5 THE POPULATION DYNAMICS AND CONTROL OF PERNICIOUS WEEDS

5.1 Introduction

Improvements in the wildlife conservation value of field margins must be preceded or accompanied by effective control of pernicious weeds if they are to gain acceptability with farmers. Indeed, it is usually the case that conservation measures can best gain acceptability with farmers when they are seen to accompany agronomic or financial benefits. This principle has been effectively demonstrated by the success of the Game Conservancy Trust's Cereals and Game Birds Project in promoting conservation headlands through their benefits to game rearing (Potts 1986).

In this chapter we examine the extent to which one of our original hypotheses, that the re-establishment of grassy perennial swards on field margins should exclude annual weeds, is upheld. We consider the effects of competition from the developing successional swards, and the sown swards, on the abundance of key crop weeds. Weed abundance can also be influenced by mowing, both indirectly through its effects on the competing swards, and through direct effects on the plants themselves (see Chapter 4.1). For each of the species considered, we describe the gross changes in their abundance during the experiment, and the ways in which mowing and sowing influenced this pattern.

We have analyzed the data for three annual grasses (*Bromus sterilis, Avena* species (*A. fatua* and *A. sterilis* subsp *ludoviciana* combined) and *Alopecurus myosuroides*) and one forb, *Galium aparine*. *G. aparine* and *B. sterilis* are both common weeds of degraded field margins as well as of crops. They are the only two species for which Marshall (1989) found good evidence to support the widely held prejudice amongst farmers that field margins form reservoirs for weeds that subsequently re-infect the crop. The three grass species are the commonest annual grass weeds of cereal crops in England (Froud-Williams & Chancellor 1982) and all can result in serious crop yield losses (Cousens *et al* 1988, Hubbard *et al* 1986, Wilson & Peters 1982, Martin & Field 1987). We have also analyzed the data for three species of perennials that are frequently the subject of agricultural weed control. *Cirsium arvense* is a notifiable weed, *Elymus repens* can become a problem weed in cereal crops and *Urtica dioica* is frequently controlled in field boundaries. Although it is unlikely that the occurrence of these species in field margins seriously increases weed nuisance in the crop, the fact that farmers perceive a problem is likely to determine the acceptability or otherwise of a field margin management strategy.

For each species we discuss overall trends in abundance with time and responses to sowing, mowing and spraying, first in the new and second in the old margins. We also describe the relative abundance of each species in the old and the new margins because, even where a problem weed increases in the new margin, it is valuable to assess it in terms of its pre-existing control problems as well as in absolute terms. The analyses presented are for June dates only, and therefore reflect the abundance relevant to flowering and seed production, rather than peak abundance. The data were all collected immediately prior to the June cut and so reflect the effects of the spring, and previous year's cutting, rather than any proximate effects.

5.2 Results and discussion

The results are all based on analyses of the mean frequencies (or densities) per quadrat for each plot. We measured panicle densities as well as relative frequencies for the annual grass weeds (see Chapter 2.2.5) to give a more accurate and sensitive measure of change in abundance. The density data also enabled us to relate the abundances encountered in the field margins to the many published estimates of abundance for these species in crops. For each species we use figures to show the time trends in the relative frequencies and in panicle densities in each zone of the margin. The significance of the results of analyses of variance of the frequencies are tabulated for each species, zone and date. Where analyses of panicle densities gave rise to significant results that were not also obtained from the frequency data, tables of these results are presented in addition to those for frequencies. We discuss additional significant results arising from unplanned comparisons of means but, because of the volume of data, we do not tabulate the means on which these are based.

The relative frequency data cover 1987 to 1990 for all species and 1992 for the annual grasses and *Cirsium arvense*. The density data are for 1989 to 1992 (Chapter 2.2.5).

5.2.1 *AVENA* SPECIES

The new margins

Temporal trends The gross changes in the abundance of *Avena* species in the new margins are similar to those of most other annual species. Abundance peaked in the first year of fallow, when the seed bank in the old crop edge was expressed, and declined rapidly thereafter (Figure 5.1). The increasingly dense perennial sward caused failure either of germination or of establishment of the annuals. This decline was more rapid than is often reported for *Avena* populations in whole-field set-aside, where the greater distances from sources of perennial colonists delays the development of a dense sward.

Mowing We found no significant difference between *Avena* populations in swards cut in summer only and in uncut swards (unplanned comparisons), despite our summer cutting regime removing the majority of bolting heads and effectively preventing seed return. This is because the *Avena* species have very large, persistent seed banks which buffer the short-term effects of controlling seed return. Thus, summer cutting does not help in the short-term control of this species although it may still be desirable both for aesthetic reasons (farmers find it an anathema) and to prevent seeds being shed into the crop edge. Where the field margins are part of a set-aside scheme, and the intention is to return to arable at the end of the set-aside period, summer cutting is also advantageous to prevent augmenting the seed bank.

The only significant effect of our mowing regimes on the *Avena* species was that cutting in spring and autumn resulted in much worse control than other regimes (Tables 5.1 and 5.2). In both unsown and sown swards, frequencies under this regime were very significantly higher than under the spring and summer cut regime, suggesting that cutting in autumn was responsible for the difference. This effect appeared to result from the favourable conditions created for the germination of *Avena* seeds by autumn cutting. Like most annuals, *Avena* seeds require light gaps in which to germinate and these are provided in the very short, open, autumn-cut swards.

Sowing Sowing a wild flower seed mixture greatly accentuated this decline by providing a very dense sward at an earlier stage (Figure 5.1). It resulted in very significant reductions in the frequencies and densities of *Avena* species from the second year of fallow onwards (Tables 5.1 and 5.2), with almost negligible densities remaining in sown plots.

Spraying The effects of spraying on *Avena* varied from year to year. Densities in sprayed swards much higher in sprayed than in uncut swards in 1991 and 1992 and showed no sign of declining. In 1991 this difference was highly significant but in 1992 the significance could not be tested because the data could not be normalised (Table 5.2). Spraying maintained an open, early-successional sward (see Chapter 4.2.3) in which *Avena* could germinate and establish successfully. Spraying usually prevented seed return but the seed bank buffered this effect, at least on the five year time-scale of this experiment.

The old margins

In the established vegetation of the old margins (Figure 5.2, Table 5.3) *Avena* populations remained around their pre-experiment levels. These were similar to those reached on the new margins by 1990. In all treatments there was evidence of a slight increase in 1990 which was likely to have resulted from the drought of 1989 creating relatively uncompetitive conditions in the sward. We were unable to detect any significant effects of sowing but we show in Chapter 6 that the sown species established only at very low densities in the old margins. The deleterious effects of autumn cutting were not apparent in the old margins, where the sward base was dominated by low-growing *Poa trivialis* (see Chapter 3) and was likely to have remained relatively dense in all treatments during the winter.

Summary

Although *Avena* species can be very abundant in successional swards at field edges in the first year after fallowing, they decline rapidly thereafter, even in the absence of management. Sowing a wild flower seed mixture virtually eliminates *Avena* by the second year after fallowing. Cutting in late June prevents flowering, and although this does not assist short-term control, it is likely to be desirable both to prevent build-up of the seed bank in the crop edge and because many farmers find it visually unacceptable. Cutting in autumn substantially worsens *Avena* control. Annual spraying allows *Avena* to persist at much higher levels than in unsprayed swards over a period of five years. In established swards on field margins neither sowing nor any of our mowing regimes appear to influence the abundance of these species over a four year period.

5.2.2 *ALOPECURUS MYOSUROIDES*

The new margins

Temporal trends The distribution of *A. myosuroides* around the fields was extremely patchy, within as well as between blocks of the experiment. The significant differences between treatments in 1987 and 1988 are artifacts resulting from this distribution. By 1991 there were so few, patchily distributed, plants that the data could not be analyzed. However, where *A. myosuroides* was abundant it showed the same temporal pattern as the *Avena* species, with a peak in the first year after fallowing and a rapid decline thereafter (Figure 5.3).

Mowing Our summer mowing regime failed to control *A. myosuroides* because some of its seeds were ripe by late June (Table 5.4). It seems likely, however, that an earlier cut would help significantly in control of this species. We found that, in 1989 and 1990, removal of hay containing ripe seeds after the summer cut resulted in significantly lower frequencies the following season than when the hay was left lying. This suggests that reductions in seed input can influence the population size the following year. This is contrary to our conclusion for *Avena* and suggests, as is supported by the literature, that *A. myosuroides* has a smaller, shorter-lived seed bank that is less able to buffer the population size between years. By 1992 *A. myosuroides* was completely absent from the treatment in which the hay was removed but persisted in that in which it was left lying.

Sowing Sowing resulted in very significant reductions in the frequency of *A. myosuroides* to negligible levels in 1989, the second year of fallow, and 1990 (Table 5.4). By 1991 it had disappeared completely from sown swards (Figure 5.3).

Spraying In 1991 and 1992 spraying resulted in very much higher densities of *A. myosuroides* than did other treatments (Figure 5.3b). Much of this effect must have been due to removal of perennial competition for the seedlings, rather than from direct effects on seed production, because the early June spraying date in 1990 would have prevented much of the seed input for that year. Much of the 1991 cohort must therefore have come from the seed bank.

The old margins

A. myosuroides was very uncommon in the old field margin, where densities were never greater than a mean of three plants per metre square in any treatment (Figure 5.4). It is typically most abundant in the compacted soils of arable headlands (Marshall 1989) and the densities that we found in the newly fallowed margins in 1988 reflected this distribution. We were unable to detect significant differences between treatments (data not presented) and there were no discernable trends in abundance during the course of the experiment.

Summary

In summary, *A. myosuroides* declines naturally in successional swards on fallowed arable land but this decline is much more rapid in sown swards. Mowing this species when it is bolting is likely to reduce further its population in the following year. If summer cutting is delayed until the seeds are ripening, removal of the hay helps to reduce the population the following year. *A. myosuroides* is unlikely to be sufficiently abundant to require control measures in more established field margin vegetation.

5.2.3 *BROMUS STERILIS*

The new margins

Temporal trends *B. sterilis* exhibited a temporal pattern of abundance that differed conspicuously from that of *Avena* species and *A. myosuroides* in two respects. First, the increase in its population size was delayed until the second year of fallow. This resulted from the way we set up the experiment on land ploughed in October 1987. Because *B. sterilis* germinates primarily in late summer, much of the 1987/88 cohort was destroyed at this stage. The second and more important difference was the persistence of this species at high frequencies, which only started to decline in unmanaged swards in 1992 (Figure 5.5b). The persistence of this annual species in successional swards in the first four years after fallowing is attributable to the atypical ability of its seeds to germinate in the dark.

Mowing Our summer mowing regime came too late to prevent *B. sterilis* shedding it seeds, which mature in early June. An earlier cut, in late May, would almost certainly have resulted in very effective control of this species because it has almost no persistent seed bank. Cutting in spring as well as summer resulted in significantly lower densities of *B. sterilis* than cutting only in summer in 1990 (cut once v twice comparison, Table 5.6). Although we were unable to detect this effect in subsequent years we also found that spring cutting reduced *B. sterilis* panicle numbers when it was grown in monoculture under controlled conditions (paper in prep.). As with *A. myosuroides*, we found that removal of hay following the cut resulted in significantly lower densities in 1990 and 1991, than when the hay was left lying (Table 5.6). As with *Avena* species, we found that cutting in spring and autumn resulted in significantly higher frequencies the following year than did cutting in spring and summer. This again appears to be due to the openness of the autumn-cut swards during the winter. For *Avena*, this promoted germination but for *B. sterilis*, which germinates in late summer, it allowed seedling establishment in a low competitive environment.

Sowing Although *B. sterilis* competed successfully in the naturally regenerating swards, it could not compete successfully in the much denser, sown swards (Figure 5.5). There was a highly significant difference in frequencies and densities between sown and unsown swards from 1989 onwards (Tables 5.5 and 5.6). From 1990, except in swards cut in spring and autumn, *B. sterilis* was virtually eliminated from sown swards. We have previously shown that fecundity, as well as the density of *B. sterilis* is also much lower in sown than in unsown swards (Watt *et al* 1990).

Spraying The effects of spraying varied between years but it resulted in a significant increase in *B. sterilis* in 1992. In 1991 we sprayed after the *B. sterilis* seed was ripe and the resulting seedlings thrived in the absence of competition from a perennial sward.

The old margins

In the old margins *B. sterilis* was common throughout the experiment, although it increased between 1987 and 1988 (Figure 5.6). Neither sowing nor mowing had significant effects on frequencies (Table 5.7) but in both 1990 and 1991 the effect of cutting on panicle densities was highly significant (Table 5.8). As on the new margins, most of this effect resulted from higher densities on treatments cut in spring and autumn than on those cut in spring and summer.

Summary

B. sterilis is likely to present longer-term management problems in successional swards than are other annual weeds. Summer cutting of bolting panicles should give more effective control of this species than of either *A. myosuroides* or *Avena* species because of its lack of a persistent seed bank. Autumn cutting should be avoided and if *B. sterilis*-infested swards are cut in summer after seeds have started to mature, hay should be removed. Sowing produces relatively rapid and very effective control. Well-timed spraying should control this species but spraying after the seeds are ripe results in its proliferation. In established field margin swards, sowing and mowing are much less effective management tools for this species over a four year period.

5.2.4 *GALIUM APARINE*

The new margins

Temporal trends In the new margins *G. aparine* increased slightly in 1988, from very low frequencies in the old crop edge, but in most treatments it neither became common nor did the increase continue (Fig 5.7).

Mowing Only when the new margins were left uncut was this increase sustained until 1990, when it was last measured. This effect was not quite significant in June in any individual year (Table 5.9, P=0.08 in 1989 and 0.054 in 1990, but see old margins below). In 1990 cutting in spring and autumn resulted in significantly higher frequencies than cutting in spring and summer. *G. aparine* germinates in autumn and, like *Avena* species, appeared to thrive in swards that are open during the winter.

Sowing Sowing reduced significantly the frequency of *G. aparine* in 1990 (Table 5.9). It appeared to be slightly less effective in controlling this species than it was other annuals, but failure to detect significant effects may have resulted from the low numbers in both sward types.

Spraying Although until 1989 the sprayed treatment was equivalent to the uncut treatment, *G. aparine* mean frequencies were higher in sprayed than in uncut plots from

1987 onwards. This difference resulted from baseline variability in the species distribution within blocks. The magnitude and significance of this difference increased after the spray treatment commenced, with *G. aparine* reaching frequencies of over 50% in 1990. By 1992 the sprayed plots were often dominated by *G. aparine*, although it was inconspicuous in all other treatments (pers. obs.).

The old margins

G. aparine frequencies in the old margins fluctuated considerably between years (Figure 5.8). In all except the sprayed treatment they remained higher than on the new margins. Frequencies were significantly higher in the uncut treatment than in the cut treatments by 1990 (Table 5.10). We were unable to detect any significant effect of the timing of mowing or of sowing or spraying.

Summary

G. aparine does not establish in extended field margins as prolifically as the annual grass weeds. Both sowing and mowing reduce its frequency although mowing in autumn should be avoided. Spraying can very significantly increase the abundance of this species.

5.2.5 *ELYMUS REPENS*

The new margins

Temporal trends *E. repens* became progressively more abundant in the new margins during the first three years after fallowing. It reached frequencies of over 80% in some treatments by 1990, the last year in which it was monitored (Figure 5.9). It was impractical to measure the density of this species but it should be borne in mind that high frequencies of a grass species do not necessarily reflect high densities. *E. repens* increases primarily by rhizomatous extension and the gradual increase reflected progressive invasion from the old margin and proliferation of rhizome fragments that were present in the old crop edge. Future analyses of the data for this species will include estimates of its rate of lateral spread.

Mowing None of our mowing regimes prevented this progressive increase in *E. repens* (Table 5.11), although there was some evidence that it was exacerbated by mowing in spring and summer (see old margins below).

Sowing The increase in *E. repens* frequencies was considerably and significantly reduced by sowing (Figure 5.9). Its frequencies in sown plots appeared to have stabilised between 1989 and 1990. Marshall (1990) demonstrated a similar reduction in the rhizome growth of *E. repens* when it was grown amongst *Arrenatherum elatius* and, to lesser extents, *Dactylis glomerata* and *Agrostis stolonifera*.

Spraying Spraying resulted in a significant reduction in the frequency of *E. repens* relative to that in uncut plots in 1990 (Table 5.11). No effect was expected in June 1989 because the June data were collected before the spray was applied.

The old margins

E. repens was abundant in the old margin from the start of the experiment and its levels there remained fairly constant, with slight evidence of an increase only in treatments cut in summer (Figure 5.10). The analyses for individual years provide further evidence of a deleterious effect of spring and summer cutting on the control of *E. repens*. Treatments cut in spring and summer had significantly higher frequencies than those cut in spring and autumn from 1989 onwards (Table 5.12). In the new margins detection of this effect is complicated by an initial difference between these treatments, caused by the patchy distribution of this species within blocks. The importance of this effect will be clearer when the data for patchily distributed species are re-analyzed (see 5.3.2).

Summary

E. repens is likely to spread progressively from existing foci into successional swards on expanded field margins. It is possible that mowing more than twice a year might help in its control but none of our regimes prevented its increase. Its abundance was limited at much lower levels in sown swards. Spraying reduced significantly its frequency but was no more effective than sowing. Where natural regeneration is used to establish swards on expanded field margins, however, and *E. repens* is perceived as a problem, spot treatment with glyphosate, at an early stage, may be a desirable option. By 1990 *E. repens* frequencies in the new margins were similar to those in the old margins in summer cut treatments but remained lower than those in the old margin in uncut and spring and autumn cut treatments. Further years' data are needed to assess whether this species will continue to increase or whether it will stabilise or decline.

5.2.6 *CIRSIUM ARVENSE*

The new margins

Temporal trends *Cirsium arvense* was more patchily distributed and less abundant than *E. repens* but it is clear that it also increased progressively in the new margins in the absence of management (Figure 5.11). The 1987 data show that it was already present in the crop edge, probably as rhizome fragments, and these are likely to have acted as foci for its subsequent increase in the new margins. As early as 1988 it was as abundant in the new as in the old margins and in most treatments it subsequently became more abundant in the new than the old margin. Future analyses of the data for this species will enable us to assess the relative extents to which this increase was attributable to rhizomatous extension and to seedling establishment.

Mowing None of our mowing regimes controlled the increase in this species (Table 5.13).

Sowing Sowing was more effective in controlling *C. arvense* than *E.repens*. It resulted in frequencies significantly lower than those in unsown treatments in 1990 and 1992 (not measured in 1991). Frequencies in sown swards decreased at a time when they were still increasing in naturally regenerating swards (Figure 5.11).

Spraying Spraying resulted in a significant reduction in the frequency of *C. arvense* relative to that in uncut treatments in 1992. Frequencies in sprayed plots were nevertheless higher than in uncut, sown plots.

The old margin

In the old margin, *C. arvense* increased slightly during the experiment but neither sowing nor mowing had significant effects on its frequency (Figure 5.12, Table 5.14).

Summary

Cirsium arvense increases slowly in extended field margins for at least five years, although there is some evidence that this increase will not be sustained. None of our mowing regimes controlled this species although, as with *E. repens*, it is likely that control could be achieved by cutting more than twice a year. Sown swards control *C. arvense* very effectively, even when uncut. Spraying with glyphosate resulted in a significant reduction in its frequency but was a less effective control measure than sowing. As with *E. repens*, spot spraying of *C. arvense* with glyphosate at an early stage in the establishment of swards by natural regeneration may be a useful option.

5.2.7 *URTICA DIOICA*

The new margins

Temporal trends Although *U. dioica* was virtually absent from the crop edge in 1987 it increased very rapidly in the first year of fallow (Figure 5.13). It was the single most abundant species in the seed bank on the farm (Chapter 3) and this rapid increase reflected germination from seed rather than rhizomatous spread. However, in contrast to *E. repens* and *C. arvense*, this increase did not continue, with numbers fluctuating around their 1988 levels in 1989 and 1990 (the last year of measurement). By 1989 and 1990, *U. dioica* frequencies in most treatments in the new margins were similar to those in the old margins.

Mowing The very patchy distribution of *U. dioica* within the blocks of the experiment makes any effect of frequency or timing of mowing difficult to evaluate without further analyses. The significantly lower frequencies in cut than in uncut treatments in 1988 are likely to have resulted from this distribution (Table 5.15, Figure 5.14). We did however, detect a significant increase in *U. dioica* frequencies in treatments in which the hay was left lying, in 1990. The mean frequencies of *U. dioica* were higher in this treatment than in all others. This effect is compatible with the well-established preference of this species for high-fertility soils (Pigott & Taylor 1964) but it requires confirmation with further years' data.

Sowing Sowing resulted in a rapid decrease in *U. dioica* frequencies to very low levels. Frequencies in sown treatments were significantly lower than those in unsown treatments from 1989 onwards.

Spraying In contrast to the previous two perennial species, the glyphosate application in 1989 was ineffective in controlling *U. dioica*. Not only did its frequencies in the sprayed treatment not differ significantly from those in the uncut treatment (Figure 5.15), but by June 1990 the sprayed treatment was second in the rank order of treatment means.

The old margins

In the old margins, substantial differences between the baseline treatment means, resulting from the patchy distribution within blocks, were sustained throughout the experiment (Table 5.16). As in the new margins, significant differences between the uncut and cut treatments, which were first detected in November 1987, are attributable at least in part to these problems. This contrast cannot be properly evaluated until the analyses are repeated, taking account of these problems. Cutting twice a year resulted in significantly lower *U. dioica* frequencies than cutting once, in September 1989 and in April and September 1990 (data not presented). In June 1990 (Table 5.16), this difference is not quite significant (P=0.06). The higher frequencies seen in the treatments in which the hay was left lying on the new margins were not detected in the old margins. Sowing had no effect on this species in the old margins.

Summary

U. dioica increases very rapidly in newly extended field margins but, unlike the previous two perennials, it does not continue to increase. It seems likely that it will remain at frequencies similar to those in the old margins although continued monitoring is needed to confirm this. Cutting twice reduced its frequency relative to that in plots cut once but its patchy distribution meant that we were unable to assess the effects of cutting once against not cutting at all without further analyses. Leaving hay lying favours this species. Once again, sowing resulted in very effective control, reducing frequencies to low levels. Annual spraying with glyphosate was ineffective in controlling *U. dioica*.

5.3 Discussion

5.3.1 CONCLUSIONS AND PRACTICAL IMPLICATIONS

Our results lead to some general and some species-specific conclusions about the use of sowing, mowing and annual spraying as weed control measures on extended arable field margins. In general, the denser the sward, the better the control of both annual and perennial weeds. In this context the seed mixture can be seen as a means of achieving a denser sward more quickly. Most annual weeds proliferate early in the succession, when the seed bank in the former crop edge is expressed in the absence of perennial competition, but decline rapidly as perennial cover increases, even in the absence of any management. The naturally regenerating swards were not sufficiently dense to prevent a gradual increase in the abundance of rhizomatous perennials during the course of the experiment. The sown swards were sufficiently dense after only one year to effectively eliminate annuals and to prevent or restrain the increase in perennials, even in the absence of any management.

It is often suggested that the high fertility of former agricultural soils will lead eventually to complete domination of successional swards by small numbers of the so called 'aggressive' perennial species, such as *U. dioica* and *C. arvense*. We do not yet have sufficient years' data to confirm this but the static or downward trend in the abundance of such species in the sown swards suggests that, if naturally-regenerating swards become sufficiently dense, the increase in such species might be limited. However, this conclusion is likely to depend on colonisation by grass species that produce a dense sward base.

Sowing did not reduce significantly the abundances of either the annual or perennial weed species in the old field margins, despite seeds being sown into the swards and subsequent gradual colonisation by sown species (see Chapter 6). It is clear that rapid weed control benefits are only obtained from sowing the seed mixture into well-prepared seed beds to ensure good establishment. We suggested in Chapter 4.3 that there are good *a priori* reasons for expecting changes in the vegetation of established field margins to be much slower than those in early successional swards. It seems likely that if the frequency of sown species continues to increase in the old field margins, this will eventually result in benefits for pernicious weed control.

Weed control can be augmented by carefully-timed mowing but, equally, it can be significantly worsened by badly-timed mowing. Mowing successional swards in autumn significantly exacerbated problems with *Avena* species, *B. sterilis* and *G. aparine*, and should be avoided until annual weeds are controlled at acceptable levels. Mowing that is timed to coincide with the flower production of pernicious annual species can very significantly hasten their decline although its effectiveness will be species-specific for the reasons discussed above. Where more than one species is perceived as a problem, the timing of mowing will have to be a compromise between the optimum times for the species concerned. Our data do not support the suggestion of Wilson (1988) that frequent mowing of set-aside swards from mid-May onwards is likely to maximise annual weed control by minimising seed production. Frequent mowing from mid-summer onwards, during periods when problem species germinate and establish, is likely to have similar effects to our autumn mowing and exacerbate weed problems by reducing the competitive ability of the swards.

Of the pernicious perennial species that we examined, only *U. dioica* was reduced in frequency by mowing. It seems likely that more frequent, as opposed simply to better-timed, mowing would be needed to reduce significantly the abundance of these species in the absence of sowing.

In Chapter 4 we showed that mowing in autumn rather than summer had significant benefits for the development of species richness. In Chapters 8 to 10 we show that summer cutting also has deleterious effects on several important invertebrate groups. Autumn cutting particularly favoured the perennial component of the swards although our results in this chapter show that some individual annual species also benefit from this regime. The increases in both *B. sterilis* and *Avena* species under this regime clearly resulted from improved opportunities for germination and establishment rather than from increased seed production. There is an obvious conflict of interest between the need to control these two species and the development of species richness. Where either or both species are perceived as problems, priority should be given to their control by avoiding autumn cutting. Once their populations have been satisfactorily reduced, the cutting regime should be changed to benefit the development of diversity.

The still-common practise of spraying-out hedge bottoms annually with glyphosate results in the perpetuation of early-successional, annual-dominated swards. It thus ensures the need to continue the practise and removes the possibility of biological weed control through perennial sward development. Glyphosate application resulted in a significant reduction in *E. repens* abundance after only one year and so may be a useful tool in removing foci of this species when expanded field margins are established. Spot-treatment with this and other selective herbicides may also be appropriate to control weed patches that the farmer finds unacceptable at later stages, although this practise is always likely to result in replacement of the target species by annual weeds. Although *E. repens*-dominated swards are ecologically monotonous we found no evidence that they are an agricultural problem. There was no significant movement of *E. repens* from the margins into the crop on the time-scale of this experiment (unpublished data for crop edge quadrats, see Chapter 2.2.5).

Management of field margin vegetation to encourage selectively broad-leaved species, using selective herbicides and growth retardants, is currently being actively and successfully promoted to a wide farming audience by C & G Willmot Agrochemical Merchants and Contractors Ltd. (Nowakowski & Marshall 1991). However, as in the more extreme case of glyphosate use, the suppression of grasses inevitably results in less effective weed control by sward density and a need to perpetuate agrochemical use (see also Chapter 6.3).

Whilst it is imperative that farmer's perceptions of weed nuisance resulting from field margins are addressed, it is also important to establish which species present real problems and to encourage recognition of the conservation value of species such as *U. dioica* which rarely become problems in the crop. The value of both *U. dioica* and *C. arvense* in relation to butterfly conservation on field margins is considered in Chapters 9 and 10.

5.3.2 FUTURE ANALYSES

Four additional areas of analysis are planned for the data on the abundance of individual species. (1) The data from times of year other than June will be analyzed. These analyses should further increase our understanding of the biology underlying each species response to sward management, and so improve our ability to extrapolate our results to other management regimes and other sites. (2) As in Chapter 4, the analyses do not take account of differences in the baseline that result from the very patchy distribution of some of these species within blocks of the experiment. Analyses that take this factor into account are being developed. Again, these should not obviate any of the significant effects that we have attributed to treatments but it is possible that they will reveal additional, significant treatment effects. (3) As in Chapter 4, we plan to analyze more formally the effects of treatment on temporal trends in abundance, as opposed to absolute abundances at specific points in time. This is likely to reveal additional significant effects of treatment. (4) For the rhizomatous perennial species we will use the detailed data on occurrence in individual cells of the quadrats in the old and new margins, and crop edge, to estimate rates of lateral spread under the different treatments.

5.3.3 FUTURE MONITORING

Although most of the annual pernicious weeds occurred at low frequencies in the new field margins by 1992, agronomically important weedy perennials and *B. sterilis* were still common and many of the former were still increasing. Future monitoring of the abundance of these species is vital to assessing the weed control problems and associated acceptability of expanded field margins in the medium term. It is particularly important to evaluate the prediction that the soil nutrient status on field margins will be sustained sufficiently to allow these species eventually to dominate the swards.

We suggested in Chapter 4 that the rates of change in species number will be slower in more established swards, necessitating less frequent monitoring. This is also likely to be true for individual species. Since estimation of species richness entails the recording all species in each quadrat, and data on individual species requires recording of relative frequencies in each quadrat, the two data sets can continue to be collected in the same, single monitoring round, at two or three yearly intervals (see Chapter 4.3).

Although monitoring of densities, as well as frequencies, yielded important additional information on the population dynamics of the annual grass weeds in the early years of the experiment, it is unlikely to continue to be cost-effective. By 1992 the same patterns of significant results were obtained from both variables. The decline in these species had also made them less important influences in determining management strategies.

5.3.4 IMPLICATIONS FOR SET-ASIDE MANAGEMENT

Our conclusions on weed population development, and its control by sowing and mowing, in expanded field margins are equally applicable to set-aside. All of these species are commonly recorded on set-aside land where they are perceived as major problems. However, it is likely that the time-scale both of the decrease in abundance of annuals and increase in that of perennials will be greater towards the centres of fields where colonisation by sward-forming grasses is likely to be slower.

Table 5.1 *Avena species* frequencies in the new margin 1987-1992
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90		JUN '92	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig	P [1]	Sig
BLOCK effect	5,45	.0005	***	.0003	***	.0002	***	.0048	**	data	
TREAT effect	9,45	.9863	ns	.9607	ns	.0005	***	.0001	***	non-	
										normal	
Planned comparisons:											
Remove v leave hay	1,45	.8157	ns	.9354	ns	.5194	ns	.5728	ns		
Spray v uncut	1,45	.5826	ns	.4801	ns	.7356	ns	.8326	ns		
from 3-way ANOVA:											
SOWING effect	1,35	.6489	ns	.5110	ns	.0036	**	.0001	***		
CUTTING effect	3,35	.8081	ns	.7064	ns	.0006	***	.0007	***		
INTERACTION	3,35	.8850	ns	.8919	ns	.3438	ns	.1566	ns		
Planned comparisons:											
Cut v uncut	1,35	.6109	ns	.3183	ns	.1585	ns	.3743	ns		
Cut once v twice	1,35	.6083	ns	.9811	ns	.0254	*	.3037	ns		
Cut sp + su v sp + au	1,35	.5144	ns	.5421	ns	.0005	***	.0001	***		

[1] In 1992 *Avena* was found at frequencies >1% only in spring and autumn cut treatments (both sown and unsown) and in the sprayed treatment.

Table 5.2 *Avena* species densities in the new margin 1989-1992
Summary of significance of differences for selected comparisons

Comparison:		JUN '89		JUN '90		JUN '91		JUN '92	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig
BLOCK effect	5,45	.0124	*	data		.0001	***	data	
TREAT effect	9,45	.0001	***	non-		.0001	***	non-	
				normal				normal	
Planned comparisons:									
Remove v leave hay	1,45	.4681	ns			.8207	ns		
Spray v uncut	1,45	.2016	ns			.0001	***		
from 3-way ANOVA:									
SOWING effect	1,35	.0271	*			.0002	***[1]		
CUTTING effect	3,35	.0002	***			.0001	***		
INTERACTION	3,35	.1442	ns			.0081	**		
Planned comparisons:									
Cut v uncut	1,35	.3663	ns			.0270	*[1]		
Cut once v twice	1,35	.0194	*			.0183	*		
Cut sp+su v sp+au	1,35	.0001	***			.0001	***		

[1] Significance levels should be treated with caution because of significant interaction term

Table 5.3 *Avena species* frequencies in the old margin 1987-1992
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90		JUN '92
from 2-way ANOVA:	d.f	P	Sig	P[2]	Sig	P	Sig	P	Sig	not
BLOCK effect	5,45	.0471	*			.0001	***	.0001	**	recorded
TREAT effect	9,45	.9065	ns			.2256	ns	.5896	ns	
Planned comparisons:										
Remove v leave hay	1,45	.8193	ns			.5983	ns	.9204	ns	
Spray v uncut	1,45	.6768	ns			.6778	ns	.7068	ns	
from 3-way ANOVA:										
SOWING effect	1,35	.8982	ns	.3084	ns	.0524	ns	.9344	ns	
CUTTING effect	3,35	.5143	ns	.6083	ns	.1427	ns	.1874	ns	
INTERACTION	3,35	.9882	ns	.8952	ns	.7848	ns	.8350	ns	
Planned comparisons:										
Cut v uncut	1,35	.3748	ns	.4493	ns	.2869	ns	.1062	ns	
Cut once v twice	1,35	.2495	ns	.3490	ns	.3865	ns	.5334	ns	
Cut sp + su v sp + au	1,35	.9671	ns	.5490	ns	.0577	ns	.1749	ns	

[1] In 1992 *Avena* was found at frequencies >1% only in spring and autumn cut treatments (both sown and unsown) and in the sprayed treatment.
[2] 1988 were non-normal for the two-way ANOVA but normalised for the 3-way ANOVA

Table 5.4 *Alopecurus myosuroides* frequencies in the new margin 1987-1992
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90		JUN '92[1]
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig	data
BLOCK effect	5,45	.0001	***	.0001	ns	.0001	***	.0031	**	non-
TREAT effect	9,45	.2344	ns	.1691	ns	.0088	**	.0307	*	normal
Planned comparisons:										
Remove v leave hay	1,45	.5353	ns	.9267	ns	.0436	*	.0396	*	
Spray v uncut	1,45	.5223	ns	.7280	ns	.5637	ns	.9653	ns	
from 3-way ANOVA:										
SOWING effect	1,35	.8608	ns	.9706	ns	.0055	**	.0015	**	
CUTTING effect	3,35	.0668	ns	.0290	*	.3961	ns	.3288	ns	
INTERACTION	3,35	.7748	ns	.5731	ns	.3851	ns	.4355	ns	
Planned comparisons:										
Cut v uncut	1,35	.0322	*	.0050	**	.3497	ns	.4442	ns	
Cut once v twice	1,35	.6198	ns	.4822	ns	.4611	ns	.2534	ns	
Cut sp + su v sp + au	1,35	.1156	ns	.4267	ns	.2140	ns	.2123	ns	

[1] In 1992 no plants were recorded in sown treatments and in the unsown treatment cut in spring and summer

Table 5.5 *Bromus sterilis* frequencies in the new margin 1987-1992
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90		JUN '92	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig	P	Sig
BLOCK effect	5,45	.0001	***	.0001	***	.0001	***	.0453	*	.0627	ns
TREAT effect	9,45	.2158	ns	.2540	ns	.0001	***	.0001	***	.0001	***
Planned comparisons:											
Remove v leave hay	1,45	.5070	ns	.9716	ns	.3093	ns	.0767	ns	.8056	ns
Spray v uncut	1,45	.2093	ns	.4569	ns	.0040	**	.9530	ns	.0083	**
from 3-way ANOVA:											
SOWING effect	1,35	.7596	ns	.9275	ns	.0001	***	.0001	***	.0001	***
CUTTING effect	3,35	.2423	ns	.0593	ns	.0752	ns	.0153	*	.0006	***
INTERACTION	3,35	.1187	ns	.5489	ns	.4835	ns	.4889	ns	.1071	ns
Planned comparisons:											
Cut v uncut	1,35	.0513	ns	.6196	ns	.9419	ns	.5014	ns	.7858	ns
Cut once v twice	1,35	.6305	ns	.0083	ns	.1694	ns	.0627	ns	.2463	ns
Cut sp+su v sp+au	1,35	.7934	ns	.7787	ns	.0244	*	.0084	**	.0001	***

Table 5.6 *Bromus sterilis* densities in the new margin 1989-1992
Summary of significance of differences for selected comparisons

Comparison:		JUL '89		JUN '90		JUN '91		JUN '92	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig
BLOCK effect	5,45	.0002	***	.0139	*	.0184	*	.0301	*
TREAT effect	9,45	.0001	***	.0001	***	.0001	***	.0001	***
Planned comparisons:									
Remove v leave hay	1,45	.4411	ns	.0140	*	.0488	*	.8500	ns
Spray v uncut	1,45	.0810	ns	.9903	ns	.0897	ns	.0001	***
from 3-way ANOVA:									
SOWING effect	1,35	.0001	***	.0001	***	.0001	***	.0001	n/a[1]
CUTTING effect	3,35	.3349	ns	.0187	*	.0475	*	.0002	n/a
INTERACTION	3,35	.8313	ns	.1530	ns	.0613	ns	.0042	**
Planned comparisons:									
Cut v uncut	1,35	.6972	ns	.8959	ns	.3008	ns	.9721	n/a
Cut once v twice	1,35	.1735	ns	.0198	*	.2977	ns	.1521	n/a
Cut sp + su v sp + au	1,35	.2403	ns	.0262	*	.0144	**	.0001	n/a

[1] Note that significance of effects from 3-way ANOVA cannot be interpreted because interaction term is significant

Table 5.7 *Bromus sterilis* frequencies in the old margin 1987-1992
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90		JUN '92
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig	P
BLOCK effect	5,45	.0420	*	.0226	*	.0061	**	.13330	***	not
TREAT effect	9,45	.5315	ns	.7818	ns	.6549	ns	.4197	ns	recorded
Planned comparisons:										
Remove v leave hay	1,45	.9305	ns	.4446	ns	.1356	ns	.0942	ns	
Spray v uncut	1,45	.1891	ns	.0949	ns	.2230	ns	.9112	ns	
from 3-way ANOVA:										
SOWING effect	1,35	.1727	ns	.6719	ns	.9234	ns	.5939	ns	
CUTTING effect	3,35	.9441	ns	.7576	ns	.4711	ns	.1062	ns	
INTERACTION	3,35	.2542	ns	.7024	ns	.5268	ns	.7814	ns	
Planned comparisons:										
Cut v uncut	1,35	.9871	ns	.3213	ns	.9772	ns	.8390	ns	
Cut once v twice	1,35	.6881	ns	.9709	ns	.6683	ns	.1207	ns	
Cut sp+su v sp+au	1,35	.6465	ns	.6821	ns	.1310	ns	.0530	ns	

Table 5.8 *Bromus sterilis* densities in the old margin 1989-1992
Summary of significance of differences for selected comparisons

Comparison:		JUL '89		JUN '90		JUN '91		JUN '92
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	not
BLOCK effect	5,45	.0183	*	.2556	ns	.0359	*	recorded
TREAT effect	9,45	.6833	ns	.6003	ns	.0018	**	
Planned comparisons:								
Remove v leave hay	1,45	.1456	ns	.1560	ns	.8942	ns	
Spray v uncut	1,45	.1950	ns	.6590	ns	.0519	ns	
from 3-way ANOVA:								
SOWING effect	1,35	.8769	ns	.7713	ns	.1186	ns	
CUTTING effect	3,35	.3185	ns	.1334	***	.0007	***	
INTERACTION	3,35	.8384	ns	.8930	ns	.2371	ns	
Planned comparisons:								
Cut v uncut	1,35	.4541	ns	.8434	ns	.1195	ns	
Cut once v twice	1,35	.2091	ns	.3534	ns	.0390	*	
Cut sp + su v sp + au	1,35	.2388	ns	.0311	*	.0003	***	

Table 5.9 *Galium aparine* frequencies in the new margin 1987-1990
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig
BLOCK effect	5,45	.0002	***	.0001	***	.0001	***	.0001	***
TREAT effect	9,45	.2305	ns	.6519	ns	.0043	**	.0001	***
Planned comparisons:									
Remove v leave hay	1,45	.0540	ns	.6744	ns	.7359	ns	.7456	ns
Spray v uncut	1,45	.0735	ns	.2264	ns	.0271	*	.0015	**
from 3-way ANOVA:									
SOWING effect	1,35	.4679	ns	.1832	ns	.1697	ns	.0171	*
CUTTING effect	3,35	.3233	ns	.5700	ns	.1981	ns	.0303	*
INTERACTION	3,35	.3052	ns	.7582	ns	.7807	ns	.9561	ns
Planned comparisons:									
Cut v uncut	1,35	.5249	ns	.5328	ns	.0880	ns	.0540	ns
Cut once v twice	1,35	.0997	ns	.7677	ns	.6603	ns	.6087	ns
Cut sp + su v sp + au	1,35	.5683	ns	.206	ns	.2088	ns	.0218	*

Table 5.10 *Galium aparine* frequencies in the old margin 1987-1990
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig
BLOCK effect	5,45	.0001	***	.0001	***	.0001	***	.0001	***
TREAT effect	9,45	.9061	ns	.5687	ns	.3966	ns	.0851	ns
Planned comparisons:									
Remove v leave hay	1,45	.5590	ns	.8042	ns	.6616	ns	.8985	ns
Spray v uncut	1,45	.8142	ns	.5002	ns	.3255	ns	.1677	ns
from 3-way ANOVA:									
SOWING effect	1,35	.8783	ns	.5316	ns	.6452	ns	.9033	ns
CUTTING effect	3,35	.6341	ns	.5627	ns	.4757	ns	.1640	ns
INTERACTION	3,35	.6446	ns	.2496	ns	.3871	ns	.9259	ns
Planned comparisons:									
Cut v uncut	1,35	.9763	ns	.3169	ns	.1398	ns	.0259	*
Cut once v twice	1,35	.8052	ns	.3734	ns	.6832	ns	.9624	ns
Cut sp+su v sp+au	1,35	.2050	ns	.6313	ns	.7530	ns	.9315	ns

Table 5.11 *Elymus repens* frequencies in the new margin 1987-1990
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig
BLOCK effect	5,45	.0001	***	.0213	*	.0047	**	.0111	**
TREAT effect	9,45	.2469	ns	.2347	ns	.0137	*	.0005	***
Planned comparisons:									
Remove v leave hay	1,45	.1156	ns	.3682	ns	.8852	ns	.9330	ns
Spray v uncut	1,45	.3742	ns	.8421	ns	.1617	ns	.0032	**
from 3-way ANOVA:									
SOWING effect	1,35	.9380	ns	.7911	ns	.0073	**	.0001	***
CUTTING effect	3,35	.0665	ns	.0191	*	.0576	ns	.2727	ns
INTERACTION	3,35	.7983	ns	.6969	ns	.9759	ns	.9948	ns
Planned comparisons:									
Cut v uncut	1,35	.4866	ns	.1182	ns	.0765	ns	.2997	ns
Cut once v twice	1,35	.4020	ns	.6030	ns	.3722	ns	.3950	ns
Cut sp+su v sp+au	1,35	.0144	*	.0062	**	.0509	*	.1458	ns

Table 5.12 *Elymus repens* frequencies in the old margin 1987-1990
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90	
from 2-way ANOVA:	d.f.	P	Sig.	P	Sig.	P	Sig.	P	Sig.
BLOCK effect	5,45	.0099	**	.0087	**	.0004	***	.0029	**
TREAT effect	9,45	.6272	ns	.2993	ns	.1717	ns	.0437	*
Planned comparisons:									
Remove v leave hay	1,45	.7976	ns	.7166	ns	.7296	ns	.5984	ns
Spray v uncut	1,45	.9586	ns	.5033	ns	.6174	ns	.4814	ns
from 3-way ANOVA:									
SOWING effect	1,35	.3170	ns	.3356	ns	.2770	ns	.1657	ns
CUTTING effect	3,35	.2931	ns	.1510	ns	.0748	*	.0233	*
INTERACTION	3,35	.6453	ns	.7575	ns	.7784	ns	.4979	ns
Planned comparisons:									
Cut v uncut	1,35	.3114	ns	.7416	ns	.3978	ns	.2873	ns
Cut once v twice	1,35	.2965	ns	.0887	ns	.2112	ns	.1639	ns
Cut sp + su v sp + au	1,35	.2019	ns	.1255	ns	.0292	*	.0094	**

Table 5.13 *Cirsium arvense* frequencies in the new margin 1987-1990
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90		JUN '92	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig	P	Sig
BLOCK effect	5,45	data		data		.0001	***	.0001	***	.0247	*
TREAT effect	9,45	non-		non-		.2668	ns	.1116	ns	.0176	*
		normal		normal							
Planned comparisons:											
Remove v leave hay	1,45					.3792	ns	.5868	ns	.3648	ns
Spray v uncut	1,45					.0884	ns	.2233	ns	.0344	*
from 3-way ANOVA:											
SOWING effect	1,35	.8005	ns			.0890	ns	.0011	**	.0001	***
CUTTING effect	3,35	.9294	ns			.6165	ns	.4756	ns	.6076	ns
INTERACTION	3,35	.0695	ns			.8022	ns	.6192	ns	.7014	ns
Planned comparisons:											
Cut v uncut	1,35	.8812	ns			.7850	ns	.8012	ns	.6789	ns
Cut once v twice	1,35	.5185	ns			.2534	ns	.1241	ns	.9858	ns
Cut sp+su v sp+au	1,35	.9987	ns			.5366	ns	.9410	ns	.2032	ns

Table 5.14 *Cirsium arvense* frequencies in the old margin 1987-1990
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90		JUN '92
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig	not
BLOCK effect	5,45	data		data		.0001	***	.0002	***	recorded
TREAT effect	9,45	non-		non-		.2195	ns	.9277	ns	
		normal		normal						
Planned comparisons:										
Remove v leave hay	1,45					.6205	ns	.8483	ns	
Spray v uncut	1,45					.0186	*	.9416	ns	
from 3-way ANOVA:										
SOWING effect	1,35					.2753	ns	.2026	ns	
CUTTING effect	3,35					.3640	ns	.7859	ns	
INTERACTION	3,35					.4963	ns	.7401	ns	
Planned comparisons:										
Cut v uncut	1,35					.5586	ns	.9864	ns	
Cut once v twice	1,35					.1193	ns	.3583	ns	
Cut sp+su v sp+au	1,35					.5376	ns	.6591	ns	

Table 5.15 *Urtica dioica* frequencies in the new margin 1987-1990
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig
BLOCK effect	5,45	Data		.0001	***	.0004	***	.0004	***
TREAT effect	9,45	non-		.1505	ns	.0241	*	.0001	***
		normal							
Planned comparisons:									
Remove v leave hay	1,45			.7939	ns	.4061	ns	.0471	*
Spray v uncut	1,45			.5110	ns	.3533	ns	.2837	ns
from 3-way ANOVA:									
SOWING effect	1,35			.0473	*	.0017	**	.0001	***
CUTTING effect	3,35			.1147	ns	.6075	ns	.7372	ns
INTERACTION	3,35			.6390	ns	.7007	ns	.1978	ns
Planned comparisons:									
Cut v uncut	1,35			.0267	*	.2487	ns	.7267	ns
Cut once v twice	1,35			.4023	ns	.5847	ns	.2965	ns
Cut sp+su v sp+au	1,35			.5864	ns	.6775	ns	.8786	ns

Table 5.16 *Urtica dioica* frequencies in the old margin 1987-1990
Summary of significance of differences for selected comparisons

Comparison:		JUL '87		JUN '88		JUN '89		JUN '90	
from 2-way ANOVA:	d.f	P	Sig	P	Sig	P	Sig	P	Sig
BLOCK effect	5,45	.0033	**	.0006	***	.0002	***	.0005	***
TREAT effect	9,45	.2758	ns	.1259	ns	.1653	ns	.2742	ns
Planned comparisons:									
Remove v leave hay	1,45	.9687	ns	.9547	ns	.8414	ns	.9641	ns
Spray v uncut	1,45	.8593	ns	.5189	ns	.5830	ns	.8789	ns
from 3-way ANOVA:									
SOWING effect	1,35	.9257	ns	.7341	ns	.9359	ns	.6815	ns
CUTTING effect	3,35	.1980	ns	.0532	ns	.0516	*	.0600	ns
INTERACTION	3,35	.4624	ns	.4782	ns	.7252	ns	.6963	ns
Planned comparisons:									
Cut v uncut	1,35	.0782	ns	.0094	**	.0130	*	.0379	*
Cut once v twice	1,35	.3427	ns	.3504	ns	.2138	ns	.0678	ns
Cut sp+su v sp+au	1,35	.4086	ns	.9789	ns	.7747	ns	.9317	ns

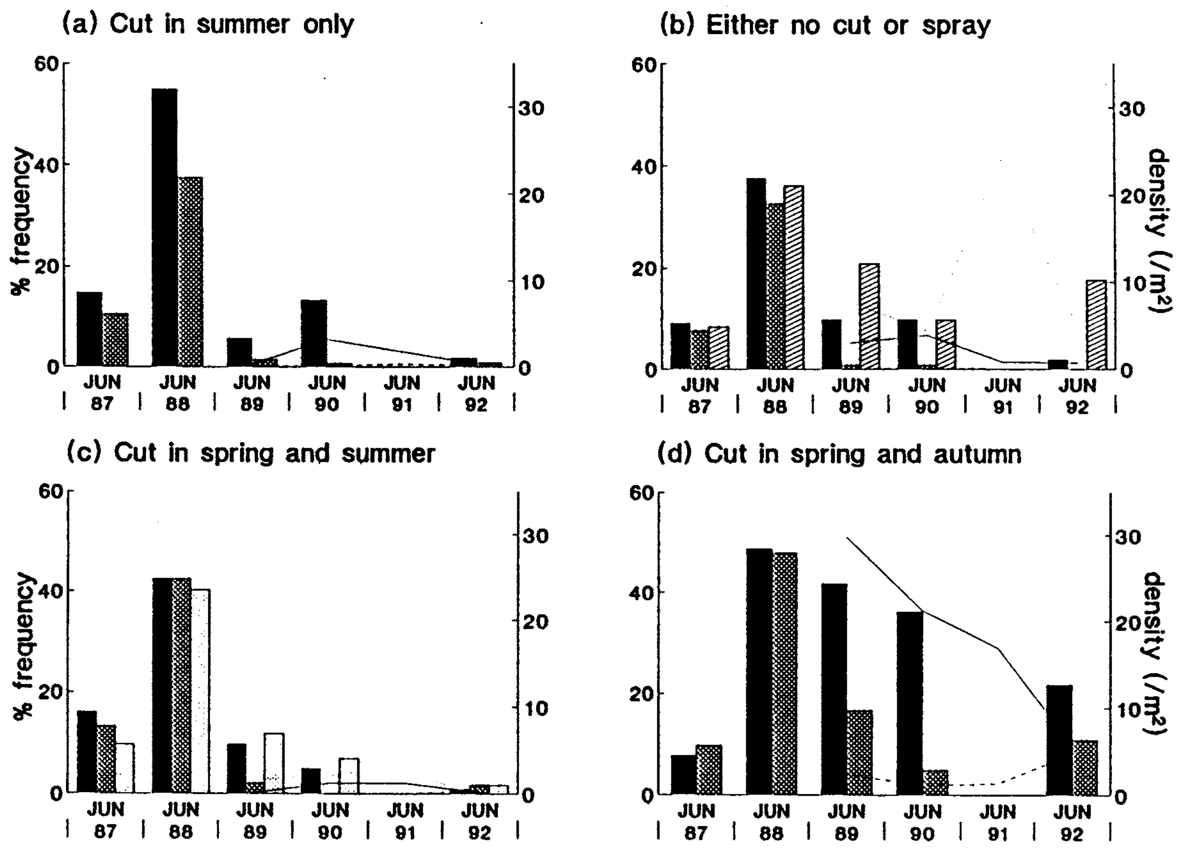


FIG.5.1 Changes in *Avena* species abundance in the new margin
Bars represent frequencies and lines densities
sown, unsown, sprayed (b), cut/hay left (c)
-- sown, — unsown, ...sprayed (b), ... cut/hay left (c)

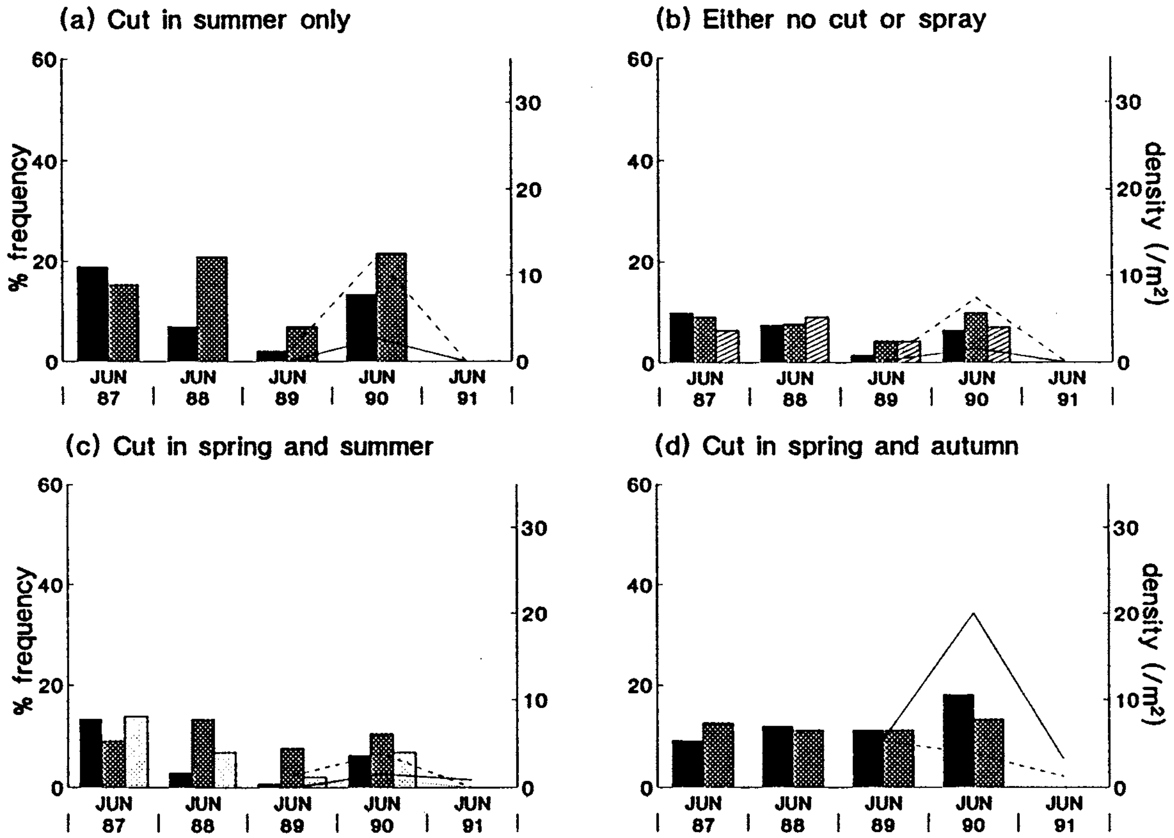


FIG.5.2 Changes in *Avena* species abundance in the old margin

Bars represent frequencies and lines densities

sown, unsown, sprayed (b), cut/hay left (c)

-- sown, — unsown, ...sprayed (b), ... cut/hay left (c)

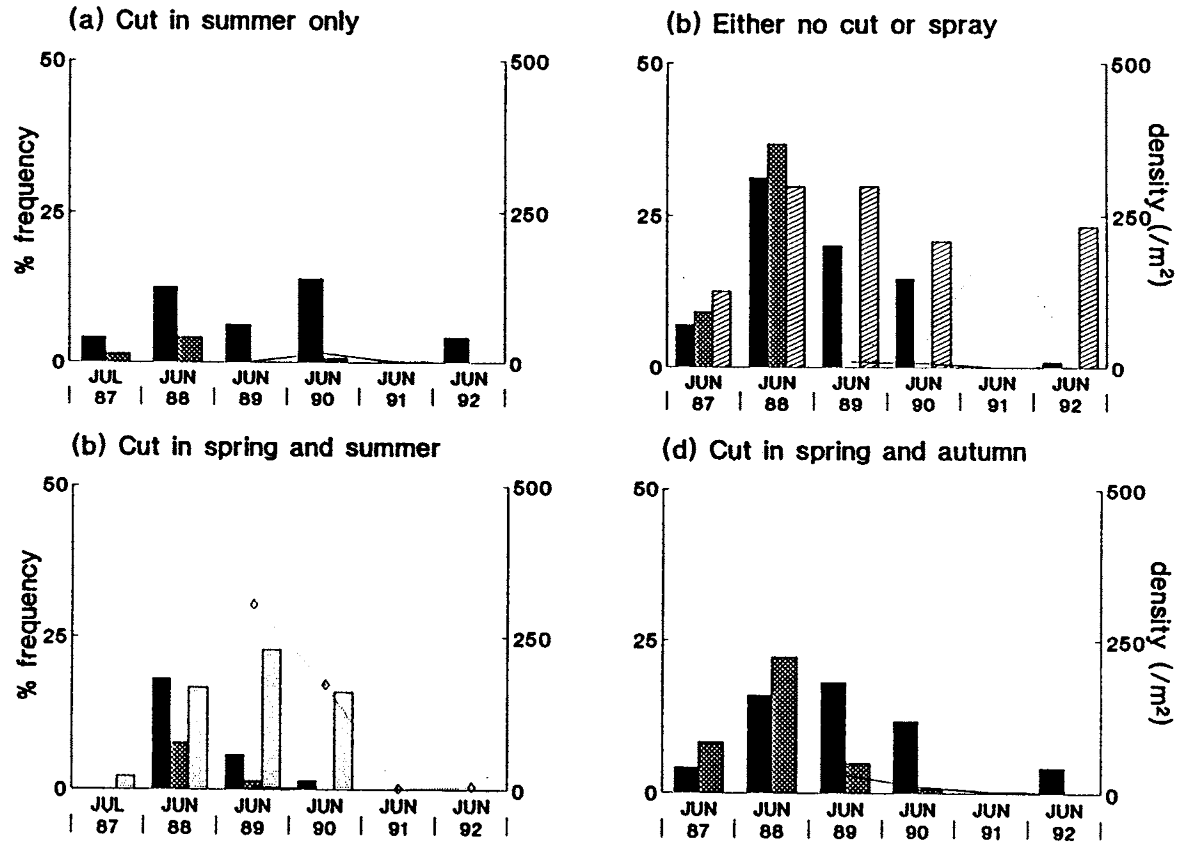


FIG.5.3 Changes in *A.myosuroides* abundance in the new margin
Bars represent frequencies and lines densities
sown, unsown, sprayed (b), cut/hay left (c)
-- sown, — unsown, ...sprayed (b), ... cut/hay left (c)

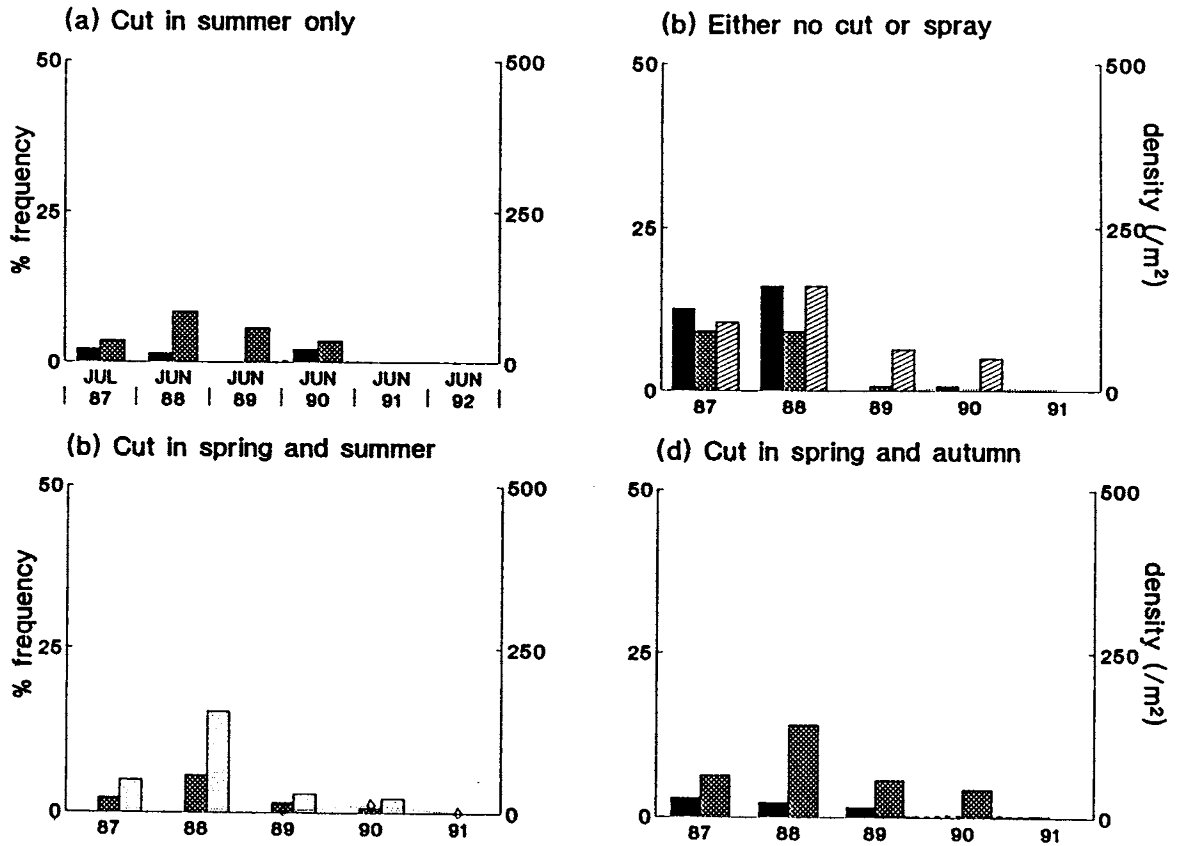


FIG.5.4 Changes in *A.myosuroides* abundance in the old margin
Bars represent frequencies and lines densities
sown, unsown, sprayed (b), cut/hay left (c)
-- sown, — unsown, ...sprayed (b), ... cut/hay left (c)

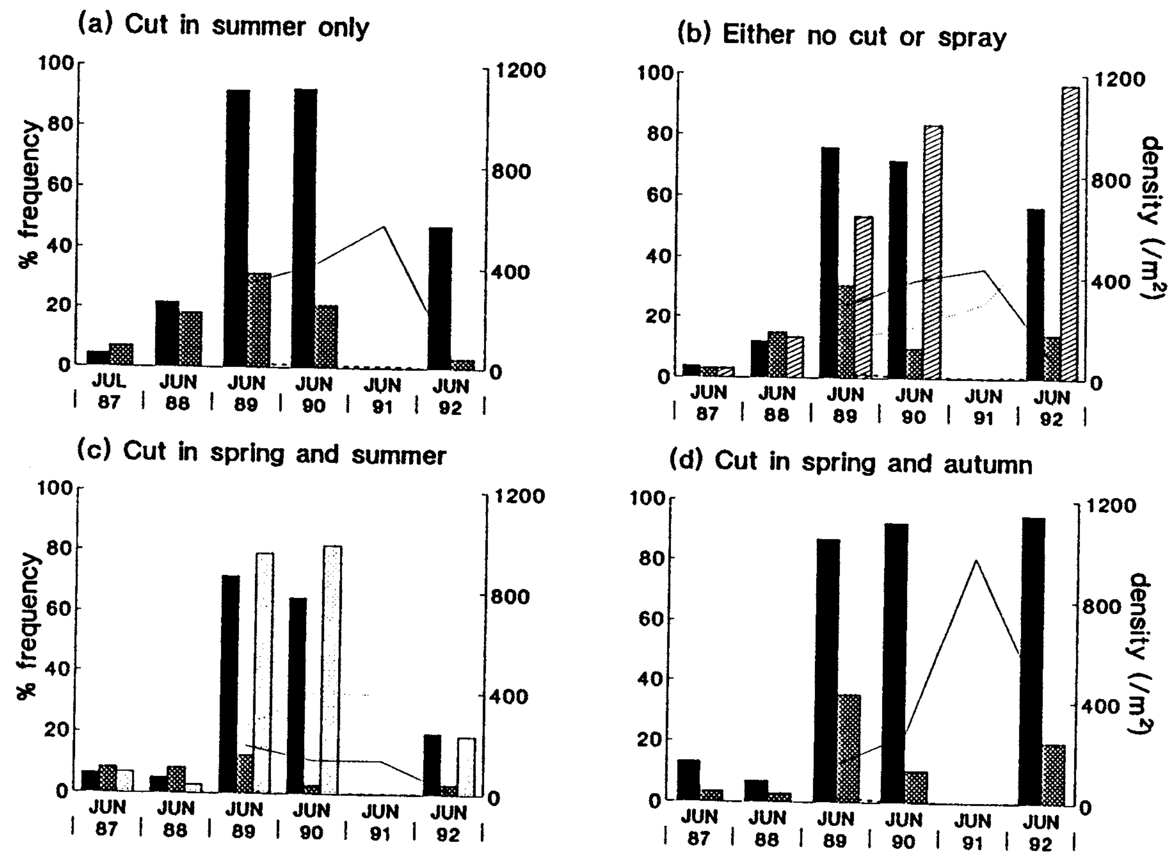


FIG.5.5 Changes *in B. sterilis* abundance in the new margin
Bars represent frequencies and lines densities
sown, unsown, sprayed (b), cut/hay left (c)
-- sown, — unsown, ...sprayed (b), ... cut/hay left (c)

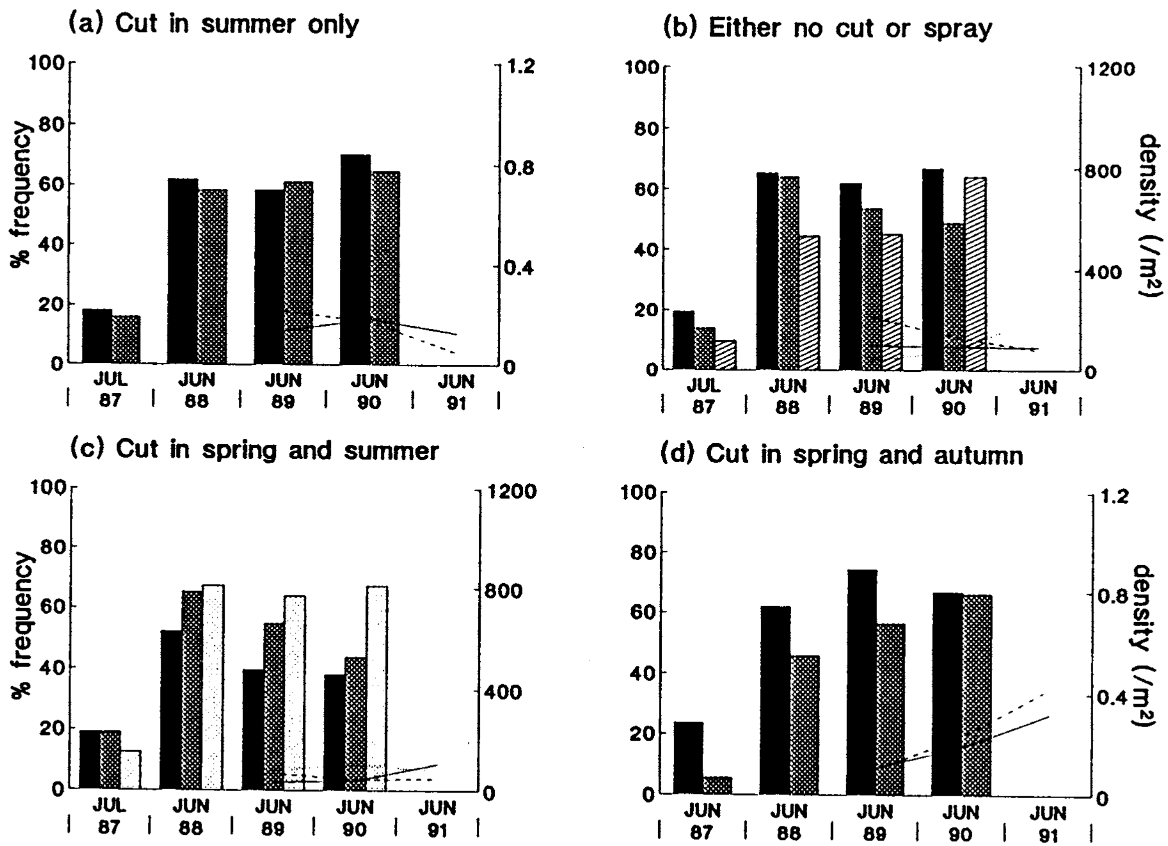


FIG.5.6 Changes *in B. sterilis* abundance in the old margin
Bars represent frequencies and lines densities
sown, unsown, sprayed (b), cut/hay left (c)
-- sown, — unsown, ...sprayed (b), ... cut/hay left (c)

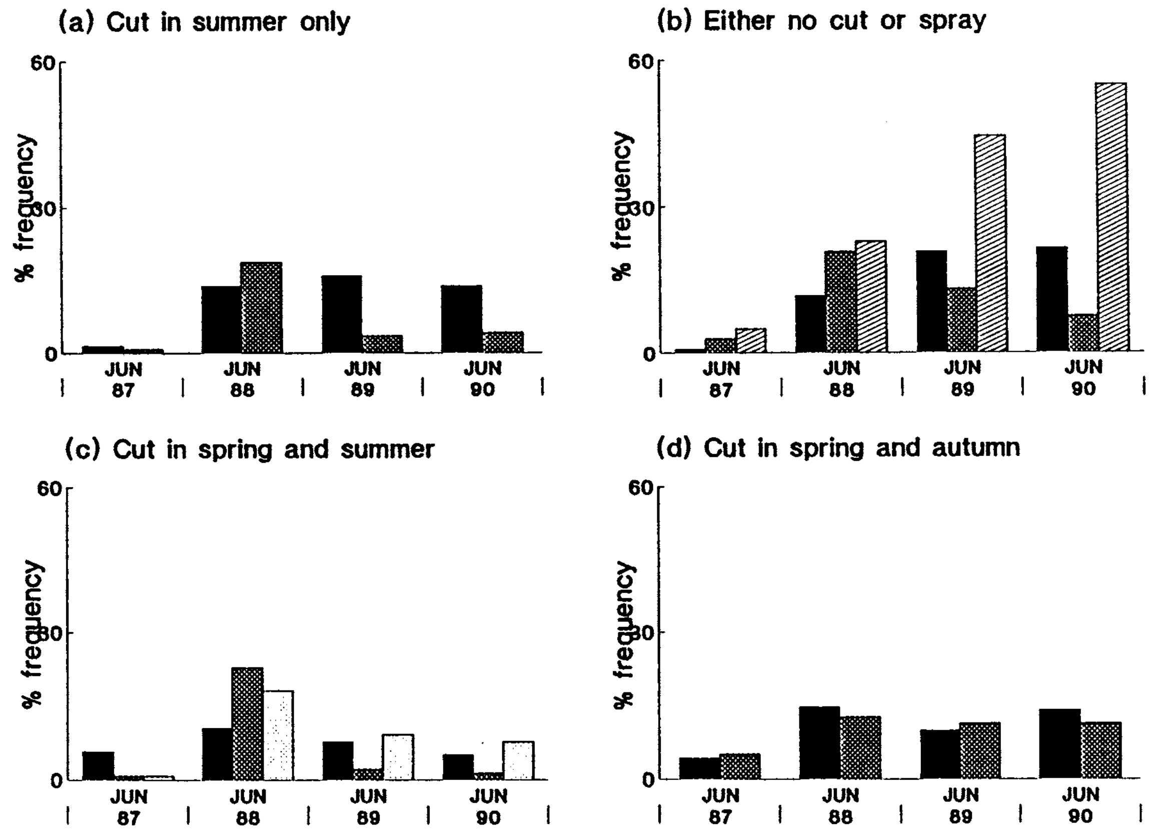


FIG.5.7 Changes *in G.aparine* abundance in the new margin
Bars represent frequencies:
sown, unsown, sprayed (b), cut/hay left (c)

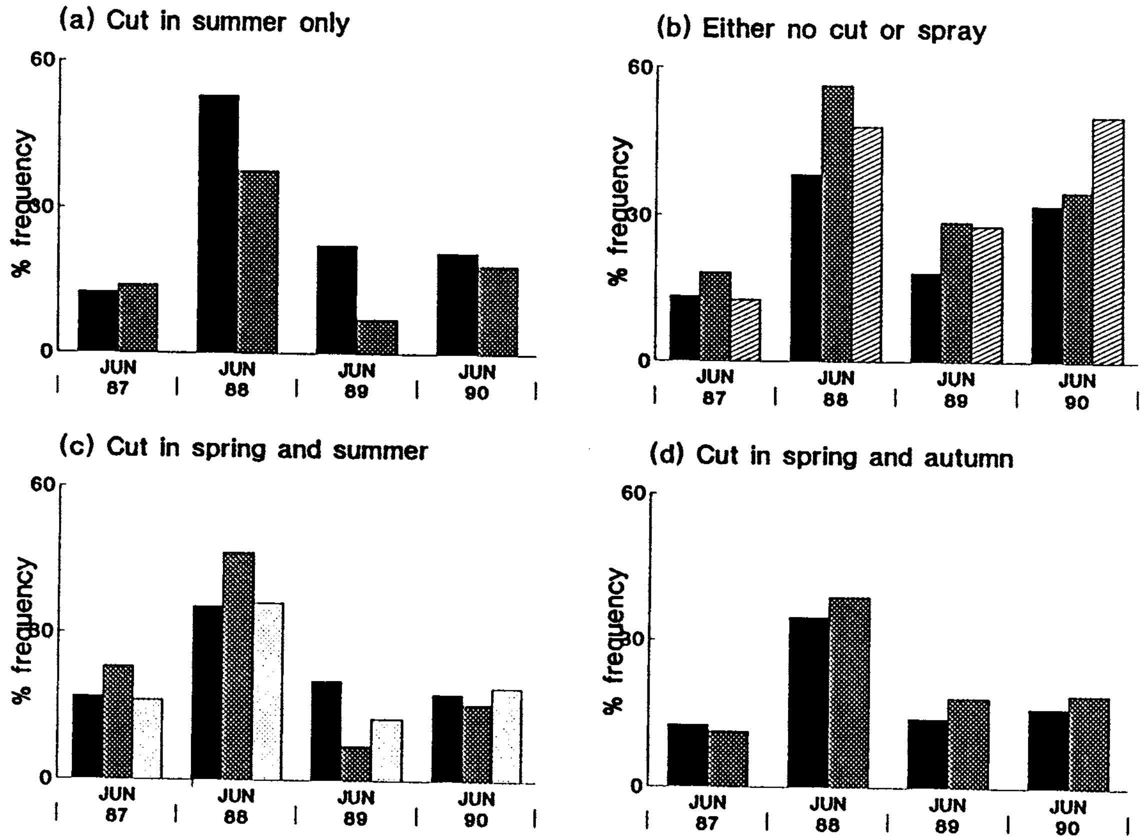


FIG.5.8 Changes *in G. aparine* abundance in the old margin
Bars represent frequencies:
sown, unsown, sprayed (b), cut/hay left (c)

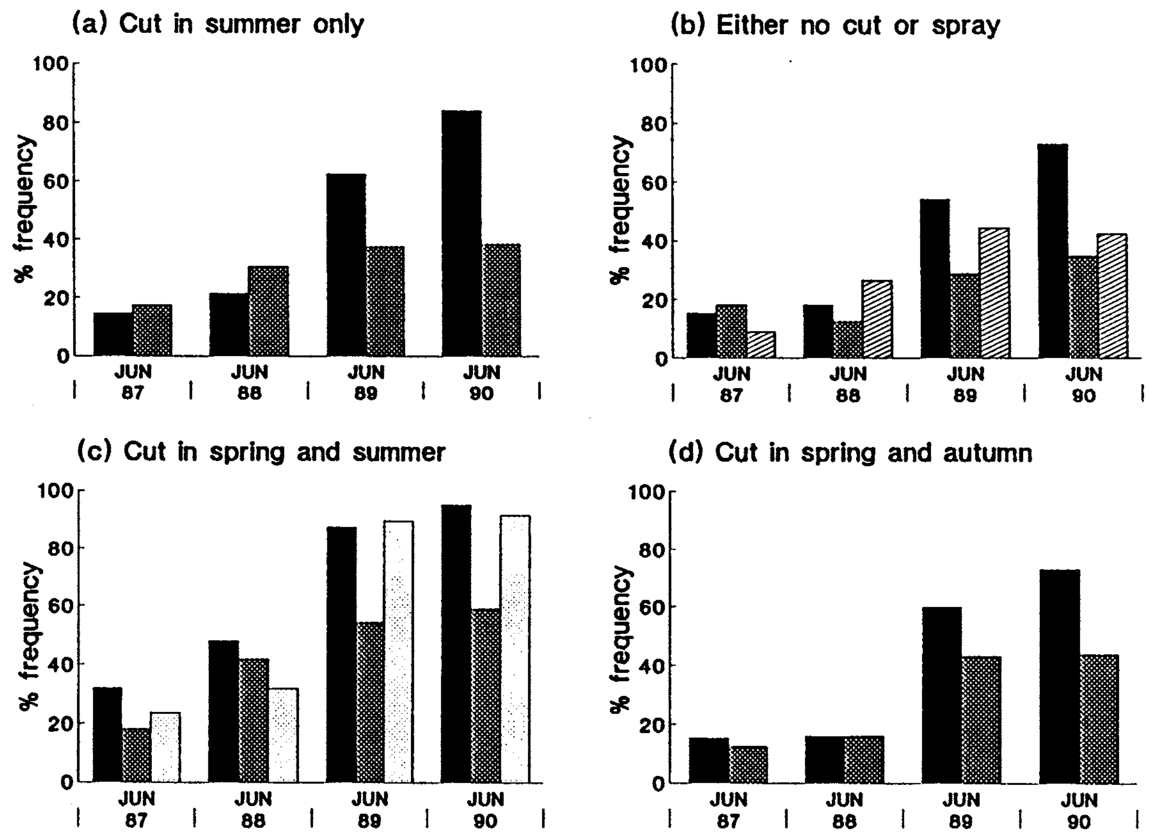


FIG.5.9 Changes *in E.* repens a*b*undance in the new margin
Bars represent frequencies:
sown, unsown, sprayed (b), cut/hay left (c)

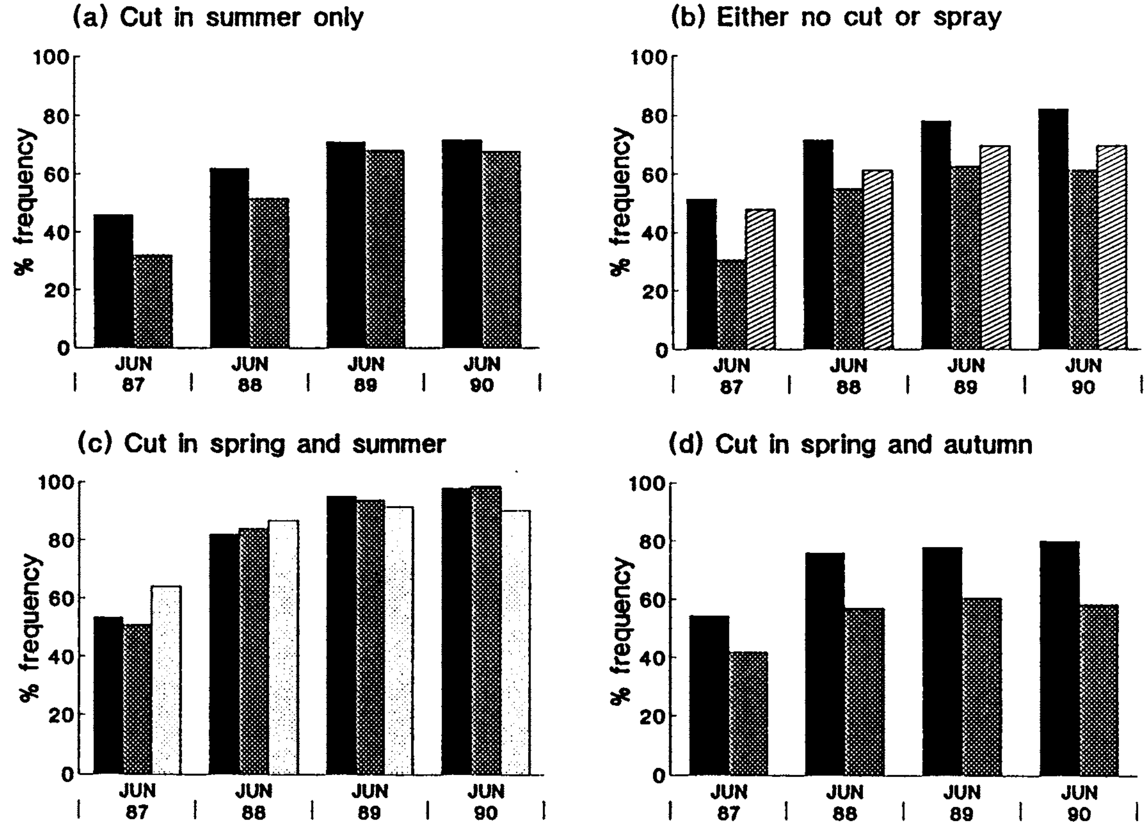


FIG.5.10 Changes *in E.* repens abundance in the old margin
Bars represent frequencies:
sown, unsown, sprayed (b), cut/hay left (c)

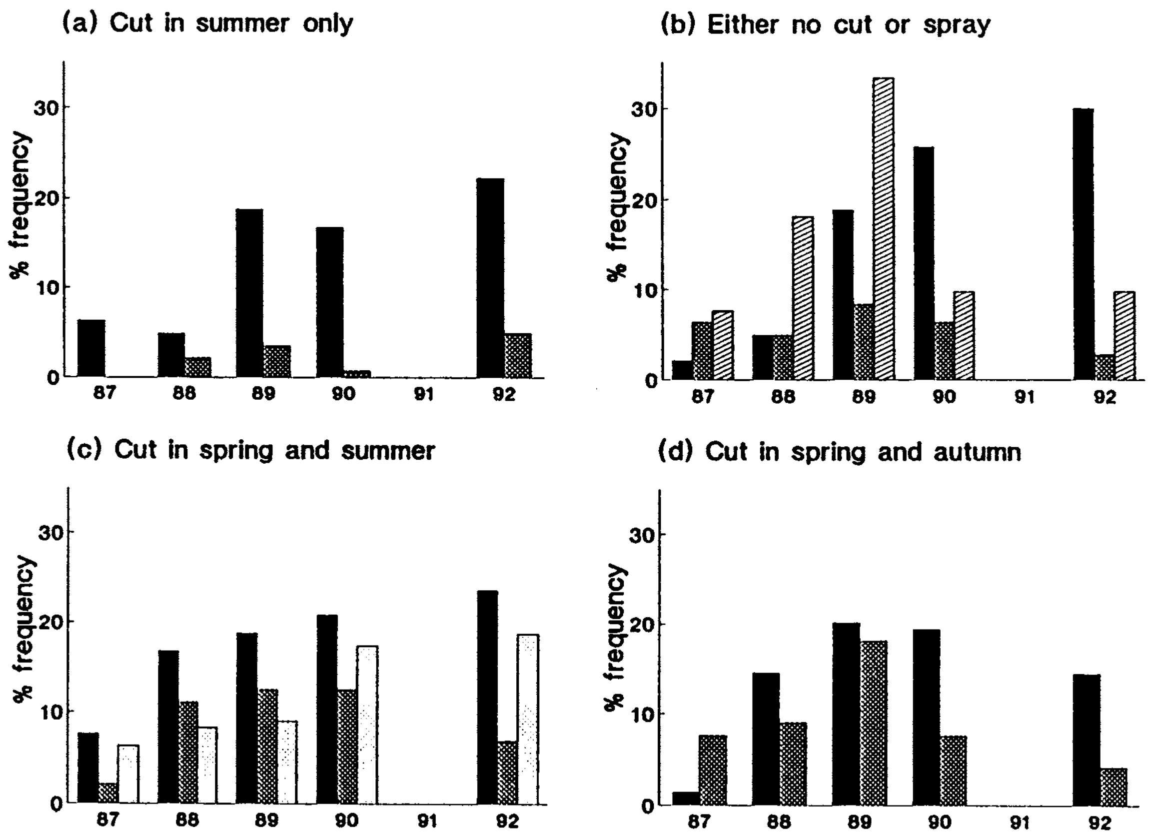


FIG.5.11 Changes *in C.* arvense abundance in the new margin
Bars represent frequencies:
sown, unsown, sprayed (b), cut/hay left (c)

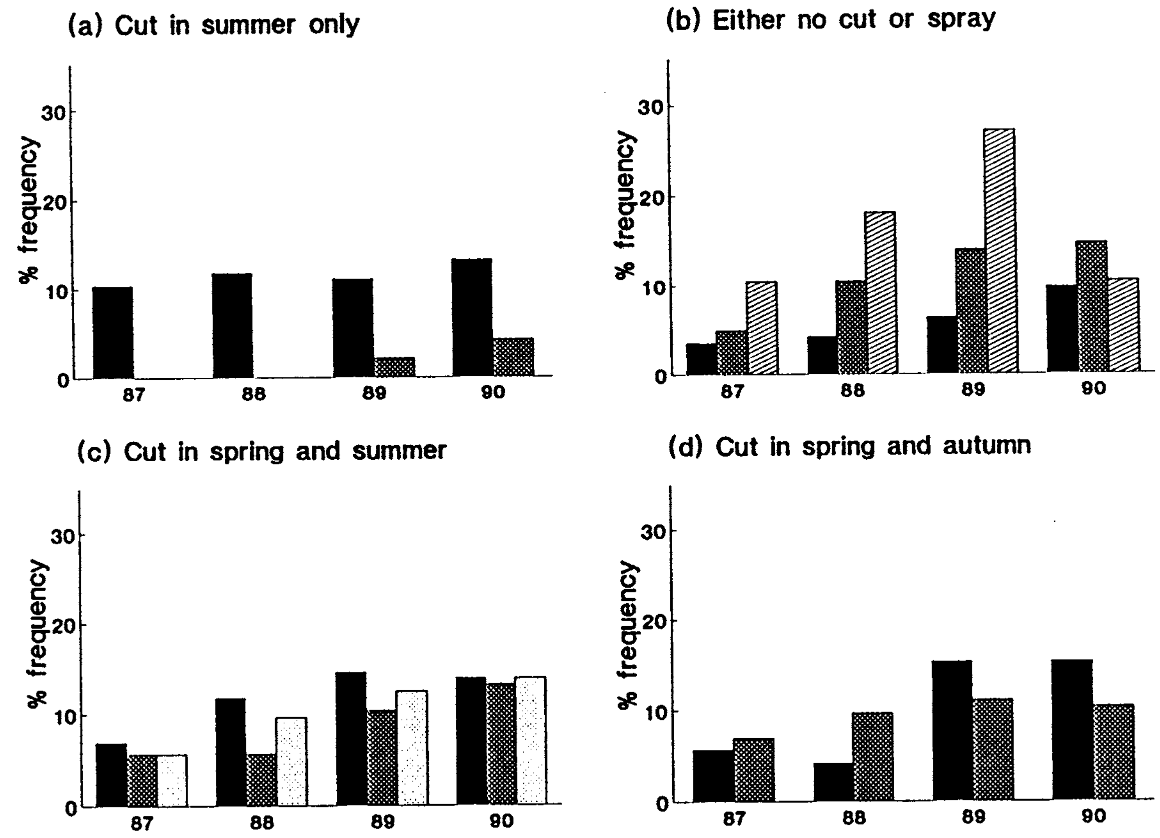


FIG.5.12 Changes in *C. arvense* abundance in the old margin

Bars represent frequencies:

sown, unsown, sprayed (b), cut/hay left (c)

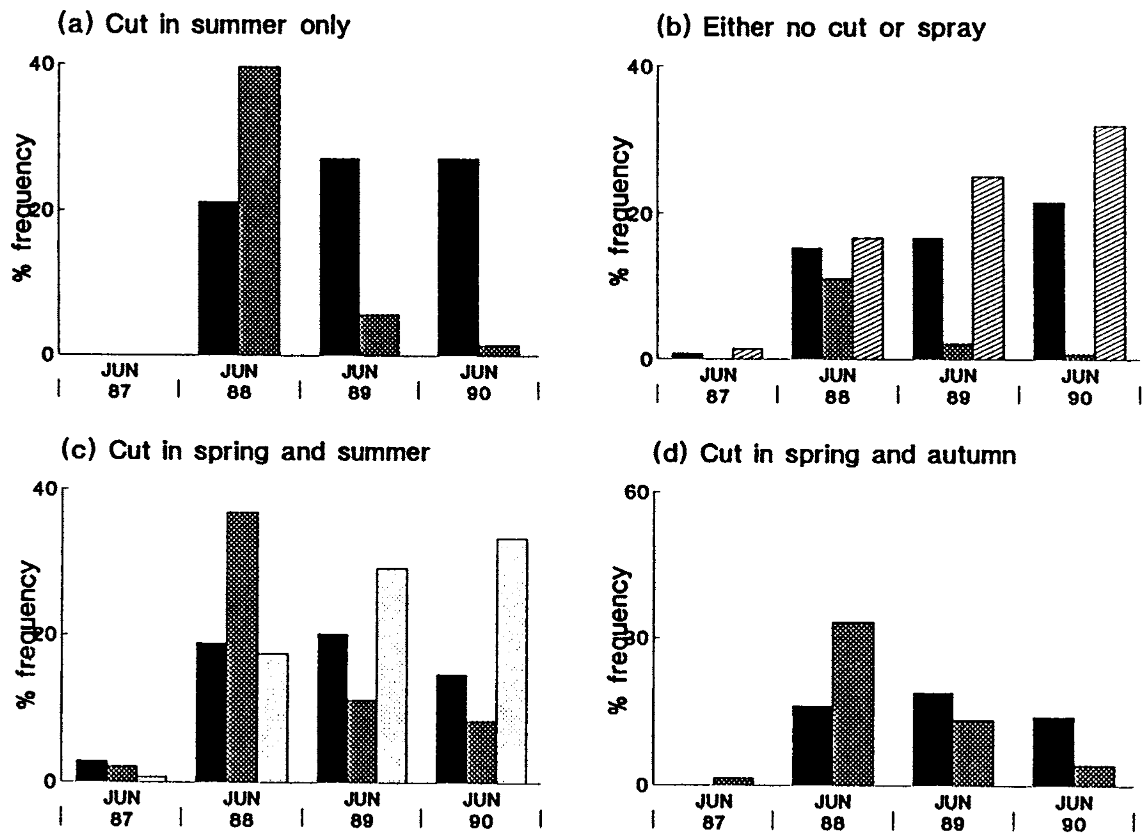


FIG.5.13 Changes in *U. dioica* abundance in the new margin
Bars represent frequencies:
sown, unsown, sprayed (b), cut/hay left (c)

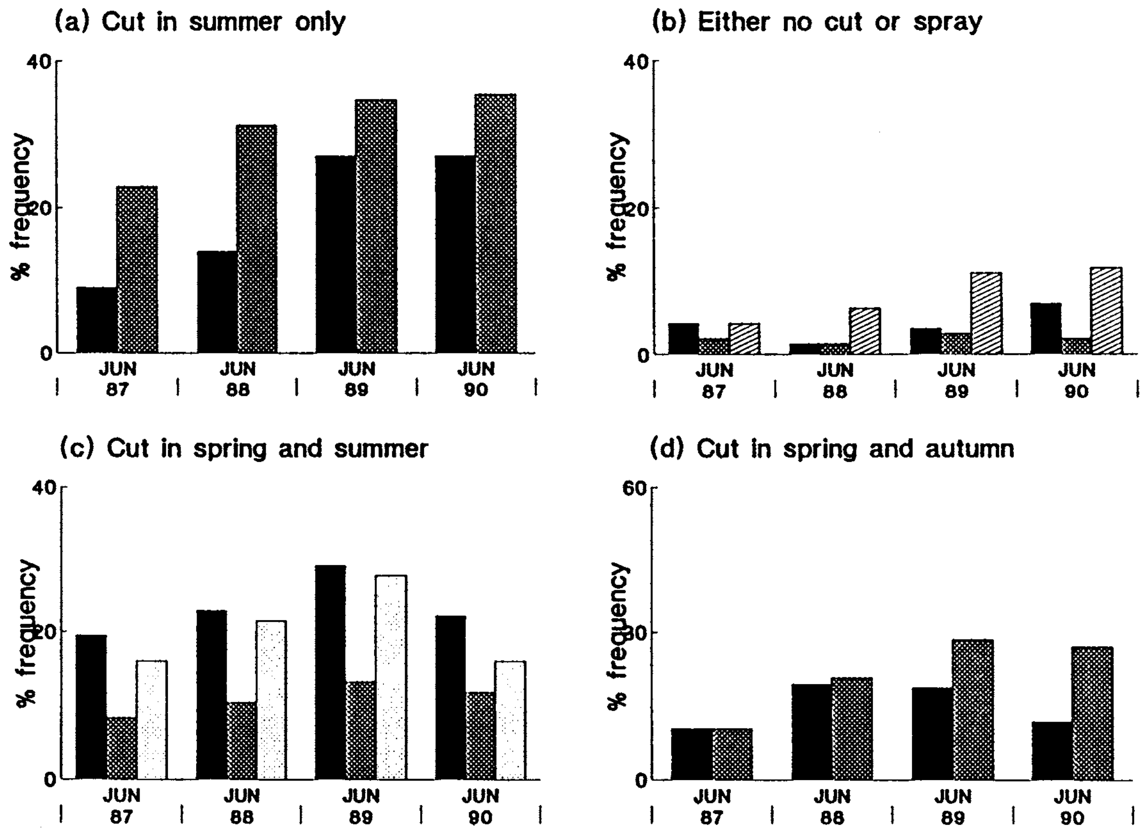


FIG.5.14 Changes in *U. dioica* abundance in the old margin
Bars represent frequencies:
sown, unsown, sprayed (b), cut/hay left (c)

6 THE WILD FLOWER SEED MIXTURE

6.1 Introduction

We showed in Chapter 4 that wild flower seed mixtures can be used successfully to reinstate an attractive perennial flora on arable field margins. Their use is particularly appropriate in situations where suitable sources of colonists have been eliminated by insensitive field margin management practices. We also show, in Chapter 9, that these mixtures can have an enormous impact on the abundance of butterflies and other nectar-feeding insects on field margins. However, considerable prejudice surrounds the use of wild flower seed mixtures on agricultural land. It is generally believed that their expense and the difficulty of establishing them cannot justify the benefits to wildlife and amenity that are likely to accrue.

We have shown in Chapter 5 that the cost-effectiveness of such mixtures should be evaluated not only in terms of their benefits to wildlife and amenity, which inevitably appeal only to a limited sector of the farming community, but also in terms of their direct benefits to agricultural weed management. We demonstrated that mixtures containing fine grasses can completely exclude pernicious annual grass weeds and can limit the spread of perennial weeds. This benefit must be set against very variable purchase costs: simple, and therefore relatively inexpensive, seed mixtures can be as effective for weed control as complex mixtures and can also have considerable benefits for wildlife and amenity.

The expense of any wild flower seed mixture, however simple, makes it imperative that all of the components of the mixture establish well. The success of wild flower seed mixtures, both as weed barriers and conservation assets, depends on how well their components establish. This depends in turn on both careful seed bed preparation and sowing, and on selection of species that are likely to thrive in a given situation. The subsequent success of a mixture is dependent on selection of species that will both thrive under the proposed management regime and which will fulfil the farmer's or land manager's aspirations for the sward. These aspirations may be restricted to weed control but may also include benefits to amenity, to specific species or groups of species, or to species richness in general. Thus, we showed in Chapter 4.2.1, that the species richness of sown swards on the new margins was maximised by mowing in spring and autumn, while least species persisted when sown swards were either cut once or were left unmanaged. In Chapter 4.2.2. we further showed that the species richness of the sown component of sown swards was also greatest in treatments cut in spring and autumn, and was greater in treatments cut twice than in those cut once.

In this chapter we look first at the changes in the number of sown species with time. We describe establishment not only in the new zones of the sown plots, where the seed mixture was sown into a well-prepared seed bed, but also in the old zones, where it was sown into an existing sward. Data are also presented on the subsequent lateral spread of established components of the mixture into adjacent unsown plots. The greater part of the chapter is then devoted to analysis of the performance of the individual components of the seed mixture. In Section 6.2.2. we describe the overall patterns of relative abundance and the ways in which they changed with time. In Section 6.2.3 we present detailed accounts for each species of changes in abundance with time and of the effects of the experimental treatments on abundance. In both of these sections we evaluate the success of the species establishment in terms of both the temporal trends in abundance and the relative abundance in the sward in relation to sowing density. Recommendations are made about the relative ease of establishment of different species and about their suitability for inclusion in swards managed by particular regimes. Summaries of the critical information are given at the end of each species account. In Chapters 9 & 10 we discuss the relative importance of the species in the mixture as nectar sources for butterflies. We do not attempt to evaluate the species performance in terms of either their cost or their nature conservation or aesthetic value. Although all of these factors are of importance in selecting species for seed mixtures, the cost varies from year to year according to the supply and demand and conservation and aesthetic value must be defined in the context of the aims of a particular field margin restoration scheme.

Most of the analyses that we present are of data for 1989 and 1990. The seed mixture was sown in spring 1988 and, although data on the establishment of many individual species have been analyzed for that year, data on total numbers of species establishing in 1988 are unreliable because of the difficulty of identifying seedling grasses. We have therefore used data from 1989 for our first assessment of the numbers of species that established. 1990 was the last year in which all species were recorded. The forbaceous component of the mixture was additionally recorded in 1991 and 1992, and the data on the changes in the numbers of forbaceous species and on the relative abundance of some individual forbs are presented for these two years. However, we interpret some of the data from these two years with caution because records were collected only on one, relatively late date (Chapter 2.2.5).

6.2 Results and discussion

6.2.1 THE EFFECTS OF TIME AND MANAGEMENT ON NUMBERS OF SOWN SPECIES

The new margins

On the new margins of sown plots, there was a slight decrease in the mean number of sown species between 1989, the year after sowing, and 1990 under all experimental treatments (Table 6.1). Although we are unable to examine the trend in total species richness after September 1990 (above), comparison of the numbers of forbs from 1988 to 1992 suggests that numbers of sown species in these plots remained fairly constant over a five year period (Table 6.2). The effects of the experimental treatments on the numbers of sown species in the plots over this period are fully described in Chapter 4.2.2.

The old margins

The numbers of sown species that had established in the old margins by June 1989, the year after sowing, was very low (Table 6.3). Numbers had increased only very slightly by June 1990, the last year in which species were recorded on the old margins. In

Chapter 4.2.2 we show that we were unable to detect any effects of treatment on the numbers of sown species in the old margin on any sampling date in either year.

Adjacent unsown plots

By 1990 most of the sown grasses and some of the forbs had colonised unsown plots although numbers were low and most colonists were in the areas immediately adjacent to sown plots. Very few sown species were recorded in the permanent quadrats of unsown plots but it should be borne in mind that the quadrats constituted very small areas, a minimum of 12m from the boundary with the sown plots. By 1990 the mean numbers of species recorded in the quadrats of unsown plots neighbouring sown plots remained too low to analyze but ranged from zero to 2.3.

6.2.2 OVERALL CHANGES IN ABUNDANCE OF THE COMPONENTS OF THE SEED MIXTURE

The new margins

Although the total numbers of sown species on the new margins of sown plots were relatively constant during the first four years after establishment (above), the relative abundances of many of the species showed substantial changes. In this section we describe the general patterns of relative abundance amongst the species in the mixture. We examine first the relative frequencies of the sown species in the swards and the way in which these changed with time, and secondly the relationship between frequency and sowing density. Frequency has been estimated as the proportion of the maximum possible number of quadrat cells occupied in all plots, irrespective of treatment (the effects of treatment are analyzed in Section 6.2.3). Data are presented for all sown species in 1988, the year of sowing, 1989 and in 1990. Because the phenologies of the species differ, the datum presented for each species in each year is based on the quadrat recording round in which the species was most abundant. In 1988 the definitive identification of the seedlings of some species was not possible until relatively late in the season and so the frequencies presented for these species are likely to be anomalously low (see Table 6.4). Data are presented for 1991 and 1992 only for those forbs for which the July data were thought to be a reliable measure of abundance.

Most of the sown grass species established at high frequencies in 1988 (Table 6.4). *Poa pratensis* L. Smooth Meadow-grass and *Hordeum secalinum* Schreber Meadow Barley were less abundant but both increased substantially over the next two years. By 1990 *H. secalinum* was the only grass species that was not present in the great majority of quadrat cells. *Cynosurus cristatus* L. Crested Dog's-tail was the only grass species that decreased, following a very high level of establishment, but we show below that this decrease occurred only in some treatments.

The only forb that established at high frequencies was *Leucanthemum vulgare* Lam. Oxeye Daisy, while several forb species established at very low frequencies. Most forb species declined between 1988 and 1990. Seven increased but none of the increases was substantial. Between 1990 and 1992 three of the declining forb species started to increase although six species present in low numbers appeared to have been lost completely from the quadrats. The trends for individual species are described below (6.2.3).

It was not possible to derive a precise quantitative relationship between sowing density and subsequent abundance because relative frequency, rather than density, of plants was recorded. We therefore derived a relative measure by regressing relative frequency (arcsine square root transformed) on sowing density (log transformed) and ranked the species by their deviations from the regression line (i.e. by the residuals). The regression for 1990 is given as an example in Figure 6.1 and the residuals for 1989 and 1990 are ranked by species in Table 6.5. The rank abundances of the species in the seed mixture and in the sward in 1989 (see Chapter 2.2.2 for sowing densities) are also given for reference in Table 6.5.

When the performance of many of the sown species in the swards is evaluated in relation to the density at which their seeds were sown, some of the forbs which occurred at low frequencies can be seen to have established as well from seed as some of the commoner grasses. Thus, some relatively infrequent species, such as *Tragopogon pratensis* L. Goat's-beard and *Knautia arvensis* (L.) Coulter Field Scabious, were sown at low density but established relatively well from seed while other species, such as *Poa pratensis*, were more abundant because they were sown at high densities, but nevertheless established relatively poorly from seed. The three most abundant grass species and *L. vulgare* established very well in relation to their sowing density. At the opposite extreme, the two *Hypericum* species were very infrequent in the swards. Although they were sown at high density they established extremely badly from seed.

The old margins

In the old margin quadrats most species increased from very low frequencies in 1988 (Table 6.6). The greatest increases were amongst the grasses. As on the new margins, *L. vulgare* was the only forb that increased substantially. Five species of forb were not recorded in the old margin quadrats on any date. Of these, *Hypericum perforatum* L. Perforate St John's-wort, *H. hirsutum* Hairy St John's-wort, *Silene latifolia* Poiret subsp. *alba* and *S. vulgaris* also performed relatively poorly on the new margins but *Centaurea nigra* L. Common Knapweed was one of the most successful forbs on the new margins.

6.2.3 THE EFFECTS OF ESTABLISHMENT AND MANAGEMENT ON THE ABUNDANCE OF SOWN SPECIES

In this section we describe in detail for each species in the seed mixture the changes in relative frequency during the experiment and the results of formal analyses of the effects of the experimental treatments. Analyses of variance were performed on the relative frequencies of all sown species in the four sown treatments for which sufficient data were available. We used the same planned comparisons of means as in previous chapters, comparing cut with uncut treatments, treatments cut once with those cut twice, and treatments cut in spring+autumn with those cut in spring+summer. Because of the large number of analyses, the results are described and significant results are presented in the text, but all of the results are not tabulated.

Grasses

***Festuca rubra* L. Red Fescue** We sowed a mixture of two sub-species of *F. rubra* (subsp *commutata* and subsp. *littoralis*) and did not attempt to distinguish between them when recording. The *F. rubra* mixture was the second most frequent component of the sown swards and ranked second in abundance in relation to its sowing density in both 1989 and 1990 (Table 6.4 and 6.5). We were unable to detect any effects of our experimental treatments on its abundance.

In the old margins *F. rubra* increased steadily to become the second most frequently recorded sown species by 1990. Again, we were unable to detect any significant or consistent effects of treatment on its frequency (Table 6.6).

Summary *F. rubra* was a very successful and valuable component of the wild flower seed mixture. In addition to its excellent establishment on very fertile soils, and wide tolerance of management regimes, it was the primary contributor to forming a dense sward base. It was this feature of the sown swards that conferred their ability to exclude both annual and perennial pernicious weeds (Chapter 5).

***Phleum pratense* subsp. *bertolonii* (DC.) Bornm Smaller Cat's-tail** *P. pratense* subsp *bertolonii* established at very high frequencies in 1988 and had increased slightly by 1990 (Table 6.4). It was the third most frequent species in the swards and also established very well from seed, ranking third in abundance in relation to its sowing density in 1989 (Table 6.5). By 1990 it was the highest ranked species in relation to sowing density. It was common in all treatments and we were unable to detect any consistent or significant effects of treatment on its abundance. It should be noted, however, that our recording method can be insensitive to increases in abundance in very common species. Increases in density within quadrat cells would not be detected.

In the old margins it increased gradually but was less abundant there in 1990 than either *Cynosurus cristatus* or *Festuca rubra* (Table 6.6). As on the new margins, we were unable to detect any significant effects of treatment.

Summary *P. pratense* subsp *bertolonii* is a long-lived species and appears to be a very successful constituent of wild flower seed mixtures on fertile soils, having excellent establishment and very broad tolerance of sward heights and densities. Grime *et al* (1988) suggest that the *Phleum* species are intolerant of trampling and are best suited to regimes involving only occasional cutting or grazing. Although it appeared to be well suited to our twice-annual cutting regimes, this suggests that it may be an unsuitable species for inclusion in swards that are to be cut frequently or used for amenity and access purposes. It should not be sown into existing swards.

Cynosurus cristatus In 1989 *C. cristatus* was the most frequent species recorded but it also established better in relation to sowing density than any other species in the seed mixture (Table 6.4 and 6.5). However, in contrast to the other grass species, its frequency decreased between 1989 and 1990.

This decrease was restricted to the treatments that were cut once or were left uncut. In the former, frequency decreased by 27.8%, and in the latter by 70%, between June 1989 and 1990. There was no evidence of this effect during 1989 but on all dates from January 1990 onwards the contrast between cut and uncut treatments was highly significant (Jan. 1990; $F_{(1,15)}=16.70$, $P<0.001$: Apr. 1990; $F_{(1,15)}=36.43$, $P<0.001$: Jun. 1990; $F_{(1,15)}=36.43$, $P<0.001$: Sept. 1990; $F_{(1,15)}=41.74$, $P<0.001$). In June 1990 comparison of treatments cut once with those cut twice was also significant ($F_{(1,15)}=14.03$, $P<0.01$) and in September 1990 this comparison was almost significant ($P=0.058$). Observations suggested that this decline continued in 1991 and 1992, when it became difficult to find this species in uncut swards. The onset of the decline may not have been as abrupt as these data suggest, because our recording method was insensitive to changes in density in very common species (above). Thus *C. cristatus* could have declined in density for some time before it was lost from sufficient cells to register as a decline in frequency.

In the old margins *C. cristatus* was the most abundant sown species in 1988, 1989 and 1990, and showed the greatest increase between 1989 and 1990 (Table 6.6). In uncut treatments it increased only very slowly. Uncut treatments had significantly lower frequencies than cut treatments in September 1990 ($F_{(1,15)}=6.67$, $P<0.05$). Low frequencies in all treatments at earlier dates made it unlikely that significant effects would be detected. Most of the increase in the old margins must have resulted from seed shed from plants in the new margins since seed from the original sowing probably remained viable only for one year (see below). By late 1990 there was some evidence that the increase in *C. cristatus* on the old margins was greatest in the spring and autumn-cut treatments (June 1990; $F_{(1,15)}=2.65$, $P=0.073$ and Sept. 1990; $F_{(1,15)}=6.67$, $P=0.021$). Under this regime the seed return from both the new margins, and from plants establishing in the old margins swards, would be expected to be greatest (see below).

Our results are consistent with the finding of Grime *et al* (1988) that this species is markedly restricted to heavily grazed, short turf, and of Lodge (1959) that it has low shade tolerance. It is likely that its high frequencies in spring+summer cut treatments during the first three years after sowing will decline. *C. cristatus* flowers in June and sets seed in July and so much of the seed production is removed by cutting at the end of June. Loss of seed production is likely to be reflected in a decline in abundance at a relatively early stage because it is a short-lived species with no persistent seed bank. It is much more likely to persist at high frequency in spring and autumn-cut treatments: not only is seed production higher but establishment opportunities are also likely to be greater. Further years' data are needed to test these predictions.

Summary Despite excellent establishment from seed, *C. cristatus* was lost rapidly from unmanaged swards and only slightly less rapidly from swards cut once a year on fertile soils. Although it should not be included in seed mixtures intended for such low intensity management, it is a highly successful constituent in swards managed by twice-annual mowing. Although the timing of mowing did not appear to be critical during the first three years after establishment, we suggest that this species is more likely to persist at high frequency in swards cut in spring and autumn than in those cut in spring and summer. *C. cristatus* should only be sown into a well prepared seed bed since it established badly from seed sown into the old margins. Of our sown species it was the best colonist of the old margin swards over a three year period but nevertheless achieved frequencies of only 25% compared with over 90% in the new margins.

Trisetum flavescens **(L.) Beauv. Golden Oat-grass** *T. flavescens* was the fourth most abundant grass in the sown swards with a frequency of 90% in 1989 but some evidence of a slight decline in 1990 (Table 6.4). It performed relatively less well in relation to its sowing density, ranking seventh in 1989 and eighth in 1990 (Table 6.5).

The slight overall decline recorded for 1990 resulted almost exclusively from a drop in frequency in the uncut treatments between 1989 and 1990. The decline between the June recording rounds in the two years was 16.7%: increases or decreases and decreases of under 5% were recorded in the other treatments. The planned contrast between cut treatments and the uncut treatment was almost significant in September 1989 ($F_{(1,15)}=4.51$, $P=0.051$) and was significant on all subsequent dates (Jan. 1990; $F_{(1,15)}=5.36$, $P<0.05$: Apr. 1990; $F_{(1,15)}=5.62$, $P<0.05$: Jun. 1990; $F_{(1,15)}=6.35$, $P<0.05$: Sept. 1990; $F_{(1,15)}=14.03$, $P<0.01$:). There were no significant differences in the abundance of *T. flavescens* in swards cut once and those cut twice.

In the old margins *T. flavescens* increased slowly following poor establishment from the original sowing in 1988. It is thought to have an annual seed bank and so most of the increase must have come from seed shed into the old margin swards from plants in the new margins. The increase was smallest in the uncut treatments, suggesting that establishment, as well as persistence, was restricted by dense swards. However, the frequencies were too low to detect any significant effects of treatment.

T. flavescens showed a similar, although less extreme, response to cutting to *Cynosurus cristatus*. Grime *et al* (1988) found that in unmanaged grassland this species was restricted to sites where the growth of more productive species was checked. They describe it as a 'congenital subordinate', being a minor component of grassland, irrespective of turf height, and capable of persisting through changes in management that are likely to bring about more radical changes in the abundance of dominants. These conclusions support our own data in suggesting that this species is likely to persist only at very low frequency in unmanaged swards.

Summary *T. flavescens* can be a major and attractive component of wild flower seeded swards on fertile soils where the sward is mown at least once a year. Although it is possible that it will persist at higher frequencies in swards cut twice than in those cut once, we found no evidence of this by the third year after sowing. This species should not be included in seed mixtures on fertile soils where the intention is to mow less than once a year or leave swards completely unmanaged. It should never be sown into existing turf.

Poa pratensis *P. pratensis* was recorded at much lower frequencies than any of the preceding grasses in 1988 but increased very rapidly to reach an overall frequency of 84% by 1990. Its establishment from seed was much poorer than that of any of the other grasses (Table 6.5). It was probably under-recorded in 1988, although both vegetative spread and seed germination are also likely have contributed to the increase by 1989. There is debate about the longevity of its seeds (see Grime *et al* 1988) and so we do not know whether seeds sown in 1988 could have germinated in subsequent years. *P.*

pratensis was not recorded flowering on the margins until 1989 and so could not have regenerated by seed from established plants until 1990.

Although this species increased in all treatments, by June 1989 the two summer-cut treatments had higher frequencies than either the treatment that was cut in spring and autumn or the uncut treatment. The uncut treatment had the lowest frequencies. This pattern persisted and by September 1989 the planned comparisons between both spring+summer *vs* spring+autumn cut treatments and between cut *vs* uncut treatments were significant ($F_{(1,15)}$=9.48, P<0.01: $F_{(1,15)}$=5.83, P<0.05, respectively). These comparisons remained either significant or nearly significant on all subsequent dates. Unplanned comparisons between all treatment means showed that these significant differences resulted from higher frequencies in treatments that were cut in summer than in those left uncut in summer. The differences between the two summer cut treatments and between the spring+autumn cut and uncut treatments were never significant.

In the old margins *P. pratensis* increased very slowly and by 1990 it was still not sufficiently abundant to analyze treatment effects (Table 6.6). If increase in this species results primarily from rhizomatous extension, it is likely that its spread into the old margins will continue to be slow. Further analyses of the data are required to determine the mode of increase.

Our data show that, although *P. pratensis* reached high frequencies more slowly than the other grasses in the seed mixture and established relatively poorly from seed, it nevertheless became a very frequent component of the swards within three years of sowing. It responded particularly well to cutting in summer but increased even in the absence of summer cutting. Grime *et al* (1988) report that this species is tolerant of grazing and trampling and Spedding & Diekmahns (1972) that it is potentially high-yielding. Our data support those of Grime *et al* (1988) in showing that in tall herb communities, it persists as a more minor component. We found that in these situations it develops extremely long leaves: this phenomenon is also reported by Grime *et al* (1988).

Summary These characteristics make *P. pratensis* a very suitable candidate for inclusion in wild flower seed mixtures on fertile soils. Its inclusion is of doubtful value only where the intention is never to cut swards during the summer, but its ability to persist at low frequency in unmanaged swards makes it a valuable candidate for swards in which the management is likely to be varied either temporally or spatially.

Hordeum secalinum *Hordeum secalinum* was the least frequently recorded grass species in the mixture, increasing steadily to only 34% by 1990 (Table 6.4). Its establishment in relation to its sowing density, however, was slightly better than that of *Poa pratensis* (Table 6.5). It was also the least abundant sown grass in the old margins and showed the smallest increase between 1988 and 1990.

We were unable to detect any consistent and significant effects of treatment on the abundance of this species. In contrast to all of the other sown grass species there were consistent significant effects of experimental block on its frequency on the new margins. These appeared to be related to soil type, with this species establishing at higher frequencies on the heavier clay soils than on the lighter loams. Further analyses are required to confirm this association.

Summary Our data suggest that this species is likely to be worth including in seed mixtures where the intention is to create swards resembling those of traditional hay-meadows, on relatively heavy soils. It appears to be tolerant of, and able to increase in swards cut up to twice annually and in uncut swards. It should never be sown into existing swards.

Forbs

Full analyses of treatment effects were possible for only some of the commoner species described below. Data for the remainder are described as far as possible but were too few for rigorous analysis.

Leucanthemum vulgare This species was much the commonest forb on the sown plots throughout the experiment. Although it was sown at a relatively high density it also established extremely well from seed. It increased between 1988 and 1991, with a slight overall drop recorded in 1992.

The temporal trends for individual treatments showed that this drop was confined to treatments that were unmanaged, where frequencies dropped from 87 to 57%. Planned comparisons following analysis of variance also showed a significant effect of leaving treatments uncut in July 1992 ($F_{(1,15)}=12.87$, $P<0.01$). We were unable to detect other consistent and significant effects of treatment although, as discussed above, our recording method was insensitive to changes in density in very abundant species.

L. vulgare colonised the old field margins at greater frequency than any other forb in the seed mixture (Table 6.6). Although few plants established in 1988, numbers increased substantially over the next two years. This increase was likely to have resulted both from dormant seeds from the original sowing and from seed shed from the plants established on the new margins. We were unable to detect any consistent effects of treatment but in September 1990 frequencies on the old margins were sufficiently high for unplanned comparisons to show a significant effect of cutting in summer. This effect requires confirmation in future years but it is possible that it reflects greater seed rain from the new margins in plots where seed production was not diminished by mowing.

Grime *et al* (1988) suggest that this species does best on soils of low fertility where competition from dominants is restricted by, for example, mowing for hay. On the very high fertility soils of the Wytham field margins this species proved to be an extremely successful competitor for four years, even in the absence of any mowing. The reasons for the delay in its decline in uncut treatments until 1992 are unclear. Although mowing in summer removed most of the annual seed production it had no detectable effect on the rate of increase in frequency. There are two likely reasons for this. First *L. vulgare* has a persistent seed bank and so seed from the original sowing may continue to germinate for a number of years. Second, this species flowered earlier than many of the forbs in the mixture and regrowth and flowering following cutting was more prolific. Its seed production is prolific (Howarth & Williams 1968) and so even limited re-flowering may substantially augment the seed bank.

Summary This species was the most successful forbaceous component of our seed mixture. Its established extremely well from seed and it increased over a four-year period, spreading into the old field margins and into adjacent unsown plots. It flowered well even in the year of establishment, following a spring sowing. Its relatively early flowering time not only made it the predominant nectar resource on the field margins in June and early July (Chapters 9 & 10) but also allowed some re-flowering following mowing in late June. This species should not be sown into existing swards on fertile soils but can be expected progressively to colonise grassland adjoining seeded areas.

Knautia arvensis *K. arvensis* was relatively uncommon on the new margins. Its frequency fell slightly between 1988 and 1989. It increased again, to slightly above its 1988 level, in 1992, probably as a result of seedling establishment (Table 6.4). Despite its relatively low frequency in the swards, its rank in relation to sowing density shows that its performance was better than average in 1989 and 1990 (Table 6.5).

Analyses of variance and examination of trends in abundance in the different treatments provided little clear evidence that *K. arvensis* was affected by our management regimes. There was slight but not statistically significant evidence that it tended to increase in treatments that were left uncut in summer, while remaining at the levels at which it established in 1988 in summer cut treatments. Summer cutting prevents seed return in this species, which has a largely transient seed bank (Grime *et al* 1988) and so it seems likely that an increase in treatments that were left uncut in summer resulted from the establishment of seedling progeny of plants that established from the 1988 sowing. Further data comprising larger sample sizes, are required to confirm this trend.

On the old margins very little *K. arvensis* established from the original sowing in 1988 and there was no subsequent increase in its frequency (Table 6.6).

Summary Amongst the sown forbs *K. arvensis* established moderately well from seed. It can be expected to increase gradually in swards in which it is allowed to flower and seed. Much of the interest in including this species in seed mixtures results from the value of its flowers for amenity and for nectar for insects and are not realised when it is cut in summer. However, where the intention is to use summer cutting for a few years (e.g. to control annual weeds) or on an occasional basis (e.g. to provide variety in turf height) our data suggest that it is still likely to be worth including this species in seed mixtures because it persists under this regime and its benefits can still be realised when the regime is relaxed. It should not be sown into existing swards.

Centaurea nigra *C. nigra* was one of the commoner forbs on the new margins and it established relatively well from seed. Its frequency fell slightly between 1988 and 1989, probably as a result of death of some seedlings, but it increased steadily over the next three years.

The increase in plots that were cut in summer was much smaller than in those left uncut in summer. The rank orders of the treatment means and unplanned comparisons following analyses of variance also suggested that this species was more abundant in treatments left uncut in summer from June 1990 onwards. This species has a largely transient seed bank (Grime *et al* 1988) and vegetative spread is both slow and limited in extent (Marsden-Jones & Turrill 1954). Summer cutting reduced substantially its potential seed return and so its increase in swards left uncut in summer must be attributed largely to seed produced by the plants that established in 1988.

Very little *C. nigra* established in the old margins in 1988 (Table 6.6). The plants that established at that time persisted but there had been no increase in frequency by 1990.

Summary This species, like *K. arvensis*, performed relatively well in our seed mixture in relation to its sowing density. In sown swards, on fertile soils, it can be expected to increase progressively, particularly where swards are left uncut in summer. Like *K. arvensis* it persists even in summer-cut swards and so is likely to be worth including in mixtures where the intention is to cut in summer for a limited period or on an occasional basis. It should not be sown into existing perennial swards.

***Torilis japonica* (Houtt.) DC. Upright Hedge-parsley** On the new margins *T. japonica* established at relatively low frequencies in the sward (Table 6.4) although its abundance and establishment from seed were middle ranking (Table 6.5). It increased steadily over the next four years.

This increase was restricted to treatments that were not cut in summer. In treatments that were cut in summer it persisted at very low levels. Analyses of variance, with unplanned comparisons of means, showed that treatments cut in summer (cut in summer only and cut in spring+summer) had significantly lower frequencies of *T. japonica* than treatments left uncut at this time (uncut and cut in spring+autumn) from September 1989 onwards.

Although very few plants established on the old margins in 1988, numbers increased substantially in subsequent years, and constituted the largest increase in any forb except *L. vulgare* (Table 6.6). The data for the old margins were too few for formal analysis but, as on the new margins, frequencies were conspicuously higher in treatments that were left uncut in summer than in those that were cut.

Although typical of perennial-dominated hedgerow and woodland edge floras, *T. japonica* is a biennial or winter annual. It has a transient seed bank and so its persistence depends on annual production of seeds. Its inability to increase in our summer-cut swards is thus attributable to the majority of its flower heads being removed by mowing (it flowers from July onwards) and therefore preventing seed return. Some flowering on regrowth following summer mowing was observed, and this is likely to have allowed the species to persist at low frequencies under this regime.

Summary *T. japonica* was a moderately successful component of the wild flower seed mixture. However, it should not be included in wild flower seed mixtures where the intention is to mow during the summer months. It is unlikely to be cost-effective to sow it into existing swards but it can be expected to colonise them from nearby sown swards.

***Prunella vulgaris* L. Selfheal** *P. vulgaris* established relatively badly from seed. There was some evidence that its frequency dropped slightly in 1989 as a result of seedling mortality, but it then increased steadily. This increase was likely to have resulted from both vegetative spread and regeneration from seed produced by the plants that first flowered in 1989. There is debate about whether this species forms any persistent seed bank (see Winn 1985 *vs* Roberts 1986) and the relative importance of regeneration by seed and by vegetative spread varies considerably between populations (Grime *et al* 1988).

Because this species was relatively uncommon we were unable to detect significant effects of treatment. However, at every monitoring round from June 1990 onwards, treatments cut twice had higher frequencies of *P. vulgaris* than those cut once or not at all. The comparison between treatments cut twice and those cut once approached significance in June 1992 ($P<0.06$). This trend requires confirmation using larger sample sizes but is consistent with the commonly reported association of this species with short-grazed turf and lawns. Although *P. vulgaris* increased in frequency only in treatments cut twice, it persisted at low densities in treatments that were uncut or cut once.

On the old margins *P. vulgaris* established at extremely low frequency in 1988 but increased slowly over the next two years (Table 6.6).

Summary Although *P. vulgaris* established relatively poorly from seed in our mixture, its progressive increase over a four year period suggests that it is worth considering for inclusion in mixtures for fertile soils when the intention is to mow at least twice a year.

***Galium verum* L. Lady's Bedstraw** *G. verum* was the second most frequently recorded forb in the sown swards in 1988 and also established relatively well from seed (Tables 6.4 and 6.5). Its frequency declined during 1988 to a low point early in 1989, as a result of seedling mortality, but then increased again. It then declined again between 1991 and 1992 but further year's data are required to assess the significance of this decline. The first increase is likely to have resulted from stoloniferous extension and possibly also from germination of seeds from the original sowing (Grime *et al* 1988 'suspect' that this species has a persistent seed bank). This species did not flower until 1990 and seed set is thought to be poor (Grime *et al* 1988). Increase as a result of regeneration by seed of the established plants is therefore likely to be slow.

G. verum occurred at higher frequencies in treatments cut in spring and autumn than in those cut in spring and summer from June 1989 onwards. This effect was significant in June in 1989 and in 1990 ($F_{(1,15)}=13.26$, $P<0.01$ and $F_{(1,15)}=5.86$, $P<0.05$, respectively). It was also more abundant in treatments cut twice than in those cut once. This effect was significant in September 1989 ($F_{(1,15)}=6.03$, $P<0.05$) and in June 1990 ($F_{(1,15)}=6.03$, $P<0.05$). We were unable to distinguish between the effects of cutting once and of leaving swards uncut. In both of these treatments the population remained stable between 1990 and 1992. *G. verum* is relatively low growing and cutting twice a year appears to promote its increase by reducing competition from taller-growing species. The greater effectiveness of cutting in autumn than in summer is likely to have resulted from opportunities for this winter-green species to increase in the low competitive environment of autumn-cut swards during the winter months. It is also possible that autumn cutting favours germination and establishment but no information is available on the phenology of its germination.

On the old margins *G. verum* established at low frequency in 1988 and had increased only slightly by 1990 (Table 6.6).

Summary *G. verum* established very well from seed relative to most other forbs although, in the highly competitive environment on our fertile soils it then declined from its establishment levels. Although it persisted at low frequencies in unmanaged swards it should mainly be considered for inclusion in seed mixtures where the intention is to mow twice annually, and can be expected to reach its highest frequencies where swards are cut in autumn.

***Clinopodium vulgare* L. Wild Basil** *C. vulgare* was the sixth most abundant forb in 1988 but its frequency halved between 1990 and 1991. Its establishment in relation to its sowing density was very poor. Its frequency increased again in 1992, probably as a result of germination of seeds produced by the plants that established from the original sowing.

C. vulgare declined in all treatments but by 1992 it was nearly twice as abundant in spring+autumn cut treatments as in any other treatment. Further data are needed to confirm the statistical significance of this effect and to see whether or not the 1992 increase was sustained.

It established at very low frequency in the old margins but had doubled in frequency there by 1990 (Table 6.6).

Summary The results for *C. vulgare* to-date should be treated cautiously but suggest that, despite its relatively successful establishment, it is rarely likely to be a cost-effective component of wild flower seed mixtures on very fertile soils.

Tragopogon pratensis *T. pratensis* was sown at low density and was a minor component of the sown swards, although its density had increased slightly by 1992 (Table 6.4). It was likely to have been slightly under-recorded, particularly at the seedling stage, because of the grass-like morphology of its leaves. Despite the fact that it ranked only eighteenth in recorded frequency, it ranked as the fifth and fourth best establishing species overall in 1989 and 1990 respectively when sown density was taken into account (Table 6.5). This species is a short-lived and often monocarpic perennial. It first flowered in 1989 and so the plants present in 1992 were likely to have been the progeny of the plants that germinated in 1988.

There were too few data to detect any differences in abundance between treatments. Larger sample sizes are required to assess treatment effects.

No *T. pratensis* established in the permanent quadrats on the old margins in 1988 but a few plants had appeared by 1990 (Table 6.6). These were likely to have resulted from seed dispersed from plants that established in the new margins rather than from the 1988 sowing: this species is thought to have a predominantly annual seed bank. Its seed dispersal distances are potentially greater than those of most of the other species in the mixture and so its potential for longer-distance colonisation is likely to be greater. *T. pratensis* plants were conspicuous on some unsown plots in the areas adjacent to sown plots. Further years' data are needed to ascertain whether the efficient dispersal of this species will enable it to establish effectively in unsown areas of the field margins.

Summary Our data are insufficient to assess the effects of management on *T. pratensis* but suggest that it establishes well and can subsequently reproduce successfully by seed in swards on fertile soils. It should not be sown into existing swards but is likely gradually to colonise grassland in the vicinity of sown swards.

***Centaurea scabiosa* L. Greater Knapweed** This species established at low frequency on the new margins in 1988, declined during the following two years and was not recorded in the permanent quadrats in either 1991 or 1992 (Table 6.4). Its sowing density was low and although it was the twenty-first most abundant species, its rank in abundance in relation to sowing density was fifteenth (Table 6.5).

C. scabiosa was never recorded in the old margins quadrats (Table 6.6).

C. scabiosa is a spring germinator, the seed of which probably remain viable for only one year (Grime *et al* 1988). Sown seeds that failed to germinate in spring 1988 would thus be likely to have lost viability. The decrease in frequency between 1988 and 1989 as a result of seedling mortality could not have been compensated for by new germination. Although this species flowered on the margins in 1989, either seed production or seedling establishment was evidently insufficient to reverse this decline. Dickie (1977) reported very low seed production in this species in chalk grassland as a result of poor seed set and insect predation.

Summary Although *C. scabiosa* was lost from the permanent quadrats by the fourth year after sowing, it remained in the new margin swards at low frequency. By 1992 the plants were large and prominent and contributed to the interest of the sward. It is possible that these plants will provide foci for the spread of this species in the swards over the next few years. In general, however, our data suggest that in many circumstances *C. nigra* is likely to be a more reliable constituent of wild flower seed mixtures for fertile soils than *C. scabiosa*, which is generally a constituent of low-fertility calcareous grassland.

***Ranunculus bulbosus* L. Bulbous Buttercup** Both *Ranunculus* species in the seed mixture established better than the 1988 data suggest because at the seedling stage they were often identified only to the genus. *R. bulbosus* was at least the third most abundant forb in the sown swards in 1988 and 1989 (Table 6.4) and established very well in relation to its sowing density (Table 6.5). It declined between 1989 and 1990 and our data suggest that it had disappeared from the permanent quadrats by 1991. However, it is likely that this species was under-recorded rather than lost in 1991 and 1992. Between 1988 and 1990 we recorded maximum abundances of *R. bulbosus* in March but, the data for these two years were collected in July (above). This species aestivates as a below-ground 'corm' from mid-July until autumn (Harper 1957).

R. bulbosus established on the old margins at low frequency but had increased slightly by 1990 (Table 6.6). There was some evidence of treatment effects on this species but further data are needed to confirm them. During 1989 it was consistently most abundant in autumn-cut treatments and this was reflected in a significant difference between the spring+autumn and spring+summer cutting treatments in June ($F_{(1,15)}=10.46$, $P<0.01$). This species germinates in autumn (Harper 1957) and so it is likely that most of the sown seed germinated in autumn 1988. Mowing that autumn would have created more gaps suitable for germination than were available in other treatments, resulting in higher frequencies in autumn-cut treatments in 1989. There was also some slight evidence that *R. bulbosus* was more abundant when cut than when left uncut. Throughout 1990 its abundance was lowest in the uncut treatment and in June this effect approached significance ($F_{(1,15)}=3.31$, $P=0.089$). A preference for more frequent mowing is consistent with the finding of Grime *et al* (1988) that this species is most abundant in grassland where shading is prevented by heavy grazing or by low fertility.

Summary Our results suggest that *R. bulbosus* performs well in wild flower seed mixtures on fertile soils but confirmation is needed of the trend in its abundance after the third season. It likely that it would establish better from autumn than from spring sowing and that it should not be included in mixtures for swards that are to be left unmanaged.

Ranunculus acris *R. acris* was less abundant in the swards in 1989 than *R. bulbosus* and it established very badly in relation to its sowing density (Tables 6.4 and 6.5). Like *R. bulbosus* it declined between 1989 and 1990 and was not recorded in the quadrats in 1991 or 1992. Again, however, the latter result is unlikely to be a true reflection of this species status because we recorded maximum abundances in March, with substantial die-down after mid-summer. Further years' recording in spring are required before conclusions can be drawn about the trends in this species abundance in the sown swards.

Like *R. bulbosus, R. acris* established and persisted at low frequency on the old margins.

Despite its relatively low frequencies we were able to detect consistent and significant effects of our experimental treatments on this species abundance. Planned comparisons showed that it was consistently more abundant in treatments that were cut than in those that were left uncut. There was also some evidence that it was more abundant in treatments that were cut twice than in those cut once. The former effect was either significant or almost significant from April 1989 onwards (Apr. 1989; $F_{(1,15)}=4.31$, $P=0.056$: June 1989 $F_{(1,15)}=8.59$, $P<0.01$: Jan. 1990; $F_{(1,15)}=3.6$, $P=0.077$: Apr. 1990; $F_{(1,15)}=6.24$, $P<0.05$: June 1990; $F_{(1,15)}=9.55$, $P<0.01$). The latter effect was significant in January 1990 ($F_{(1,15)}=7.21$, $P<0.05$), was almost significant in April 1990 ($F_{(1,15)}=4.49$, $P=0.051$) but was not significant in June 1990.

Summary *R. acris* is typical of grazed or mown grassland and it is clear that it is only worth sowing in wild flower seed mixtures for fertile soils where the intention is to mow, preferably at least twice a year. Although its establishment was poor, it can be a prominent component in the sward even at relatively low densities and may often be desirable where the intention in sowing is to re-create swards resembling traditional hay meadows. Conversely, where there is a likelihood of swards containing this species being grazed, for example on the margins of fields in an arable-grass rotation, this species should not be included. It is unpalatable to, and avoided by, stock and is an anathema to many farmers who believe that it is toxic to cattle (it contains the toxin protoanemonin: see Cooper & Johnson 1984).

Hypericum perforatum* and *H. hirsutum These two species had not only the lowest frequencies amongst the sown species but also the poorest establishment in relation to sowing density (Tables 6.4 and 6.5). *H. perforatum* was present at low but increasing frequency from 1988 to 1990 but was not recorded in the permanent quadrats in 1991 or 1992. *H. hirsutum* was not recorded in permanent quadrats until 1990 and, like *H. perforatum*, was not recorded in 1991 or 1992. Both of these species form persistent seed banks and so germination of the original sown seeds over a number of years is likely to account for increase in numbers in 1989 and 1990.

H. perforatum was recorded in quadrats on the old margins at extremely low frequency in 1989 and 1990 but *H. hirsutum* was never recorded in old margin quadrats.

Grime *et al*(1988) suggest that both *Hypericum* species are spring germinators and that germination is dependent on the existence of relatively large areas of bare ground. Although this does not explain the poor establishment following sowing in spring 1988, when large areas of bare ground were available, it may explain the lack of recruitment in subsequent years, when dense vegetation growth would have restricted germination sites. They further suggest that, although these species are tall-growing, they are likely to thrive only on soils where infertility restricts competition from other tall, clonal species. It seems likely that these species were unable to compete successfully in the highly productive swards on the field margins.

Summary Both *H. perforatum* and *H. hirsutum* performed extremely badly in the sown swards. This effect was so extreme and consistent that neither species can be recommended for inclusion in mixtures for use on high fertility arable soils.

Silene latifolia* subsp *alba *S. latifolia* was uncommon in the sown swards and declined from 1988 to 1990. It was not recorded in the permanent quadrats in 1991 or 1992 (Table 6.4). Its also established very badly in relation to its sowing density (Table 6.5). There were too few data to detect any effects of the experimental treatments on abundance. *S. latifolia* was never recorded in the quadrats on the old margins (Table 6.6).

It is unclear why this species established so badly in the sown plots. On some unsown plots, where it was present in the seed bank (it has a persistent seed bank), it established well and was a conspicuous flowering component of the sward by 1989. It is likely that it was to some extent excluded by the very dense sown swards although this does not account for the low frequency of seedlings recorded in 1988.

***Silene vulgaris* (Moench) Gaertner** *S. vulgaris* was extremely infrequently recorded in the sown plots on the new margins and also established very badly in relation to its sowing density. It declined from 1988 to 1990 and was not recorded in 1991 or 1992 (Tables 6.4 and 6.5). The data were too few to detect any effects of experimental treatment and it was never recorded on the old margins (Table 6.6). Again, it seems likely that this species was excluded by competition from other components of the sown swards on these productive agricultural soils, although it grew amongst dense, fine grasses on road verges adjacent to the field margins.

Summary Neither *Silene* species would appear to be reliable candidates for inclusion in wild flower seed mixtures on productive soils although they may fare better on thin, calcareous soils.

***Leontodon hispidus* L. Rough Hawkbit** *L. hispidus* was infrequent in the swards but ranked tenth overall in relation to its sowing density (Table 6.4). However, despite this relatively good establishment, it declined from 1988 to 1990 and was not recorded in the quadrats in 1991 or 1992 (Table 6.5). It occurred at very low frequency in the old margins in 1988 but was not recorded there on any subsequent date.

The data were too few to analyze for treatment effects but *L. hispidus* had disappeared completely from quadrats in uncut plots by 1990 while it remained at low frequency in cut plots. Larger sample sizes are required to verify this effect. Grime *et al* (1988) suggest that this species is suppressed by larger species in rank vegetation and it is likely that its poor persistence on the field margins resulted from competition from the sward on these very productive soils.

Summary Our data should be treated with caution but suggest that *L. hispidus* is unlikely to persist in sown swards on very fertile soils. It may, however, be worth consideration as a component for mown swards on less fertile soils.

***Primula veris* L. Cowslip** *P. veris* established at low frequency on sown plots and its establishment was very poor relative to its sowing density. It declined slightly in the permanent quadrats between 1989 and 1990. However, between 1991 and 1992, when we recorded the numbers of plants flowering in entire sown plots, rather than in the quadrats (Chapter 2.2.5), the numbers of plants almost doubled and the number of plots on which it was recorded increased from 14 to 21.

P. veris usually germinates either as fresh seed or in spring, following vernalization. However, we first recorded seedlings in summer 1988, following a spring sowing of seed harvested the previous year. Few additional plants were recorded the following spring and summer but it seems likely that the much denser vegetation at that stage may have inhibited germination or resulted in mortality of seedlings before they were recorded. *P. veris* flowered for the first time on the new margins in 1990. In that year, however, it flowered on only two plots, one of which was immediately adjacent to, and the other separated by a track from, ditch banks with natural *P. veris* populations. We were thus unable to tell whether the flowering plants originated from the seed that we sowed or from the field boundary populations. It is possible that plants from the latter source were present as vernalised seed in the soil in spring 1988 and so were able to germinate earlier than many of the sown seeds. By 1991 *P. veris* flowered on the new margins of many plots. Some of the additional plants flowering in 1992 may have been the progeny of plants that flowered in 1991, but the increase in the numbers of plots on which plants flowered suggests that many of the plants must have originated from dormant seed from the original sowing.

We were unable to detect any significant effects of treatment on the numbers of *P. veris* plants flowering in the plots in either 1991 or 1992. Although the mean values for each treatment type in 1992 suggest that the number of plants increased as the cutting frequency increased, the variation between plots remained very large (Table 6.7). The numbers of flowering plants per plot ranged from zero to 16 in 1992. The increase in density between 1991 and 1992 also suggests the same effect of cutting but analysis of variance of the percentage change again failed to reveal significant results. Further increase in abundance of this species is likely to reduce the variance sufficiently to yield significant results.

P. veris was not recorded on the old margins in the routinely monitored blocks 1 to 6 of the experiment until 1990 (Table 6.6). In block 8, however, which was not recorded systematically (see Chapter 2.2.5), *P. veris* occurred at high density on the old margin adjacent to a ditch bank population. The density on the ditch bank and field margin increased substantially, to form a large and conspicuous colony during the course of the experiment, probably as a result of exclusion of herbicides.

Summary Our results show that, once established, *P. veris* can thrive on fertile soils adjacent to intensively managed arable crops, where care is taken to exclude agrochemical drift. It is likely to be worth including in seed mixtures for fertile soils where the intention is to create a permanent sward. Its extremely slow establishment makes it an unsuitable for inclusion in mixtures for semi-permanent grassland (e.g. five-year set-aside). We have some evidence that it is likely to increase more rapidly when cut twice a year than when cut once or not at all, but this requires confirmation with future years' data.

6.3 Discussion

6.3.1 CONCLUSIONS AND PRACTICAL IMPLICATIONS

The wild flower seed mixture used on our experimental plots was sown into a well prepared seed bed (Chapter 2.2.1.). Although this practise is recommended by most of the major suppliers of wild flower seed, failure to follow it is a common cause of poor results from sowing. Our results show clearly that it is never likely to be cost effective to sow wild flower seed mixtures into existing swards or into weedy stubbles. None of the species sown established in the old margins in 1988 at frequencies of more than 4% of those achieved on the new margins. Several sown species were never recorded on the old margins. Even three years after sowing only four species had reached frequencies greater than 10% on the old margins and much of the increase was attributable to seed shed from plants that had established and flowered in the adjacent new margins, rather than from the original sowing. Not only are these frequencies an extremely poor return for the sowing density but we showed in Chapter 5 that they are also inadequate to have any measurable effect on weed control.

We have also shown that, by using common species typical of local semi-natural grasslands, sown into a well prepared seed bed and protected by simple and inexpensive means from agrochemical drift, many species of wild flowers can be established immediately adjacent to intensively managed arable crops. Five years after they were sown, although relatively species-poor, the swards were an attractive imitation of semi-natural grassland, and on some treatments this effect was achieved within two to three years.

The mean species richness of the sown component of the sown swards showed no sign of diminishing after five years although a few species had declined to very low levels. In such highly fertile situations it might be predicted that 'aggressive' perennials might invade the swards and result in loss of diversity. In Chapter 5 we showed that *Elymus repens* increased much more slowly in sown than in naturally regenerating swards and that *Cirsium arvense* appeared to stop increasing in two year old sown swards. Although analyses of other aggressive perennials are required, these results suggest that decline in sown species richness from this cause is likely to be slow. On these time-scales other factors may have opposing influences on sown species richness. Thus, for example, decline in soil fertility on the margins as a result of fertiliser exclusion, together with continuity of mowing and hay removal, may reduce the competitive advantage of invading perennials. It is also possible that forbaceous species richness may increase over the next few years as a result of increased seed production. The time-scale of our monitoring was short in which to record the effects of seedling establishment from plants from the original sowing, many of which were not of sufficient size to flower prolifically until 1990 or 1991. Because we have no reliable grounds for predicting the future maintenance of species richness of the sown swards it is imperative that it is measured. This information is essential if wild flower seeding is to be recommended as a means of establishing permanent perennial swards on high fertility soils.

Although all of the sown species occurred in the local area there were large differences in how well they established. Many factors are likely to have contributed to these differences. The numbers germinating are affected by innate differences in dormancy and germination requirements, which are in turn modified by local soil conditions and by temperature (viability should not be a problem in seed sold commercially). The relative abundance of different species is also likely to be influenced by their germination phenology in relation to the timing of sowing. Thus, for example, species that germinate in spring are likely to be at a competitive disadvantage in autumn-sown swards. The precise composition of the seed mixture influences the abundance of each of its components by influencing the competitive environment in which they establish. Small-scale variation in soil conditions also alters the relative abundance of some species: for example we suggested that soils conditions were responsible for the significant differences in the abundance of *Hordeum secalinum* on the margins of different fields.

A number of the forbaceous species in our seed mixture established very badly from seed and in many species seedling mortality during the first season was high. One possible explanation for this was damage by molluscs. Slugs and snails were extremely abundant on the field margins and in the crops, where levels were well above the thresholds for severe commercial damage, in spring 1988 and during the 1988/1989 winter. Molluscicides were used to control the outbreak in the crops. Work undertaken as part of an undergraduate research project in 1990 provided some circumstantial support for this explanation (Sitch 1991). Laboratory feeding preference experiments and a field experiment in which plants of four species of wild flowers were planted into sown plots, both with and without barriers to protect them from grazing by molluscs, suggested that levels of grazing damage were inversely related to abundance in the swards. Thus, seedlings of *Prunella vulgaris* and *Silene latifolia* subsp *alba* tended to be grazed more by molluscs than *Tragopogon pratensis*, while *Leucanthemum vulgare* was grazed least. The common occurrence of pest-level outbreaks of molluscs in arable fields together with this evidence, suggests that seedlings on field margins could suffer a high level of grazing damage. Further detailed work is required to investigate the potential role of molluscs in determining sward composition in wild flower seed mixtures. It has important implications for the choice of species for use on arable field margins.

A second possible explanation for the relatively poor performance of many forbs was that they were competitively excluded by the grass species in the mixture. We showed in Chapter 4 that the sown swards effectively excluded or restricted the frequency of naturally regenerating species. However, the sown forbs were likely to be relatively less disadvantaged than these species because most germinated at the same time as the sown grasses. Many of the sown forbs were also species adapted to germinating in small gaps in perennial grassland. Although more detailed work on the causes of establishment failure and decline of many of the forbs should help to elucidate the role of competition from the sward, a dense sward base is not a feature that should be readily sacrificed for greater forb frequency on field margins. Marshall (1988) showed that the use of the growth retardant mefluidide restricts the growth of grasses resulting in an increase in the numbers of annuals and biennials in a pasture sward. It has been recommended for use on wild flower seed mixtures on field margins (Nowakowski & Marshall 1991) to promote forb species richness but the cost of this is inevitably a reduction in the effectiveness of weed control. The weed control properties of wild flower seed mixtures are of critical importance in determining their acceptability to farmers.

Because the sorts of factors discussed above ensure that the relative abundance of species establishing from wild flower seed mixtures will vary from site to site, and mixture to mixture, it is difficult to predict with precision the success of a seed mixture or of its components in a given situation. However, the data now available from our own work and that of Wells *et al* (1986) on the performance of species in wild flower-seeded swards, combined with autecological information from other sources, give a reasonable basis for evaluating the chances of successful establishment.

The effects of management on the subsequent abundance of species establishing from wild flower seed mixtures are equally critical in determining success but are likely to be much more consistent and therefore predictable. We have shown in this chapter how the timing and frequency of mowing affects the abundance of many species. For example, some species are lost from swards that are never mown while others increase under these conditions but decline in swards that are mown twice a year. Because the cost of failure of wild flower seed mixtures is high, this information should always be a vital element in deciding which species to include. If used in conjunction with information on establishment probabilities and attractiveness to invertebrates, together with judgements on visual attractiveness and nature conservation value, wild flower seed mixtures should become a more cost-effective option for field margin restoration.

While this information helps to determine which species are suitable for inclusion in a seed mixture, the numbers of suitable species included must depend on the objectives for the sward. Although our mixture was complex, because we were interested in the responses to management of a large range of species, very simple, and hence inexpensive, mixtures are usually likely to most suitable for use on field margins. Any simple mixture of grasses that will rapidly form a dense sward base is likely to be effective in fulfilling the requirement that the sward excludes annual weeds (Chapter 5). Conventional agricultural grass leys with *Lolium perenne* L. Rye-grass as the major constituent, which are available very cheaply to farmers, may be as effective in excluding annual weeds as mixtures containing fescues and other fine grasses but research is needed to evaluate this (our species-rich ley which was compared with a conventional ley in the wide margins experiment did not contain red fescues, Chapter 11). Fine grass mixtures are preferable for nature conservation and for their value to wildlife. On fertile soils, they are also likely to be less productive and therefore require less intensive management (see Chapter 11).

Addition of even one forb species to a grass mixture increases disproportionately its visual attractiveness and its value to invertebrates. *Leucanthemum vulgare*, for example, is inexpensive, establishes reliably, flowers in the year of establishment, has enormous visual appeal and provides both vertical structure in the sward and abundant nectar (favouring spiders (Chapter 8) and butterflies (Chapters 9 & 10) respectively). Addition of a later flowering species, such as *Centaurea nigra* or *Knautia arvensis*, would provide continuity of visual appeal and of nectar. We show in Chapter 9 that continuity of nectar supply is vital in supporting breeding populations of many relatively immobile species of butterflies.

With the exception of atypical annual species, such as *Torilis japonica*, which are adapted to survive in predominantly perennial grassland communities, annual species should not normally be included in wild flower seed mixtures designed for permanent grass field margins (with the possible exception of 'nurse' species such as *Lolium multiflorum* Lam. Italian Rye-grass). Inclusion of annuals is sometimes recommended to give colourful results in the establishment year (Nowakowski & Marshall 1991). However, if guidelines are followed and sward establishment is rapid, such species should be largely excluded by the second season (Chapter 5). They thus give a very short-lived return for the expenditure. Inclusion of species like *Leucanthemum vulgare*, however, can give results in the first season as well as a much more sustained return on the investment.

The benefits to both agricultural weed management, and to nature conservation and amenity, of using wild flower seed mixtures to create grassy perennial field margins are enormous. A substantial body of research information is now available to ensure that the species included in such mixtures can be selected to give a very high probability of successful establishment and therefore of cost-effective investment. However, even simple wild flower seed mixtures are inevitably slightly more expensive than conventional agricultural grass mixtures. Extension of their use to farms other than those managed by committed conservationists, will depend on the introduction of a subsidy mechanism.

6.3.2 FUTURE ANALYSES

In addition to the analyses presented in this chapter of frequencies at specific points in time, additional information on the effects of treatment on the sown species will be sought by analyses of changes in frequency. Analyses of the information on the presence of seedlings (Chapter 2.2.5), and of the locations of new records in the quadrats (using the individual cell records), will provide further information on the species' patterns and modes of increase and on the causes of decline.

6.3.3 FUTURE MONITORING

The data presented in this chapter show clearly that the species composition of the wild flower-seeded swards was changing rapidly even five-years after sowing. Continued monitoring is required to answer two outstanding questions of critical importance to the provision of reliable advice on the use of wild flower seed mixtures on arable land. First, we need to know whether the diversity of sown species will be sustained in the medium term or whether aggressive perennials will invade and exclude the sown species. Secondly, further information is needed on the responses of the sown species to competition and to management. This experiment provides a unique opportunity for rigorous and realistic assessment of the effects of management on many species commonly included in wild flower seed mixtures.

The information needed to answer these questions can in part be provided by continuing the routine monitoring of permanent quadrats. As recommended in Chapter 4, a lower frequency a monitoring (e.g. once every two to three years) would suffice at this stage to give a broad picture of trends in abundance. However, we recommend that for some of the rarer species in the wild flower seed mixture, for which permanent quadrat data were insufficient to detect treatment effects, counts of plants in whole plots should be undertaken. In order not to waste the information on these species that is available from the experiment, this monitoring should be undertaken within the next two years, preferably at points in the season when maximum frequencies are likely to be detected. Monitoring density in this way has the additional advantage that a more precise quantitative relationship can be derived between sowing density and density in the sward.

6.3.4 IMPLICATIONS FOR SET-ASIDE MANAGEMENT

Most of the conclusions in this chapter are as applicable to the management of non-rotational set-aside as to field margins. The potential benefits of wild flower seed mixtures for both weed control and wildlife enhancement on set-aside are in some senses greater even than on field margins because the probability of annual weed control by the development of an acceptable, naturally regenerated, perennial sward is lower (Chapter 5). Investment in simple mixtures (containing eg. two forbs), chosen and sown according to our guidelines, should be considered for five year set-aside, while more complex mixtures become more cost-effective over longer periods.

Further information on the use of wild flower seed mixtures on set-aside is provided by our wide margins experiment, described in Chapter 11.

Table 6.1 Mean numbers of sown species in the new margins of sown plots in 1989 and 1990

Treatment	Date	
	June 1989	June 1990
Cut in spring and autumn	12.4 (1.09)	11.15 (1.08)
Cut in spring and summer	10.8 (1.04)	9.93 (1.04)
Cut in summer only	10.3 (1.01)	9.35 (1.02)
Uncut	10.5 (1.02)	9.90 (1.04)
Min. sig. diff.	0.08	0.10

Means are of six plots and are back-transformed from log-transformed data. Numbers in parentheses are log-transformed data (to 2 d.p.). The M.S.D. applies to the transformed data.

Table 6.2 Mean numbers of sown forbs per quadrat in the new margin plots from 1989 to 1992

Treatment	Date			
	June 1989	June 1990	July 1991	July 1992
Cut in spring and autumn	6.98 (0.85)	6.67 (0.82)	7.10 (0.85)	7.41 (0.87)
Cut in spring and summer	4.92 (0.69)	5.05 (0.70)	5.48 (0.74)	5.17 (0.72)
Cut in summer only	4.50 (0.65)	4.54 (0.66)	4.86 (0.69)	4.20 (0.62)
Uncut	4.87 (0.69)	5.29 (0.72)	4.90 (0.69)	4.90 (0.69)
Min. sig. diff.	0.17	0.2	0.20	0.19

Means are back-transformed from log-transformed data. Numbers in parentheses are log-transformed data (to 2 d.p.). The M.S.D. applies to the transformed data.

Table 6.3 Mean numbers of sown species in the old margins of sown plots in 1989 and 1990

Treatment	Date	
	June 1989	June 1990
Cut in spring and autumn	1.97 (0.30)	2.13 (0.50)
Cut in spring and summer	1.75 (0.24)	1.79 (0.45)
Cut in summer only	2.54 (0.40)	2.76 (0.58)
Uncut	1.61 (0.21)	1.95 (0.47)
Min. sig. diff.	0.339	0.403

Means are back-transformed from log-transformed data. Numbers in parentheses are log-transformed data (to 2 d.p.). The M.S.D. applies to the transformed data.

Table 6.4 Changes in the relative frequency of species in the wild flower seed mixture on the new margins

Species	Year						
	1988	1989	1990	1991	1992	Change[2] from	
						88-90	90-92
Grasses:							
Festuca rubra	97.6	99.7	99.5	-	-	+1.9	
Phleum bertolonii	90.1	95.7	95.8	-	-	+5.7	
Cynosurus cristatus	98.4	99.7	91.0	-	-	-7.4	
Trisetum flavescens	74.7	90.5	87.0	-	-	+12.3	
Poa pratensis	34.5	70.3	84.2	-	-	+49.6	
Hordeum secalinum	11.3	30.7	34.9	-	-	+23.6	
Forbs:							
Leucanthemum vulgare	71.2	74.2	79.2	86.5	82.3	+8.0	+3.1
Galium verum	25.9	17.9	19.3	20.5	16.8	-6.6	-2.5
Centaurea nigra	18.1	15.6	16.7	19.8	23.6	-1.4	+6.9
Ranunculus bulbosus[1]	17.2	17.7	12.3	-	-	-4.9	-[3]
Clinopodium vulgare	16.1	12.3	8.0	8.5	10.9	-8.1	+2.9
Knautia arvensis	7.6	5.6	6.4	5.7	11.1	-1.2	+4.7
Torilis japonica	6.9	7.1	11.8	11.3	10.6	+4.9	-1.2
Prunella vulgaris	5.7	5.2	6.1	7.1	10.4	+0.4	+4.3
Ranunculus acris[1]	5.0	14.4	9.0	-	-	+4.0	-[3]
Silene latifolia alba	3.8	1.9	1.7	0	0	-2.1	-1.7
Leontodon hispidus	3.6	2.8	1.6	0	0	-2.0	-1.7
Centaurea scabiosa	2.3	0.7	0.7	0	0	-1.6	-0.7
Tragopogon pratensis	1.7	2.6	3.3	1.2	4.3	+1.6	+1.0
Primula veris	1.6	1.7	0.9	0	0	-0.7	-[3]
Silene vulgaris	1.6	0.7	0.5	0	0	-1.1	-0.5
Hypericum perforatum[1]	0.2	1.0	1.4	0	0	+1.2	-1.1
Hypericum hirsutum[1]	0	0	0.4	0	0	+0.4	-1.4

Data are maximum numbers of quadrat cells occupied on any date in each year, expressed as percentages of the total number of quadrat cells (Chapter 2.2.5).

[1] Percentage for 1988 anomalously low because recorded to genus and not species on some dates.

[2] Change in percentage of cells in which spp. were recorded between 1988 and 1990, or 1988 and 1992 for some forbs (see text).

Table 6.5 Relative abundance of sown species in the new margins in relation to sowing density

Species	Rank density sown[1]	1989 rank rel. freq.[2]	1989		1990	
			residual[3]	rank[4]	residual	rank
Cynosurus cristatus	3	=1	0.447	1	0.213	5
Festuca rubra	2	=1	0.400	2	0.399	2
Phleum bertolonii	5	3	0.397	3	0.411	1
Leucanthemum vulgare	=7	5	0.290	4	0.358	3
Tragopogon pratensis	3	17	0.279	5	0.298	4
Ranunculus bulbosus	19	9	0.253	6	0.179	6
Trisetum flavescens	4	4	0.206	7	0.163	8
Knautia arvensis	=20	14	0.157	8	0.176	7
Galium verum	=15	8	0.120	9	0.141	9
Leontodon hispidus	22	16	0.104	10	0.062	13
Centaurea nigra	17	10	0.103	11	0.120	11
Hordeum secalinum	10	7	0.067	12	0.116	12
Torilis japonica	18	13	0.053	13	0.136	10
Centaurea scabiosa	=20	=21	0.002	14	0.003	15
Ranunculus acris	=13	11	-0.014	15	-0.094	16
Poa pratensis	1	6	-0.142	16	0.037	14
Silene latifolia alba	=15	18	1.061	17	-0.181	18
Prunella vulgaris	12	15	-0.199	18	-0.176	17
Clinopodium vulgare	9	12	-0.249	19	-0.315	19
Primula veris	11	19	-0.300	20	-0.334	21
Silene vulgaris	=13	=21	-0.321	21	-0.327	20
Hypericum perforatum	6	20	-0.731	22	-0.706	23
Hypericum hirsutum	=7	23	-0.746	23	-0.679	22

[1] Rank order of density in the seed mixture (see Chapter 2.2.2 for absolute densities)
[2] Rank order of relative frequencies in the sward in 1989
[3] Residuals are from regressions of sowing density on subsequent maximum frequency in 1989 and in 1990 (see text)
[4] Rank orders of residuals. The species list is ordered by the ranks for the residuals for 1989.

Table 6.6 Changes in the relative abundance of species in the wild flower seed mixture on the old margins

Species	Year			
	1988	1989	1990	Change[2] from '88-'90
Grasses:				
Festuca rubra	3.8	10.2	20.5	+16.7
Phleum bertolonii	3.6	7.8	14.1	+10.5
Cynosurus cristatus	4.0	17.2	25.2	+21.2
Trisetum flavescens	1.2	4.3	7.8	+6.6
Poa pratensis	2.1	3.3	5.4	+7.5
Hordeum secalinum	0.2	0.2	3.5	+3.3
Forbs:				
Leucanthemum vulgare	1.0	3.3	18.2	+17.2
Galium verum	0.4	0.7	1.0	+0.6
Centaurea nigra	0.2	0.2	0.2	0
Ranunculus bulbosus[1]	1.7	2.1	2.6	+0.9
Clinopodium vulgare	0.7	1.0	1.4	-0.7
Knautia arvensis	0.7	0.5	0.5	-0.2
Torilis japonica	0.2	0.2	5.2	+5.0
Prunella vulgaris	0.2	0.9	1.4	+1.2
Ranunculus acris[1]	0.3	1.0	0.9	+0.6
Leontodon hispidus	0.2	0	0	-0.2
Primula veris	0	0	0.2	+0.2
Hypericum perforatum[1]	0	0.2	0.2	+0.2
Tragopogon pratensis	0	0	1.0	+1.0
Silene latifolia alba	0	0	0	0
Silene vulgaris	0	0	0	0
Centaurea scabiosa	0	0	0	0
Hypericum hirsutum[1]	0	0	0	0

Data are maximum numbers of quadrat cells occupied on any date in each year, expressed as percentages of the total number of quadrat cells (Chapter 2.2.5.1).

[1] Percentage for 1988 anomalously low because recorded to genus and not species on some dates.

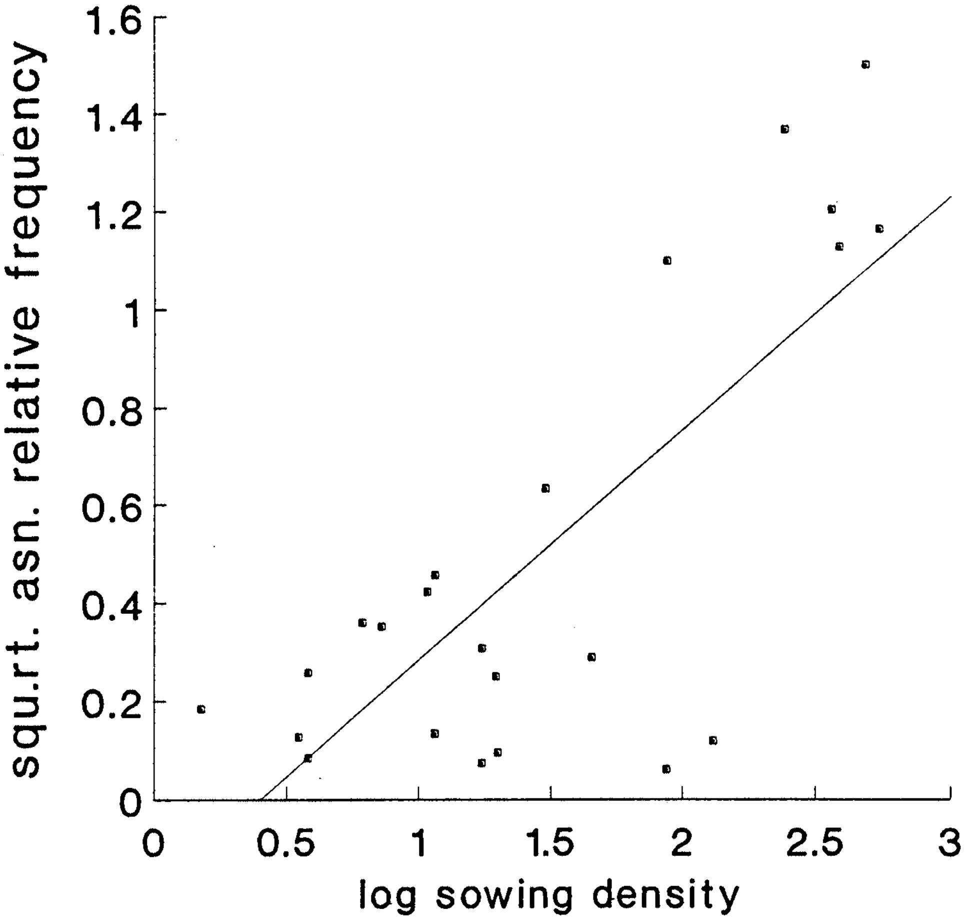
[2] Change in percentage of cells in which spp. were recorded between 1988 and 1990 (see text).

Table 6.7 The density of flowering plants of *Primula veris* in sown treatments on the new margins in 1991 and 1992

Treatment	Mean no.[1] flowering plants		Mean increase 1992-'92
	1991	1992	
Uncut	0.86 (0.55)	1.29 (0.57)	0.429 (0.65)
Cut in summer	0.29 (0.18)	2.00 (1.02)	1.714 (0.92)
Cut in spring+summer	0.43 (0.30)	3.43 (1.13)	3.000 (0.98)
Cut in spring+autumn	1.71 (0.71)	5.00 (2.31)	3.286 (1.73)

[1] Mean over seven blocks of the experiment, includes plots with no plants
Numbers in parentheses are standard errors

Figure 6.1 The relationship between sowing density and relative frequency of sown species in 1990



N.B. Each point represents one species
Regression equation: y=0.485x-0.201

7 HABITAT USE BY SMALL MAMMALS ON FARMLAND

In this chapter we report on work on small mammals on field margins undertaken by Susanne Plesner Jensen and supported by grants from the Danish Research Academy, Statens Uddannelsesstotte and the Whitley Animal Protection Trust.

7.1 Introduction

We assess the effects of contrasting field margin management regimes, and of other features of field boundaries, on small mammals. Five rodent species were studied: wood mice *Apodemus sylvaticus* L., bank voles *Clethrionomys glareolus* Schreb., field voles *Microtus agrestis* L., harvest mice *Micromys minutus* Pallas and house mice *Mus domesticus* Schwartz & Schwartz, as well as three insectivorous species: common shrews *Sorex araneus* L., pygmy shrews *S. minutus* L. and water shrews *Neomys fodiens* Pennant.

Because the scale of the experimental treatments was small in relation to the known home-ranges of small mammals on farmland (Tew *et al* 1992) we confined this study to comparisons of treatments which we predicted would differ substantially in their attractiveness to small mammals, and to comparisons between small mammal populations on the two metre margins, wide margins and conventionally-managed field margins. We use data from both Longworth trapping on individual plots, and radio tracking of individual animals in the vicinity of the experimental field margins, to attempt to assess the extent to which small mammals are influenced by field margin type. Multivariate analyses of the effects on small mammals of other features of the field boundary, including the presence of hedges, trees and ditches, are presented.

7.2 Methods

7.2.1 FIELD METHODS

The Longworth trapping regimes for the two metre and wide field margin experiments are described in Chapter 2 (Sections 2.2.5 and 2.3.2 respectively). Trapping was also carried out on two field edges with conventionally-managed, narrow field margins, for four days in October 1989 (with 16 trap-points each, the equivalent of 8 plots). These field margins were *ca* 0.5m in width, were left unmanaged and were not protected from fertiliser and spray drift. Both of these field edges bordered ploughed arable land and were separated from grazed pasture, one with by ditch and a hedge, the other by a fence only.

Some comparisons are also made in this chapter with small mammal populations in Wytham Great Wood, which is adjacent to the University Farm. These data were collected as part of the Mammal Society's six-monthly national mammal survey. Longworth live-traps were placed in two 2-acre grids in oak-ash-sycamore woodland. The grid consisted of 15 trap points with five traps at each point, bringing the total to 150 traps. The traps were pre-baited for 48 hours and then set. The catch was examined on the evening of the same day and on the following morning. In both studies, captured animals were weighed and sexed and the reproductive state of the females recorded.

7.2.2 ANALYSES

When the numbers of animals captured per plot were compared for each treatment, an individual rodent captured in adjoining plots during one trapping session would be recorded only for the plot in which it was captured most often (or first, in the case of ties). If it was recaptured in plots not immediately adjacent to the initial capture, its use of both plots would be recorded. This conservative use of the data was chosen because, while the animal might have been enticed into the neighbouring plot by the presence of baited traps or by all the traps in the preferred plots being occupied, a move of more than the length of one plot (i.e. >50m) was more likely to be a deliberate one.

For shrews, which were not marked individually, the trap-round or rounds which had the highest numbers of captures within each trapping session were used on the assumption that 1) no animal was captured twice during one trap-round and 2) the distribution of the animals on the margins in that round was representative of that session. In the case of several rounds having the maximum number of captures, each of the rounds was analyzed separately and compared, thus testing the second assumption above.

To ensure statistical independence, data from different trapping sessions were analyzed separately and not treated as replicates.

The effects of the presence or absence of various habitat features (Figure 7.1), and vegetation heights, on the numbers of animals captured per plot were assessed using stepwise multiple regression (STEPWISE, SAS Institute Inc. 1988). The independence of these factors was tested and in cases where two factors were correlated, the less significant of the two was excluded from the model. When the presence of tracks, ditches, trees or adjacent margins was shown to affect numbers captured, plots with the relevant feature would be selected and the effect of the following variables would be tested: the width of the track; the side of the plot on which a track was located; the width of ditch; the depth of ditch; the side of the plot on which the ditch was located and the type of margin on the opposite side of the boundary feature. Treatment effects were tested using a generalised linear model in which the residuals for the appropriate multiple regression model were treated as the dependent variable (GLM, SAS Institute Inc. 1988). The radio-tracking data were analyzed using the WILDTRAK software package (Todd 1992).

7.3 Results

7.3.1 ANNUAL POPULATION FLUCTUATIONS

Rodents

Numbers of rodents captured on wide and 2m margins fluctuated with season and showed a downward trend from year to year (Figure 7.2a). Where data were available for the same month in more than one year, the numbers captured per plot were compared between years using a Student's t-test (Table 7.1). In each case the decline in numbers of rodents captured was significant. This pattern also applied to each of the two most common species of rodent, the wood mice and bank voles. For the wood mice, the decline was non-significant only between February 1989 and February 1991. Numbers of bank voles declined on each occasion except between October 1988 and 1989. The other rodent species were captured in insufficient numbers for statistical comparison, but almost all showed a decline in numbers in each comparison. The only exception to this was an increase in numbers of field voles and harvest mice on the 2m margins between October 1988 and 1989.

The decline in numbers of wood mice was not restricted to the arable field margins. A comparison between the numbers of wood mice captured on the farm and in nearby Wytham Great Wood in December 1989 and December 1990 (using a 2x2 contingency table) showed a good correspondence in the decline in numbers of mice at the two sites ($X^2=0.002$, $P=1.0$). Over the same period the numbers of bank voles captured in the woods remained unchanged ($X^2=10.453$, $P<0.002$) although an overall downward trend was apparent between 1988 and 1991 for bank voles as well as for wood mice (Figure 7.2c).

Insectivores

No annual differences were detectable in the numbers of insectivores captured (Figure 7.2b). They did not vary significantly between the same month in different years (Table 7.1).

7.3.2 THE EFFECTS OF EXPERIMENTAL TREATMENTS

Wide margins

Rodents The total numbers of rodents captured per plot showed a skewed distribution towards zero in all sessions except two, and for five of the sessions, no simple transformation produced normality. The non-normal session samples showed no significant effect of treatment type on numbers of rodents captured and neither did the seven sessions in which transformed data were normally distributed (deviations of this sort from normality do not in general markedly affect the power of the analysis (Ryan *et al* 1985). None of the probabilities approached significance: ANOVA: $F_{(3,28)}=0.14\text{-}2.70$, $P=0.06\text{-}1.0$).

The numbers of individuals of each species captured per plot were non-normally distributed. The only exception to this was for wood mice in one session (4 November 1988). There was no evidence that treatment type affected the numbers of any rodent species captured in any session ($F_{(3,28)}$=0.17-2.95, P=0.06-0.9).

Insectivores All data sets were distributed non-normally. We were unable to detect any effect of treatment on the numbers of any insectivore captured in any session ($F_{(3,28)}$=0.18-2.81, P=0.06-0.9 and ($F_{(3,26)}$=0.35-2.54, P=0.08-0.8).

2m margins

Rodents We were unable to detect any effect of treatment on total rodent numbers on the 2m margins (treatment effect from ANOVA: $F_{(3,21)}$=0.09-1.61, P=0.2-1.0). Separate analyses of wood mice and bank voles also failed to reveal any significant effects of treatment (treatment effect: $F_{(3,21)}$=0.71-1.92, P=0.2-0.9). The numbers of field voles captured on the 2m margins were too low for this analysis.

Insectivores Similarly, there was no evidence that total numbers of insectivores captured on the 2m margins were affected by experimental treatment (treatment effect: $F_{(3,21)}$=0.09-3.03, P=0.05-1.0). No effects were detected for individual species (common shrews: $F_{(3,21)}$= 0.15-2.39, P=0.1-0.9; pygmy shrews: $F_{(3,21)}$= 0.0-3.49 P=0.03-1.0; water shrews: $F_{(3,21)}$= 0.09-3.03, P=0.52-1.0).

Since analyses of variance failed to detect any significant effects of the experimental treatments we tested further for treatment effects by removing the residual variance due to other habitat features. Following Stepwise multiple regression to determine the habitat factors affecting numbers of animals captured (below), we re-tested for treatment effects. Again, however, treatment failed to contribute significantly to explaining any of the residual variation ($F_{(3,28)}$=0.31-0.58, P=0.6-0.8 for tests on either the 2m or wide margins; $F_{(7,56)}$=0.52-1.74, P=0.1-0.8 for tests involving both margin types).

7.3.3 COMPARISON OF WIDE, TWO METRE AND CONVENTIONAL MARGINS

Since we were unable to detect significant effects of the experimental treatments on either the two metre or wide margins, we compared the gross numbers of animals captures in these two margin types and on the conventionally-managed, narrow margins.

Rodents

The numbers of rodents captured on wide and 2m margins fluctuated in a similar fashion, and in none of the trapping sessions did numbers on the two types of margins differ more than between different treatments within each experiment (Table 7.2). Bank voles were the only species of rodent which did not follow this pattern. In October 1988 they were captured in significantly greater numbers on 2m than on wide margins (Permutation test, n=4 and 4, P=0.03).

The numbers of wood mice, bank voles and house mice captured per 50m on conventionally managed, narrow field edges without expanded margins in October 1989 (2.63, 1.75 and 0.13 per 50m) did not differ significantly from those captured on either the wide margins (2.56, 1.41 and 0.09 per 50m plot) or 2m margins (2.0, 2.37 and 0 per plot). The number of field voles was, however, significantly higher on conventional (0.25 per 50m) than on the wide margins (0.03 per plot, $t_{(3)}=-7.0$, $P=0.006$). The greatest number of field voles was captured on the 2m margins (0.56 per plot), but this figure did not differ significantly from that for wide or conventional margins.

Insectivores

Of the insectivores, common shrews were by far the most numerous, followed by pygmy shrews and water shrews. Numbers of insectivores did not differ between wide and 2m margins in any session (Table 7.2g) and the numbers captured on the wide and 2m margins did not differ from those on field edges without expanded margins ($t_3=0$ and 2.83, $P=1.0$ and 0.7).

7.3.4 THE EFFECTS OF HABITAT FEATURES AND VEGETATION HEIGHT

Rodents

In most months, the numbers of wood mice captured were either positively correlated with hedge height or were affected by the presence of hedges or trees (Table 7.3a). Tree height did not affect numbers of wood mice captured (mean numbers of animals captured per plot in each category are shown in Table 7.4a). In several sessions, the height of the taller level of vegetation was a significant factor, with greater height generally being preferred. However, amongst the lower level of vegetation, shorter heights were selected. This may have been due to the different structure of the two levels of vegetation. The shorter level formed a dense ground cover, often of grass, while the taller level tended to consist of forbs and be more open. The mice may have been avoiding the dense ground cover and selecting the taller stands of forbs.

In November, plots next to a track were generally avoided by wood mice and the width of the track was also negatively correlated with numbers of wood mice captured ($F_{(1,8)}=5.87$, $P=0.04$). It is likely that cover was at a premium at this time of year. The side of the margin on which the track was found did not affect the numbers captured.

Numbers of bank voles were positively affected by some measure related to hedges in six out of seven trapping sessions (Table 7.3b). The mean numbers of animals captured per plot in the presence of significant habitat features are shown in Table 7.4b. The second most frequent significant factor was the presence of a ditch, which had positive effects on numbers captured in the first spring in which the field margins were fallowed. Vegetation heights affected numbers captured only in the first session, with taller vegetation being preferred.

In one of the cases in which the presence of ditches was significant (May 1989), the width of the ditch had a negative effect on the numbers of bank voles captured

($F_{(1,47)}$=4.25, P=0.04). The depth of the ditch and the side of the margin on which it was found were not significant factors, nor were track widths, position of tracks or the type of margin on the opposite side of the boundary.

Field voles did not respond either to habitat features or to vegetation heights in any session, when the data for wide and 2m margins were combined for analysis. Analysis of data from the wide margins alone suggested that the presence of tracks had a positive effect on numbers captured in February (Table 7.3c: 0.35 animals captured per plot adjacent to tracks *cf* 0.02 for plots without a track). However, track width was not a significant factor, nor was the side of the margin on which the track was found.

Harvest mice were captured in larger numbers on wide than on 2m margins in February while, in November, plots without hedges were preferred (Table 7.3d).

Insectivores

There was no clear pattern in the response of Common shrews to habitat features. They appeared to respond to a different feature in each session (Table 7.3e). In the first summer, the depth of water in the ditches had a positive effect on numbers captured, whereas in November and the following March, they responded positively to the height of the taller level of the vegetation on the original part of the margin.

In the only session in which the numbers of pygmy shrews were high enough to reveal a response to the features measured, a positive effect was found of the height of both the taller level of vegetation on the expanded part of the margin and the height of the vegetation on the tracks (Table 7.3f).

Water shrews were captured in insufficient numbers for this analysis.

7.3.5 RADIO-TRACKING

Seasonal differences were found in the use of field margins by wood mice and also in their use of wide and 2m margins. In summer, the four male wood mice tracked spent most of their time in the fields (Figure 7.3). While the 2m margins provided a nest site for one of the animals tracked (Figure 7.3a), the wide margins were never ventured into at this time of year, once the baited traps had been removed (Figure 7.3b). By October, both the male and female mice tracked on the wide margins experiment used the hedgerows exclusively, so that their home ranges were only as wide as the hedges in which they were living (Figure 7.3c&d). A female tracked on this experiment in January was captured near an area of young trees and bushes at the edge of the field. Again, it did not venture into the wide margins once the baited traps had been removed but it spent most of its time in the hedgerow and was regularly located at the height of about 1-1.5m. By contrast, the other female tracked in January was captured on a 2m margin and confined its movements entirely to the margins and hedgerow (Figure 7.3e).

7.4 Discussion

Our failure to demonstrate any significant effects of the experimental treatment on the two metre margins on any small mammal species requires careful interpretation. Since the home ranges of these species were likely to include several field margins plots as well as adjacent habitats, the number of captures of individuals per treatment is likely to be an insensitive measure of their overall activity patterns. It is likely that an index of activity on the different treatments would provide a more sensitive measure of relative use but it is difficult to obtain reliable indices from Longworth trapping because of biases created by individual animals that become 'trap happy' or 'trap shy'.

Our limited radio-tracking data show clearly that wood mice utilised the two metre margins at least at some times of year, it seems improbable that the very different vegetation structures and plant and invertebrate assemblages on the different treatments did not influence the distribution of this and other small mammal species. This suggestion is supported both by our demonstration that vegetation structure affected numbers of captures of several species (see also below) and by a separate experiment on the field margins in which the amount of predation of weed seeds by small mammals was shown to be significantly affected by treatment (Povey *et al* 1993). The predation of annual weed seeds attributable to small mammals was significantly greater in the taller, denser swards on uncut plots than in swards than in those cut in spring and summer, probably because the former afforded greater protection from predators (see also Birny *et al* 1976). Grass weed seeds are known to be important components in the diets of wood mice and to a lesser extent of bank voles, the two most abundant small mammal species on the field margins (*eg* see Watts 1968; Green 1989; Hansson 1971, 1985). More definitive resolution of the effects that changes in arable field margins management have on small mammals are likely to require either very intensive radio tracking or the establishment of much larger experimental plots.

The radio tracking data clearly suggest that the two metre margins were more attractive to wood mice than the wide margins sown with agricultural grass leys. The latter were unlikely to provide useful resources for small mammals. We show in Chapter 11 that their plant species richness was relatively low and included a low frequency of forbs. Because they were cut in mid-summer, they provided little food for granivorous species and little cover during much of the year. The most important role of the field margins to wood mice appeared to be the provision of food and nesting sites in winter, when the fields were bare.

Failure to reveal this difference in the use of the two types of margin in the direct comparisons between numbers captured in each (Section 7.3.3) may be attributable to several factors: 1) mice may have been attracted to the wide margins by the baited traps 2) the effect of edge type may have been weak relative to the other habitat features and 3) since the traps were positioned close to the field boundary feature, rather than in the middle of the margin, they may have sampled the animals travelling along the hedgerow. The preference for 2m margins by wood mice and bank voles was, however, revealed by the stepwise regression when the effects of the other habitat features were removed.

Although attempts to radio collar bank voles and field voles were unsuccessful because of problems with fitting the collars securely, it seems likely that field margins may be more important to these species than to wood mice. These species were rarely captured in arable fields (see Plesner Jensen 1993b) but were captured in large numbers on the field margins. Five bank voles which were radio collared for a short period on the 2m margins all had nests in the margins. Since the voles are the most herbivorous of the species recorded, they may benefit most from the establishment of grassy field margins in otherwise arable landscapes. In three winter months (November 1988, February and March 1989) larger numbers of bank voles were captured on 2m margins than on wide margins. In an enclosure-based, choice experiment which tested the preferences of bank and field voles for various combinations of soil and vegetation types and foods, Hansson (1982) showed that the availability of safe retreats was of over-riding importance. The tall, dense vegetation of uncut plots on the two metre margins was more likely to provide safe retreats than the wide margin swards. Successful radio-tracking of voles would be likely to reveal much more information about the role of field margins and of different sward types in their ecology in arable landscapes.

Although further data are required to determine the extent to which small mammals are influenced by field margin management, our data clearly showed that aspects of field boundary structure have very important influences on small mammals.

The numbers of wood mice captured were positively correlated with some aspect of trees or hedges both in winter, when the mice tended to use field boundary habitats exclusively, and in spring and autumn, when home ranges stretched across both the fields and boundaries. Trees and hedges probably served different functions for wood mice at different times of the year. In autumn and winter, when fruit was abundant, the mice ate seeds (Plesner Jensen 1993a) and nested between the roots (revealed by radio-tracking). In spring, when both the margins and fields were relatively bare, the hedges provided shelter and bolt holes for foraging mice. The taller vegetation, which tended to more open at ground level than the shorter swards, may have served a similar dual purpose of providing food and shelter. Shorter swards, which were usually denser and lusher, provided neither food nor shelter. Amongst these swards, shorter heights were preferred. One exception to this pattern was found in March, when the numbers of wood mice were negatively correlated with the height of the taller level of vegetation on the new margins. However, in this month, the vegetation classified as belonging to the taller level was not much taller than the lower level (7.25-30.5 cm compared with 2.25-14.5 cm). Both levels may have represented ground cover to the mice.

For bank voles, which have a different mode of movement from wood mice, running along the ground underneath the vegetation rather than leaping over it (King 1985), the shorter level of vegetation could have provided cover. Two months after establishment of the margins, the height of both of these levels of vegetation had a positive effect on numbers captured probably as a result of the relatively sparse nature of the vegetation at this stage in the succession (more detailed discussion of the effects of vegetation height is given by Plesner Jensen 1993b). In the remaining trapping sessions other factors had more influence on small mammals than vegetation height. These factors included the presence of hedges and ditches, the effects of which were always positive. This finding is supported by other studies of this species (reviewed by Corbet & Harris 1991).

The numbers of field voles captured on the field margins were too low to reveal any effects of the factors measured. The isolated observation of a positive effect of the presence of tracks in February is not easily explained.

The availability of food is more likely to be more important than the habitat structure in determining the abundance of shrews in arable habitats. Little is known of the differences in the habitat requirements that allow common shrews and pygmy shrews to coexist in the same area or about the preferred habitats of either species. The general consensus (see *eg* Corbet & Harris 1991, Macdonald & Barrett 1993) is that pygmy shrews need plenty of ground cover. However, Butterfield *et al* (1981) suggested that the importance of vegetation cover may generally have been over-stressed and that other environmental factors, particularly food supply, play a major part in determining their distribution. Common shrews feed on earthworms and are known to dig for their food, whereas pygmy shrews are not known to do any digging and instead feed on surface-living invertebrates. The abundance of common shrews is therefore thought to be primarily dependent on the distribution of earthworms, while the density of surface-living invertebrates determines pygmy shrew abundance (Butterfield *et al* 1981). The factors found to influence the numbers of shrew captures may thus have had their effects via their influence on the abundance of earthworms and other invertebrates. This may explain the seasonal differences in the factors which were significant. Future analyses of these data will include examination of the relationships between insectivore abundance and invertebrate numbers (see Chapter 8).

We recommend that the conservation of small mammals in farmland is likley to benefit from tall, grassy field margin vegetation which is left uncut in summer, providing both cover and a diversity of plant and invertebrate foods. Conventionally managed grass leys are likely to be of limited benefit to small mammals. The presence of hedges and ditches are probably the most important features of small mammal habitat in arable farmland. Careful management of field boundary habitats can thus encourage a diversity of small mammal species. This can have additional benefits, both to conservation and agriculture, by increasing predation of weed seeds (Povey *et al* 1993, Tew *et al* 1992) and of insect pests (Pernetta 1976) and by providing prey for larger mammals and birds (eg Southern 1970).

Table 7.1 Results of t-tests comparing numbers of animals captured per 50m strip in the same months of different years (* $P < 0.05$, ** $P < 0.01$)

	Oct.1988 vs. Oct.1989	Feb.1989 vs. Feb.1991	Dec.1989 vs. Dec.1991
Rodents			
Wide margins	-2.21*	-9.64**	-
2m margins	-2.79**	-3.91**	-4.45**
Wood mice			
Wide margins	-2.83**	-9.23**	-
2m margins	-3.78**	-2.01*	-2.33*
Bank voles			
Wide margins	0.23	-9.94**	-
2m margins	-0.66	-4.10**	-3.63**
Insectivores			
Wide margins	-0.84	+0.79	-
2m margins	-0.46	0.61	-1.77

Table 7.2a, b and c Total numbers of animals captured on plots of the different treatments
* applies to sessions 5-13, in sessions 2-4 U/SpSu/L was monitored

Trapping session		Wide Margins					Narrow Margins					Permutation test
		D/F	D/-	C/F	C/-	Total	U/Spray	U/NC	S/SpSu*	U/SpSu	Total	P
Rodents												
1	June 1988	29	29	35	36	129	-	-	-	-	-	-
2	August 1988	27	33	25	30	115	39	30	35	31	135	0.1
3	October 1988	53	46	53	27	179	65	56	50	46	217	0.3
4	Nov. 1988	38	60	56	28	182	63	77	53	73	266	0.1
5	February 1989	23	35	34	16	108	36	32	20	25	113	0.8
6	March 1989	18	23	10	5	56	18	27	19	19	83	0.2
7	May 1989	20	16	11	10	57	9	13	4	9	35	0.1
8	July 1989	8	4	7	8	27	14	14	8	8	44	0.2
9	October 1989	57	25	23	20	125	31	49	39	29	148	0.6
10	December 1989	26	43	29	24	122	16	27	24	27	94	0.3
11	December 1990	-	-	-	-	-	12	11	6	5	34	-
12	February 1991	15	6	5	3	29	13	9	7	10	39	0.5
13	April 1991	-	-	-	-	-	1	9	4	16	30	-
Wood mice												
1	June 1988	7	15	13	14	49	-	-	-	-	-	-
2	August 1988	11	19	12	9	51	19	13	13	7	52	1.0
3	October 1988	36	27	40	20	123	42	35	19	27	123	1.0
4	Nov. 1988	22	31	28	19	100	37	49	22	31	139	0.2
5	February 1989	10	13	14	8	45	10	12	4	13	39	0.7
6	March 1989	5	4	0	1	10	6	8	5	8	27	0.06
7	May 1989	4	0	1	0	5	7	3	0	0	10	0.7
8	July 1989	1	1	2	4	8	4	2	2	2	10	0.7
9	October 1989	38	11	14	13	76	20	13	6	6	45	0.4
10	December 1989	14	26	9	15	64	7	8	11	22	48	0.5
11	December 1990	-	-	-	-	-	8	10	4	3	25	-
12	February 1991	2	0	1	1	4	6	3	1	7	17	0.1
13	April 1991	-	-	-	-	-	1	5	1	0	7	-
Bank voles												
1	June 1988	19	12	18	12	61	-	-	-	-	-	-
2	August 1988	12	13	12	21	58	13	14	19	18	64	0.7
3	October 1988	11	17	9	7	44	22	19	31	18	90	0.03
4	Nov. 1988	16	18	24	8	66	24	24	26	31	105	0.09
5	February 1989	11	12	12	7	42	19	15	14	11	59	0.1
6	March 1989	13	10	8	4	35	7	15	13	8	43	0.6
7	May 1989	15	15	10	10	50	1	10	4	9	24	0.09
8	July 1989	6	3	5	2	16	9	12	6	6	33	0.09
9	October 1989	17	13	8	6	44	9	11	25	15	60	0.4
10	December 1989	9	9	18	6	42	5	9	10	5	29	0.5
11	December 1990	-	-	-	-	-	3	0	1	1	5	-
12	February 1991	6	1	3	1	11	6	2	5	2	15	0.7
13	April 1991	-	-	-	-	-	0	2	3	7	12	-

Table 7.2d, e and f Total numbers of animals captured on plots of the different treatments
* applies to sessions 5-13, in sessions 2-4 U/SpSu/L was monitored

Trapping session		Wide Margins					Narrow Margins					Permutation test
		D/F	D/-	C/F	C/-	Total	U/Spray	U/NC	S/SpSu*	U/SpSu	Total	*P*
Field voles												
1	June 1988	4	2	1	2	9	-	-	-	-	-	-
2	August 1988	2	0	1	0	3	4	2	0	3	6	0.3
3	October 1988	0	0	2	0	2	0	0	0	0	0	0.4
4	Nov. 1988	0	6	0	0	6	1	2	2	5	10	0.6
5	February 1989	1	1	0	1	3	6	5	2	1	14	0.1
6	March 1989	0	4	2	0	6	3	3	1	3	10	0.5
7	May 1989	1	0	0	0	1	1	0	0	0	1	1.0
8	July 1989	1	0	0	2	3	0	0	0	0	0	0.4
9	October 1989	0	1	0	0	1	1	3	8	6	18	0.06
10	December 1989	0	3	0	0	3	4	8	1	0	13	0.3
11	December 1990	-	-	-	-	-	0	1	1	1	3	-
12	February 1991	7	5	1	0	13	1	4	1	1	7	0.6
13	April 1991	-	-	-	-	-	0	0	0	0	0	-
House mice												
1	June 1988	0	0	0	0	0	-	-	-	-	-	-
2	August 1988	2	1	0	0	3	3	1	3	3	10	0.09
3	October 1988	3	2	1	0	6	0	2	0	1	3	0.6
4	Nov. 1988	0	4	1	0	5	0	2	1	4	7	0.8
5	February 1989	0	0	0	0	0	0	0	0	0	0	1.0
6	March 1989	0	0	0	0	0	0	0	0	0	0	1.0
7	May 1989	0	1	0	0	1	0	0	0	0	0	1.0
8	July 1989	0	0	0	0	0	1	0	0	0	0	1.0
9	October 1989	1	0	1	1	3	0	0	0	0	0	1.0
10	December 1989	0	0	0	0	0	0	0	0	0	0	1.0
11	December 1990	-	-	-	-	-	0	0	0	0	0	-
12	February 1991	0	0	0	0	0	0	0	0	0	0	1.0
13	April 1991	-	-	-	-	-	0	0	0	0	0	-
Harvest mice												
1	June 1988	0	0	0	0	0	-	-	-	-	-	-
2	August 1988	0	0	0	0	0	0	0	0	0	0	1.0
3	October 1988	3	0	1	0	4	0	0	0	0	0	0.4
4	Nov. 1988	0	1	3	1	5	1	0	2	2	5	1.0
5	February 1989	1	4	8	0	13	1	0	0	0	1	0.3
6	March 1989	0	5	0	0	5	2	1	0	0	3	1.0
7	May 1989	0	0	0	0	0	0	0	0	0	0	1.0
8	July 1989	0	0	0	0	0	0	0	0	0	0	1.0
9	October 1989	1	0	0	0	1	0	2	0	2	4	0.4
10	December 1989	3	3	2	2	10	0	2	2	0	4	0.2
11	December 1990	-	-	-	-	-	0	0	0	0	0	-
12	February 1991	0	0	0	1	1	0	0	0	0	0	1.0
13	April 1991	-	-	-	-	-	0	0	0	0	0	-

Table 7.2g, h and i Total numbers of animals captured on plots of the different treatments
* applies to sessions 5-13, in sessions 2-4 U/SpSu/L was monitored

Trapping session		Wide Margins D/F	D/-	C/F	C/-	Total	Narrow Margins U/Spray	U/NC	S/SpSu*	U/SpSu	Total	Permutation test P
Insectivores												
1	June 1988	7	4	0	1	7	-	-	-	-	-	-
2	August 1988	4	4	7	1	16	6	7	5	9	27	0.17
3	October 1988	1	1	2	1	5	6	1	7	3	17	0.09
4	Nov. 1988	1	3	1	0	5	3	3	3	2	11	0.03
5	February 1989	2	0	1	0	3	2	2	3	0	7	0.4
6	March 1989	3	1	3	0	7	4	5	5	6	20	0.3
7	May 1989	7	5	2	3	17	6	3	7	4	20	0.7
8	July 1989	8	4	3	5	20	8	3	2	3	16	0.6
9	October 1989	2	4	0	2	8	8	2	6	8	24	0.1
10	December 1989	1	5	5	3	14	3	0	2	1	6	0.2
11	December 1990	-	-	-	-	-	0	1	0	0	1	-
12	February 1991	0	0	1	0	1	1	1	1	0	3	0.5
13	April 1991	-	-	-	-	-	1	1	2	1	5	-
Common shrews												
1	June 1988	1	0	4	5	10	-	-	-	-	-	-
2	August 1988	4	4	5	1	14	4	5	3	8	20	0.5
3	October 1988	0	1	2	1	4	5	0	4	2	11	0.3
4	Nov. 1988	1	1	1	0	3	3	3	2	0	8	0.2
5	February 1989	1	0	1	0	2	1	2	1	0	4	0.7
6	March 1989	1	1	3	0	7	4	4	3	5	16	0.06
7	May 1989	6	5	1	3	15	4	1	7	3	15	1.0
8	July 1989	3	3	3	5	14	8	2	0	3	13	1.0
9	October 1989	2	2	0	1	5	8	2	5	4	19	0.09
10	December 1989	1	5	4	3	13	3	0	2	0	5	0.2
11	December 1990	-	-	-	-	-	0	1	0	0	1	-
12	February 1991	0	0	1	0	1	1	1	0	0	2	1.0
13	April 1991	-	-	-	-	-	1	0	0	0	1	-
Pygmy shrews												
1	June 1988	2	0	0	0	2	-	-	-	-	-	-
2	August 1988	0	0	1	0	1	2	1	1	1	5	0.1
3	October 1988	3	0	0	1	4	1	1	1	0	3	1.0
4	Nov. 1988	0	1	0	0	1	0	0	1	1	2	1.0
5	February 1989	1	0	0	0	1	1	0	1	0	2	1.0
6	March 1989	1	1	0	0	2	0	0	0	2	2	1.0
7	May 1989	1	0	1	0	2	1	1	0	1	3	1.0
8	July 1989	3	1	0	0	4	0	0	2	0	2	0.7
9	October 1989	0	1	0	0	1	0	1	1	3	4	0.7
10	December 1989	0	0	1	0	1	0	0	0	1	1	1.0
11	December 1990	-	-	-	-	-	0	0	0	0	0	-
12	February 1991	0	0	0	0	0	0	0	0	0	0	1.0
13	April 1991	-	-	-	-	-	0	0	2	1	3	-
Water shrews												
1	June 1988	0	0	0	0	0	-	-	-	-	-	-
2	August 1988	0	0	1	0	1	0	1	1	0	2	1.0
3	October 1988	0	0	0	0	0	0	0	2	1	3	0.4
4	November 1988	0	1	0	0	1	0	0	0	1	1	1.0
5	February 1989	0	0	0	0	0	0	0	1	0	1	1.0
6	March 1989	0	0	0	0	0	0	1	1	0	2	0.4
7	May 1989	0	1	0	0	1	7	1	0	0	2	1.0
8	July 1989	2	0	0	0	2	0	1	0	0	1	1.0
9	October 1989	0	1	0	1	2	0	0	0	1	1	1.0
10	December 1989	0	0	0	0	0	0	0	0	0	0	1.0
11	December 1990	-	-	-	-	-	0	0	0	0	0	-
12	February 1991	0	0	0	0	0	0	1	0	0	1	1.0
13	April 1991	-	-	-	-	-	0	0	0	0	0	-

Table 7.3a Effect of habitat features and vegetation height on numbers of wood mice captured per margin plot as determined by STEPWISE Regression for wide and 2m margins (64 plots) except where indicated otherwise. In each instance, the overall model was significant at the 5% level. One asterisk denotes a 5% significance level, 2 asterisks, a 1 % level. Variables included in the models were: presence/absence of hedge, ditch, trees, road/track/path, adjoining pasture, adjoining experimental margin, and whether a plot was an end-plot (ie joined to another experimental plot at one end only), height of hedge, as well as measurements of features *a-o*, (Figure 7.1) and number of major hedge species present

Month	Trapping Session	No. animals	Significant factors	Parameter estimates
June 1988 (wide margins only)	1	49	Trees, presence/absence	+ 1.110**
November 1988	4	239	Hedge height	+ 0.003**
			Track, presence/absence	- 0.475**
			Height of taller level of veg., extended part of margin	+ 0.009**
February 1989	5	84	None	
March 1989	6	37	Edge type[1]	+ 0.288*
			Hedge, presence/absence	+ 0.342**
			Height of taller level of veg., extended part of margin	- 0.029**
May 1989	7	15	Height of taller level of veg., extended part of margin	+ 0.015**
			Height of shorter level of veg., extended part of margin	- 0.011*
October 1989 (narrow margins only)	9	45	None	
December 1989	10	112	Trees, presence/absence	+ 0.903**
			Height of taller level of veg., extended part of margin	+ 0.002**
			Hedge height	+ 0.018*

[1]Wide margins given a value of 1, 2m margins of 2

Table 7.3b Effect of features and vegetation height on numbers of bank voles captured per margin plot as determined by STEPWISE Regression (see Table 7.3a for details)

Month	Trapping Session	No. animals	Significant factors	Parameter estimates
June 1988 (wide margins only)	1	61	Height of taller level of veg., original part of margin Height of shorter level of veg., extended part of margin	+ 0.009* + 0.027*
November 1988	4	171	Hedge, presence/absence Edge type[1]	+ 1.003** + 0.542**
February 1989	5	161	Edge type[1] Ditch, presence/absence Hedge height	+ 0.409** + 0.430* + 0.005**
March 1989	6	78	Edge type[1] Ditch, presence/absence Hedge height	+ 0.487* + 0.347* + 0.006**
May 1989	7	74	Ditch, presence/absence Other margin, presence/absence Hedge height	+ 0.613** - 0.487** + 0.004**
October 1989 (narrow margins only)	9	60	No of Hedge species	+ 0.386**
December 1989	10	71	Hedge, presence/absence Track, presence/absence	+ 0.467** + 0.421*

[1]Wide margins given a value of 1, 2m margins of 2

Table 7.3c Effect of features and vegetation height on numbers of field voles captured per margin plot as determined by STEPWISE Regression (see Table 7.3a for details)

Month	Trapping session	No. animals	Significant factors	Parameter estimates
June 1988 (wide margins only)	1	9	None	
November 1988	4	16	None	
February 1989 (for wide margins only)	5	17	Track, presence/absence	+ 0.322**
March 1989	6	16	None	
May 1989	7	2	None	
October 1989 (narrow margins only)	9	18	None	
December 1989	10	16	None	

Table 7.3d Effect of features and vegetation height on numbers of harvest mice captured per margin plot as determined by STEPWISE Regression (see Table 7.3a for details)

Month	Trapping Session	No. animals	Significant factors	Parameter estimates
June 1988 (wide margins only)	1	0	-	
November 1988 (wide margins only)	4	5	Hedge, presence/absence	- 0.387**
February 1989	5	14	Edge type[1]	- 0.224**
March 1989	6	8	None	
May 1989	7	0	-	
October 1989 (narrow margins only)	9	4	None	
December 1989	10	17	None	

[1]Wide margins given a value of 1, 2m margins of 2

Table 7.3e Effect of features and vegetation height on numbers of common shrew captured per margin plot as determined by STEPWISE Regression (see Table 7.3a for details)

Month	Trapping Session	No. animals	Significant factors	Parameter estimates
June 1988 (wide margins only)	1	10	Water depth in ditch	+ 0.084**
November 1988	4	11	Height of taller level of veg., original part of margin	+ 0.004*
February 1989	5	6	None	
March 1989	6	23	Pasture, presence/absence Height of taller level of veg., original part of margin	+ 0.220* + 0.013*
May 1989	7	30	None	
October 1989 (narrow margins only)	9	29	Hedge, presence/absence	+ 0.355*
December 1989	10	18	Track, presence/absence	+ 0.190*

Table 7.3f Effect of features and vegetation height on numbers of pygmy shrew captured per margin plot as determined by STEPWISE Regression (see Table 7.3a for details)

Month	Trapping Session	No. animals	Significant factors	Parameter estimates
June 1988 (wide margins only)	1	2	-	
November 1988	4	3	-	
February 1989	5	3	-	
March 1989	6	4	None	
May 1989	7	5	Height of taller level of veg., extended part of margin Height of shorter level of veg. on track	+ 0.005** + 0.080**
October 1989 (narrow margins only)	9	4	None	
December 1989	10	2	-	

Table 7.4a Mean numbers of wood mice captured per plot in presence of and in absence of significant habitat features shown in Table 7.3a

Month	Trapping Session	Effect of presence/absence of habitat features	Mean nos. per plot±SE	N (plots)
November 1988	4	Hedge, no track	4.90±0.46	39
		No hedge, no track	2.57±0.64	14
		Hedge and track:	2.38±0.68	8
		Track, no hedge:	1.00±1.10	3
March 1989	6	Narrow margin with hedge:	1.19±0.37	21
		Wide margin with hedge:	0.38±0.13	26
		Narrow margin, no hedge:	0.36±0.36	11
		Wide margin, no hedge:	0.17±0.17	6
May 1989	7	Trees:	5.33±0.88	3
		No trees:	1.48±0.33	29
December 1989	10	Trees:	4.00±0.95	5
		No Trees:	1.63±0.25	59

Table 7.4b Mean numbers of bank voles captured per plot in presence of and in absence of significant habitat features shown in Table 7.3b

Month	Trapping Session	Effect of presence/absence of habitat features	Mean nos. per plot±SE	N (plots)
November 1988	4	Narrow margin with hedge:	4.67±0.90	21
		Wide margin with hedge :	2.62±0.67	26
		Narrow margin, no hedge:	0.91±0.46	11
		Wide margin, no hedge:	0.00±0.27	6
February 1989	5	Narrow margin, no ditch:	2.00±1.00	6
		Narrow margin with ditch:	1.85±0.45	26
		Wide margin with ditch:	1.52±0.30	25
		Wide margin, no ditch:	0.57±0.37	7
March 1989	6	Narrow margin, no ditch:	2.33±1.11	6
		Narrow margin with ditch:	1.38±0.39	26
		Wide margin with ditch:	1.32±0.30	25
		Wide margin, no ditch:	0.14±0.14	7
May 1989	7	Ditch, no other margin:	2.37±0.47	27
		itch, no other margin:	0.77±0.43	13
		Ditch and other margin:	0.38±0.28	24
		Other margin, no ditch:	-	0
December 1989	10	Narrow margin, no ditch:	2.00±1.00	6
		Narrow margin with ditch:	1.85±0.45	26
		Wide margin with ditch:	1.52±0.30	25
		Wide margin, no ditch:	0.57±0.37	7

Table 7.4c Mean numbers of field voles captured per plot in presence of and in absence of significant habitat features shown in Table 7.3c

Month	Trapping Session	Effect of presence/absence of habitat features	Mean nos. per plot±SE	N (plots)
February 1989 (wide margins only)	5	Track:	0.35±0.02	28
		No track:	0.02±0.20	4

Table 7.4d Mean numbers of harvest mice captured per plot in presence of and in absence of significant habitat features shown in Table 7.3d

Month	Trapping Session	Effect of presence/absence of habitat features	Mean nos. per plot±SE	N (plots)
November 1988 (for wide margins only)	4	Wide margin, no hedge:	0.67±0.33	6
		Narrow margin with hedge:	0.24±0.15	21
		Narrow margin, no hedge:	0.18±0.12	11
		Wide margin with hedge:	0.04±0.04	26
February 1989	5	Wide margins:	0.41±0.07	32
		Narrow margins:	0.03±0.03	32

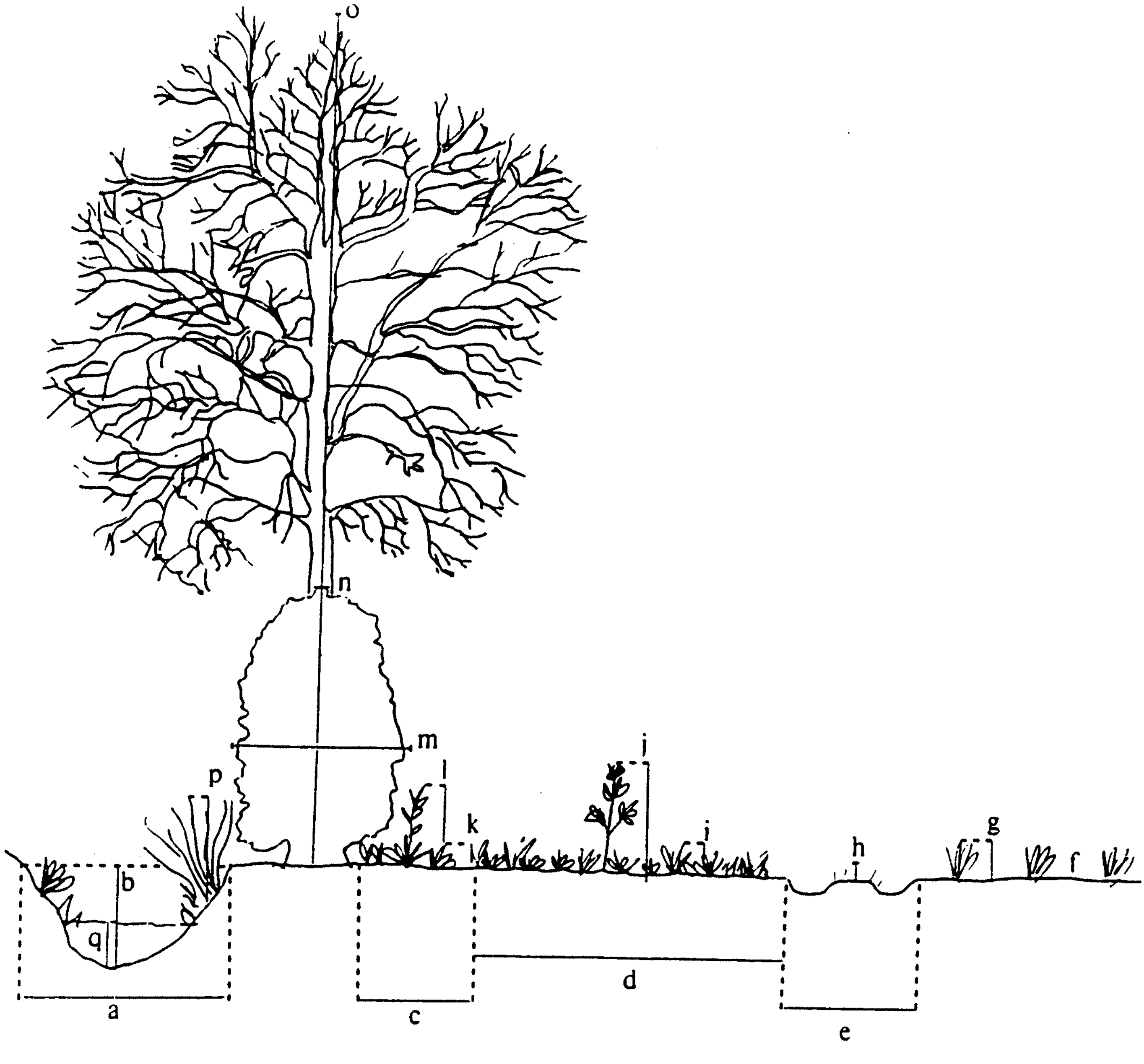


Figure 7.1 Habitat features measured at the beginning of the study:
a) width of ditch; b) depth of ditch; c) width of old margin; d) width of new margin; e) width of path, track, or road; o) height of trees;

and after each trapping session:

f) density of crop; g) height of crop; h) height of vegetation on path or track; i) height of shorter vegetation on new margin; j) height of taller vegetation on new margin; k) height of shorter vegetation on old margin; l) height of taller vegetation on old margin; m) width of hedge; n) height of hedge; p) height of vegetation in ditch; q) depth of water in ditch

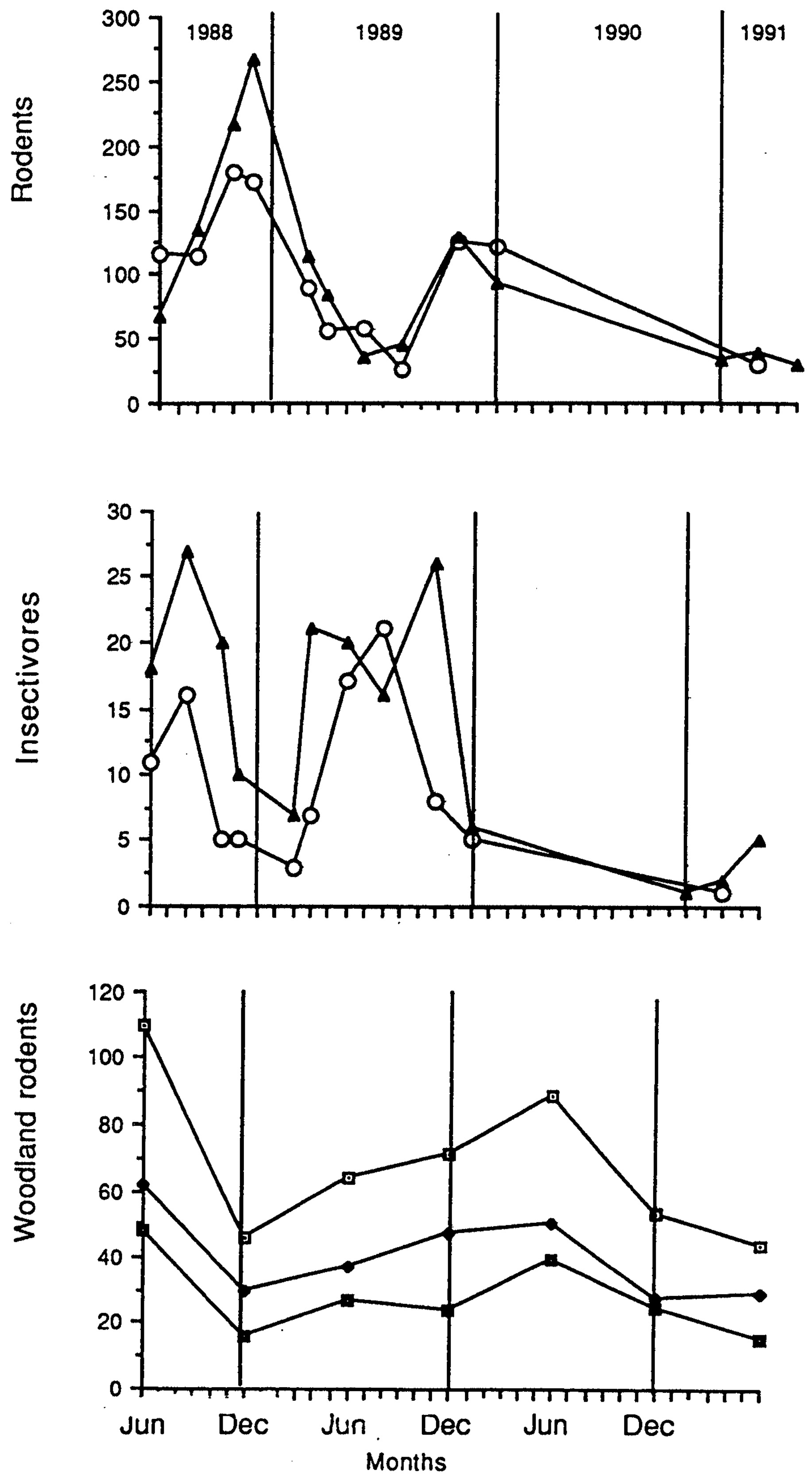


Figure 7.2 Total numbers of rodents (a) and insectivores (b) captured on wide margins (circles) and 2m margins (triangles). c): Woodland rodents (top line), wood mice (2nd line) and bank voles (bottom line) captured during the same period in nearby Wytham Wood

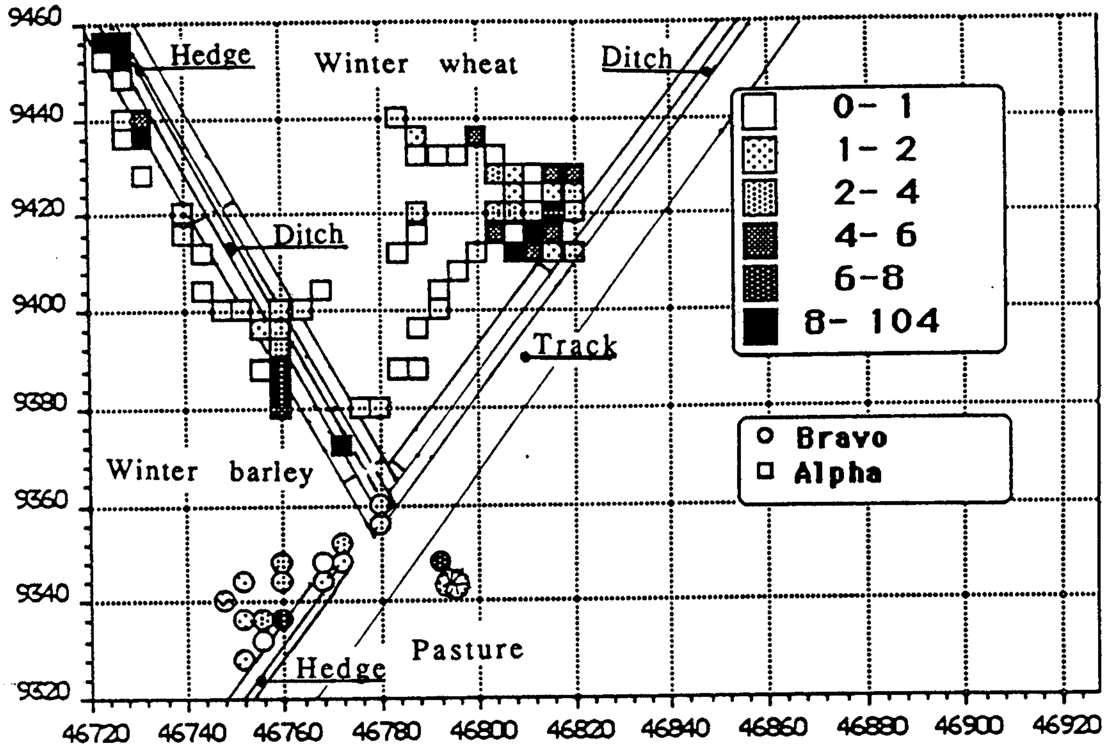


Figure 7.3a Number of fixes per 4m cells for 2 adult male wood mice, 2m margins, June

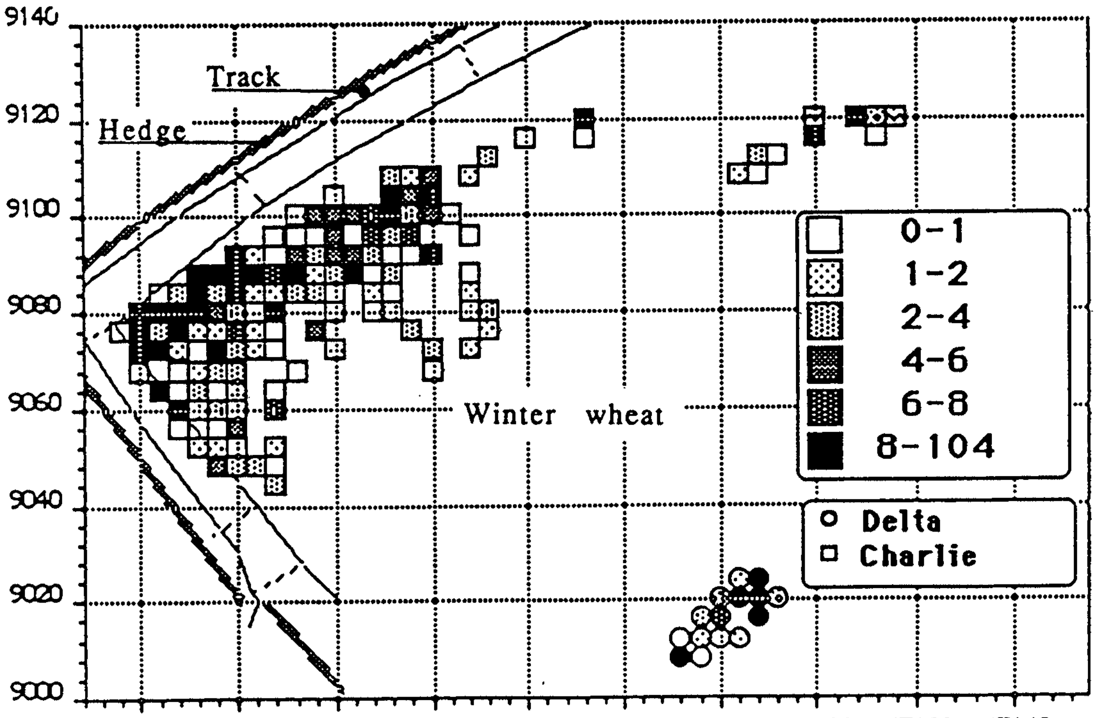


Figure 7.3b Number of fixes per 4m cells for 2 male wood mice, wide margins, June

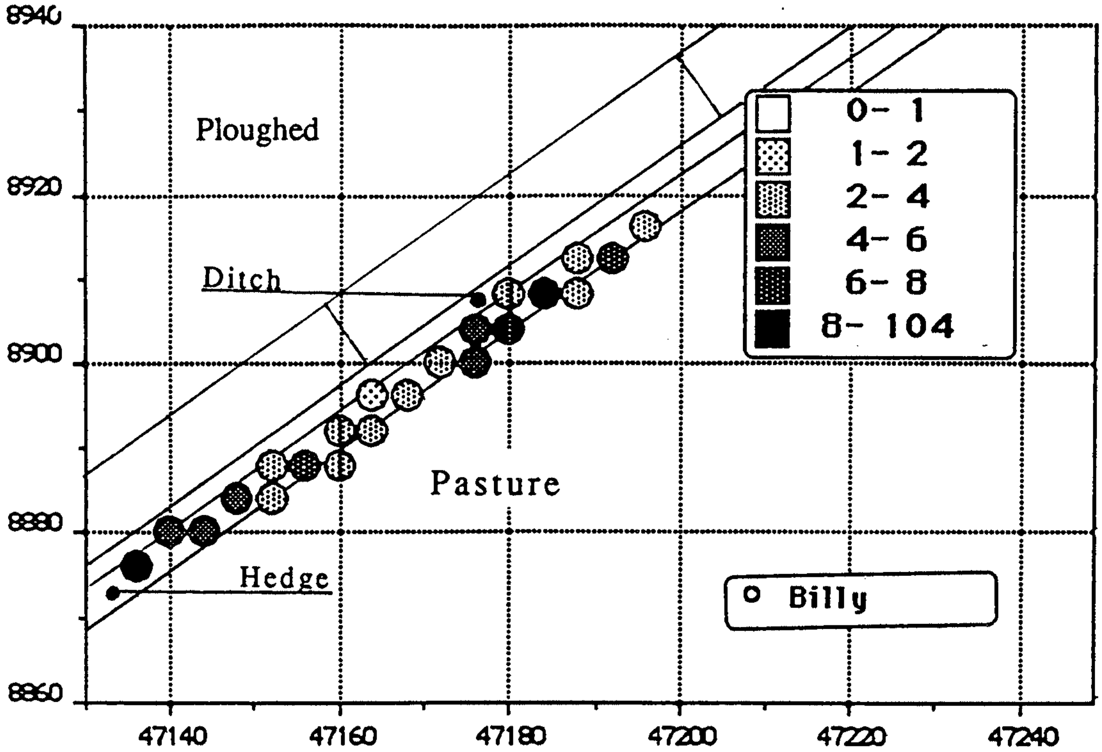


Figure 7.3c Number of fixes per 4m cells for 1 male wood mouse, wide margins, October

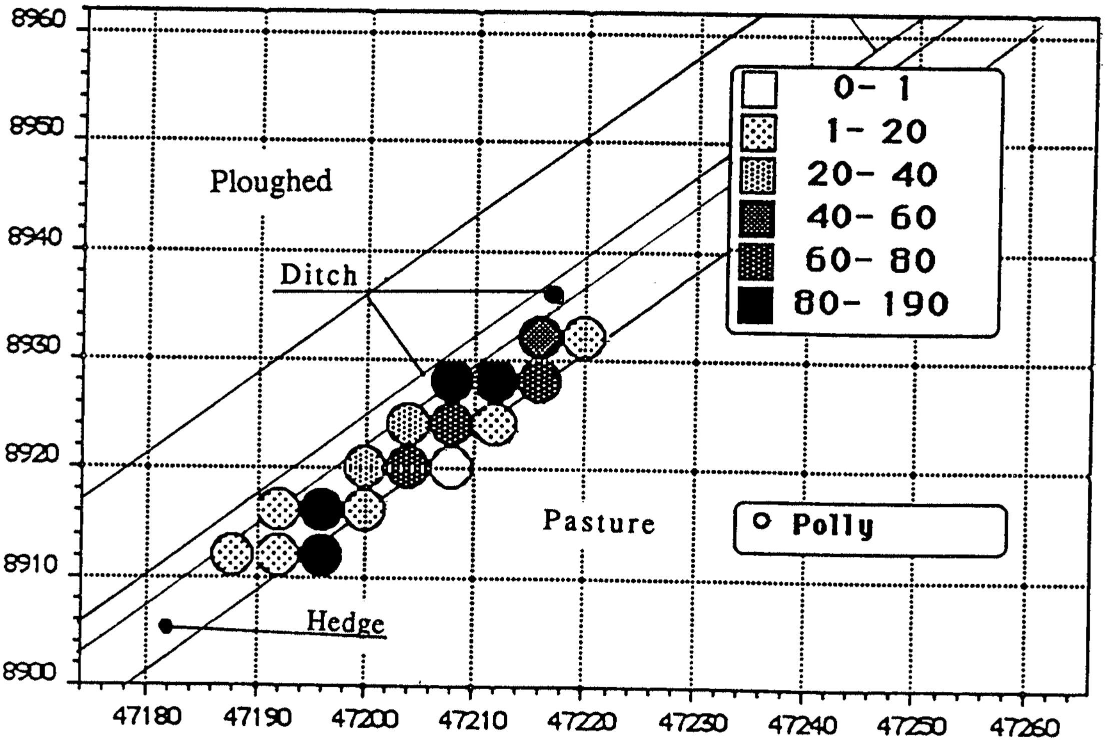


Figure 7.3d Number of fixes per 4m cells for 1 female wood mouse, wide margins, October

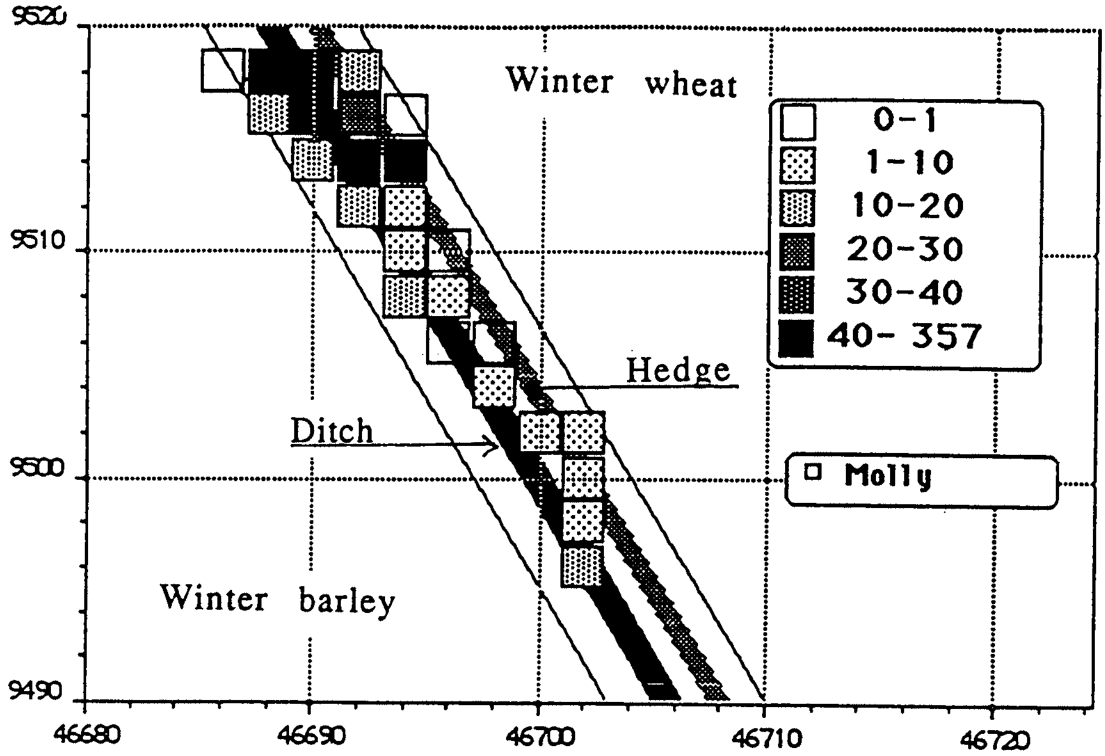


Figure 7.3e Number of fixes per 2m cells for 1 female wood mouse, 2m margins, January

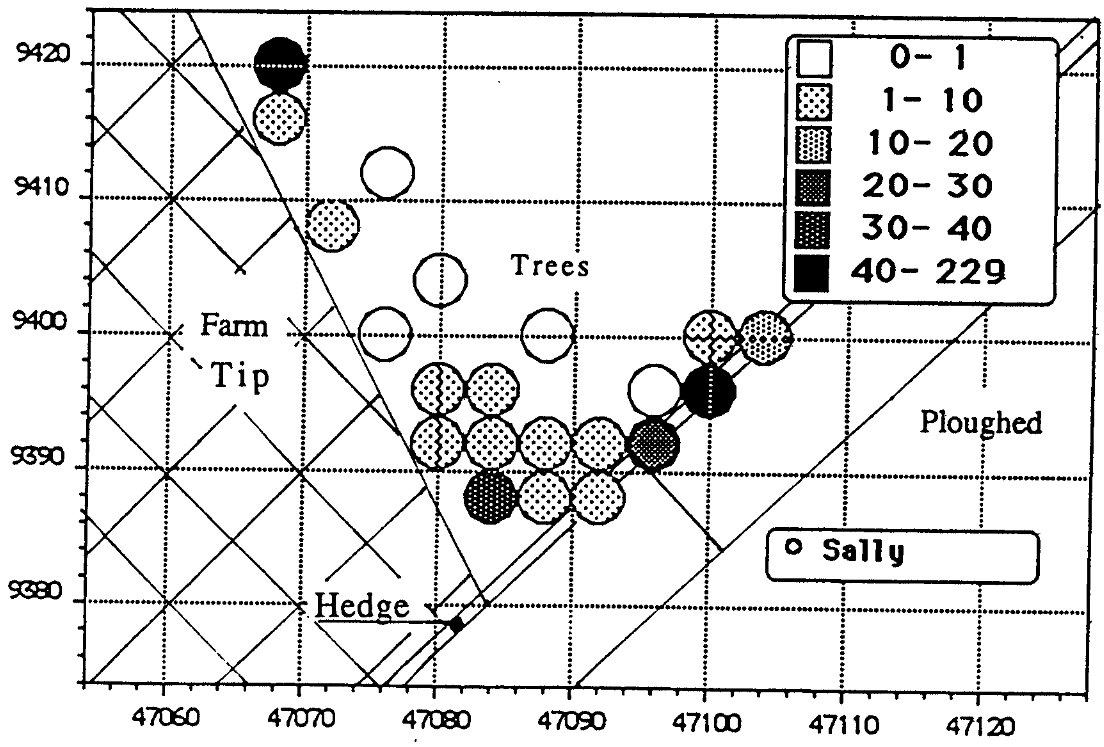


Figure 7.3f Number of fixes per 4m cells for 1 female wood mouse, wide margins, January