8 THE EFFECTS OF MANAGEMENT ON INVERTEBRATES

8.1 Introduction

In this chapter we describe the effects of our field margin management regimes on the abundance and diversity of invertebrates that could be caught by D-Vac suction sampling. Equivalent results for butterflies are presented in Chapter 9 and those for invertebrates caught by pitfall trapping will be presented elsewhere (see Section 8.2.1).

Modern farming methods do not provide high quality habitats for the great majority of invertebrates; many species of agricultural weeds which formerly supported a rich and varied insect fauna are now rare, and are associated primarily with field edges (Morris & Webb 1987). Heavy use of pesticides, as well as herbicides, within the crops has greatly exacerbated this loss of invertebrate interest by causing direct mortality. Even in the weedier areas at the crop edge and on adjoining permanent grass field margins, mechanical disturbance (Duffey 1975, Morris & Plant 1983) and pesticide and herbicide drift are likely to impoverish the remaining insect fauna. Most research on invertebrate populations in field boundary grassland to-date has concentrated either on pest species or on the potentially beneficial role of this habitat in harbouring overwintering populations of invertebrate predators of crop pests (eg Thomas *et al* 1992). We assess the extent to which extended grassy margins can benefit these and other invertebrates of nature conservation interest.

It might be expected that extending the area of field margins by expanding their width and minimising the influence of agrochemicals would, in itself, have beneficial effects on invertebrates. However, our experiment was designed primarily to quantify the effects of different management options for extended field margins. In this chapter we therefore assess the relative merits of the different management strategies in terms of the diversity and abundance of invertebrates that were supported.

Management is essential to preserve the character of grassland and prevent rapid succession to scrub. Early and mid-successional species are likely to become scarce or extinct under a *laissez faire* regime (Usher & Jefferson 1987). However, it is well established that the timing of cutting is critical for many groups of invertebrates (e.g. Morris 1981a & b, Morris & Lakhani 1979, Morris & Plant 1983). Our data allow us to assess the effects on field margin invertebrates of varying both the frequency and timing of mowing and of more radically manipulating the plant species composition by comparing naturally regenerating and wild-flower seeded swards.

We have concentrated our analyses on estimates of total invertebrate abundance (see Section 8.2.2) and on the species richness and abundance of the following important and ecologically contrasting groups. First, Araneae (spiders) are a relatively mobile and entirely carnivorous group which might be expected to respond to plant architecture rather than to plant species composition. The frequency and timing of cutting are therefore likely to be critical. As an entirely predatory group they are also of potential benefit to farmers. Second, Auchenorrhyncha (leaf-hoppers) are highly mobile herbivores characteristic of grasslands. They have previously been used by other workers as indicators of the impact of different mowing regimes (Morris & Lakhani 1979). Third, the Heteroptera, which include both carnivorous and herbivorous species and, fourth, the Aphids, most of which are potential crop pests.

In Section 8.3 we present analyses of the effects of cutting, sowing, spraying and leaving cut material *in situ* on each of these groups on both the old and the new zones of the field margin. We then examine critical differences between the invertebrate faunas of the old and new zones of the margins and analyse the effects of vegetation height, rather than of treatment type, on the invertebrate groups. The ecological and practical management implications of the results for each group are discussed in Section 8.4. We also discuss the extent to which management regimes that most benefitted invertebrates also benefitted weed control and plant diversity and consider practical ways in which field margins may be used to optimise benefits to invertebrate conservation.

8.2 Methods

8.2.1 SAMPLING

The sampling protocol for D-Vac suction sampling is described in detail in Section 2.2.5. We considered this to be the best available method for quantifying the abundance of our target groups. Although D-Vac sampling becomes less efficient in taller vegetation (Duffey 1980) it is generally accepted that the bias is not critical for many groups, and that reasonably accurate estimates of abundance and species richness can be made (Morris 1990, Tumala 1982). We also sampled intensively by pitfall trapping, to obtain samples of cursorial groups, particularly Carabid beetles, which are not efficiently sampled by D-Vac suction sampling (see Section 2.2.5). However, despite the extremely common use of this method in invertebrate studies, our own validation experiments (Green, unpublished report) for this method and those of Topping & Sunderland (1992) showed clearly that abundances measured by pitfall traps were misleading indicators of the suitability of the habitat for the species concerned. Green (*ibid.*) showed that trapping rates of Carabid beetles declined as vegetation density increased. Because of these problems we are seeking new methods of analysing pitfall trap data and will present the results in the literature when they can be interpreted with greater confidence.

8.2.2 ANALYSES

Most of the analyses presented in this chapter follow the structure described in Chapter 2.2.7. Additional *a priori* contrasts were included, primarily to compare each cutting treatment with the unmanaged plots. Other methods of analysis are described in the main text. Abundance data were log-transformed ($\ln x+1$) before analysis. Species richness data were square-root transformed.

We estimated the total abundance of invertebrates as the sum of the number of individuals in all major groups (excluding Collembola and Acaria) sampled by D-Vac suction sampling on each plot. These estimates include the individuals recorded from the following groups: Auchenorrhyncha, Aphids, Coleoptera, Lepidoptera (adults & larvae), Harvestmen, Thrips (Thysanura), Heteroptera, Spiders, Woodlice, Hymenoptera, Diptera and Psocoptera.

The core results presented for the abundance and species richness of the invertebrate groups comprise separate analyses for each sample round so that both the proximate and medium term effects of management can be evaluated. It is possible, however, that counts based on the numbers of species at single points in time may give misleading under-estimates of the overall species richness supported under a particular management regime. This is particularly likely to be the case when a taxonomic group includes species with widely differing phenologies. For spiders and Auchenorrhyncha we have therefore presented additional analyses of the minimum number of species recorded on each treatment type throughout both 1990 and 1991.

The data are presented as figures, showing the numbers of invertebrates in the different groups caught on differernt treatments on different dates, and as tables summarising the results of the analyses of variance. To facilitate comparison of numbers caught in this and other studies, the numbers caught are also presented in tables in Appendix 2.

8.3 Results

Analysis of the 1987 baseline data provided no evidence for any significant differences in either the number of species recorded or the abundance of any of the groups investigated, between the plots within each experimental block.

8.3.1 THE EFFECTS OF MOWING

Overall invertebrate abundance

The old margins Mowing was almost always associated with an immediate reduction in invertebrate abundance on the old field margins. From September 1989 onwards, the effect of mowing was consistently significant (Table 8.1 & Figures 8.1-8.3). Invertebrates were significantly more abundant on the uncut plots than on those managed by cutting.

Plots cut in summer only remained poorer in total numbers of invertebrates than uncut plots in September and, to a lesser extent, in May the following year. Plots cut in spring as well as summer had even lower numbers of invertebrates. They were significantly lower than on uncut plots in seven of the nine sample rounds after September 1988. By contrast, invertebrate numbers on plots cut in spring and autumn recovered more quickly than on plots which were cut in summer. While abundance was highly significantly lower than on uncut treatments in May, a few weeks after the spring cut, in both 1990 and 1991, no significant difference remained by July.

The new margins The effects of mowing on the total abundance of invertebrates on the new margins were essentially similar to those on the old margins (Table 8.2 & Figures 8.1-8.3). The only notable difference was the absence of any detectable effect of mowing in September 1991. There was also an interaction between cutting and sowing in July 1991 which is described more fully in Section 8.3.2.

Summary Mowing was associated with a significant reduction in the abundance of invertebrates on both the old and new margins. The effect of cutting in summer was more persistent than that of cutting in spring and autumn.

Spiders

The old margins Mowing had a substantial and significant influence on both the abundance and species richness of spiders (Tables 8.3 & 8.4). The effect of cutting on the abundance of spiders was significant on every date after the baseline sample round in September 1987. The species richness of spiders was significantly affected by cutting on all dates after September 1989.

In general both the abundance and species richness of spiders were reduced by cutting (Figs 8.4-8.9) but different cutting regimes differed in their impact. The two treatments that involved cutting in summer had the most marked effects on abundance and species richness. Both variables were lower than on uncut plots in July 1990 and 1991, and there was no evidence of any recovery by September. Plots cut only in summer were still significantly impoverished in numbers of spider species the following May, although abundances had recovered to levels recorded on uncut plots by that stage. By contrast, plots cut in spring and autumn, recovered relatively quickly. Both abundance and species richness were lower in May, immediately after the spring cut, but in most years both variables had recovered to the levels recorded on uncut plots by July and September. The only exception to this was in July 1991, when significantly fewer species continued to be recorded on spring and autumn-cut plots ($P<0.05$). That timing of the summer cut, rather than the frequency of cutting was critical is confirmed by the significantly higher numbers and abundances of spiders on plots cut in spring and autumn than on those cut in spring and summer on several dates (planned comparisons, Tables 8.3 and 8.4).

Analyses of the total numbers of spider species caught in 1990 and 1991 show very similar effects of cutting to the individual sample dates (Tables 8.5 and 8.6). Species richness was significantly reduced by cutting, with the most severe effects resulting from cutting in summer.

The new margins The responses of spider species richness and abundance on the new and old margins were very similar (Tables 8.7 & 8.8, Figures 8.4-8.9). There was some evidence that spiders on the new margins were less affected by cutting in the early stages of the experiment: no overall effects of cutting on either abundance or species richness were demonstrated in September 1988. In September 1989, however, the abundance of spiders was significantly greater on uncut than on cut plots only on the new margins.

The results of the planned comparisons between uncut treatments and the various cutting regimes also differ in detail between the old and new margins but tend to re-enforce the general conclusions (Tables 8.7 & 8.8). First, there was stronger evidence that the deleterious effects of cutting on the abundance of spiders persisted for a full year. In May 1990 and 1991, treatments cut the previous summer had significantly less spiders than the uncut treatment on the new but not the old margins. At the same time, the evidence for persistent deleterious effects of summer cutting on species richness were weaker on the new than the old margins. No significant differences between species richness on summer-cut and uncut plots were found for the new margins in May in either 1990 or 1991, although significant effects were recorded at this stage for plots cut in spring and summer. Second, in September 1991, the numbers of spiders on uncut plots and on plots cut in summer differed significantly only on the old margins, although the probabilities for the new margins approached significance. It seems likely that these results from the two zones of the margin are complementary rather than contradictory.

A significant interaction between the effects of cutting and sowing on spider abundance in September 1989, appears to suggest that the influence of the cutting regimes differed on sown and naturally regenerating plots. Figure 8.4 shows that treatments that were cut in either summer or spring and summer, had fewer spiders when sown, while treatments left uncut or cut in spring and autumn, had more spiders when sown. However, since there is no evidence of this effect on any other date, it should be treated with extreme caution.

Similar results were obtained from analyses of the total numbers of spiders recorded during 1990 and 1991 (Table 8.5). The only substantive difference between these results and those for individual sampling dates was that the significant differences between plots cut in spring and summer and those cut in spring and autumn were no longer detectable in 1990.

Summary Cutting caused a substantial reduction in both the abundance and species richness of spiders. Cutting in summer was particularly deleterious. Cutting in summer only and in both spring and summer had much more persistent effects than cutting in spring and autumn.

Auchenorrhyncha

The old margins The effects of cutting on Auchenorrhyncha were similar to, but much less pronounced than those on spiders. Both abundance and species richness declined immediately after the swards were cut (Figures 8.10-8.15) although the overall effects of cutting were significant on relatively few dates (Tables 8.9 & 8.10). The planned contrasts between abundances on cut and uncut plots show that Auchenorrhyncha abundance was significantly lower on cut plots on several dates from September 1988 onwards. Species richness showed a similar trend. Most of this effect resulted from significantly lower abundances and numbers of species on plots that were cut in summer (both summer only and spring and summer) although plots cut in spring and autumn also had significantly less Auchenorrhyncha than uncut plots on some dates.

The effects of summer cutting on Auchenorrhyncha appeared to be less severe than on spiders. On plots cut in summer only, neither the reduction in abundance nor in species richness persisted to the May sample of the following year. In 1990, we failed to demonstrate a significant reduction in species richness immediately after the summer cut, although a significant difference was demonstrated in September, but in 1991 summer cutting had no significant effects.

Cutting in spring and autumn appeared to have less severe effects on Auchenorrhyncha than cutting in summer. Abundances on spring and autumn cut plots were significantly lower than on uncut plots on only two dates and species richness was significantly lower on only one date. However, direct comparison of plots cut in spring and summer with those cut in spring and autumn, showed that the former had significantly less Auchenorrhyncha on only one occasion.

Analyses of the annual total numbers of Auchenorrhyncha species again showed a similar pattern to the individual sample rounds (Table 8.5 cf 8.10). In 1990 the significant reduction in species richness in treatments cut in only summer was lost, although treatments cut in spring and summer remained significantly poorer in species than uncut treatments. The effect of cutting in spring and autumn remained significant.

The new margins In general the effects of cutting on the Auchenorrhyncha were similar on the new and old field margins (Tables 8.11 & 8.12). There was some evidence that the effect of the summer cut persisted until May the following year. Species richness in May 1990 remained significantly lower on plots cut the previous summer than on uncut plots. In May in both 1990 and 1991, abundances were also higher on uncut plots than on those cut the previous summer although the differences just failed to reach significance ($P=0.0526$ and 0.0629 respectively). Deleterious effects on Auchenorrhyncha of cutting in spring and autumn were also more pronounced on the new than the old margins. The differences between uncut plots and those cut in spring and autumn were significant on more dates than on the old margins.

Analyses of the total numbers of species of Auchenorrhyncha on the new margin in 1990 differed in two respects from the patterns observed from analysis of individual sample rounds. Plots cut in spring and autumn no longer differed significantly either from those cut in spring and summer or from uncut plots. In 1991 the difference between uncut plots and those cut in spring and autumn also disappeared (Table 8.5 cf Table 8.12).

Summary Cutting reduced both the abundance and species richness of Auchenorrhyncha. The effects of cutting in summer (either alone or in addition to cutting in spring) appeared to be less persistent than those on spiders although they were sometimes detectable over a whole year. Cutting in spring and autumn also reduced Auchenorrhyncha abundance and species richness. In contrast to the results for spiders, where summer-cutting was often significantly more deleterious than spring and autumn cutting, few significant differences between these regimes were detected for Auchenorrhyncha.

Heteroptera

The old margins The responses of the Heteroptera to the cutting regimes were broadly comparable with those of both spiders and Auchenorrhyncha; cutting reduced abundance and species richness (Figures 8.16-8.21). No effects of cutting were detected in September 1988 but in May and July 1989 Heteropteran abundance was significantly higher on uncut plots than on plots cut in spring and summer ($P<0.001$ on both dates, Table 8.13). Species richness was also significantly higher on uncut plots on both dates ($P<0.05$, Table 8.14). By September 1989 plots cut only in summer still had significantly fewer individuals and species of Heteroptera than uncut plots, although numbers on plots cut in spring and summer were no longer significantly different. Although the effects of cutting in summer in 1989 could not be detected in May the following year, the decline following cutting in 1990 persisted strongly in May 1991. No significant effects of cutting were detectable in September 1991, despite a strong effect immediately after the cut in July.

The effects of cutting in spring and autumn were much less severe than those of cutting in summer. Abundance was significantly lower than on uncut plots on only two dates, and species richness on one date, all in 1990 ($P<0.05$ in all cases). As expected from this result, both abundance and species richness tended to be significantly lower on plots cut in spring and summer than on those cut in spring and autumn (Tables 8.13 and 8.14).

The new margins As with the other groups, the patterns of Heteropteran abundance and species richness were similar on the new and old margins (Tables 8.15 & 8.16). Again, the minor differences in the pattern of significant results tend to re-enforce rather than contradict our general conclusions. Thus, on the new margins, the effect of summer cutting persisted until May the following year in 1990 as well as 1991. The contrast between plots cut in spring and summer and those cut in spring and autumn was also significant on more occasions on the new margins.

A single significant interaction between sowing and cutting was obtained for abundance in July 1990. It suggests that sowing was associated with an increase in abundance on plots cut in summer only, the converse of the result for unsown plots (Figure 8.17). However, since this is an isolated result, its interpretation must be treated with caution.

Summary Summer cutting resulted in large and persistent decreases in both the abundance and species richness of Heteroptera. Additional cutting in spring did not result in more marked differences. The effect of cutting in spring and autumn was much less severe than that of cutting in either spring and summer or summer only.

Aphids

Aphids were present in sufficient numbers for comparisons between treatments to be feasible in only five samples: those of May 1989, May 1990, July 1990, July 1991 and September 1991. They were not identified to species level and the analyses presented are of total abundance only.

The old margins No effect of cutting was detectable in May 1989 or in May or July 1990 (Table 8.17). In July 1991, abundance was significantly lower on plots cut in summer. The distribution of aphids in September 1991 was anomalous, with no individuals being recorded on the uncut plots, and significantly more individuals on plots cut in spring and summer than on those cut in spring and autumn.

The new margins As on the old margins, no effect of cutting could be detected on aphid abundance on the new margins in 1989. In May 1990, the overall effect of cutting approached significance ($P=0.0607$) and abundance on plots cut in spring and summer was significantly higher than on those cut in spring and autumn ($P<0.05$). In July 1990, however, while the overall effect of cutting was again non-significant, abundance was significantly higher on plots cut in spring and autumn than on those cut in spring and summer ($P < 0.05$). No significant effects of cutting were detectable in July or September 1991.

Summary Aphids were sporadic in their occurrence and numbers obtained by D-Vac suction sampling were low. Further sampling, using methods designed to obtain larger sample sizes, is required to detect any responses to cutting.

8.3.2 THE EFFECTS OF SOWING

Overall invertebrate abundance

As expected from the poor establishment of the wild flower seed mixture in the existing swards on the old margins (Chapter 6.2.1), we were unable to detect any significant effects of sowing on total invertebrate abundance on the old margins (Table 8.1). On the new margins, however, invertebrates tended to be more abundant on plots sown with wild flower seed mixture than on those with naturally regenerating swards (Figures 8.1-8.3). This effect was significant in September 1989 and in May and July in 1990 (Table 8.2) but not on subsequent dates. Although no significant effect of sowing was detected in 1991, the rank order of means was the same as in May and July in 1990. The mean abundance was higher under most cutting regimes on sown than on unsown plots. The general pattern of higher numbers on sown than on unsown plots on the new but not the old margins is illustrated in Figure 8.22. The data in this figure are the natural logarithms of the mean numbers of invertebrates recorded in sown plots, expressed as a percentage of those in unsown plots. These percentages were calculated separately for each sown and unsown pair of treatments under the same cutting regime (four pairs) in six blocks of the experiment. Where the effect of sowing was significant this is indicated as asterisks denoting the significance level above the appropriate bars.

A significant interaction between sowing and cutting was obtained in July 1990 (Table 8.2). Abundance appeared to be unaffected by sowing on plots cut in spring and summer but, like other isolated significant interactions, this result should be treated with caution.

Summary Swards sown with wild flower seed mixture tended to support higher total numbers of invertebrates than unsown swards under all cutting regimes except the spring and summer cut. However, this effect was not consistently significant. No effect of sowing on invertebrate abundance was detectable on the old margins, where wild flower seed establishment was poor.

Spiders

On the new margins spiders were significantly more abundant on sown than on unsown plots on three dates (May 1989, May 1990 and July 1991: Table 8.7) although no significant effects were detected on the old margins (Table 8.3). Although the effect of sowing was not significant on other dates, the mean percentage differences between sown and unsown plots were always positive (Figure 8.23).

Spider species richness on the new margins was also increased by sowing. The results were significant on only two dates (Table 8.8) but species richness values were higher on sown than on unsown plots on most other dates (Figures 8.7, 8.8 & 8.9). Again, no trends or significant differences in spider species richness resulting from sowing were detected on the old margins.

Summary Sowing was associated with higher numbers of individuals and species of spiders on the new margins. The effect on abundance was most clear in May in 1989 and 1990 and in July 1991. Sowing had no significant effect on the old margins, where the seed mixture established poorly as a result of being sown into the existing swards.

Auchenorrhyncha

Sowing did not affect Auchenorrhyncha on the old margins but significantly increased their abundance on the new margins on three dates: May 1989, September 1989, and July 1990 (Table 8.11, Figure 8.24). On most other dates, the mean abundances were higher on the sown treatments but the differences were not significant (Table 8.11, Figures 8.10, 8.11 & 8.12). By contrast, species richness differed significantly between sown and unsown plots on only one date (September 1991) when significantly fewer species were found on sown plots (Table 8.12, Figures 8.13, 8.14 & 8.15).

Summary Sowing resulted in an increase in the abundance of Auchenorrhyncha on the new margins, which was significant on some dates. There was no good evidence for an equivalent effect on species richness. No effect of sowing was detected on the old margins.

Heteroptera

We were unable to detect either any significant effects of sowing on the abundance of Heteroptera on the new margins (Tables 8.13 & 8.15) or any consistent patterns in mean abundance on sown and unsown plots (Figures 8.16, 8.17 and 8.18). In July 1990 there was a single significant interaction between sowing and cutting: Heteroptera appeared to be more abundant on sown than unsown plots when they were cut in summer but less abundant under the other cutting regimes (Figure 8.17).

Sowing had no clear-cut, consistent effects on the species richness of Heteroptera on the new margins. On one date significantly fewer species were recorded on sown than on unsown plots ($P<0.05$, Table 8.16). Significant interactions between sowing and cutting in September in 1989 and 1991 were both associated with greater species richness on sown than on unsown plots which were left uncut in summer (uncut or cut in spring and autumn) but relatively low values on sown plots cut in summer (either summer only or spring and summer (Figures 8.19 & 8.21)).

On the old margins evidence that sowing affected the Heteroptera was equally equivocal. On one date (September 1990, Table 8.13), Heteroptera were significantly less abundant on sown than on unsown plots, with lower numbers being recorded under all cutting regimes (Figure 8.17). Significantly fewer species were also recorded on unsown plots on this date (Table 8.14). A single significant interaction between sowing and cutting in May

1991, resulted from lower mean values of species richness on sown than on unsown plots under all cutting regimes except the spring and autumn cut, where the mean value of species richness was almost twice as high on sown plots (Figure 8.21).

Summary The effects of sowing on Heteroptera were much less clear than those on spiders and Auchenorrhyncha. There was no evidence that this group was more abundant on sown swards and some, weak evidence that it could be less abundant on sown than on naturally regenerating swards.

Aphids

There was little evidence that sowing had any influence on aphid abundance on the old margins (Tables 8.17 and 8.18). Sown plots had significantly less aphids than unsown plots on only one date (July 1990, $P<0.05$) but this was not part of any consistent pattern and should therefore be treated with caution.

Summary The numbers of aphids sampled, together with their patchy spatial and temporal distributions, were too low to assess with confidence any effects of sowing.

8.3.3 THE EFFECTS OF SPRAYING

Total Invertebrate Abundance

The old margins Invertebrate numbers on sprayed plots were significantly lower than those on uncut plots in September in both 1990 and 1991 (Table 8.1), although spraying had no significant effects in 1989. No effects of spraying were detectable when the July samples were collected. This was 30 days after spraying in 1990 but only 10 days in 1991. This result is consistent with the fact that it took several weeks for the spray to become fully effective, and well over a month before it affected the structure, in addition to the live species composition, of the vegetation.

The new margins On the new margins spraying resulted in significantly lower abundance of invertebrates only in September 1990 (Table 8.2). However, the mean abundances on sprayed plots were lower than on uncut plots on all other dates (Figures 8.1-8.3).

Spiders

The old margins Spiders were significantly less abundant on sprayed than on uncut plots on the old margins in both September 1990 and May 1991 (Table 8.3). Species richness was also significantly lower on sprayed plots in May 1991 (Table 8.4). As with total invertebrate abundance, the effects of spraying were not detectable in the July samples, collected soon after spraying, and no effect of spraying was detected in 1989.

The new margins We were unable to detect any significant effects of spraying on either the abundance or the species richness of spiders on the new margins (Tables 8.7 & 8.8), although there were consistently fewer spiders on sprayed than on uncut plots (Figures

8.4-8.6). However, spiders were also consistently more abundant on sprayed than on cut plots, suggesting that the effects of spraying were less important than those of cutting.

Auchenorrhyncha

The old margins Auchenorrhyncha were significantly less abundant on sprayed than on uncut plots only in July 1991 (Table 8.9). Spraying had no significant effects on species richness (Table 8.10).

The new margins There were significantly lower numbers of Auchenorrhyncha on sprayed than on uncut plots on the new margins in both September 1990 and July 1991 (Table 8.11). Significantly fewer species of Auchenorrhyncha were recorded on sprayed plots in the September 1991 (Table 8.12).

Heteroptera

The old margins Spraying reduced significantly the abundance on Heteroptera relative to that on uncut plots only in September 1990 (Table 8.13). As for spiders, spraying had no effect on Heteropteran abundance in July, immediately following application of the spray (Figures 8.17 & 8.18). Species richness was also significantly reduced by spraying in September 1990 although, anomalously, in July 1990, species richness was significantly higher on sprayed than on uncut plots (Table 8.14).

The new margins On the new margins Heteroptera abundance was significantly lower on sprayed than on uncut plots only in July 1990 (Table 8.15). Species richness was significantly reduced on sprayed plots in both July and September in 1990 but again, no significant effects were detected in 1989 or 1991 (Table 8.16).

Aphids

There was little evidence that spraying influenced aphid numbers (Tables 8.17 & 8.18). An isolated significant effect was detected on the new margins in September 1991, when aphid abundance was significantly higher on sprayed than on uncut plots ($P<0.05$).

Summary

Our results suggest that, for most of the groups examined, annual spraying with glyphosate was associated with reduced abundance and species richness. This effect was not usually detectable until some time after spraying. This effect did not appear to be persistent or cumulative.

8.3.4 THE EFFECTS OF COLLECTING OR LEAVING CUT MATERIAL

Planned comparisons between the treatment cut in spring and summer in which the cut hay was removed and that in which it was left *in situ* revealed very few significant differences for any invertebrate group. This comparison has therefore been omitted from the tables of results.

Figures 8.1-8.21 show that there was no consistent pattern in the rank order of the mean values for these two treatments. Only two significant results were obtained amongst tests for abundance and species richness in all groups on both the old and new margins. Since these were not part of consistent trends, and the number of tests carried out was large, they cannot be interpreted with confidence.

Summary

There was no evidence that removal of cut hay had any influence on the abundance or species richness of any group of invertebrates on either the old or new margins during the first four years of the experiment.

8.3.5 COMPARISON OF THE OLD AND NEW MARGINS

In this section we consider first, the extent to which the species richness and abundance of invertebrates differed on the old and new zones of the field margins at the outset of the experiment and during the subsequent years and, second, whether treatments differed in their effects on invertebrates on the two zones.

We compared the abundance and species richness of the invertebrate groups on the two zones using paired t-tests for the experiment as a whole. These tests involved all 60 plots (giving 59 degrees of freedom) except for the first two sample rounds in 1989 when only 30 plots were sampled (Chapter 2.2.5). As there were no *a priori* grounds for expecting a direction in these comparisons, the tests were two-tailed. Because large numbers of separate tests increase the probability of type one errors, we concentrate on detecting temporal patterns in the results and attach little weight to isolated results at the 0.05 probability level.

We used analyses of variance of the ratios of both abundance and species richness on the old and new zones of the margins to detect any differential effects of the experimental treatments on the two zones.

Absolute differences between the zones

In September 1988, six months after the new margins were rotovated and either sown or left to colonise naturally, there were significantly more individuals and species of both spiders and Auchenorrhyncha on the old than the new zones of the margins (Table 8.19). For Auchenorrhyncha this difference was very short-lived, with no substantial differences in either variable between the two zones on any subsequent date. The effect on both the abundance and species richness of spiders was more persistent. Species richness was consistently higher on the old than the new margins although the differences were not always significant. Abundances were not always higher although they were significantly higher on some dates, as late as May 1991. In contrast to the spiders and Auchenorrhyncha, no consistent differences between the two zones of the margins could be detected for Heteroptera at any stage.

Although these data suggest that Auchenorrhyncha and Heteroptera assemblages on the two zones of the margins became increasingly similar, analyses of the species composition of the groups on the two zones are required to confirm this conclusion. Convergence in numbers of individuals and species may not necessarily have been accompanied by convergence in species composition.

Differential effects of treatment on the old and new zones

In Section 8.3.1 we showed that while the results of analyses of the effects of management on invertebrate abundance and species richness on the old and new zones of the margins often differed in detail, the general conclusions to emerge from the two zones were very similar. Formal comparison of the effects of management on the two zones confirmed this conclusion. Few consistent or significant differences between the zones in the effects of treatment on the three invertebrate groups were detected (the results have not been tabulated). The only significant differences were for spiders. Spider species richness was significantly lower on the old than the new margins on sown plots in May 1989 ($P=0.0352$) and spider abundance was relatively lower in May 1990. These results are compatible with the finding in Section 8.3.2 that spider species richness and abundance were increased by sowing, but this effect was not detected on other dates.

Spider abundance also tended to be relatively lower on the old than the new zones of the margin on cut plots in the samples collected soon after cutting. It seems possible that the plant communities on the new margins recovered to provide conditions favourable for spiders more rapidly than those on the old margins. Alternatively, it is possible that the dominant spider species on the new margins were better able to recover from the effects of cutting than those on the old margins. This is compatible with the suggestion above that the spider communities on the two zones remained distinct, and will be further investigated by analysis of the species composition and ecological characteristics of the spider assemblages on the two zones.

We were unable to detect any consistent or significant effects of treatment on the relative abundances or species richness of either the Auchenorrhyncha or Heteroptera on the old and new zones of the margins. There was slight evidence that spraying had more severe effects on Auchenorrhyncha on the new than the old zones of the margins. Fewer species and individuals occurred on sprayed than on uncut plots on the new than on the old zones in September in both 1990 and 1991. This effect requires confirmation but would be consistent with a less effective application of the spray on the old zones (see Section 2.2.3).

Summary

We were unable to detect differences in the abundance and species richness of Heteroptera on the old and new zones of the field margins only six months after fallowing and differences in the Auchenorrhyncha disappeared within a year of fallowing. Differences in the abundance and species richness of spiders persisted for at least four years. Further analyses are required to ascertain whether the species composition of Heteroptera and Auchenorrhyncha on the two zones also converged.

There was little evidence that management had differential effects on the invertebrates on the old and new zones of the margins. The only conspicuous difference in the effects of management, the relative failure of establishment of the wild flower seed mixture on the old margins, was reflected in a lower abundance and species richness of spiders on the latter. Spiders on the new margins also recovered more rapidly from the effects of cutting.

8.3.6 THE EFFECTS OF VEGETATION HEIGHT ON INVERTEBRATES

In the following section we present analyses of the relationship between vegetation height (see Chapter 2.2.5) and the abundance and diversity of invertebrates found on the new margins in September in three successive years. The September data were collected *ca* 12 weeks after the summer cut and therefore avoid any severe proximate effects of cutting. Mean values of vegetation height (using the largest disc, see Chapter 2.2.5) are regressed on mean values of abundance and species richness for each treatment. The data are presented as coefficients of determination (r^2), which represents the variation in abundance and species richness which can be explained by vegetation height.

Total invertebrate abundance

In both 1989 and 1990 there was a strong relationship between vegetation height and total invertebrate abundance (Table 8.20). This relationship was not significant in 1991. This was attributable in part to high residual variation for mean abundance on the sprayed plots in that year (ie mean abundance was much lower on these plots than would tend to be predicted from the vegetation height alone).

Spiders

Both the abundance and species richness of spiders were highly significantly correlated with vegetation height in all three years, with relationships explaining up to 83% of the variation (Table 8.20). The greater part of the effect resulted from the difference between treatments cut in summer and those left uncut. However, even amongst the latter a significant relationship remained between vegetation density and spider abundance (r^2=91.7, P=0.007). For species richness, however, the effect was entirely dependent on the summer cut. Similar results were obtained in 1990 and 1991. In 1991 much less of the variation in species richness was explained by vegetation height. As for total invertebrate abundance, this resulted from high residual variation for the sprayed plots, on which the number of species recorded tended to be much lower than would be predicted from the simple regression relationship.

Auchenorrhyncha

Vegetation height was a much less important factor in explaining the abundance and species richness of Auchenorrhyncha than of spiders. The only significant relationship was for species richness in 1989 (Table 8.20).

Heteroptera

In 1989 there was a significant relationship between the species richness of Heteroptera and vegetation height. In 1990 both species richness and abundance were significantly related to vegetation height but in 1991 neither relationship was significant (Table 8.20).

Other Groups

There was a significant relationship between the abundance of Coleoptera and vegetation height in both 1989 and 1991, and the result approached significance in 1990 ($P=0.079$). The abundance of the other two groups investigated, Hymenoptera and Diptera, was not significantly related to vegetation height on any date (Table 8.20).

Summary

A high proportion of the variation in the abundance and species richness of spiders could be predicted by a simple measure of vegetation height in all three September samples. The abundance and diversity of Heteroptera and Coleoptera were much less reliably predicted by this measure and that of Auchenorrhyncha and Diptera were unrelated to vegetation height.

8.4 Discussion

In this section we discuss the ecological basis of the above results and their implications for both pest-control and conservation aspects of field margin management. We then consider how our understanding of these problems may be improved by further analysis of the existing data and we assess how future monitoring may be planned to give a more complete picture of both the effects of management and of longer term successional effects. Finally, we consider the relevance of these results from fallowed field margins to invertebrate conservation on whole fields fallowed under the set-aside schemes.

8.4.1 SPIDERS

During the first four years after establishment of the experiment the abundance and diversity of spiders was much higher on plots that were left uncut. Cutting in mid-summer had larger and more persistent negative effects on both the abundance and diversity of spiders than cutting in either the spring or the autumn. However, it is possible that cutting in spring has disproportionately important effects by reducing the abundance of spiders at a time when they may have a critical role in controlling crop pests. While our data provide good evidence that spider numbers recover quickly after spring cutting, this is a critical period in the life cycle of important pest species. Cereal aphids, for example, which overwinter on grassland and hedgerow species, colonise crops in May and June (Hand 1989).

The strong dependence of spider abundance and diversity on vegetation height results from the dependence of many species on finding suitable web-building sites. Gibson *et al*

(1992) found that web-building spiders of all types were more abundant in plots associated with taller vegetation.

The dependence of spiders on relatively complex plant architecture is likely to explain the delayed impact of spraying. Spraying had relatively little immediate impact on the physical complexity of the vegetation although the dead stems started to collapse after several months. Spraying may have other indirect delayed effects on spiders through its influence on prey species which may be more dependent on plant species composition than on architectural complexity. Similarly, it is more likely that the beneficial effects of sowing on spiders, which we observed on the new margins, resulted from the sown species increasing structural diversity, rather than plant species diversity. Further analyses of the vegetation density measurements are required to quantify the relative importance of these two factors.

The spider assemblages on the new zone of the field margins remained poorer in numbers of individuals and species of spiders for at least four years after fallowing.

8.4.2 AUCHENORRHYNCHA

Auchenorrhyncha were more resilient than spiders to the effects of mowing. Our results agree with those of Morris & Lakhani (1979) in showing that, at least in the short term, unmanaged grassland supports a richer community of Auchenorrhyncha than mown grassland. Although we found that mowing reduced the abundance and species richness of Auchenorrhyncha, and that cutting in summer had more severe effects than cutting in spring, these effects rarely persisted into the following year. Morris & Lakhani (1979) also found that cutting in spring was less deleterious than cutting in summer but, in their study, cutting caused more substantial reductions in Auchenorrhyncha abundance and species richness, and the effects of summer cutting persisting into the following year. The causes of the apparently greater resilience of Auchenorrhyncha to cutting in our study than in that of Morris & Lakhani (1979) are not clear although the differing requirements of the Auchenorrhyncha species present at the two sites and the differing cutting dates (both the spring and summer cut were *ca* three weeks later in Morris & Lakhani's study) are likely to be important.

The less severe effects of cutting on Auchenorrhyncha than on spiders may be explained by weaker dependence on the vegetation height and structure. Plant species composition is likely to be a more important factor for Auchenorrhyncha and this has a more complex relationship with the mowing regimes. Although the group is considered to have 'rather generalised phytophagous habits' (Morris 1971), 31 of the 51 British species are known to prefer grasses to other vegetation and some feed exclusively on grasses (Morris 1990).

The dependence of this group on grasses, and the positive effects of mowing on tillering in grasses, as well as on overall plant species richness (Chapter 4), suggest that in the medium term, some mowing regimes could benefit Auchenorrhyncha. Morris (1981a) found that some species of Auchenorrhyncha responded positively to cutting and Southwood & Van Emden (1967) found that phytophagous insects were more abundant on cut than on uncut grasses. This could explain the lack of any significant deleterious effects of mowing in our experiment in 1991 and the lack of any tendency for mown swards to harbour less species or individuals of Auchenorrhyncha than uncut swards by September 1991. Further years' data are required to evaluate this possibility.

The beneficial effects of sowing with a wild flower seed mixture on the abundance of Auchenorrhyncha are likely to have resulted from the significantly higher numbers of grass species in these swards than in those resulting from natural regeneration.

8.4.3 HETEROPTERA

Our study, like that of Morris & Lakhani (1979), showed that the effects of cutting on Heteroptera were similar to those on Auchenorrhyncha. Both studies show that summer cutting can have persistent effects on Heteroptera, and that the effects of cutting in spring are less severe. Although Morris & Lakhani (1979) found that Heteroptera recovered more rapidly from cutting in both in spring and in summer than Auchenorrhyncha, our results showed that the effects of summer cutting tended to be more persistent in the latter group. This difference between the results from the two studies may again have resulted from the differing ecological requirements of the Heteropteran species present at the two study sites. The Heteroptera are more diverse in their requirements than the Auchenorrhyncha, including both phytophagous and predatory species, and so different assemblages may be more likely to respond differently to management.

In contrast to the Auchenorrhyncha, sowing had no significant or consistent effects on the Heteroptera. The predatory habits of some species are likely to make them less dependent on plant species composition. Amongst the herbivorous species, one of the most numerous species in our samples, *Lygus rugullipennis*, the tarnished plant bug, feeds largely on *Urtica dioica*, which was very significantly less abundant in sown than in naturally regenerating swards (Chapter 5.2.7). Analyses of the effects of treatment on individual abundant species are required to evaluate the importance of such species-specific effects to the results for the group as a whole.

8.4.4 TEMPORAL TRENDS

It is inherently difficult to identify temporal trends in any study of invertebrate communities. The enormous variation in weather conditions between and within years has large effects on the phenologies of different species and on population size. The complex inter-relationships between phytophagous species, their food plants, and their predators and parasitoids, are also likely to result in unpredictable fluctuations. Within the context of our experiment, any cumulative effects of management over time may be confounded by opposing temporal trends resulting from successional change on the new field margins. Differences between managed and unmanaged plots would have to be large in relation to normal interannual fluctuations in order to disentangle these two effects.

Examination of our longest run of data for one time of year, the September samples of 1987 to 1991, shows large between-year fluctuations for all groups, which are independent of any aspect of management. The most striking feature is the large number of individuals and species of most groups in September 1991. The total abundance of invertebrates was also higher than at this time in previous years although this did not result from increases in all groups. The increase was particularly marked for the spiders, where abundances were roughly twice those in the previous September and mean numbers of species were higher on every treatment. By contrast, the Heteroptera were no more abundant in September 1991 than 1990. It is impossible to attribute the size of this sample to any particular cause without further sampling but it is possible that since this phenomenon overwhelmed any treatment effects, it resulted from unusually high immigration and an exceptional breeding season.

Gibson *et al* (1992) reported a gradual accumulation in annual totals of spider species recorded in secondary successional limestone grassland in Wytham Woods. Because our numbers of sample rounds varied between years we can only generate comparable measures for this variable for 1990 and 1991 (Table 8.6). Between these years the mean annual totals of spider species increased under all treatments. The numbers of species of Auchenorrhyncha also increased under the majority of treatments and remained unchanged under the remainder. Detailed examination of changes in the species composition and ecological characteristics of the different groups is required to further elucidate evidence of successional changes. The comparison of rates of convergence in species richness and abundance of the different invertebrate groups in Section 8.3.5 suggest that successional change may be much more rapid in some groups than in others. Comparisons of species composition on the two zones are required to confirm this conclusion but are likely to be complicated by the changes in plant species composition which were recorded on the old as well as the new zones of the margin during the early years of the experiment (Chapter 3).

We found no evidence in our data that the deleterious effects of mowing were cumulative. Morris & Lakhani (1979) were able to detect cumulative effects of deleterious mowing regimes in the period July to September over a three year period in ancient limestone grassland. However, their sampling intensity was much greater than ours and their data were subject to much smaller interannual fluctuations and were uncomplicated by the effects of rapid early successional change. A much longer time period would be required for low-intensity sampling to reveal these sorts of trends.

It is also likely that some aspects of our management regimes would not be expected to have measurable effects on invertebrates over a time scale of five years. For example, we were unable to detect changes in plant species richness resulting from leaving mown hay *in situ* because changes in soil nutrient status on field margins would be likely to very slow (Chapter 4). Changes in invertebrate assemblages may be expected to follow those in plant species composition and structural complexity.

8.4.5 GENERAL CONCLUSIONS FOR MANAGEMENT

Our results show clearly that most invertebrate groups, and the largest and richest invertebrate assemblages, on expanded and existing field margins are encouraged in the absence of regular, annual mowing. However, whilst lack of management may benefit invertebrate conservation in the short-term, some management is essential to prevent succession to scrub in the medium term. Invertebrate conservation is rarely likely to be the primary aim of field margin management, but where this is the case, some form of rotational mowing, possible on a two-year cycle is likely to be of most benefit to the species richness.

Where more frequent mowing is demanded by other objectives, mowing in spring and autumn is greatly preferable to mowing in summer. We reach precisely the same conclusions for butterflies in Chapter 9. Spring and autumn mowing, particularly in early succession, has additional benefits for invertebrate conservation. This regime allows moderately complex vegetation architecture to develop during the summer, maximises the abundance of nectar sources (Chapters 9 & 10) and has the positive benefit of maximising plant species richness (Chapter 4). In Chapter 5 we showed that spring and autumn mowing cannot be recommended in naturally regenerating, early successional swards where annual weed control is a priority but suggest that it should be instated as soon as weed control problems are overcome by using mowing regimes which are less sympathetic to conservation aims.

Sowing with our wild flower seed mixture also benefitted the invertebrate groups examined, with the possible exception of the Heteroptera. The weed control properties of these swards mean that mowing regimes more sympathetic to invertebrate conservation can be employed at an earlier stage. However, the benefits to invertebrates of sown swards are likely to depend on their precise species composition. It is likely that a reasonable number of grass species, and sufficient forbs to provide continuity of nectar supply and structural diversity, would best encourage invertebrate diversity. The addition of specific plant species might be considered to encourage particular species or groups of phytophagous invertebrates. Similarly, the addition of plant species with specific characteristics might be included to encourage other groups. Thus, for example, Thomas *et al* (1992) show that grass species which form dense tussocky growth provide a high density of overwintering sites for Carabid beetles, which are important aphid predators in adjoining crops in the summer.

Field margin management by annual herbicide application is likely to reduce the abundance and species richness of invertebrates. The effects on phytophagous and nectar-feeding species (see Chapters 9 & 10) are likely to be more severe than those on predators. Our data suggest that spraying has less severe effects than mowing on predatory groups such as spiders. However, further analyses of our data are required to ascertain the extent to which species composition, in addition to species richness and abundance, of the invertebrate assemblage, is altered by spraying.

Further analyses of our data are required to reveal the extent to which wild flower-seeded swards encourage assemblages of invertebrates which differ in species composition from those on naturally regenerating swards. Any such differences may have important implications for invertebrate conservation.

8.4.6 FUTURE ANALYSES

In addition to the requirements for further analyses mentioned in the above sections, several major additional analyses of the invertebrate data are planned. Completion of analysis of the pitfall trapping data (see Section 8.2) will provide additional information on the above groups and equivalent data for two more ecologically and agriculturally important groups, the Carabid and Staphylinid beetles.

Further analysis of the D-Vac data will examine in more detail changes in the species composition and ecological characteristics of the different invertebrate groups in relation both to the effects of management and to succession. This information will allow finer-tuning of management advice, particularly where specific species or assemblages are the targets of conservation or agricultural objectives for field margin management.

Multivariate methods of analysis will be used to examine further the relationship between the species composition of the invertebrate assemblages and a range of environmental factors in addition to the experimental treatments. These analyses will be used to examine the importance of management and other environmental factors to species associations rather than simply to taxonomic groups.

8.4.7 IMPLICATIONS FOR SET-ASIDE MANAGEMENT

Our data are of direct relevance to the management of set-aside swards. Although it is possible that the invertebrate assemblages in the centres of set-aside field may be poorer in phytophagous species than those at the edges, because the plant community is less rich (Chapter 4), our data are in general likely to be representative of five-year set-aside. The conclusions for management of set-aside are precisely the same as those for field margins: principally that invertebrate species richness is best encouraged by confining mowing to the spring and autumn. Sown swards containing a few forb species to provide continuity of nectar and structural diversity are also a very desirable option for set-aside (see also Chapters 9 & 10). In addition to benefitting most groups of invertebrates, the weed control properties of these swards, even in the absence of summer mowing (Chapter 5), provide a means of overcoming the conflict of interest between the requirements of weed control and invertebrate conservation.

Table 8.1 Total invertebrate abundance on the old margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CUTTING	ns	-	-	0.0052 **	0.0001 ***	0.0002 ***	0.0001 ***	0.0116 *	0.0001 ***	0.0107 *
SOW*CUT	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	0.0204 * >	0.0001 *** >	0.0002 *** >	0.0001 *** >	0.0023 ** >	0.0001 *** >	0.0330 * >
Cut SpSu vs Cut SpAu	ns	-	-	ns	ns	0.0091 ** <	0.0353 * <	ns	0.0015 ** <	ns
Not Cut vs Cut SpSu	ns	0.0085 ** >	0.0020 ** >	ns	0.0001 *** >	0.0001 *** >	0.0008 *** >	0.0081 ** >	0.0001 *** >	(0.0623) >
Not Cut vs Cut Su	ns	-	-	0.0008 *** >	0.0273 * >	0.0003 *** >	0.0001 *** >	(0.0556) >	0.0001 *** >	0.0050 ** >
Not Cut vs Cut SpAu	ns	-	-	ns	0.0001 *** >	ns	ns	0.0016 ** >	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	0.0003 *** <	ns	ns	0.0168 * <

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.2 Total invertebrate abundance on the new margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	ns	ns	0.0247 * >	0.0279 * >	0.0010 ** >	ns	ns	ns	ns
CUTTING	ns	-	-	0.0311 *	0.0033 **	0.0001 ***	0.0413 *	0.0004 ***	0.0001 ***	ns
SOW*CUT	ns	-	-	ns	ns	0.0315 *	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	0.0038 ** >	0.0004 *** >	0.0001 *** >	0.0085 ** >	0.0004 *** >	0.0001 *** >	ns
Cut SpSu vs Cut SpAu	ns	-	-	ns	ns	0.0002 *** <	ns	ns	0.0036 ** <	ns
Not Cut vs Cut SpSu	ns	ns	0.0005 *** >	0.0038 ** >	0.0019 ** >	0.0001 *** >	0.0435 * >	0.0004 *** >	0.0001 *** >	ns
Not Cut vs Cut Su	ns	-	-	0.0091 ** >	0.0106 * >	0.0001 *** >	0.0122 * >	ns	0.0001 *** >	ns
Not Cut vs Cut SpAu	ns	-	-	0.0183 * >	0.0006 *** >	ns	ns	0.0004 *** >	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	0.0377 * <	ns	ns	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.3 Spider abundance on the old margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CUTTING	0.0498 *	-	-	0.0014 **	0.0031 **	0.0001 ***	0.0001 ***	0.0040 **	0.0003 ***	0.0001 ***
SOW*CUT	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Uncut vs Cut	0.0248 * >	-	-	ns	0.0030 ** >	0.0003 *** >	0.0001 *** >	0.0010 *** >	0.0020 ** >	0.0008 *** >
Cut SpSu vs Cut SpAu	ns	-	-	(0.0597) <	ns	0.0043 ** <	0.0295 * <	ns	0.0025 ** <	0.0009 *** <
Not Cut vs Cut SpSu	ns	0.0044 ** >	0.0100 ** >	ns	(0.0550) >	0.0001 *** >	0.0001 *** >	0.0066 ** >	0.0009 *** >	0.0001 *** >
Not Cut vs Cut Su	0.0101 * >	-	-	0.0029 ** >	ns	0.0003 *** >	0.0001 *** >	ns	0.0012 ** >	0.0001 *** >
Not Cut vs Cut SpAu	ns	-	-	ns	0.0012 ** >	ns	ns	0.0036 ** >	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	0.0056 ** <	0.0402 * <	ns	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.4 Numbers of species of spiders on the old margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CUTTING	ns	-	-	ns	0.0011 **	0.0040 **	0.0002 ***	0.0001 ***	0.0002 ***	0.0153 *
SOW*CUT	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	ns	0.0003 *** >	0.0014 ** >	0.0002 *** >	0.0001 *** >	0.0001 *** >	0.0330 * >
Cut SpSu vs Cut SpAu	ns	-	-	ns	(0.0504) >	ns	0.0333 * <	ns	(0.0533) <	0.0319 * <
Not Cut vs Cut SpSu	ns	0.0027 ** >	ns	ns	0.0280 * >	0.0039 ** >	0.0001 *** >	0.0001 *** >	0.0001 *** >	0.0123 * >
Not Cut vs Cut Su	ns	-	-	ns	0.0117 * >	0.0087 ** >	0.0001 *** >	0.0005 *** >	0.0001 *** >	0.0091 ** >
Not Cut vs Cut SpAu	ns	-	-	ns	0.0002 *** >	ns	ns	0.0001 *** >	0.0308 * >	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	ns	0.0043 ** <	ns	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.5 Results of the analyses of annual species richness values of spiders and Auchenorrhyncha (three sample rounds treated as single unit)

Effect or Comparison	Spiders				Auchenorrhyncha			
	1990		1991		1990		1991	
	Old	New	Old	New	Old	New	Old	New
SOWING	ns	ns	ns	ns	ns	ns	ns	(.06)
CUTTING	0.0017 **	0.0020 **	0.0004 ***	0.0001 ***	0.0197 *	0.0017 **	ns	ns
SOW*CUT	ns	ns	ns	ns	ns	ns	ns	ns
Uncut v Cut	0.0001 *** >	0.0006 *** >	ns	0.0001 *** >	0.0040 ** >	0.0009 *** >	ns	ns
Cut SpSu vs Cut SpAu	ns	ns	0.0189 * <	0.0065 ** <	ns	ns	ns	ns
Not Cut vs Cut SpSu	0.0101 * >	0.0003 *** >	0.0001 *** >	0.0001 *** >	0.0039 ** >	0.0011 ** >	ns	ns
Not Cut vs Cut Su	0.0039 ** >	0.0013 ** >	0.0002 *** >	0.0001 *** >	ns	0.0002 *** >	ns	ns
Not cut vs Cut SpAu	0.0042 ** >	(0.06) >	0.0439 * >	0.0104 * >	0.0233 * >	ns	ns	ns
Spray U/Spray vs U/NC	ns	ns	ns	ns	ns	ns	ns	ns

ns = not significant, * $P <= 0.05$, ** $P <= 0.01$, *** $P <= 0.001$, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.6 Mean values of species richness (three sample rounds treated as one catch)

Spiders				Auchenorrhyncha			
1990		1991		1990		1991	
Old Margin	New Margin	Old Margin	New Margin	Old Margin	New Margin	Old Margin	New Margin
U/NC 16.2	S/NC 16.5	S/NC 19.2	S/NC 18.2	S/NC 10.7	U/NC 10.2	U/NC 10.8	U/SpSu 11.5
S/NC 14.5	U/NC 12.2	U/NC 17.0	U/NC 16.5	U/NC 10.2	S/NC 10.0	S/SpAu 10.3	S/NC 10.5
U/Spray 14.2	S/SpAu 12.0	U/Spray 15.7	S/SpAu 15.5	U/Su 9.3	U/SpSu/L 9.3	U/SpSu/L 10.2	U/NC 10.2
U/SuSu/L 13.6	U/Spray 12.0	U/SpAu 15.3	U/Spray 13.7	U/Spray 9.2	S/SpAu 8.8	U/SpAu 10.2	U/Su 10.0
U/SpAu 12.7	S/Su 10.8	S/SpAu 15.3	U/SpSu/L 12.8	U/SpAu 9.0	U/SpAu 8.4	S/NC 9.5	U/SpSu 10.0
U/SpSu 11.6	U/SpAu 10.0	S/Su 13.5	U/SpAu 12.5	U/SpSu/L 9.0	U/Spray 8.2	U/SpSu 9.5	S/SpAu 9.3
S/SpAu 11.0	U/SpSu/L 9.8	S/SpSu 13.0	U/Su 11.8	S/Su 8.8	U/SpSu 8.0	S/SpSu 9.2	U/Sp/Au 8.8
S/SpSu 11.0	U/SpSu 8.8	U/SpSu/L 13.0	S/Su 11.2	S/Su 8.8	U/Su 7.0	U/Spray 9.0	S/SpSu 8.8
S/Su 10.5	S/Su 8.8	U/Su 12.7	S/SpSu 10.5	S/SpAu 8.2	S/Su 7.0	S/Su 9.0	U/Spray 8.8
U/Su 9.8	S/SpSu 8.7	U/SpSu 11.7	U/SpSu 10.3	S/SpSu 7.7	U/Su 5.2	U/Su 8.7	S/Su 7.7

Table 8.7 Spider abundance on the new margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	0.0101 * >	ns	ns	0.0003 *** >	ns	ns	ns	0.0033 ** >	ns
CUTTING	ns	-	-	0.0001 ***	0.0001 ***	0.0001 ***	0.0009 ***	0.0001 ***	0.0002 ***	0.0207 *
SOW*CUT	ns	-	-	0.0192 *	ns	ns	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	0.0001 *** >	0.0001 *** >	0.0001 *** >	0.0005 *** >	0.0001 *** >	0.0027 ** >	(0.0600) >
Cut SpSu vs Cut SpAu	ns	-	-	0.0001 *** <	ns	0.0001 *** <	0.0217 * <	ns	0.0017 ** <	0.0233 * <
Not Cut vs Cut SpSu	ns	0.0003 *** >	0.0001 *** >	0.0001 *** >	0.0001 *** >	0.0001 *** >	0.0001 *** >	0.0001 *** >	0.0021 ** >	(0.0760) >
Not Cut vs Cut Su	ns	-	-	0.0001 *** >	0.0146 * >	0.0001 *** >	0.0034 ** >	0.0196 * >	0.0013 ** >	(0.0791) >
Not Cut vs Cut SpAu	ns	-	-	ns	0.0001 *** >	ns	0.0474 * >	0.0001 *** >	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	ns	ns	ns	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.8 Numbers of species of spiders on the new margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	0.0201 * >	ns	ns	ns	ns	ns	ns	0.0420 * >	ns
CUTTING	ns	-	-	0.0001 ***	0.0032 **	0.0001 ***	0.0017 **	0.0178 *	0.0001 ***	0.0015 **
SOW*CUT	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	0.0005 ***	0.0037 ** >	0.0001 *** >	0.0006 *** >	0.0065 ** >	0.0001 *** >	0.0081 ** >
Cut SpSu vs Cut SpAu	ns	-	-	0.0079 ** <	ns	0.0038 ** <	0.0448 * <	ns	0.0023 ** <	0.0022 ** <
Not Cut vs Cut SpSu	0.0499 * >	0.0049 ** >	0.0005 *** >	0.0013 ** >	0.0026 ** >	0.0001 *** >	0.0001 *** >	0.0029 ** >	0.0001 *** >	0.0007 *** >
Not Cut vs Cut Su	ns	-	-	0.0001 *** >	ns	0.0001 *** >	0.0011 ** >	ns	0.0001 *** >	0.0208 * >
Not Cut vs Cut SpAu	ns	-	-	ns	0.0011 ** >	0.0453 * >	0.0347 * >	0.0095 ** >	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	ns	ns	ns	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.9 Auchenorrhyncha abundance on the old margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CUTTING	ns	-	-	ns	ns	0.0053 **	ns	ns	0.0001 ***	ns
SOW*CUT	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Uncut vs Cut	0.0388 * >	-	-	ns	0.0287 * >	0.0008 *** >	ns	ns	0.0008 *** >	ns
Cut SpSu vs Cut SpAu	ns	-	-	ns	ns	ns	ns	ns	0.0096 ** <	ns
Not Cut vs Cut SpSu	0.0457 * >	0.0489 * >	0.0137 * >	ns	0.0325 * >	0.0017 ** >	ns	ns	0.0160 * >	ns
Not Cut vs Cut Su	ns	-	-	0.0314 * >	ns	0.0044 ** >	0.0288 * >	ns	0.0004 *** >	ns
Not Cut vs Cut SpAu	0.0329 * >	-	-	ns	ns	0.0312 * >	ns	ns	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	ns	ns	0.0485 * <	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.10 Numbers of species of Auchenorrhyncha on the old margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CUTTING	ns	-	-	0.0492 *	0.0242 *	ns	0.0390 *	ns	ns	ns
SOW*CUT	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	0.0108 * >	ns	0.0433 * >	0.0060 ** >	ns	ns	ns
Cut SpSu vs Cut SpAu	-	-	-	ns	ns	ns	ns	ns	ns	ns
Not Cut vs Cut SpSu	ns	ns	ns	0.0463 * >	0.0208 * >	0.0200 * >	0.0334 * >	ns	ns	ns
Not Cut vs Cut Su	ns	-	-	0.0041 ** >	ns	ns	0.0424 * >	ns	ns	ns
Not Cut vs Cut SpAu	ns	-	-	ns	ns	ns	0.0059 ** >	ns	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	ns	ns	ns	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.11 Auchenorrhyncha abundance on the new margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	0.0001 *** >	ns	0.0186 * >	ns	0.0001 *** >	ns	ns	ns	ns
CUTTING	0.0046 **	-	-	ns	ns	0.0003 ***	ns	0.0230 *	0.0128 *	ns
SOW*CUT	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	0.0424 * >	0.0120 * >	0.0001 *** >	ns	0.0034 ** >	0.0128 * >	ns
Cut SpSu vs Cut SpAu	0.0044 ** >	-	-	ns	ns	ns	ns	ns	ns	ns
Not Cut vs Cut SpSu	ns	0.0017 ** >	0.0460 * >	ns	0.0247 * >	0.0014 ** >	ns	0.0084 ** >	0.0393 * >	ns
Not Cut vs Cut Su	0.0320 * <	-	-	ns	(0.0526) >	0.0001 *** >	ns	(0.0629) >	0.0019 ** >	ns
Not Cut vs Cut SpAu	ns	_	-	0.0291 * >	0.0443 * >	0.0074 ** >	ns	0.0118 * >	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	0.0223 * <	ns	0.0354 * <	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.12 Numbers of species of Auchenorrhyncha on the new margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	0.0058 ** >	ns	ns	ns	ns	ns	ns	ns	0.0056 ** <
CUTTING	ns	-	-	0.0146 *	(0.0560)	0.0004 ***	ns	0.0143 *	ns	ns
SOW*CUT	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	0.0033 ** >	0.0080 ** >	0.0002 *** >	0.0311 * >	0.0024 ** >	ns	ns
Cut SpSu vs Cut SpAu	ns	-	-	ns	ns	0.0480 <	ns	ns	ns	ns
Not Cut vs Cut SpSu	ns	ns	ns	0.0067 ** >	0.0121 * >	0.0003 *** >	ns	0.0089 ** >	ns	ns
Not Cut vs Cut Su	ns	-	-	0.0024 ** >	0.0493 * >	0.0001 *** >	0.0230 * >	(0.0526) >	ns	ns
Not Cut vs Cut SpAu	0.0489 * >	-	-	ns	0.0376 * >	ns	ns	0.0029 ** >	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	ns	ns	ns	0.0335 * <

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.13 Heteroptera abundance on the old margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	ns	ns	ns	ns	ns	0.0042 ** <	ns	ns	ns
CUTTING	ns	-	-	ns	0.0352 *	0.0001 ***	0.0076 **	0.0002 ***	0.0001 ***	ns
SOW*CUT	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	ns	ns	0.0001 *** >	0.0017 ** >	0.0016 ** >	0.0001 *** >	ns
Cut SpSu vs Cut SpAu	ns	-	-	ns	0.0091 ** <	0.0062 ** <	ns	ns	0.0001 *** <	ns
Not Cut vs Cut SpSu	ns	0.0010 *** >	0.0006 *** >	ns	0.0145 * >	0.0001 *** >	0.0006 *** >	0.0066 ** >	0.0001 *** >	ns
Not Cut vs Cut Su	ns	-	-	0.0236 * >	ns	0.0001 *** >	0.0053 ** >	0.0001 *** >	0.0001 *** >	ns
Not Cut vs Cut SpAu	ns	-	-	ns	ns	0.0452 * >	0.0444 * >	ns	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	ns	0.0003 *** <	ns	ns	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.14 Numbers of species of Heteroptera on the old margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	ns	ns	ns	ns	ns	0.0228 * <	ns	ns	ns
CUTTING	ns	-	-	(0.0547)	ns	0.0001 ***	0.0030 **	0.0089 **	0.0001 ***	ns
SOW*CUT	ns	-	-	ns	ns	ns	ns	0.0290 *	ns	ns
Uncut vs Cut	ns	-	-	0.0477 * >	ns	0.0003 *** >	0.0009 *** >	0.0073 * >	0.0060 ** >	ns
Cut SpSu vs Cut SpAu	ns	-	-	ns	ns	0.0002 *** <	ns	ns	0.0001 *** <	ns
Not Cut vs Cut SpSu	ns	0.0417 * >	0.0154 * >	ns	ns	0.0001 *** >	0.0001 *** >	(0.0626) >	0.0001 ** >	ns
Not Cut vs Cut Su	ns	-	-	0.0072 ** >	ns	0.0001 *** >	0.0053 ** >	0.0002 *** >	0.0007 *** >	ns
Not Cut vs Cut SpAu	ns	-	-	ns	ns	ns	0.0356 * >	ns	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	0.0155 * >	0.0001 *** <	ns	ns	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.15 Heteroptera abundance on the new margin 1988-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND									
	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
SOWING	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CUTTING	ns	-	-	ns	0.0001 ***	0.0001 ***	0.0250 *	0.0001 ***	0.0001 ***	ns
SOW*CUT	ns	-	-	ns	ns	0.0185 *	ns	ns	ns	ns
Uncut vs Cut	ns	-	-	ns	0.0001 *** >	0.0001 *** >	0.0160 * >	0.0003 *** >	0.0001 *** >	ns
Cut SpSu vs Cut SpAu	ns	-	-	ns	0.0001 *** <	0.0002 *** <	ns	0.0025 ** <	0.0007 *** <	ns
Not Cut vs Cut SpSu	ns	0.0083 ** >	0.0202 * >	ns	0.0001 *** >	0.0001 *** >	(0.0616) >	0.0001 *** >	0.0001 *** >	ns
Not Cut vs Cut Su	ns	-	-	ns	0.0001 *** >	0.0001 *** >	0.0070 ** >	0.0004 *** >	0.0001 *** >	ns
Not Cut vs Cut SpAu	ns	-	-	ns	ns	(0.0536) >	ns	ns	0.0495 * >	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	0.0209 * <	ns	ns	ns	ns

ns = not significant, * P < = 0.05, ** P < = 0.01, *** P < = 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.16 Numbers of species of Heteroptera on the new margin 1988-1991
Summary of significance of differences

Effect or Comparison	Sep 88	May 89	Jul 89	Sep 89	May 90	Jul 90	Sep 90	May 91	Jul 91	Sep 91
	SAMPLING ROUND									
SOWING	ns	ns	ns	ns	ns	0.0297 * <	ns	ns	ns	ns
CUTTING	ns	-	-	ns	0.0197 *	0.0001 ***	0.0189 *	ns	0.0001 ***	ns
SOW*CUT	ns	-	-	0.0478 *	ns	ns	ns	ns	ns	0.0114 *
Uncut vs Cut	ns	-	-	ns	0.0059 ** >	0.0001 *** >	0.0164 * >	ns	0.0024 ** >	ns
Cut SpSu vs Cut SpAu	ns	-	-	ns	ns	0.0036 ** <	ns	ns	0.0001 *** <	ns
Not Cut vs Cut SpSu	ns	0.0305 * >	(0.0730) >	0.0451 * >	0.0056 ** >	0.0002 *** >	ns	(0.0511) >	0.0001 *** >	ns
Not Cut vs Cut Su	ns	-	-	ns	0.0089 ** >	0.0001 *** >	0.0015 ** >	ns	0.0006 *** >	ns
Not Cut vs Cut SpAu	ns	-	-	ns	ns	ns	ns	ns	ns	ns
Spray U/Spray vs U/NC	ns	-	-	ns	ns	0.0067 ** <	0.0071 ** <	ns	ns	ns

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.17 Aphid abundance on the old margins 1989-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND				
	May 89	May 90	Jul 90	Jul 91	Sep 91
SOWING	ns	ns	0.0347 * <	ns	ns
CUTTING	-	ns	ns	0.0288 *	0.0031 **
SOW*CUT	-	0.0122 *	ns	ns	ns
Uncut vs Cut	-	ns	ns	ns	ns
Cut SpSu vs Cut SpAu	-	ns	ns	ns	0.0032 ** >
Not Cut vs Cut SpSu	ns	ns	ns	ns	0.0076 ** <
Not Cut vs Cut Su	-	ns	ns	0.0197 * >	ns
Not Cut vs Cut SpAu	-	ns	ns	ns	ns
Spray U/Spray vs U/NC	-	ns	ns	ns	ns

ns = not significant, * P < = 0.05, ** P < = 0.01, *** P < = 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.18 Aphid abundance on the new margins 1989-1991
Summary of significance of differences

Effect or Comparison	SAMPLING ROUND				
	May 89	May 90	Jul 90	Jul 91	Sep 91
SOWING	ns	ns	ns	ns	ns
CUTTING	-	(0.0607)	(0.0851)	ns	ns
SOW*CUT	-	ns	ns	ns	ns
Uncut vs Cut	-	ns	ns	ns	(0.0587) <
Cut SpSu vs Cut SpAu	-	0.0180 * >	0.0116 * <	ns	ns
Not Cut vs Cut SpSu	ns	0.0183 .* <	ns	ns	0.0471 * <
Not Cut vs Cut Su	-	ns	ns	ns	(0.0793) <
Not Cut vs Cut SpAu	-	ns	ns	ns	ns
Spray U/Spray vs U/NC	-	ns	ns	ns	0.0407 * >

ns = not significant, * P <= 0.05, ** P <= 0.01, *** P <= 0.001, (P values close to 0.05 bracketed)
Arrows on lines below P values denote direction of significant contrast

Table 8.19 Mean differences per sample unit (0.5 m^2) between old and new margin[1]
Results of paired t-tests (P values and significance levels given in parentheses[2])

Sampling Round	Spiders		Auchenorrhyncha		Heteroptera	
	Abundance	No. species	Abundance	No. species	Abundance	No. species
Sep 1988	17.8 (0.0003 ***)	1.02 (0.0338 *)	10.5 (0.0001 ***)	1.29 (0.0001 ***)	-2.1 (0.1016 ns)	0.17 (0.5461 ns)
May 1989	30.4 (0.0003 ***)	2.03 (0.0016 **)	3.1 (0.6008 ns)	0.14 (0.2933 ns)	1.1 (0.4887 ns)	-0.27 (0.1995 ns)
Jul 1989	-3.7 (0.6422 ns)	0.20 (0.7523 ns)	4.3 (0.3233 ns)	0.93 (0.0177 *)	-0.3 (0.7227 ns)	0.17 (0.6235 ns)
Sep 1989	18.4 (0.0033 **)	0.86 (0.0284 *)	-3.0 (0.0510 ns)	-0.53 (0.0102 *)	0.4 (0.3459 ns)	0.08 (0.6194 ns)
May 1990	8.9 (0.0038 **)	1.00 (0.0184 *)	2.2 (0.6436 ns)	-0.33 (0.1306 ns)	-5.6 (0.1337 ns)	-0.14 (0.5534 ns)
Jul 1990	-4.9 (0.0693 ns)	0.14 (0.7138 ns)	-1.3 (0.6914 ns)	0.08 (0.7994 ns)	3.6 (0.0191 *)	0.67 (0.0633 ns)
Sep 1990	2.8 (0.6002 ns)	1.03 (0.0229 *)	-18.6 (0.0233 *)	0.16 (0.5105 ns)	0.9 (0.1892 ns)	0.22 (0.3753 ns)
May 1991	12.2 (0.0001 ***)	1.38 (0.0044 **)	-1.2 (0.7055 ns)	0.15 (0.5150 ns)	-0.5 (0.6713 ns)	0.46 (0.0218 *)
Jul 1991	-2.6 (0.1464 ns)	0.10 (0.7636 ns)	3.1 (0.3007 ns)	-0.27 (0.3665 ns)	0.0 (0.9917 ns)	0.00 (1.0000 ns)
Sep 1991	8.3 (0.4564 ns)	1.20 (0.0051 **)	6.5 (0.4455 ns)	0.28 (0.4016 ns)	-0.6 (0.6625 ns)	-0.47 (0.3762 ns)

[1]Positive values indicate abundance/number of species greater on old than on new margin
[2]ns = not significant, * $P <= 0.05$, ** $P <= 0.01$, *** $P <= 0.001$

Table 8.20 Values of r-squared for the regression relationships between vegetation height and abundance or species richness of invertebrates

Group	Year	Abundance	SR
Total Invertebrates	1989	61.8 ***	-
	1990	54.8 ***	-
	1991	0.0 ns	-
Spiders	1989	82.6 ***	79.8 ***
	1990	58.1 ***	61.2 ***
	1991	65.4 ***	39.8 ***
Auchenorrhyncha	1989	1.5 ns	38.9 *
	1990	0.0 ns	13.6 ns
	1991	15.5 ns	0.0 ns
Heteroptera	1989	20.4 ns	36.6 *
	1990	54.6 ***	37.2 *
	1991	30.3 ns	0.0 ns
Coleoptera	1989	32.5 *	-
	1990	25.5 ns	-
	1991	45.3 *	-
Diptera	1989	0.0 ns	-
	1990	0.0 ns	-
	1991	23.0 ns	-
Hymenoptera	1989	16.8 ns	-
	1990	0.0 ns	-
	1991	23.2 ns	-

ns = not significant, * $P <= 0.05$, ** $P <= 0.01$, *** $P <= 0.001$

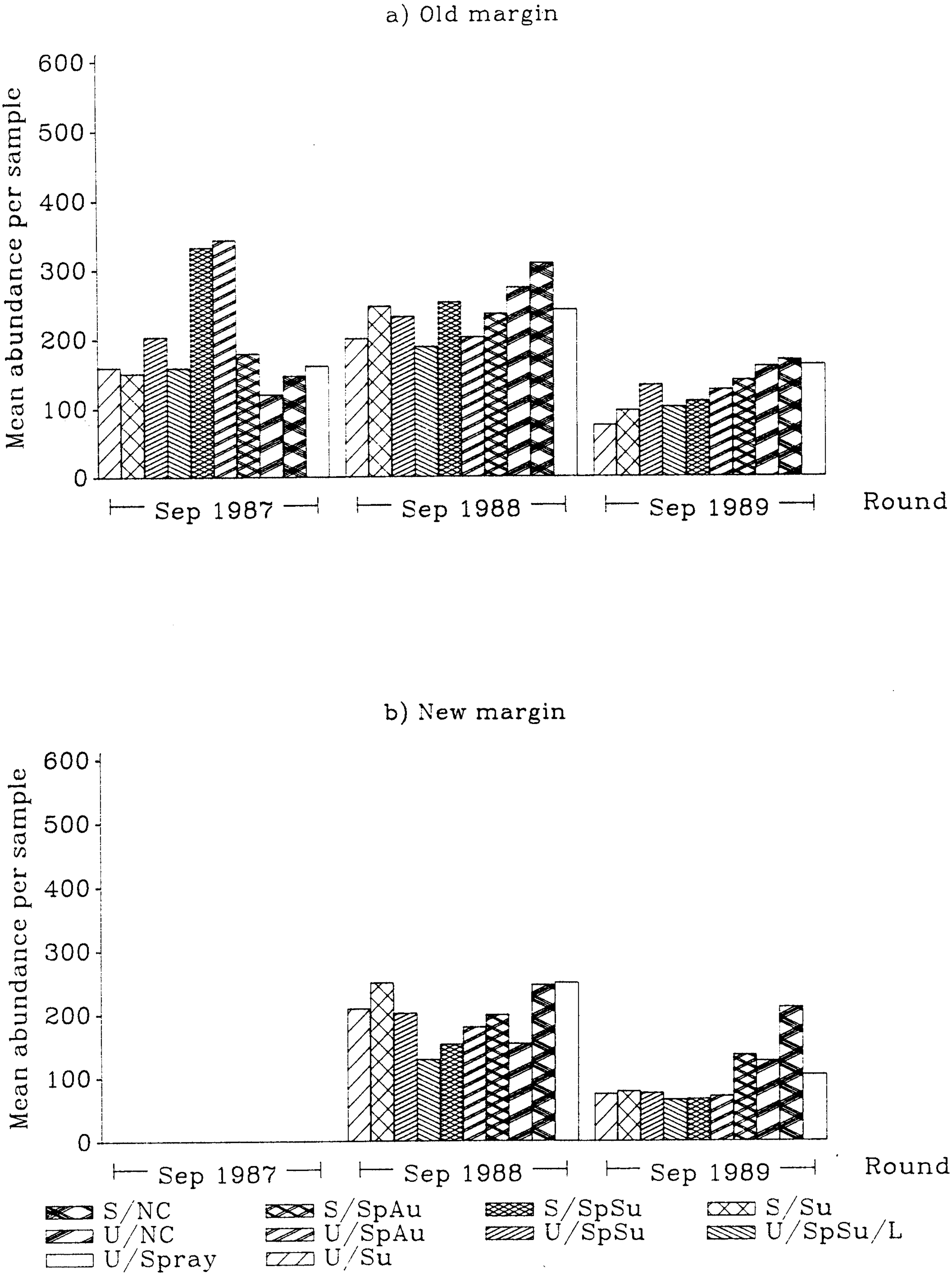


Figure 8.1 Total invertebrate abundances in 1987, 1988 and 1989
Sown treatments crosshatched

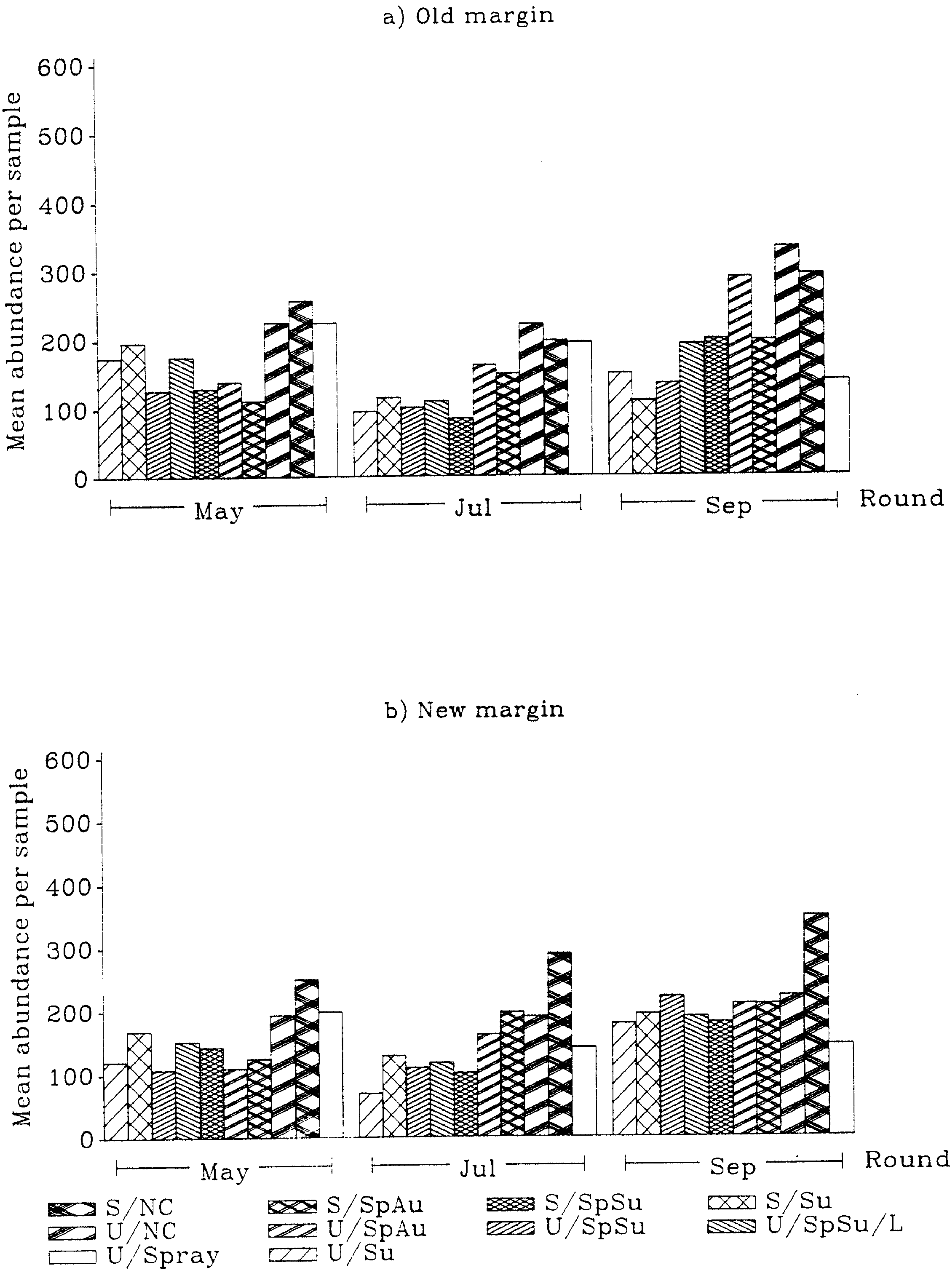


Figure 8.2 Total invertebrate abundance in 1990
Sown treatments crosshatched

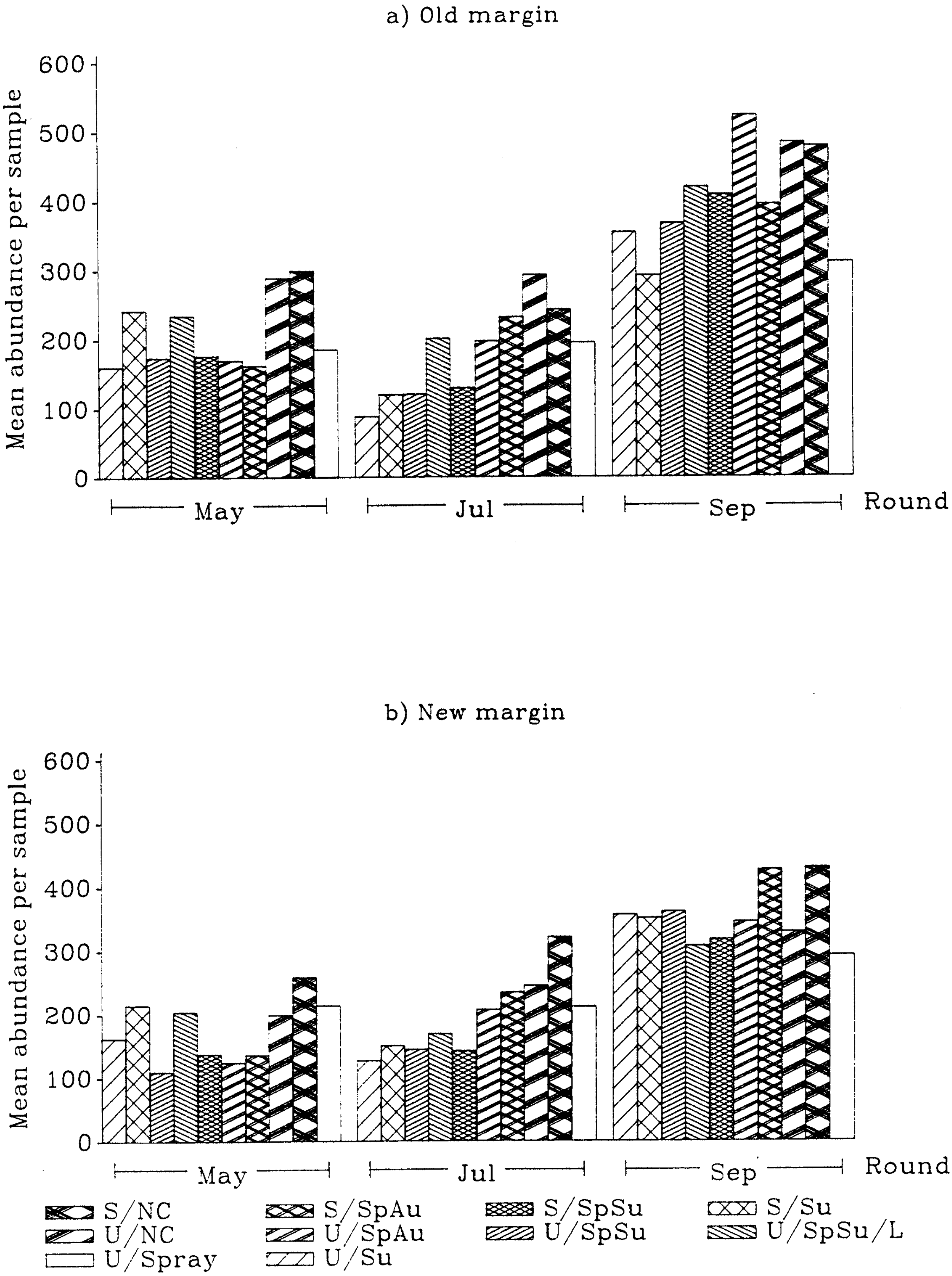
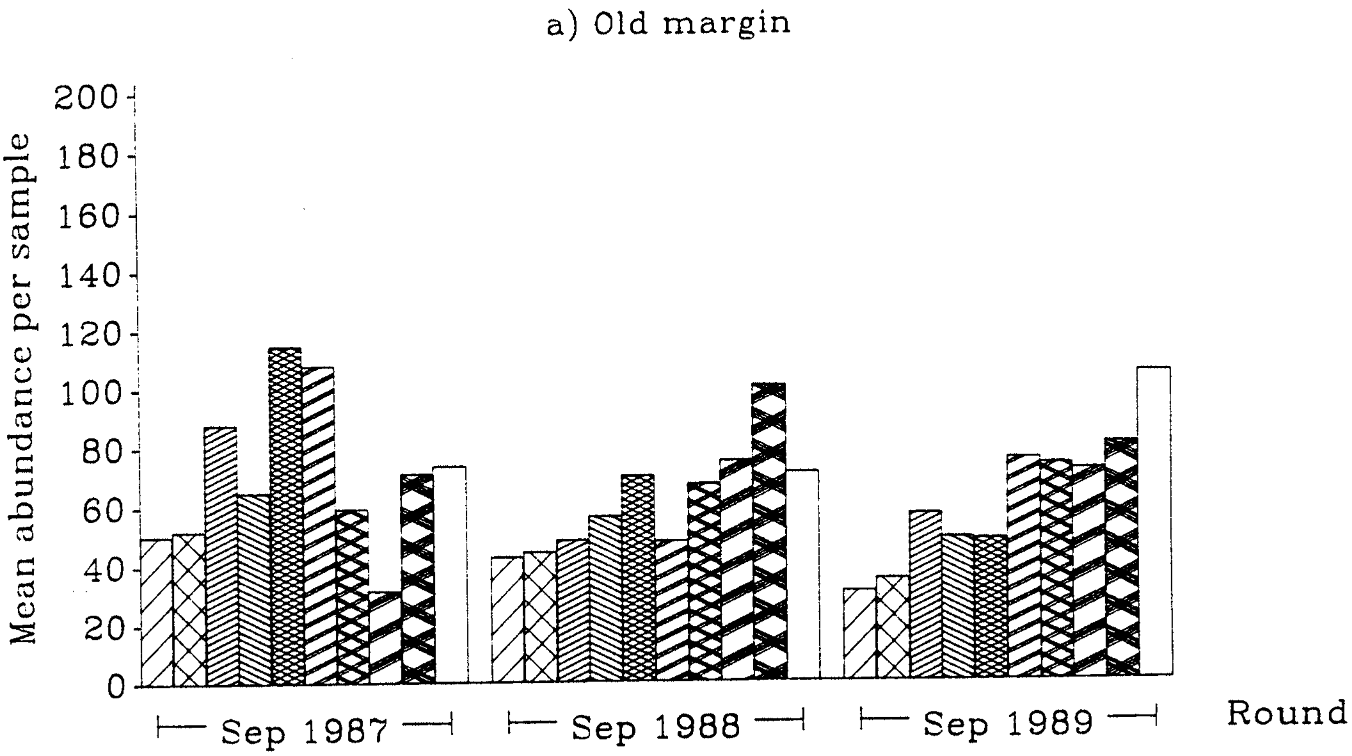


Figure 8.3 Total invertebrate abundance in 1991
Sown treatments crosshatched



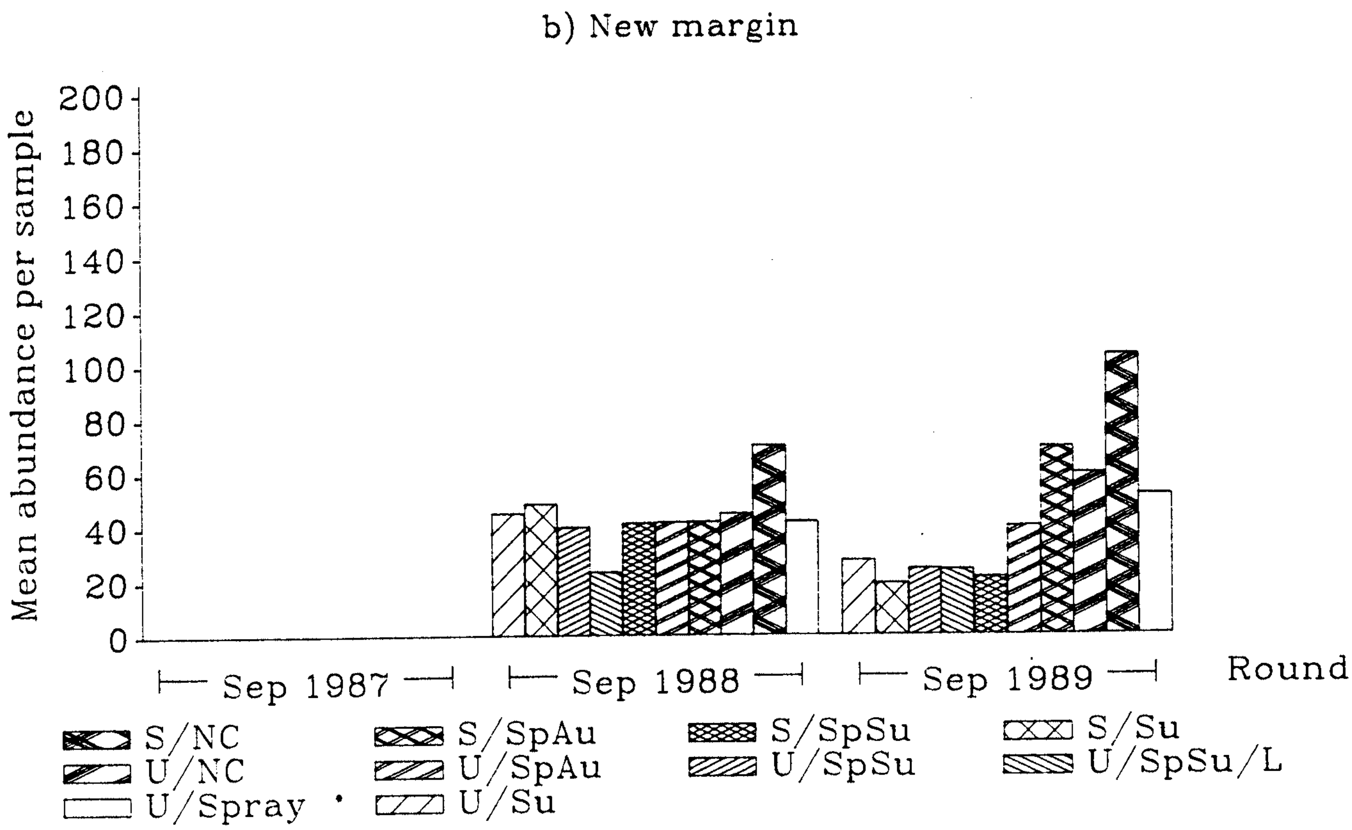


Figure 8.4 Spider abundances in 1987, 1988 and 1989
Sown treatments crosshatched

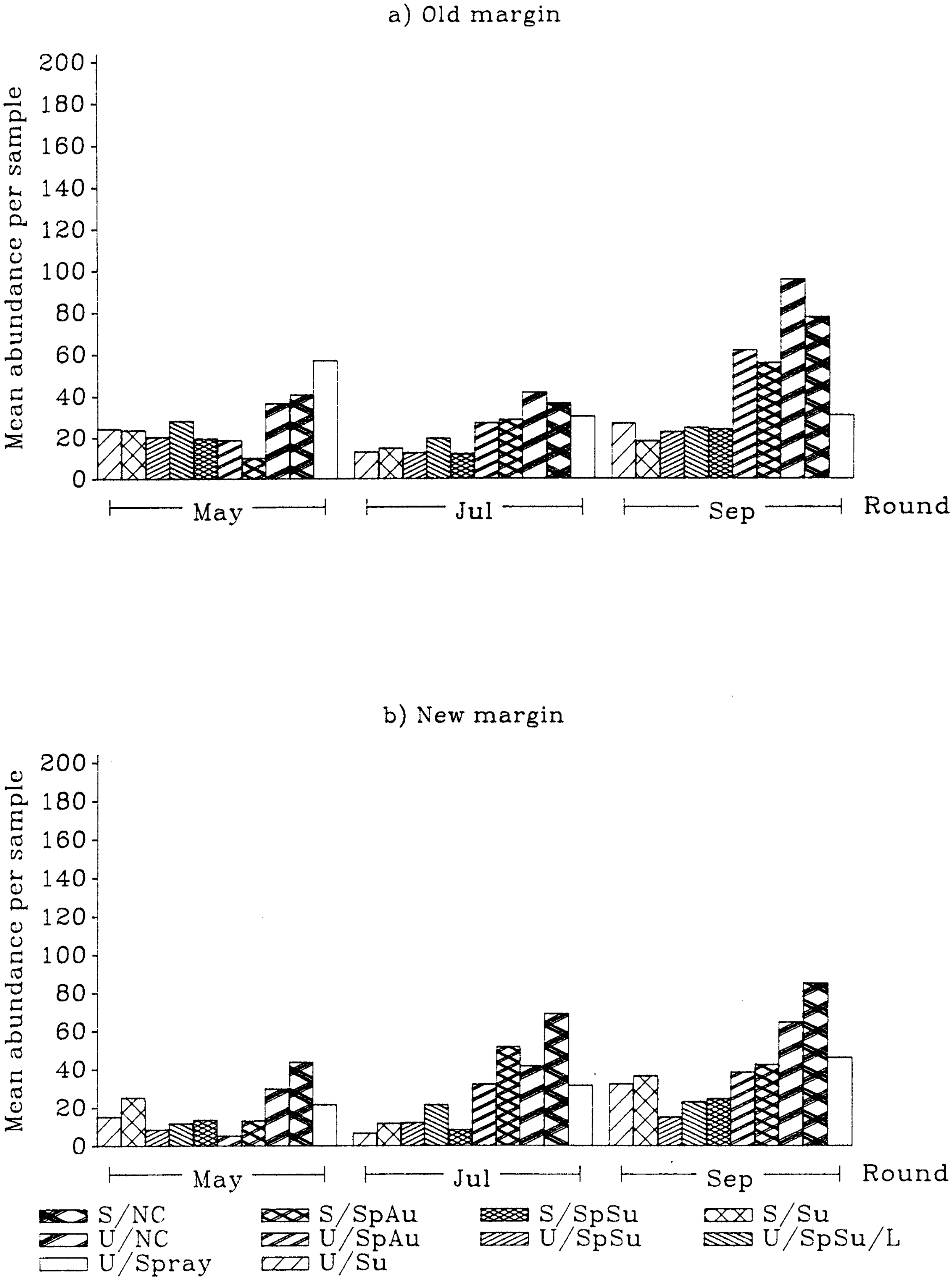


Figure 8.5 Spider abundance in 1990
Sown treatments crosshatched

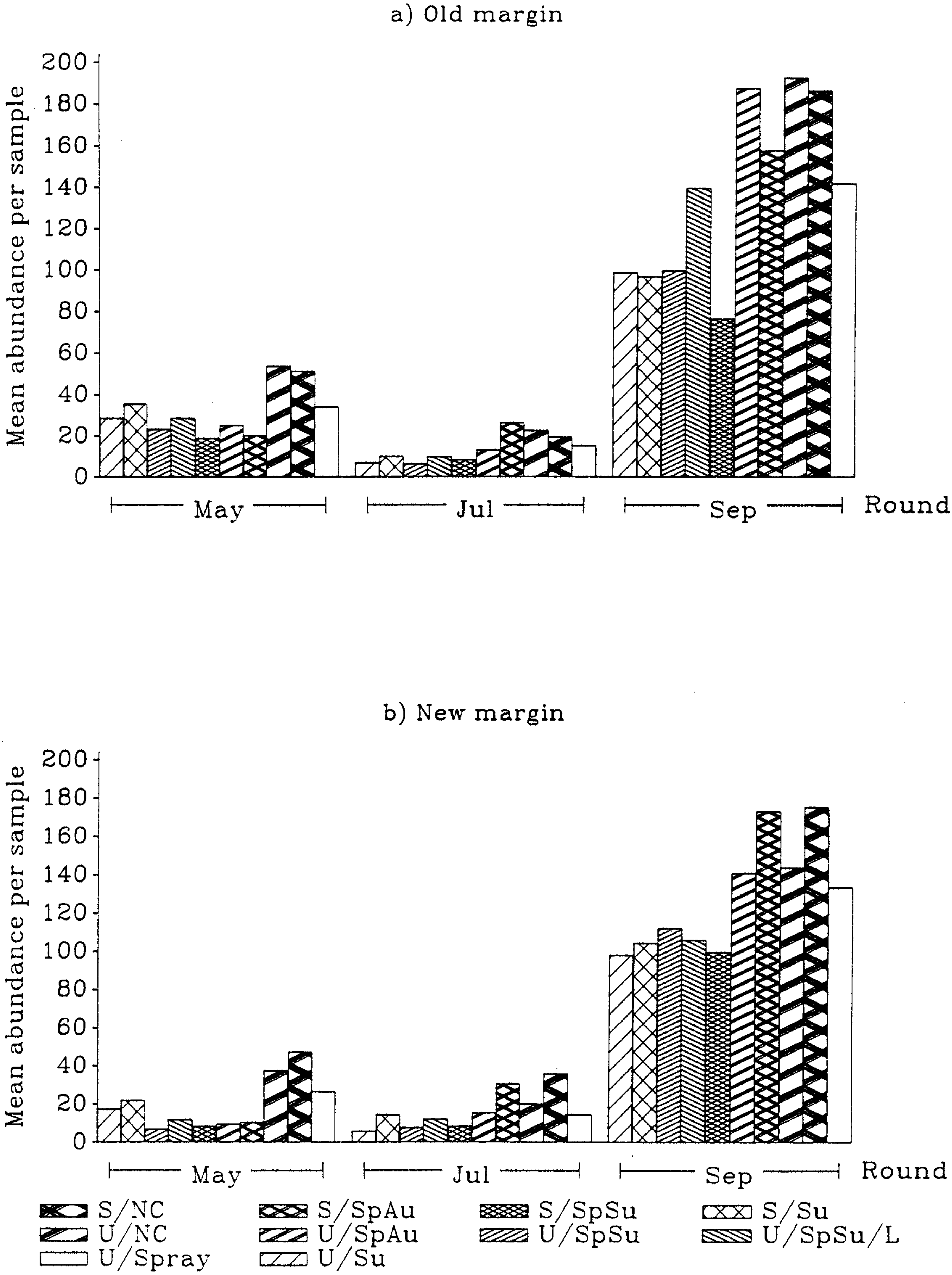


Figure 8.6 Spider abundance in 1991
Sown treatments crosshatched

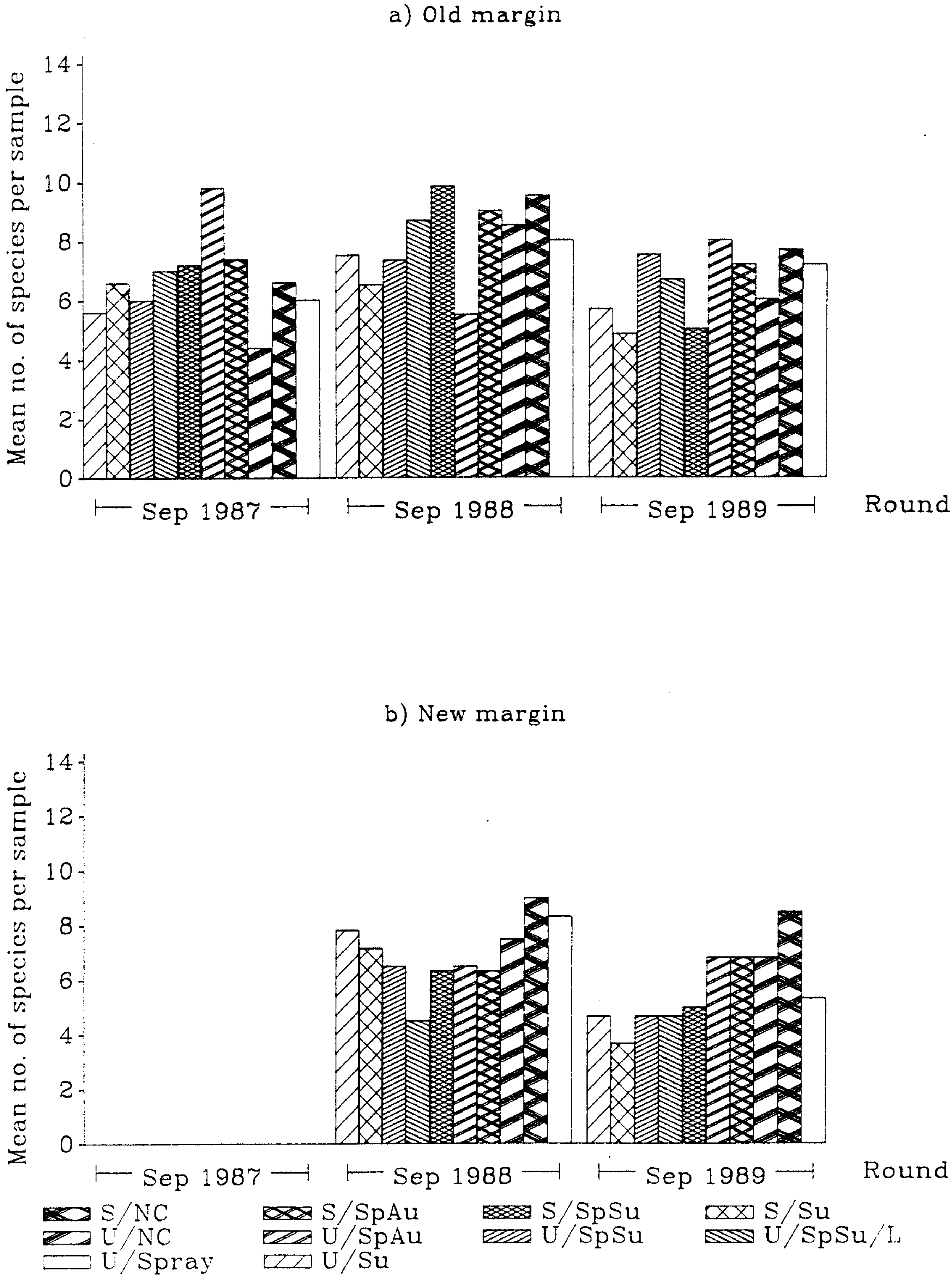


Figure 8.7 Minimum number of species of spiders in 1987, 1988 and 1989
Sown treatments crosshatched

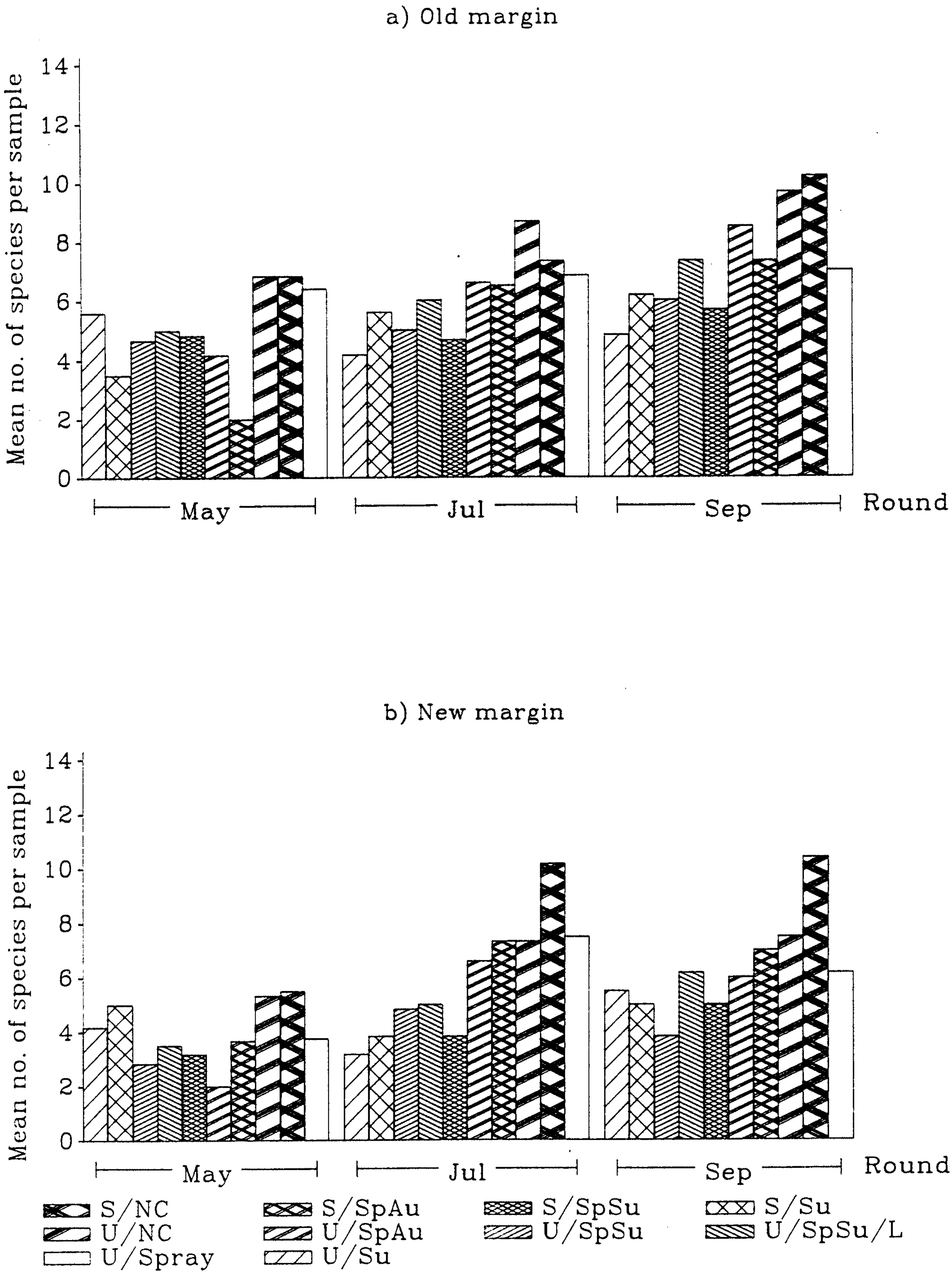


Figure 8.8 Minimum number of species of spiders in 1990
Sown treatments crosshatched

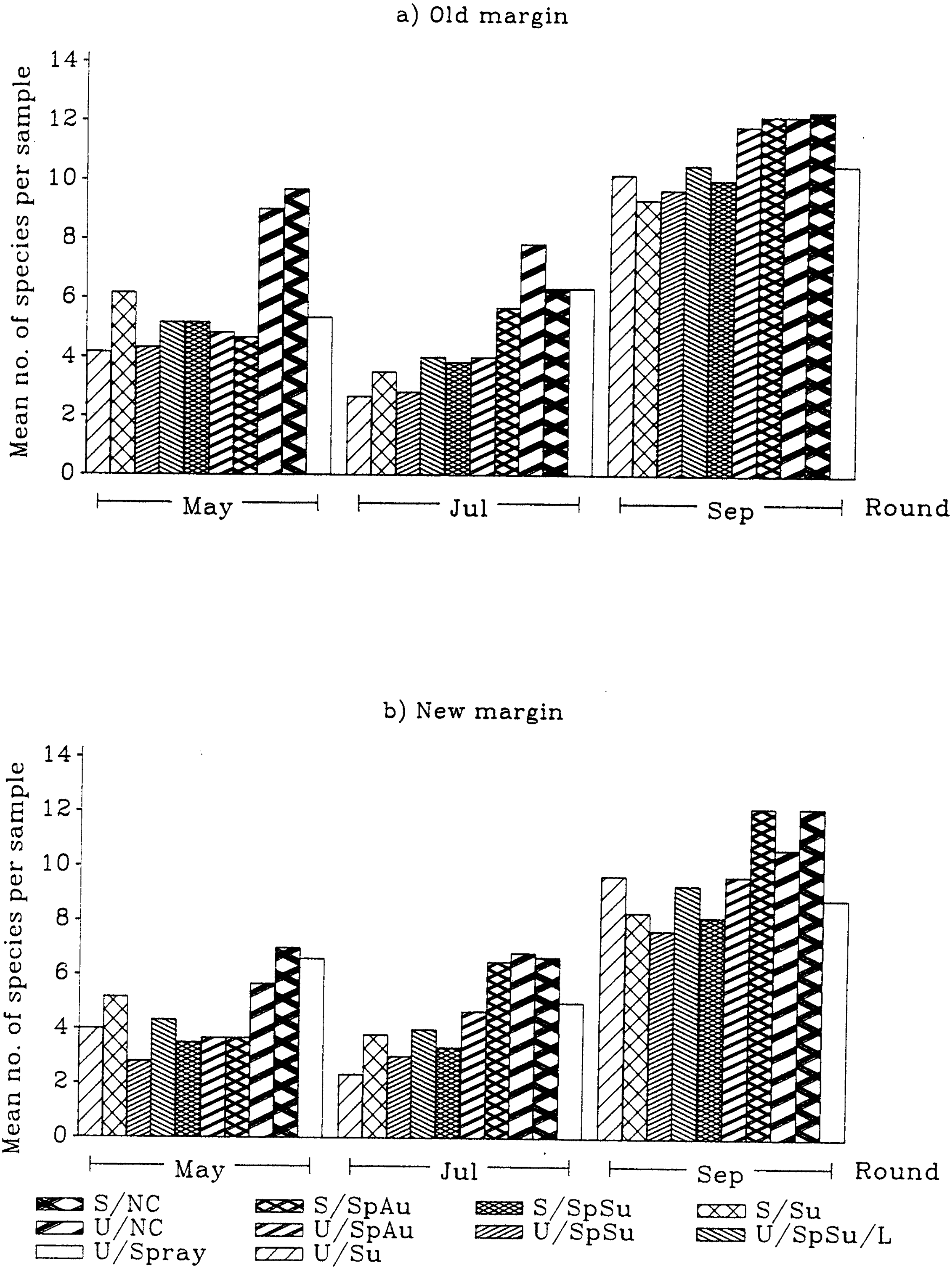


Figure 8.9 Minimum number of species of spiders in 1991
Sown treatments crosshatched

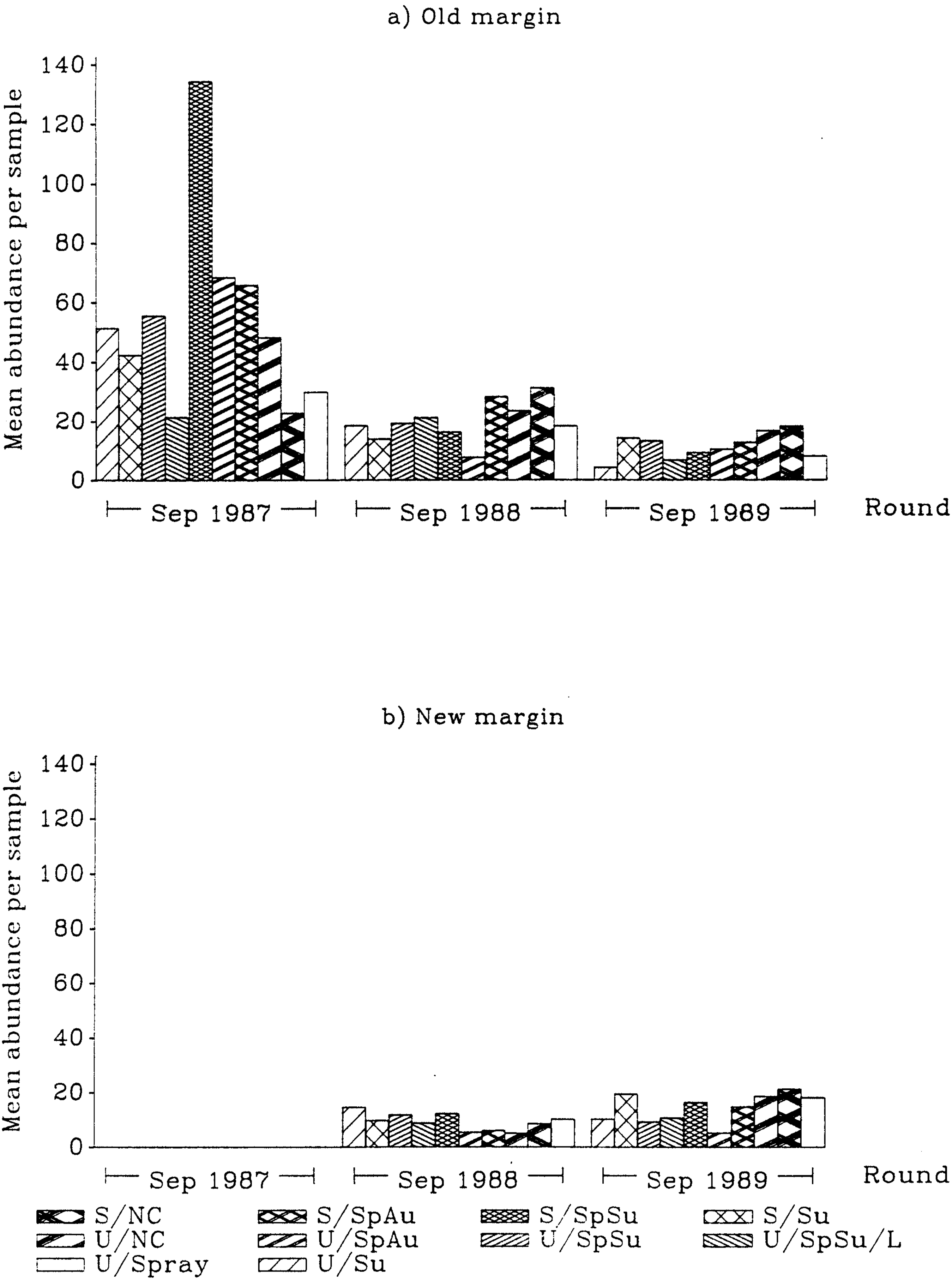


Figure 8.10 Auchenorrhyncha abundances in 1987, 1988 and 1989
Sown treatments crosshatched

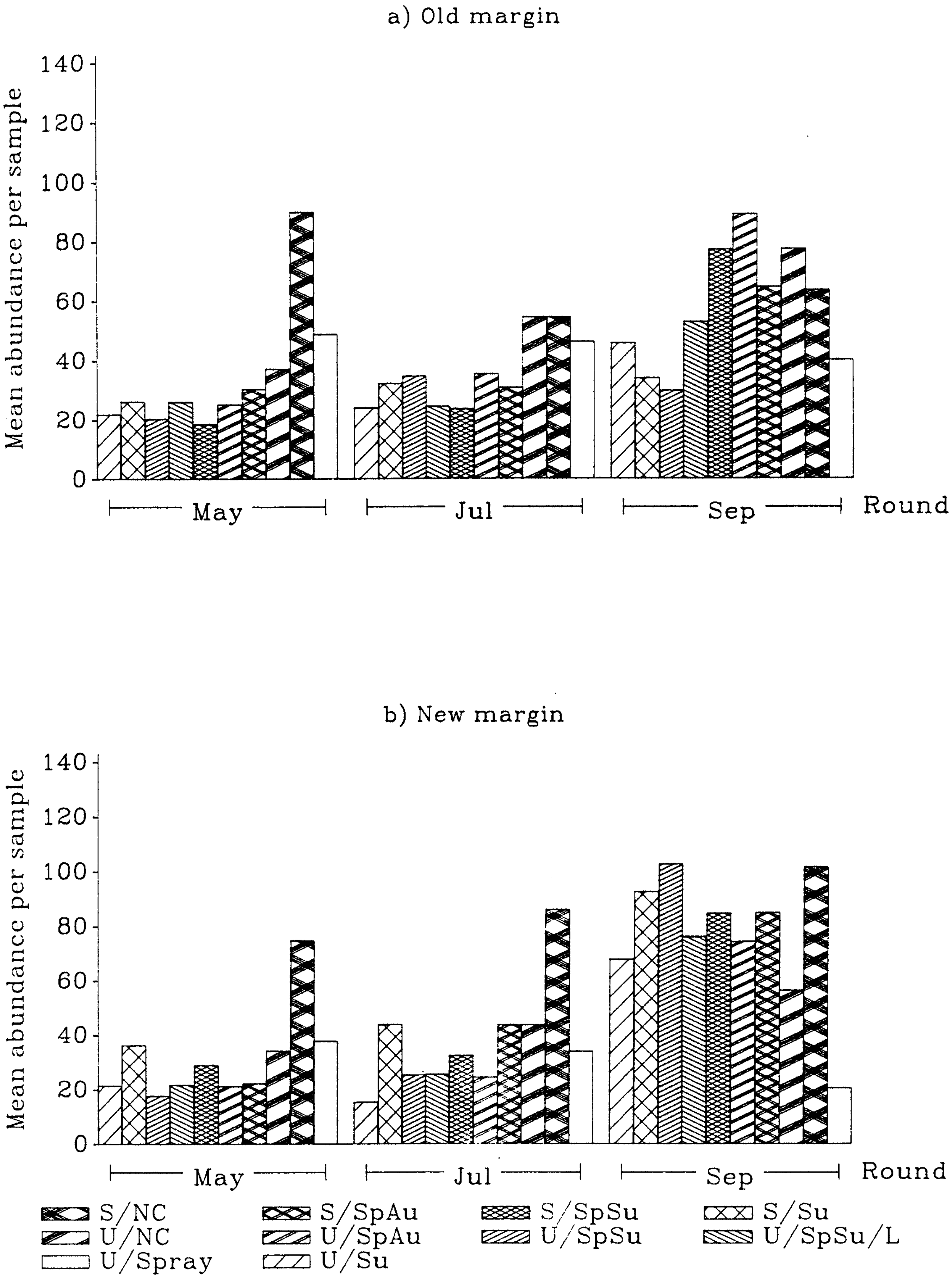


Figure 8.11 Auchenorrhyncha abundance in 1990
Sown treatments crosshatched

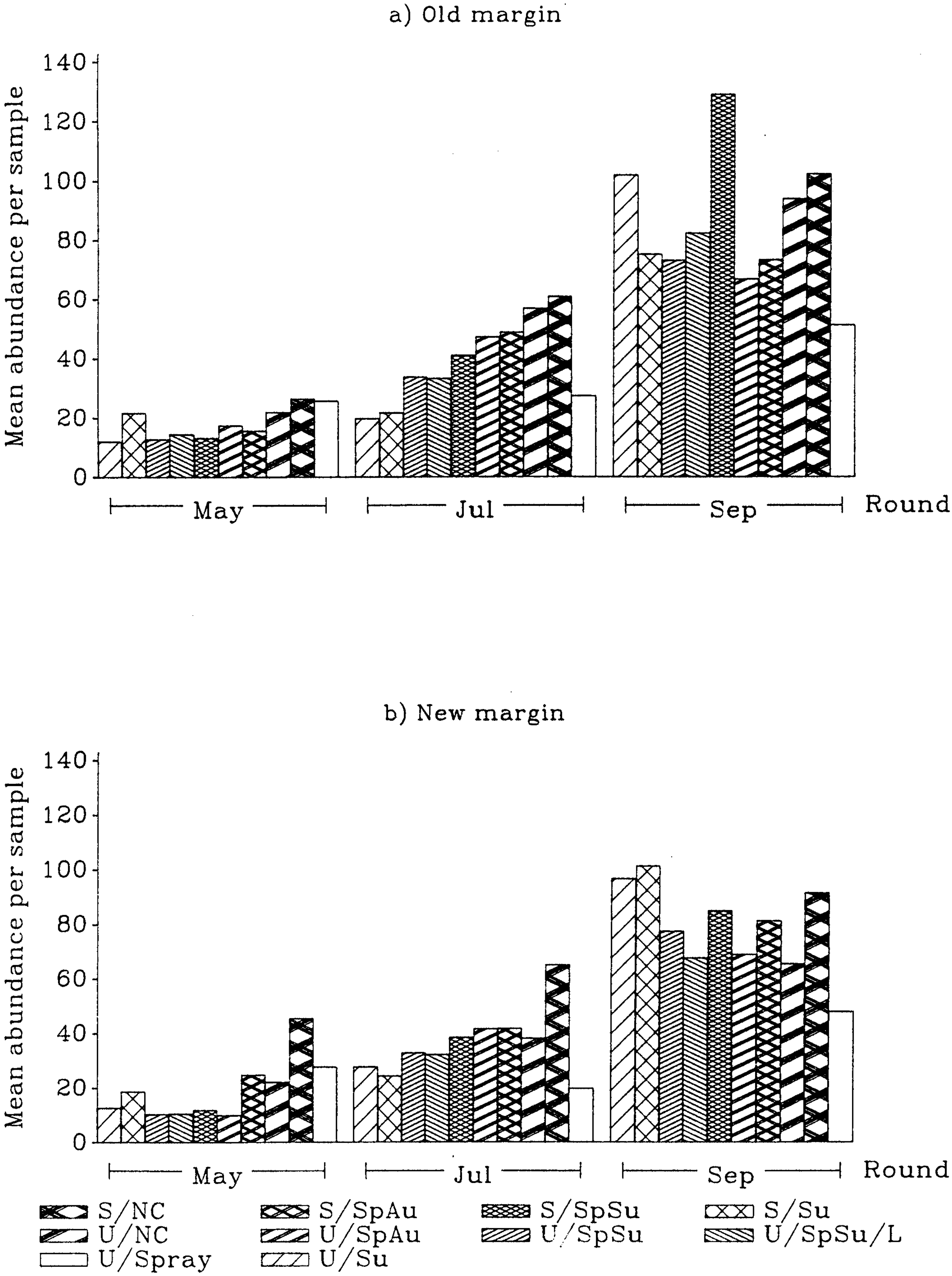


Figure 8.12 Auchenorrhyncha abundance in 1991
Sown treatments crosshatched

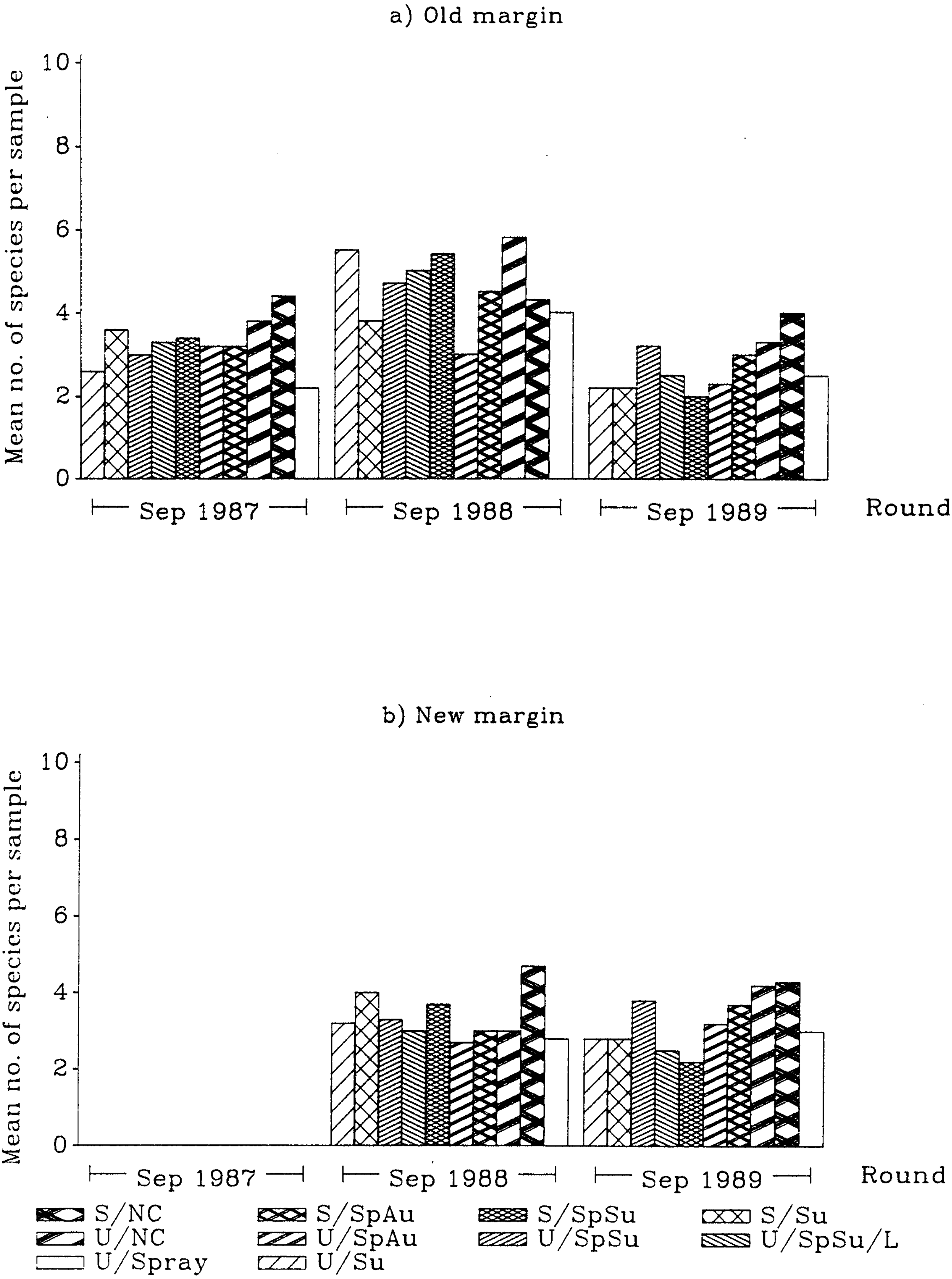


Figure 8.13 Minimum number of species of Auchenorrhyncha in 1987, 1988 and 1989
Sown treatments crosshatched

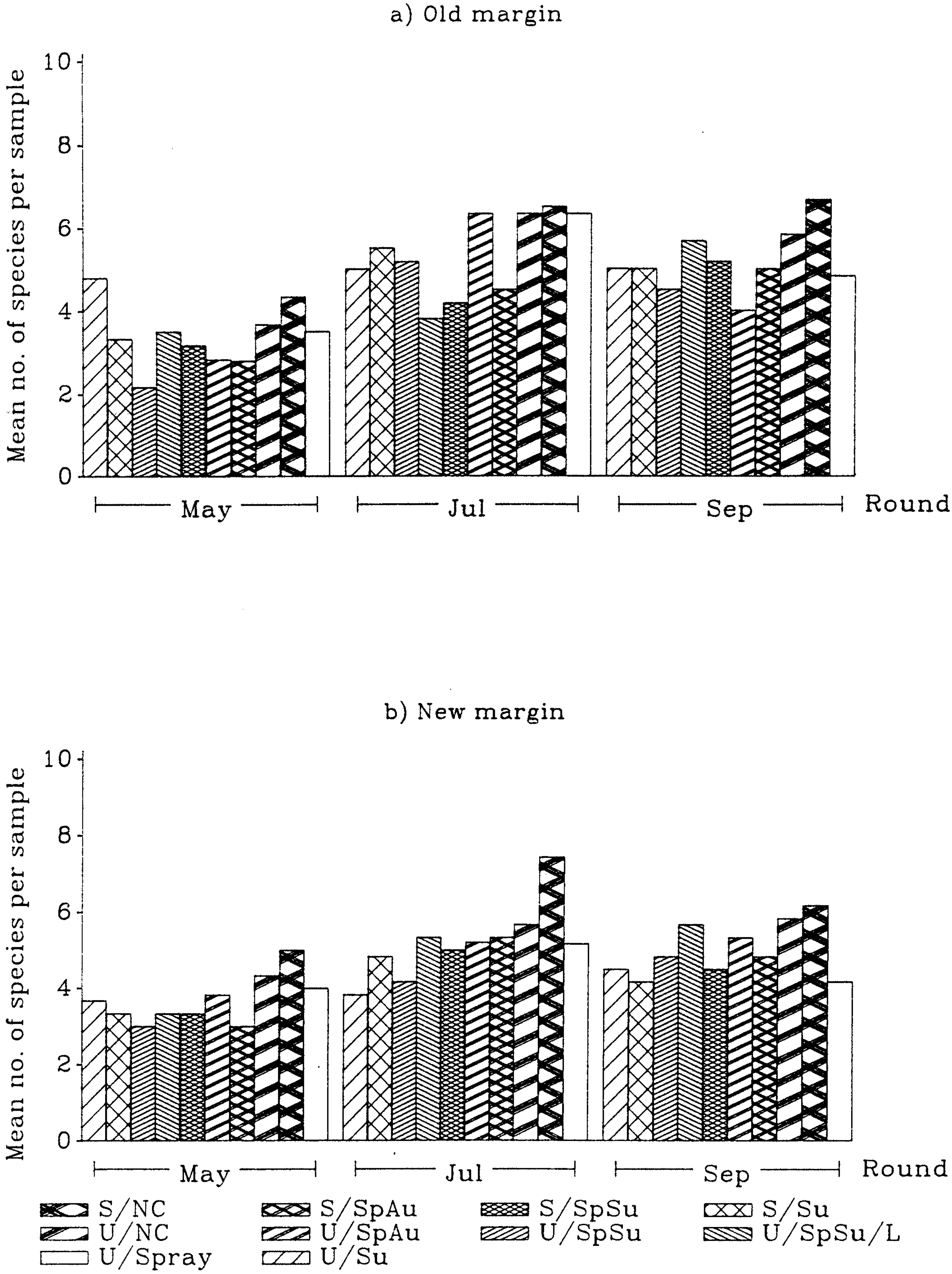


Figure 8.14 Minimum number of species of Auchenorrhyncha in 1990
Sown treatments crosshatched

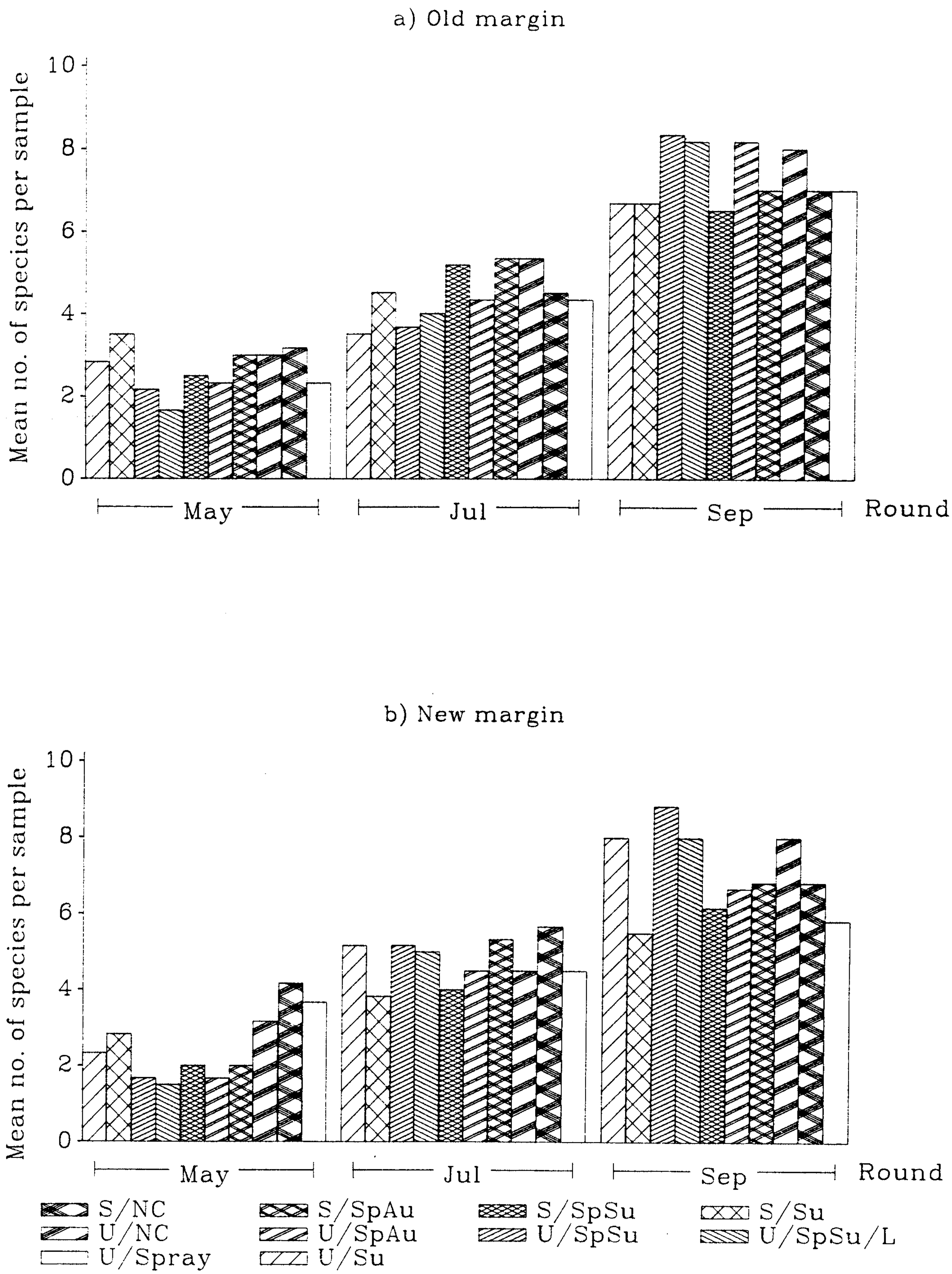


Figure 8.15 Minimum number of species of Auchenorrhyncha in 1991
Sown treatments crosshatched

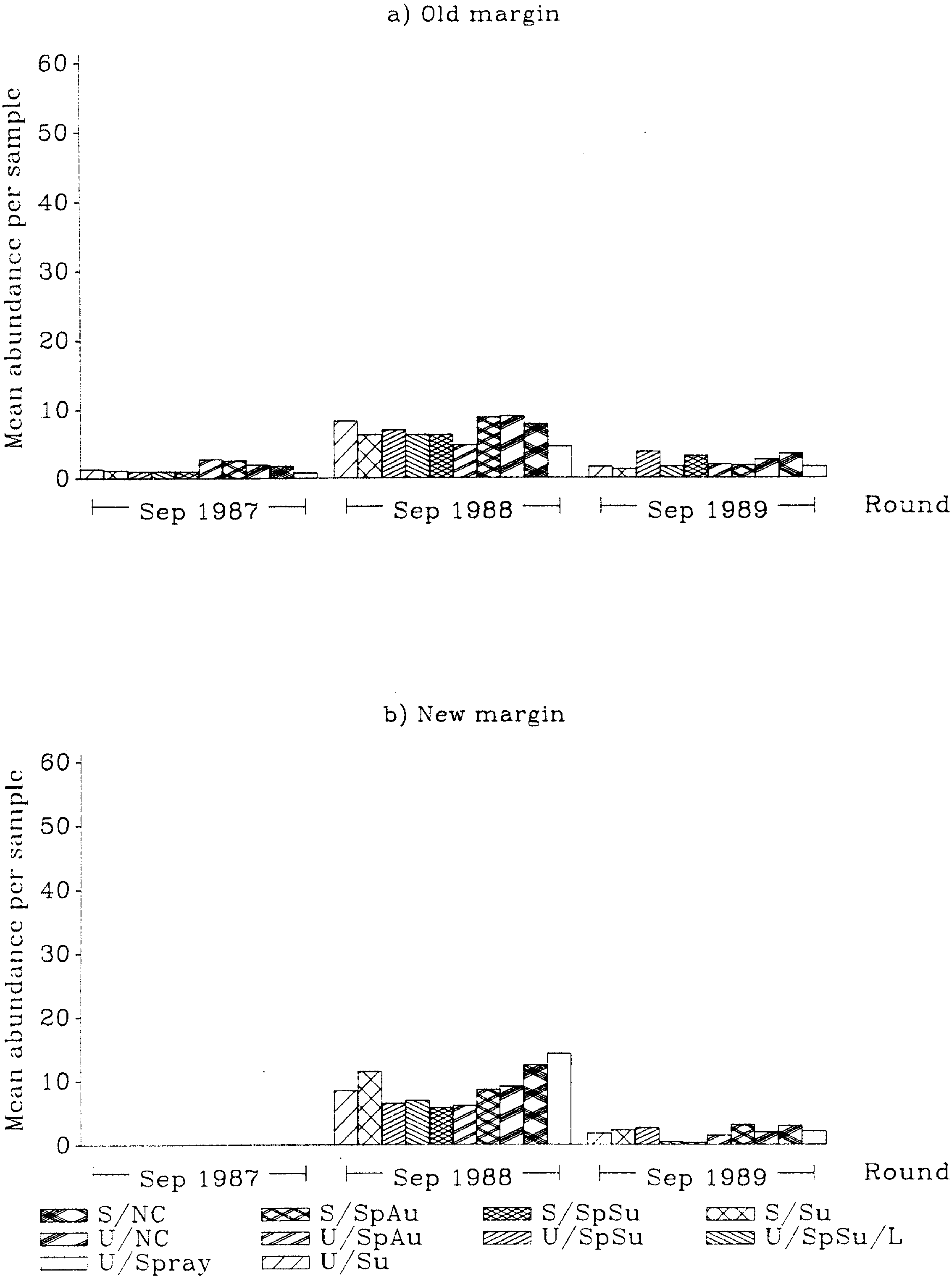


Figure 8.16 Heteroptera abundances in 1987, 1988 and 1989
Sown treatments crosshatched

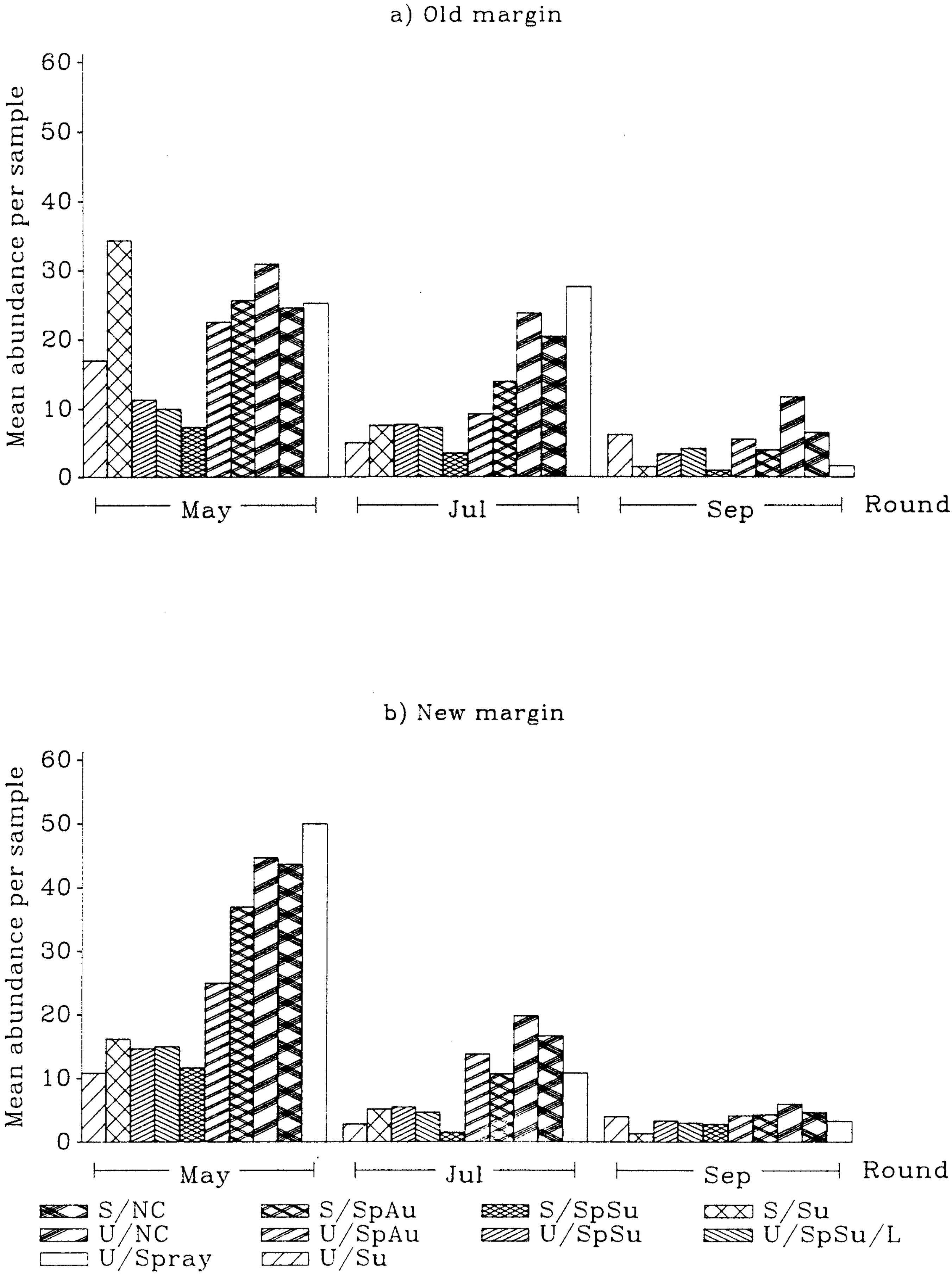


Figure 8.17 Heteroptera abundance in 1990
Sown treatments crosshatched

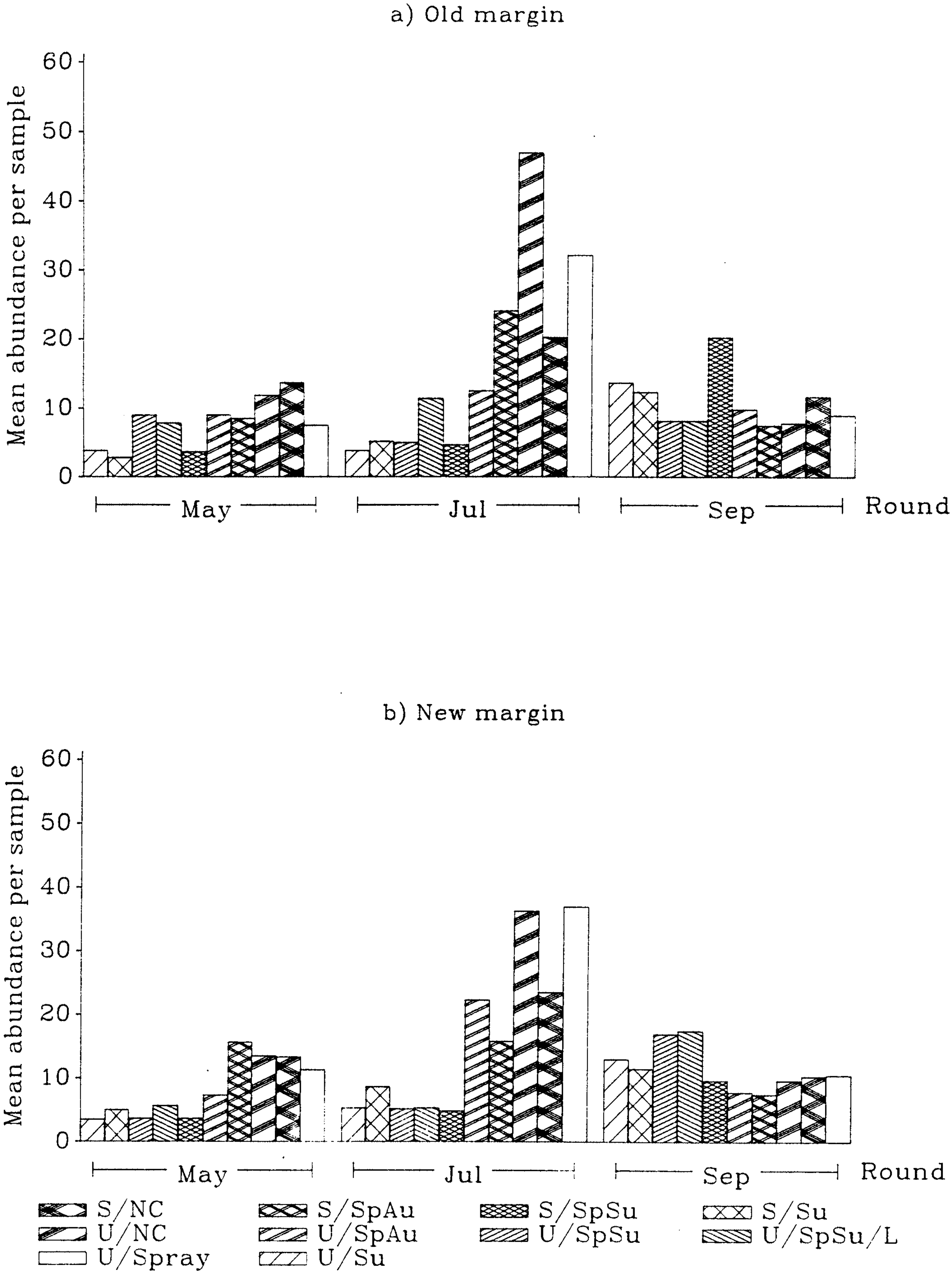
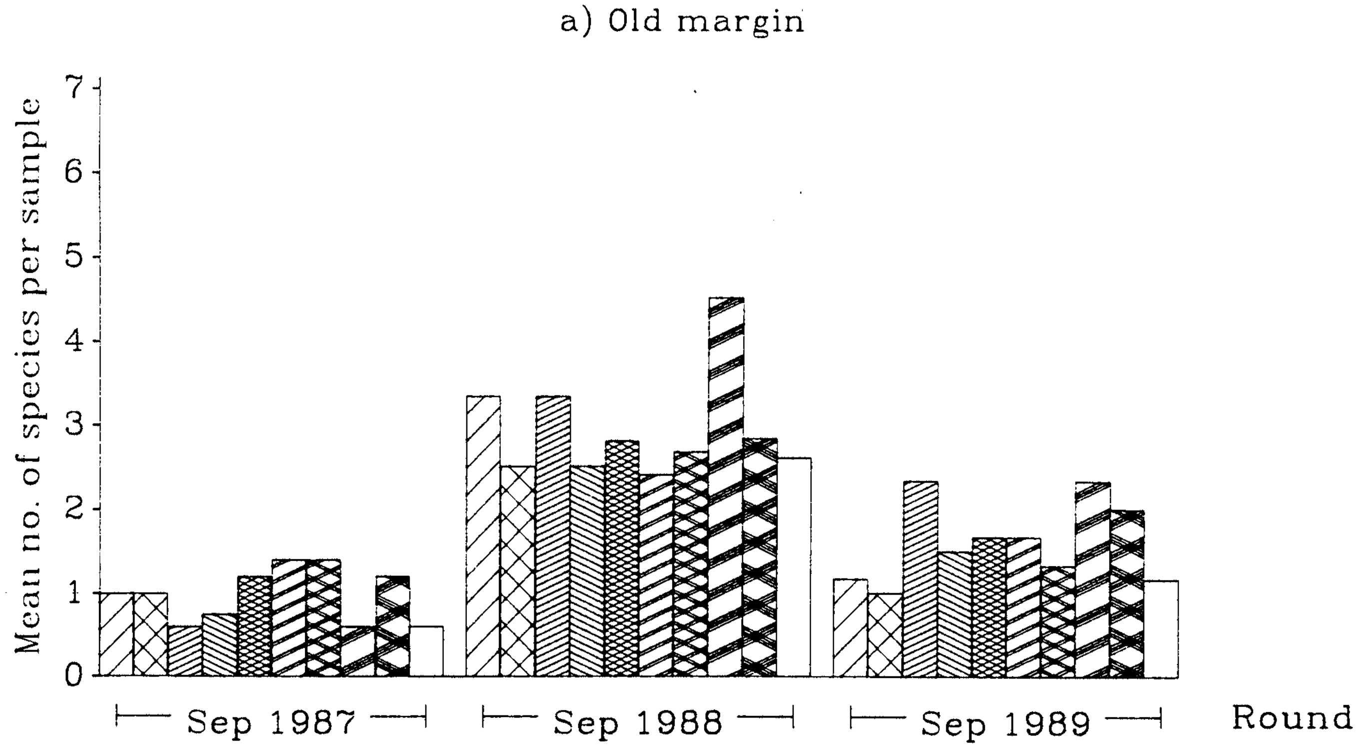


Figure 8.18 Heteroptera abundance in 1991
Sown treatments crosshatched



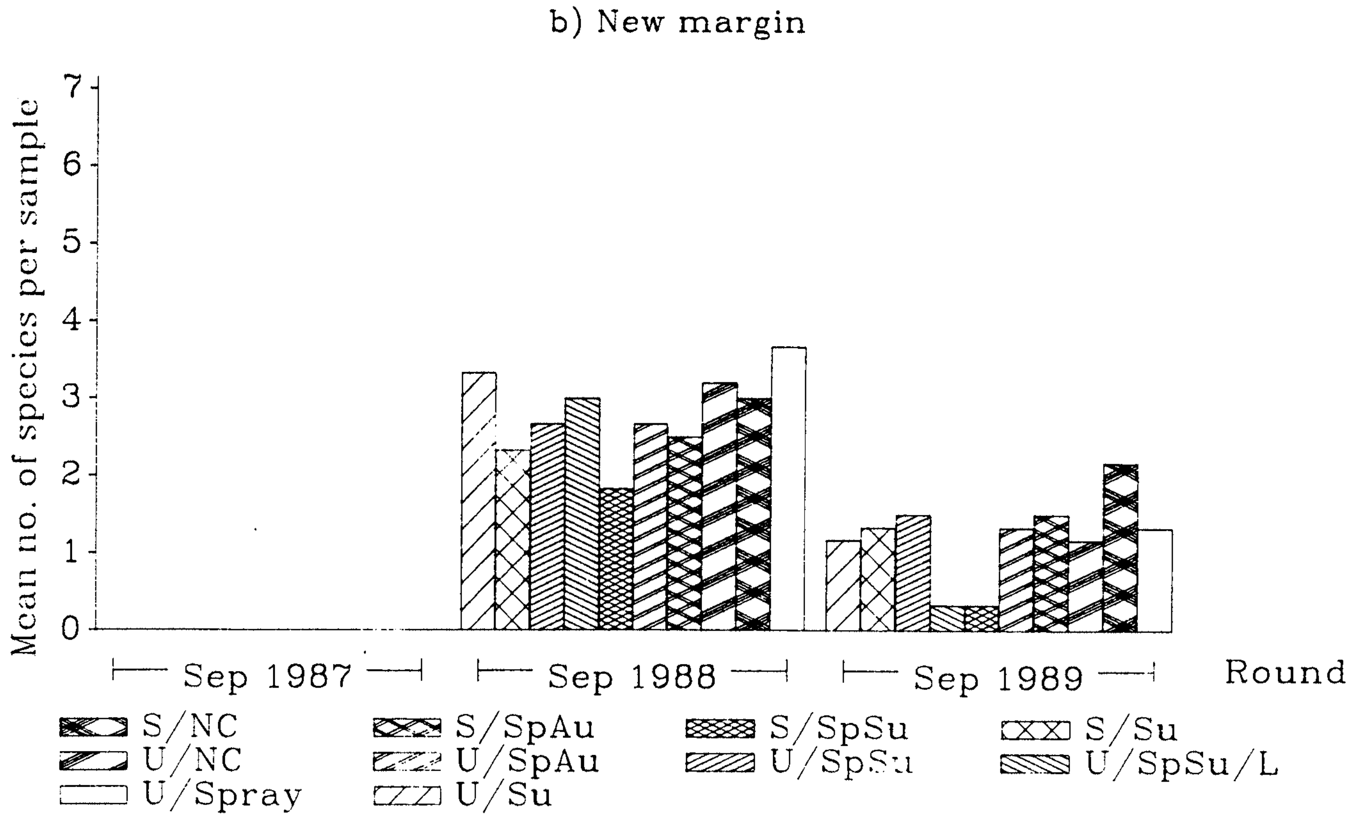


Figure 8.19 Minimum number of species of Heteroptera in 1987, 1988 and 1989
Sown treatments crosshatched

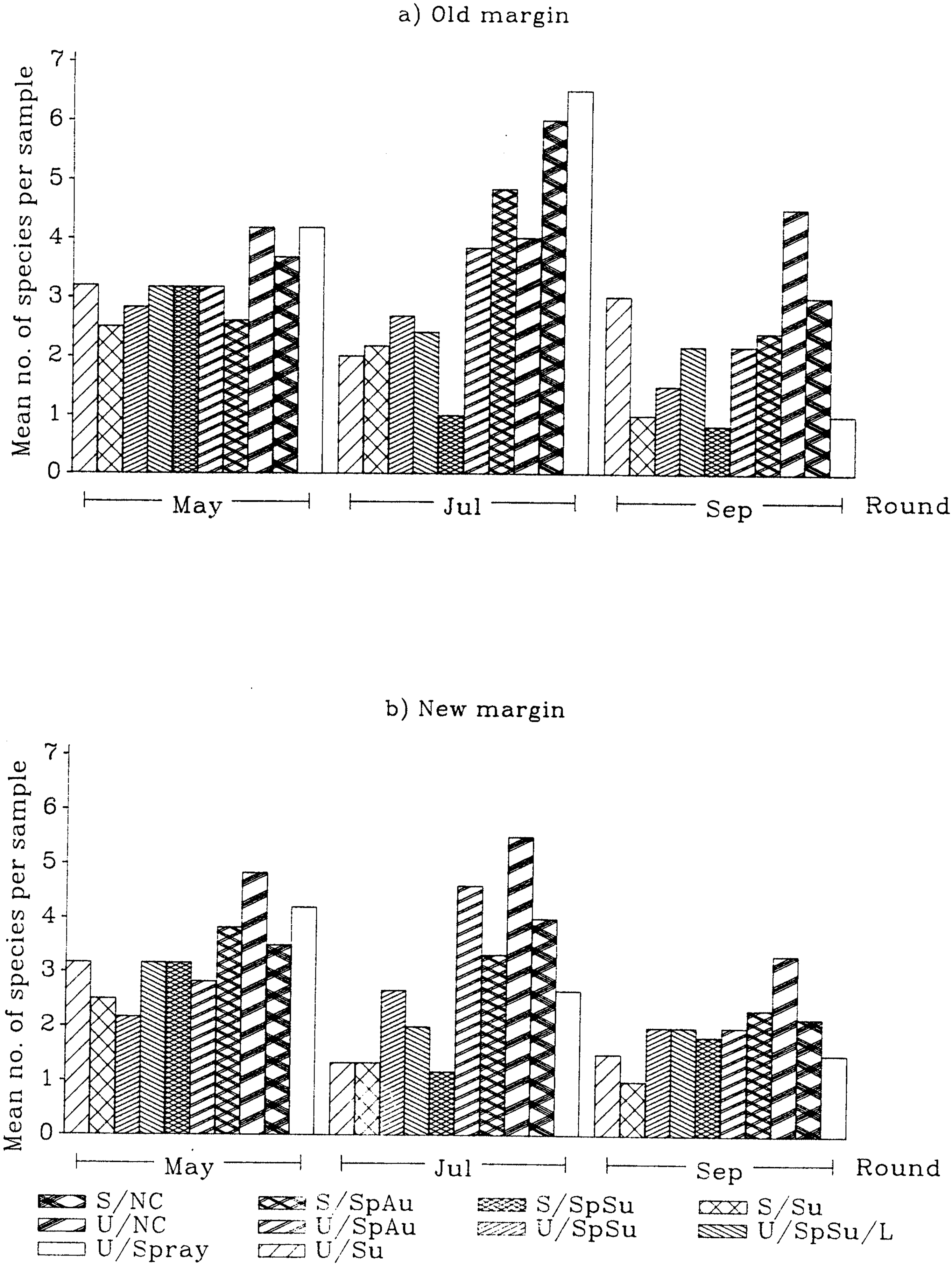


Figure 8.20 Minimum number of species of Heteroptera in 1990
Sown treatments crosshatched

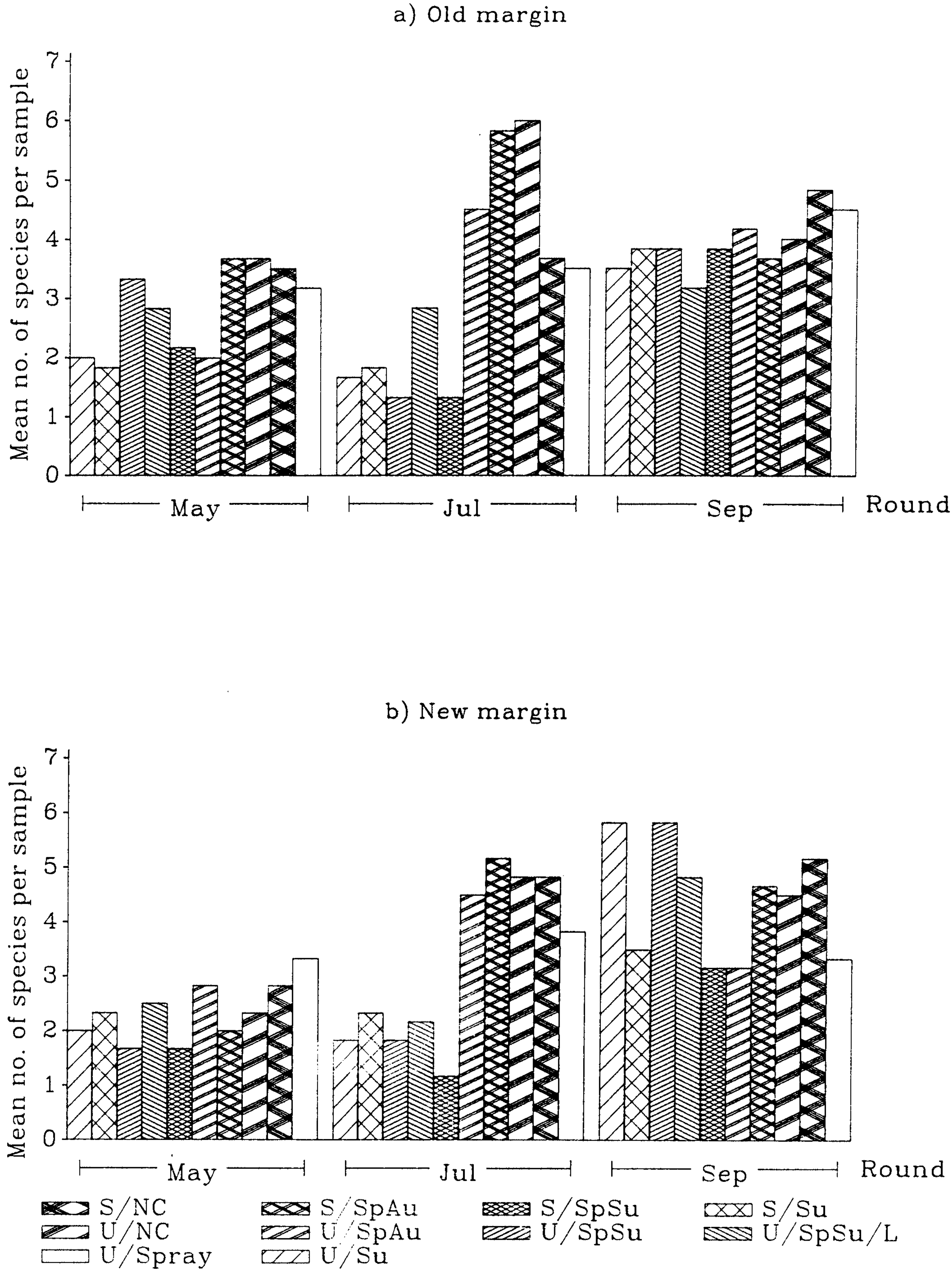
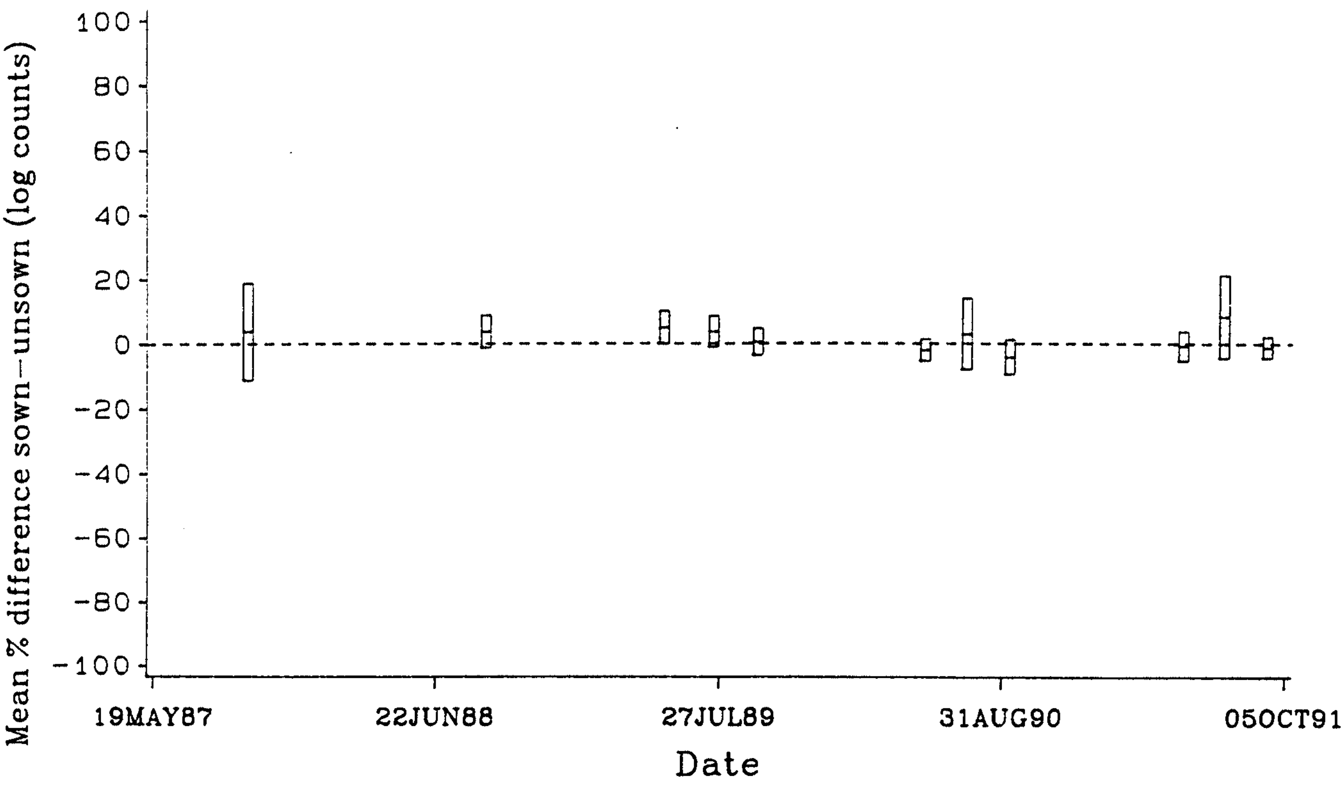


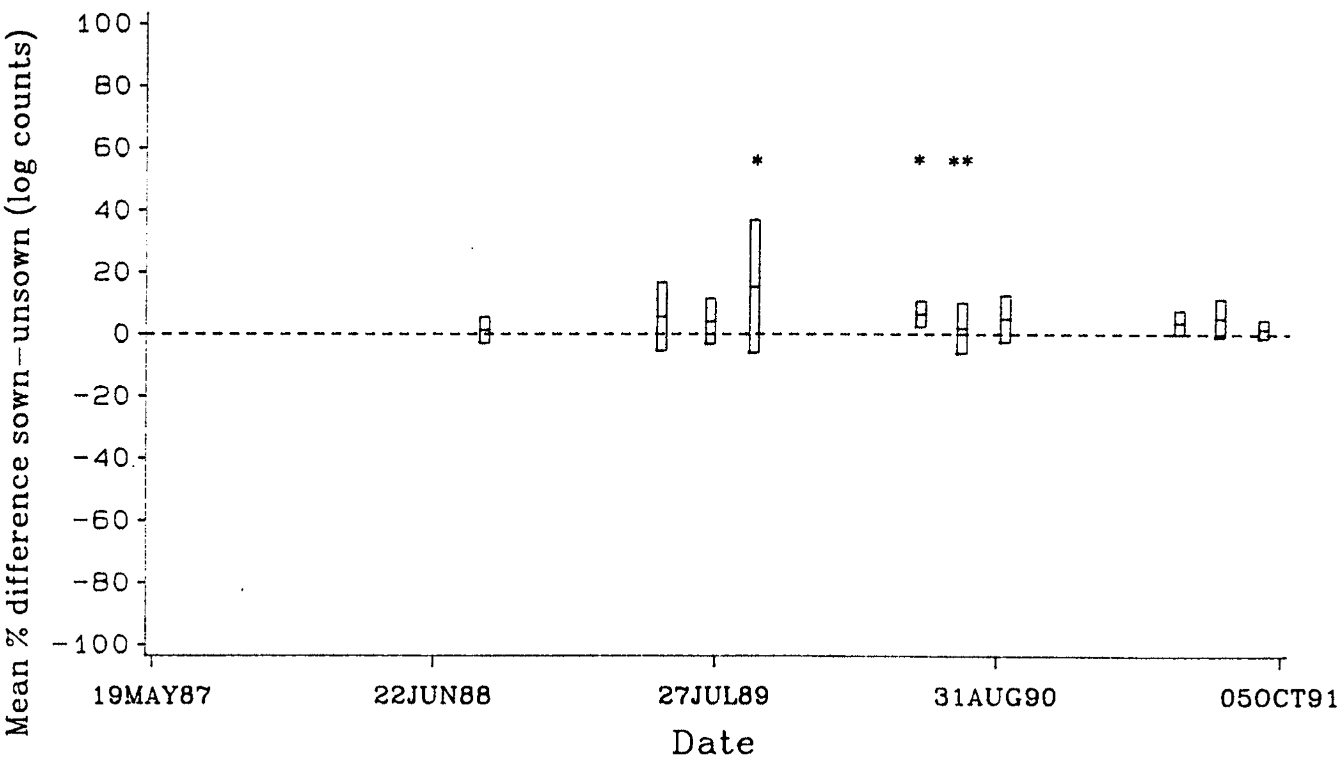
Figure 8.21 Minimum number of species of Heteroptera in 1991
Sown treatments crosshatched

a) Old margin



Bars are 1 x SE of the difference

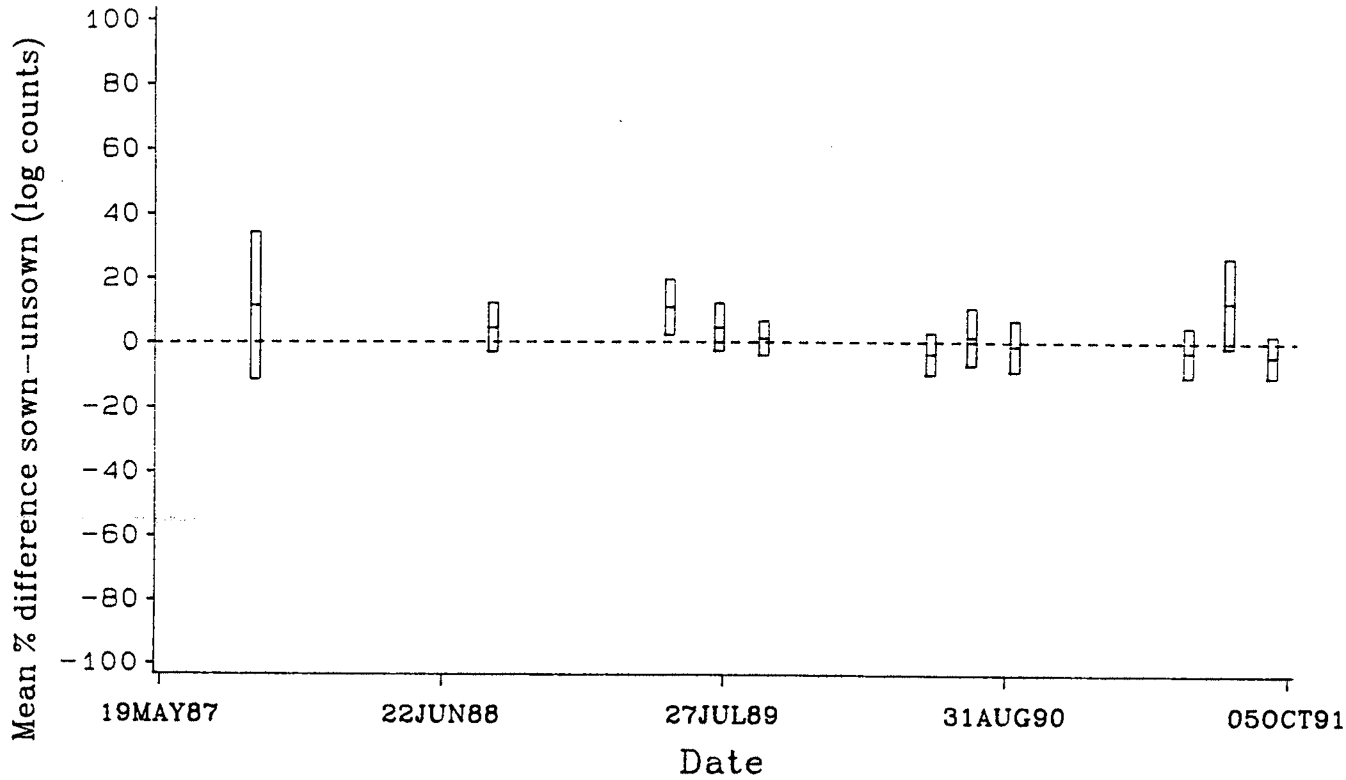
b) New margin



Bars are 1 x SE of the difference
Stars refer to the sig. level for SOWING in GLM for the date concerned

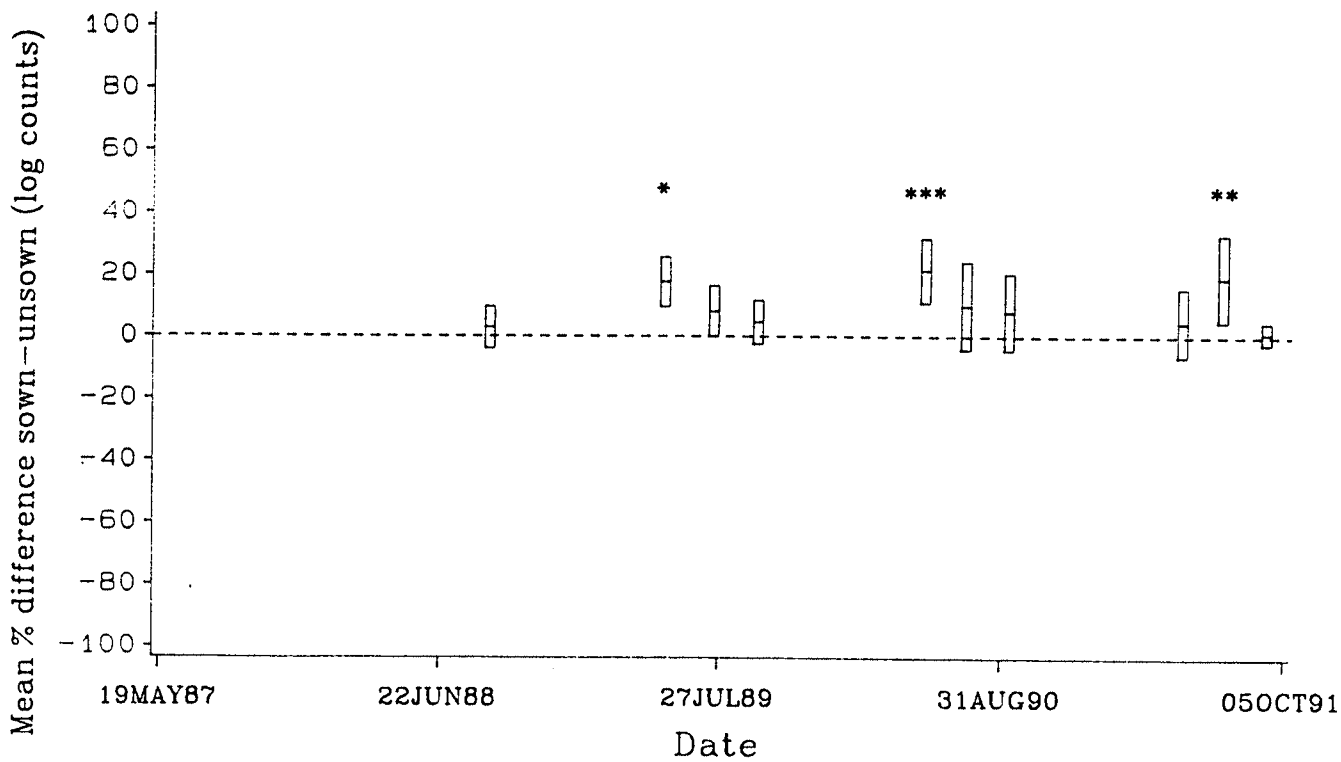
Figure 8.22 The effect of sowing on total invertebrate abundance

a) Old margin



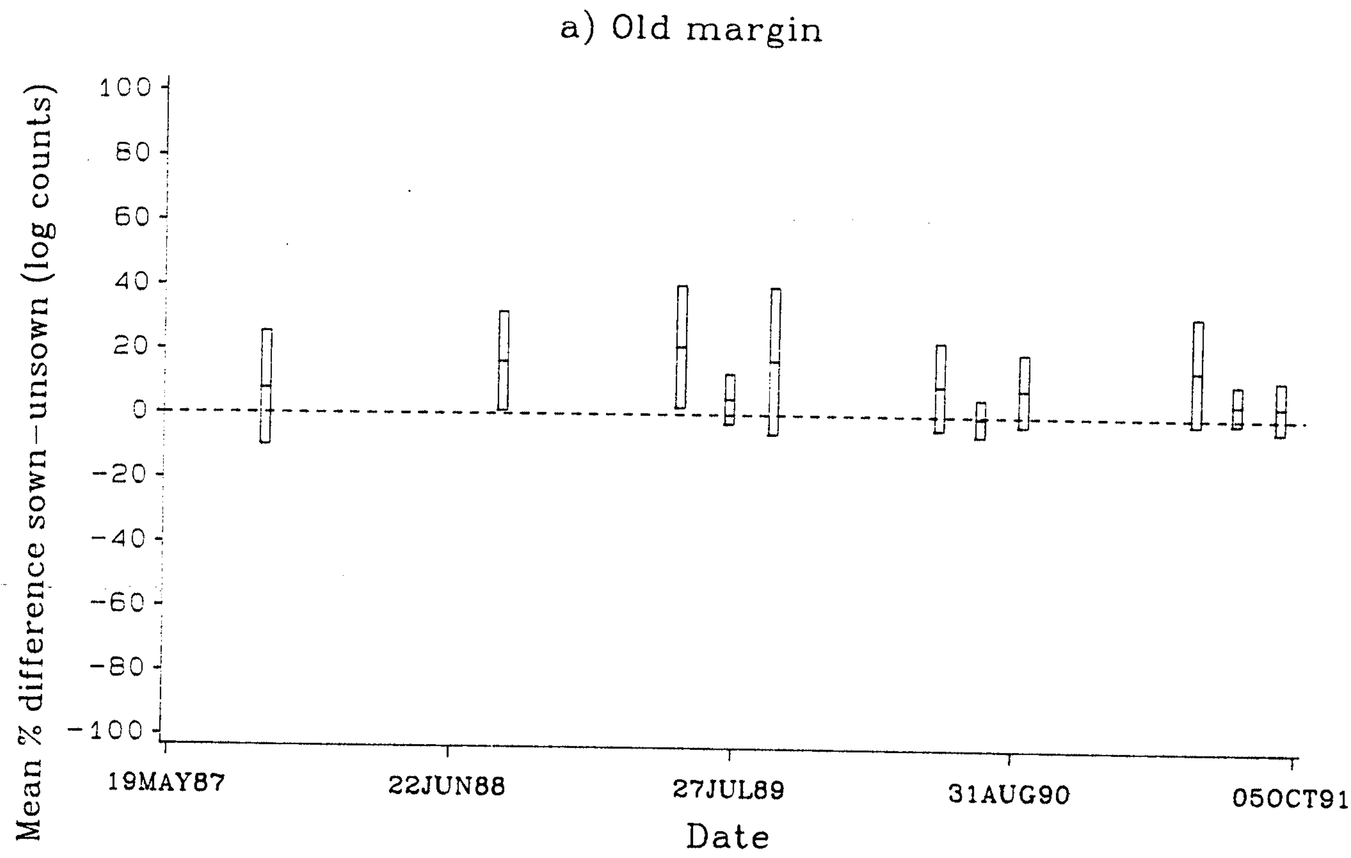
Bars are 1 x SE of the difference

b) New margin

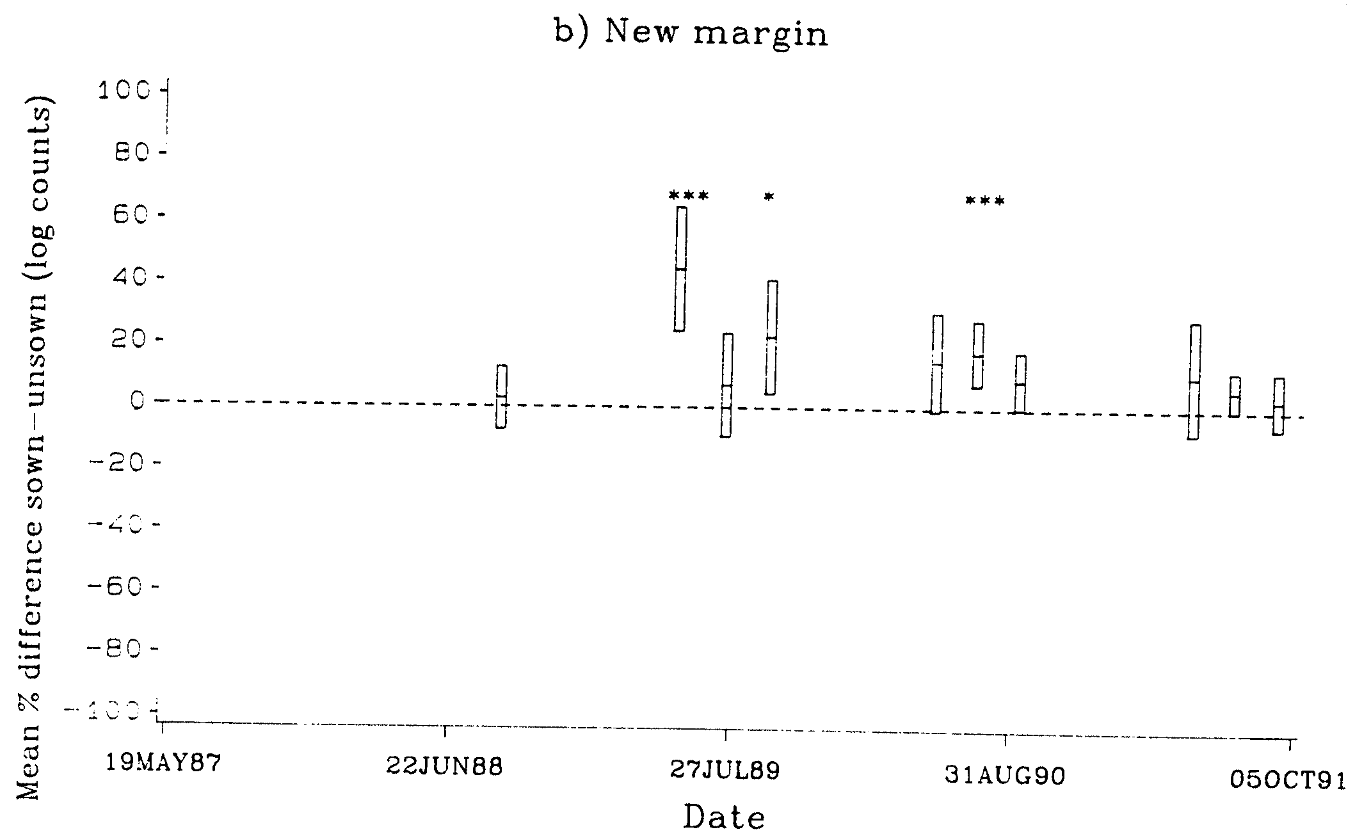


Bars are 1 x SE of the difference
Stars refer to the sig. level for SOWING in GLM for the date concerned

Figure 8.23



Bars are 1 x SE of the difference



Bars are 1 x SE of the difference
Stars refer to the sig. level for SOWING in GLM for the date concerned

Figure 8.24 [illegible]

9 THE ABUNDANCE AND DISTRIBUTION OF BUTTERFLIES ON THE FIELD MARGINS

The work described in this chapter and in Chapter 10 formed part of a doctoral research project on butterflies undertaken by Ruth Feber. Other aspects of her research on butterflies on the field margins are presented fully in her D. Phil. thesis (Feber 1993).

9.1 Introduction

During the last 150 years there have been substantial changes in the distribution and abundance of butterflies in Britain. The pattern is mostly one of decline (Heath *et al* 1984, Thomas 1984). Changes in butterfly numbers have been attributed to a variety of causes (reviewed by Thomas 1984). There is particularly strong evidence that weather and climatic influences, and changes in habitat, have been the major causes of fluctuations in numbers.

The strong synchrony of population changes of several butterfly species over wide areas of Britain (Pollard 1991), and over the Netherlands (Pollard, van Swaay & Yates 1993), suggests a major impact of weather on butterfly populations. Butterflies are ectothermic and are thus particularly responsive to temperature changes. A rise in temperature reduces the time required to raise body temperatures above their flight activity thresholds, and therefore increases the opportunity for flight dependent activities such as mate location, oviposition, foraging and dispersal (Dennis & Shreeve 1991). Faster development time may also lead to additional broods of bi- and multivoltine species, such as *Coenonympha pamphilus* small heath (Lees 1962) and *Aglais urticae* small tortoiseshell (Pullin 1986). Conversely, heat stress may result from excessive temperatures, reducing activity (Dennis & Bramley (1985) and decreasing longevity and fecundity (Stern & Smith 1960). Weather can also influence the degree of parasite infestation experienced by some species, for example *Euphydryas aurinia* marsh fritillary (Porter 1983). In addition to direct effects on the insects, climatic variation affects their host plants and nectar sources. Thus increased desiccation and nectar viscosity in the host can potentially reduce adult longevity and fecundity, and result in larval starvation (Wiklund & Ahberg 1978; Ehrlich *et al* 1980).

In an analysis of ten years of transect counts, Pollard (1988) concluded that there was a striking association between increased numbers of butterflies and warm, dry summers, whilst also supporting the view of Beirne (1955) that drought can have a detrimental effect in the following season. The effects of rainfall were variable, influencing both larval survival as well as plant growth. The response of individual species to climatic variation can to some extent be predicted since it depends on their physiological tolerances, life-history flexibility and behavioural and morphological characteristics. In general, though, such weather-dependent fluctuations make between year comparisons of butterfly abundance difficult to interpret and inconclusive for short-term studies.

Although weather is thought to cause short-term fluctuations in butterfly numbers, changes in habitat are considered to be responsible for many longer term declines in butterfly populations. In addition to widespread destruction of habitats caused by, for example, deforestation and urbanisation, butterflies have increasingly been shown to be sensitive to relatively minor changes in their habitats. Most studies have focused on Britain's rarer species. Overgrown swards resulting from undergrazing, for example, have caused the decline or loss of populations of several species whose foodplants are outcompeted by invasive grasses. Colonies of *Lysandra bellargus* adonis blue have suffered extinction even where large colonies of its foodplant exist; where the turf is not heavily grazed soil surface temperatures may be too low for the ants which may play a role in the species' survival (Thomas 1983a). In some instances, however, changes have had a positive effect. *Ladoga camilla* white admiral, for example, has benefitted from the shadier conditions that have resulted from the abandonment of coppice management (Pollard 1979). As well as local extinctions of rare species, there is also evidence of declines in Britain's commoner butterfly species. During the last twenty-five years, of 55 resident species only three have increased in number, eight have remained at a static level, while 44 have declined in at least a major part of their range (Thomas 1984). In areas dominated by intensive agriculture, the pattern of extinction and decline is likely to be even more severe.

Farmland has undergone some of the most extensive changes of any ecosystem in Britain over the past forty years (Chapter 1). Increased use of agrochemicals, abandonment of traditional rotations, field enlargement and hedgerow loss have all reduced the suitability of farmland for butterflies (Anon. 1977). Farmland is currently regarded as supporting an impoverished butterfly fauna consisting mainly of mobile species such as *Pieris brassicae* large white and *Pieris rapae* small white (Thomas 1984). However, with farmland occupying some 80% of Britain, changes in management of both cropped and uncropped areas could have considerable benefits for butterfly populations.

Butterfly communities have a number of requirements which have been summarised by Gilbert & Singer (1975) and are further discussed by Gilbert (1984). Within the scope of agricultural practices at least two of these requirements, the food resources for larvae and adults, could readily be manipulated. As a group, butterflies are relatively specialised on plant taxa used for larval food. Nevertheless, some species are either oligophagous, or utilise foodplants which are common or widespread in rough grassland. The adults of many temperate species also utilise a wide range of nectar sources. Thus, the number of species that could potentially utilise many arable areas could be increased by relatively minor changes in management. For example, the simple exclusion of pesticides from the headlands of cereal fields has been shown to increase the abundance of butterflies on two farms in southern England (Rands & Sotherton 1986; Dover *et al* 1990).

In this chapter we present data to test the prediction that creation and management of extended field margins can be an effective conservation strategy for butterflies on arable farmland. The establishment on field margins of grassy, perennial swards from which pesticides and fertilisers are excluded, could provide not only a transitory foraging habitat for mobile butterfly species, but also breeding areas for more sedentary species.

The data were obtained from counts of adult butterflies on fixed transects around the experimental field margins over a three year period. Such counts provide a basis for comparing the experimental treatments both within and between years. The methods are fully described in Chapter 2.2.5.3. In this chapter we describe first, the gross patterns in the abundance of butterflies, and in species richness and species diversity, on the field margins in 1988, 1989 and 1991 (Section 9.2.1). In Section 9.2.2 we present analyses of variance with means comparisons to show how each of these variables was affected by the experimental treatments (see Chapter 2.2.7). As well as testing for the overall effects of sown against naturally regenerating (unsown) swards, we used planned comparisons to test the effects of cutting against leaving swards uncut, of cutting in summer (when nectar abundance peaks) against not cutting in summer, and of cutting in spring and autumn against not cutting at all. The analyses that we present of the effects of treatment on abundance and species richness in each year of the study, are based on the yearly mean counts, over all blocks. For diversity indices, however, we present separate analyses for each transect round in each year of the study: the method of calculating diversity indices gives spurious results when annual means are used. We go on to describe the assemblage of butterfly species found on the field margins and present analyses of the effects of the experimental treatments on five of the commoner species, chosen for their contrasting habitat requirements. Finally, we compare overall butterfly abundance on the 2m experimental field margins with butterfly abundance on a second site with conventionally managed margins (see 2.2.5). We use the results to predict the potential effects of field margin management strategies on butterfly populations in the arable ecosystem and discuss the compatibility of butterfly conservation strategies with other aims of field margin management.

9.2 Results

9.2.1 THE PHENOLOGY OF BUTTERFLY ABUNDANCE AND SPECIES RICHNESS ON THE FIELD MARGINS

Butterfly abundance

The total numbers of butterflies on the transect showed large fluctuations between years and peaked at different times each year (Figure 9.1). Butterflies were most abundant in 1990 with a high early peak in numbers at the end of June due largely to the early emergence in that year of *Maniola jurtina* meadow brown (Section 9.2.5). In 1991 emergence of *M. jurtina* and *Pyronia tithonus* gatekeeper, the two most abundant species, was almost a month later and so the peak butterfly abundance for that year was at the beginning of August. In 1989 there was no distinct peak in numbers. The highest numbers of butterflies were recorded in the second and third weeks of July and were substantially lower than those in either 1990 or 1991. There is widespread evidence that yearly fluctuations in many species are a direct or indirect response to weather conditions in the current or previous season (Section 9.1).

Species richness

The number of butterfly species recorded through the season showed similar patterns in each of the three years (Figure 9.2). In April and May of 1990 and 1991, up to nine species were recorded on any one transect date, although their overall abundance was low (Figure 9.1). The numbers of species recorded peaked in the middle of July in 1989 and

1990, but not until the end of July and the beginning of August in 1991. The number of species recorded on any one date reached a maximum of 15 in 1990 and 1991 and in all years the number of species declined steadily during the latter half of August and through September.

Diversity

The overall diversity each year, calculated as the Shannon-Wiener function, is shown in Figure 9.3. Despite relatively large fluctuations in butterfly abundance and flight period over the three years, the pattern of diversity was very similar. There were two distinct peaks in each year (the first peak was prolonged in 1991) and a drop in diversity around the end of June and the beginning of July.

9.2.2 THE EFFECTS OF THE EXPERIMENTAL TREATMENTS ON BUTTERFLY ABUNDANCE AND SPECIES RICHNESS

Butterfly abundance

The transect data for 1989, 1990 and 1991 showed distinct differences in the total numbers of butterflies recorded both between the experimental treatments and over the three years. The mean total numbers of butterflies recorded on each treatment in each year is shown in Figure 9.4. In 1989, treatments which were left uncut in the summer had significantly higher butterfly abundance than treatments which were cut in the summer ($P<0.01$, Table 9.1). Sowing had no significant effect on the abundance of butterflies in 1989.

By 1990, both sowing and cutting had significant effects on the distribution of butterflies (Figure 9.4, Table 9.2). Sown swards attracted significantly more butterflies than unsown ($P<0.001$). As in 1989, treatments which were left uncut in summer had significantly higher mean numbers of butterflies than those that were cut ($P<0.001$). The sprayed treatment showed the effects of the first glyphosate application, the previous year, having significantly lower mean numbers of butterflies than the other uncut treatments, whether sown or unsown ($P<0.001$).

In 1991, sowing and cutting again had significant effects on butterfly numbers ($P<0.001$ and $P<0.001$ respectively, Figure 9.4, Table 9.3). As in the previous two years, treatments that were not cut in summer had significantly higher mean numbers of butterflies than treatments that were cut in summer. By 1991, the sprayed treatment attracted significantly fewer butterflies not only than uncut treatments but also than all other treatments (see planned comparisons in Table 9.3).

In all years there was no significant difference in butterfly abundance between treatments which were cut in the spring and autumn, and treatments which were never cut (planned comparisons, Tables 9.1-9.3).

Butterfly species richness

The mean number of butterfly species recorded also differed between treatment and year (Figure 9.5). In 1989 there was no significant overall effect of treatment on the mean number of species recorded (Table 9.4). Neither sowing nor cutting had significant effects although planned comparisons showed that sprayed plots had significantly lower mean numbers of species than the other plots which were left uncut in summer ($P<0.05$). Plots which were cut in summer had significantly lower number of butterfly species than plots which were not cut in summer ($P<0.05$). By 1990 there was a significant main effect of treatment on the numbers of species (Table 9.5), again, with significantly lower numbers on the sprayed and summer cut plots than on those left uncut in summer. Significantly more species were also recorded on sown than on unsown swards ($P<0.05$). In 1991 the main effect of treatment was not significant but, as in 1989 and 1990, planned comparisons showed that sprayed plots attracted significantly fewer species than plots left uncut in summer (Table 9.6). Plots left uncut in summer had higher numbers of butterfly species than plots which were cut in summer, and this approached a significant level ($P=0.057$). Although we were unable to detect any significant effect of sowing in 1991, as in 1990 the sown, uncut plots supported the highest numbers of butterfly species. In all three years, there was no significant difference in species richness between treatments cut in spring and autumn and treatments which were never cut.

Over the three years the range of the mean numbers of species on the treatments increased steadily: in 1989 the range was 5.88-8.88, in 1990 6.00-9.63 and in 1991, 6.88-10.25 per 50m plot. In 1989 recording did not begin until June and some of the increase between 1989 and 1990 was attributable to this relatively short recording season. Nevertheless, the increase over the three years may well have reflected a wider occurrence of some species on the field margins.

Butterfly diversity

In 1989 the highest diversities (calculated as the Shannon-Weiner function for each treatment and date) occurred on the sown but uncut treatments on 17 and 20 July (Table 9.7). Diversities on these treatments remained consistently high in comparison with the other treatments throughout the recording period. Significant differences in diversity were detected between treatments on 13 July and 4 August using Friedman's non-parametric method in lieu of two-way ANOVA (the data could not be normalised), but *a postiori* comparisons (see Chapter 2.2.7) did not attribute these results to differences between any particular treatments (Table 9.7). The two treatments with the highest diversities on both of those dates were the sown, uncut treatment and the unsown, spring and autumn cut treatment.

In 1990, highly significant differences in butterfly diversities were found between different treatments on 25, 26 and 29 June although, as in 1991, the peak diversities were not reached until 17 July (Table 9.8). On 26 June the diversity on the sown treatment cut in spring and summer was significantly higher than that on the unsown treatments that were sprayed, or were left uncut, or were cut either in summer or in spring and autumn (non-parametric *a postiori* tests). This result was consistent with the significant effect of sowing in 1990 discussed above (Section 9.2.3). Significant effects of treatment on diversity were also detected on two dates in July, after the summer cut. On these dates, although we were unable to detect significant differences between any pairs of means (post-hoc tests), the highest diversities were on treatments which had been left uncut in the summer. The sown, uncut treatment and the unsown spring and autumn cut treatment, which in June had supported significantly lower butterfly diversities than other treatments, supported the highest diversities in July.

In 1991, in contrast to 1990, the highest mean butterfly diversities were not reached until the end of August. There were significant differences between treatments on four dates in August (Table 9.9). As in 1990, the highest mean diversity was recorded on the sown treatment which was left uncut; on 1 August in 1991, butterfly diversity was significantly higher on these plots than on the sprayed plots. On 8 August, the sown, uncut treatment again had significantly higher diversities than the sprayed treatment, and also higher then the unsown treatment cut in summer only. Although butterfly abundance was generally lower in 1991 than 1990, the mean diversity indices were higher than in both previous years.

9.2.3 THE BUTTERFLY SPECIES ON THE FIELD MARGINS

Twenty-two species of butterfly were recorded on the field margins between 1989 and 1991 (Table 9.10). This represents 38.3% of the butterfly species currently found in the U.K. Although most of those found were common species, their populations were large and the range of species included several more typical of semi-natural habitat or rough grassland such as *Melanargia galathea* marbled white, *C. pamphilus*, *Thymelicus sylvestris* small skipper and *Ochlodes venata* large skipper. Additionally, there was one record in 1991 of *Strymonidia w-album* white-letter hairstreak, on a wild flower seeded treatment, and four sightings of *Aricia agestis* brown argus, and two of *Quercusia quercus* purple hairstreak, on sections of field margin which were under management but not included in the randomised block design. All species except for *S. w-album*, *A. agestis* and *Q. quercus* were recorded in all three years but there was a great deal of variation in numbers between years (section 9.2.4).

9.2.4 PHENOLOGY OF SPECIES OCCURRING ON THE FIELD MARGINS

Of the twenty-two species recorded on the field margins, two were migrants (*Cynthia carduii* painted lady and *Vanessa atlanta* red admiral). The flight periods of all the resident species over the years 1989, 1990 and 1991 in the study area, with the total numbers of butterflies of each species recorded plotted against the transect date, are shown in Appendix III.

Individual species showed a great deal of variation in both numbers and time of flight period between years. For many species, emergence time is related to temperature or photoperiod, which may delay or hasten eclosion (Brakefield 1987). However, in general there were two peaks in numbers of species, the first associated with the flight period of the spring-flying butterflies such as *Anthocharis cardamines* orange tip and with spring broods *(eg A. urticae)*, and the second associated with the main flight period of the satyrid butterflies, such as *M. jurtina* and *P. tithonus*.

9.2.5 RESPONSES OF INDIVIDUAL SPECIES TO THE EXPERIMENTAL TREATMENTS

In this section we describe the responses to the experimental treatments of five of the species which occurred on the field margins in 1990 and 1991. *P. tithonus*, *M. jurtina*, *A. urticae*, *T. sylvestris* and *C. pamphilus* all maintained populations on the field margins in both years, and yet have different habitat requirements. We have grouped the treatments into following categories, both to increase sample size and to clarify the important management factors: sown and cut in summer, sown and left uncut in summer, unsown and cut in summer, unsown and left uncut in summer, and unsown and sprayed.

Pyronia tithonus

In both years the flight period of this species occurred after the summer management cut. In 1990, abundance of *P. tithonus* was almost identical on uncut treatments, whether sown or unsown; similarly, abundance on sown, cut treatments was virtually the same as on unsown, cut treatments (Table 9.11; Figure 9.6). Although the sprayed treatment was left uncut, abundance of *P. tithonus* on these plots resembled that on cut rather than uncut plots. There was an overall treatment effect on *P. tithonus* abundance on two dates in July, but significant differences were not detected between any pairs of means. In 1991, the flight period of this species was almost a month later than in 1990, but numbers reached a peak more quickly. Uncut treatments, both sown and unsown, had significantly greater abundance than unsown, cut treatments and sprayed treatments by 8 August (Table 9.12). The sprayed plots had significantly lower abundance of this species than the plots which were not cut in summer (whether sown or unsown) on 1 and 14 August. Of the cut treatments, the sown swards attracted more butterflies than the unsown swards; the difference between sown and unsown swards in the uncut treatments was less apparent (Figure 9.7).

Maniola jurtina

In 1990, *M. jurtina* showed a clear response to the summer cutting management at the end of June (Figure 9.8; Table 9.13). Butterfly abundance increased steadily on sown plots until the summer cut, when a rapid fall in abundance occurred on the cut treatments while abundance rose sharply to a peak on the sown, uncut treatments. At this point, on 29 June, numbers of *M. jurtina* were significantly higher on sown, uncut treatments than all treatments cut in the summer, whether sown or unsown, and the sprayed treatment (post-hoc comparisons, Table 9.13). Unsown treatments did not attract high numbers of *M. jurtina* in 1990, but abundances did rise slightly towards the end of the season, and by 12 July were, in fact, higher on unsown swards than sown swards. In 1991, *M. jurtina* was not on the wing until after the summer management cut. Abundance was greatest throughout this season on sown, uncut treatments and was significantly higher on these swards than on sprayed swards on most dates (Table 9.14); abundance also increased on unsown, uncut treatments in August (Figure 9.9). During August there was a low increase in butterfly abundance on swards which had been cut in summer (Table 9.14). Our preliminary analyses of the abundance of flowers of *Leucanthemum vulgare*, one of the principal nectar sources for this species in both years, suggest that this resulted from reflowering of this species after the cut.

Aglais urticae

A. urticae showed a similar response to the summer cut in 1990 as *M. jurtina* (Figure 9.10), and treatment had a significant effect on abundance on four dates in 1990 (Table 9.15). Butterfly abundance was highest on sown treatments, and until the end of June was similar on both summer cut and uncut treatments. After the summer cut, abundance rose to a peak on the sown, uncut treatments, and fell immediately on the cut treatments. The autumn brood in that year was also associated with the uncut treatments, sown or unsown. In 1991, the flight period of the summer brood was around a month later. Abundance was greatest, and similar, on both sown and unsown treatments which were not cut in the summer (Figure 9.11; Table 9.16), although butterflies also utilised treatments which had been cut in the summer, a month before the peak flight period in this year. Because *A. urticae* larvae are specialist nettle feeders, this species showed some spatial separation of breeding and foraging habitat; analyses of nettle and nectar source abundance, together with butterfly distribution, showed that treatments with highest nettle abundance were not necessarily optimal foraging areas (Feber 1993).

Thymelicus sylvestris

Uncut treatments attracted the highest numbers of *T. sylvestris* in both 1990 (Table 9.17; Figure 9.12) and 1991 (Table 9.18; Figure 9.13). There was also a noticeable increase in abundance of this species over the two years, and a longer flight period in 1991. In 1990, numbers rose to an initial peak on unsown, uncut swards, then fell on these treatment types as they rose on sown, uncut swards. In 1991, six out of seven transect records showed a significant treatment effect ($P<0.05$; Table 9.18) with sown, uncut swards attracting the greatest abundance of *T. sylvestris* throughout the flight period.

Coenonympha pamphilus

In contrast to the four species above, there was only one date over the two years when *C. pamphilus* abundance showed a significant treatment effect (Tables 9.19 and 9.20). This species was found on all sward types in 1991, but was absent from sprayed plots in 1990 (Figure 9.14, Figure 9.15). Although the sample sizes were small, abundance of this species was similar on cut and uncut treatments, both sown and unsown, with slightly higher numbers of *C. pamphilus* on the cut swards. In 1991, there was a significant treatment effect in the second week of July; although the highest butterfly abundance was recorded on sown, cut swards no significant differences were detected between particular pairs of treatments (Table 9.20). However, that there was not a correspondingly high abundance on the unsown, cut swards suggests that components of the seeded swards may have been particularly attractive to *C. pamphilus*, as well as indicating some degree of preference for shorter turf.

9.2.6 BUTTERFLY ABUNDANCE ON DENMAN'S FARM

Butterfly records for seven transects conducted concurrently on Denman's Farm and the 2m margins at the University Farm were analysed for differences in butterfly abundance (Table 9.21). The abundance of each species per kilometre was calculated and a Wilcoxon signed rank test performed on the results. Of the sixteen species recorded both at Denman's Farm and the University Farm, none was significantly more abundant at Denman's than at the University Farm. However, the University Farm had significantly greater abundance of eight species compared to Denman's. These included *T. sylvestris*, *L. phlaeas*, *C. pamphilus*, *M. jurtina* and *P. tithonus*. All these species are typical of rougher grassland areas, with a more diverse vegetation. Some of these species were very much higher per kilometre at the University Farm; *T. sylvestris*, for example, was recorded at least ten times more frequently at the University Farm than at Denman's on most dates during its flight period. Three species were recorded only at the University Farm over the recording period for both farms: *P. icarus*, *M. galathea* and *O. venata*. There were no significant differences in numbers of the more mobile species commonly associated with farmland habitat such as *P. brassicae*, *P. rapae* and *I. io*. Species generally associated with high hedgerow, such as *Celastrina argiolus* holly blue, *Pararge aegeria* speckled wood and *Polygonia c-album* comma, were also not significantly diffferent in abundance between the two farms.

9.3 Discussion

9.3.1 FIELD MARGINS AS BUTTERFLY HABITAT

The butterfly assemblage on our experimental field margins was unusually large and diverse for intensively managed arable farmland during the three years of the study. Species recorded included several more typical of unimproved or rough grassland such as *M. galathea*, *C. pamphilius*, *T. sylvestris* and *O. venata*, and these were significantly more abundant on the experimental field margins than on conventionally managed field boundaries. The numbers of butterflies on the conventional boundaries were lower than on the University Farm and a much higher proportion of the butterflies recorded on the conventional boundaries were pierid species, typical of arable land.

The proximity of the University Farm to source populations of these species on grassland enclaves around Wytham Hill must have increased the probability of colonisation. However, we attribute the maintenance of populations of so many species, at such high densities to the extended field margin management.

The responses of the butterflies to the different experimental treatments on the field margins, leads to some general and some species-specific conclusions about the most effective management regimes for butterfly conservation on field boundaries.

9.3.2 THE EFFECTS OF MOWING

Some experimental treatments attracted significantly more butterflies over the recording period than others, despite variations in the foodplant requirements and phenologies of the species concerned. In all years there was a significant effect of cutting on the abundance of butterflies. Treatments which were left uncut, or were cut in spring and autumn, were preferred by the majority of butterfly species. Prior to the summer cut, however, other treatments, and particularly sown treatments, were also widely utilised. The summer cut in all three years was in the last week of June, and affected the species which were on the wing at that time. Two species examined in detail, *M. jurtina* and *A. urticae* (Section 9.2.5 (ii) & (iii)) responded immediately by moving from the cut to uncut treatments. This change in distribution was typical of the majority of species whose flight period spanned the time of the cut. Munguira & Thomas (1992), in a study of road verge butterfly populations, noted a similar sharp decline in total butterfly numbers following mowing, and a slow recovery of numbers due to the invasion of mobile species such as *Pieris* spp. and *Lycaena phlaeas*. We also recorded a slow recovery on cut treatments, particularly on those that were sown, but this was largely attributable to *Leucanthemum vulgare*, an important nectar source, reflowering several weeks after cutting. However, neither abundance nor species richness regained levels comparable with those on treatments which had not been cut in the summer.

Uncut, or spring and autumn cut treatments, had two advantages for butterfly populations. First, they provided a continuity of nectar supply. In most arable areas nectar sources are likely to be patchily distributed in both time and space. This is likely to limit the potential for sedentary species to establish populations. Had a high proportion of the field margin grassland been cut in summer, the field margins would have been ineffective in providing nectar for any but the most mobile species of butterflies. Secondly, treatments that were left uncut in summer provided a relatively undisturbed environment for the developmental stages of many species of butterflies. During the summer months adult females of most of the species recorded on the field margins were ovipositing, and the larvae of some species were feeding or completing their development on their foodplants. Mowing during any of the summer months would have a disruptive effects on any of these stages and would be likely to be particularly severe for species whose larvae were feeding rather than in diapause. Amongst these, species such as *A. cardamines*, the larvae of which remain on one plant to complete their development, would be most affected.

Although mowing in summer is an undesirable management operation for most butterfly species, it may be desirable for other management objectives, such as the control of annual weeds (see Chapter 5). The pronounced annual variability in the flight periods of the majority of species examined in this study makes it difficult to predict the least damaging time to cut. Where summer mowing is considered essential but butterfly conservation is also an aim of field margin management, either the extent of the area that is mown in summer should be restricted or the mowing should be timed to follow the peak flight period of the most important butterfly species. Priority should be given to timing mowing to benefit sedentary species of semi-natural grassland since these are least likely to recover from badly-timed management.

In contrast to the majority of species, larval development of *A. urticae* may benefit from mowing during the summer. Pullin (1987) has shown that this species prefers to lay on young stinging nettle regrowth after mowing, because of its high nitrogen levels. Our own studies of this species support this (Feber 1993), but the variation both between and within years in the timing of adult and larval stages was so great (see 9.2.4) that it is impossible to predict with any accuracy the best time to cut. Cutting too late is detrimental to the survival of larvae already hatched and feeding on the plants (pers. obs.).

Although, during the three years of this study, we were unable to detect differences in either the abundance or the species richness of butterflies between swards that were never cut and swards cut in spring and autumn, it is likely that such effects will become apparent in the longer term. The primary factor determining butterfly abundance on these two sward types was the prolonged abundance of nectar resulting from the lack of summer cutting. However, we showed in Chapter 4 that plant species diversity was significantly lower on unmanaged than on spring and autumn-cut swards from 1988 onwards. As these underlying differences increase, they are likely to have increasing impacts on the availability of nectar and of larval foodplants. In the medium term, lack of management of field margins adjacent to hedges is likely to result in the development of dense scrub. Invasion by woody species was apparent as early as 1989 (Chapter 3). Loss of butterfly diversity, and particularly of species characteristic of established grassland, is likely to result from the development of scrub. Erhardt (1985) showed that numbers of butterfly species decreased in later successional stages of abandoned alpine grassland, as dwarf shrubs colonised and plant species richness fell. Studies on chalk grassland have also attributed undesirable shifts in the species composition of butterfly communities, with the loss of the rarer Lycaenidae and Hesperiidae, to the cessation of grazing and development of taller swards (Frazer and Hyde, 1965; Thomas 1983a, 1983b).

Ideally, the creation and maintenance of a heterogenous habitat, composed of both short and overgrown swards, would maximise the potential of field margins as a habitat for butterfly populations. Indeed, the success of the experimental field margins in maintaining such a diverse butterfly assemblage was probably due in part to their heterogeneous nature, which originated as consequence of the experimental design.

9.3.3 THE EFFECTS OF SOWING

In both 1990 and 1991 adult butterflies were significantly more abundant on sown than on naturally regenerating swards. In 1990 sown swards also attracted significantly more species of butterflies. This difference resulted from much greater availability of nectar on sown swards and suggests that nectar may be a limiting resource on farmland. Wild flower seed mixtures are likely to act as an effective supplements to, or replacements for, nectar supplied by naturally-established plant species on arable farmland. They could be particularly important where plant communities are very depauperate (see Chapter 3). Feber (1993) presents detailed analyses of the factors influencing butterfly abundance on the experimental treatments in 1991. The abundance of most butterfly species was determined primarily by the abundance of nectar sources. However, the results showed that, rather than the overall abundance of flowers, the important variables were the abundance of certain types and species of nectar sources. Perennial, rather than annual, species, were consistently associated with butterfly abundance, and *Leucanthemum vulgare*, *Centaurea nigra* and *C. scabiosa*, and *Knautia arvensis* were amongst the significant predictors of abundance of seven butterfly species under analysis. These plants were all components of the seed mixture.

The wild flower seed mixture had no significant impact on total butterfly numbers in 1989, the second year after establishment. Although *Leucanthemum vulgare* provided an abundant nectar source in mid-summer that year, later flowering species in the mixture, that were attractive to butterflies, were less abundant than in the following years (Chapter 6). *Knautia arvensis*, *Centaurea scabiosa* and *C. nigra* were particularly important in this respect, especially to satyrid species such as *M. jurtina* and *P. tithonus*. Wild flower mixtures will be most beneficial to butterflies, and to other nectar-feeders, on farmland if they include early and late flowering species to provide nectar throughout the season. The dominant nectar sources in late summer in 1989 were provided by species such as *Cirsium arvense*, which were most abundant in naturally regenerating swards but which are often the targets of weed control measures on farmland (see Chapter 5). This emphasises the importance of selecting broad-leaved species for wild flower seed mixtures to give continuity of nectar supply throughout the summer.

There was also some indication, from the rank order of the treatment means and the degree of significance, that the preference for wild flower-seeded swards was less marked in 1991 than in 1990. This is likely to have resulted from the earlier flight period of most butterflies in 1990. Those butterflies that were on the wing before the summer cut (particularly the abundant *M. jurtina)* were able to utilise the summer-cut, flower-rich, wild flower seeded treatments for foraging before the summer cut at the end of June. Because of the later flight period in 1991, these treatments were only available as cut swards and the butterflies could not demonstrate a preference for them at a comparable stage. This variability in the butterflies' phenology again demonstrates the importance of ensuring continuity of nectar supply both by avoiding mowing at critical periods and by providing plant species with appropriate flowering phenologies.

The overall preference of adult butterflies for sown swards appeared to result primarily from the availability of nectar rather than from any selection of these swards for egg laying. Provision of food for butterfly larvae was not used as a criterion in the selection of species for the wild flower seed mixture. Of the butterfly species found on the field margins, none utilised broad-leaved plants in the seed mixture as larval foodplants, although members of the Satyridae and Hesperiidae laid eggs on species of grass included in the seed mixture as well as on naturally-occurring grass species (see Chapter 10.3). The broad-leaved species utilised for oviposition and larval feeding were present mainly in naturally regenerated swards and on field boundary features, such as ditch banks, adjacent to the experimental margins (Table 9.22). Many of these species, such as *Urtica dioica* and *Alliaria petiolata*, are common components of field edge and hedge bottom plant communities and their populations are likely to benefit from extension of field margin width and exclusion of agrochemicals.

Species of butterflies which rely for larval food on broad-leaved plant species associated with more established grassland, are likely to benefit from inclusion of the host species in a seed mixture. This was illustrated by our wide field margins experiment (Chapters 2.3 and 11) in which *Rumex acetosa*, the preferred host plant of *L. phlaeas*, was included in one of the seed mixtures. A substantial number of larvae of this species was found on these plants in 1989 and 1990 (unpublished data).

9.3.4 THE EFFECTS OF SPRAYING

We showed in Chapter 4 that spraying annually with glyphosate resulted in the development of species-poor plant communities dominated by annuals. Spraying also had deleterious effects on butterflies. By 1991, significantly fewer butterflies were recorded on the sprayed treatments than on any other treatment. The numbers of species of butterflies were also lowest on the sprayed treatment, although they were not significantly lower than on treatments that were cut in summer.

The loss of adult butterflies from the sprayed treatments is likely to have been attributable to the loss of suitable nectar sources. However, the selective loss of perennial plant species from these treatments must also have resulted in the loss of the larval food plants of the majority of butterfly species. The pierid species, which feed on annual Crucifers and are generally regarded as pests, are the only group likely to maintain sizable breeding populations where spraying-out hedge bottoms is a widespread management practice.

9.3.5 ADDITIONAL ANALYSES

Analyses of the relationship between the availability of nectar on the experimental treatments and butterfly numbers, within and between years, are presented in Feber (1993). Resource requirements of vanessid and satyrid larvae are also presented in Feber (1993).

Feber (1993) addresses the question of the probability of butterfly species colonising new field margins from source populations. This is a critical problem because efforts to provide suitable resources for some species could be thwarted by the species mobility. We hope to compare data for the two farms with regional trends from the National Butterfly Monitoring Scheme.

9.3.6 FUTURE MONITORING

We suggest that butterfly monitoring on the experimental field margins should be continued for two reasons. First, although the effects of cutting in summer are already obvious, we are not yet able to evaluate our prediction that cutting in spring and autumn will result in more diverse butterfly communities than leaving swards unmanaged. Since significant differences in the plant communities on these two types of treatment are already apparent, resultant differences in the butterfly populations might be expected to be detectable within the next few years. Second, a longer run of years is needed to evaluate differences between trends in butterfly numbers on our extended width field margins and those on other arable areas covered by the National Butterfly Monitoring Scheme.

Both of these objectives could be achieved by continuing to monitor numbers of butterflies on our standard transect route.

9.3.7 IMPLICATIONS FOR SET-ASIDE MANAGEMENT

Many of our conclusions on the conservation management of butterflies on field margins are equally applicable to set-aside management. Mowing should, wherever possible, be avoided during the summer months. Nectar provision is likely to present greater problems on set-aside. Education is needed to encourage greater tolerance of species such as *Cirsium arvense* and other weedy composites on set-aside, since these are likely to provide the greatest resources of nectar for butterflies and other nectar-feeding species, such as bees and hoverflies. Where top-up schemes are available for measures to enhance the conservation value of set-aside, greater emphasis should be put on inclusion of nectar sources in recommended seed mixtures. Species should again be chosen to give continuity of nectar supply throughout the summer. Inclusion of such species also has very substantial amenity benefits (see Chapter 6).

9.4 Summary

We have shown that the margins of arable fields can support breeding populations of a large number of species of butterflies, including some less common and declining species typically associated with semi-natural grassland. The diversity of butterflies increased over the three years of the experiment although comparison with regional trends from the National Butterfly Monitoring Scheme is needed to evaluate this increase. The simple management changes that were central to the establishment of our experimental field margins - extension in width and exclusion of agrochemicals - maintained the presence of larval foodplants which supported populations of up to twenty-two species of butterfly. However, additional management effort will usually be required to ensure the provision of suitable and sufficient nectar sources for such a butterfly assemblage. On many arable farms the existing flora is unlikely to provide adequate nectar resources. Moreover, the most abundant nectar sources in early-successional swards on fallowed arable land are likely to be species such as *C. arvense*, that the farmer will wish to control. Sowing wild flower seed mixtures containing species that together give abundant and continuous of nectar supply during the summer can improve very significantly the numbers of butterflies that can be supported on arable field margins. Inclusion of appropriate species in wild flower seed mixtures can also be used to encourage species of butterflies whose larval food plants are absent from the farm flora.

In the early successional stages of the newly-fallowed field margins, butterflies were most abundant on unmanaged swards and on those cut in spring and autumn. Both sward types supported an abundance of nectar sources during the main summer flight period of most species. Although we found no significant differences in butterfly abundance on these two sward types, we predict that in the medium term, the lower plant diversity and the increase in woody species on unmanaged swards, will result in relatively lower numbers of butterflies. Spring and autumn cut swards are thus likely to support the richest butterfly as well as plant communities.

Mowing at any time during the summer is likely to be detrimental to some species of butterflies. It has major impacts on the availability of nectar to adults and is likely to result in losses of earlier developmental stages. It is not even possible to recommend dates for summer mowing that would reliably minimise damage to specific species because the inter-annual variation in each species phenology is so great. The best management advice, where summer mowing cannot for other reasons be avoided, is to avoid mowing the whole of the area used by the butterflies and if possible to mow when the numbers of the most important species start to decline. We suggest that where sufficient area of field margin is available, the heterogeneity resulting from mowing some areas and leaving others uncut is likely to benefit the greatest number of butterfly species.

Table 9.1 The effect of treatment on the abundance of butterflies on the field margins in 1989

Treatment	Mean No. Butterflies[1]
sown, no cut	48.48 (3.88)
unsown, cut, spring & autumn	36.88 (3.61)
unsown, no cut	29.08 (3.69)
unsown, sprayed	27.92 (3.33)
unsown, cut, spring & summer	26.46 (3.28)
sown, cut, spring & summer	25.58 (3.24)
sown, cut, spring & autumn	24.40 (3.19)
sown, cut, summer only	21.22 (3.05)
unsown, cut, spring & summer leave hay	14.16 (2.65)
unsown, cut, summer only	14.09 (2.65)

[1] Means presented are back-transformed. Analyses were performed on log-transformed means (shown in parentheses). Minimum Significant Difference = 1.00.

2-Way Analysis of Variance (all treatments)

Main Effects	d.f.	F value	p	Sig. level
Block	7	2.93	0.010	*
Treatment	9	3.12	0.0036	**
Planned comparisons				
Spray vs uncut in summer	1	0.58	0.448	ns
Spray vs cut in summer	1	2.27	0.137	ns

3-Way Factorial Analysis of Variance

Main Effects	d.f.	F value	p	Sig. level
Sowing	1	0.70	0.410	ns
Cutting	3	5.30	0.003	**
Sow*Cut	3	2.26	0.093	ns
Planned comparisons				
Cutting vs not cutting	1	7.75	0.008	**
Cut in summer vs not cut in summer	1	10.49	0.002	**
Cut spring & autumn vs no cut	1	1.25	0.2684	ns

Table 9.2 The effect of treatment on the abundance of butterflies on the field margins in 1990

Treatment	**Mean No. Butterflies**[1]
sown, cut, spring & autumn	82.46 (4.41)
sown, no cut	76.20 (4.33)
sown, cut, spring & summer	41.62 (3.73)
sown, cut, summer only	34.99 (3.55)
unsown, no cut	29.06 (3.37)
unsown, cut, spring & autumn	22.41 (3.11)
unsown, sprayed	15.59 (2.75)
unsown, cut, spring & summer leave hay	14.86 (2.70)
unsown, cut, summer only	14.78 (2.69)
unsown, cut, spring & summer	13.86 (2.63)

[1] Means presented are back-transformed. Analyses were performed on log-transformed means (shown in parentheses). Minimum Significant Difference = 1.02

2-Way Analysis of Variance (all treatments)

Main Effects	d.f.	F value	p	Sig. level
Block	7	1.95	0.0760	ns
Treatment	9	9.36	0.0001	***
Planned comparisons				
Spray vs uncut in summer	1	18.56	0.0001	***
Spray vs cut in summer	1	1.70	0.1974	ns

3-Way Factorial Analysis of Variance

Main Effects	d.f.	F value	p	Sig. level
Sowing	1	45.43	0.0001	***
Cutting	3	5.88	0.0016	**
Sow*Cut	3	0.37	0.7758	ns
Planned comparisons				
Cutting vs not cutting	1	7.52	0.0085	**
Cut in summer vs not cut in summer	1	17.42	0.0001	***
Cut spring & autumn vs no cut	1	0.17	0.6848	ns

Table 9.3 The effect of treatment on the abundance of butterflies on the field margins in 1991

Treatment	**Mean No. Butterflies**[1]
sown, cut, spring & autumn	54.21 (3.99)
sown, no cut	47.04 (3.85)
unsown, cut, spring & autumn	35.45 (3.57)
sown, cut, spring & summer	25.22 (3.23)
unsown, no cut	23.89 (3.17)
sown, cut summer only	18.44 (2.92)
unsown, cut, spring & summer leave hay	16.99 (2.83)
unsown, cut, summer only	15.40 (2.73)
unsown, cut, spring & summer	15.38 (2.73)
unsown, sprayed	10.93 (2.39)

[1] Means presented are back-transformed. Analyses were performed on log-transformed means (shown in parentheses). Minimum Significant Difference = 0.9165

2-Way Analysis of Variance (all treatments)

Main Effects	d.f.	F value	p	Sig. level
Block	7	3.34	0.0043	**
Treatment	9	7.00	0.0001	***
Planned comparisons				
Spray vs uncut in summer	1	32.25	0.0001	***
Spray vs cut in summer	1	5.27	0.0251	*

3-Way Factorial Analysis of Variance

Main Effects	d.f.	F value	p	Sig. level
Sowing	1	10.60	0.0001	***
Cutting	3	10.76	0.0001	***
Sow*Cut	3	0.57	0.6385	ns
Planned comparisons				
Cutting vs not cutting	1	4.05	0.0498	*
Cut in summer vs not cut in summer	1	29.70	0.0001	***
Cut spring & autumn vs no cut	1	1.93	0.1707	ns

Table 9.4 The effect of treatment on numbers of butterfly species on the field margins in 1989

Treatment	**Mean no. species**[1]
unsown, cut, spring and autumn	8.88
sown, no cut	8.75
unsown, no cut	7.63
sown, cut, summer only	7.38
sown, cut, spring & autumn	7.25
unsown, cut, spring & summer	7.00
sown, cut, spring & summer	6.75
unsown, sprayed	6.25
unsown, cut, summer only	6.00
unsown, cut, spring & summer, leave hay	5.88

[1] Minimum Significant Difference = 3.83

2-Way Analysis of Variance (all treatments)

Main Effects	d.f.	F value	p	Sig. level
Block	7	1.81	0.101	ns
Treatment	9	1.59	0.139	ns
Planned comparisons				
Sprayed vs uncut in summer	1	4.12	0.048	*
Sprayed vs cut in summer	1	0.15	0.700	ns

3-Way Factorial Analysis of Variance

Main Effects	d.f.	F value	P	Sig. level
Sowing	1	0.08	0.782	ns
Cutting	3	1.94	0.136	ns
Sow*Cut	3	1.52	0.220	ns
Planned comparisons				
Cutting vs not cutting	1	2.28	0.138	ns
Cut in summer vs not cut in summer	1	5.73	0.021	*
Cut spring & autumn vs no cut	1	0.02	0.876	ns

Table 9.5 The effect of treatment on numbers of butterfly species on the field margins in 1990

Treatment	**Mean no. species**[1]
sown, no cut	9.63
sown, cut, spring & summer	9.50
sown, cut, spring & autumn	8.88
unsown, cut, spring & autumn	8.13
unsown, no cut	7.75
unsown, cut, summer only	7.00
unsown, cut, spring & summer leave hay	6.63
sown, cut, summer only	6.50
unsown, cut, spring & summer	6.25
unsown, sprayed	6.00

[1] Minimum Significant Difference = 4.01

2-Way Analysis of Variance (all treatments)

<u>Main Effects</u>	d.f.	F value	p	Sig. level
Block	7	0.65	0.715	ns
Treatment	9	2.45	0.015	*
<u>Planned comparisons</u>				
Spray vs uncut in summer	1	7.19	0.009	**
Spray vs cut in summer	1	1.54	0.219	ns

3-Way Factorial Analysis of Variance

<u>Main Effects</u>	d.f.	F value	p	Sig. level
Sowing	1	4.55	0.030	*
Cutting	3	1.93	0.138	ns
Sow*Cut	3	1.61	0.199	ns
<u>Planned comparisons</u>				
Cutting vs not cutting	1	2.28	0.138	ns
Cut in summer vs not cut in summer	1	4.14	0.047	*
Cut spring & autumn vs no cut	1	0.04	0.834	ns

Table 9.6 The effect of treatment on numbers of butterfly species on the field margins in 1991

Treatment	**Mean no. species**[1]
sown, no cut	10.25
sown, cut, spring & autumn	9.13
unsown, cut, spring & autumn	9.00
sown, cut, spring & summer	8.88
unsown, no cut	8.50
unsown, cut, spring & summer	8.00
sown, cut, summer only	8.00
unsown, cut, summer only	7.63
unsown, cut, spring & summer leave hay	7.25
unsown, sprayed	6.88

[1] Minimum Significant Difference = 3.63

2-Way Analysis of Variance (all treatments)

Main Effects	d.f.	F value	p	Sig. level
Block	7	4.66	0.0003	***
Treatment	9	1.65	0.122	ns
Planned comparisons				
Spray vs uncut in summer	1	7.16	0.0095	**
Spray vs cut in summer	1	1.57	0.215	ns

3-Way Factorial Analysis of Variance

Main Effects	d.f.	F value	p	Sig. level
Sowing	1	1.93	0.171	ns
Cutting	3	1.52	0.221	ns
Sow*Cut	3	0.41	0.748	ns
Planned comparisons				
Cutting vs not cutting	1	2.09	0.155	ns
Cut in summer vs not cut in summer	1	3.79	0.057	ns
Cut spring & autumn vs no cut	1	0.15	0.695	ns

Table 9.7 Shannon-Wiener diversity indices on each treatment (averaged over blocks) in 1989

	Treatment										
Date	U/Su	U/SpAu	U/SpSu	U/SpSu/L	U/NC	S/Su	S/SpAu	S/SpSu	S/NC	U/Spray	Sig.[1]
130689	0.000	0.000	0.092	0.000	0.000	0.087	0.000	0.080	0.000	0.000	ns
160689	0.000	0.166	0.237	0.000	0.070	0.208	0.186	0.136	0.000	0.000	ns
250689	0.070	0.262	0.137	0.164	0.191	0.000	0.173	0.207	0.202	0.185	ns
040789	0.278	0.286	0.316	0.338	0.349	0.193	0.398	0.288	0.378	0.627	ns
060789	0.290	0.582	0.571	0.286	0.546	0.219	0.427	0.166	0.613	0.344	ns
130789	0.366	0.543	0.507	0.210	0.504	0.166	0.000	0.360	0.790	0.370	* [2a]
170789	0.296	0.410	0.159	0.167	0.473	0.311	0.217	0.533	1.044	0.525	ns
200789	0.586	0.730	0.289	0.442	0.642	0.549	0.468	0.213	0.948	0.319	ns
240789	0.278	0.882	0.392	0.379	0.570	0.417	0.325	0.339	0.339	0.322	ns
310789	0.087	0.359	0.293	0.280	0.323	0.087	0.080	0.210	0.333	0.000	ns
040889	0.157	0.711	0.195	0.166	0.354	0.520	0.306	0.137	0.826	0.087	** [2b]
070889	0.000	0.166	0.000	0.087	0.390	0.224	0.224	0.173	0.522	0.000	ns
210889	0.000	0.137	0.087	0.157	0.000	0.087	0.080	0.080	0.000	0.000	ns
310889	0.000	0.000	0.087	0.000	0.087	0.000	0.000	0.000	0.000	0.000	ns
050989	0.000	0.087	0.267	0.087	0.000	0.000	0.000	0.000	0.000	0.000	ns
210989	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.087	0.000	ns

Codes:

U/Su	Unsown, cut, summer only	S/Su	Sown, cut, summer only
U/SpAu	Unsown, cut, spring & autumn	S/SpAu	Sown, cut, spring & autumn
U/SpSu	Unsown, cut, spring & summer	S/SpSu	Sown, cut, spring & summer
U/SpSu/L	Unsown, cut, spring & summer, leave hay	S/NC	Sown, no cut
U/NC	Unsown, no cut	U/Spray	Unsown, sprayed

[1] Friedmans Test for null hypothesis that treatment has no influence on diversity index. Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

[2] Non-parametric post-hoc comparisons (McDonald and Thompson 1967) show significant differences ($P \leq 0.05$) for the following pairs of treatment means:

[a] None. [b] None.

Table 9.8 Shannon-Wiener diversity indices on each treatment (averaged over blocks) in 1990

	Treatment										
Date	U/Su	U/SpAu	U/SpSu	U/SpSu/L	U/NC	S/Su	S/SpAu	S/SpSu	S/NC	U/Spray	Sig.[1]
090490	0.267	0.000	0.087	0.173	0.087	0.000	0.087	0.000	0.080	0.000	ns
240490	0.000	0.150	0.173	0.166	0.000	0.000	0.166	0.000	0.087	0.000	ns
300490	0.267	0.000	0.087	0.173	0.087	0.000	0.087	0.000	0.080	0.000	ns
030590	0.000	0.000	0.087	0.087	0.000	0.150	0.000	0.159	0.087	0.137	ns
220590	0.087	0.137	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	ns
240590	0.000	0.000	0.000	0.000	0.087	0.000	0.000	0.000	0.000	0.000	ns
280590	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	ns
310590	0.000	0.000	0.000	0.087	0.087	0.000	0.087	0.000	0.000	0.000	ns
150690	0.087	0.000	0.000	0.000	0.000	0.463	0.296	0.621	0.426	0.087	ns
250690	0.000	0.000	0.087	0.157	0.000	0.391	0.387	0.602	0.447	0.000	*** [2a]
260690	0.000	0.203	0.087	0.000	0.087	0.192	0.517	0.038	0.570	0.087	*** [2b]
290690	0.084	0.166	0.087	0.087	0.272	0.000	0.394	0.087	0.255	0.083	*** [2c]
030790	0.348	0.173	0.000	0.132	0.123	0.063	0.174	0.202	0.445	0.080	ns
110790	0.224	0.452	0.000	0.000	0.290	0.149	0.403	0.000	0.533	0.150	* [2d]
120790	0.137	0.246	0.236	0.253	0.366	0.080	0.379	0.190	0.585	0.242	ns
170790	0.336	0.646	0.435	0.344	0.663	0.470	0.572	0.200	1.172	0.354	ns
310790	0.080	0.351	0.143	0.080	0.378	0.000	0.513	0.419	0.684	0.134	* [2e]
090890	0.080	0.194	0.275	0.000	0.080	0.130	0.253	0.419	0.332	0.080	ns
220890	0.000	0.087	0.166	0.087	0.000	0.000	0.236	0.166	0.087	0.000	ns
290890	0.000	0.000	0.224	0.173	0.087	0.087	0.173	0.303	0.253	0.000	ns
130990	0.000	0.000	0.087	0.139	0.116	0.000	0.000	0.190	0.116	0.222	ns

[1] Friedmans Test for null hypothesis that treatment has no influence on diversity index. Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

[2] Non-parametric post-hoc comparisons (McDonald and Thompson 1967) show significant differences ($P \leq 0.05$) for the following pairs of treatment means:

[a] None

[b] Sown, cut, spring & summer > unsown, sprayed. Sown, cut, spring & summer > unsown, cut, summer only. Sown, cut, spring & summer > unsown, cut spring & autumn. Sown, cut, spring & summer > unsown, no cut.

[c] None. [d] None. [e] None.

Table 9.9 Shannon-Wiener diversity indices on each treatment (averaged over blocks) in 1991

Date	Treatment										
	U/Su	U/SpAu	U/SpSu	U/SpSu/L	U/NC	S/Su	S/SpAu	S/SpSu	S/NC	U/Spray	Sig.[1]
080491	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	ns
280491	0.000	0.087	0.217	0.149	0.000	0.000	0.087	0.000	0.000	0.000	ns
070591	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	ns
090591	0.000	0.080	0.080	0.087	0.000	0.087	0.087	0.000	0.000	0.087	ns
210591	0.080	0.217	0.166	0.347	0.173	0.397	0.198	0.000	0.000	0.080	ns
200691	0.000	0.099	0.087	0.080	0.000	0.099	0.000	0.000	0.070	0.000	ns
020791	0.000	0.000	0.000	0.000	0.087	0.000	0.063	0.000	0.000	0.000	ns
050791	0.087	0.000	0.087	0.000	0.000	0.000	0.000	0.000	0.173	0.000	ns
070791	0.080	0.087	0.070	0.000	0.000	0.080	0.137	0.166	0.070	0.000	ns
110791	0.087	0.330	0.000	0.000	0.080	0.000	0.111	0.224	0.166	0.166	ns
250791	0.126	0.490	0.571	0.421	0.361	0.345	0.680	0.449	0.747	0.253	ns
290791	0.279	0.541	0.291	0.448	0.599	0.324	0.780	0.253	0.683	0.301	ns
010891	0.542	0.664	0.555	0.540	0.704	0.624	1.117	0.845	1.226	0.249	*** [2a]
080891	0.166	0.807	0.383	0.303	0.707	0.333	1.036	0.574	1.342	0.130	*** [2b]
140891	0.303	0.558	0.173	0.303	0.662	0.463	0.860	0.556	1.091	0.311	** [2c]
200891	0.195	0.424	0.167	0.000	0.080	0.294	0.477	0.340	0.789	0.087	* [2d]
270891	0.087	0.173	0.166	0.087	0.000	0.137	0.080	0.080	0.211	0.173	ns
030991	0.304	0.000	0.296	0.303	0.260	0.166	0.130	0.000	0.217	0.173	ns
120991	0.260	0.000	0.084	0.166	0.087	0.506	0.166	0.173	0.157	0.000	ns
190991	0.000	0.000	0.087	0.000	0.000	0.000	0.000	0.070	0.000	0.000	ns
101091	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	NS

[1] Friedmans Test for null hypothesis that treatment has no influence on diversity index. Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

[2] Non-parametric post-hoc comparisons (McDonald and Thompson 1967) show significant differences ($P \leq 0.05$) for the following pairs of treatment means.

[a] Sown, no cut > unsown, sprayed.

[b] Sown, no cut > unsown, sprayed.
Sown, no cut > unsown, cut, summer only.

[c] None. [d] None.

Table 9.10 Butterfly species recorded on transects in 1989, 1990 and 1991 on the experimental field margins at Wytham. Nomenclature follows Emmet and Heath (1990).

SPECIES	TREATMENT U/Su	U/SpAu	U/SpSu/L	U/SpSu	U/NC	S/Su	S/SpAu	S/SpSu	U/Spray	S/NC
Hesperiidae										
Thymelicus sylvestris Ochs.	+ + +	+ + +	- - +	+ - +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Ochlodes venata B.& G.	+ + +	+ + +	- + -	+ + +	+ + +	+ + +	+ + -	+ + +	+ - -	+ + +
Pieridae										
Gonepterix rhamni L.	+ - -	+ + +	+ + +	- - +	+ + +	- - -	- + +	- + -	- + +	+ + +
Anthocharis cardamines L.	- + +	- + +	- + +	- + +	- - +	- + +	- + +	- + +	- + +	- - -
Pieris brassicae L.	+ + +	+ + +	+ + +	+ + +	+ + +	+ - +	+ + +	+ + +	+ + +	+ + +
Pieris rapae L.	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Pieris napae L.	- + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Lycaenidae										
Satyrium w-album Knoch	- - -	- - -	- - -	- - -	- - -	- - +	- - -	- - -	- - -	- - -
Lycaena phlaeas L.	+ + +	+ + +	+ - -	- + +	+ + +	+ - +	+ + +	+ + +	+ + +	+ + +
Polyommatus icarus Rott.	- - +	- - +	+ - +	+ - +	- - +	+ - +	- + +	- + +	- + +	+ + +
Celastrina argiolus L.	- - +	- - +	- - +	- - -	- - +	- - +	- - -	- - +	- - -	- - +
Nymphalidae										
Vanessa atlanta L.	+ + +	+ - -	+ + +	- - +	+ - +	+ - -	+ + -	+ + +	+ - -	+ + +
Cynthia cardui L.	- - -	+ + -	- - -	- - -	+ - -	+ + -	- - -	+ + -	- - +	+ + -
Aglais urticae L.	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Inachis io L.	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Polygonia c-album L.	- - -	+ - -	- - +	+ - +	- - -	- - +	+ - +	+ - +	- + +	- + -
Satyridae										
Pararge aegeria L.	+ - +	+ + +	+ - +	+ - +	+ - +	+ + -	+ + -	+ - +	+ - +	+ + +
Melanargia galathea L.	- + -	- - -	- - +	- - -	+ + -	- + +	- + +	- + +	- - -	+ + +
Pyronia tithonus L.	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Maniola jurtina L.	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +
Aphantopus hyperantus L.	+ + +	+ + +	+ - +	+ + +	+ + +	+ - -	+ + +	+ + +	+ + +	+ + +
Coenonympha pamphilus L.	- + +	- + +	- + +	- + -	- + +	- + +	+ + +	- + +	- - +	- + +

Symbols: + indicates presence of the species on at least one plot of given treatment, out of eight blocks. - indicates absence of the species in all eight blocks. The three symbols for each treatment show the results for 1989, 1990 and 1991 respectively. Note: in 1989 records did not begin until 13 June.

Treatment codes:

U/Su	Unsown, cut summer only	S/Su	Sown, cut, summer only
U/SpAu	Unsown, cut spring & autumn	S/SpAu	Sown, cut, spring & autumn
U/SpSu/L	Unsown, cut spring & summer, leave hay	S/SpSu	Sown, cut, spring & summer
U/SpSu	Unsown, cut spring & summer	U/Spray	Unsown, sprayed
U/NC	Unsown, no cut	S/NC	Sown, no cut

Table 9.11 Mean abundance of *P. tithonus* per 50m margin of indicated treatment type in 1990

Date	Treatment sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	Sig.[1]
110790	0.2500	0.2500	0.2500	0.0625	0.0000	ns
120790	0.1250	0.1875	0.5000	0.1875	0.1250	ns
170790	2.0000	0.3125	1.8750	0.3750	1.5000	** [2a]
310790	2.6875	1.1250	2.6250	1.2500	1.2500	* [2b]
090890	0.6875	0.4375	0.6875	0.3125	0.5000	ns
220890	0.0000	0.0000	0.0625	0.0000	0.0000	ns

[1] Friedmans Test for null hypothesis that treatment has no influence on abundance. Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.
[2] Rank sum multiple comparison test of McDonald and Thompson (1967) shows significant differences ($P \leq 0.05$) for the following pairs of treatment means: [a] None. [b] None.

Table 9.12 Mean abundance of *P. tithonus* per 50m margin of indicated treatment type in 1991

Date	Treatment sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	Sig.[1]
250791	0.9375	1.0625	0.5000	0.3125	0.1250	ns
290791	1.0625	0.3125	0.8750	0.5625	0.5000	ns
010891	3.4375	2.0000	3.3750	1.0625	1.3750	*** [2a]
080891	2.3750	1.2500	2.8125	0.4375	0.5000	*** [2b]
140891	3.0000	1.1875	2.4375	0.6875	0.3750	*** [2c]
200891	0.7500	0.3750	0.8750	0.5000	0.0000	* [2d]
270891	0.0000	0.0625	0.0625	0.0625	0.0000	ns

[1] Friedmans Test for null hypothesis that treatment has no influence on butterfly abundance.
Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.
[2] Rank sum multiple comparison test of McDonald and Thompson (1967) shows significant differences ($P \leq 0.05$) for the following pairs of treatment means: [a] Sown, uncut in summer > unsown, sprayed. Unsown, uncut in summer > unsown, sprayed. [b] Sown, uncut in summer > unsown, sprayed. Sown, uncut in summer > unsown, cut in summer. Unsown, uncut in summer > unsown, cut in summer. Unsown, uncut in summer > sprayed.
[c] Sown, uncut in summer > unsown, sprayed. Unsown, uncut in summer > unsown, sprayed [d] None

Table 9.13 Mean abundance of *M. jurtina* per 50m margin of indicated treatment type in 1990

Date	Treatment: sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	Sig.[1]
310590	0.6250	0.3125	0.1250	0.0625	0.0000	ns
150690	4.4370	5.1250	0.8125	0.3125	0.5000	***[2a]
250690	8.3750	9.6875	0.6875	0.7500	0.8750	***[2b]
260690	17.9375	4.1875	1.1250	0.6250	0.1250	***[2c]
290690	11.7500	0.5625	0.8750	0.7500	1.6250	***[2d]
030790	5.0625	1.0625	1.3750	0.7500	0.1250	***[2e]
110790	1.8125	1.1875	2.5000	0.8125	0.7500	ns
120790	2.8125	0.4375	3.5000	0.9375	1.2500	** [2f]
170890	2.2500	0.8750	3.6250	0.9735	1.3750	ns
310790	0.8175	0.1250	0.0000	0.0625	0.0000	ns
090890	0.0625	0.0625	0.0000	0.0000	0.0000	ns

[1] Friedmans Test for null hypothesis that treatment has no influence on abundance.
Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

[2] Rank sum multiple comparison test of McDonald and Thompson (1967) shows significant differences ($P \leq 0.05$) for the following pairs of treatment means:

[a] Sown, cut in summer > unsown, sprayed. Sown, cut in summer > unsown, cut in summer. Sown, cut in summer > unsown, cut in summer.

[b] Sown, cut in summer > unsown, sprayed. Sown, cut in summer > unsown, cut in summer. Sown, cut in summer > unsown, uncut in summer. Sown, uncut in summer > unsown, uncut in summer.

[c] Sown, uncut in summer > unsown, sprayed. Sown, uncut in summer > unsown, cut in summer.

[d] Sown, uncut in summer > sown, cut in summer. Sown, uncut in summer > unsown, sprayed. Sown, uncut in summer > unsown, cut in summer.

[e] Sown, uncut in summer > unsown, cut in summer. Sown, uncut in summer > unsown, sprayed.

[f] Unsown, uncut in summer > sown, cut in summer.

Table 9.14 Mean abundance of *M. jurtina* per 50m margin of indicated treatment type in 1991

Date	Treatment					Sig.[1]
	sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	
020791	0.9375	0.0625	0.1250	0.0000	0.0000	** [2a]
050791	0.6875	0.1250	0.5000	0.3125	0.0000	ns
070791	4.1250	0.5625	0.3125	0.3125	0.2500	** [2b]
110791	2.7500	0.4375	0.7500	0.6250	0.3750	** [2c]
250791	2.5625	2.1250	0.8125	1.0000	0.7500	* [2d]
290791	0.8125	0.6875	0.6875	0.4375	0.5000	ns
010891	3.6250	1.3125	1.2500	0.6875	0.1250	***[2e]
080891	1.7500	0.3125	1.1875	0.1875	0.1250	***[2f]
140891	0.6250	0.0625	0.4375	0.2500	0.0000	* [2g]
200891	0.1250	0.1875	0.0000	0.0000	0.0000	ns
270891	0.0000	0.0000	0.0000	0.0625	0.0000	ns

1 Friedmans Test for null hypothesis that treatment has no influence on abundance.
Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.
2 Rank sum multiple comparison test of McDonald and Thompson (1967) shows significant differences ($P \leq 0.05$) for the following pairs of treatment means:
a None.
b Sown, uncut in summer > unsown, sprayed. Sown, uncut in summer > unsown, uncut in summer. Sown, uncut in summer > unsown, cut in summer.
c Sown, uncut in summer > unsown, sprayed.
d Sown, uncut in summer > unsown, sprayed.
e Sown, uncut in summer > unsown, sprayed.
f Sown, uncut in summer > unsown, cut in summer. Sown, uncut in summer > unsown, sprayed.
g None.

Table 9.15 Mean abundance of *A. urticae* per 50m margin of indicated treatment type in 1990

	Treatment					
Date	sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	Sig.[1]
090490	0.2500	0.0000	0.3125	0.1875	0.6250	ns
240490	0.1875	0.0625	0.2500	0.1875	0.1250	ns
300490	0.0625	0.1250	0.0625	0.1250	0.0000	ns
030590	0.0000	0.1250	0.0000	0.1250	0.2500	ns
240590	0.1250	0.0000	0.0625	0.0000	0.0000	ns
310590	0.0625	0.0625	0.0625	0.0000	0.0000	ns
150690	1.8125	1.7500	0.0000	0.2500	0.1250	***[2a]
250690	3.3125	4.0000	0.0625	0.2500	0.2500	***[2b]
260690	7.7500	0.6250	0.3750	0.0625	0.1250	***[2c]
290690	1.8125	0.1875	0.1875	0.0625	0.3750	** [2d]
030790	0.4375	0.0625	0.1875	0.0625	0.3750	ns
110790	0.3125	0.0000	0.3125	0.0000	0.2500	ns
120790	0.3125	0.0000	0.5625	0.0000	0.1250	ns
170790	0.9375	0.6250	0.9375	0.0625	1.1250	ns
310790	0.1875	0.0000	0.1250	0.0000	0.0000	ns
090890	0.1875	0.1250	0.0000	0.0625	0.1250	ns
220890	0.1250	0.0000	0.0625	0.0625	0.0000	ns
290890	0.0000	0.1250	0.1250	0.1875	0.0000	ns

1 Friedmans Test for null hypothesis that treatment has no influence on butterfly abundance. Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

2 Rank sum multiple comparison test of McDonald and Thompson (1967) shows significant differences ($P \leq 0.05$) for the following pairs of treatment means:

a Sown, uncut in summer > unsown, sprayed. Sown, uncut in summer > unsown, uncut in summer.

b Sown, cut in summer > unsown, sprayed. Sown, uncut in summer > unsown, uncut in summer.

c Sown, uncut in summer > unsown, sprayed. Sown, uncut in summer > unsown, cut in summer. Sown, uncut in summer > unsown, uncut in summer

d Sown, uncut in summer > unsown, cut in summer. Sown, uncut in summer > sprayed.

Table 9.16 Mean abundance of *A. urticae* per 50m margin of indicated treatment type in 1991

Date	Treatment					Sig.[1]
	sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	
080491	0.0000	0.0000	0.0625	0.0625	0.0000	ns
280491	0.0625	0.1250	0.1875	0.1875	0.1250	ns
070591	0.0000	0.0000	0.0625	0.1875	0.1250	ns
090591	0.4375	0.0000	0.1875	0.1875	0.1250	ns
210591	0.3125	0.2500	0.3125	0.1250	0.2500	ns
050791	0.0000	0.0000	0.0000	0.0000	0.0000	ns
070791	0.1250	0.0000	0.0000	0.0000	0.0000	ns
110791	0.1875	0.0625	0.2500	0.1875	0.2500	ns
250791	0.2500	0.1250	0.7500	0.4375	0.5000	ns
290791	0.5625	0.2500	1.5000	0.2500	0.3750	* [2a]
010891	1.8125	0.1875	2.0625	0.6250	0.3750	* [2b]
080891	0.6250	0.0625	0.2500	0.0000	0.0000	* [2c]
140891	0.0625	0.0625	0.0625	0.0000	0.0000	ns
200891	0.0625	0.0625	0.0625	0.0000	0.0000	ns
270891	0.0000	0.1250	0.1250	0.0000	0.1250	ns
030991	0.5000	0.6250	0.5000	0.4375	0.3750	ns
120991	0.1875	0.7500	0.2500	0.3125	0.0000	ns
190991	0.9375	0.5625	0.0625	0.3750	0.1250	ns
101091	0.0000	0.1875	0.0000	0.0000	0.1250	ns

1 Friedmans Test for null hypothesis that treatment has no influence on butterfly abundance. Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

2 Rank sum multiple comparison test of McDonald and Thompson (1967) shows significant differences ($P \leq 0.05$) for the following pairs of treatment means:

a None.

b None.

c None.

Table 9.17 Mean abundance of *T. sylvestris* per 50m margin of indicated treatment type in 1990

Date	Treatment: sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	Sig.[1]
290690	0.0000	0.0000	0.1875	0.0000	0.1250	ns
030790	0.0625	0.0000	0.0625	0.1250	0.0000	ns
110790	0.1875	0.0000	0.3750	0.0000	0.0000	ns
120790	0.0000	0.1875	0.3125	0.0000	0.0000	ns
170790	0.2500	0.0625	0.6875	0.0000	0.0000	* [2a]
310790	0.6875	0.0000	0.0625	0.0000	0.0000	* [2b]

1 Friedmans Test for null hypothesis that treatment has no influence on butterfly abundance. Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

2 Rank sum multiple comparison test of McDonald and Thompson (1967) shows significant differences ($P \leq 0.05$) for the following pairs of treatment means: [a] None. [b] None.

Table 9.18 Mean abundance of *T. sylvestris* per 50m margin of indicated treatment type in 1991

Date	Treatment: sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	Sig.[1]
250791	0.9375	0.1875	0.4375	0.0000	0.0000	*** [2a]
290791	0.9375	0.1250	0.5625	0.0000	0.1250	** [2b]
010891	1.9375	0.1875	0.3750	0.3125	0.1250	*** [2c]
080891	1.6875	0.3125	0.2500	0.0625	0.1250	** [2d]
140891	1.1250	0.1875	0.0625	0.0625	0.2500	* [2e]
200891	0.6875	0.2500	0.0625	0.2500	0.0000	* [2f]
270891	0.1875	0.0000	0.0000	0.0000	0.0000	ns

1 Friedmans Test for null hypothesis that treatment has no influence on butterfly abundance. Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

2 Rank sum multiple comparison test of McDonald and Thompson (1967) shows significant differences ($P \leq 0.05$) for the following pairs of treatment means:

a Sown, uncut in summer > unsown, cut in summer. Sown, uncut in summer > unsown, sprayed. [b]None.

c Sown, uncut in summer > unsown, sprayed. [d] None. [e] None. [f] None.

Table 9.19 Mean abundance of *C. pamphilus* per 50m margin of indicated treatment type in 1990

Date	Treatment					Sig.[1]
	sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	
220590	0.0000	0.1250	0.0000	0.0000	0.0000	ns
260690	0.0625	0.0000	0.0625	0.0000	0.0000	ns
290690	0.1250	0.0000	0.0000	0.0000	0.0000	ns
170790	0.0625	0.0000	0.0625	0.0625	0.0000	ns
090890	0.1250	0.1250	0.1250	0.0625	0.0000	ns
220891	0.0000	0.1250	0.0625	0.0625	0.0000	ns
290891	0.0625	0.0000	0.0000	0.0625	0.0000	ns
130990	0.0000	0.0625	0.0000	0.0000	0.0000	ns

[1] Friedmans Test for null hypothesis that treatment has no influence on butterfly abundance. ns not significant.

Table 9.20 Mean abundance of *C. pamphilus* per 50m margin of indicated treatment type in 1991

Date	Treatment					Sig.[1]
	sown, uncut summer	sown, cut summer	unsown, uncut summer	unsown, cut summer	unsown, sprayed	
200691	0.0625	0.0000	0.1250	0.0625	0.0000	ns
020791	0.0000	0.1250	0.0000	0.0000	0.0000	ns
050791	0.0000	0.0000	0.0000	0.1250	0.0000	ns
070791	0.0000	0.3125	0.0625	0.0625	0.0000	* [2a]
110791	0.0625	0.1250	0.0000	0.0000	0.0625	ns
290791	0.0625	0.0625	0.0000	0.0625	0.0625	ns
080891	0.0000	0.0625	0.0625	0.0000	0.0000	ns
140891	0.0625	0.0000	0.0625	0.0000	0.0000	ns
200891	0.0000	0.0625	0.0000	0.1250	0.0000	ns
270891	0.0000	0.0000	0.0000	0.1250	0.0000	ns
030991	0.1250	0.0000	0.0625	0.1250	0.0000	ns
120991	0.0625	0.0625	0.0000	0.0000	0.0000	ns

1 Friedmans Test for null hypothesis that treatment has no influence on butterfly abundance. Statistic based on row mean score differences of ranks, controlled for block. ns not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

2 Rank sum multiple comparison test of McDonald and Thompson (1967) shows significant differences ($P \leq 0.05$) for the following pairs of treatment means: [a] None.

Table 9.21 Mean butterfly abundance per km at the University Farm (U) and Denman's Farm (D) on seven pairs of transect in 1991. Probability derived from Wilcoxon paired sample analysis for difference between means.

	1 Aug 91		8 Aug 91		14 Aug 91		20 Aug 91	
	D	U	D	U	D	U	D	U
T. sylvestris	1.33	11.50	0.53	9.00	1.07	6.25	0.27	4.50
O. venata	0.00	0.75	0.00	0.50	0.00	0.00	0.00	0.50
G. rhamni	0.00	0.50	0.79	0.75	0.00	0.25	0.00	0.50
P. brassicae	3.46	1.50	4.27	2.50	1.07	3.25	2.13	1.00
P. rapae	0.53	2.50	3.73	6.00	1.07	0.75	3.19	0.25
P. napae	2.39	2.75	0.53	2.00	3.47	5.50	1.87	8.00
L. phlaeas	0.00	0.25	0.00	0.00	0.27	0.75	0.27	0.50
P. icarus	0.00	0.00	0.00	0.50	0.00	1.50	0.00	0.00
C. argiolus	1.59	2.50	7.46	0.75	2.39	0.50	1.87	0.25
V. atlanta	0.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00
A. urticae	3.47	17.50	3.19	3.75	0.27	0.70	0.00	0.75
I. io	0.00	3.00	1.87	3.00	2.39	1.50	0.27	0.25
P. c-album	0.27	0.75	0.27	0.00	0.00	0.25	0.00	0.00
P. aegeria	0.00	0.00	0.27	0.00	1.07	0.00	1.59	0.00
P. tithonus	9.86	42.25	14.13	29.25	9.86	31.50	2.67	10.25
M. jurtina	13.59	29.00	7.73	14.75	3.73	5.75	0.79	1.25
A. hyperantus	0.53	2.50	0.27	0.25	0.00	0.50	0.00	0.25
C. pamphilus	0.00	0.00	0.00	0.50	0.00	0.50	0.00	0.75
M. galathea	0.00	0.25	0.00	0.00	0.00	0.00	0.00	0.00

	27 Aug 91		3 Sep 91		12 Sept 91			
	D	U	D	U	D	U	*P*	Sig.
T. sylvestris	0.00	0.75	0.00	0.00	0.00	0.00	0.04	*
O. venata	0.00	0.00	0.00	0.00	0.00	0.00	0.18	ns
G. rhamni	0.00	0.50	0.00	0.00	0.00	0.00	0.07	ns
P. brassicae	0.79	1.50	0.27	0.75	0.00	0.00	0.75	ns
P. rapae	0.27	1.00	0.53	0.75	0.27	0.50	0.31	ns
P. napae	2.67	2.75	0.00	1.25	0.53	2.00	0.02	*
L. phlaeas	0.27	0.25	0.00	0.50	0.00	0.50	0.04	*
P. icarus	0.00	0.50	0.00	1.50	0.00	0.00	0.04	*
C. argiolus	1.07	0.25	0.53	0.25	0.00	0.00	0.12	ns
V. atlanta	0.00	0.00	0.00	0.00	0.27	0.75	0.59	ns
A. urticae	0.53	1.50	2.93	10.75	1.33	6.75	0.02	*
I. io	0.00	0.00	0.27	0.00	0.00	0.50	0.89	ns
P. c-album	0.00	1.75	0.27	2.25	0.27	0.75	0.07	ns
P. aegeria	2.67	1.75	1.59	2.25	1.59	0.75	0.07	ns
P. tithonus	0.79	1.00	0.00	0.00	0.00	0.00	0.04	*
M. jurtina	0.00	0.25	0.00	0.00	0.00	0.00	0.04	*
A. hyperantus	0.00	0.00	0.00	0.00	0.00	0.00	0.14	ns
C. pamphilus	0.00	0.50	0.27	1.25	0.00	0.50	0.02	*
M. galathea	0.00	0.00	0.00	0.00	0.00	0.00	0.32	ns

Table 9.22 Common larval foodplants of the butterfly species recorded on the experimental field margins. All the plant species except those marked with an asterisk were recorded on, or in the vicinity of, the experimental margins. Table compiled from Howarth (1973) and Emmet and Heath (1990).

SPECIES	FOODPLANTS
Hesperiidae	
Thymelicus sylvestris	*Holcus lanatus, H. mollis, Phleum pratense, Brachypodium sylvaticum*
Ochlodes venata	*Dactylis glomerata, Brachypodium sylvaticum, Calamagrostis epigejos*
Pieridae	
Gonepterix rhamni	*Rhamnus catharticus*
Anthocharis cardamines	Cruciferae, esp. *Cardamine pratensis, Alliaria petiolata, Sinapis arvensis*
Pieris brassicae	Cruciferae esp. cultivated brassicas, also Leguminosae (10 species)
Pieris rapae	Cruciferae (wild and cultivated)
Pieris napae	Wild Cruciferae, esp. *Cardamine pratensis, Alliaria petiolata, Sisymbrium officinale*
Lycaenidae	
Satyrium w-album	*Ulmus* spp.
Lycaena phlaeas	*Rumex acetosa, R. acetosella**, occasionally broad-leaved docks.
Polyommatus icarus	Leguminosae, esp. *Lotus corniculatus, L. uliginosus, Medicago lupulina, Trifolium repens*
Celastrina argiolus	*Ilex aquifolium** (spring brood), *Hedera helix* (summer brood), also *Cornus sanguinea*.
Nymphalidae	
Vanessa atlanta	*Urtica dioica*
Cynthia cardui	*Cirsium vulgare, C. palustre*, also *C. arvense, Urtica dioica*
Aglais urticae	*Urtica dioica, U. urens*
Inachis io	*Urtica dioica*, occasionally *Humulus lupulus*.
Polygonia c-album	*Urtica dioica*, occasionally *Humulus lupulus, Ribes* spp., *Ulmus* spp., *Salix* spp.
Satyridae	
Pararge aegeria	Grasses, esp. *Brachypodium sylvaticum, Dactylis glomerata, Holcus lanatus*
Melanargia galathea	Grasses, esp. *Festuca rubra, F. ovina**, *Brachypodium pinnatum**
Pyronia tithonus	Grasses, esp. *Festuca* spp. and *Agrostis* spp.
Maniola jurtina	Grasses, esp. *Poa* spp., *Agrostis* spp., *Lolium* spp.
Aphantopus hyperantus	Grasses, esp. *Deschampsia cespitosa, Agrostis stolonifera*
Coenonympha pamphilus	Grasses, esp. *Poa* spp. and *Festuca* spp.

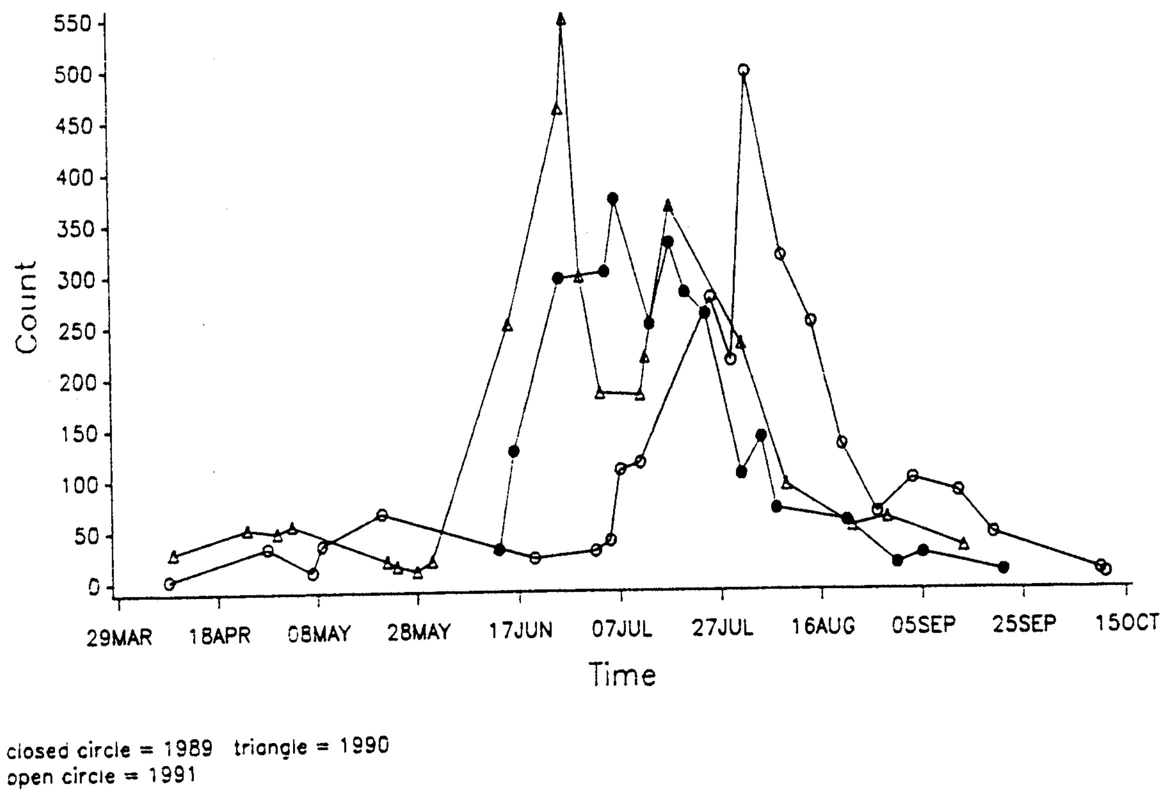


Figure 9.1 Total number of butterflies on each transect date (all treatments) in 1989, 1990 and 1991

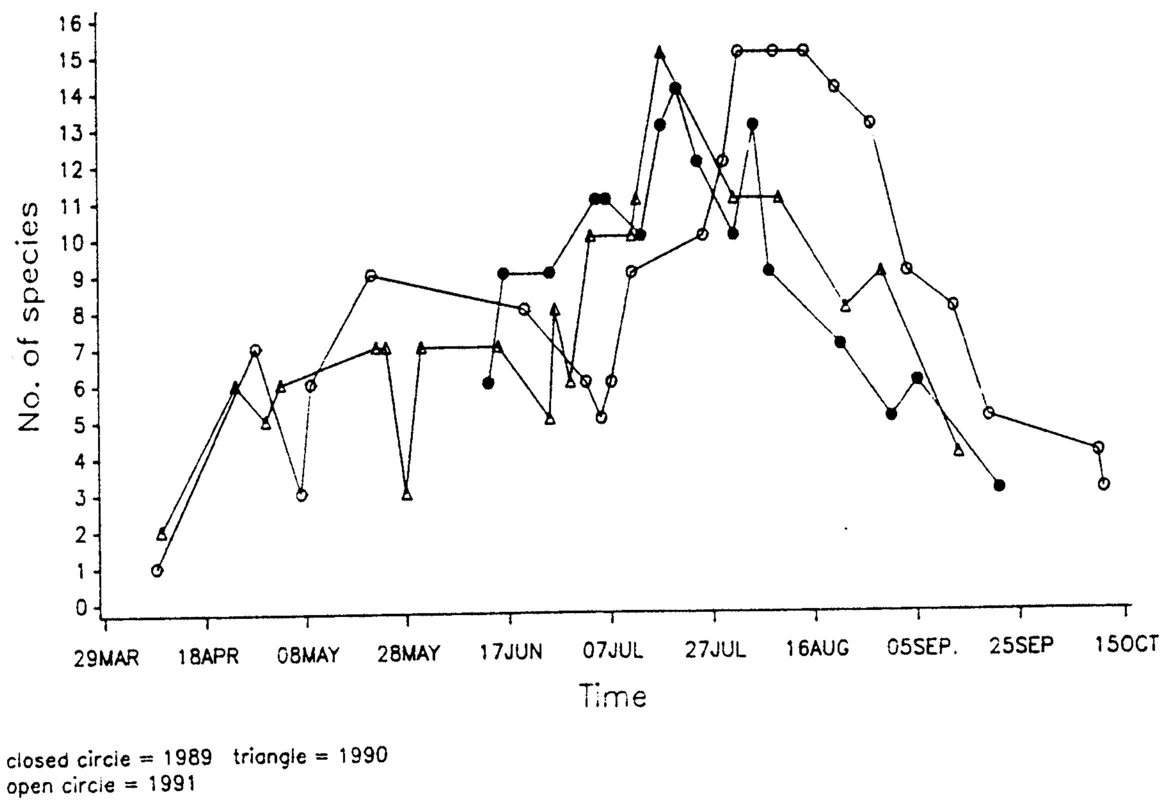
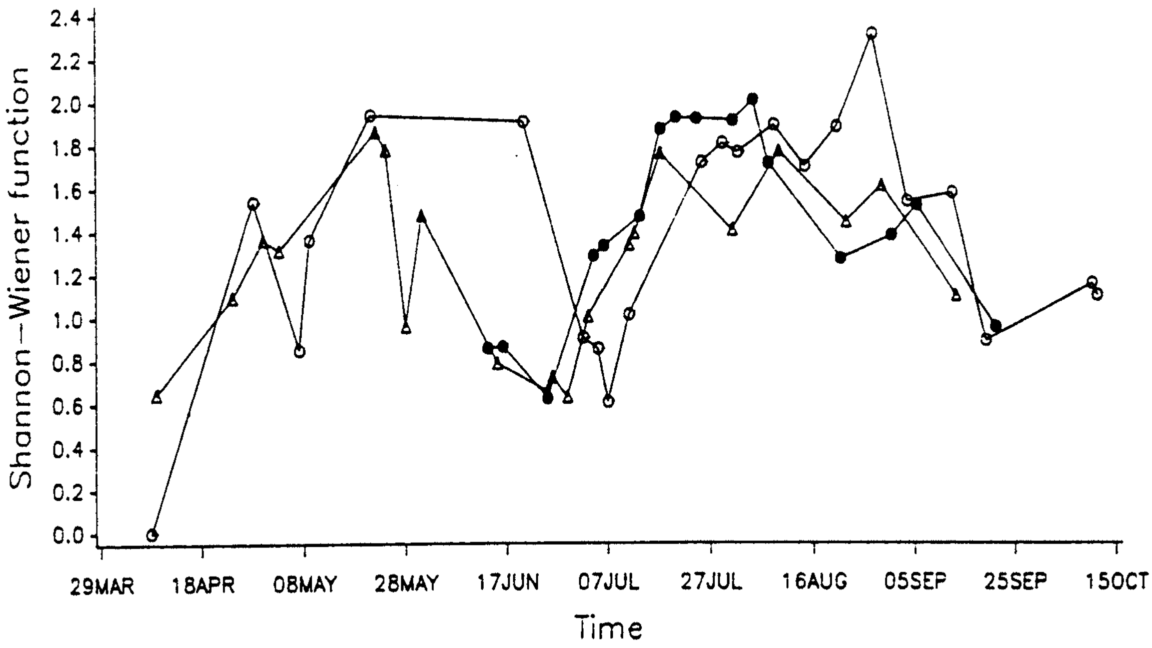


Figure 9.2 Total number of species on each transect date (all treatments) in 1989, 1990 and 1991



closed circle = 1989 triangle = 1990
open circle = 1991

Figure 9.3 Diversity (Shannon-Wiener function) on each transect date (all treatments) in 1989, 1990 and 1991

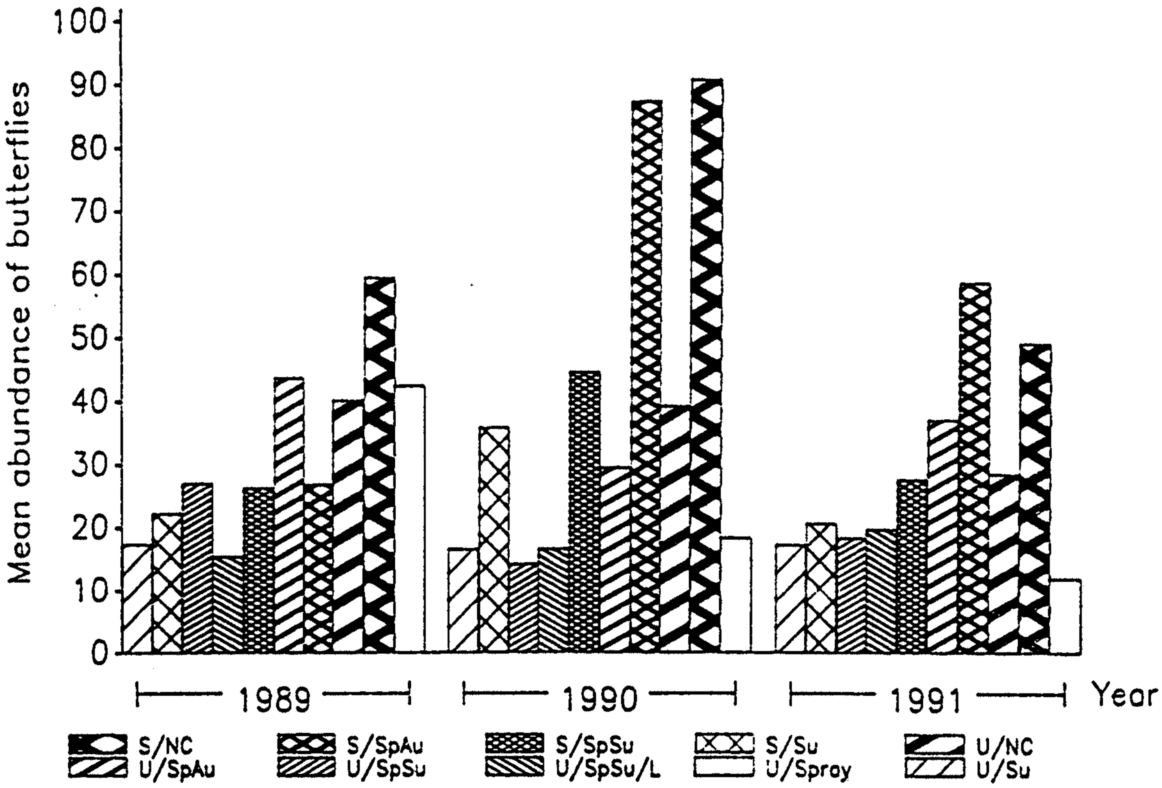


Figure 9.4 Mean butterfly abundance per treatment (all dates) in 1989, 1990 and 1991

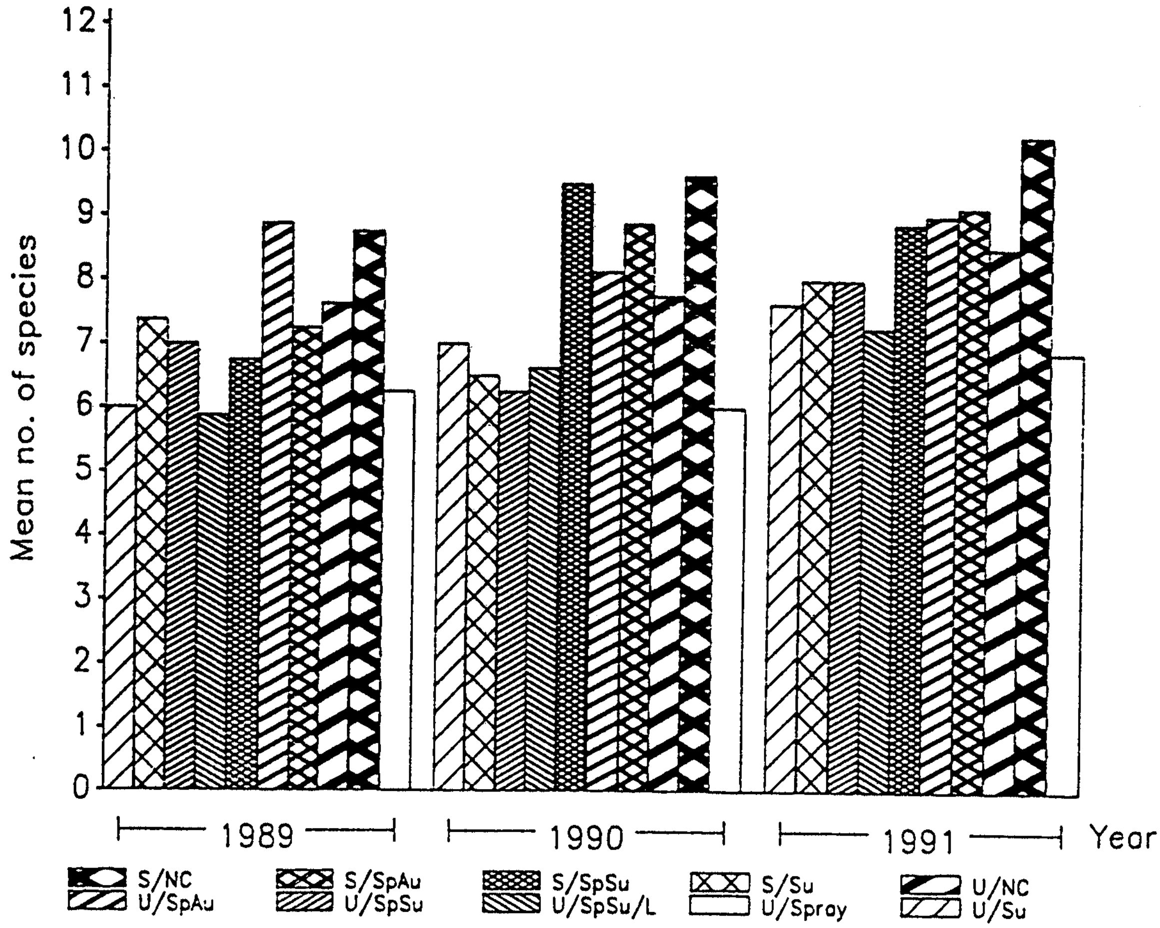


Figure 9.5 Mean number of species per treatment (all dates) in 1989, 1990 and 1991

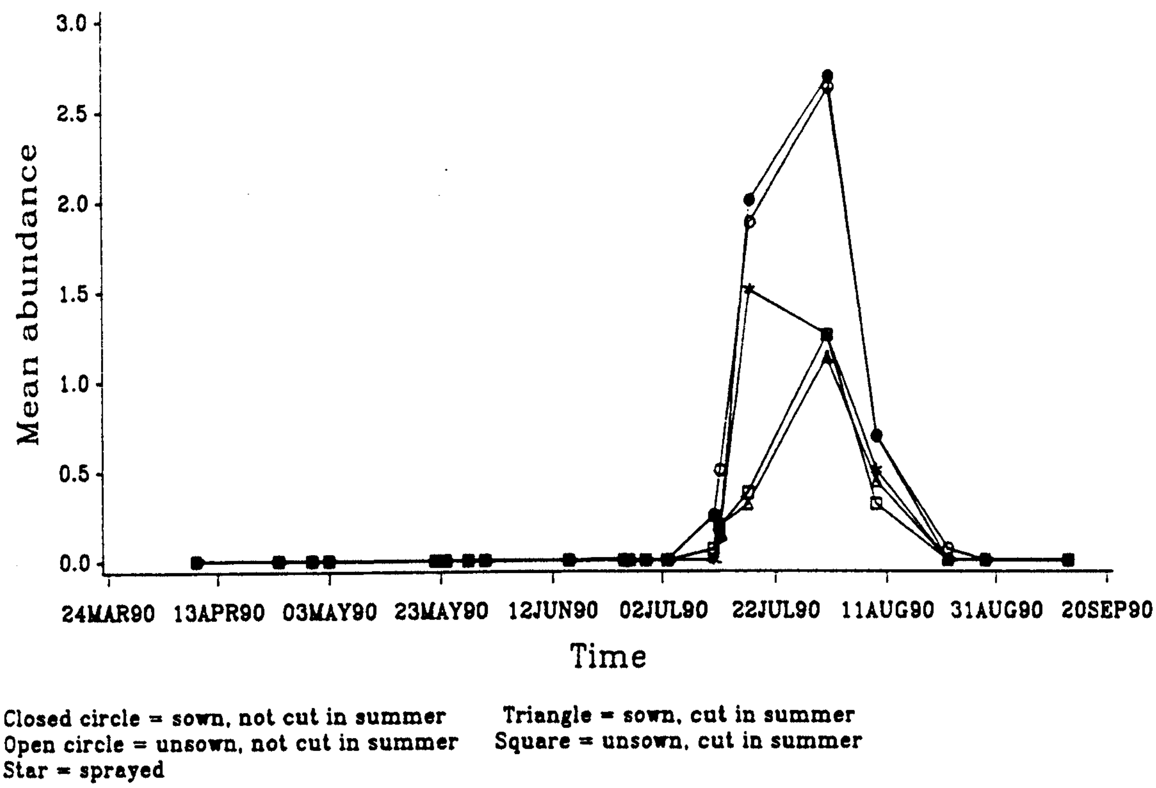


Figure 9.6 Mean abundance of *P. tithonus* per plot in 1990

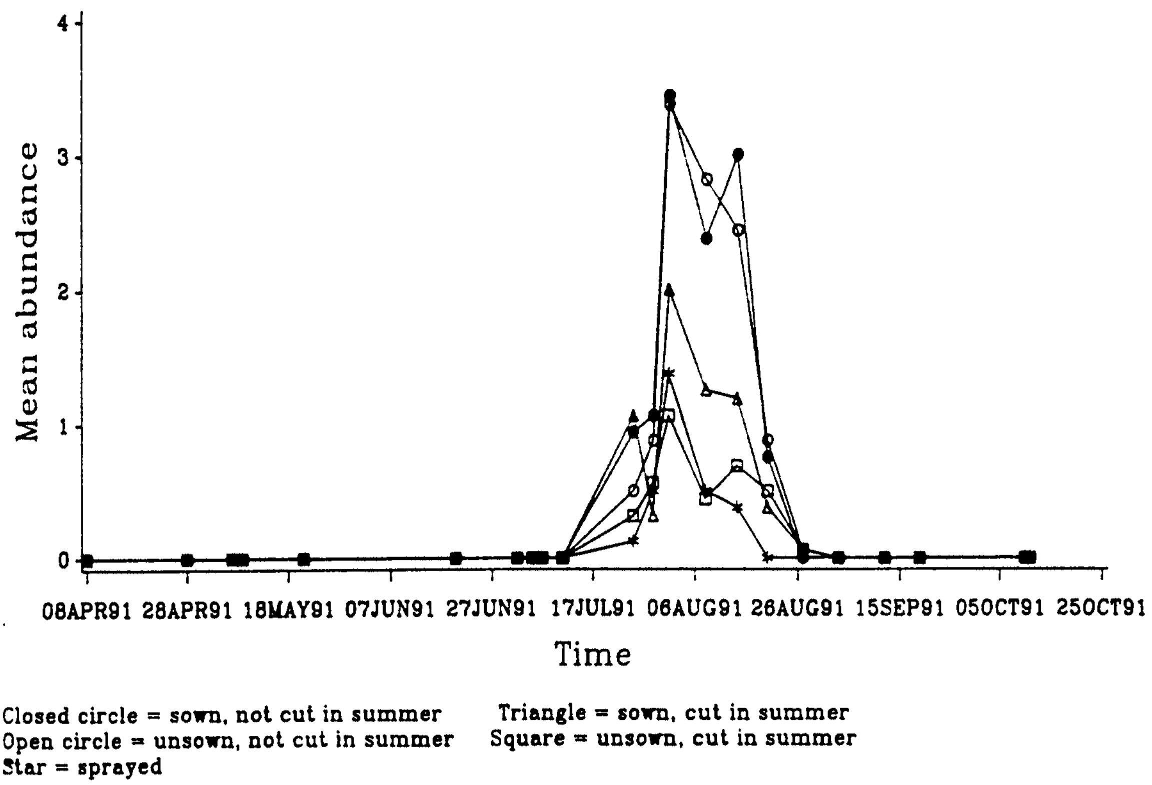
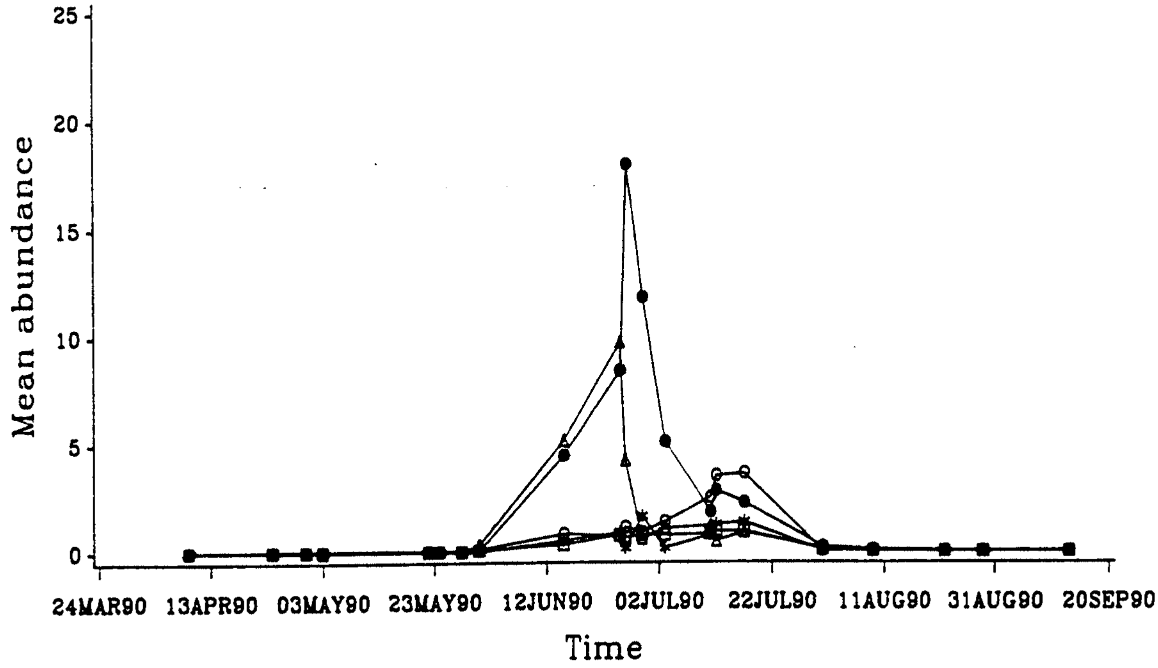
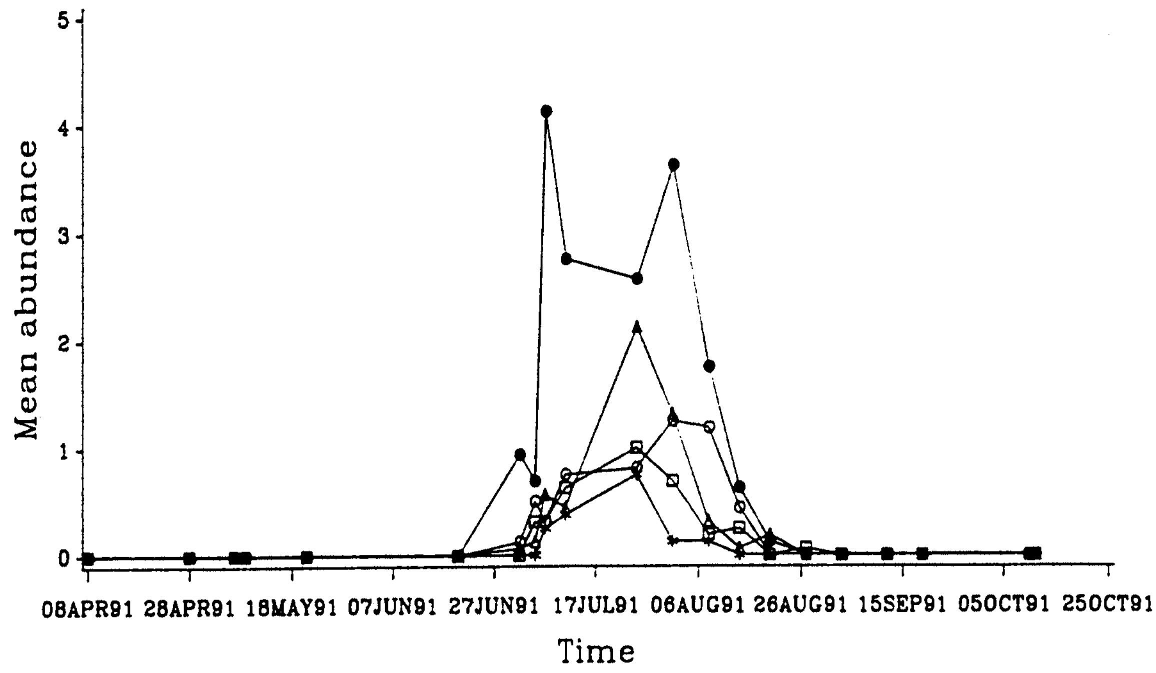


Figure 9.7 Mean abundance of P. *tithonus* per plot in 1991



Closed circle = sown, not cut in summer
Open circle = unsown, not cut in summer
Star = sprayed
Triangle = sown, cut in summer
Square = unsown, cut in summer

Figure 9.8 Mean abundance of *M. jurtina* per plot in 1990



Closed circle = sown, not cut in summer
Open circle = unsown, not cut in summer
Star = sprayed
Triangle = sown, cut in summer
Square = unsown, cut in summer

Figure 9.9 Mean abundance of *M. jurtina* per plot in 1991

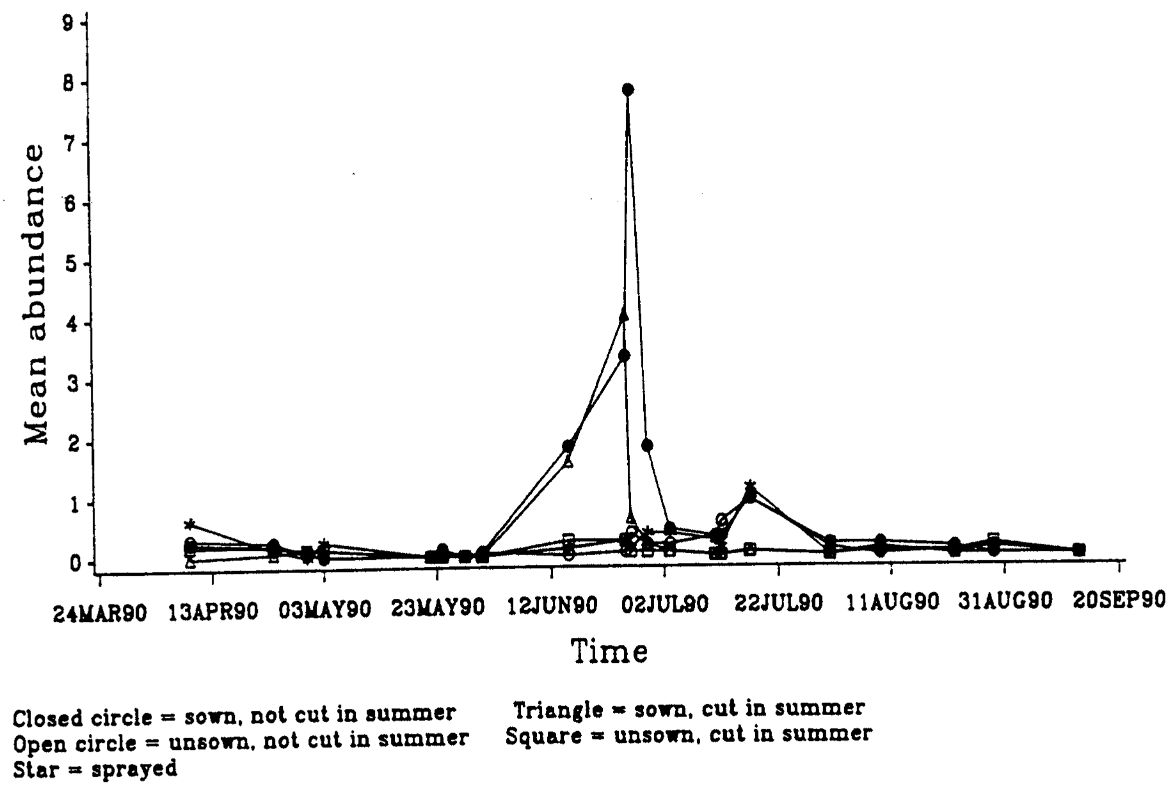


Figure 9.10 Mean abundance of *A. urticae* per plot in 1990

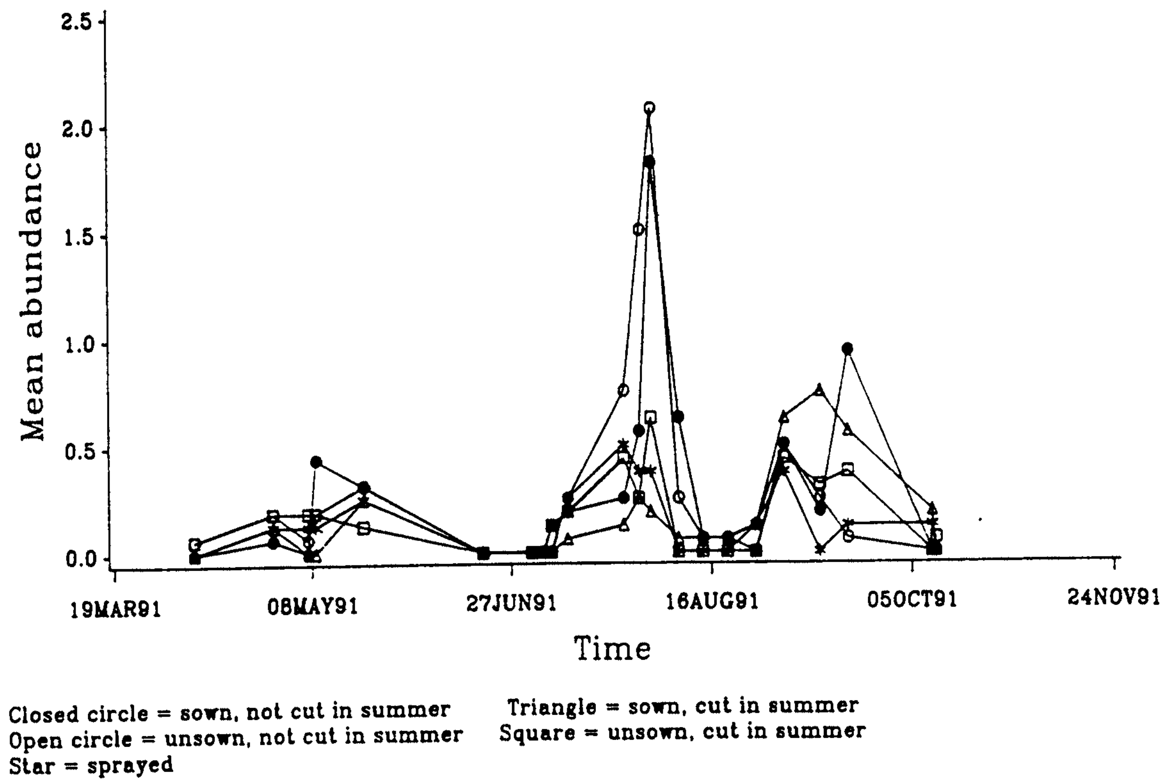


Figure 9.11 Mean abundance of *A. urticae* per plot in 1991

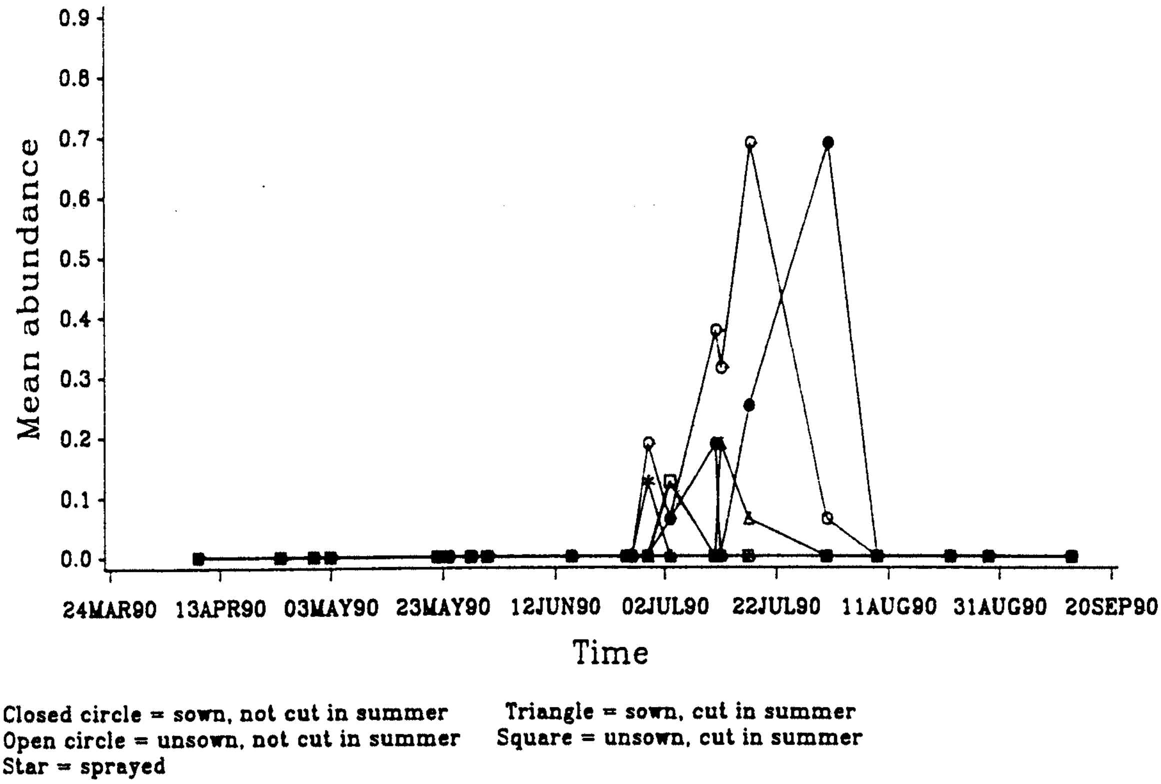


Figure 9.12 Mean abundance of *T. sylvestris* per plot in 1990

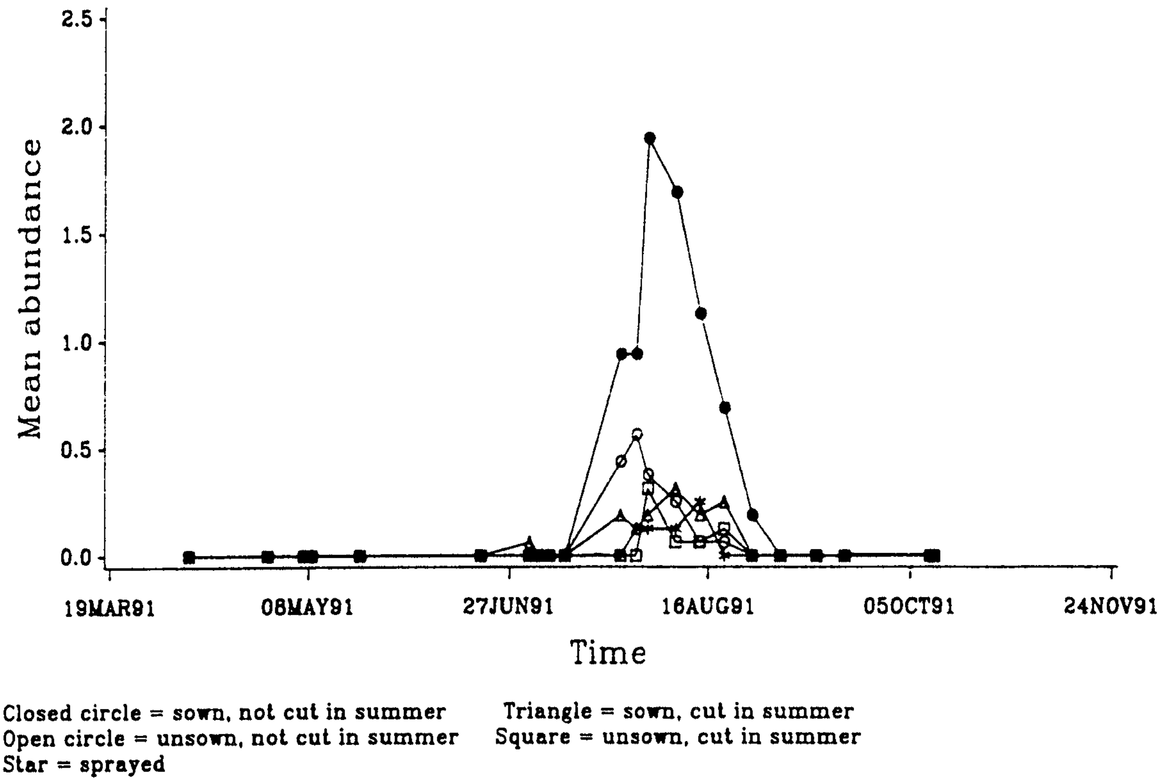


Figure 9.13 Mean abundance of *T. sylvestris* per plot in 1991

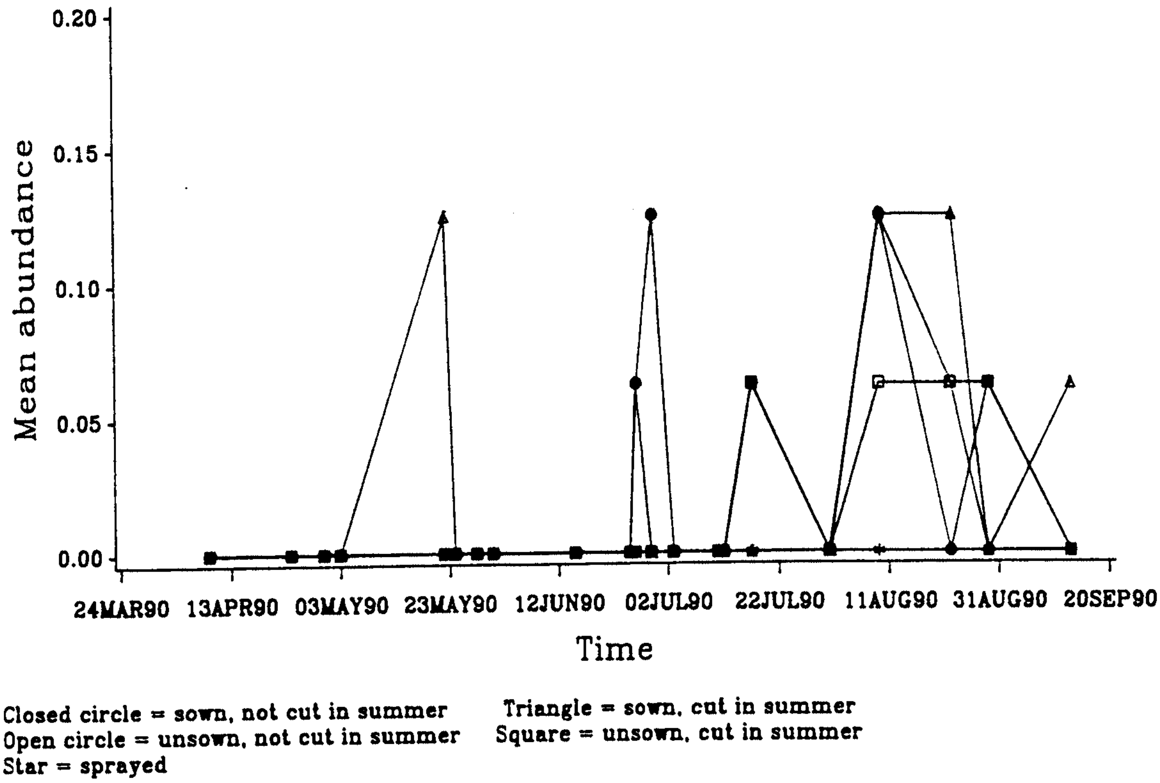


Figure 9.14 Mean abundance of *C. pamphilus* per plot in 1990

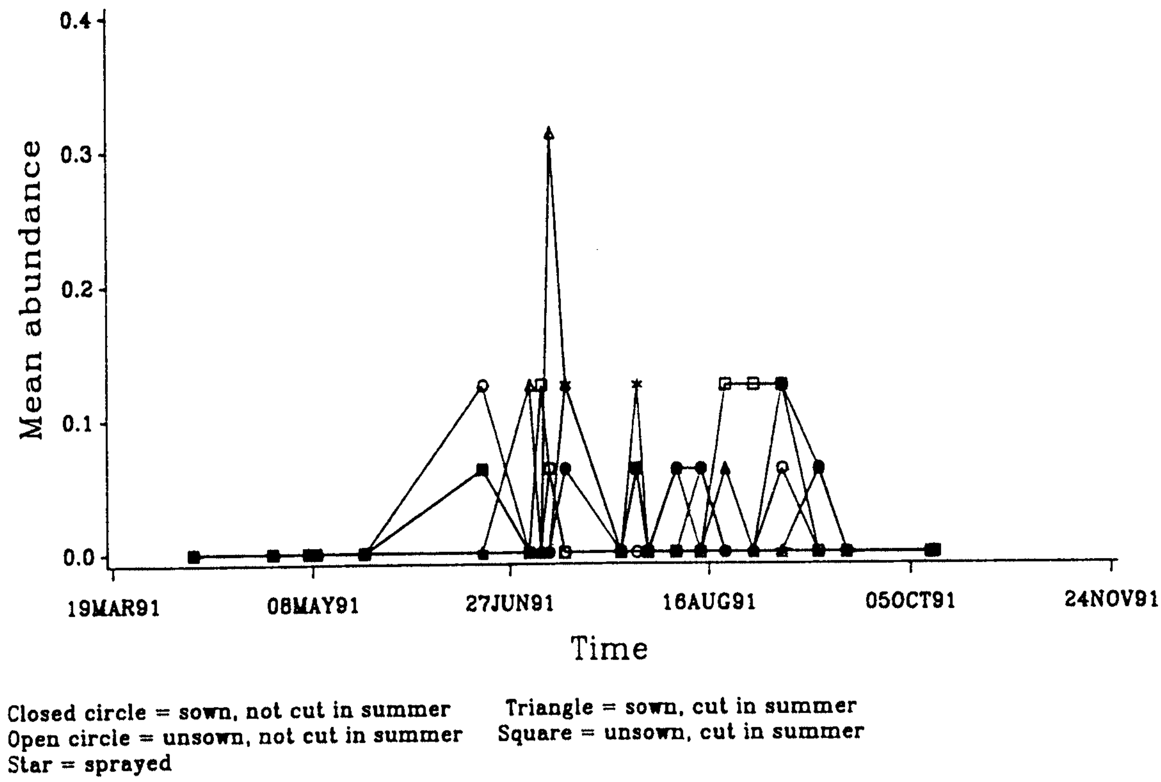


Figure 9.15 Mean abundance of *C. pamphilus* per plot in 1991