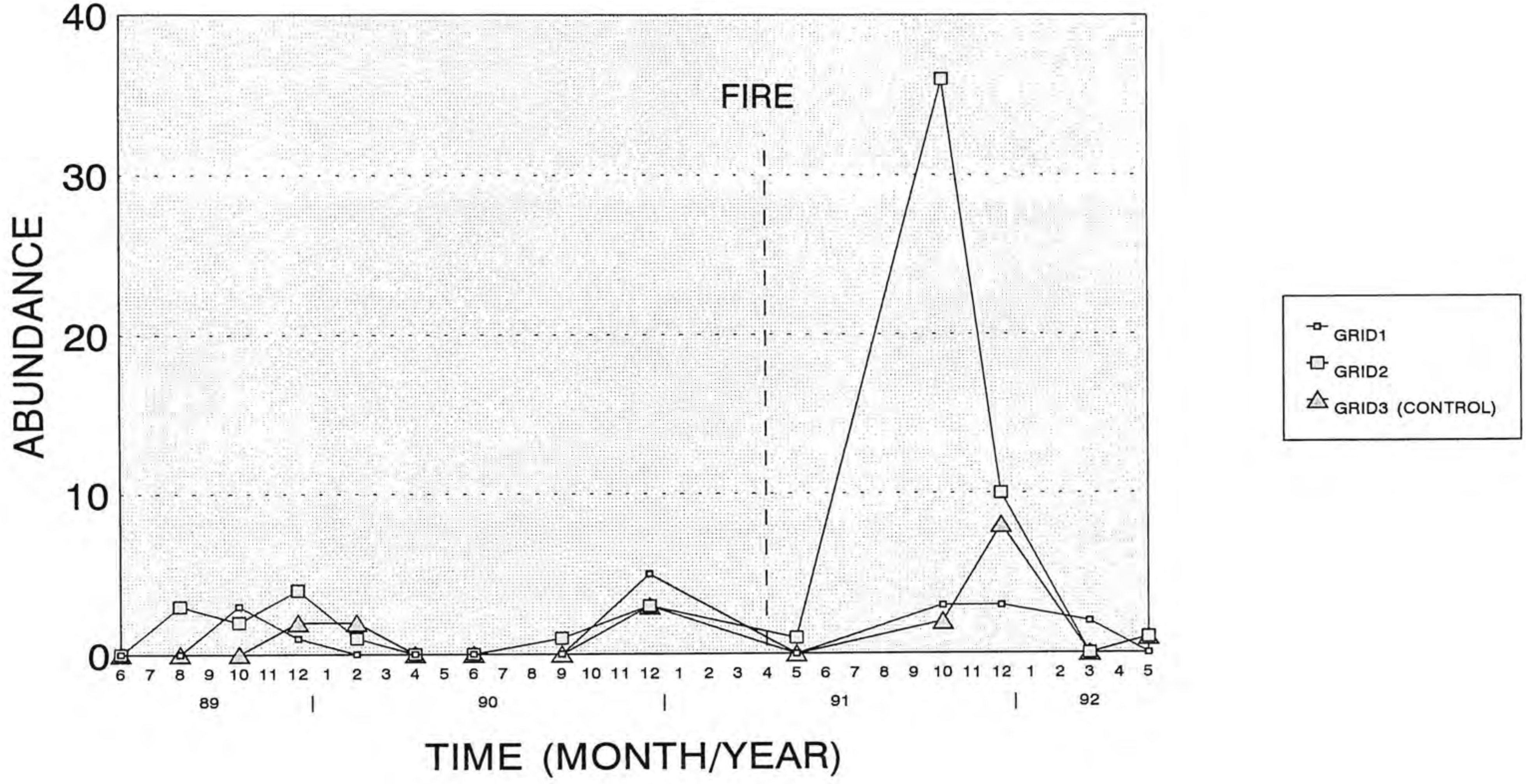

FIG.13 - ABUNDANCE VS TIME

SCARABAEIDAE

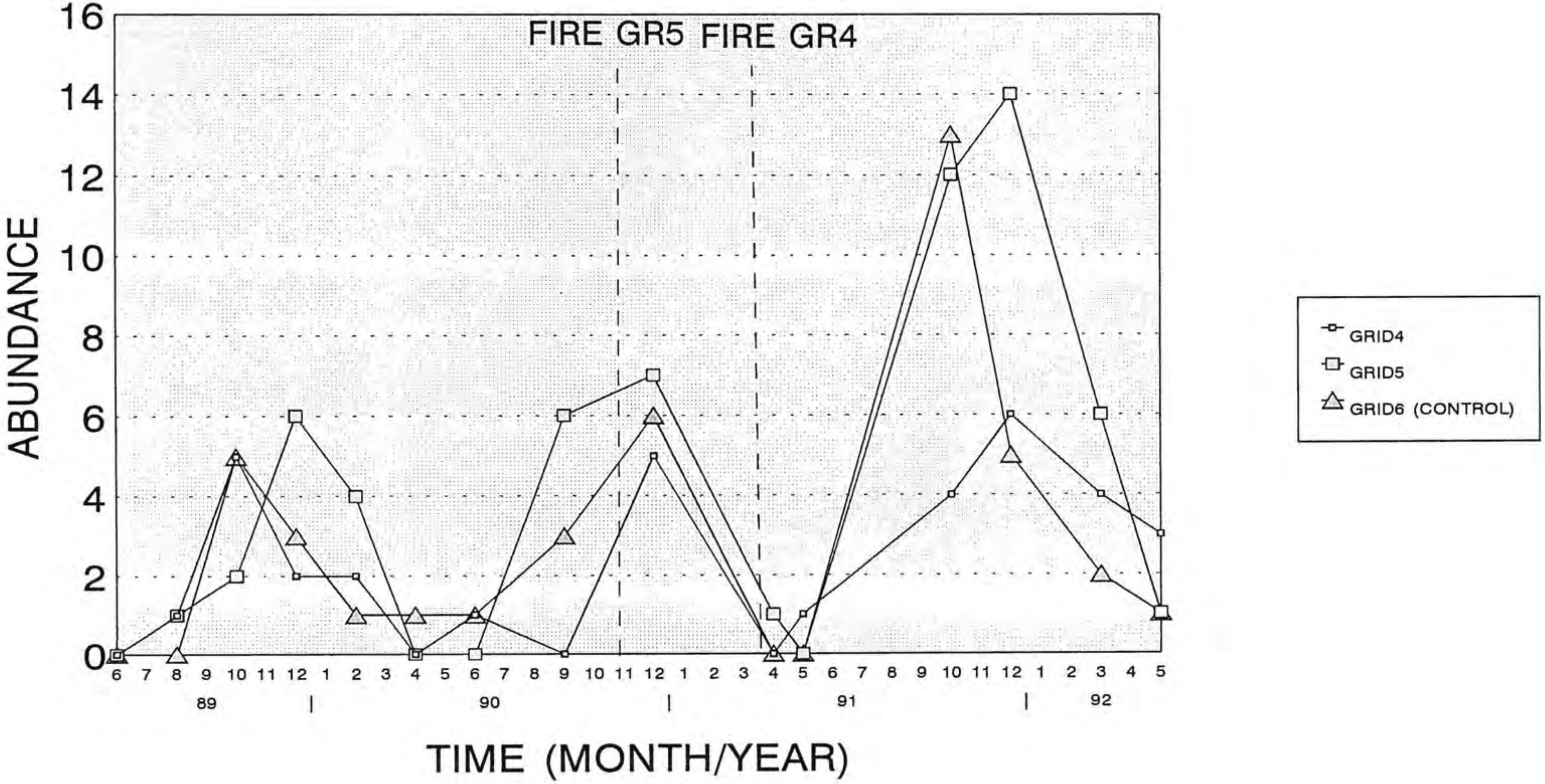

FIG.14 - ABUNDANCE VS TIME

SCARABAEIDAE

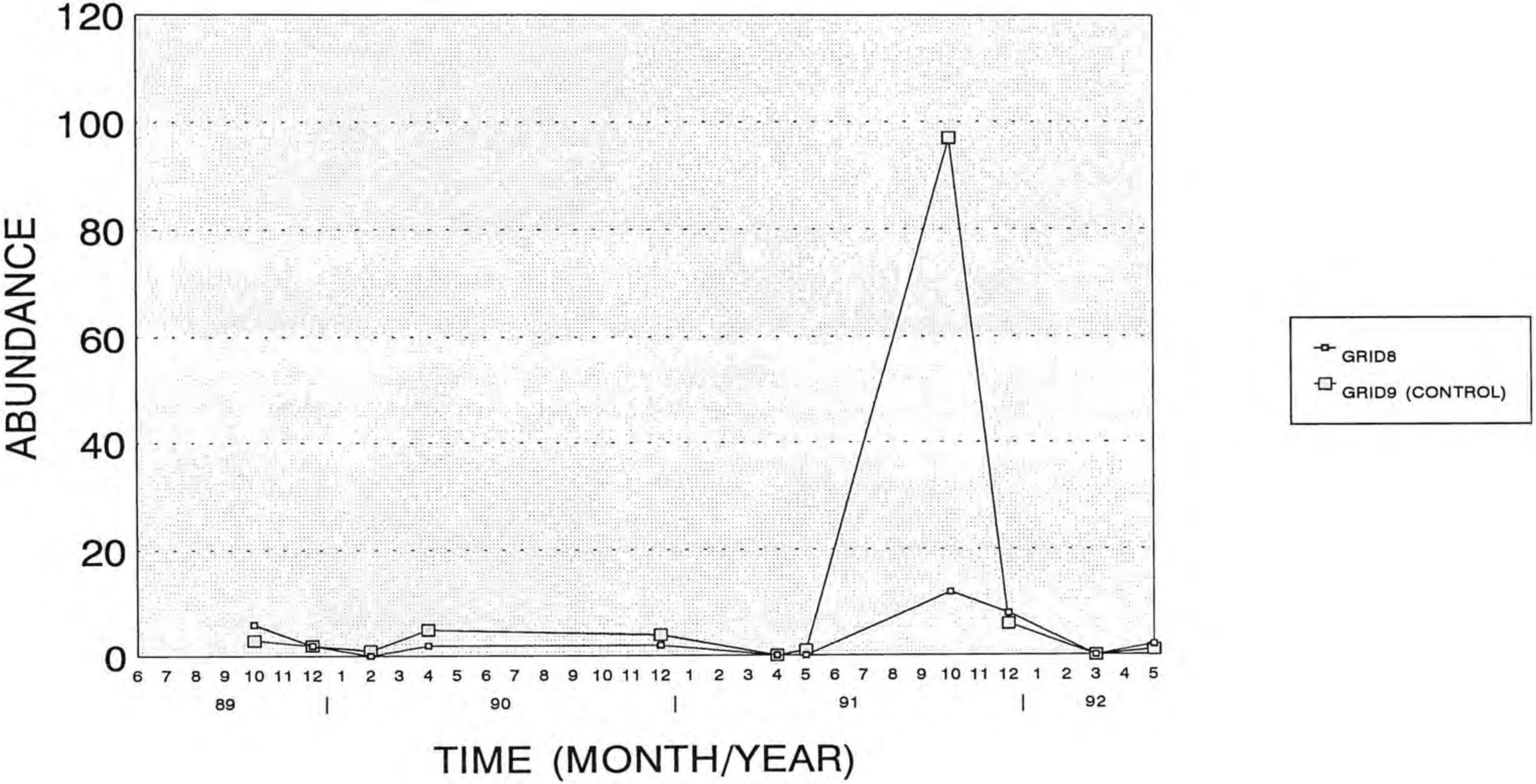

FIG.15 - ABUNDANCE VS TIME

CURCULIONIDAE

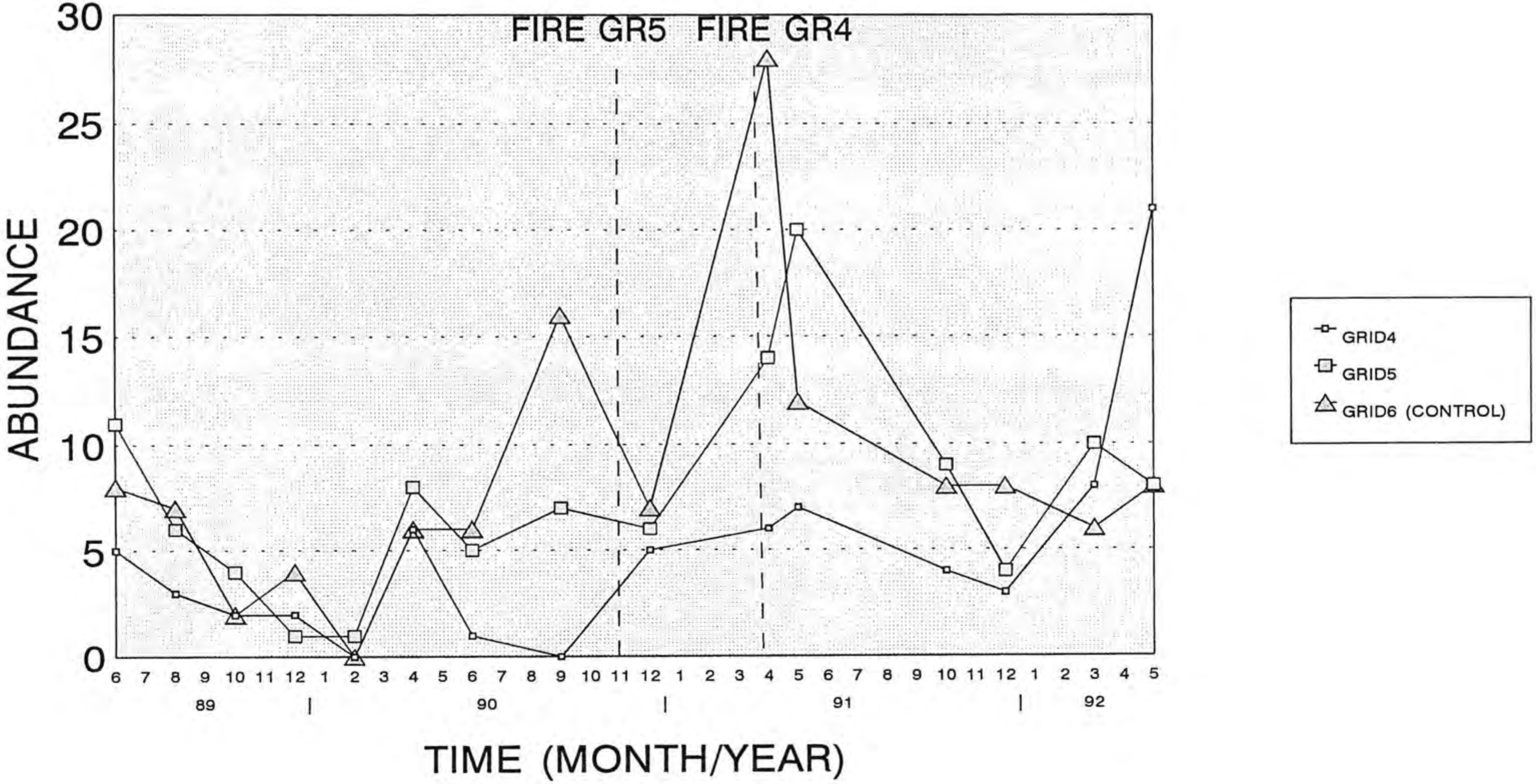

FIG.16 - SPECIES RICHNESS VS TIME

BEETLES

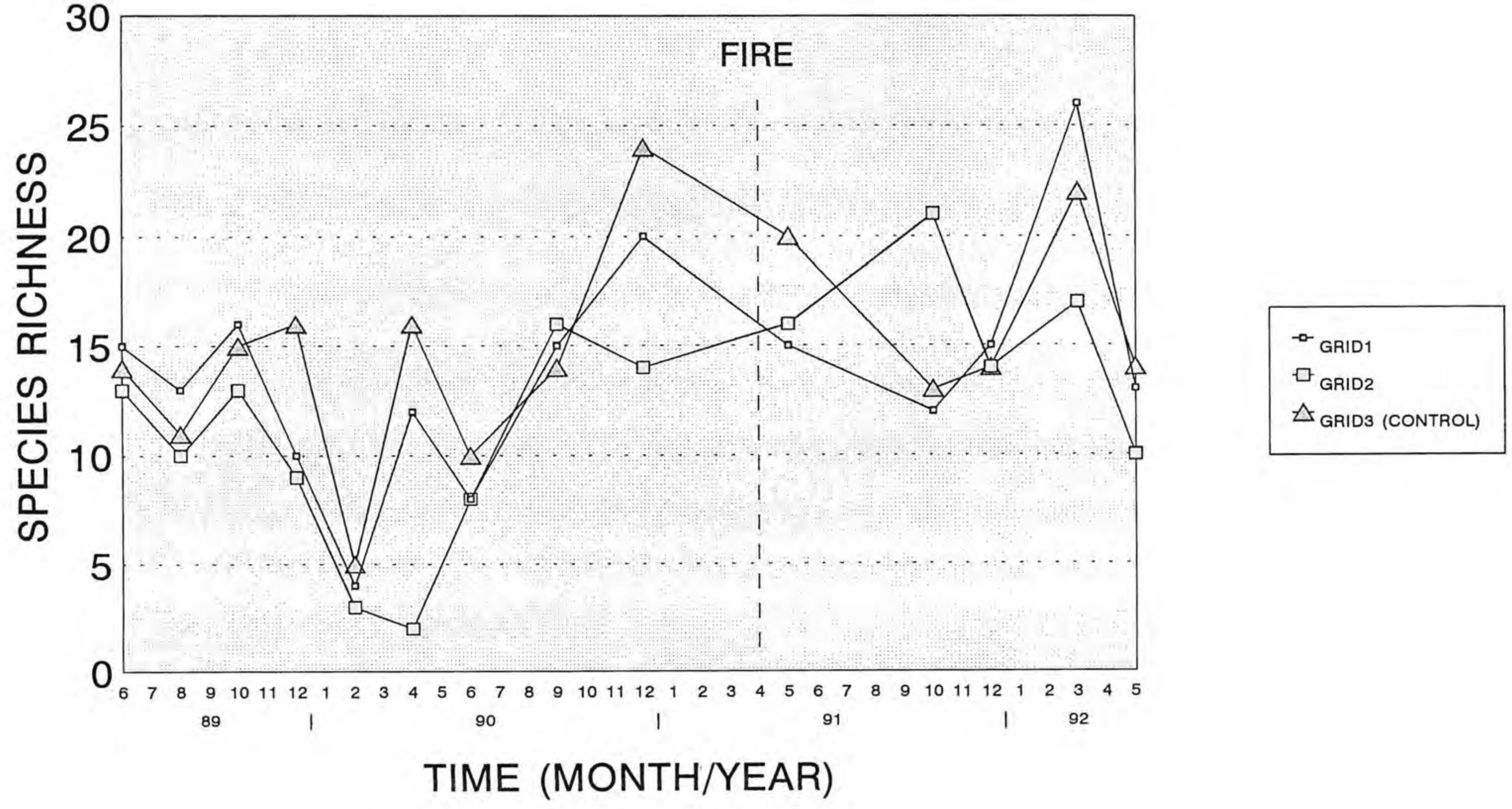

FIG.17 - SPECIES RICHNESS VS TIME

BEETLES

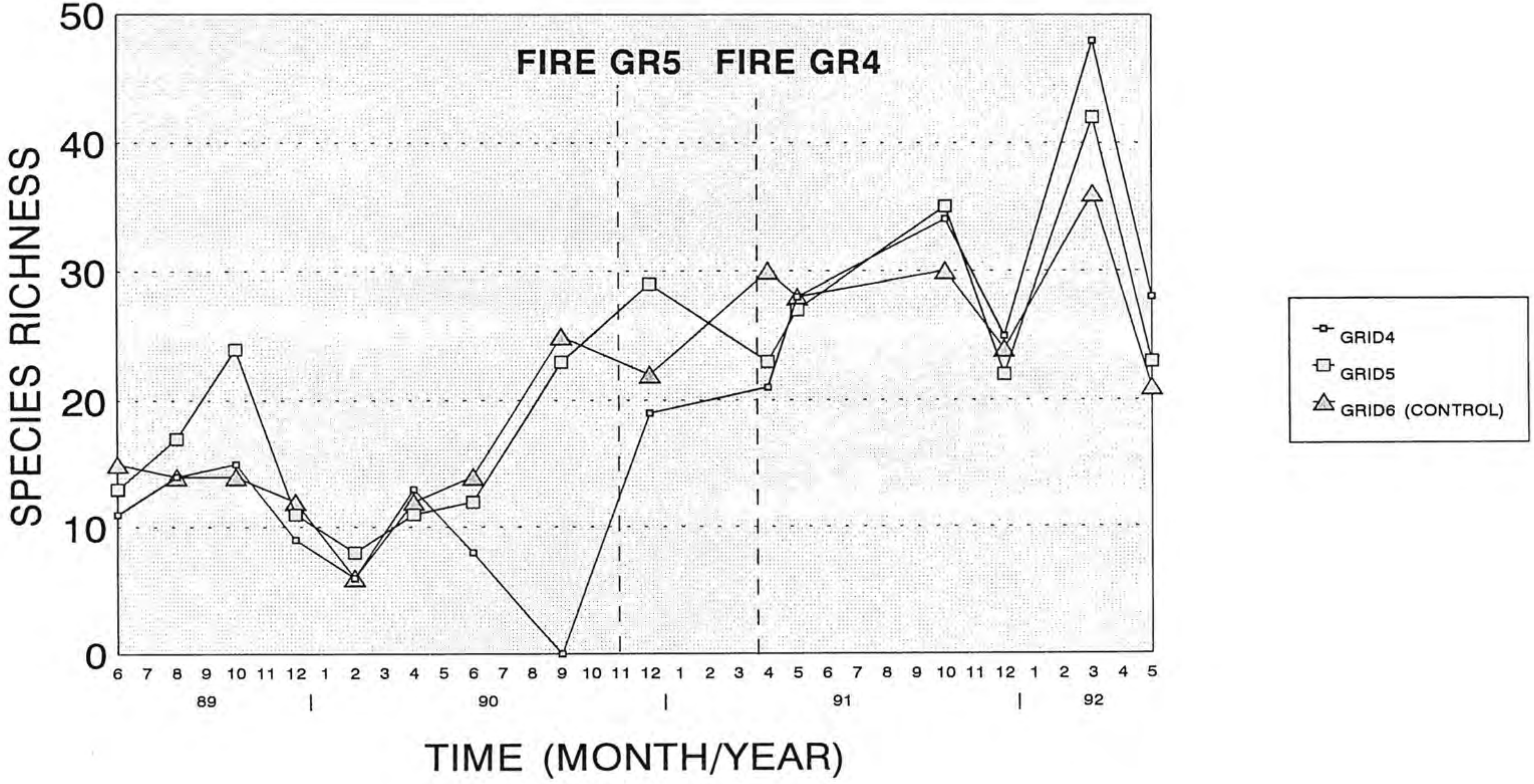

FIG.18 - SPECIES RICHNESS VS TIME

BEETLES

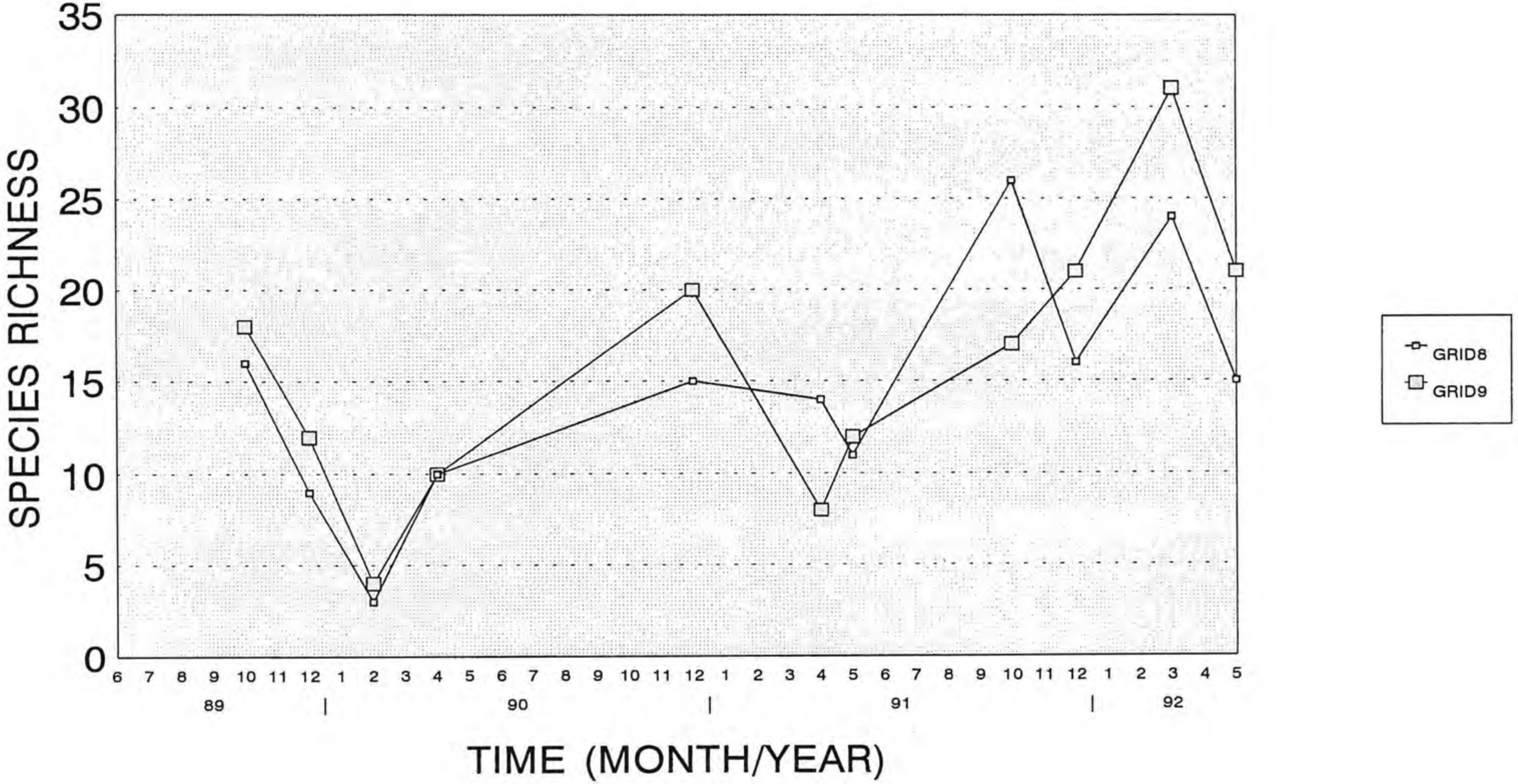

FIG.19 - SPECIES RICHNESS v AGE OF STAND

COLEOPTERA

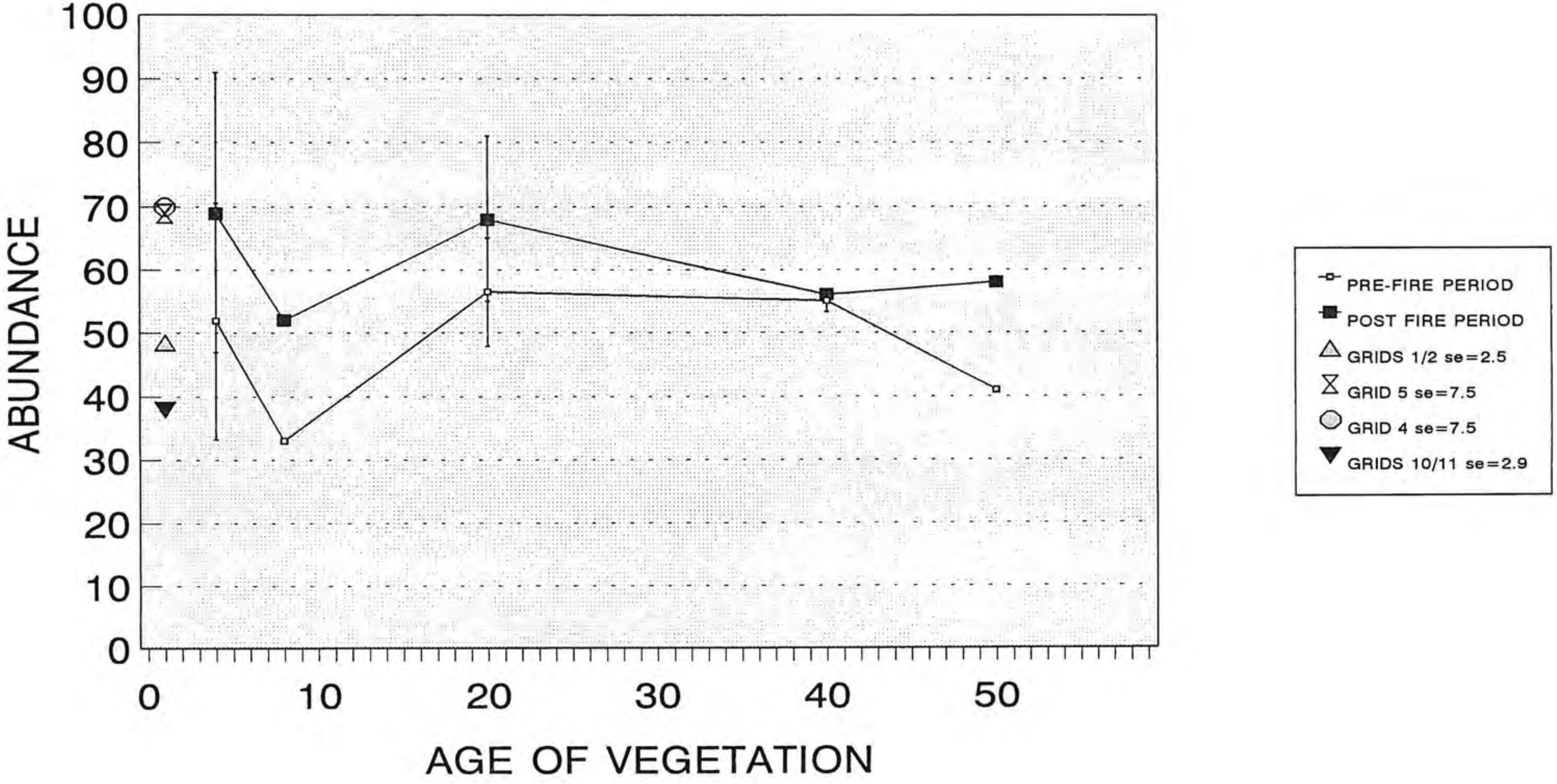

FIG.20 - ABUNDANCE VS TIME

DIPTERA

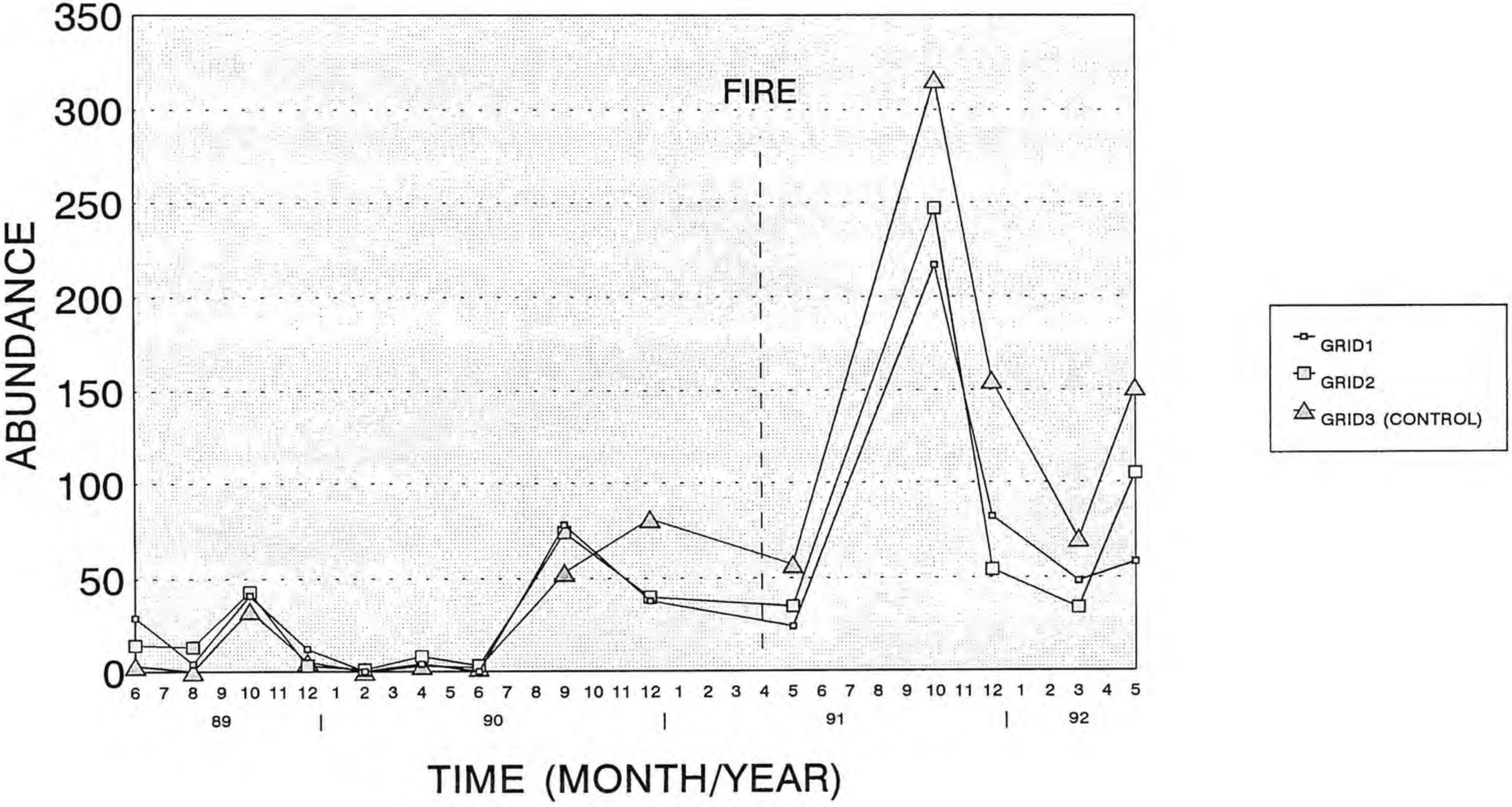

FIG.21 - ABUNDANCE VS TIME

DIPTERA

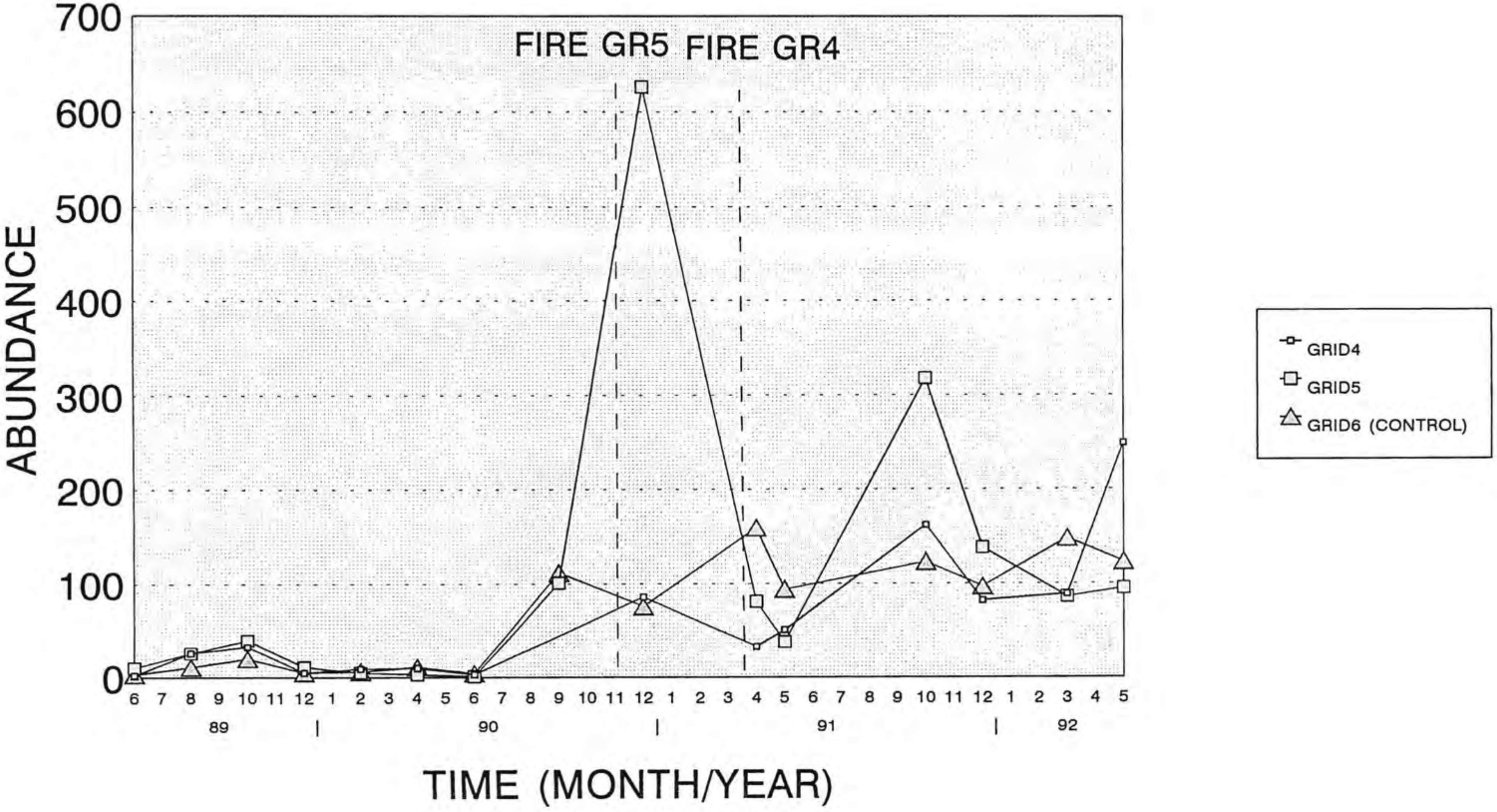

FIG.22 - ABUNDANCE VS TIME

DIPTERA

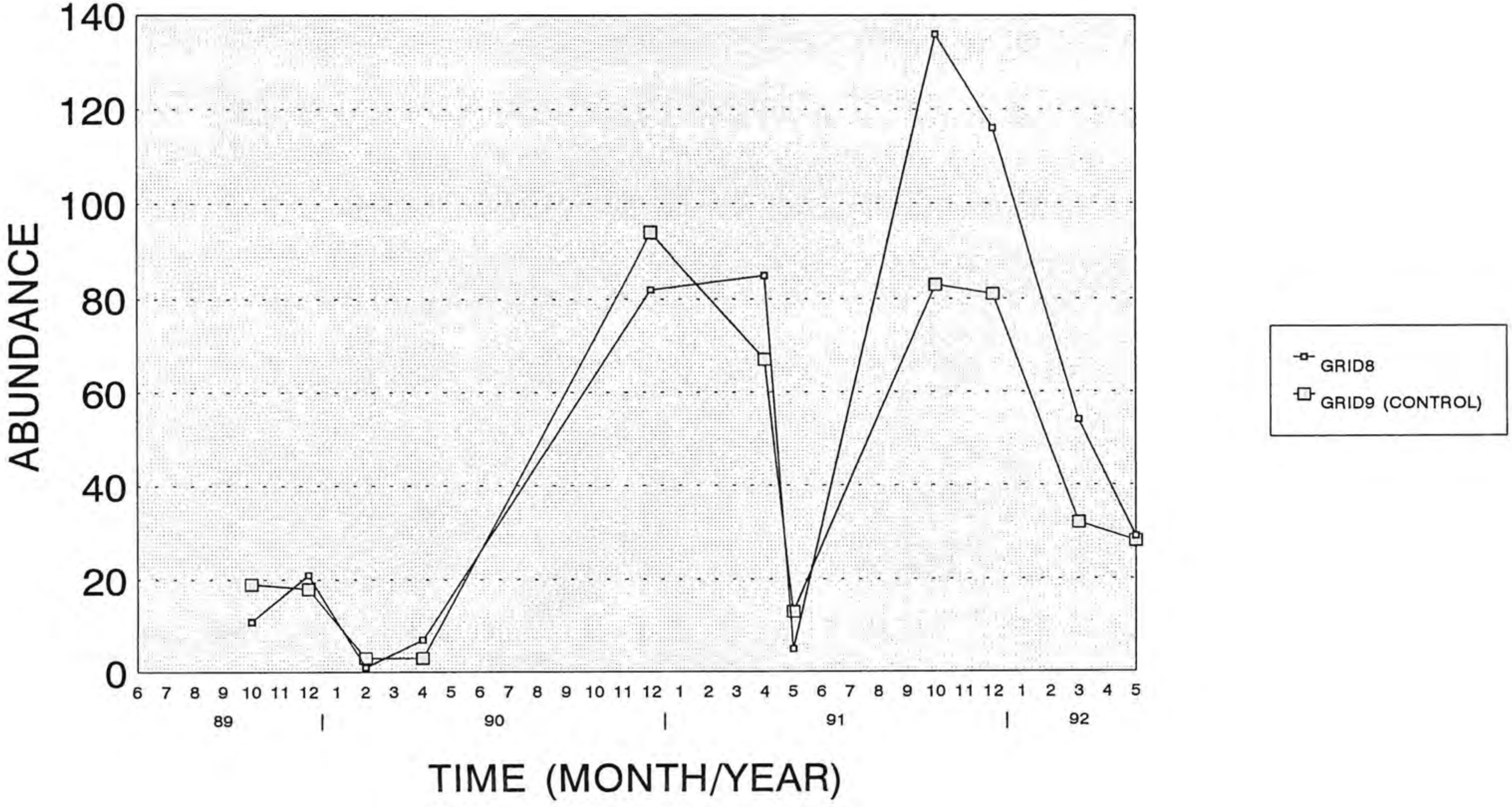

FIG.23 - ABUNDANCE VS TIME

DIPTERA

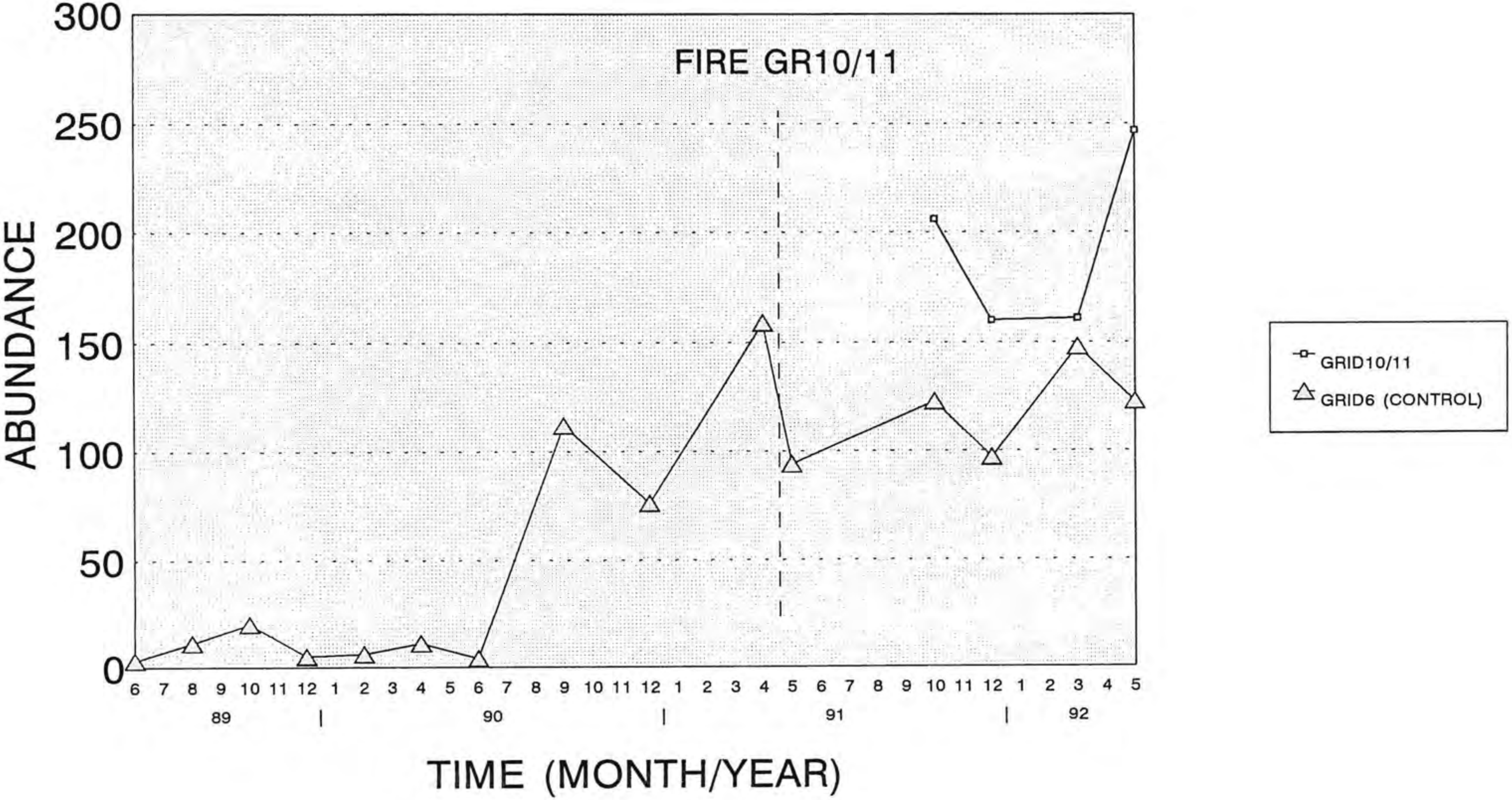

FIG. 24 - MEAN ABUNDANCE v AGE OF STAND

DIPTERA

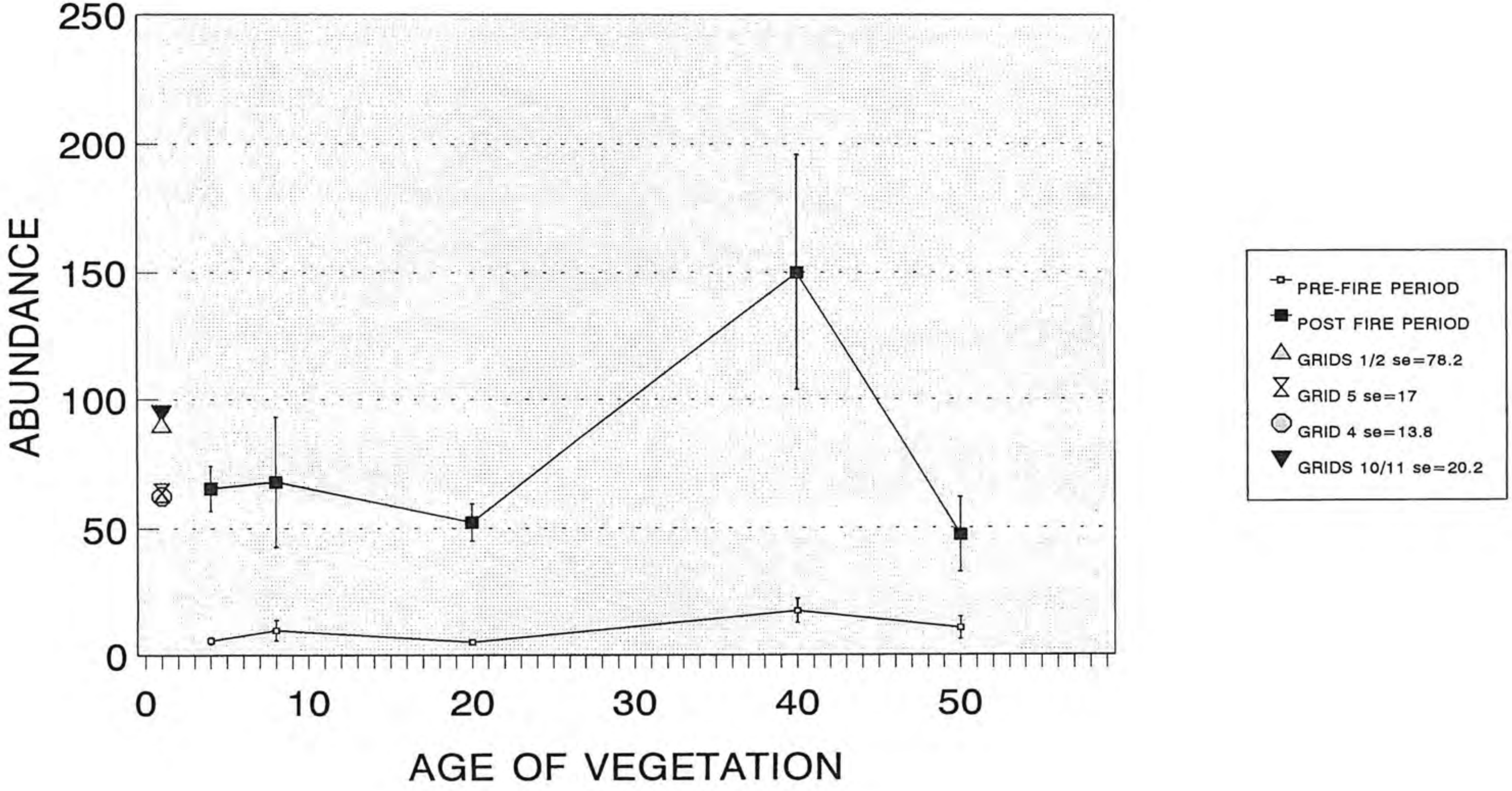

FIG.25 - ABUNDANCE VS TIME

HEMIPTERA

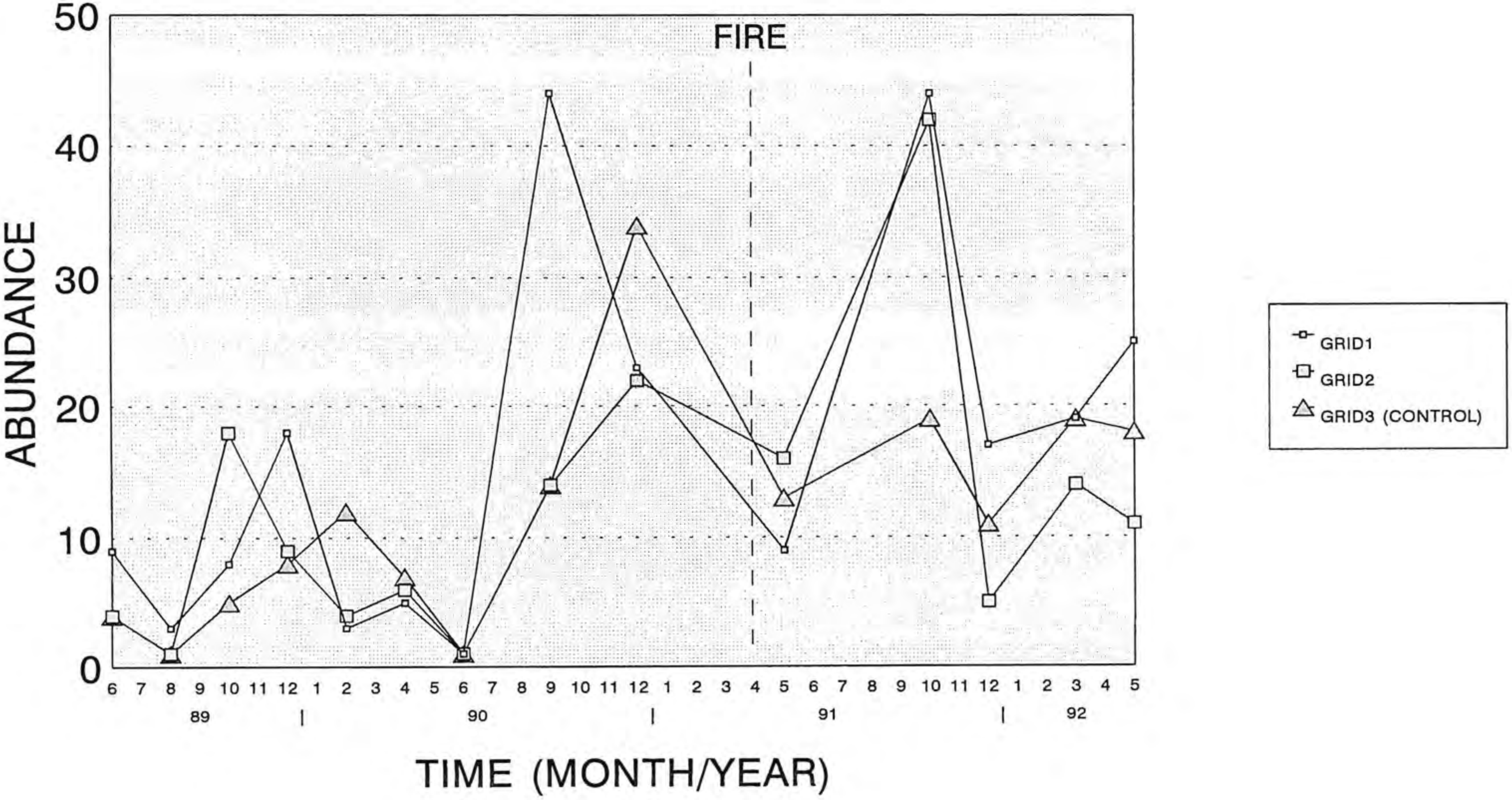

FIG.26 - ABUNDANCE VS TIME

HEMIPTERA

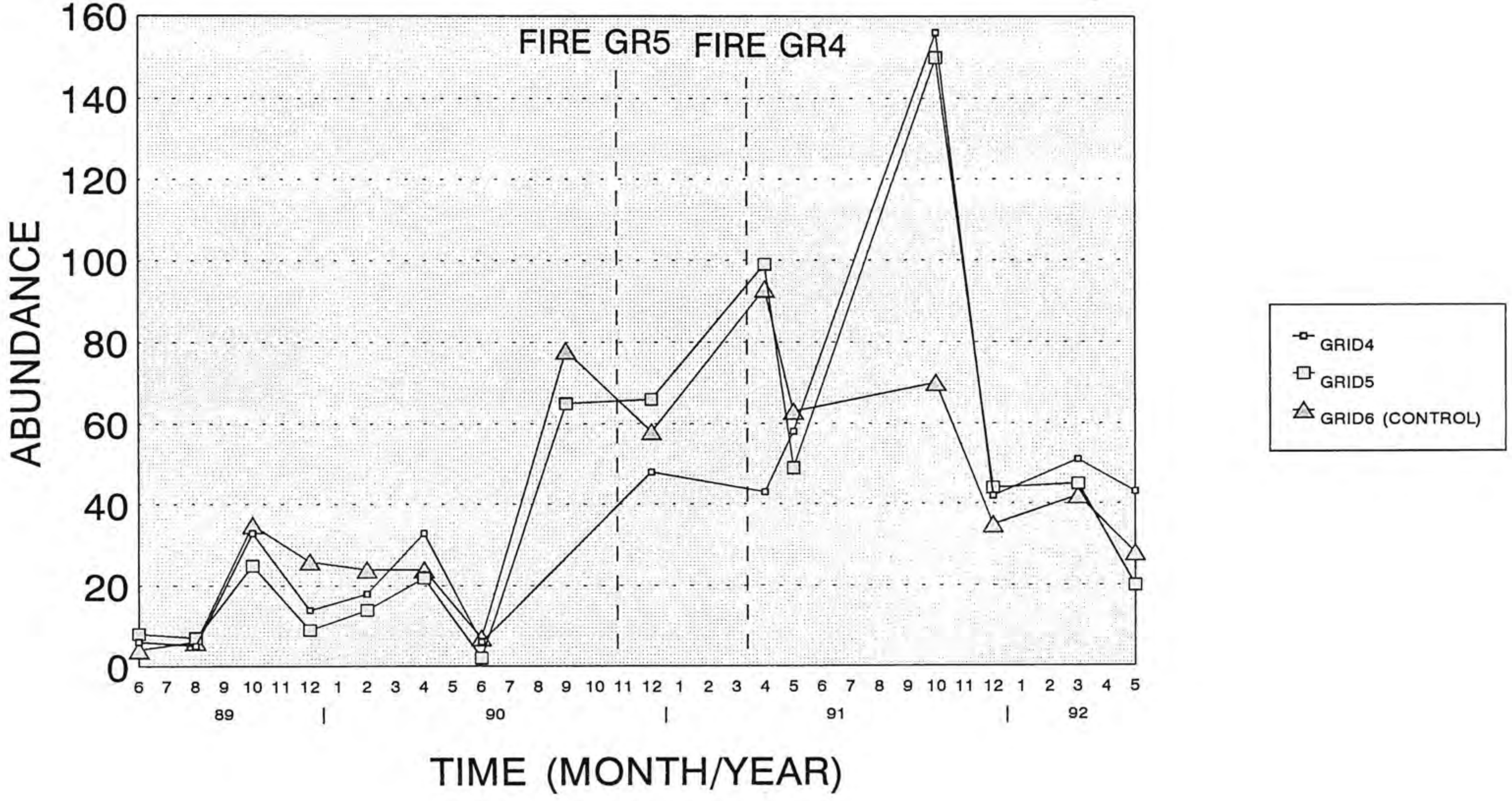

FIG.27 - ABUNDANCE VS TIME

HEMIPTERA

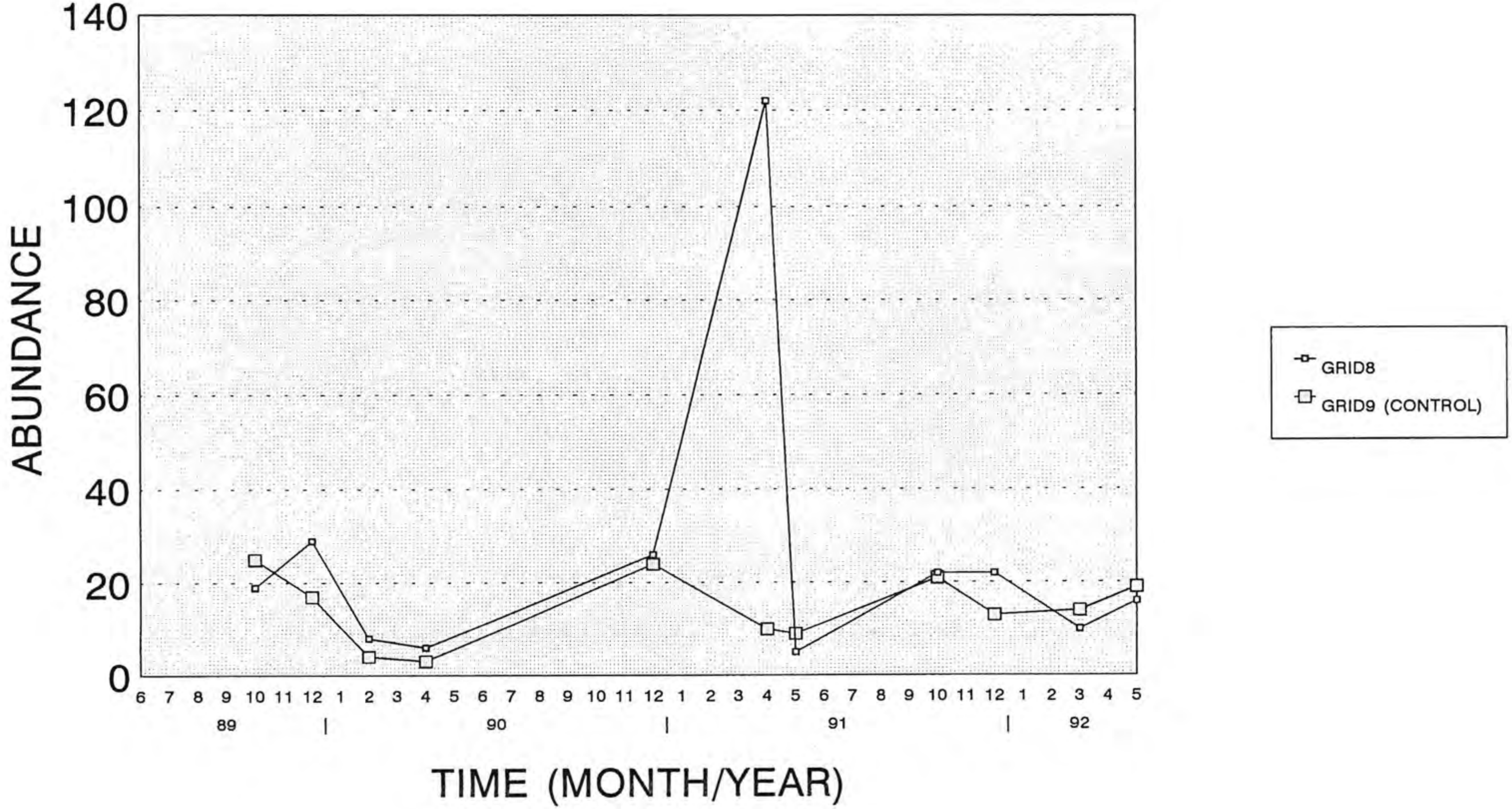

FIG.28 - ABUNDANCE VS TIME

HEMIPTERA

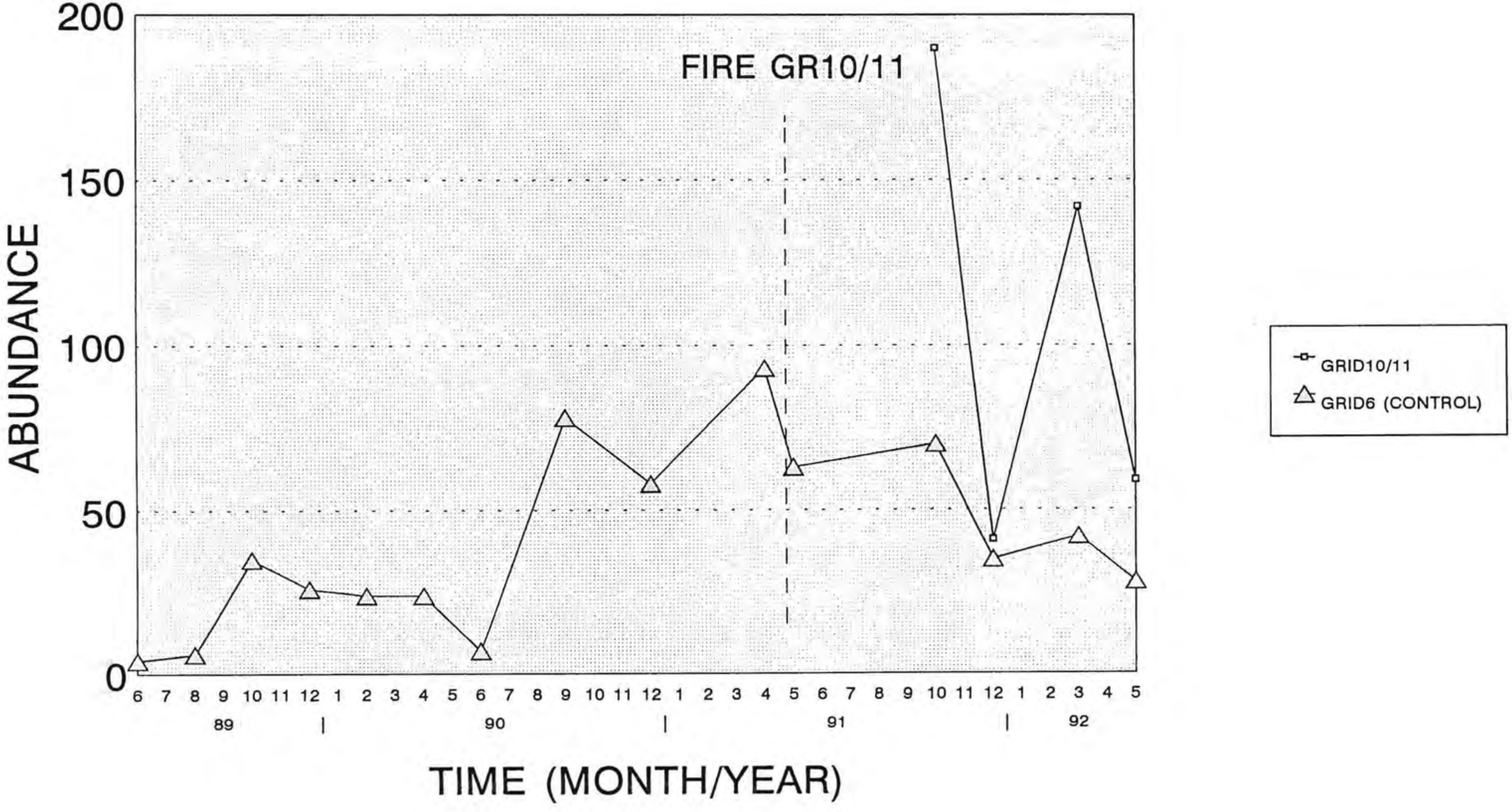

FIG.29 - MEAN ABUNDANCE v AGE OF STAND

HEMIPTERA

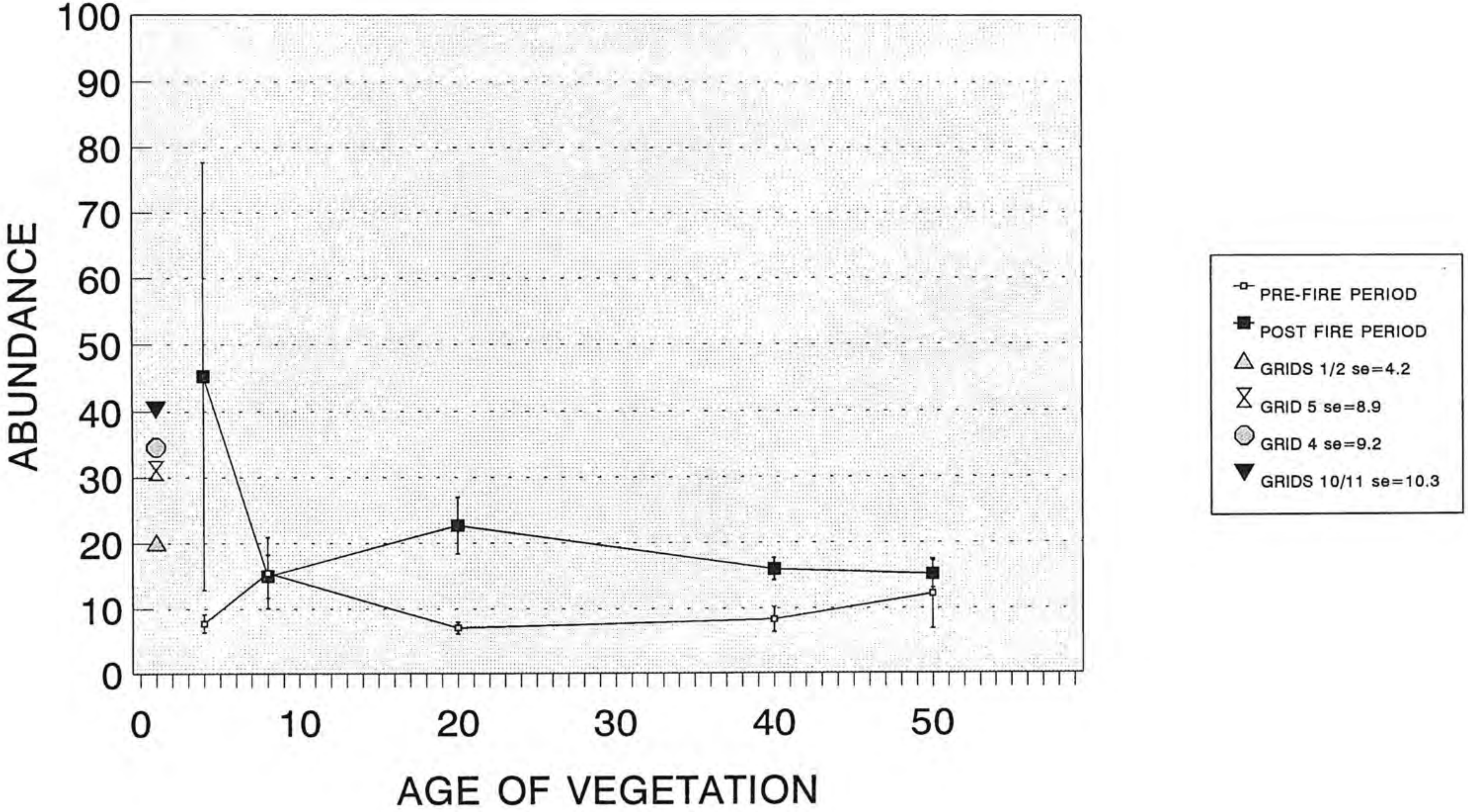

FIG.30 - ABUNDANCE VS TIME
HYMENOPTERA

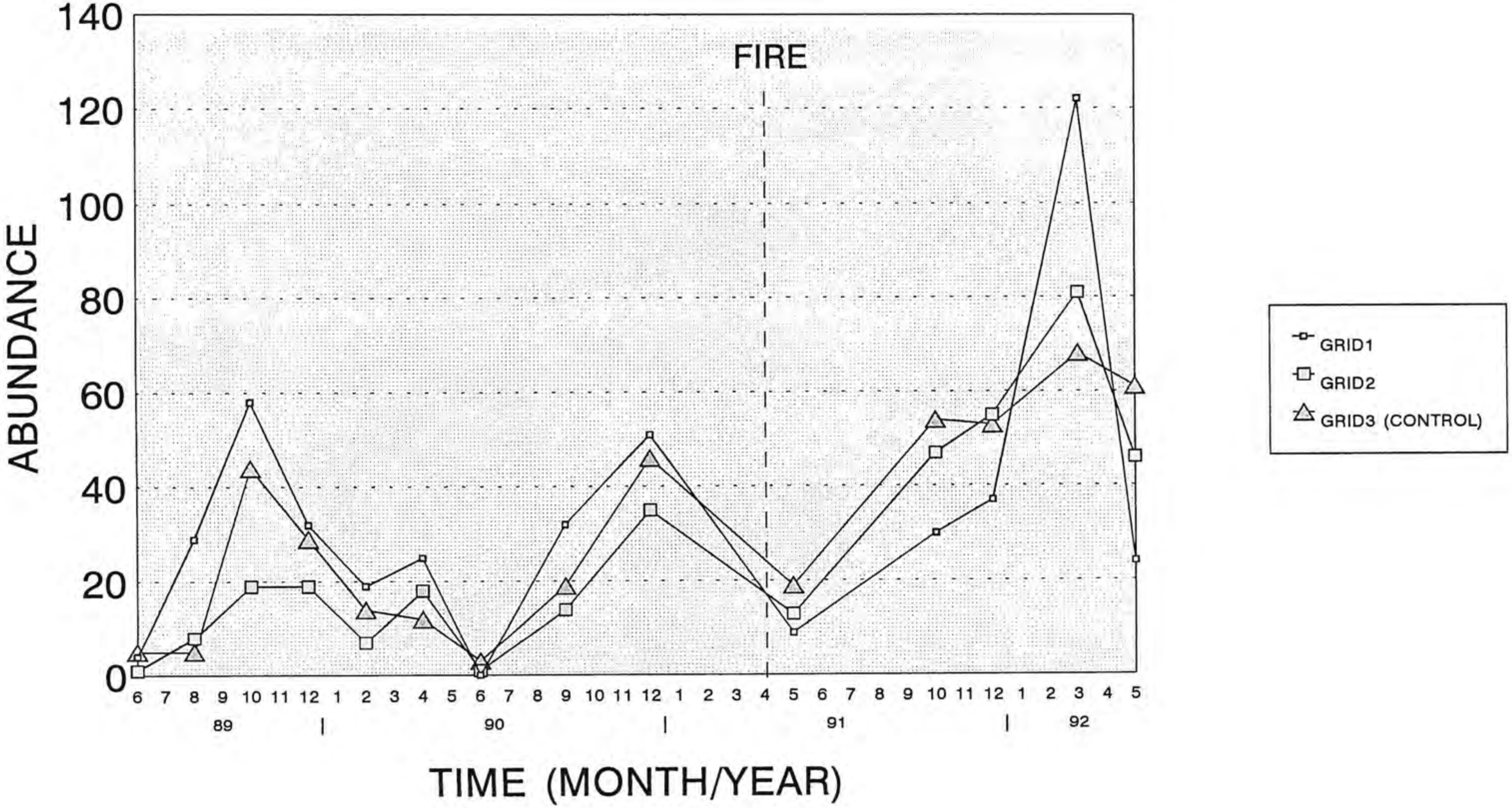

FIG.31 - ABUNDANCE VS TIME

HYMENOPTERA

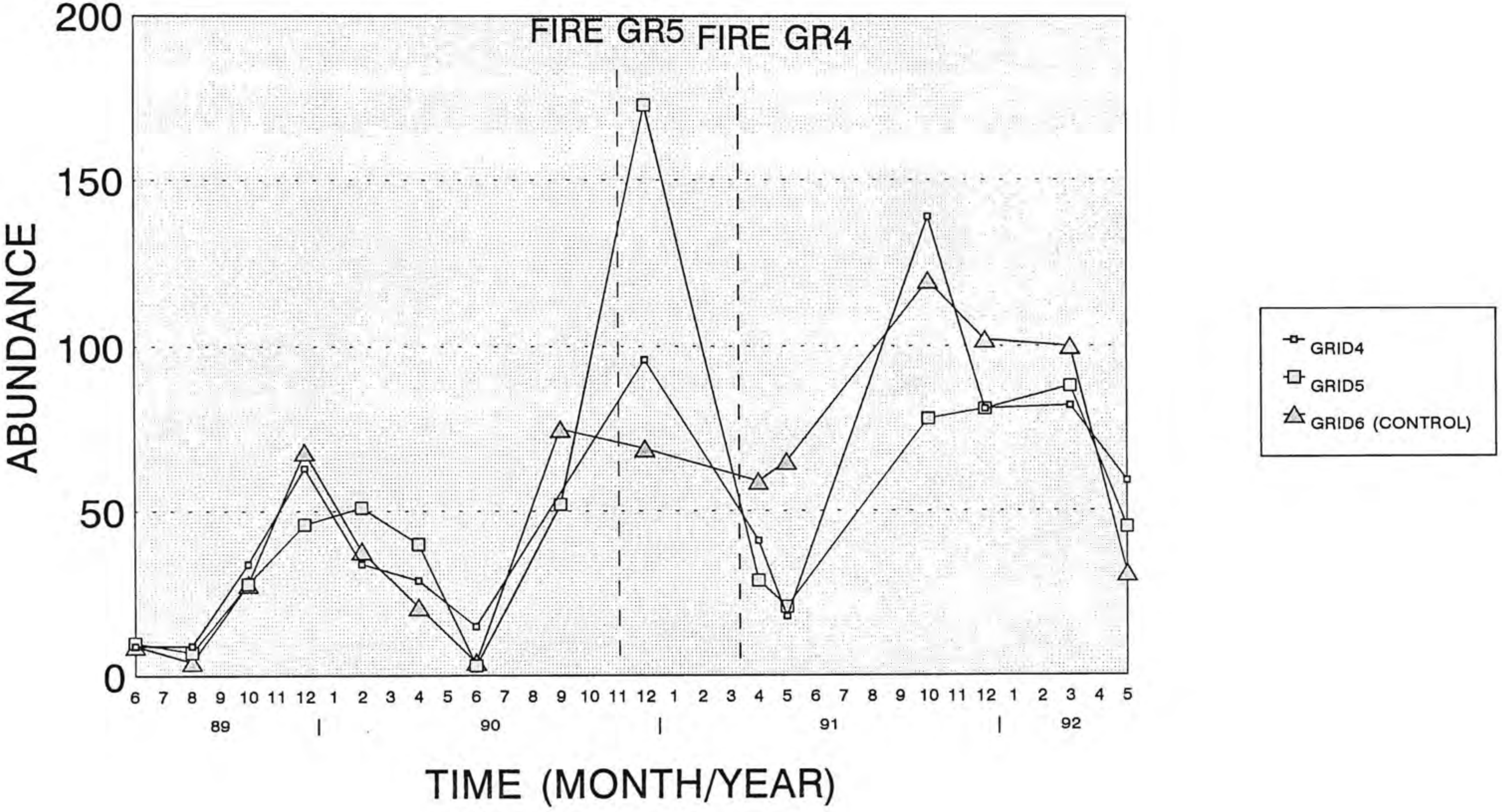

FIG.32 - ABUNDANCE VS TIME
HYMENOPTERA

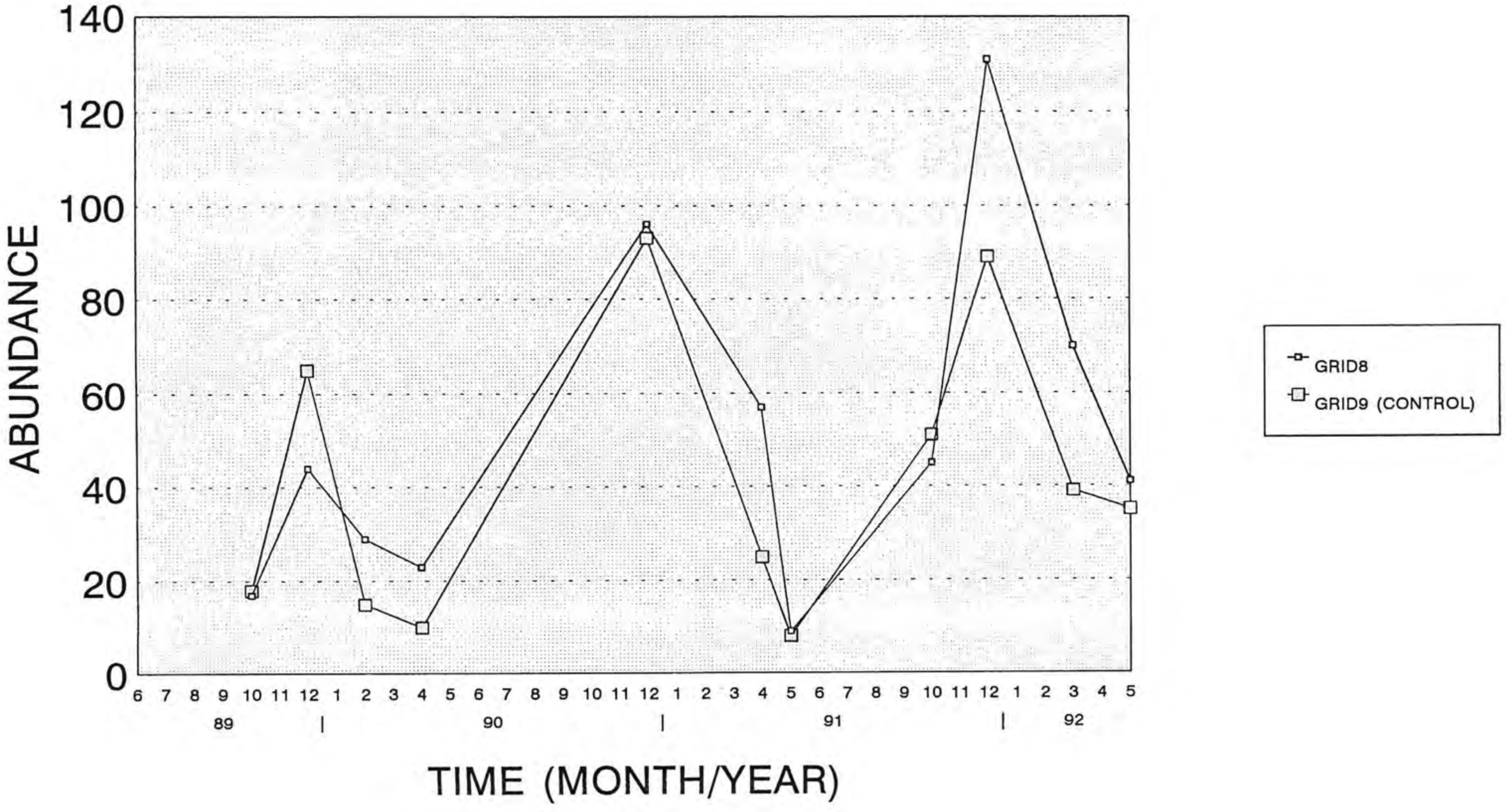

FIG.33 - ABUNDANCE VS TIME

HYMENOPTERA

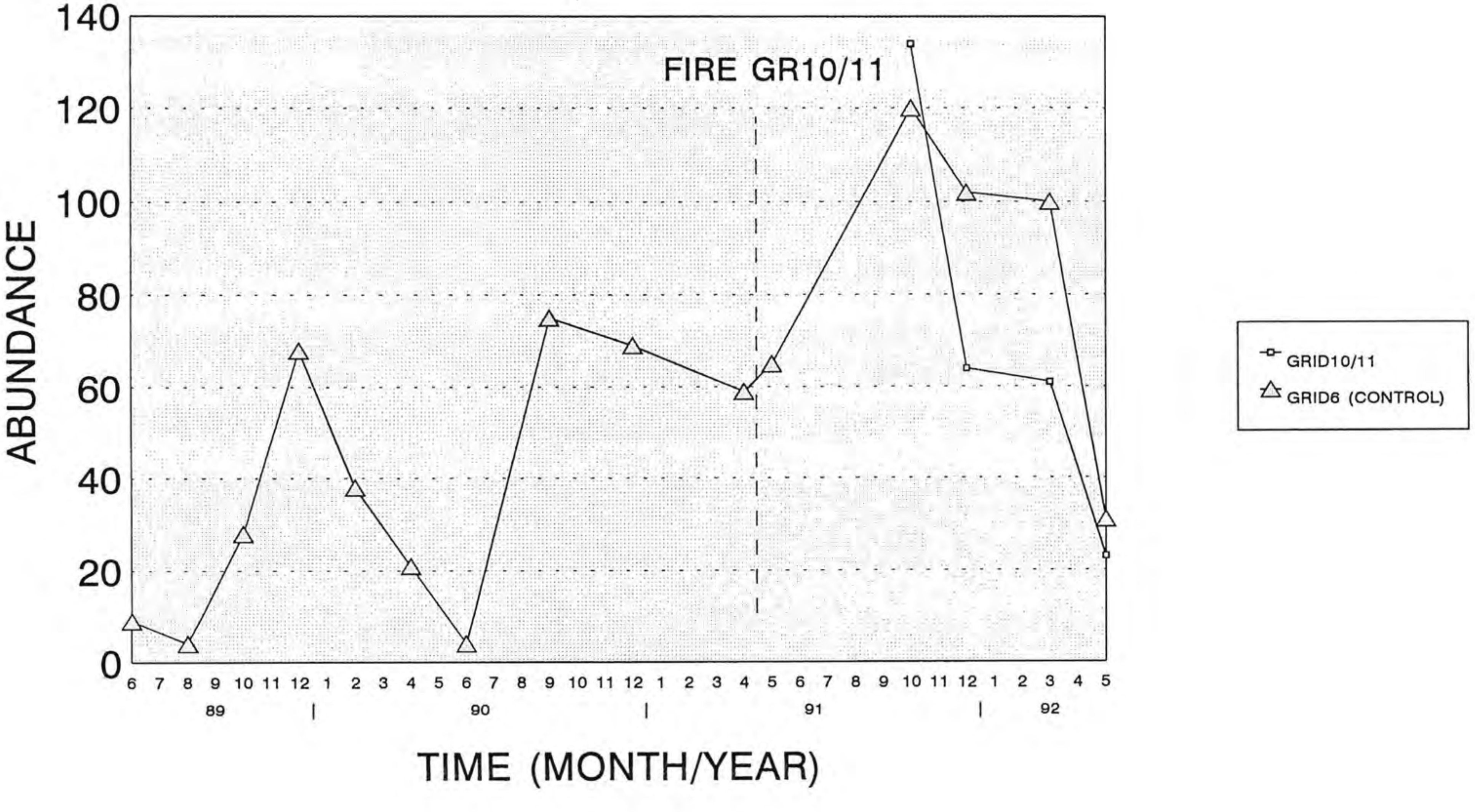

FIG.34 - MEAN ABUNDANCE v AGE OF STAND

HYMENOPTERA

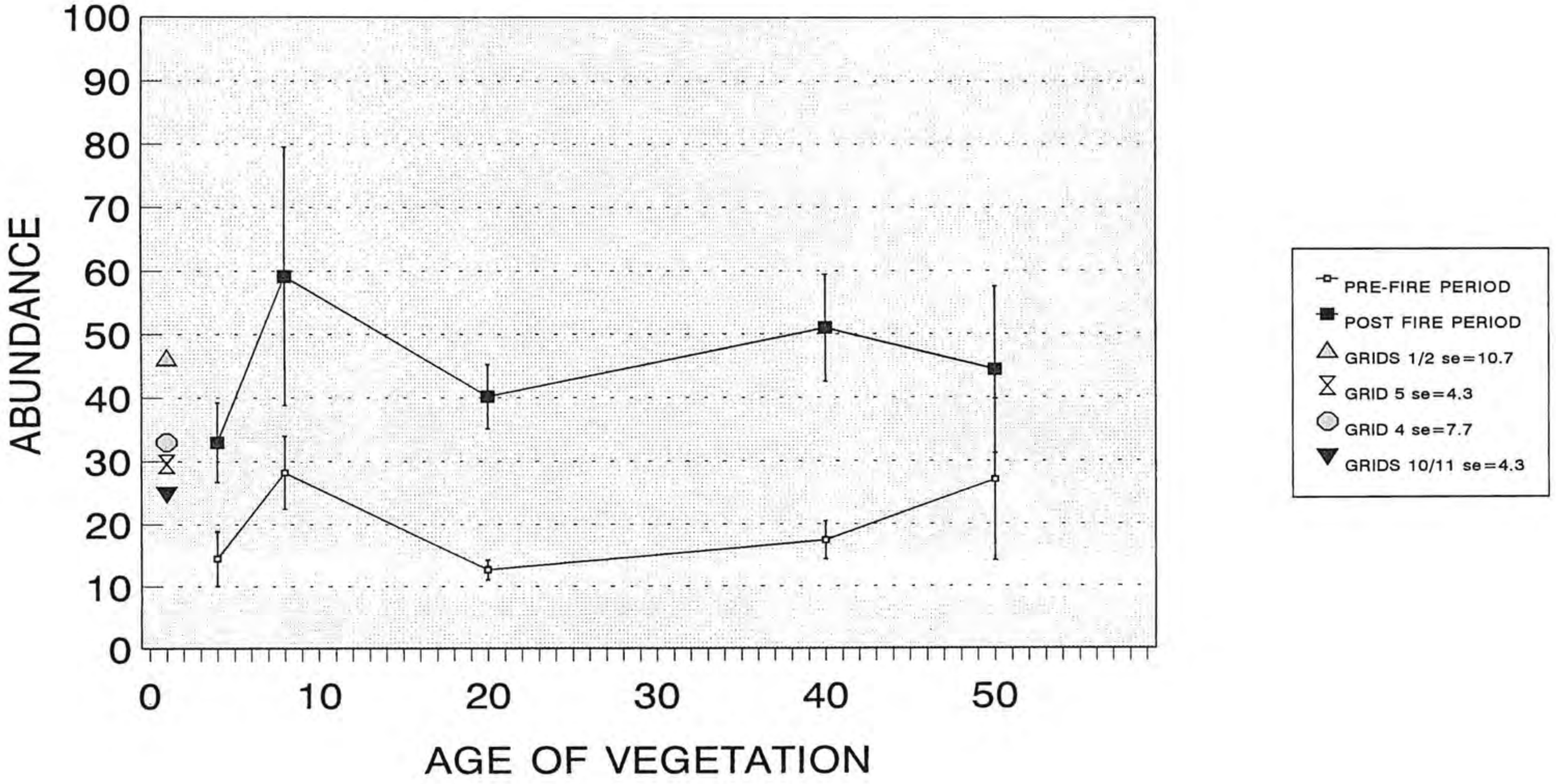

FIG.35 - ABUNDANCE VS TIME

ORTHOPTERA

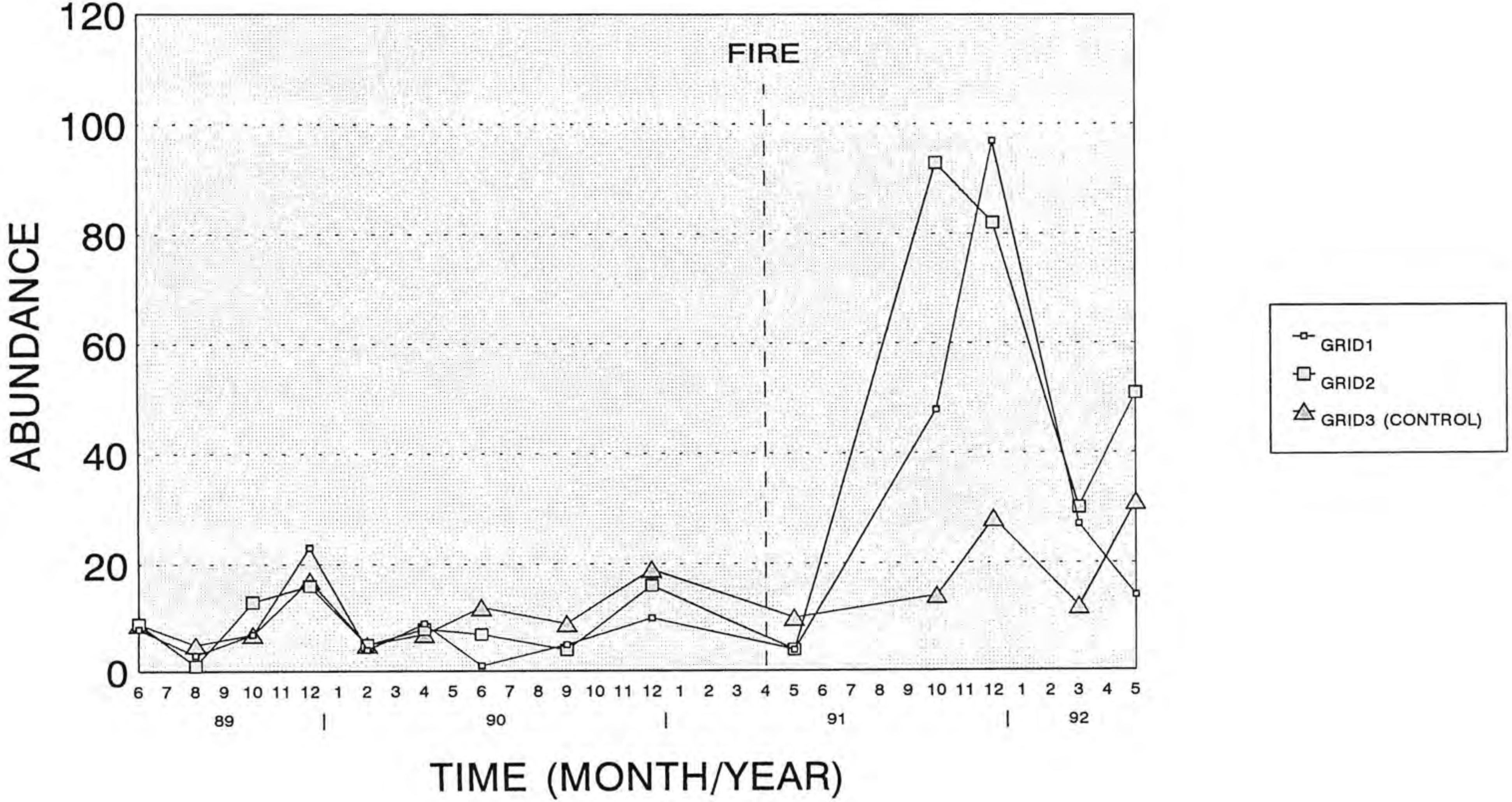

FIG.36 - ABUNDANCE VS TIME

ORTHOPTERA

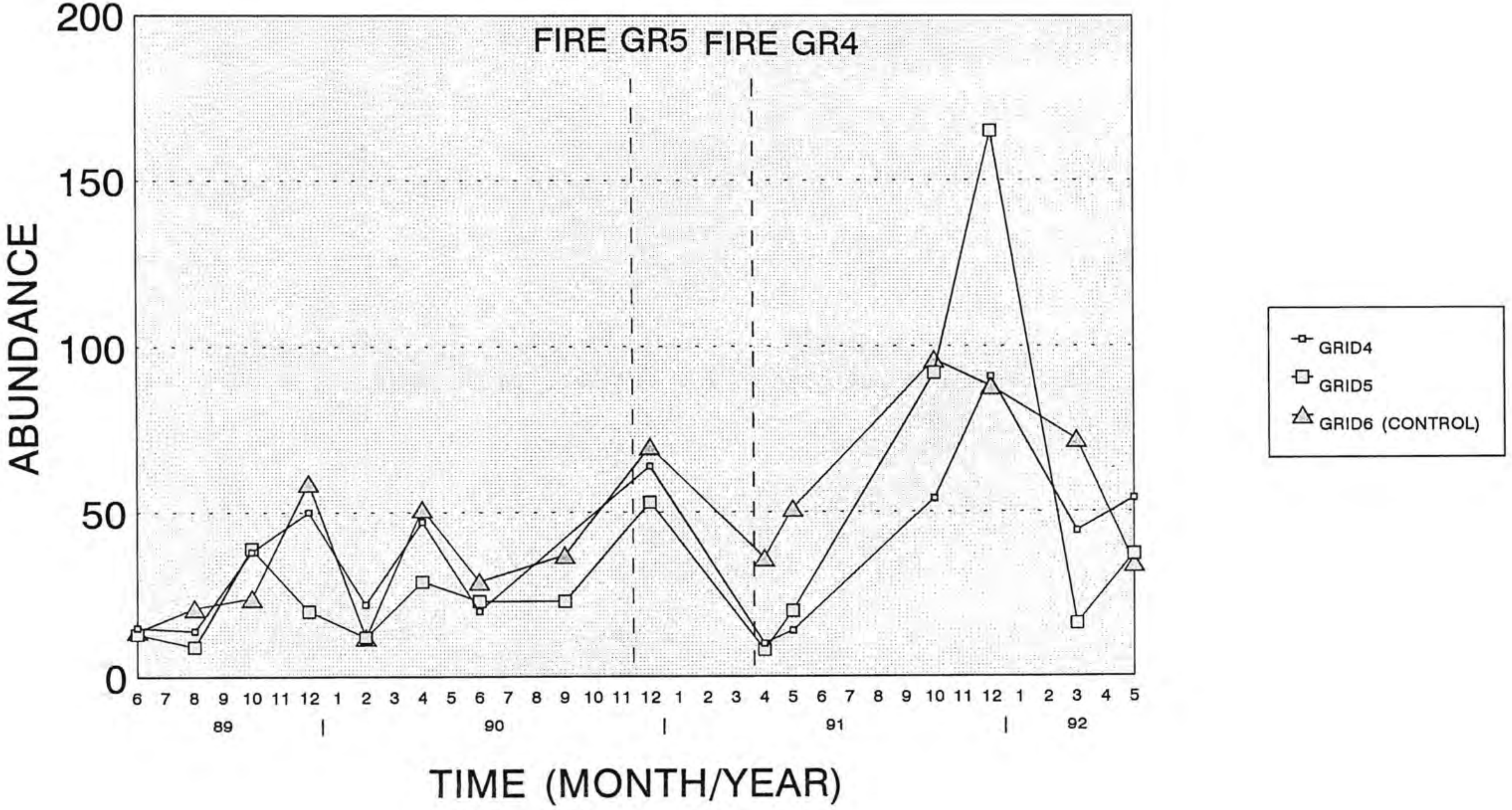

FIG.37 - ABUNDANCE VS TIME

ORTHOPTERA

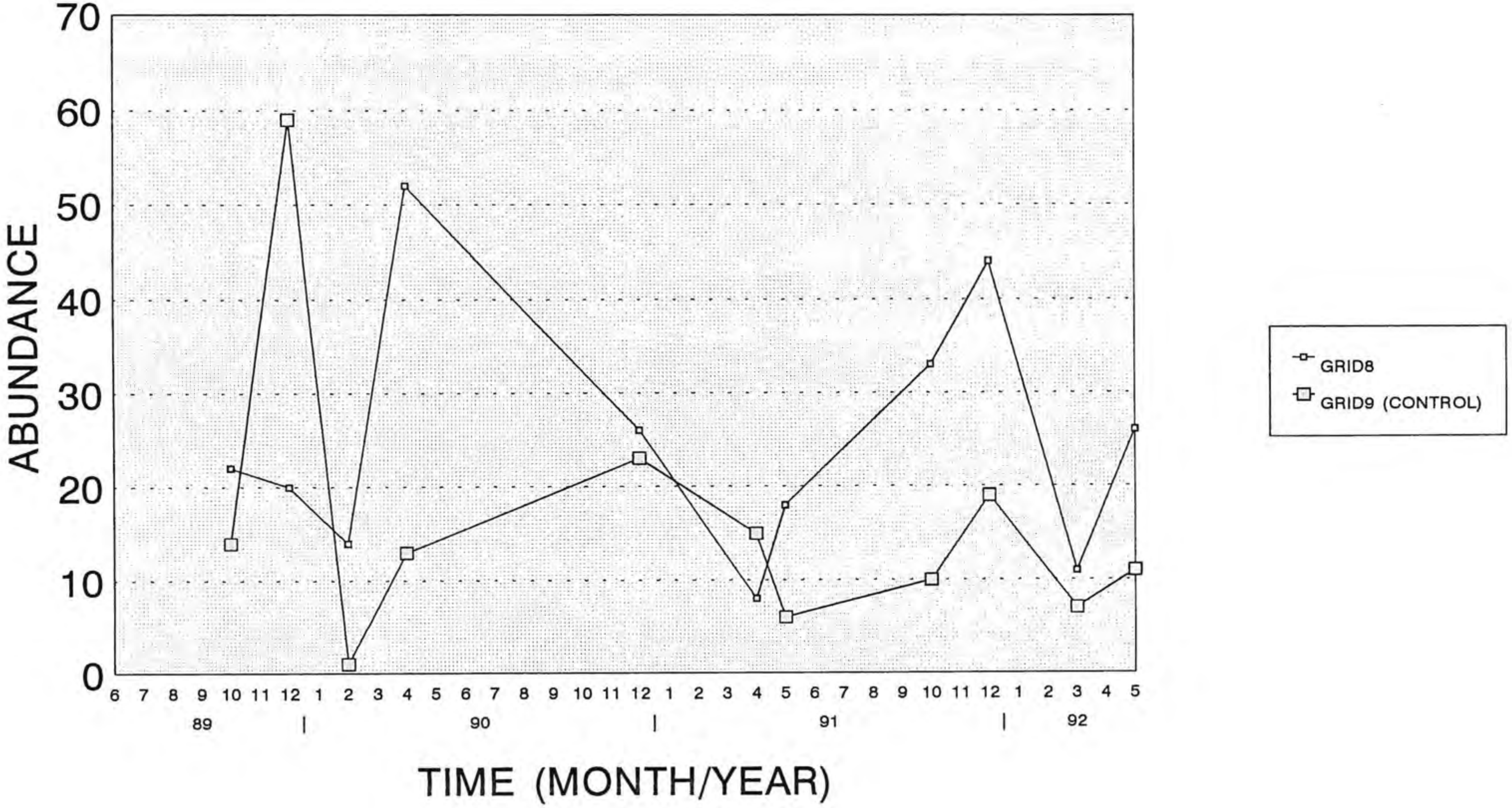

FIG.38 - ABUNDANCE VS TIME

ORTHOPTERA

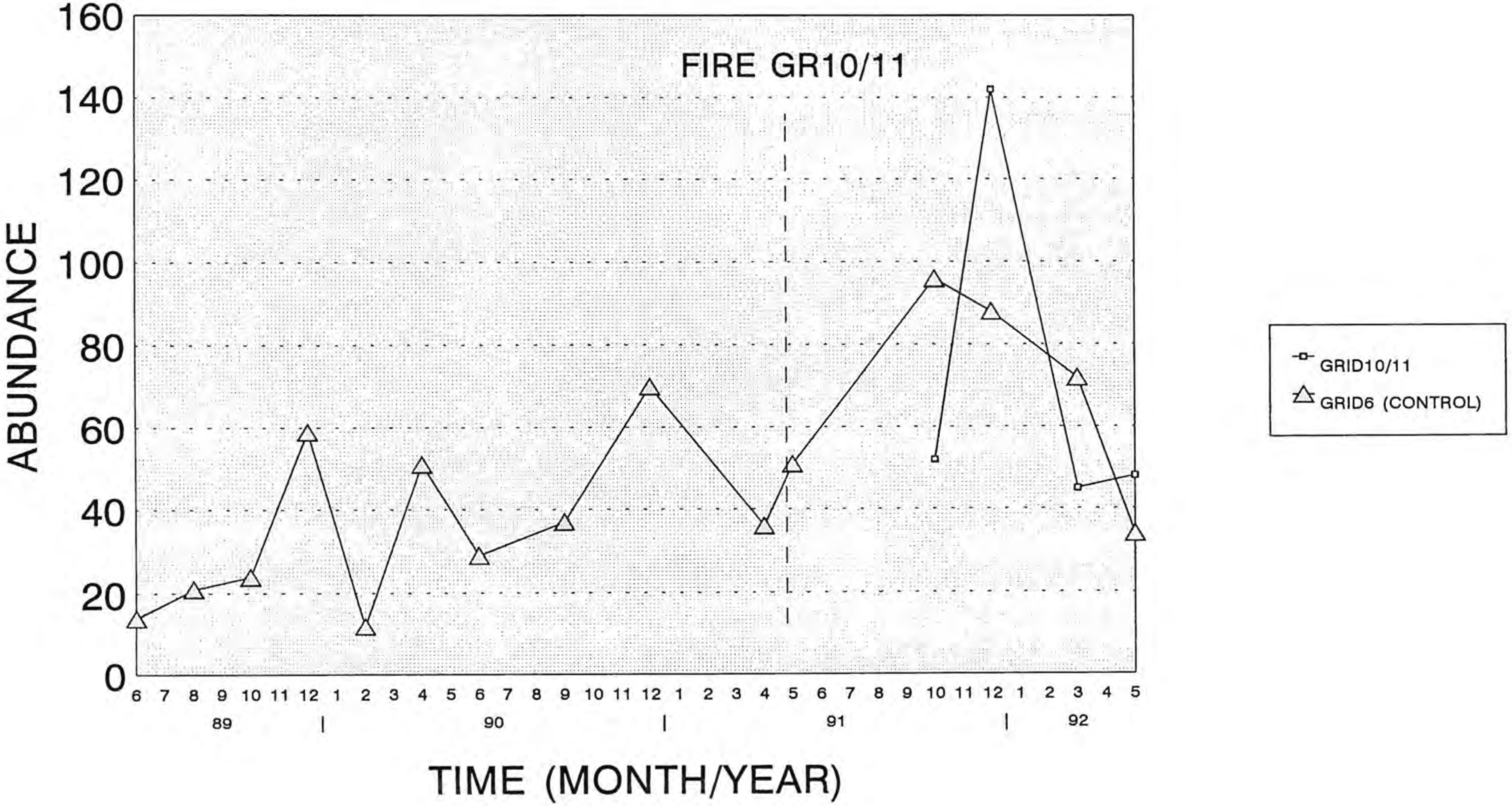

FIG.39 - MEAN ABUNDANCE v AGE OF STAND
ORTHOPTERA

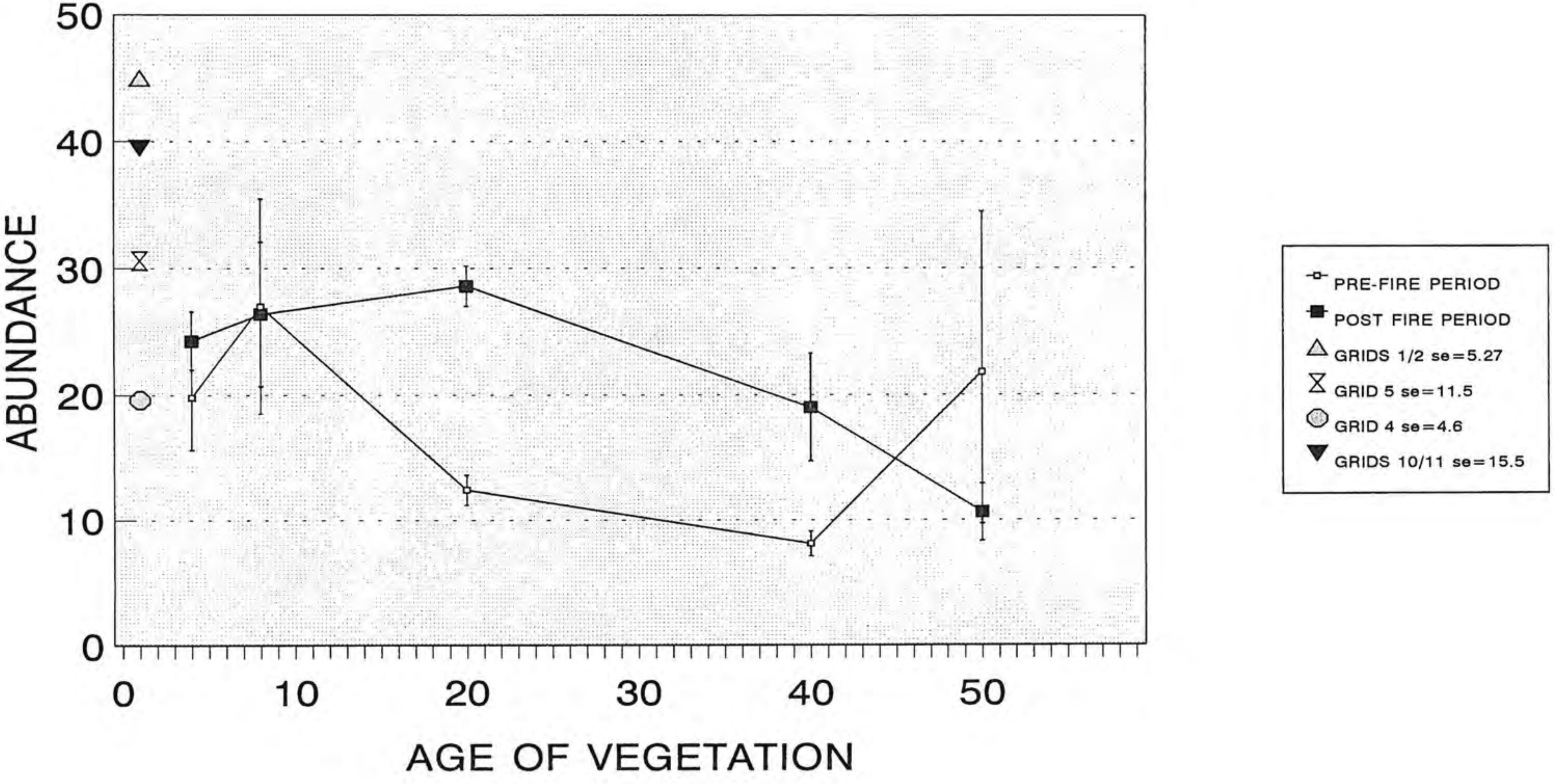

FIG.40 - ABUNDANCE VS TIME

ARANEAE

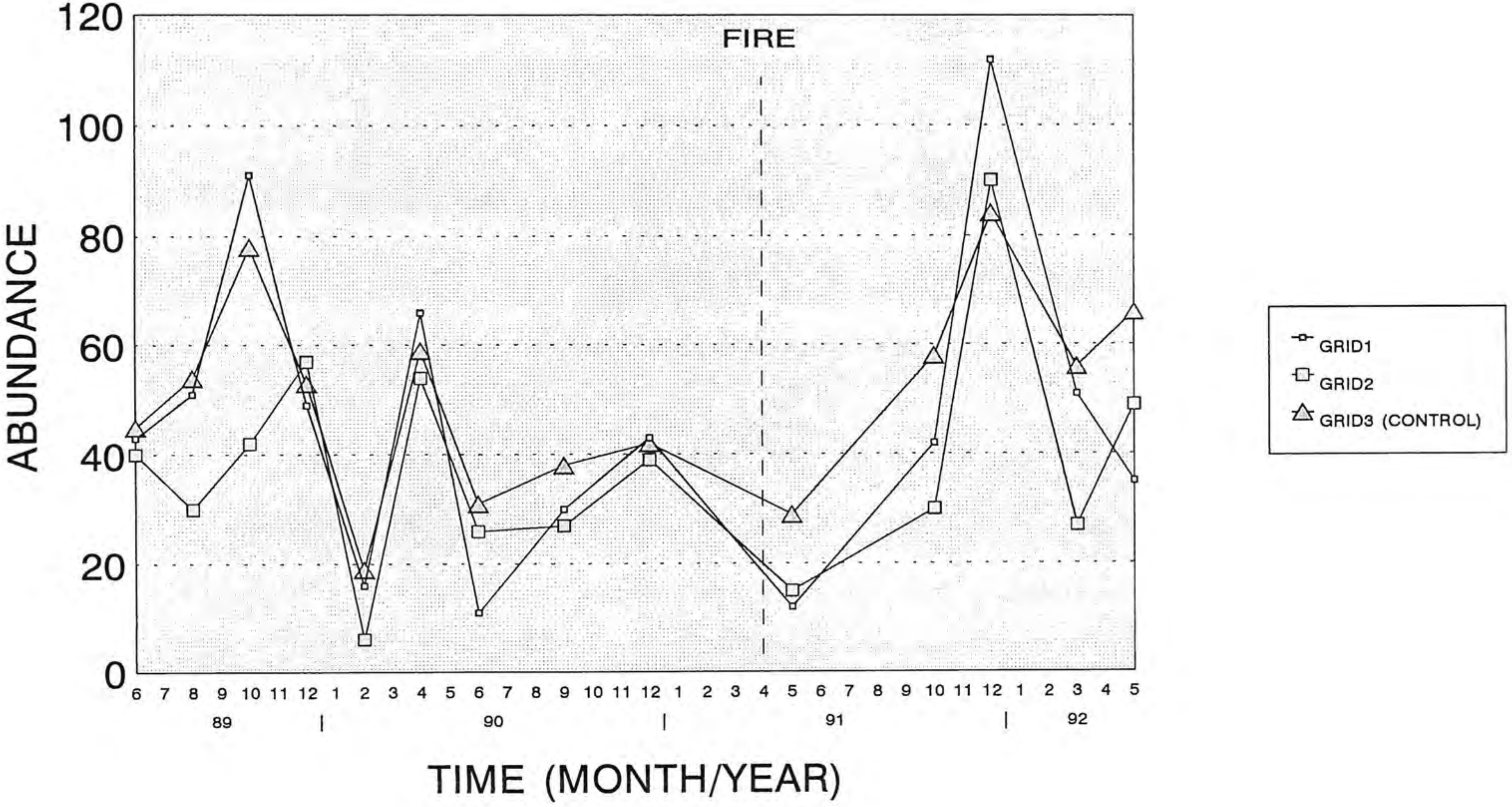

FIG.41 - ABUNDANCE VS TIME

ARANEAE

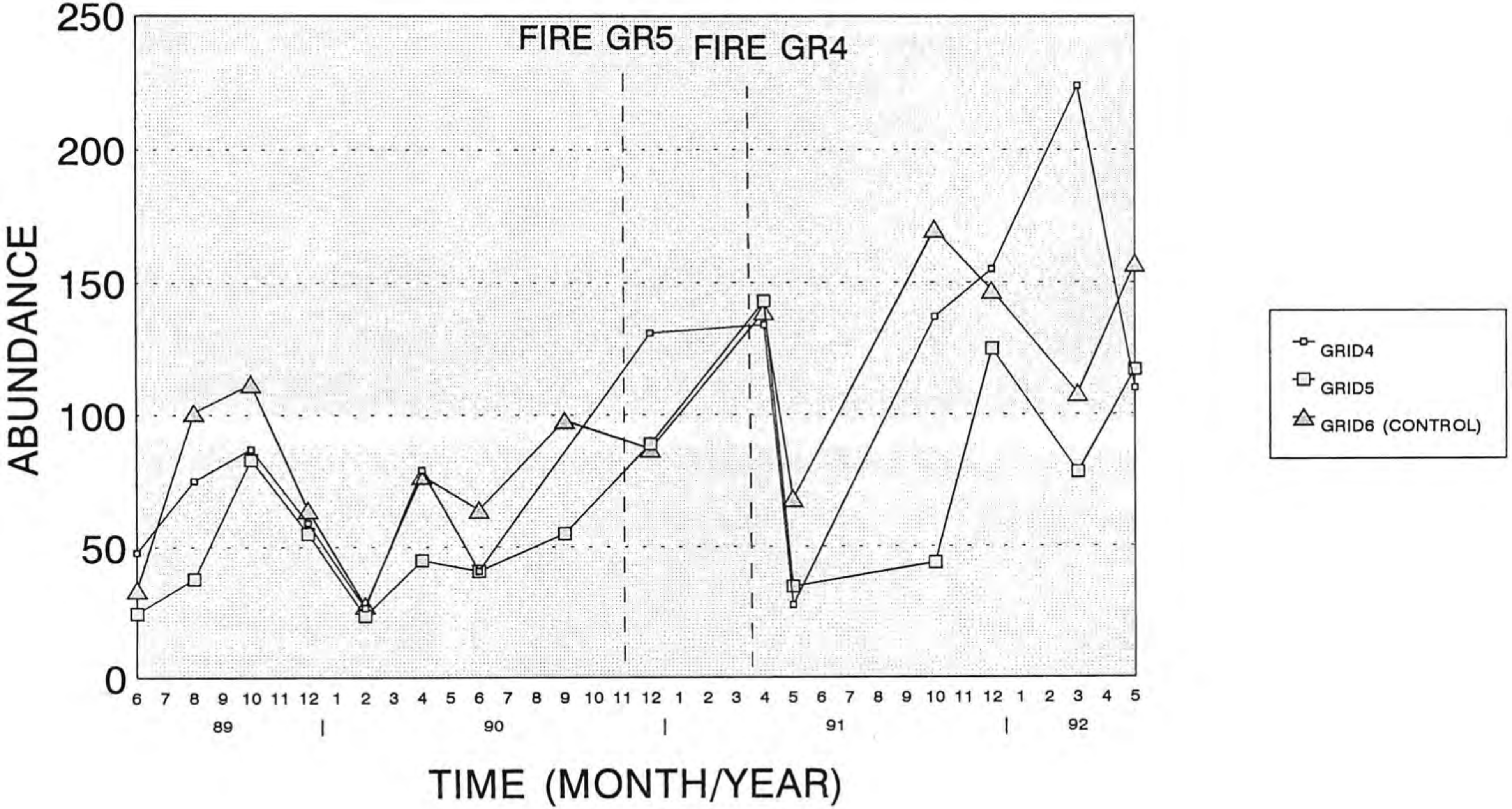

FIG.42 - ABUNDANCE VS TIME

ARANEAE

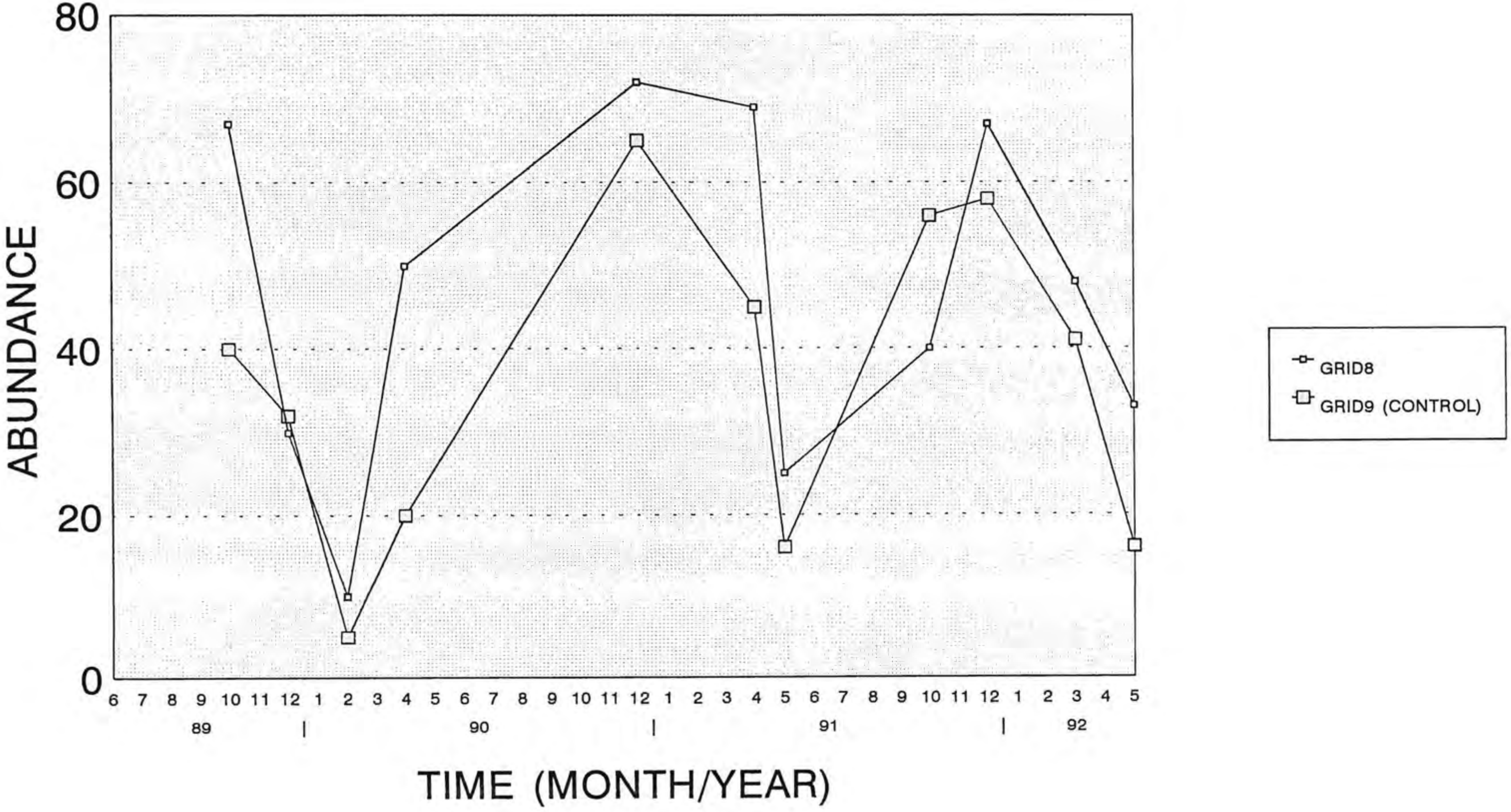

FIG.43 - ABUNDANCE VS TIME

ARANEAE

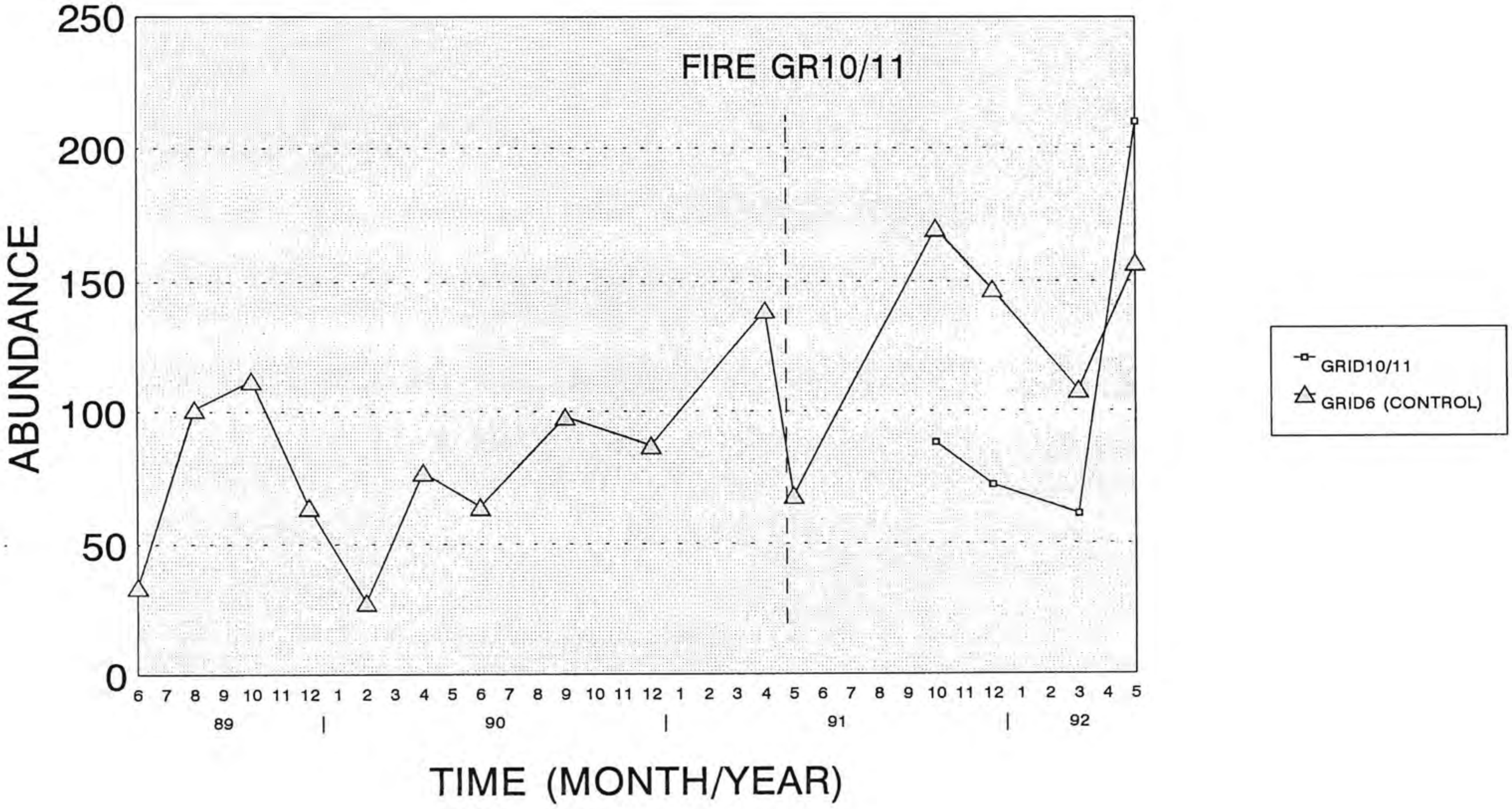

FIG.44 - MEAN ABUNDANCE v AGE OF STAND

ARANEAE

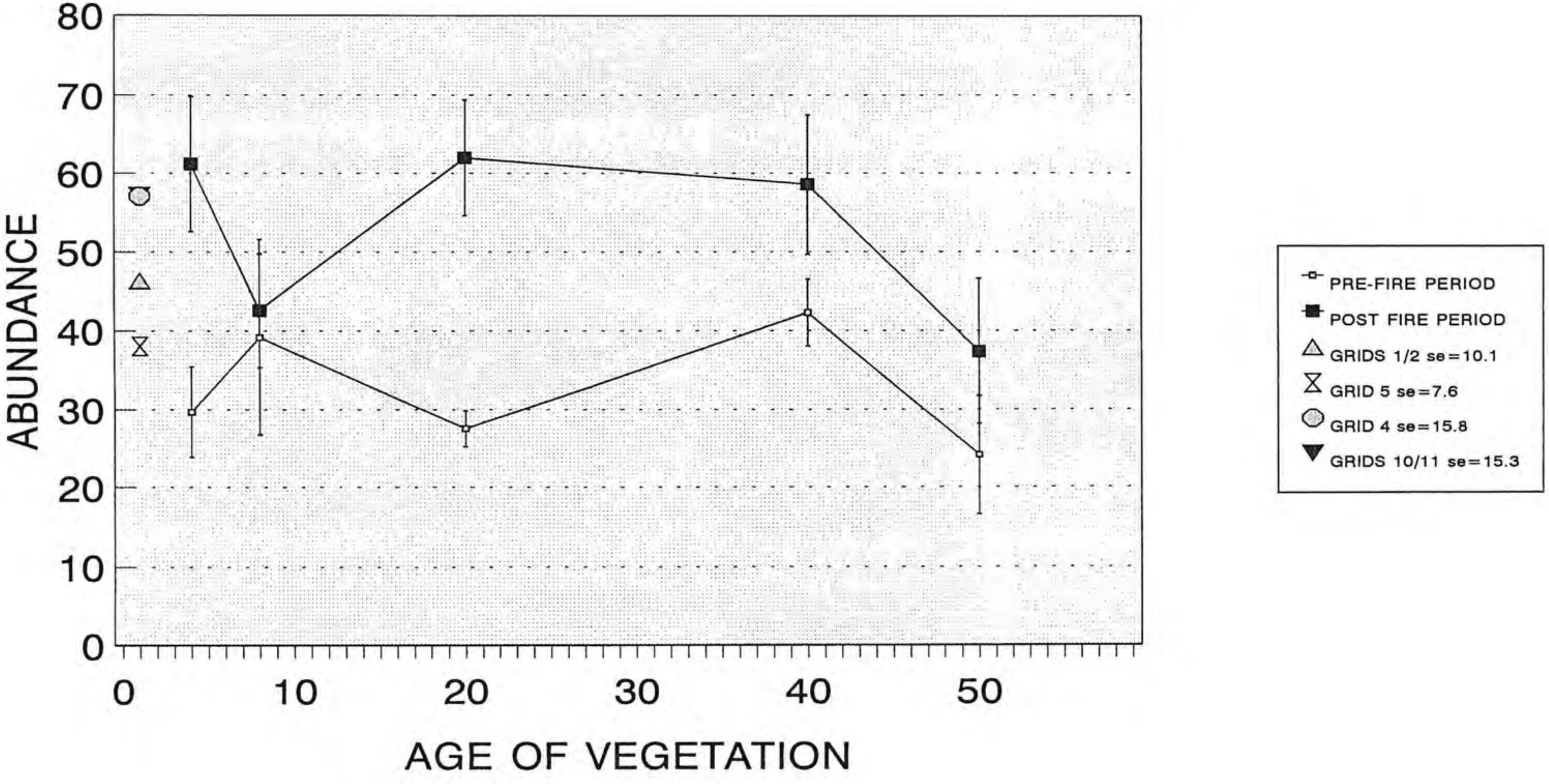

FIG.45 - BRAY-CURTIS DISSIMILARITY, GRIDS 1-3

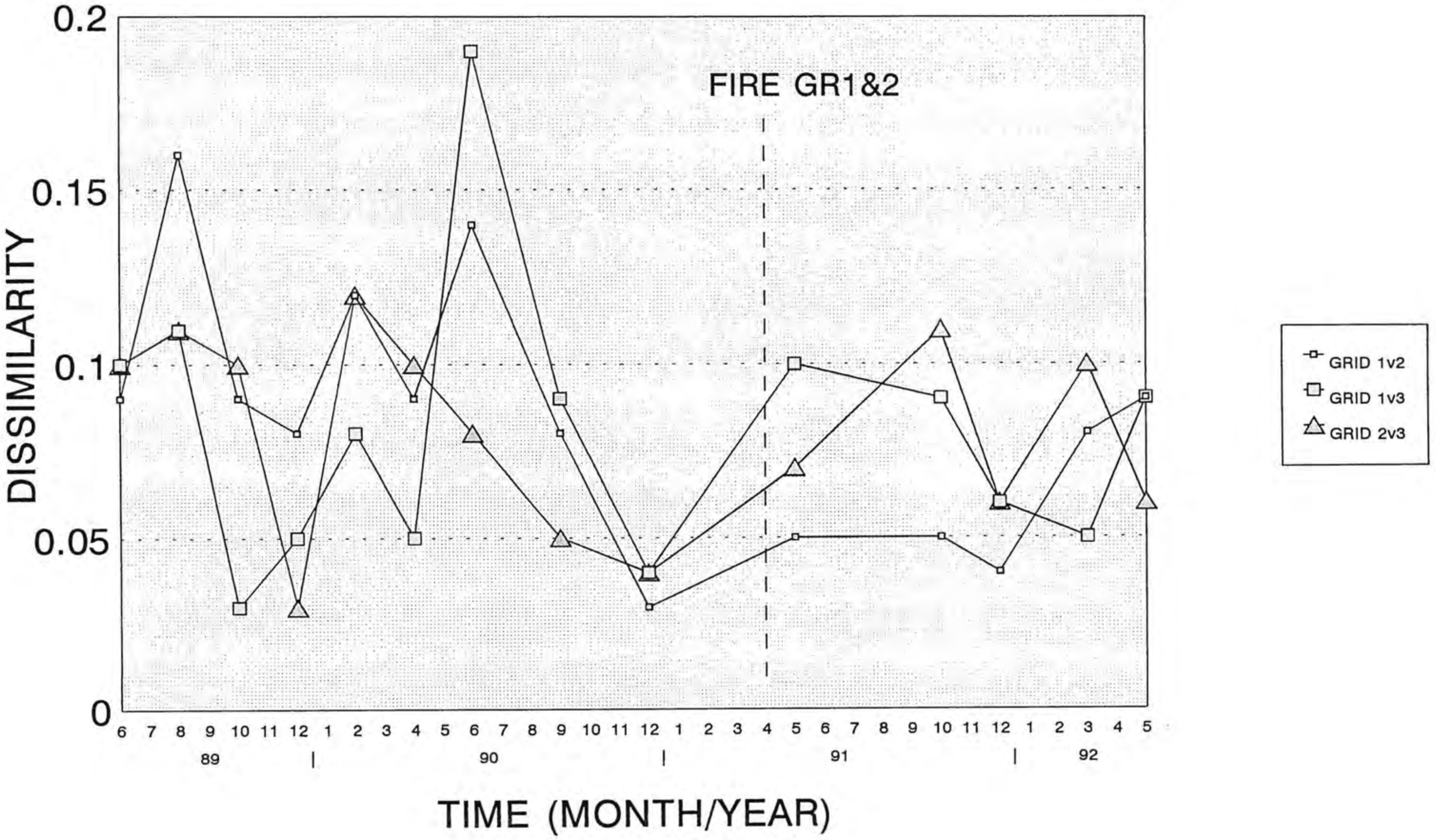

FIG.46 - BRAY-CURTIS DISSIMILARITY, GRIDS 4-6

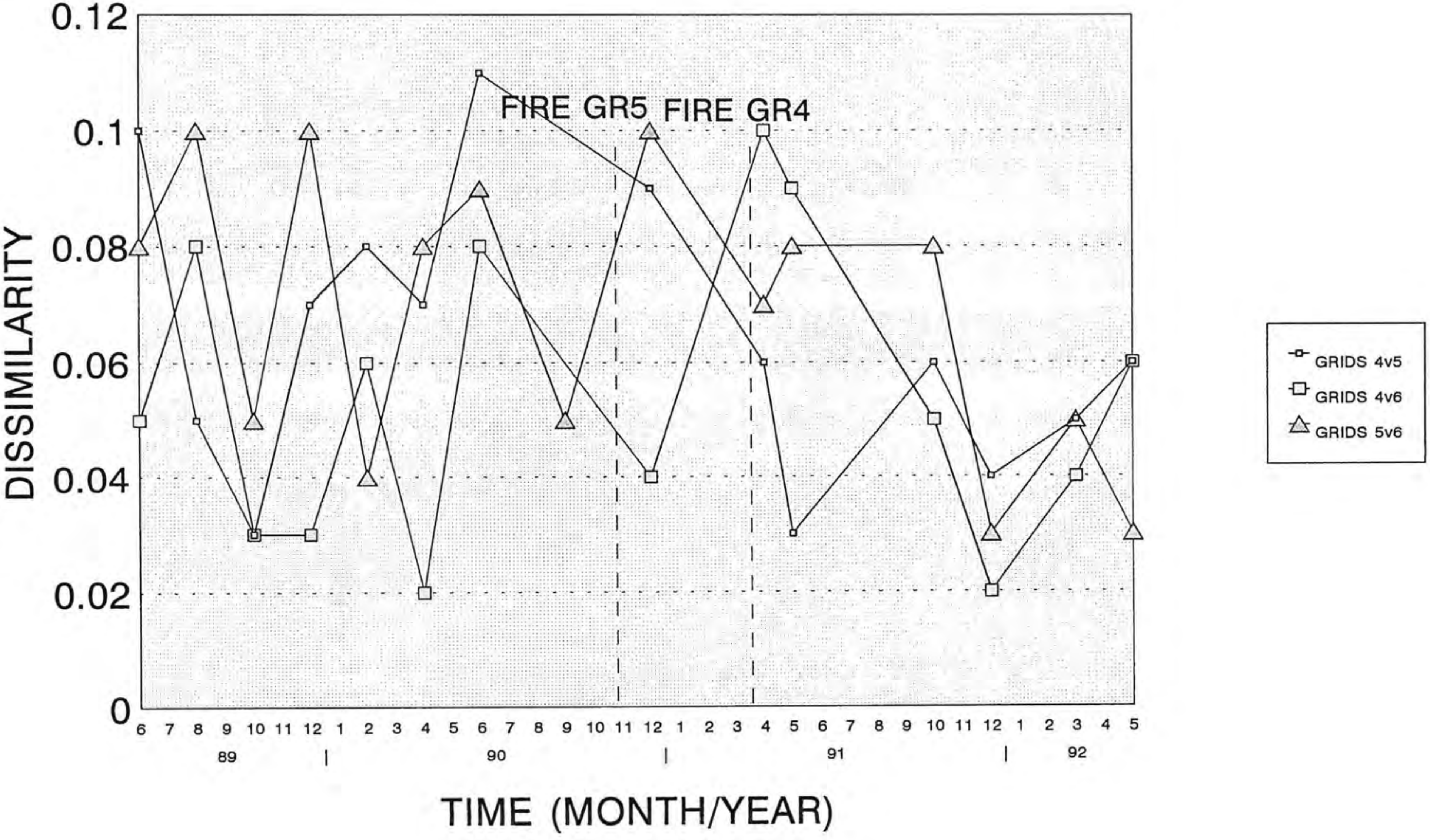

Fig.47. PCA Ordination of sampling occasions by Orders

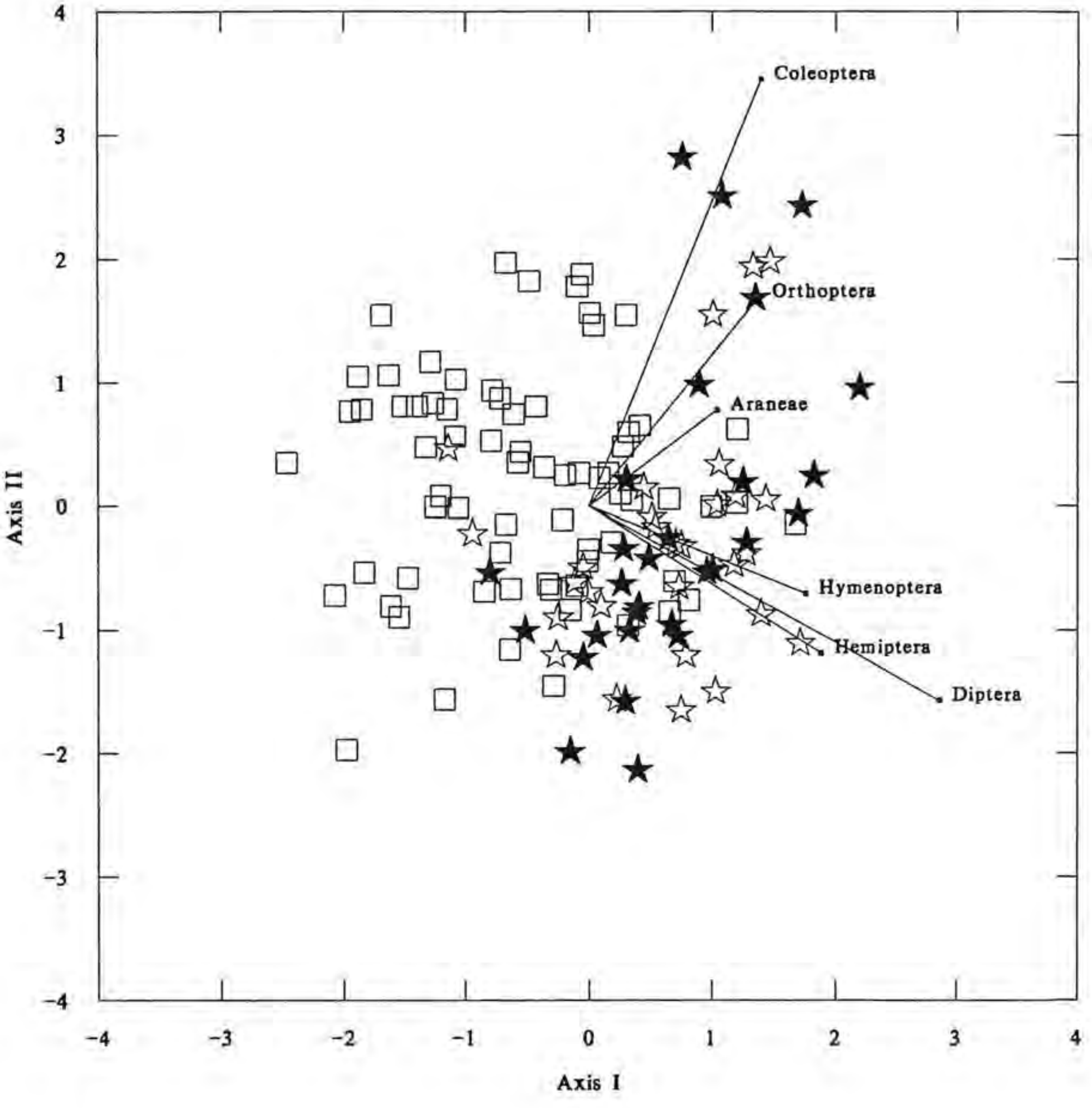

Fig.48. PCA Ordination of sampling occasions by Orders, doubly centered

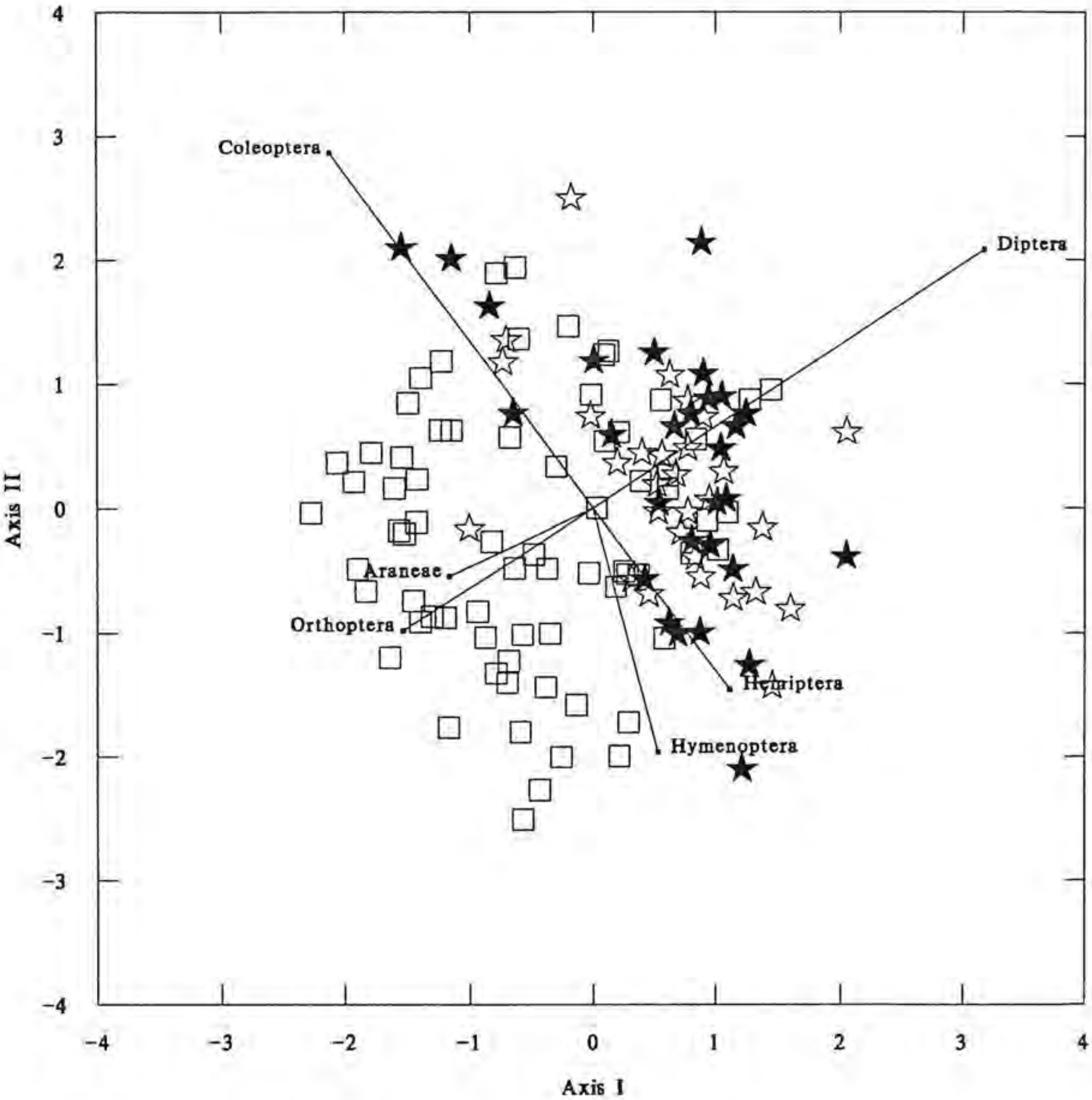

Fig.49. PCA Ordination of grids pre- and post-fire by Orders

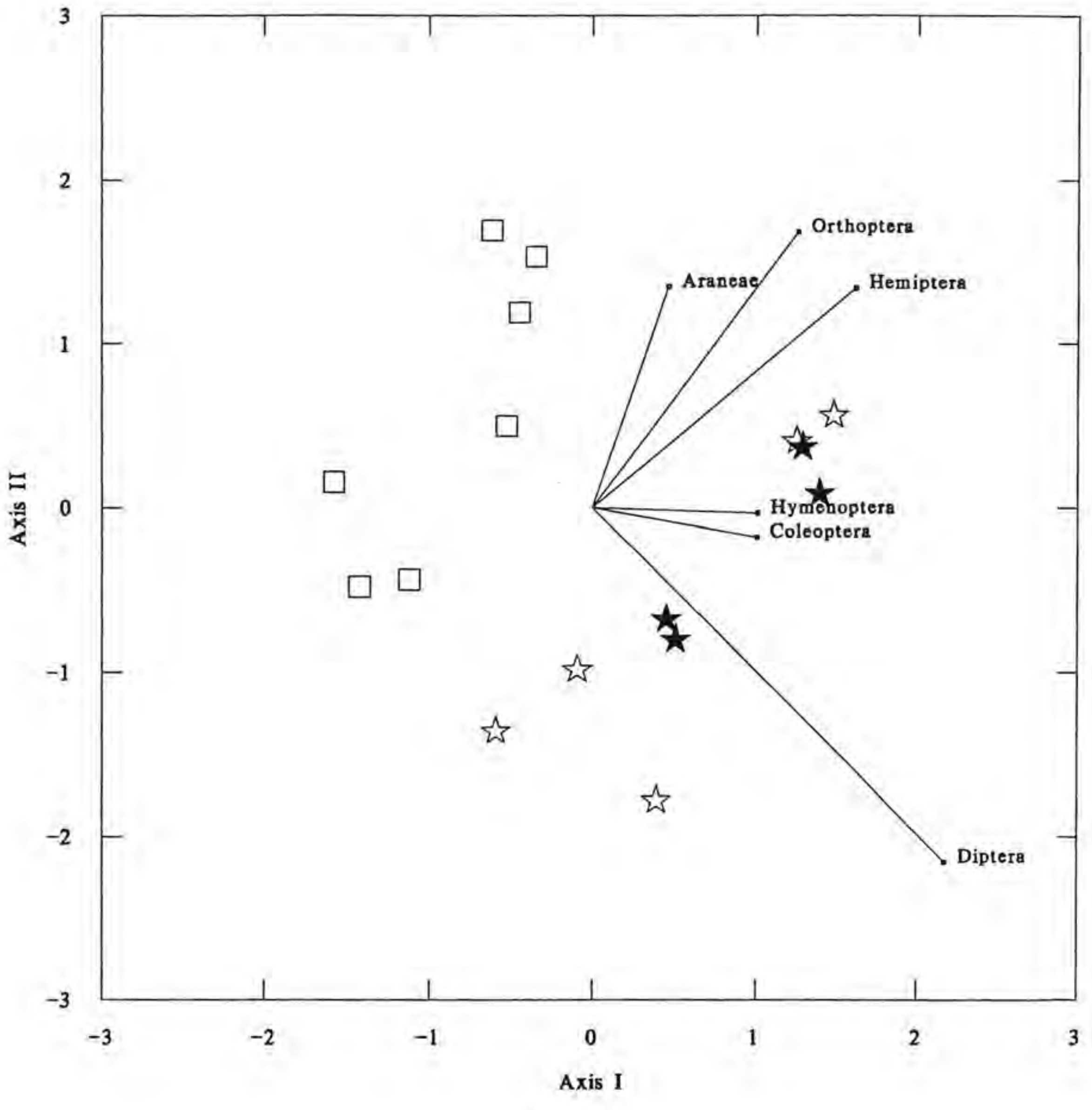

Fig.50. PCA Ordination of grids pre- and post-fire by Orders, doubly centred

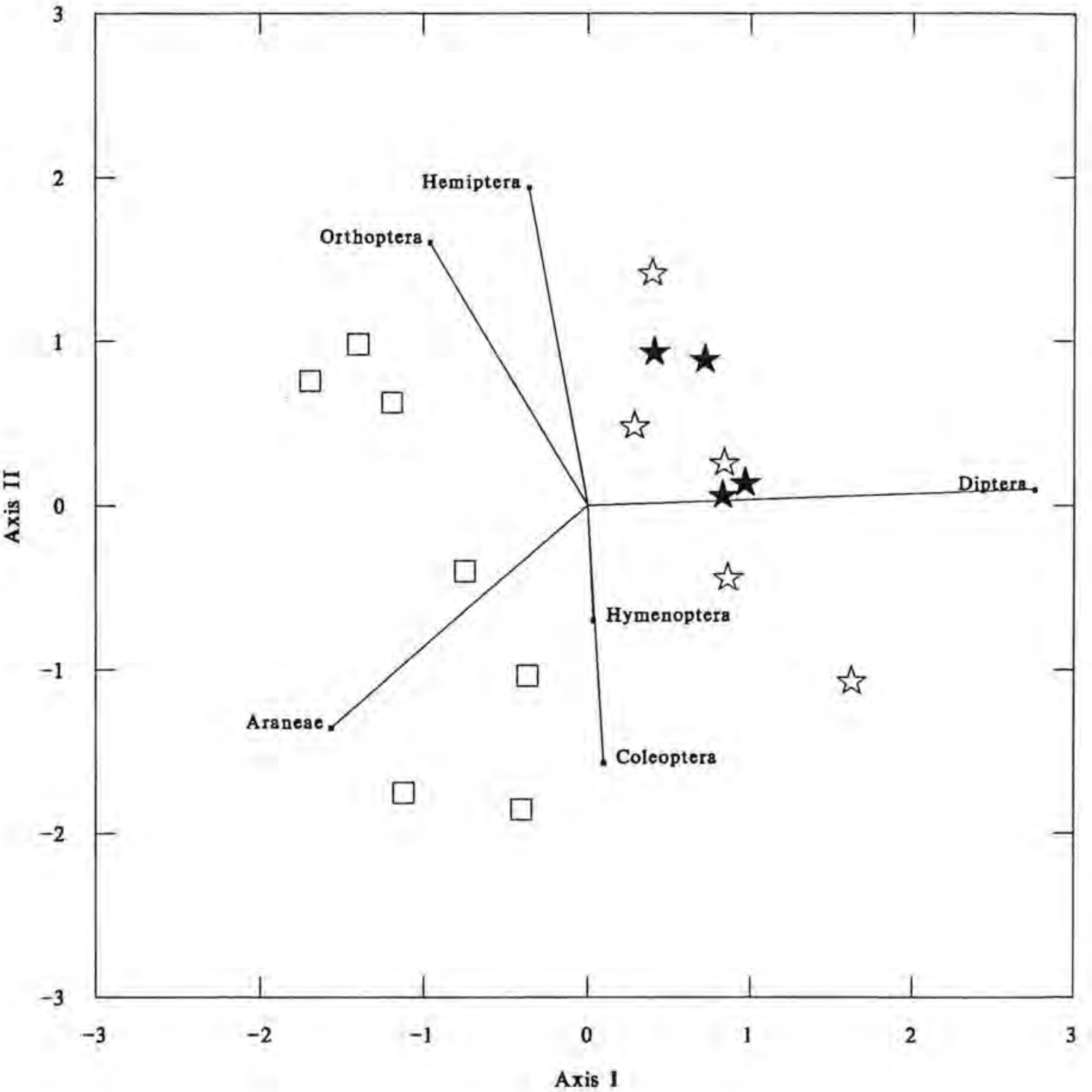

Fig.51. PCA Ordination of grids pre- and post-fire by Coleoptera

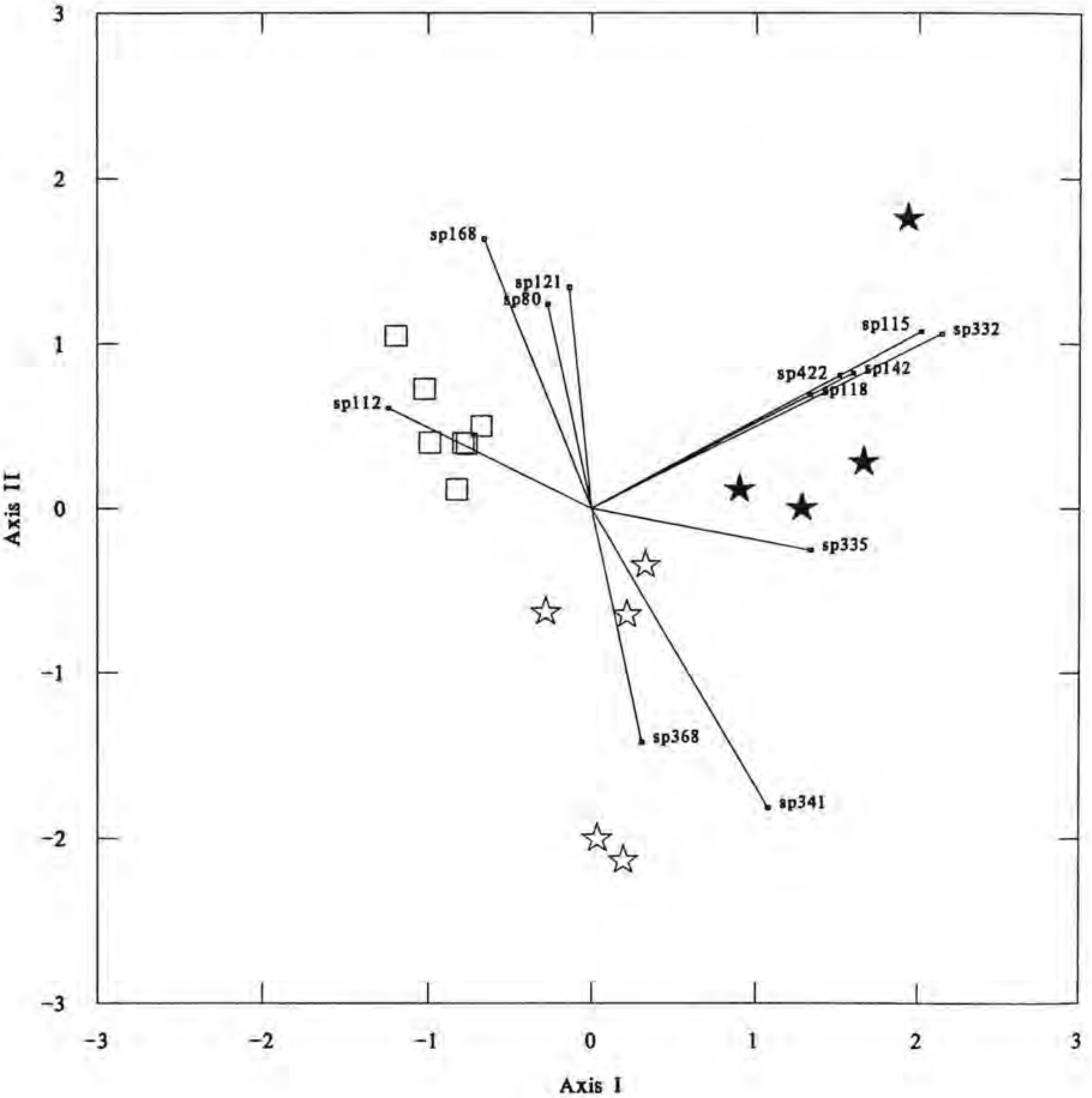

Fig.52. PCA Ordination of grids pre- and post-fire by Coleoptera, doubly centred

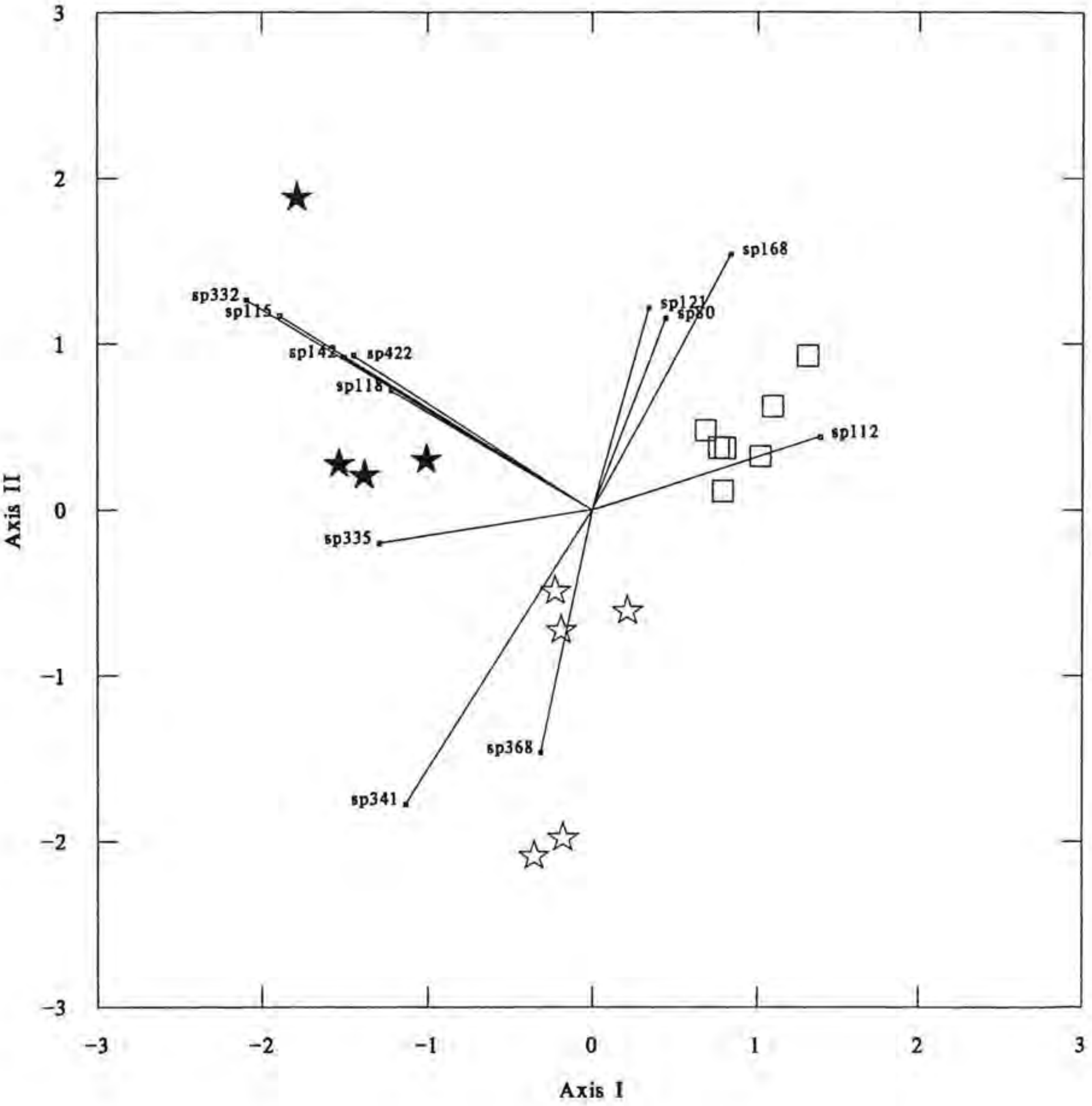

Fig.53. PCA Ordination of grids pre- and post-fire by floristic data

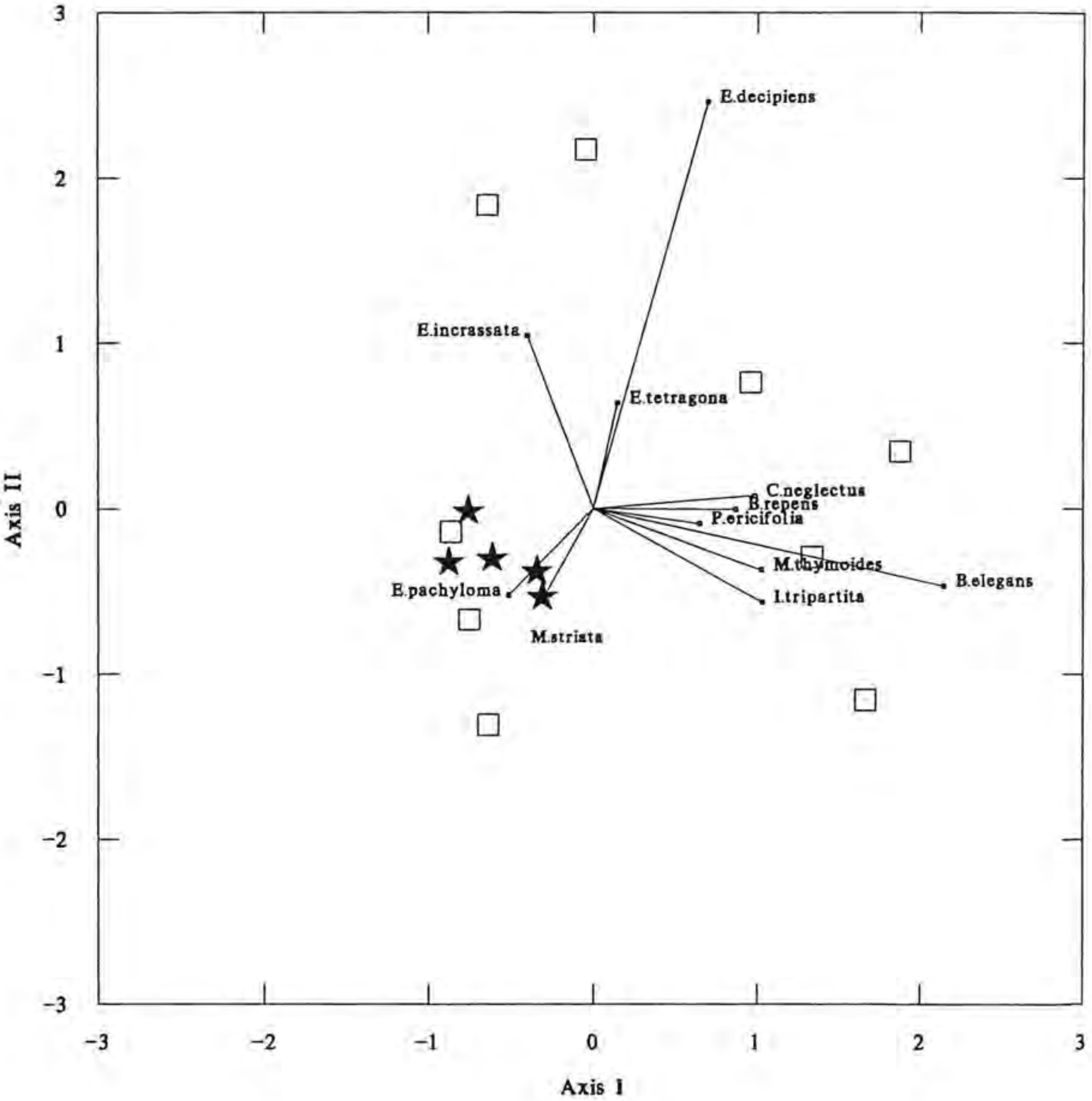

Fig.54a. PCA Ordination of grids pre- and post-fire by structure data

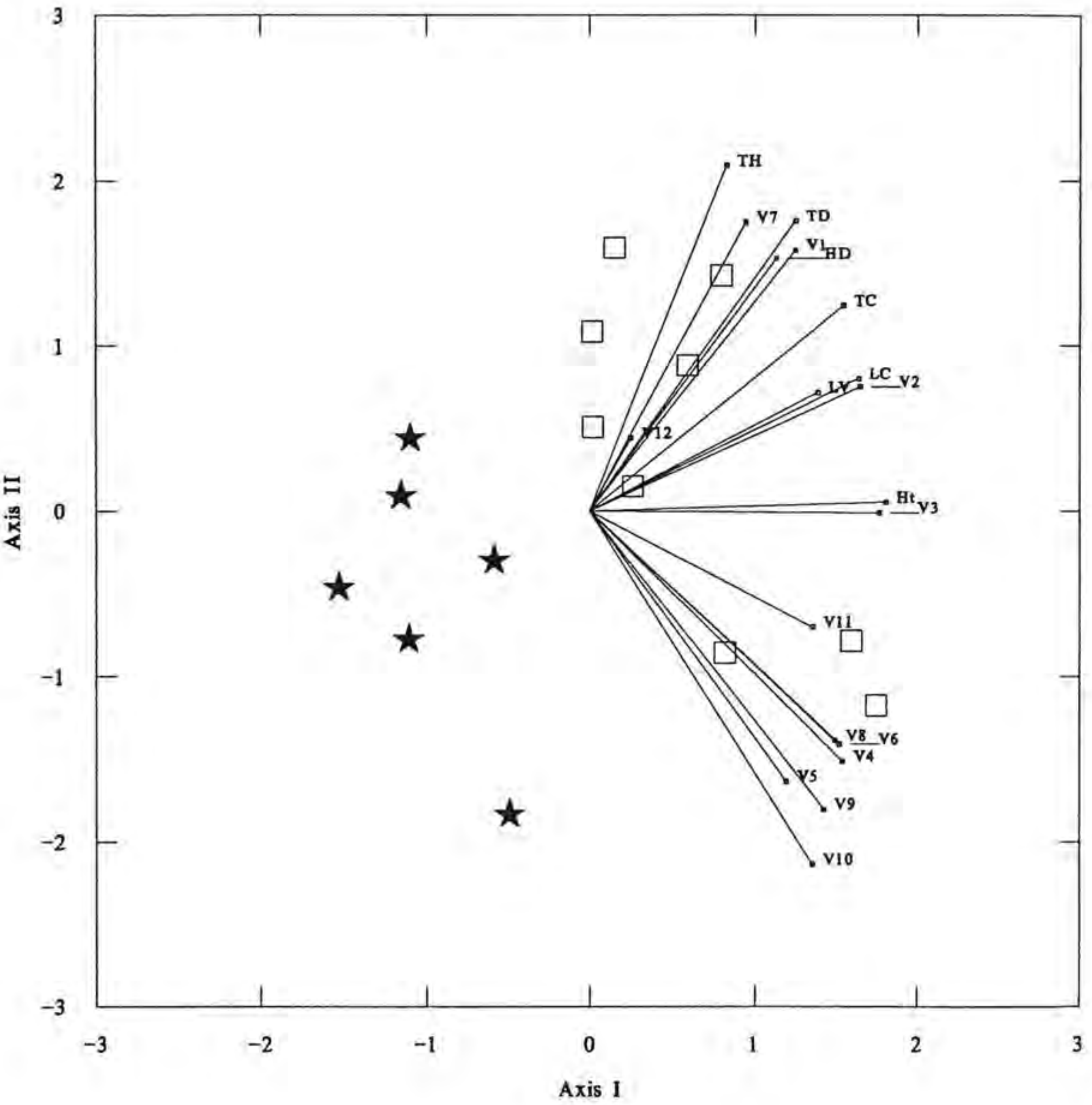

Fig.54b. PCA Ordination of grids pre- and post-fire by structure data

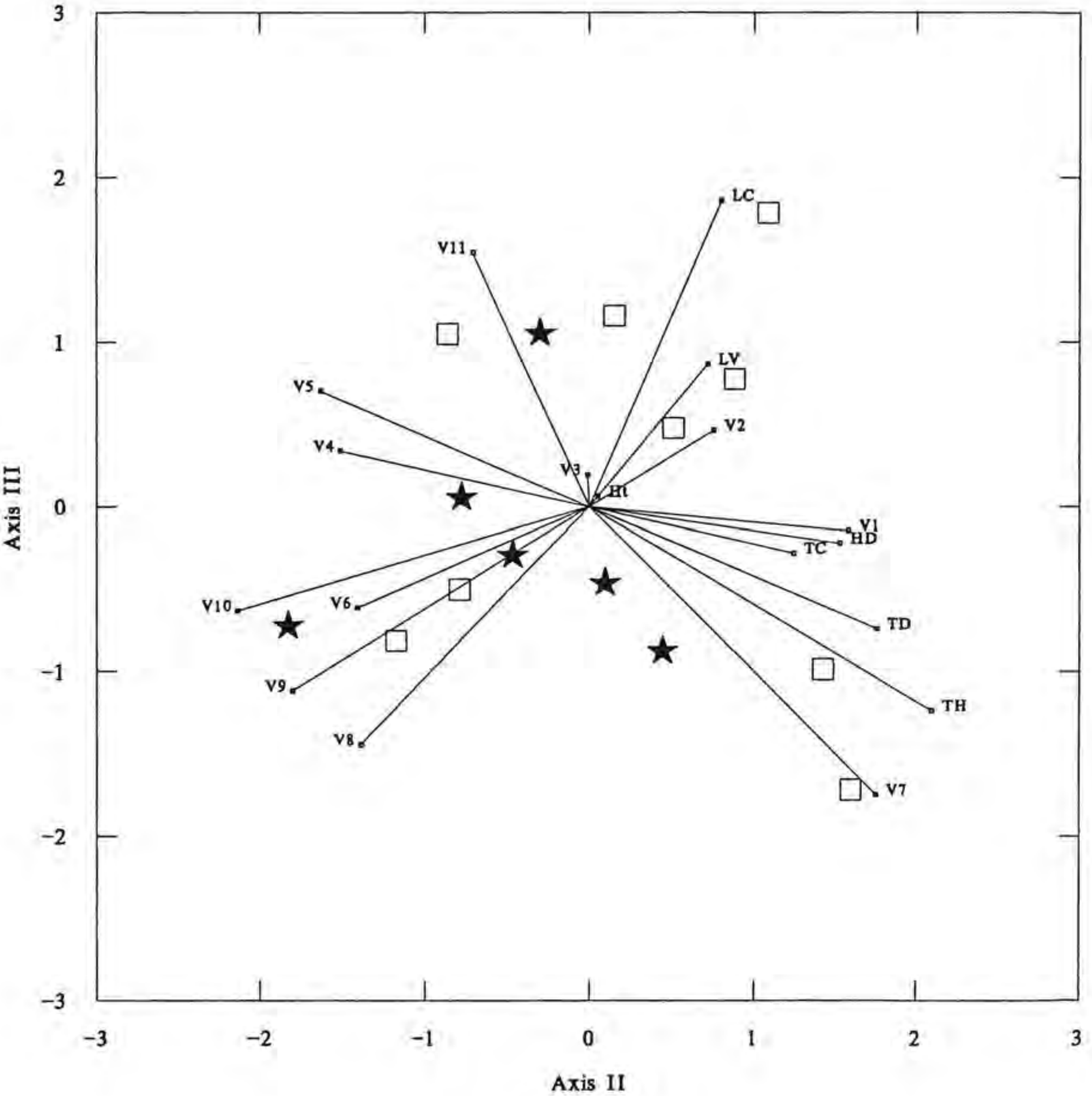

Fig.55. Procrustes analysis showing comparison of ordinations