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CONTENTS

EXECUTIVE SUMMARY

Chapter 1: **Introduction**

Field margins are the primary uncropped habitats in lowland English farmland which could be exploited for nature conservation. As well as forming extensive networks of landscape corridors, they are potentially very rich habitats in their own right. Post-war agricultural intensification has resulted in severe degradation, as well as loss, of field boundary habitats, resulting in both loss of wildlife interest and severe weed control problems. In particular, erosion in width, elevation of soil nutrient status, pesticide drift and deliberate management with herbicides, have resulted in the perpetuation of species-poor, weedy floras on field margins.

The objectives of the two experiments described in this report were to seek practical ways of restoring the nature conservation interest of field boundaries whilst at the same time addressing weed control problems. The experiments were designed to elucidate general principles rather than to optimise the likelihood of achieving specific goals. In both of our experiments we assumed that exclusion of fertilisers and pesticide drift, and expansion in width of eroded boundaries, were essential prerequisites for restoration. We postulated that wildlife interests and weed control might both best be served by establishing dense, predominantly perennial, grassy swards.

Chapter 2: **Methods**

Both experiments were established at the Oxford University Farm at Wytham, west of Oxford, in autumn 1987.

In one experiment field margins were expanded to a total width of two metres. The effects were examined on plants, small mammals and invertebrates, of swards established either by natural regeneration or by sowing a wild flower seed mixture, and subsequently managed by contrasting mowing regimes (listed in Table 2.2). These varied in the timing and frequency of mowing and in whether or not the hay was collected. No treatment was mown more than twice a year. One treatment involved annual application of broad-spectrum herbicide. Ten experimental treatments were replicated eight times in complete randomised blocks. Within each block the ten treatments occupied contiguous 50m plots. The extended and original zones of the field margin were managed as a single unit. We refer to these two zones respectively as the 'new' and 'old' margins.

The relative frequencies of all plant species, the flowering densities of key weed species and the vegetation heights were monitored in permanent quadrats in the old and new zones of the field margin, in the crop edge and 10m into the crop. A total of 720 quadrats was monitored fifteen times over a four year period. Butterflies were monitored weekly during the summer months for three years, using standard transect methods. A more intensive study of two species using mark-release-recapture techniques was undertaken for one season. Other invertebrate groups were monitored over a four year period by D-Vac suction sampling and pitfall trapping. During this period the contents of 4,560 pitfall traps and 1,320 D-Vac samples were sorted. Small mammals were monitored over a 35 month period by Longworth trapping (a total of 58,368 trap-days) and radio telemetry (a total of 109 tracking hours)

In the second experiment, wider fallowed margins were sown with either a species rich or a conventional Timothy/Rye-grass/White clover ley. Both leys were managed with and without fertiliser. These four treatments were replicated and randomised around three fields, two of which were managed as hay and the third as silage.

Chapter 3: **Colonisation and succession**

Estimates were made of the rates of colonisation by natural regeneration of both the new and old zones of the field margins, of the likely sources of the colonists, and of the minimum distances that they were likely to have travelled. The relationships between both the relative abundance of species with different ecological characteristics and the species richness of the new margin flora and of potential source floras were examined. These colonisation processes were similar for all treatments, and the analyses presented are for all plots combined.

Large numbers of species, including forbaceous, woody and grassy perennials, colonised the new margins during the first six months after fallowing. The colonisation rate then dropped rapidly but remained fairly constant over the next two years. Net numbers of species present on the new margins peaked in the first year of fallow as a result of large numbers of annual colonists. The numbers of these annual species halved by the second year of fallow and the abundance of the remaining annual species also declined. The numbers and abundances of perennial species continued to increase slowly. Most of the colonists occurred at low frequency but, of the species that were abundant, most were problem weeds. Severe annual weed infestation is an inevitable feature of early succession on fallowed arable soils. Both the likelihood of its occurrence and its short-lived nature should be clearly understood by those embarking on programmes involving fallowing.

On the old field margins, recruitment of species in the first year of the experiment was also relatively rapid although much smaller than on the new margins. The net numbers of species increased slowly over three years. Most of the old margin flora was perennial and perennials increased as a proportion of the total during the experiment. Exclusion of agrochemicals from the old field margins appeared to have more impact on their flora than management over this period.

Most of the species colonising the new field margins were likely to have come from floras in the immediate vicinity, with negligible numbers arriving from sources beyond the experimental fields. With few exceptions, the seed bank was unlikely to be a source of novel species and was not a reliable predictor of either the qualitative or quantitative characteristics of the new margin flora. The crop flora, which was predominantly annual, was a reliable predictor of the annual component of the new margin flora only in the first year of succession. The old margin and field boundary floras were the best predictors of the composition of the new margin flora in subsequent years although a higher proportion of these floras than of other sources failed to colonise the new margins within three years. We therefore suggest that where the old field margin and field boundary floras are considered inadequate bases for establishing a new margin flora, seed mixtures must be considered as an alternative to natural regeneration.

Chapter 4: **The effects of management on plant species richness and diversity**

We analyzed the effects of sowing a wild flower seed mixture, mowing and annual broad-spectrum herbicide application, on the species richness and diversity of the colonising flora on the two metre margins.

Plant species richness and diversity were greater in swards sown with a species-rich wild flower seed mixture than in naturally regenerating swards for at least three years after sowing. A high proportion of both annual and perennial species in the local flora were excluded from sown swards. This is an advantageous effect where most potential colonists are weedy, but may be a disadvantage where the local flora contains desirable species which may be excluded. It also implies that species-poor wild flower seed mixtures are likely to remain relatively species poor.

Species richness and diversity were also influenced by mowing over a three year period, with mown swards having more annual and perennial species than swards which were left uncut. Differences between swards cut once and twice a year were not significant over this period, nor were those between swards from which cut material was removed and those on which it was left lying. The timing of mowing was, however, important, with swards mown in autumn having significantly more species than those mown in summer. Autumn mowing increased the numbers of perennial species from an early stage in the succession.

The species richness of old margin swards was not affected by mowing during this period and only started to be influenced by sowing in the second and third years of the experiment. We suggest that manipulation of species richness is likely to be a slower process in established swards than in secondary successional vegetation.

Swards sprayed annually with glyphosate were species poor but never differed significantly from unmown swards in total numbers of species. Spraying effectively re-created first year successional swards each year, with significantly higher numbers of annual species and lower numbers of perennials than on other uncut treatments.

Chapter 5: **The population dynamics and control of pernicious weeds**

Management to improve the wildlife conservation interest of field margins must be accompanied by improvements in weed control if it is to be acceptable to farmers. We analyze the extent to which both the course of succession, and management by mowing and by sowing wild flower seed mixtures, influence the populations of common annual and perennial pernicious weeds. Analyses are presented for three annual grasses (*Bromus sterilis*, *Avena* species and *Alopecurus myosuroides*), one annual forb (*Galium aparine*) and three perennial species (*Elymus repens, Cirsium arvense* and *Urtica dioica*).

Optimising the management strategies for controlling each of these species depends on understanding their life-histories and phenologies. All of the annual species were effectively eliminated from sown swards after only one year. The annual grasses, except *B. sterilis*, declined naturally in successional swards even in the absence of management. *B. sterilis* could present longer-term problems because it was able to persist in perennial-dominated, naturally regenerating swards. Control of all of these species could be significantly improved by carefully-timed mowing but equally could be significantly worsened by badly-timed mowing.

U. dioica increased very rapidly in the first year of succession, reflecting its dominance of the seed bank, but showed little further increase in subsequent years. Its frequency was reduced by mowing but increased on plots where cut material was left lying. It was controlled at very low levels in sown swards. *E. repens* increased substantially and *C. arvense* more slowly, by rhizome extension, over a four year period. In sown swards the increase in *E. repens* was halted and that of *C. arvense* reversed. Neither species was controlled by any of our mowing regimes although it is likely that they would be controlled by mowing more then twice a year. Spot-treatment with selective herbicides at an early stage in succession is likely to be a useful option where these species colonise naturally-regenerating swards. Further years' data, together with monitoring of soil nutrient status, are required to determine whether these species are controlled in the medium term by decline in the soil nutrient status.

Chapter 6: **The wild flower seed mixture**

The weed control properties of the wild flower seed mixtures help to outweigh their costs in situations where the local flora is unlikely to be an adequate basis for establishing perennial swards. Effective costs can also be reduced by tailoring mixtures to include only species that are likely to thrive on the soil type, and under the intended management regime, at a particular site. We consider the success of establishment and subsequent persistence of each of the species in our wild flower seed mixture and, where possible, analyze their responses to mowing.

There was little change in the numbers of sown species present on the new field margins over a five year period. Establishment on the old margins was extremely poor, although numbers of species increased slightly with time. Colonisation of adjacent, unsown plots by components of the wild flower seed mixture was also very slow.

In general the sown grass species established and remained at high frequencies. The only forb to follow this pattern was *Leucanthemum vulgare*. Six forb species increased slightly in frequency over the three year period but most decreased. In the subsequent two years some of the declining species started to increase, as seed from established plants germinated. The reasons for the generally poor establishment of sown forbs are discussed.

Many of the sown species showed significant responses to mowing. Some species were virtually eliminated by regimes under which other species thrived. Understanding of these responses is critical to the design of successful wild flower seed mixtures.

Chapter 7: **Habitat use by small mammals on farmland**

Populations of small mammals were monitored on the two metre and wide margins experiments and on conventionally-managed, narrow field margins, by trapping and radio-tracking. The responses of five species of rodent and three species of insectivore to contrasting management regimes and to other features of the field boundary were analyzed.

The numbers of both rodents and insectivores captured on the field margins showed annual fluctuations, with an overall decline between 1988 and 1991. This decline was unlikely to be attributable to the experimental manipulation of the margins because a similar decline was observed in nearby woodland.

We were unable to detect any effects of the experimental treatments on small mammals. We suggest that this resulted from the small size of the plots in relation to the animals' home ranges, and to the trapping technique used. In general the two metre margins were preferred to the wide margins sown with agricultural grass leys, particularly by bank voles. The presence or absence of certain habitat features often affected the numbers of small mammals captured and were more important than vegetation height. In particular, the presence of hedges and ditches had a positive effect on numbers of most of the small mammal species.

Radio-tracking of nine adult wood mice revealed a seasonal difference in their relative use of fields and field margins. In autumn and winter, when the fields were bare, the tracked animals confined their movements entirely to hedgerows and margins.

Small mammal conservation in arable farmland can be promoted by the presence of tall grassy field margin swards which provide both cover and food in winter, and by careful management of field boundary habitats.

Chapter 8: **The effects of field margin management on invertebrates**

The effects of mowing, sowing with a wild flower seed mixture and annual spraying with broad-spectrum herbicide, on the total abundance of invertebrates and on the abundance and species richness of spiders, leafhoppers and Heteropteran bugs, were investigated.

Mowing resulted in a significant reduction in the total numbers of invertebrates. The effects of mowing in summer were more severe and persistent than those of mowing in spring and autumn. The same effects were particularly pronounced for spiders and Heteroptera. They were slightly less severe for Auchenorrhyncha. For spiders, and to a lesser extent for Heteroptera, the deleterious effects of mowing were related to loss of structural complexity of the vegetation. The effects on Auchenorrhyncha were likely to be more dependent on the species composition of the swards. Although lack of management benefitted invertebrates in the short term, some management to prevent succession to scrub is essential in the medium term. Invertebrates are best conserved on field margins by avoiding summer mowing and by mowing once a year or less, preferably rotating the areas which are cut each year.

Swards sown with wild flower seed mixture supported higher total numbers of invertebrates than naturally regenerating swards. The species richness and abundance of spiders and the abundance of Auchenorrhyncha were higher on sown plots. Heteroptera, however, were unaffected by sowing.

Annual spraying with broad-spectrum herbicide was associated with reduced abundance and species richness of most of the groups considered. The effect was not usually detectable until some time after spraying, when the vegetation structure, rather than live plant species composition, started to be affected.

Chapter 9: **The abundance and distribution of butterflies on the field margins**

Butterfly transects were conducted to assess the distribution and abundance of all butterfly species on the two metre margins between 1989 and 1991. Butterfly abundance, species richness and diversity differed between experimental treatments. Plots which were either cut in spring and autumn or left uncut attracted more butterflies than plots cut in summer. Swards which were left uncut during the summer provided a continuity of nectar supply for adults, as well as optimising the chances of survival of earlier developmental stages. Butterflies were more abundant on wild flower seeded swards than on naturally regenerating swards. The wild flower seed mixture contained abundant nectar sources.

In 1991 transects were also conducted on a neighbouring farm with conventionally managed, narrow field boundaries. Butterflies were much more abundant on the expanded, experimental field margins than on conventionally managed margins. Species which were more abundant on the experimental margins included *Thymelicus sylvestris*, *Pyronia tithonus*, *Maniola jurtina* and *Coenonympha pamphilus*. These results indicated that extended-width, managed field margins supported larger populations of less mobile species, typical of semi-natural grassland, than conventionally managed field boundaries.

We conclude that field margins which are left uncut during the summer will be most beneficial for the majority of butterfly species. Wild flower seed mixtures are likely to act as effective supplements to, or replacements for, established plant species on arable farmland where the vegetation is impoverished. Although in our experiment the advantage of the sown swards to butterflies lay in their provision of nectar for adults, larval foodplants may also be included in seed mixtures.

Chapter 10: **Resource use by the meadow brown *Maniola jurtina* and the gatekeeper *Pyronia tithonus* on arable farmland**

A programme of mark-release recapture and behavioral observations of *Maniola jurtina* and *Pyronia tithonus* was conducted on the two metre margins experiment in 1991 to determine the ways in which their abundance was related to resource availability on the different field margin habitats.

All butterflies on both the grass margins and adjacent habitats within the study area were caught and marked. Significantly more individuals were captured on the field margins than on the field boundary or crop. On the margins more butterflies were captured on plots that were either cut in spring and summer or left uncut than on those cut in summer.

Perennial-dominated, grassy field margins thus appeared to be key elements in supporting these species in substantial numbers. Many aspects of butterfly behaviour also differed between the experimental treatments and between the sexes.

Both species fed on nectar from a very restricted range of the plant species flowering on the field margins. Of these, some species were preferred greatly to others. *Knautia arvensis, Centaurea* species, *Carduus acanthoides* and *Cirsium* species were the most important nectar sources and were utilised more than would be expected from their abundance in the swards. The supply of suitable and sufficient nectar sources must be ensured where butterfly conservation is an objective of field margin management.

Oviposition by both species was recorded on the field margins on a variety of sward types. Both species showed relatively low mobility although there was evidence of limited immigration into the study area during the flight season. We suggest from this, and from data on other life-history stages, that the extended field margins can provided the resources necessary to support substantial breeding populations of these two declining species.

Chapter 11: **The wide margins experiment**

Species rich and conventional Timothy/Rye-grass/White Clover leys, managed both with and without fertiliser, were used to examine the problems of promoting nature conservation, and of practical management, on set-aside land. The species rich ley, when cut in June only and grown without fertiliser, accommodated more sown and unsown species than any other treatment in both the establishment year and three years later. Over this period the numbers of sown species declined under all other treatments. This decline was exacerbated by the high rates of fertiliser applied under silage management. The numbers of unsown species declined under all treatments but the decline was greater under silage than under hay management and greater in the conventional than the species-rich ley.

The responses of the sown species to fertiliser had important influences on diversity. In the species rich ley *Dactylis glomerata* became strongly dominant under the fertiliser levels associated with silage management, resulting in a substantial loss of diversity. Fertiliser addition to the conventional ley promoted the dominance of *Lolium perenne* at the expense of *Trifolium repens* in the first year, although *L. perenne* dominated all treatment after three years. Inclusion of perennial cultivars of *L. perenne* in grass seed mixtures is likely to result in low species richness even in the absence of fertiliser addition. Where the aim is to encourage plant species richness, inclusion of *D. glomerata* in seed mixtures for very fertile soils should also be avoided. *Trifolium* cultivars should be excluded from leys intended for soils of low or declining fertility.

Fertiliser addition increased substantially the productivity of both the species rich and conventional leys. The unfertilised, species rich ley was least productive and is likely to present least problems under set-aside management, where cut material is left *in situ*. Although it contained the smallest biomass of sown species it contained the greatest biomass of unsown species. It nevertheless contained fewer problem weed species than other treatments, probably because most of these species compete most successfully on high fertility soils. We conclude that the use of relatively species rich grass leys for green cover on set-aside land has considerable advantages over conventional leys, both for nature conservation and for ease of management.

Chapter 12: **Discussion**

Realistic nature conservation objectives for field margin management must take into account agricultural requirements, such as weed control and access. The data in this report provide a robust basis for designing field margin management strategies that can increase the species richness of plant and animal communities and conserve populations of attractive, widespread but declining species, while effecting weed control. Many of the more detailed results in the report allow much finer-tuning of management advice to specific situations. Such advice is most likely to give the successful results which are essential if better conservation management practices are to be widely adopted. We therefore recommend that these and similar results are best communicated to farmers by trained advisors. Approaches such as expert systems need to be developed to improve the accessibility of this information to advisors.

The results of these experiments also provide a reliable basis for designing incentive schemes to capitalise on the immense nature conservation potential of the field margins network. Many of the results are of direct relevance to both nature conservation and agricultural objectives for the management of set-aside and other fallowed agricultural land.

1 INTRODUCTION

In this report we describe the results of experiments on the management of arable field margins conducted by the University of Oxford's Wildlife Conservation Research Unit between April 1987 and April 1992 under contract to The Nature Conservancy Council (1897-April 1991) and English Nature (1991-1992) (Contract F72-02-02).

1.1 Background

Field boundaries are the only uncropped habitat that is common to all lowland English farmland and on which all farmers could practise management favourable to the conservation of wildlife. They form an important unifying element in the farmed landscape and constitute corridors along which some species can move between remaining pockets of semi-natural habitats. They can also be very rich habitats in their own right, often comprising a woody element (the hedge), a wetland (the ditch), and grassland (the field margin). The juxtaposition of these elements can create a habitat much richer in wildlife than the sum of the individual elements. Our study is largely concerned with the grassy strips that adjoin boundary features such as tracks, hedges and ditches. Greaves & Marshall (1987) described these as 'boundary strips' but we follow the more common usage and refer to them as field margins.

Despite the enormous potential importance of field margins for wildlife and landscape conservation in the wider countryside, conservationists who are not actively involved in farmland issues have rarely considered them to be important, while farmers usually consider them to be a major management problem. There are good reasons for both of these views. The post-war drive for agricultural self-sufficiency, augmented by improved mechanisation and by the introduction of synthetic agrochemicals in the 1950's, led to drastic intensification of agriculture in lowland England (Mellanby 1981, Sly 1981). In addition to the well-documented loss of large areas of both unfarmed and agricultural semi-natural habitats (NCC 1984), the area and quality of smaller, uncultivated areas within the arable landscape was decimated. Hedge losses and changes in the suitability of the cereal headland for game birds have received considerable attention (Hooper 1987, Potts 1970, Sotherton *et al.* 1989) but until the late 1980's the concomitant losses of associated grassland were deplored only in the context of losses of foraging territory for barn owls *Tyto alba* (Bunn *et al.* 1982, Shawyer 1987).

Agricultural intensification resulted in three interconnected and deleterious changes to field margins. First, they were eroded in width by close-ploughing in attempts to maximise the area under cultivation. This loss of area relative to the periphery must have increased substantially the probability of chance local extinctions. The wildlife must have been further impoverished because most or all of the remaining width of the grassy margin and the boundary feature was then more vulnerable to agrochemical drift. Second, the soil nutrient status of field boundaries was increased by the use of broadcasting distributors which spread fertiliser across the field margin. This resulted in impoverishment of the plant communities as highly competitive species, such as *Urtica dioica* L. Common Nettle[1] and *Cirsium arvense* (L.) Scop. Creeping Thistle, that are able

[1] Scientific botanical nomenclature follows Clapham *et al* (1987) and English names follow Dony *et al* (1986)

to utilise high nutrient levels, increased. The proliferation of noxious and notifiable weeds at the crop edge led farmers to seek control by the best method then available: the use of herbicides. The bare patches of ground that these created were readily colonised by annual species, including pernicious crop weeds such as *Bromus sterilis* L. Barren Brome and *Galium aparine* L. Cleavers. This new problem elicited another round of spraying and so a vicious cycle was initiated that ensured the maintenance of a species-poor, early successional community dominated by pernicious weeds. These communities have not only failed to inspire conservationists but have also led farmers to perceive field margins as presenting severe management problems.

It is against this background that this project was commissioned by the Nature Conservancy Council (now English Nature) in 1987. Two factors made it timely to start to seek ways in which the enormous potential of field margins for wildlife conservation in the wider countryside could be realised. First, the work of the Farming and Wildlife Advisory Groups was increasingly identifying field margins as a problem area for which no reliable, research-based, management prescriptions were available. The design of the first of our two experiments, on the management of field margins expanded to a 2m width, was largely a customer-led response to a survey that we carried out of FWAG advisors in 1986. Second, it had become inevitable that the EC would introduce incentives to reduce cereal overproduction although the details of what became the set-aside scheme were not yet formulated. Expanded-width field margins were mooted as an option for obtaining environmental benefits from land removed from production, because of their potential for creating large-scale wildlife corridors. In our second experiment, we examined the wildlife benefits of contrasting management systems imposed on conventional agricultural and more species rich grass leys on 'set-aside' field margins. The experiment on the management of 2m wide field margins provided additional information on the establishment of green cover on fallowed arable land by natural regeneration.

Both of our experiments were designed to meet the primary aim of understanding the critical ecological processes important in field margin management, so that same principles could be applied elsewhere. To achieve this the experimental treatments were kept constant to minimise sources of variation in the results and so maximise their explanatory power. The alternative of using goal-orientated, systems experiment was considered inappropriate. Such experiments involve continual modification of the methods to demonstrate the viability of achieving preset goals and are commonly used in agro-environmental research (e.g. the LIFE experiment, see Jordon *et al.* 1990). However, this use of complex and variable treatments in even more complex and variable environments means that these experiments cannot provide robust information on the ecological processes underlying the changes that are observed (Macdonald & Smith 1991). It is precisely this information that is needed if results are to be extrapolated to different circumstances and sites. Moreover, for both conservation and agriculture, many goals are likely to be required. For most farmers the priority for field margins will be to minimise weed problems and management costs but many also want to promote game or amenity interests, or encourage birds, butterflies or aphid predators. Our use of fixed treatments meant that whilst some of our experimental plots provided better visual demonstrations than others of techniques for achieving particular goals, together they provided the information required to predict how to achieve a wide range of goals.

The layout of our experimental treatments was designed to maximise our ability to detect significant treatment effects by minimising the effects of environmental variation. The agro-ecosystem is notoriously variable because its long history of different cultivations and crops is superimposed on natural environmental variability. Thus, in both experiments, the treatments were replicated as much as possible. The number of treatments used was restricted by this priority for adequate replication. The 2m margins experiment used a blocked design so that the effects of soil-type and other environmental variables could be separated from treatment effects.

1.2 The two metre margins experiment

The primary aim of this experiment was to seek management methods that would provide a unified solution to the problems of restoring diverse and attractive plant and animal communities of value for nature conservation and of controlling weeds on the degraded margins of intensively farmed, arable fields. The management methods had to be realistic in terms of finance, labour and machinery. In practise we sought to reverse the deleterious trends in field margin management described above. Our experiments were carried out at the University farm at Wytham where the field margins exemplified all of these trends.

The margins had been eroded to a width of only *ca* 0.5 m by close ploughing. We expanded them to a total width of 2m by fallowing a strip of cultivated land at the edge of the field. A width of 2m was chosen for practical reasons: it was the maximum that farmers we consulted felt that they could 'spare' from their cropped area and it would accommodate both landrovers and farm machinery that might be used in management. Other widths might be appropriate on other farms. Fertiliser had been applied to the fields with a spinning disc distributor and was consequently deposited through the entire width of the field boundaries. This, combined with pesticide drift and deliberate herbicide application to the margins, resulted in communities dominated by pernicious weeds. *Cirsium arvense*, *Urtica dioica*, *Elymus repens* L. Gould Couch Grass, *Calystegia sepium* (L.) R. Br. Hedge Bindweed, *Bromus sterilis*, *Alopecurus myosuroides* Hudson Black-grass and *Avena* Wild Oat species were all locally dominant. We prevented spray drift and further direct application of fertiliser by simple modifications to the farm's machinery.

We aimed to restore more attractive and diverse communities on both the fallowed and original parts of the field margins by establishing swards of relatively uncompetitive, predominantly perennial, species typical of semi-natural grassland. We predicted that, with appropriate management, annual weedy species would eventually be excluded from such swards. To achieve this we chose a cost-free option of allowing natural regeneration of the local flora. Since in many intensive arable situations the local flora is severely impoverished, we also sowed a mixture of wild grasses and forbs.

These two types of swards were managed using contrasting mowing regimes. The regimes selected were all used commonly in nature conservation and agricultural management practise and *a priori* ecological considerations suggested that they were likely to give contrasting results. They also had contrasting practical and financial implications. The regimes were combinations of different timings and frequencies of mowing and of whether or not the cuttings were removed. A single, broad-spectrum herbicide treatment was used as a control for the effects of past management practise. The details of the regimes are given in Chapter 2 and the specific hypotheses tested for the different variables that we measured are described in the introductions to the relevant sections.

We collected baseline botanical data for this experiment in the summer of 1987, established the expanded margins that autumn, and started to impose the management treatments on the new swards from summer 1988. The first cycle of treatments was completed by the spring of 1989. Detailed data on the processes of colonisation and succession and the ways in which these processes are modified by management were collected until 1991. Throughout each year changes in the composition and structure of the swards, in both the original and the fallowed zones of the field margins, and in the adjacent crop, were monitored in permanent quadrats. Parallel data were collected for invertebrates, with particular emphasis on Araneae (spiders), Auchenorrhyncha (leaf-hoppers), Heteroptera and Carabid and Staphylinid beetles (see Chapter 8), using intensive suction sampling and pitfall trapping regimes. More detailed studies of the effects of field margin management on butterflies and small mammals were undertaken as doctoral research projects (the latter funded by Danish Government grants).

1.3 The wide margins experiment

The aim of this experiment was to evaluate, in terms of the benefits to wildlife and the ease of management, two inexpensive, contrasting grass leys that might be suitable for green cover on land removed from arable production. This could be for set-aside and its associated appendage schemes, for ESA requirements, for amenity or for alternative cropping. We used a conventional timothy/rye-grass/clover ley because such would be both readily and cheaply available to many farmers. Our second ley was relatively species rich and although more expensive, was within the price range of more specialist agricultural grass mixtures. It was based on 19th century herbal ley mixtures and included *Achillea millefolium* L. Yarrow and *Rumex acetosa* L. Common Sorrel. We also included *Ranunculus acris* L. Meadow Buttercup to improve its amenity value and further diversify its structure. Potential problems with the forage quality of this species are discussed in Chapter 11.

We compared the performance of both of these leys under conventional management, with fertiliser application, and under a fertiliser-free regime. Although set-aside does not allow the use of fertiliser, the comparison with and without fertiliser provides a better explanation of the biological mechanisms influencing diversity and productivity and an indication of the ways in which soils of differing fertilities might affect the results. The management regimes were appropriate either for hay or for silage production, with either one or two cuts a year and appropriate fertiliser applications where used. Our results are therefore equivalent to a set-aside situation where the hay is removed from the site, rather than dumped on the sward, but the information that they provide on productivity is a good indicator of the practicality of disposal of the cuttings.

The species composition of these swards and the biomass of each component species were monitored by intensive destructive sampling in 1988, the year of establishment, and again in 1991. We also monitored the relative use of the swards by small mammals from 1988 to 1991 and by butterflies in 1991.

1.4 Structure of the report

In this report we describe the results of the core areas of the project, which were funded by EN. More detailed analyses of many of the topics covered will be undertaken at a later stage, when more of the work is published in the scientific literature. These analyses will not obviate any of the conclusions drawn in this report but should provide additional information on field margin management. Some less central aspects of our data which were funded by other bodies (see Acknowledgements) are not covered in this report but will also be available when they are prepared for publication.

In Chapter Two we describe the study site, experimental design and general monitoring and analytical methods for both the 2m and wide margins experiments. Each of the following results chapters covers a major aspect of the monitoring data from either the 2m or wide margins experiment. In the introductions to each chapter we cover the details of the questions addressed by each type of monitoring. Detailed aspects of the methodology and analyses are also covered in the appropriate chapters. Summaries of key results are given at appropriate points in each chapter. The final section in each chapter covers the salient conclusions for management of species or groups considered. We have endeavoured to indicate at the end of the conclusions to each chapter where further analyses are planned and the ways in which these are expected to contribute to our understanding of the subject. We have also considered both the relevance of our results to the management of whole-field set-aside and the contributions that could be made to our current understanding of field margin management by future monitoring of the experiments. The tables and figures are presented at the ends of the appropriate chapters rather than interspersed in the text.

In the final discussion (Chapter 12) we draw on the results of both experiments to make recommendations on appropriate management regimes for achieving different sorts of goals in field margin management. We also point to areas where there are conflicts between the optimal management requirements for different interests.

2 METHODS

2.1 The study site

The experiments were conducted at the University of Oxford's farm at Wytham, west of Oxford. The farm occupies an area of approximately 364 ha and forms part of the Wytham estate. It is run as a commercial unit with dairy and beef cattle as well as arable. The fields around which our experiments were conducted (subsequently referred to as the 'experimental' fields), lie on the gentle, east-facing slope of Wytham Hill, between Wytham Woods on the hill top (*ca* 150m), and the river Thames. Figure 2.1 shows the location of the two experiments and the soil types in the fields concerned. Blocks 1 to 3 of the two metre margins experiment were located around fields on gravel terraces above the contemporary Thames floodplain. Their soils are sandy clay loams. The remaining blocks of the experiment, and most of the wide margins experiment, were on Oxford clays, with clay loam or heavy clay soils. Wytham Hill is capped by Corallian limestones and sandstones and water percolating through these strata emerges at the top of the Oxford clays in a marked spring line. The upper, western end of the fields where the wide margins experiment was conducted is frequently waterlogged for this reason.

All of the experimental fields had a long history of intensive arable use. In the years immediately prior to establishing our experiments they had been under continuous cereal production. From 1988 onwards they were returned to a rotation, usually with two years of winter wheat, one of winter barley and the fourth with a break crop of rape, maize or winter beans. The cropping regimes and agrochemical inputs to these fields were determined by purely commercial considerations and were not modified for the purposes of our experiments.

2.2 The two metre margins experiment

2.2.1 ESTABLISHMENT OF THE TWO METRE MARGINS

The experiment was established in October 1987. At that time the field margins around the experimental fields were 0.5 m or less in width. Following normal ploughing and disc harrowing of the fields, cultivated extensions to the margins, of about 1.5m, were fallowed to create a total width of 2m. We refer to the original margin as the 'old' margin and the fallowed extension as the 'new' margin. After the crops were drilled, the new margin, as well as the crop, was rolled.

Swards were established on the new margins either by allowing natural regeneration or by sowing a wild grass and forb mixture. We had intended to sow the seed mixture in autumn 1987 but the soil was too wet. It was sown instead in mid-March 1988. By that time there was quite a dense covering of plants on the new margins and so a suitable seed bed was restored by rotavating. The new margins on both the plots that were to be sown, and those on which natural regeneration was allowed, were rotavated so that both started with equivalent probabilities of colonisation. The seed mixture was sown on both the new and the old margins, but the absence of vegetation cover on the former resulted in much higher effective sowing densities. On the new margins the seeds were raked in after sowing and the margins rolled twice with a ring roller.

From the time that they were fallowed, the field margins were protected from fertiliser drift by fitting a boundary disc to the spinning distributor. Drift from pesticide applications was minimised by fitting taps to the outer two jets of the sprayer boom and turning off one or both, according to wind conditions.

In 1989 rape was grown as a break crop in some of the experimental fields. To prevent the crop lodging across the field margins a 2 m wide sterile strip was cultivated between the crop and the margins. From 1990 onwards sterile strips were used around all of the fields because they facilitated access to the experiment for visitors and for management operations.

2.2.2 THE SEED MIXTURE

The seed mixture comprised 17 forbs and 6 grasses in a 1:4 forb:grass ratio and was sown at a rate of 30 kg ha^{-1}, using untreated saw-dust as a carrier. It was supplied by Johnson's Seeds of Boston, Lincolnshire. All of the forbs were biennial or perennial species typical of semi-natural grasslands and all were found commonly in the Wytham area. The species and sowing densities are given in Table 2.1.

2.2.3 THE EXPERIMENTAL TREATMENTS

From the summer of 1988 the sown and naturally regenerating swards on the field margins (subsequently referred to as 'sown' and 'unsown' swards) were managed according to the regimes in Table 2.2.

The 'spring' cut was in the last week of April, the 'summer' cut in the last week of June and the 'autumn' cut in the last week of September each year. The first summer and autumn cuts were in 1988 and the first spring cut in 1989, a year after the swards were established. Cutting was done with an Allen scythe or a tractor-mounted, finger-bar mower, at a height of 4-5 cm. Glyphosate was sprayed as 3 lha^{-1} Roundup in 175 l water, in late June, from 1989 onwards. We used an Oxford precision Sprayer (calor gas at 30psi) with a boom to give a 2m swath. Spraying was done only under reliably dry conditions and so the precise date varied between years. In a few occasional places where the field boundary width was slightly greater than two metres, we under-applied on the old, rather than the new, zone of the margin.

Wherever possible full descriptions of the treatments have been used in the tables and figures in the results chapters. Occasionally, however, the following abbreviations have been used:

S/NC	Sown, not cut
S/SpAu	Sown, cut Spring & Autumn, cutting collected
S/SpSu	Sown, cut Spring & Summer, cuttings collected
S/Su	Sown, cut Summer, cuttings collected
U/NC	Not sown, not cut
U/SpAu	Not sown, cut Spring & Autumn, cuttings collected
U/SpSu	Not sown, cut Spring & Summer, cuttings collected
U/SpSu/L	Not sown, cut Spring & Summer, cuttings left *in situ*
U/Spray	Not sown, not cut, sprayed
U/Su	Not sown, cut Summer, cuttings collected

2.2.4 THE EXPERIMENTAL DESIGN

The ten treatments were each imposed on contiguous, 50m lengths of field margin ('plots') arranged in a randomised complete block design with eight blocks. As far as possible, each block fell within a single field so that the variance due to cultivation practices was minimised. The layout of the blocks is shown in Figure 2.2.

2.2.5 MONITORING

For monitoring purposes each plot was sub-divided into five, 10m lengths. Most monitoring was done within the central 30m to avoid edge effects at boundaries between different treatments.

Botanical monitoring

Most monitoring operations were based on a series of permanent quadrats established on six blocks of the experiment (blocks 1-6) in July 1987, before the new margins were fallowed. Permanent quadrats were chosen to give the maximum probability of detecting temporal changes within the relatively small area that it was feasible to sample within each plot. The sample size per plot was constrained by the large number of plots resulting from the overriding importance of adequate replication. These quadrats had the additional advantage of allowing precise mapping of changes in the extent of patches of individual species. Each quadrat was 100 x 50 cm, with the long axis placed parallel with the margin. In each plot the quadrats were positioned in the old margin, the new margin, 0.5 m into the crop and 10m into the crop. There were three banks of these four quadrats arranged as shown in Figure 2.3, giving a total of 720 quadrats.

Relative frequencies We monitored the relative frequencies of all higher plants in the permanent quadrats from July 1987 onwards. Each quadrat was subdivided into eight 25x25 cm subcells, in each of which the presence/absence of all rooted species was recorded. Species that were overhanging but not rooted in a cell were recorded separately. Additional information collected for each species record included the presence of seedlings, of flowers (for grasses) and of grazing damage.

The quadrats were monitored in July and November in 1987, five times in 1988, and four times in 1989 and in 1990. Monitoring was always done just before the cutting treatments and the spray treatment, so that longer-term, rather than proximate effects of the treatments were measured. Some of the quadrats in the crop were not monitored in some sampling rounds, when recent cultivations or herbicide applications had destroyed the flora. The crop quadrats were monitored until 1990, when the sterile strips were established and weed ingress from the margins into the crop could no longer be assessed. In 1991 only the quadrats on the sprayed plots were monitored for all species and the relative frequencies of the forb species in the seed mixture were monitored on the new margins, in sown plots, in July. In 1992 the relative frequencies of *Cirsium arvense* were recorded in late May, and of sown forbs on the new margins, in sown plots, in July.

Densities The numbers of panicles of the commonest pernicious annual grass weeds of cereal crops, *Bromus sterilis, Alopecurus myosuroides, Avena fatua* L. Wild-oat and *A. sterilis* subsp *ludoviciana* (Durieu) Nyman Winter Wild-oat were counted in the permanent quadrats in mid-June in 1989, 1990, 1991 and 1992.

Primula veris L. Cowslip, which was a component of the seed mixture, occurred in quadrats at frequencies too low to give adequate statistical comparison between treatments. To increase the sample size we counted the total numbers of flowering plants in each sown plot in all sown strips, in April 1991 and 1992. These counts were made on the plots in block seven as well as in the routinely monitored blocks 1-6 (above).

Vegetation height/density in permanent quadrats From 1989 onwards, we measured relative sward height and density using a type of sward stick modified from that designed by Boorman (described in Anon. 1986). Four discs, differing in diameter and weight, were dropped sequentially down a graduated aluminium pole positioned vertically in the vegetation. The height at which each disc came to rest was recorded. The smallest disc was always dropped last to avoid disturbing the vegetation for the larger disc readings. The readings for the largest disc were used as a measure of sward height and the smaller disc readings gave relative measures of the penetrability of the sward. The largest disc was 30 cm in diameter (49.4g), the second was 15 cm in diameter (55.8g), the third 5 cm in diameter (109g) and the smallest was 3 cm in diameter (205g). Measurements were made in the permanent quadrats in the old and new zones of the field margins. Readings were taken at four points in each quadrat.

Vegetation height was measured, using the largest disc, in June and September in 1989, in April, June and September in 1990, in March, April, June and September in 1991 and in June in 1992. Vegetation density was measured, using all four discs, in June each year until 1991. The measurements were always made just before the plots were cut. In this report we use measurements taken with the largest disc to examine the relationship between vegetation height and invertebrate abundance (Chapter 8.3.6). Analyses of results from the other discs will be presented elsewhere in the literature.

Grass weed size and fecundity In 1989 a maximum of ten, randomly selected, mature culms of each of *B. sterilis*, *Avena* species, and *A. myosuroides* were harvested from an area of $1m^2$, one metre away from the permanent quadrats in the old and new margin. These measurements were repeated for both the new and the old margins in 1990. Culm heights were recorded and the lengths of the flower heads (*A. myosuroides*), or spikelets (*Avena* spp. and *B. sterilis*) were measured to give an estimate of fecundity.

The results of this work are discussed in Chapter 5.3 but are presented fully in Watt *et al* (1990), together with parallel data obtained by growing these species in monocultures subject to the same cutting regimes as in the field experiment.

The seed bank The seed bank was monitored at the outset of the experiment to provide information on the origins of species colonising the new margins. Three samples were taken from the newly fallowed margins of each plot in blocks 1-6, between 4 and 15 December 1987. One sample was taken from each of the central three, 10m sub-plots. Each comprised four, 40mm diameter cores taken from within a 1m^2 area, using a gauge auger inserted to a depth of 25-30 cm (the plough horizon). The four cores comprising each sample were broken-up and thoroughly mixed. They were spread on a 1 cm layer of horticultural sand in a 15.5 x 21.5 x 5 cm plastic seed tray, lined with newspaper. The samples were interspersed with sterile loam controls (one per 14 samples) in a randomised block, on a glasshouse flat. The glasshouse received no artificial light but was heated to maintain the temperature just above freezing during the winter. Seedlings were identified and removed, and the soil was turned regularly, until April 1991. Those seedlings for which later growth stages were required for identification were potted separately.

Nectar sources For each 50m strip of margin the abundance of flowers of all broad-leaved species was estimated on a six point scale in each of three zones of the field boundary: new margin, the old margin, and any associated hedge, ditch or track. The scale was as follows:
1. If less than 25 flowers then the actual numbers of flowers was counted
2. 25-50 flowers
3. 50-100 flowers
4. 100-200 flowers
5. 200-500 flowers
6. More than 500 flowers.

Nectar sources were recorded seven times in 1991, during the period that butterflies were recorded on transect walks (see below). Recording rounds commenced on 7 May, 21 May, 19 June, 15 July, 8 August, 11 September and 9 October. Each round took from 2 to 7 days to complete, depending on flower abundance.

The numbers of individual flowers were assessed for as many species as possible. However for some species, such as many of the Umbellifers and Labiates, this was not feasible. For such species the data collected represent the abundance of compound umbels, racemes, flower spikes, *etc*. To obtain estimates of the numbers of flowers, equivalent to those for other species, we also collected data on the number of flowers per umbel, raceme, spike, etc.

For *Leucanthemum vulgare*, which was a very important nectar source, we collected precise data on the density of flowers in 1990, as well as estimating densities in 1991. Counts of the numbers of open flowers and of buds were made in 25x25 cm quadrats positioned without bias on the new margins in each of the four sown plots in each of six blocks of the experiment. Five quadrats were counted on each strip on 6-8 June, before the summer cut, and ten on 13-14 August, when flowering had recommenced following the cut.

We refer to the results of nectar source monitoring in Chapters 9.3 and 10.3 but they are presented in full by Feber (1993).

Species lists for each 50m plot From the outset of the experiment, lists were accumulated of the dates of first record of all plant species found on each experimental plot, in addition to the permanent quadrat records. Separate lists were maintained for the boundary feature (ditch, hedge or track) behind the plot, for the old and new zones of the plot and for the first 10m width of crop adjacent to the plot.

Invertebrate monitoring (excluding butterflies)

Invertebrates on the field margins were sampled by pitfall trapping and Dietrick Vacuum (D-Vac) suction sampling (butterflies were sampled separately in an intensive study described below). These two methods complement one-another, the former catching primarily cursorial, surface-dwelling species, and the latter, species living on or amongst the vegetation.

D-Vac sampling Our D-Vac samples comprised five, 30-second 'sucks' taken at 10m intervals along each plot (Figure 2.3). This approximates to sampling a total area of 0.5 m^2 per plot. Each sample was transferred to a polythene bag and immediately cooled to reduce activity. The live invertebrates were extracted from the debris by pootering. This was always done within a few hours of collection. The samples were stored in 70% alcohol until they were sorted.

To minimise variation in sampling efficiency, sample rounds were, whenever possible, completed within two-day periods, during dry, bright weather. In 1989, 1990 and 1991 we sampled three times a year, in May, July and September. The May and July samples were collected approximately two weeks after the spring and summer cuts and the September sample was collected in the second week of the month, before the autumn cut (the weather was too unreliable to delay this sample round until October, after the autumn cut). Two samples were thus collected between the summer and autumn cuts. On each occasion separate samples were collected from the old and new zones of the margins around six blocks of the experiment. We restricted the first two sample rounds in 1989 to only five of the ten treatments but all ten treatments were sampled at subsequent rounds. We sampled only once, in September, in 1987 and 1988. The 1987 samples were taken from the old margins only because the new margins were still fallow at that stage. In May and July 1989 we also took parallel samples from the crop adjacent to the field margins at distances of two and 10 m from the edge.

All of the samples collected were sorted to order. The Carabidae and Araneae from the pitfall trap samples and the Araneae, Heteroptera, Staphylinidae and Auchenorrhyncha from the D-Vac samples, were identified to species. Since it is rarely possible to identify all individual Araneae, Auchenorhyncha or Heteroptera to species, our analyses use minimum number of species. An individual not identified to species was recognised as an additional species in any sample if it represented a genus not previously recorded within that sample.

Pitfall trapping The traps comprised 7cm diameter, 8 cm deep, plastic cups containing ethylene glycol as a preservative and a drop of detergent to reduce the surface tension. The trapping positions were permanently marked by sections of plastic pipe inserted into the ground. During sample rounds the traps were mounted in the pipes, with their rims at surface level. Dilution of the preservative by rain, and consequent damage to the catch, was minimised by Plywood covers, supported 4cm above the traps by nails.

In October 1987, five traps were placed at 10m intervals in each plot on the old field margins of six blocks of the experiment. In 1988, when the new margins had become established, the traps were moved to the interface between the old and new margin. In 1989 the number of traps was reduced to four per plot, leaving a total of 240 (Figure 2.3).

The traps were left in position for discrete, ten-day sampling sessions. In 1991 and in 1990 we ran one session each month from April to October inclusive. In 1989 we ran three sessions, in May, July and September, and in 1988 and 1987 we ran single, September sessions.

Butterfly monitoring

Transect recording of all species The relative abundance of butterflies was measured using the transect recording methods developed and described by Pollard *et al* (1975) and Pollard (1977) with slight modifications. Transect recording is the standard method for the Butterfly Monitoring Scheme (Hall 1981) and so our data are comparable with those collected nationally from a wide range of sites.

Recordings were made on eight blocks of the experiment at least once a week from 1 April to 30 September in 1990 and 1991. In 1989 the first transect was recorded at the beginning of June. The following criteria were observed to standardise the results: (1) counts were started after 10.45 h British Summer Time and completed before 15.45 h, (2) counts were not made when the temperature was below 13°C; from 13°C to 17°C counts were made in sunny conditions (60% sunshine minimum); above 17°C conditions were sunny or cloudy and (3) counts were not made in windy weather when the wind was strong enough to prevent normal flight activity. Butterfly counts vary according to the time of day (Frazer 1973) so the time of the transect was standardised to reduce the variability. Each transect took around 2.5-3.0 hours to complete depending on butterfly numbers.

The transect route was divided into 50m sections which corresponded with the 50m lengths of experimental plots. Thus a count would be made of all species on each plot on each transect date. In addition to recording the distribution of butterflies in relation to the habitat type, this also simplified counting. We walked at a uniform pace and recorded all butterflies seen within prescribed limits. The linear nature of the study area made these limits easy to define; all butterflies seen in any zone of the field boundary and up to the first tramline in the crop were recorded. Butterflies were recorded up to approximately 5m ahead, and where butterflies flew ahead of the recorder only one record was made, for the location of the initial sighting. If stops were made to resolve identification problems, recording was resumed from the point where the walk was interrupted. If, occasionally, a butterfly could not be positively identified it was recorded as the commoner of the likely alternatives present in the area at that time.

In 1991, transects were conducted on a second study site. Denman's Farm was located approximately 10 km from the University Farm and was of similar aspect. The transect route at Denman's Farm was around four arable fields which did not have managed field margins. Transects were conducted on the same day, at the same time, on both farms by two recorders. This reduced any variation in results due to differing weather conditions and allowed paired sample analyses to be performed on the data. The same recorder conducted all the transects at Denman's Farm. The transect was divided into seventeen sections which corresponded to different habitat types around the fields. Often these sections were associated with each side of a particular field, but not in every case. Counts were made of all butterflies seen along the transect route following the method described above. Transects were conducted on both farms on seven dates in 1991.

Mark-release-recapture of *Maniola jurtina*[1] meadow brown and *Pyronia tithonus* gatekeeper A programme of mark-release-recapture was conducted in the summer of 1991. The study area covered blocks 3-6 of the experiment, which were located around a block of contiguous fields (Figure 2.2).

M. jurtina and *P. tithonus* caught in this area were intensively marked from 2 July to 15 September. Four habitat zones were sampled: the field margin, the associated boundary feature, the adjacent sterile strip (see 2.2.1) and the crop edge to the first tram-line. It was not possible to sample further into the crop on a systematic basis but searches in the crop indicated that butterflies were rarely located further than the first tramline and then were generally flying at speed. The habitat zones were equally accessible and during sampling the area was searched systematically for butterflies and in a manner that was consistent from one occasion to the next. Attempts were made to capture all butterflies which were seen in each zone of the study area on each visit. One or two visits were completed on each day of sampling, depending on the weather and butterfly abundance. Poor weather prevented sampling on several days throughout this period.

Butterflies were caught using a standard net and were marked uniquely at first capture. Marks were made with fine-tipped, Staedtler Lumocolor pens, and comprised inconspicuous dots on the ventral surface of the wings. The marking system followed the 1-2-4-7 method of Ehrlich and Davidson (1961). Captive *M. jurtina* and *P. tithonus* were marked after emergence and kept with unmarked individuals to test for adverse affects on the butterflies and to assess the longevity of the marks. The marks were shown to be non-toxic and permanent.

On initial capture the following data were recorded: (1) time and date of capture (2) location of capture according to block, experimental treatment and zone (3) distance along specified treatment to the nearest 10 metres (4) sex (5) behavioural activity of the butterfly immediately prior to its disturbance and capture and (6) physical condition of the

[1] Butterfly nomenclature follows Emmet & Heath (1990)

wings. Behavioural activities were classified as flying, resting, feeding or interacting with another butterfly. Resting is a general description applied to both basking with the wings open as well as resting with closed wings. If feeding, the species of plant was recorded. Oviposition was not recorded. Wing condition was ranked on a five-point scale similar to that used by Watt *et al* (1977) for *Colias* butterflies. The physical condition of each butterfly was classified as: 1, freshly emerged, wings still damp; 2, wings and other cuticle dry and hard, no visible damage; 3, noticeable wear of scales from wings or body; 4, wings showing tearing or fraying in their cuticle; 5, wings with extensive scale wear and cuticle damage.

On recapture, time, date, capture location, behavioural activity, reference number and wing wear were recorded. All butterflies were released at their point of capture. The procedure of capture, handling (including marking), and release was undertaken as quickly as possible, taking around 30 seconds per butterfly. There was no evidence of capture-release trauma such as escape reactions or other abnormal dispersal behaviour.

Both species are strictly univoltine and were sampled from the first date of recorded emergence to the final sighting. For *M. jurtina* this was 3 July to 22 August and for *P. tithonus* from 7 July to 2 September. Their flight periods coincided with the eight week period between the summer and autumn cuts (see 2.2.3) and consequently there was no management cut during the time they were on the wing.

Behavioural observations of *Maniola jurtina* and *Pyronia tithonus* Behavioural observations of M. jurtina and P. tithonus were conducted over the same period as the mark-release-recapture study. The study was conducted in the same area and, in addition, field margins around a further two fields on the farm which were under experimental management were also included (blocks 1 and 2). Individual butterflies were followed until lost, and for the duration of each observation a verbal description of the butterfly's activities and movements was recorded using a portable battery operated tape recorder. The method was adapted from that of Dover (1989b). The tapes were transcribed later for data analysis.

Small mammals

Longworth trapping Between June 1988 and April 1991 small mammals were monitored on 13 occasions by live-trapping in Longworth traps. Each trapping session lasted for 4 days and 4 nights. Pairs of traps were situated at the junction between the old and new field margins. Four pairs of traps were placed at 10m intervals on four of the treatments in each of eight blocks of the experiment (Figure 2.3). For the last nine trapping sessions the treatments monitored were those cut in spring and summer with hay collected on both unsown and sown swards, the sprayed treatment and the unsown, uncut treatment. In the earlier sessions the unsown spring and summer-cut treatment in which the hay was left lying was monitored instead of the sown, spring and summer cut treatment.

Small mammal numbers were also monitored on two conventionally-managed field margins for 4 days in October 1989. Both margins separated ploughed fields from grazed pasture. One had a ditch and a hedge and the other a fence only.

The traps were baited with wheat for rodents and with fly pupae (*Calliphora* sp.) for shrews, and were filled with hay for bedding. They were checked every 8 h except during the hottest part of the summer, when the maximum interval during the hottest part of the day was 4 h. On initial capture rodents were numbered using fur-clipping (Twigg 1975), and at each capture they were weighed and sexed and their reproductive state was assessed. Females were classified as: not in breeding condition, perforate, pregnant or lactating. Males were classified according to whether or not they had descended testes. Insectivores were identified to species and weighed.

Habitat recording At the beginning of the study the following habitat variables were recorded: presence or absence of hedges, ditches, trees, roads/tracks/paths, bordering pasture and bordering experimental margin; whether a strip adjoined another experimental strip at one end only; the dominant hedge species at each trapping point; and the dimensions of ditches, trees and tracks. After each trapping session the maximum and minimum heights of vegetation in the old and new margins, the dimensions of hedges and the water depth and vegetation height in ditches were measured at each trap point. The crop type in the adjoining field was also recorded. The density of the crop 2m into the field was assessed on a 1 to 4 scale from dense to very sparse.

Radio telemetry The amounts of time spent by wood mice in the field, hedgerow and field margin at different times of the year were estimated from radio telemetry data. Radio-transmitters (Mouse-type collars, Biotrack, Dorset) were fitted to animals caught by Longworth trapping. This type of monitoring was confined to wood mice for several reasons. Anatomically they are more suited to radio-tagging than other small mammal species, as they have a slim neck relative to their head size. They are the most mobile of the species recorded on the field margins (Wolton 1985), feeding on a wide selection of species (Bailey 1970; Campbell 1974; Eldridge 1969; Hansson 1971; Miller 1954; Watts 1968) and needing to travel some distance every night in order to obtain sufficient food. Their movement patterns are therefore assumed to be fairly accurate reflections of their habitat preferences. Data were gathered for six adult males and three adult females (total number of tracking hours =108h 46m).

2.2.6 DATA BASES

In addition to our monitoring data we built-up several data-bases of supplementary information about both the environmental variables associated with each experimental plot and the ecological attributes of many of the plant and invertebrate species recorded. The former enable us to analyze the effects of sources of variation other than our treatments. They include plot-specific information on adjacent and opposite plots and crops (including cropping and agrochemical application), and on the dimensions and dominant species of associated ditches and hedges. The latter enable us to analyze our data by life-history or other ecological attributes as well as by species.

2.2.7 ANALYSES

The complete randomised block design of the experiment enabled us to remove environmental variation resulting from differences between blocks from the effects of our treatments. All analyses of the effects of the experimental treatments on the measured variables were performed by analyses of variance using PROC GLM of SAS (SAS Institute 1988). Specific hypotheses about the relative effects of particular treatments were tested by planned comparisons. Unplanned comparisons of treatment means were used to detect other significant differences.

For most purposes we initially performed a 2-way analysis of variance to detect significant differences between treatments. Where necessary, appropriate transformations were used to normalise the data. We used planned comparisons to test for differences (1) between the treatment in which the hay was removed and that in which it was left lying (both cut in spring and summer) and (2) between the sprayed treatment and the uncut treatment. Unplanned comparisons were then made between all treatment means in order to detect significant differences that were not predicted by our initial hypotheses.

We then excluded the treatment in which the cut hay was left lying and the sprayed treatment and performed a further, 3-way, analysis of variance on the remaining treatments, which form a 2x4 factorial structure (ie. sown or unsown x 4 types of cut x 6 (or 8) blocks). This allowed us to split the treatment effect into main effects of sowing and cutting. For most purposes we then used planned comparisons to test for differences between: (1) treatments that were cut and the uncut treatment (2) the treatments cut once and those cut twice, and (3) the spring+summer and spring+autumn-cut treatments. Other hypotheses appropriate to particular variables were also tested by planned comparisons and have been described in the relevant results chapters.

Where data could not be normalised by transformation, Friedman's non-parametric method for randomised blocks was used *in lieu* of two way analysis of variance. *A posteriori* tests between pairs of means were carried out using Wilcoxon's critical range method (Colquhoun 1971), or the rank sum multiple comparison test of Mcdonald & Thompson (1967).

2.3 The wide margins experiment

2.3.1 ESTABLISHMENT OF THE EXPERIMENT AND EXPERIMENTAL DESIGN

The experiment was conducted on the fallowed margins of three arable fields (Figure 2.1). The two smaller fields were adjacent to one another and together spanned the same range of soil types as the largest field. In each year of the experiment they were under the same crop and we therefore treated the margins around them as a single experimental unit.

Strips of land around the edges of the fields were fallowed following ploughing, in autumn 1987. Those around the largest field were 9.6 m wide and were managed as silage (the 'silage' margins). Those around the two smaller fields were 7.2m wide and were managed as hay (the 'hay' margins). We chose the different widths to accommodate the harvesting equipment available at the farm.

Two grass ley mixtures were drilled into freshly tine-harrowed ground in early April 1988. The sown margins were chain harrowed and rolled. They were subsequently protected from the drift effects of agrochemical applications in the fields by the use of a 'headland deflector' disc on the fertiliser spinner and by turning off one or two jets on the sprayer boom, according to wind conditions.

The 'conventional' grass ley comprised six varieties of *Lolium perenne*, with a wide range of maturation times, a late and an early variety of *Phleum pratense* and *Trifolium repens* (variety Blanca). The 'diverse' ley contained *Cynosurus cristatus*, *Dactylis glomerata*, *Festuca pratensis*, *Phleum pratense*, *Poa pratensis*, *Trisetum flavescens*, *Ranunculus acris*, *Achillea millefolium* and *Rumex acetosa*. Both leys were drilled at a rate of 30 kg ha^{-1}.

The margins of both the large and the two smaller fields were divided into contiguous, 50m-long plots, half of which were randomly assigned to the conventional ley and the other half to the diverse ley. Amongst each ley type, half of the plots were treated with fertiliser and half received none. Each of the four ley/fertiliser combinations managed as silage was replicated six times. Those managed as hay were replicated seven times. The layout of the plots is shown in Figure 2.2.

The fertilised plots on both the hay and the silage margins received the same fertiliser treatment during the establishment year of 1988. They were drilled with 183 kg ha^{-1} N, 97.5 kg ha^{-1} P and 140.6 kg ha^{-1} K and received a further 105 kg ha^{-1} N in mid-June. From 1989 onwards, fertiliser applications were the same as those on silage and hay crops elsewhere on the farm, and varied slightly from year to year. In general, the silage margins received a total of around 180 kg ha^{-1} N, 160 kg ha^{-1} K and 104 kg ha^{-1} P in one or two applications prior to the first cut, and 200 kg ha^{-1} N and 116 kg ha^{-1} K prior to the second cut. The hay margins received the same fertiliser application as the silage margins prior to the first cut, but received no subsequent applications. The fertiliser was applied precisely, using a pneumatic spreader.

In 1988, the establishment year, both the silage and hay margins received a single cut (with cuttings removed immediately) on 24 August. In subsequent years the silage was cut in late May and late July and the hay in the first half of July. Because of extremely dry conditions, no second silage cut was taken in 1990.

2.3.2 MONITORING

Botanical monitoring

Species composition and biomass We monitored the biomass and species composition of the plots in 1988 and 1991. All of the vegetation in four 25x25 cm quadrats, placed at random co-ordinates within 30x3 m areas positioned centrally within each 50m plot, was harvested by clipping at ground level. In 1988 this was done in the last week of July, prior to the cut. In 1991 the hay margins were monitored in mid-June, prior to the cut, and the silage margins were monitored in mid-July, just before their second cut. All samples were sorted to species and each species was dried separately (85°C for 48h) and weighed.

Butterflies On five occasions in 1991 the relative abundance of all butterfly species was recorded on a standard transect, covering all plots, using the same methodology as described above for the 2m margins (Section 2.2.5).

Small mammals Between June 1988 and April 1991 small mammals were trapped during 11, four day/four night sessions, using Longworth live-traps. Pairs of traps were positioned at 10m intervals at the junction between the old and new field margins. Four pairs of traps were used in each plot. Eight replicates of each of the four treatments (both leys and fertiliser levels) were monitored. The trapping protocol was the same as that used on the 2m margins (2.2.5 above).

2.3.3 ANALYSES

Analyses of biomass and species richness data, and of diversity indices, were performed on the mean values for the four quadrats harvested from each plot. Analyses of change in species richness or diversity between years were based on the ratio of the plot means in 1991 and 1988. Where necessary the data were normalised by appropriate transformations. They were analyzed by one-way ANOVA of the four treatments using PROC GLM in SAS (SAS Institute 1988). Tukey's Studentised Range test was used to identify significant differences between treatment means.

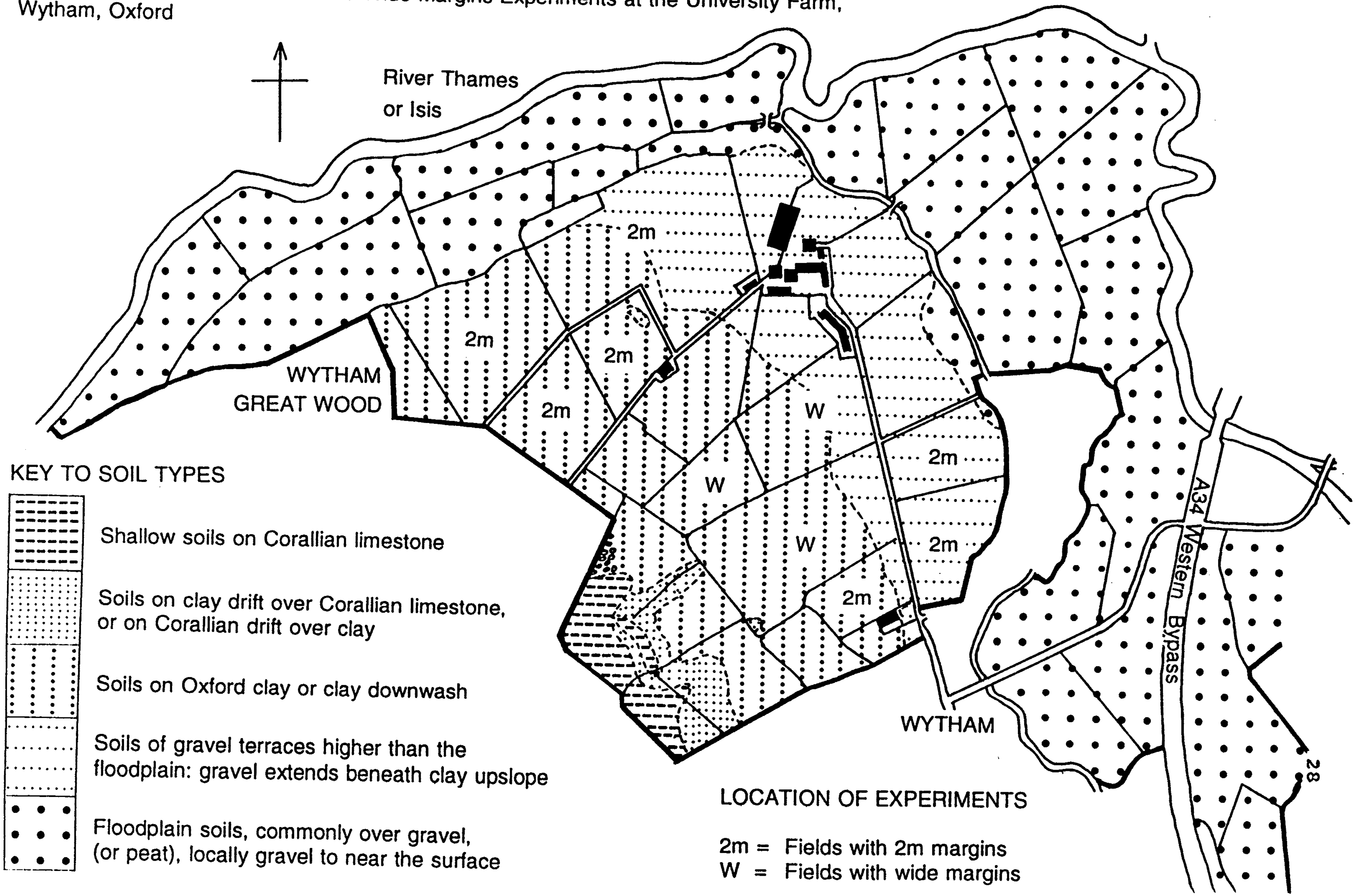
Table 2.1 The composition of the wild flower seed mixture

		Seeds sown m^{-2}
Forbs:		
Centaurea nigra	Common Knapweed	21.6
C. scabiosa	Greater Knapweed	7.5
Clinopodium vulgare	Wild Basil	90.0
Galium verum	Lady's Bedstraw	23.1
Hypericum hirsutum	Hairy St John's-wort	172.8
H. perforatum	Perforated St John's-wort	259.2
Knautia arvensis	Field Scabious	7.5
Leontodon hispidus	Rough Hawkbit	7.0
Leucanthemum vulgare	Oxeye Daisy	172.8
Primula veris	Cowslip	39.6
Prunella vulgaris	Selfheal	38.9
Ranunculus acris	Meadow Buttercup	34.6
Ranunculus bulbosus	Bulbous Buttercup	12.1
Silene latifolia subsp *alba*	White Campion	23.1
Silene vulgaris	Bladder Campion	34.6
Torilis japonica	Upright Hedge Parsley	14.4
Tragopogon pratensis	Goat's Beard	3.0
Grasses:		
Cynosurus cristatus	Crested Dog's-tail	786.0
Festuca rubra 'commutata'	Red Fescue	600.0
F. rubra 'littoralis'	"	360.0
Hordeum secalinum	Meadow Barley	60.0
Phleum pratense subsp *bertolonii*	Smaller Cat's-tail	480.0
Poa pratensis	Smooth-stalked Meadow-grass	1080.0
Trisetum flavescens	Golden Oat-grass	720.0

Table 2.2 Management regimes for the conservation margins experiment

UNSOWN	SOWN
Not cut	Not cut
Cut in summer hay collected	Cut in summer hay collected
Cut in spring and summer hay collected	Cut in spring and summer hay collected
Cut in spring and autumn hay collected	Cut in spring and autumn hay collected
Cut in spring and summer Hay left lying	
Sprayed once a year with glyphosate	

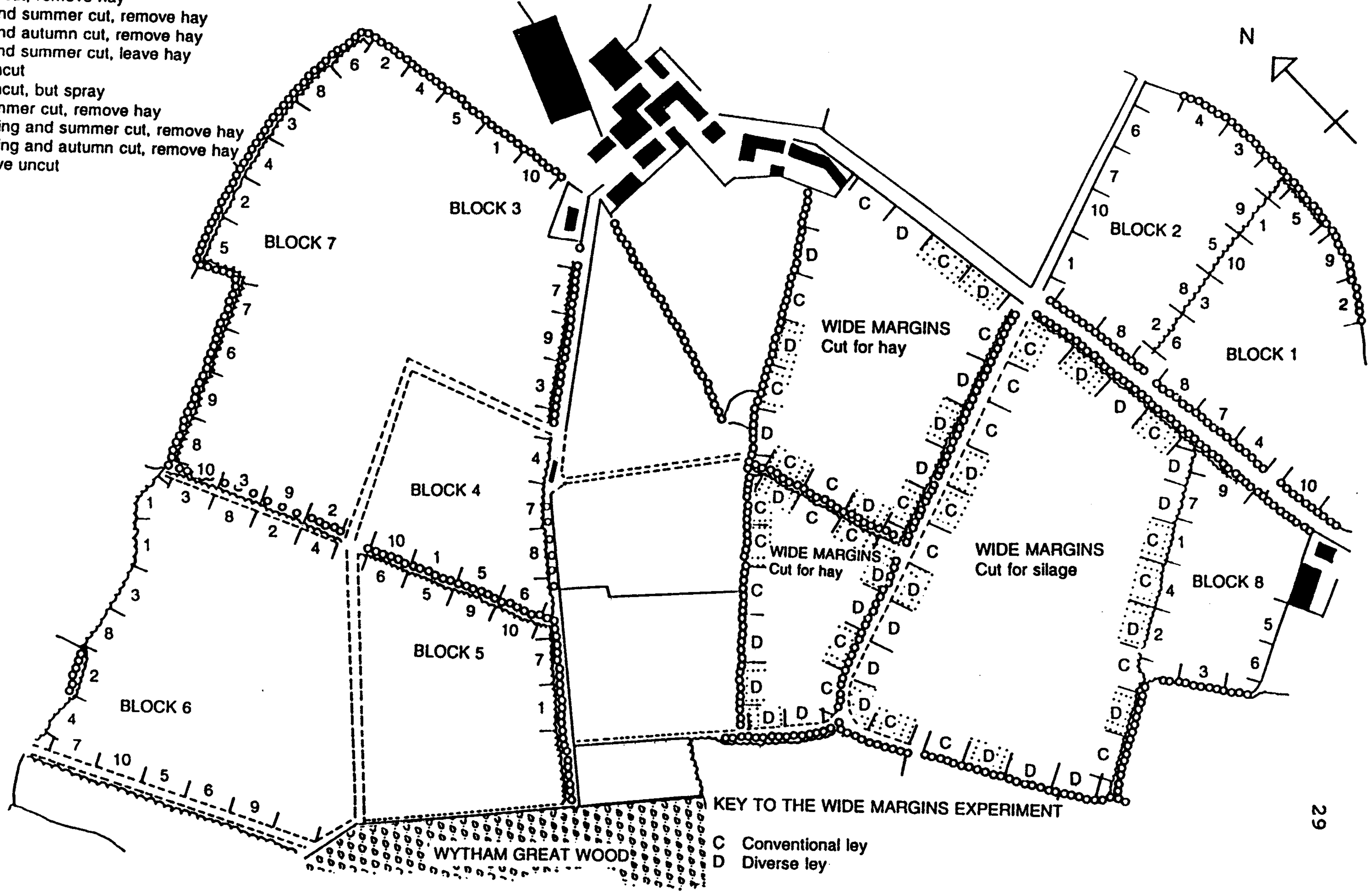
FIG. 2.1 The location of the 2m and Wide Margins Experiments at the University Farm, Wytham, Oxford



KEY TO THE 2m MARGINS EXPERIMENT

1. Summer cut, remove hay
2. Spring and summer cut, remove hay
3. Spring and autumn cut, remove hay
4. Spring and summer cut, leave hay
5. Leave uncut
6. Leave uncut, but spray
7. Sow, summer cut, remove hay
8. Sow, spring and summer cut, remove hay
9. Sow, spring and autumn cut, remove hay
10. Sow, leave uncut

FIG. 2.2 Lay-out of the 2m and Wide Margins Experiments at the University Farm, Wytham, Oxford



KEY TO THE WIDE MARGINS EXPERIMENT

C Conventional ley
D Diverse ley

Fertiliser application
No fertiliser

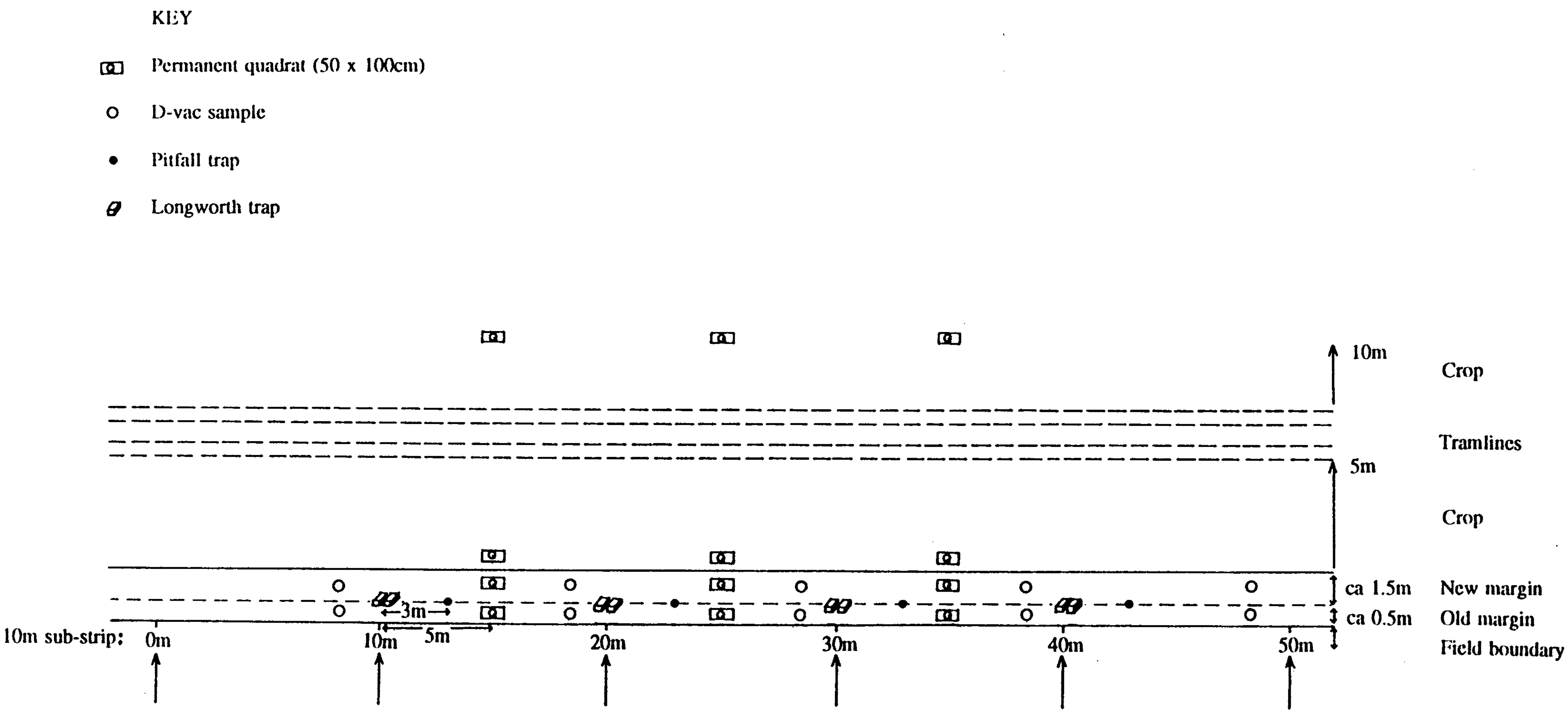


Figure 2.3 Location of permanent quadrats, pitfall traps, D-vac samples and Longworth traps within an experimental field margin plot

3 COLONISATION AND SUCCESSION

3.1 Introduction

Most of this report is devoted to an examination of the ways in which simple management regimes can be used to manipulate secondary successional communities that develop on fallowed arable field margins. In this chapter, however, we examine the processes of plant colonisation and succession on fallowed field margins. We address questions which are fundamental to predicting the likely success or failure of natural regeneration as a means either of establishing vegetation with an acceptable or 'desirable' species composition on extended field margins or of restoring degraded field margins. In particular we ask first, whether the quantity and quality of the colonising species are likely to provide the basis for developing an acceptable flora, and second what determines both of these characteristics.

Before the UK set-aside scheme was introduced in 1988 (Anon 1988), most studies of secondary succession on fallowed farmland were atypical of the majority of contemporary, intensively-farmed arable areas. Succession on the so-called 'old fields' in the USA, which is well documented in the literature (e.g. Beckwith 1954), took place on relatively low-fertility soils which had not been subject to several decades of agrochemical applications. The two most pertinent studies from the UK are also, for different reasons, atypical of modern arable farmland. Gibson & Brown (1991, 1992) studied succession on an abandoned arable field (Upper Seeds) within an enclave in Wytham Woods, close to our own field site. The soils are skeletal, overlying Corallian limestone, and the field was created only 21 years before it was abandoned in 1981, and cultivated with low inputs. The soil nutrient status was therefore likely to be lower and the seed bank richer than in most arable situations. The potential seed supply was likely to be unusually rich not only because of the seed bank but also because of the close proximity to several pockets of rich, ancient limestone grassland. The abandoned valley bottom fields studied by Graham & Hutchings (1988a & b) were also surrounded by rich seed sources from calcicolous grassland, at Castle Hill NNR in Sussex, although, in contrast to Upper Seeds, the soils were deeper and had been intensively managed. Both of these studies nevertheless provide detailed information on the relationship between sources of colonists and the composition of the secondary successional flora which can be compared with those obtained from this study.

More recent studies of secondary succession, in response to the set-aside schemes, have concentrated on more typical modern arable farmland. They have included several broad-scale surveys of the species richness and life-history composition of the flora of set-aside fields of different ages (e.g. Poulton & Swash 1992, Wilson 1992, Fisher *et al* 1992). More intensive studies have concentrated on the effects of distance from the field boundary and the soil seed bank on the species composition of the colonising flora (Rew *et al* 1992), although most of the research emphasis has been on the agricultural implications of set-aside vegetation for the seed bank and seed rain (e.g. Lawson *et al* 1992, Jones & Naylor 1992). None of these studies provides information equivalent to that from both our own, and the Upper Seeds, experiments at Wytham, relating the species composition of the successional flora to potential sources of colonists.

In the following sections we describe the rates of colonisation and the changing composition of the colonising flora on the new field margins during the first three years of fallow. We examine criteria relevant to the desirability and acceptability of the flora, including its species richness, the numbers of species with different life-histories and growth forms, and the relative abundances of species in these categories.

The old field margins were also influenced by removal of agrochemical applications and by the same management regimes that were imposed on the new margins. Since many farmers require to know the extent to which old margin vegetation may be expected to improve under these conditions we also present analyses and comparisons of the equivalent data for the old margins.

We then examine the extent to which the quality and quantity of species colonising the new margins is determined by, and can be predicted from, that in the various source floras. The source floras we consider are the seed bank, the old margins and field boundaries, and the crop. Colonists that could not be attributed to any of these sources within the experimental fields are considered to have arrived from more distant sources. We look at the minimum distances that colonists must have travelled, and the changing similarity between the source floras and new margin flora. Life-history composition, species richness, similarity in species composition and the relationship between species abundances are all used as measures of similarity. We examine the proportion of species in the sources that can be expected to colonise and the characteristics of species in the source floras that fail to colonise the new field margins.

All of the analyses in this chapter are concerned with gross changes in species composition in relation to succession, and with comparisons of the species composition of the new margin and source floras. Since the effects of the management regimes on the variables concerned were small in relation to these differences, data from the different treatments are combined in many analyses. Analyses of the effects of treatment on the plant community are presented in Chapters 4-6. The data used come both from the complete species lists that were accumulated for the different zones of each 50m plot and from the permanent quadrats. The former are used only where complete lists of species that occurred on the margins during the three year experiment are required. The permanent quadrat data provide estimates of the changes in the net numbers of species and of differences in the abundance of species. Sown plots are excluded from all analyses involving the calculation of mean values per plot because the presence of sown species reduced the numbers of naturally regenerating species present (see Chapter 4). Species included in the seed mixture are also excluded from many of the analyses when they occur in unsown plots. Most such occurrences resulted from invasion from nearby sown plots and so might bias many of the analyses. Exclusion of these species also results in a slight (downward) bias in estimates of numbers of perennial species because some of the same species also colonised naturally from local sources. It was impossible to distinguish definitively which individual colonists were derived from which source.

3.2 Results

3.2.1 CHARACTERISTICS OF THE NEW MARGIN FLORA

Colonisation rate

Over the experiment as a whole, new species arrived on the fallowed margins most rapidly during the spring and early summer of 1988, after the new margins were rotovated (cumulative totals: Figure 3.1). There was a further, but relatively slight, increase the following spring but by spring 1990 there was no equivalent increase, although a slight trend of increase was sustained throughout the year. By September 1990 a total of 181 species had been recorded in the permanent quadrats on the new margins, 77% of which arrived in the first six months after fallowing. Two hundred and three species were recorded in the complete plot lists over the same period (see Appendix 1.3).

Although the rate of arrival of novel species on the experiment as a whole was very low by 1990, new species continued to arrive in individual quadrats at a higher and undiminished rate from summer 1988 onwards, following an initial very rapid increase after the margins were rotovated that spring (Figure 3.2). This suggests that the vegetation remained very dynamic with some opportunities for seedling establishment being maintained. A relative lack of availability of propagules of novel species may have been limiting the species richness of the experiment as a whole by that stage.

We show below that the numbers of novel species remaining in the near-by source floras by the second and third years of the succession were relatively low, and so gaps were much more likely to be exploited by species already present than by a much smaller supply of seed arriving from further afield.

Species richness

The total number of species recorded in the permanent quadrats on the new margins was 143 in 1988 and 126 in 1990. The mean number of species per quadrat on the new margins also peaked in the first year of fallow. It declined rapidly during the second year, increasing slightly again during 1990 (Figure 3.3). Numbers of annual species were the main determinant of the pattern in total species numbers during this period. The numbers of annual species peaked in 1988, but halved by the following summer before showing a small second peak in 1990 which accounted for the rise in total numbers that year. This probably resulted from the extreme drought in summer 1989 and 1990 creating a more open sward with better establishment opportunities for annuals. Over the three year period the mean ratio of annual to perennial species on the field margins changed radically, with annuals comprising a greater proportion of the species present until spring 1989 (Figure 3.4a). Over the experiment as a whole, annual species comprised over 50% of the total species recorded only until June 1988 (Figure 3.5a).

As well as increasing as a proportion of the species present (above), the number of perennial species increased by 64% between June 1988 and 1990 (Figure 3.3). This increase was relatively gradual although the rate of increase amongst the forbs and grasses was conspicuously greater in spring 1988 than in subsequent seasons. A slow increase in the mean numbers of perennial grass species per quadrat was sustained throughout the three years, although the mean numbers of forbs did not increase between summer 1988 and 1990. Mean numbers of woody species and of rushes and sedges increased slightly during the experiment. Mean numbers of biennials did not increase between summer 1988 and 1990.

Species abundance

We have shown above that the total number of species arriving on the new field margins was high. By 1990, three years after fallowing, it had included 22 perennial grasses, 75 perennial forbs, 16 woody species and three *Carex* and *Juncus* species, many of which might be considered desirable components, in nature conservation terms, for the grassy perennial swards we aimed to establish (data from complete plot lists). However, although the numbers of perennial species increased, and those of annuals decreased, the abundance of the majority of 'desirable' species in the sward, remained low.

The majority of species on the new margins were recorded at very low frequency while small numbers of species were extremely common (Figure 3.6: data exclude sown plots). This pattern was more pronounced in 1989 and 1990 than in 1988. In 1988 most of the common species were annuals but in subsequent years the abundance of many of these annual species decreased substantially. Thus, as well as a decline in the number of annual species (above), the abundance of many of those that remained decreased. Analyses of the decline in *Avena* species and *Alopecurus myosuroides* are presented in Chapter 5. In 1988 the most common annuals were, respectively, *Veronica persica* Poiret Common Field-speedwell, *Avena* species, *Polygonum aviculare* L. Knotgrass, and *Hordeum distichum* Barley volunteers. By 1989 *Bromus sterilis* had become the most abundant annual species. In that year and in 1990 it was the only annual species that remained extremely common on the new margins (see Chapter 5 for detailed analyses of this species).

All of the biennials, woody species and *Juncus* and *Carex* species colonised at low frequency and remained very uncommon. Although the majority of perennial forb species were also very uncommon, *Urtica dioica* occurred at moderate frequencies and was much the most common perennial forb in 1988 (see Chapter 5 for detailed analyses of this species). By 1990 *Convolvulus arvensis* L. Field Bindweed and *Geranium dissectum* L. Cut-leaved Crane's-bill achieved similar frequencies. The only common perennial grass in 1988 was *Poa trivialis* L. Rough Meadow-grass. It increased in frequency to become the most abundant single species by 1989. *Elymus repens* had also become extremely common by 1989 and by 1990 was even more frequently recorded than *P. trivialis*. By 1990 *Arrenatherum elatius* (L.) J.& C.Presl. False Oat-grass, *Agrostis stolonifera* L. Creeping Bent, *Dactylis glomerata* L. Cock's-foot and *Holcus lanatus* L. Yorkshire-fog were also recorded at overall frequencies of over 10%.

The above suggests that although many desirable components of perennial grassy swards colonised the new field margins in the first year of the fallow, the quality of the dominant species in the new margin swards remained low and included many pernicious weeds. Figure 3.7 shows the relative frequencies of five of the commonest pernicious crop weeds (*Bromus sterilis, Avena* species, *Alopecurus myosuroides, Cirsium arvense* and *Elymus repens*). It is clear both that almost all of the dominant species were problem weeds, and that most of the problem species were common in the new margin swards. The only very abundant species in 1989 and 1990 that is not classified as a problem weed is *Poa trivialis*. This species can become a problem in cereal crops but did not present problems on the University Farm. Ways in which the abundance of the these species can be reduced by mowing management and by sown swards are discussed in the Chapter 5.

Summary Large numbers of species, including desirable forbaceous, woody and grassy perennials, colonised the new margins very rapidly during the first six months after fallowing. The rate of arrival of new species then dropped rapidly and was fairly constant over the next two years. Numbers of species present on the new margins peaked in the first year of fallow as a result of large numbers of annual colonists. The number of annual species halved by the second year of fallow while that of perennials increased. The numbers of perennials continued to increase slowly, with most of the increase being in grass species. The abundance, as well as numbers of species, of annuals decreased sharply, and that of perennials increased, by the second year of fallow. Most species were very uncommon in the flora but a few, most of which were pernicious weeds, became very abundant.

3.2.2 CHARACTERISTICS OF THE OLD MARGIN FLORA

Colonisation rate

The cumulative total of species recorded in the permanent quadrats on the old field margins also increased steadily during the first three years of the experiment (Figures 3.1 & 3.2). The rate of increase was greater at the beginning of the experiment, in spring 1988, although it was not nearly as great as on the new margins. After that time, the rate of increase over the experiment as a whole, and per quadrat, was very similar to that on the new margins.

Species richness

The net total numbers of species recorded in the permanent quadrats on the old margins were slightly higher than those on the new margins throughout the experiment. One hundred and fifty three were recorded in 1988 and 134 in 1990 (a total of 237 species was recorded in the complete plot lists for the old margin and field boundaries combined, over the same period: see Appendices 1.1 & 1.2). However, during the period that the mean numbers of species peaked and then decreased on the new margins, they showed a slight increase on the old margins (Figure 3.8).

Perennials comprised a greater proportion of the old margin species than annuals throughout the experiment (Figures 3.4b and 3.5b) and, as on the new margins, they comprised a higher proportion of the species present in 1990 than at the beginning of the experiment. Most of the sustained increase in total species numbers resulted from an increase in the number of perennial grass species (Figure 3.8). As on the new margins the numbers of annual species declined during 1989 but increased again in 1990, suggesting again that the drought in those years created new establishment opportunities.

By 1990 perennials still comprised a higher proportion of species present on the old than on the new margins (Figure 3.4). The numbers of perennial species per quadrat were very similar on the old and new margins by that stage (means±S.E.: 6.32±0.22 v 6.61±0.24 respectively) but the number of annual species on the new margins remained substantially higher than on the old margins (means±S.E.: 5.12±0.24 v 3.28±0.18 respectively).

Species abundance

On the old field margins the frequency distribution of species in the different life-history and growth-form categories was more consistent during the three years of the experiment, and was similar to that on the new margins in 1989 and 1990. The only notable exception to this was the occurrence of woody species at frequencies greater than 10%. The relative dominance of individual species was most similar to that on the new margins by 1990, although there were some consistent differences in the annual species and perennial forbs that were most abundant. In all years *Elymus repens* and *Poa trivialis* were the most abundant species. *Bromus sterilis* was only slightly less frequently recorded and was much the most abundant annual species. *Galium aparine*, which was never a common species on the new margins, was common on the old margins in 1988 but much less common in subsequent years (see Chapter 5 for detailed analysis of this species). *Convolvulus arvensis*, *Urtica dioica* and *Lamium album* L. White Dead-nettle were consistently the most common perennial forbs. *Hedera helix* L. Ivy was responsible for the appearance of woody species in the higher frequency categories, increasing from an overall frequency of 18% in 1988 to 23% in 1990.

The frequency distribution of problem weeds on the old margins was also similar in all years to that on the new margins in 1990, although there were more non-weedy species in the moderately common (20-40%) category (Figure 3.10). Thus, the new margins became more like the old margins during the experiment in the relative frequencies of species in different life-history and growth form categories, and in the pattern of dominant species.

Summary There was a burst of recruitment of new species to the old as well as the new margins in the first six months of the experiment. This was much smaller than that on the new margins but the subsequent, slower rate of arrival of new species was very similar on the two zones. The majority of species on the old margins was perennial throughout the experiment and, as on the new margins, perennials increased as a proportion of the total complement. After three years of succession the numbers of perennial species were very similar on the old and new margins although the new margin still retained significantly more annual species. The patterns of relative abundance of species with different life-histories and growth forms on the old margins were similar to those on the new margins in the second and third years of succession. By 1990 most of the dominant species in the two zones were the same.

3.2.3 THE ORIGINS OF THE NEW MARGIN FLORA

In this section we analyze the relationship between the new margin flora and potential source floras. The sources that we consider are the seed bank, the crop, and the old margin and field boundary floras. Where data from the permanent quadrats are used for the analyses only the grassy strip of old field margin is represented. Where the data from the complete plot species lists are used, the species in this strip and the boundary feature are combined.

Distances of arrival

We analyzed, in three approximate categories, the minimum distances that each species that colonised the new margin of each plot would have had to travel from source floras. The shortest distance category was within 100 metres of the plot. Because species at one end of a plot were as close to sources in the adjacent plot as to those in parts of their own plot, we pooled the species from each source in both the same and adjoining plots. The second category included all sources within the experimental fields. Species on the new margins that could not be attributed to sources in either of these categories were considered to have come from further afield.

Ninety percent of the species that colonised the new margins could have arrived from sources within 100m of the plot and over 99% could have arrived from sources within the experimental fields (Table 3.1). A higher proportion of species on the new margins could be attributed to the old margin and crop sources than to seed bank sources, although 68% of species on the new margins could be attributed to species occurring in the seed bank within the experimental fields. This difference in potential supply of species between the seed bank and the other source floras resulted from the lower species richness of the seed bank than of the other sources (see below).

Sources of colonists and their relationship with the new margin flora

Distant floras The Wytham estate as a whole has a rich and comprehensively documented flora. A total of 623 species has been recorded on the estate (Gibson 1991), most of which lies within a maximum radius of three miles of the experimental fields. However, we have shown above that sources of propagules beyond the experimental fields were extremely unlikely to have been important, since the great majority of species colonising the new margins could have arrived from source floras in close proximity to the margins. Only four species that colonised the new margins were not also recorded from source floras within the experiment. These were *Epilobium montanum* L. Broad-leaved Willowherb, *Scrophularia nodosa* L. Common Figwort, *Barbarea vulgaris* R. Br. Winter-cress and *Leontodon autumnalis* L. Autumn Hawkbit, all of which were present within the Wytham estate. We cannot, however, preclude the possibility that some species originating from further afield colonised both the new and old margins and so would not be detected as novel by our sampling regime.

The soil seed bank

Eighty six species were recorded in the soil seed bank (see Appendix 1.4). Over the experiment as a whole 55% percent of species were annuals, although a mean of 64% of species per quadrat were annuals. Only three species of biennials were recorded. The perennials comprised 23 species of forbs, five grasses, five woody species and two *Juncus* species (*J. inflexus* L. Hard Rush and *J. effusus* L. Soft Rush). Two *Carex* species have been recorded from the seed bank elsewhere on the farm (Adams, unpublished data).

Some of the experimental fields differed significantly from others in the species richness of the seed bank (Table 3.2). Blocks five and six of the experiment, which were on heavy Oxford clay soils (Chapter 2) had only about half of the number of species present in blocks one and two, which were on calcareous loams and gravels.

The fields also differed substantially and significantly in the abundance of seeds in the soil (Table 3.2). The pattern was similar to that of species richness, with blocks five and six of the experiment having only about a half of the density of seeds recorded from blocks one and two.

The majority of species in the seed bank were very uncommon while a few were very abundant (Figure 3.11). Most of the dominant species in the seed bank were annuals with *Veronica persica*, *Veronica arvensis* L. Wall Speedwell, *Papaver rhoeas* L. Common Poppy and *Avena* species, respectively, being the most abundant. However, the species most commonly recorded in the seed bank was *Urtica dioica*, which comprised 18% of the seeds. *Poa trivialis* was also very common. All woody species, *Juncus* and *Carex* species, and biennials, were uncommon.

The precise complement of species recorded in seed bank samples depends on the time of year at which the samples are collected. Our seed bank samples were collected December 1987 and so were expected to include some of that year's seed rain as well as seed which remained dormant from previous years. Autumn-germinating species with short-lived seeds were expected to be poorly represented while spring-germinating species with short-lived seeds were expected to be lost from the samples by summer 1988, leaving only species with persistent seed banks. Thus, for example, a total of only six seedlings of *Bromus sterilis*, an extremely common autumn-germinating species in the crop edge (Chapter 5), were recorded from all of our soil samples. Repeated sampling during the year should remove this bias but, since our main interest was in the longer-lived seeds, such intensive sampling was beyond the scope of this study.

Seventy-seven species germinated from the samples between collection in December and August the following year. The numbers of species germinating declined in the following two years, to 47 and 38 species respectively. Over the experiment as a whole, the proportion of species that were annuals had increased to 60% by that stage. The perennials that remained included only five species (the two *Juncus* species, *Holcus lanatus*, *Dactylis glomerata* and *Poa trivialis*) that might be regarded as desirable components of a grassy perennial sward. The total numbers of seedlings emerging from the samples also declined, by 75% over the three year period. *Urtica dioica* remained the single most abundant species, comprising 16% of the seeds germinating in the third year of the experiment.

On a farm-scale, the persistent seed bank was unlikely to contribute many novel species to the new margin flora. Only three species which colonised the new margins occurred in the seed bank and not in other near-by source floras. These were *Epilobium ciliatum* Rafin. American Willowherb, *Euphorbia peplus* L. Petty Spurge and *Glyceria fluitans* (L.) R. Br. Floating Sweet-grass. Four additional species were recorded from the seed bank that were not recorded on either the new margins or other near-by source floras. These were *Sagina apetala* Ard. Annual Pearlwort, *Dryopteris felix-mas* (L.) Schott

Male-fern, *Hypericum tetrapterum* Fries. Square-stemmed St John's-wort and *Cytisus scoparius* (L.) Link. Broom. Of these, only *D. felix-mas* and *H. tetrapterum* would be considered desirable additions to field margin grassy perennial swards (*C. scoparius* was likely to be a garden escape). It should be borne in mind, however, that in this, as in other seed bank studies, the area sampled for seeds was much smaller than that sampled for plants. This inevitably leads to a bias against finding species that are rare in the seed bank. Furthermore, it is possible that some species present in the seed bank samples may not be recorded because they fail to germinate.

On a more local scale the seed bank almost certainly contributed some species to the new margin flora that were not present in the other floras in the immediate vicinity. Thus, for example, a 10m length of a single plot developed a flora comprising a high frequency of *Juncus inflexus*, together with some *J. effusus* and *Carex otrubae* Podp. False Fox-sedge, none of which was present in the adjacent and near-by field boundaries, and all of which had long-lived seeds and were present in the seed bank.

Although the seed bank probably contributed few species to the new margins that could not also have arrived from other near-by sources, with the exception of the species discussed above, nearly all of the species (95%) recorded from the seed bank were also recorded in the colonising flora on the new margins. Because many fewer species were recorded from the seed bank than the new margins, the seed bank and new margin floras of the plots had an average of only about 50% of their species in common in 1988 (similarity coefficients, Table 3.3). The similarity in species composition between the seed bank and new margin floras was lower in the second and third years of succession as a result of the decline in numbers of annual species on the new margins. Differences in the complement of species detected in the two floras inevitably result from the sampling methods as well as from real differences. Thus, the timing of collection of seed bank samples affects the representation of species with short-lived seeds (above) while the smaller area sampled reduced the probability of detecting uncommon species. Species which propagate primarily by vegetative means, as well as some of those with short-lived seeds, will be absent from seed bank samples. These species also contribute to the lower species richness of the seed bank than of the above-ground floras.

There was a significant correlation between the species richness of the seed bank and that of the new margin flora but this relationship explained only 18.5% of the variation in the numbers of species (Table 3.4).

The rank abundance of the species common to the seed bank and new margins was also significantly correlated in 1988 but not in subsequent years (Table 3.5). The seed bank was almost certainly important in determining the colonising frequency of some species whilst the importance of other species in the seed bank and new margin floras was very different. Thus, *Urtica dioica*, the most common species in the seed bank was also the most common forbaceous perennial species on the new margins in the first year of fallow, although it was only the seventh most common species overall in the new margin flora. Amongst the common annuals, *Veronica persica*, the most common species on the new margins in 1988, was also the most common annual in the seed bank. *Veronica arvensis*, however, although the second most common species in the seed bank, was only the sixteenth most common species in the new margin flora in 1988. By 1990 the rank abundance of *Veronica arvensis* in the new margins was seventeenth but that of *Veronica persica* had declined to eighteenth.

Although abundance in the seed bank is likely to be the main determinant of abundance of some species in the colonising flora, the relative abundance of species in the seed bank was not a good general predictor of species abundance in the first year of fallow. In subsequent years this difference increased. The slower rate of colonisation and lower frequency of annuals meant that competition within the new margin swards had more influence on relative frequencies than did seed supply.

The crop flora The flora of annual arable crops is constrained by the annual trauma of ploughing and is considerably modified in each year by both the cropping regime and herbicide applications. The only perennial species that can establish persistent populations under these conditions are those such as *Elymus repens* and *Convolvulus arvensis*, that can reproduce from vegetative fragments. However, many other perennial species seed into the crop and are recorded in routine monitoring. Between 1987 and 1990 a total of 146 species was recorded from the crop, many less than were recorded in the field margins over the same period (Sections 3.2.1 and 3.2.2). Fifty percent of these were annuals but a mean of 68% of the species recorded on each plot were annuals.

Since the new margin was cropped land at the outset of the experiment, it may initially be expected to have many species in common with the crop flora. Many of these must have colonised from the seed bank during 1988 but others may have seeded into the margin from plants in the crop in 1988 and subsequent years. There is therefore considerable overlap between the role of the seed bank and the adjacent crop as sources of colonists.

Seed rain from the adjacent crop is likely to be a significant source only of annuals. Of the annual species recorded from the crop only one, which was recorded at extremely low frequency (*Erophila verna*), was not also recorded in the new field margins. Three years after fallowing there was a significant positive correlation between species richness in the crop and the new margins (based on lists for each plot). This explained more of the variation in numbers of species in the new margins than did the numbers of species in either the seed bank or the old field margins (Table 3.4). As expected from the decline in annual species in the new margins, the crop and new margin floras became less similar during the course of the experiment. The numbers of species common to the crop and new margin declined during the experiment (Similarity coefficients: Table 3.3), as did the strength of the rank relationship between the abundances of these species (Table 3.5).

The old margin and boundary flora The general characteristics of the old margin flora are described in Section 3.2.2. We showed that the old and new margin floras became more similar in the life-history and growth form characteristics of their component species during the three years after fallowing (Section 3.2.2). They also became more similar in their species composition although, by 1990, there was no significant correlation between species richness in the new margins and the adjacent field margin and boundary flora combined (Table 3.4). The numbers of species common to the two floras increased from about 42 to 60% during the three years after fallowing (Table 3.3). The rank abundances of the species common to the two floras also became significantly more similar during this period (Table 3.5).

The old margin was much the most important source of desirable perennial species that colonised the new margins. Twenty four species that colonised the new margins were not also recorded in other source floras. They were all perennial forbs, grasses and woody species typical of established meadow or woodland edge grasslands (Table 3.6). Other species on the new margins may also have come exclusively from the old margin but many of these were also recorded as seedlings in the crop flora and so are more difficult to attribute to this source.

Despite this increasing similarity between the old and new margin floras, a much higher proportion of the old field margin and field boundary flora than of the seed bank and crop flora failed to colonise the new margin during the three years of the experiment. Fifty seven species (24% of total) recorded in the old margin and boundary floras (complete plot lists) during the course of the experiment were not recorded on the new field margins. Some of these species were recorded as seedlings in the crop, showing that they could potentially colonise the new margins. Only two species in this group were annuals; both species (*Erophila verna* L. Chevall. Common Whitlowgrass and *Centaurium erythraea* Rafn Common Centaury) were typical of bare sandy patches and anthills in some of the better quality ditch-bank grassland. Thirty-one percent of perennials that failed to colonise were woody species and 50.1% forbs, while only 11.8% were grasses. The numbers of these species failing to colonise the new margins represented 60% of the *Juncus* and *Carex* species (although the sample size was small), 50% of the woody species, 27% of the perennial forbs and only 20% of the perennial grasses recorded on the old field margins. Thus, in general, grasses and to a lesser extent forbs, were more effective colonisers of the new field margins than were woody species, and *Juncus* and *Carex* species, available in the same source flora, over the same period.

Summary The great majority of plants arriving on the new field margins were likely to have come from source floras in the immediate vicinity. The contribution of sources beyond the experimental fields was negligible.

Most of the species present in the seed bank were represented on the new field margins. However, with some local, although potentially important, exceptions the persistent seed bank was unlikely to be a significant source of species that were not also present in other near-by floras. It was particularly unlikely to be an abundant source of desirable grassland perennials since few such species occurred in the persistent component of the seed bank. Neither the qualitative nor quantitative characteristics of the new margin flora could be reliably predicted from the species composition of the seed bank. Both the species richness of the seed bank and the relative abundance of species common to the seed bank and new field margins were significantly related only in the first year of fallow. Even in that year the rank abundance of many species differed considerably between the seed bank and new margin floras.

Most of the species that maintained populations within the crop were annuals. The crop flora was a reasonable predictor of the species richness and annual species complement of the new margin flora in the first year of fallow. In the second and third years, however, this relationship disappeared as the new margin flora became predominantly perennial.

Although the new margin flora had less in common with the old margin than the crop and seed bank floras during the first year of succession, most of the perennial species that became the major element in the flora from the second year onwards were derived from the old margin and field boundary. A much higher proportion of species from the old margin than from other zones failed to colonise the new margins after three years. Perennial grasses colonised most reliably and *Juncus, Carex* and woody species least reliably.

3.3 Discussion

3.3.1 CONCLUSIONS AND PRACTICAL IMPLICATIONS

These results demonstrate a clear set of principles that are vital for assessing the likely success of natural regeneration as a means of establishing vegetation on extended field margins.

First, it is clear that the great majority of colonists arrived very early in the succession. These early colonists included a high proportion of the woody, forbaceous and grassy perennials, as well as of the annuals, that arrived within the three year study. The major changes from an annual to a perennial dominated flora also happened very quickly. There are two likely reasons for the rapidity of these changes. First, the high fertility of these agricultural soils led to high productivity in the early successional swards. By mid-summer 1988 the swards were very dense and opportunities for seedling germination and establishment were much reduced. Second, we have shown both that the supply of propagules is likely to be extremely local and that a high proportion of the species available locally colonised very rapidly. The supply of novel species, as well as the opportunities for establishment therefore diminished very rapidly. A major practical implication of this conclusion is that the appearance of the swards can be expected to change radically by the second year of succession and that it should be stressed to farmers that the great majority of perceived annual weed problems on new field margins will disappear rapidly without additional intervention (see also Chapter 5). On less fertile soils these processes may be more protracted. They may also be more protracted on set-aside land further from the field boundary because the distance from the major perennial seed source is greater.

After the initial burst of colonisation, the rate of acquisition of new species was slow but constant. Although species richness declined as the numbers of annuals decreased, the numbers of perennial species increased progressively. Gradual acquisition of new species may be expected to occur for many years. Gibson & Brown (1992) suggest that this progress towards a species-rich sward is likely to continue for decades. We show in Chapter 4 that the rate of acquisition of new species can be significantly modified by management.

Although the flora of the old field margins was long-established, it also changed rapidly during the first six months of the experiments. Cessation of fertiliser application and herbicide drift allowed new species to establish in the relatively open swards. Although the subsequent rate of acquisition of new species was similar to that on the new margins, we show in Chapter 4 that the species richness of the old margin flora was relatively unresponsive to mowing management. It therefore appears that, for the first few years, cessation of deleterious management practises has a greater impact on old margin vegetation than the introduction of positive management.

The results also allow us to assess the extent to which the characteristics of the new flora can be predicted from the existing flora of the farm. The very short distances of arrival of the great majority of species suggest that the new margin flora will be a sub-set of the species already present. This has the major implication that if the existing farm flora is extremely depauperate the flora that colonises fallowed field margins will also be extremely poor. Under these circumstances, which are likely to apply on many intensive-managed farms, natural regeneration cannot be recommended as a method of establishing field margin vegetation that is either of value for nature conservation or likely to be acceptable to farmers. Seed mixtures are certain to give preferable results from the points of view both of diversity of desirable and attractive species (Chapters 4 and 6) and of weed control (Chapter 5).

It is often suggested that, even where the existing farm flora is poor, natural regeneration from long-lived seeds in the seed bank may restore a more diverse and attractive flora. Our results suggest that this is unlikely to be the case. The seed bank within our experimental fields was species rich compared with many other published estimates for arable soils. However, although most species in the seed bank appeared on the new margins, most species that were in the seed bank were also in the other source floras. Relatively few of the species in the persistent seed bank were desirable perennials. This conclusion is in agreement with that of Graham & Hutchings (1988a & b) from the Castle Hill study. Although the seed bank should not be regarded as a panacea for a depauperate flora, it may nevertheless be a quantitatively important source of some desirable species, and may be a novel source of some grassland perennials including *Juncus* and *Carex* species.

Many of the characteristics of the early successional flora could be predicted from the flora of the crop and seed bank. Almost all of the species that occurred in these floras colonised the new margins. The species richness and the rank abundance of species in the new flora were significantly correlated with that in both of these sources. However, the rank abundance of many of the component species of the new flora could not reliably be predicted from that in either source.

These significant relationships depended primarily on the annual component of the floras. By the second year of the succession, when annuals declined on the new margins as a result of competition from the perennial component of the flora, these relationships disappeared. Thus, the crop and seed bank floras only provide useful indicators of the vegetation in the first year of the succession. During the subsequent two years the new margin vegetation became more like that of the old field margins. The numbers of species common to the two floras increased and the relationship between the rank abundances of these species became significant. Species richness of the two floras was not significantly correlated during the first three years of succession because, in contrast to the other two source floras, a significant proportion of species in the old margins and field boundary failed to colonise the new margins during this period. Perennial grasses colonised more readily than other types of perennials. It is likely that the proportion of old margin species colonising the new margins will increase progressively with time.

These results augment those from the analysis of colonisation distances. They confirm that the majority of species in the new flora are likely to be derived from near-by source floras. The great majority of species in the crop and seed bank floras are likely to colonise the new margins but the perennial flora of the old margins is much the most important source of perennial grassland species. The old margin flora is thus much the best available indicator of the likely species composition of the new margins flora. The new margin flora cannot be expected to achieve the same species richness as the old margin flora within the early years of the succession because not all of the species available from this source can be expected to colonise rapidly.

We have suggested that where the species complement of the old field margins is regarded as an inadequate source for establishing the new margin flora alternatives to natural regeneration must be considered. Where natural regeneration is considered a viable option, our results suggest that although many of the components for a relatively diverse flora are likely to be present from very early in the succession, the new flora is likely to be dominated by weedy species. In Chapter 5 we address the extent to which management by mowing can be used to manipulate the populations of these species to make the establishment of field margin vegetation by natural regeneration a more realistic option.

3.3.2 FUTURE MONITORING

Continued monitoring of the species composition of the new margin flora is required to ascertain the extent to which, and the time-scales on which, more of the species present in the flora of the old margin and field boundary are acquired. It is also important to know whether species from sources beyond the immediate vicinity of the new field margins will colonise with time, or whether the composition of new flora will continue to be largely restricted to local species in the medium to long term. Continued monitoring of changes in the relative dominance of species, in both the new and old margins floras, is required to ascertain the persistent of dominance by aggressive perennials and the extent to which woody perennials and many of the more 'desirable' grassland perennials, which colonised at low frequency early in succession, can persist or increase. These issues are discussed further in Chapters 4 and 5.

3.3.3 IMPLICATIONS FOR SET-ASIDE MANAGEMENT

In general, the species richness of whole-field set-aside is likely to be influenced by that of near-by source floras in the same way as colonising floras on field edges. However, species richness is likely to decrease with increasing distance from the field boundary, and so the time taken to develop a species rich flora is also likely to be greater. The relatively poor supply of propagules further from the boundary also makes it more likely that species from further afield, and particularly wind-dispersed species, will have more establishment opportunities and be more prominent in the new flora. As on field margins, the use of seed mixtures to establish green cover on set-aside land should be considered in situations where the supply of propagules is likely to be very poor (see also Chapters 6 and 11). The dominance by annuals is also likely to be longer-lived towards the centres of fields, because colonisation by perennials is slower. This is borne-out by many reports from set-aside on previously very intensively managed farmland.

The inevitability of dominance by annuals in early secondary succession on set-aside land should be explained clearly to farmers embarking on any schemes involving fallowing, as should the relatively short-lived nature of the problem. In Chapter 5 we address the ways in which management by mowing can be used successfully to further reduce this problem.

Table 3.1 Minimum distances of arrival of species colonising the new margins by 1990

	Mean % of species on new field margin plots that could have arrived from:			
Distance	Old margin+ boundary	Crop	Seed bank	Any zone
Within 100m	68.3 ± 1.6	72.9 ± 1.1	27.6 ± 0.9	88.9 ± 0.8
Within the experimental fields	96.1 ± 0.4	96.2 ± 0.5	68.2 ± 0.7	99.4 ± 0.2
Further afield				0.6

Data are means, ± S.E., derived from total lists for each 50 m plot to 1990. See text for method of calculation.

Table 3.2 Species richness and seed abundance in the soil seed bank in different experimental blocks

Block	No. species recorded			No. seeds recorded:			
	per plot[1]			per plot[1]			per m^{-2}
	Mean	S.E.	Sig.[2]	Mean		Sig.[2]	
1	16.01	1.23	a	26.80	3.65	a	6233
2	10.97	1.54	a b	20.37	5.15	a b	4737
3	11.57	1.29	a b	17.33	2.45	a b	4032
4	10.70	0.95	a b	21.30	4.07	a b	4954
6	9.77	0.66	b	11.10	1.83	b	2977
5	7.43	0.96	b	12.80	1.00	b	2582
ANOVA between blocks: $F_{(5,54)}=4.02$, $P<0.01$				ANOVA between blocks: $F_{(5,54)}=5.59$, $P<0.001$			

[1] Number of species recorded in a total area of 151 cm^2 sampled in each plot
[2] Means with the same letter do not differ significantly (Tukey's Studentised Range Test, based on log-transformed data)

Table 3.3 Similarity between the species composition of the new margin flora and that of the old margins, crop and 1987 seed bank in June 1987-1990

	Old margin		Crop edge		Seed bank	
	Cs[1]	S.E.	Cs	S.E.	Cs	S.E.
1988	0.4183	0.021	0.5023	0.030	0.4713	0.017
1989	0.5638	0.025	0.3604	0.037	0.3408	0.016
1990	0.5985	0.014	0.4186	0.028	0.3407	0.015

Coefficients based on mean numbers of species per quadrat

1 Cs: Sorensens coefficient of similarity $Cs=2j/(a+b)$ where j is the number of species common to the two habitats, and a and b are respectively the numbers of species in each sample

Table 3.4 Relationship between species richness in the new margins plots by 1990 and that in the (a) adjacent old margins (b) adjacent crop edge (c) plot seed bank and (d) combined adjacent sources

	Old margin		Crop edge		Seed bank		All sources	
R^2=	-0.033	ns[1]	0.437	**	0.432	**	0.074	ns
r^2 [3]	0.001		0.244		0.185		0.005	

Data are from complete lists for each plot by 1990 (Chapter 2.x.x) and from seed bank samples

[1] Significance of correlation: ** P<0.01, ns not significant
[2] R: Pearson correlation coefficient
[3] r^2: Coefficient of determination

Table 3.5 The relationship between the rank abundance of species in the new margins and in (a) the old margins (b) the crop edge and (c) the 1987 seed bank, in June each year

		1988		1989		1990	
(a) Old margins	Rs[1]	0.306	*[3]	0.513	***	0.580	***
	(n)[2]	(42)		(48)		(61)	
(b) Crop edge	Rs	0.755	***	0.370	ns	0.369	*
	(n)	(57)		(25)		(29)	
(c) Seed bank	Rs	0.660	***	0.273	ns	0.193	ns
	(n)	(57)		(41)		(45)	

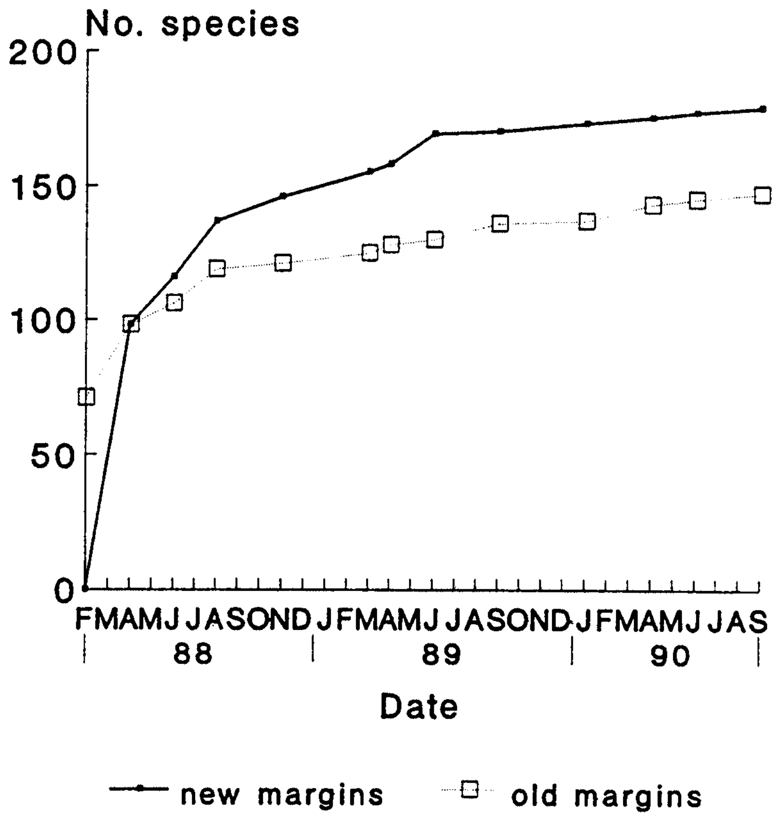
Correlations are based on rank overall abundance of species recorded from permanent quadrats and from seed bank samples collected in 1987. Sown and sprayed plots and sown species are excluded from the analysis.

[1] R_s: Spearman's rank correlation coefficient
[2] n: number of species in sample
[3] Significance of correlation: *** $P<0.001$, * $P<0.05$, ns not significant

Table 3.6 Species restricted to the new and old margin floras

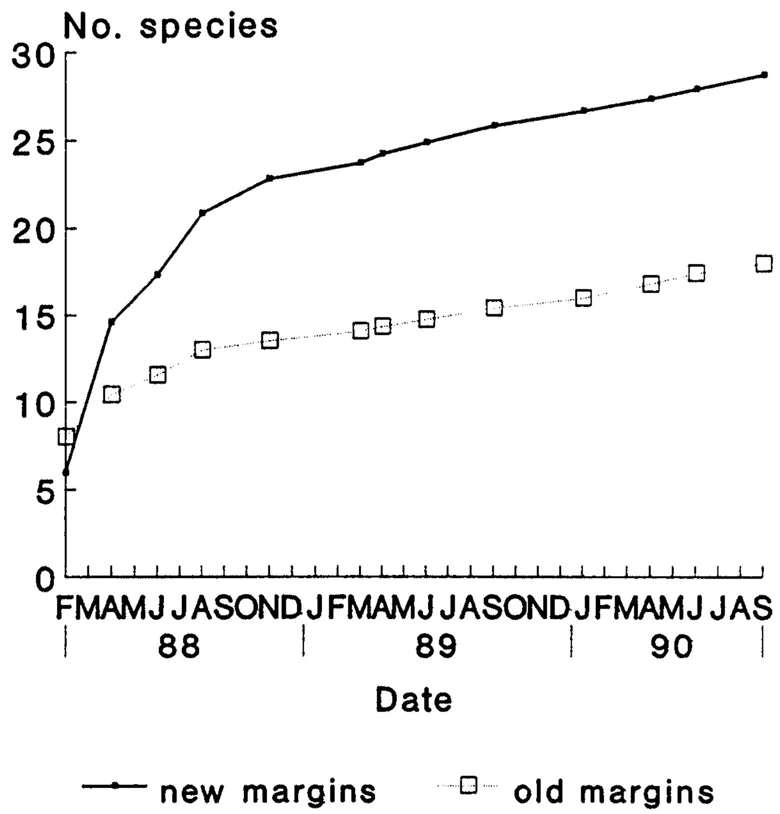
Perennial forbs	
Achillea millefolium	Yarrow
Agrimonia eupatorium	Agrimony
Allium vineale	Crow garlic
Arum maculatum	Wild Arum
Bellis perennis	Daisy
Centaurea scabiosa	Greater Knapweed
Cirsium eriophorum	Woolly Thistle
Gallium mollugo	Hedge Bedstraw
Geum urbanum	Wood Avens
Lathyrus pratensis	Meadow Vetchling
Ranunculus ficaria	Celendine
Silene dioica	Red Campion
Silene vulgaris	Bladder Campion
Stellaria holostea	Greater Stitchwort
Trifolium pratense	Red Clover
Veronica chamaedrys	Germander Speedwell
Viola odorata	Sweet Violet
Perennial grasses	
Bromus erectus	Upright Brome
Brachypodium sylvaticum	False Brome
Carex otrubae	False Fox Sedge
Deschampsia cespitosa	Tufted Hair-grass
Festuca gigantea	Giant Fescue
Woody species	
Coryllus avellana	Hazel
Solanum dulcamara	Woody Nightshade

Figure 3.1 Cumulative total of plant species that colonised the fallowed field margins



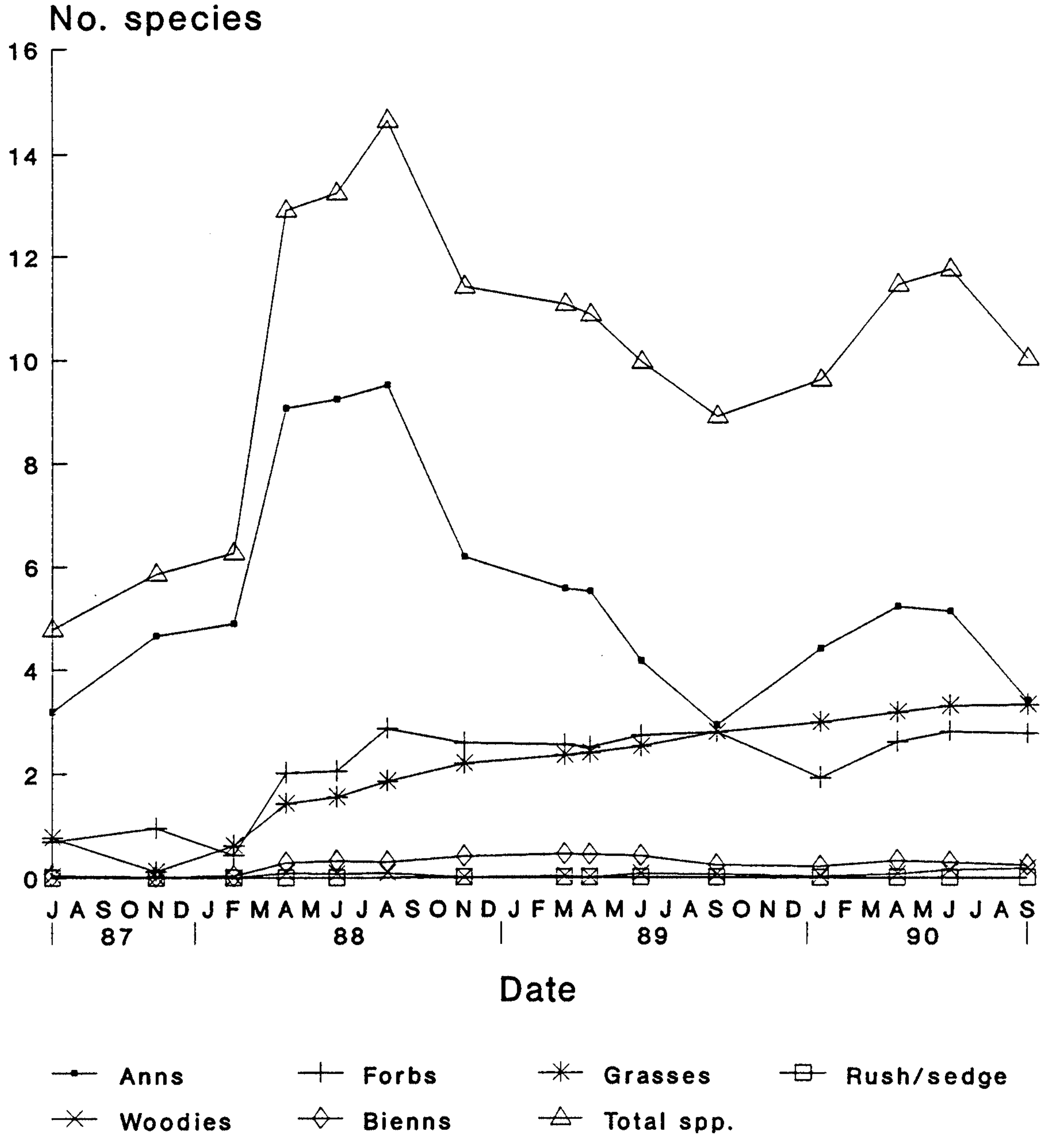
Data from 50m plot species lists

Figure 3.2 Cumulative mean total of plant species per 0.5x1.0m quadrat



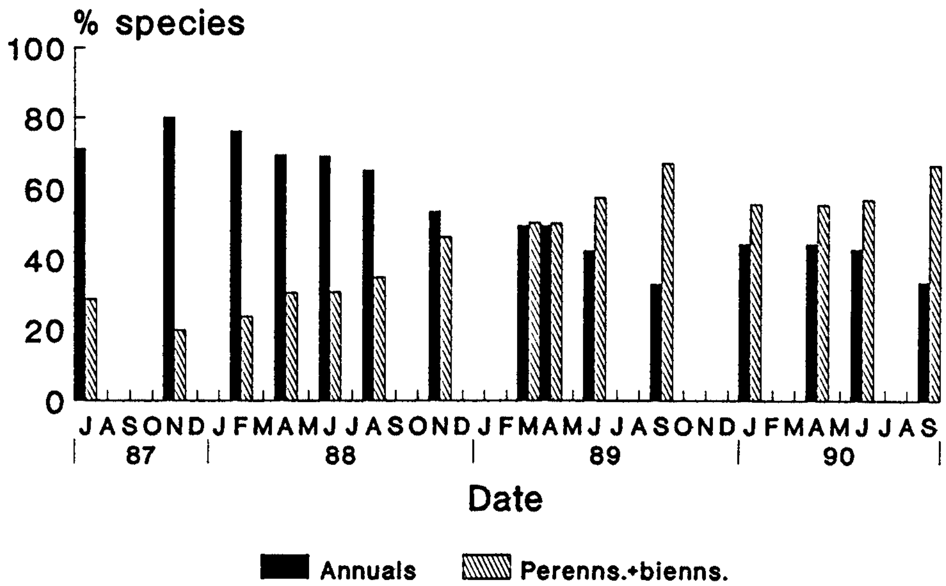
Data from 50m plot species lists

Figure 3.3 Change in numbers of species in different life-history categories (Data are means per 0.5x1m quadrat)



Forbs, grasses, rushes/sedges and woody species all refer only to perennial species

Figure 3.4 Mean percentage of annual and perennial species in permanent quadrats
(a) on the new margins



(b) on the old margins

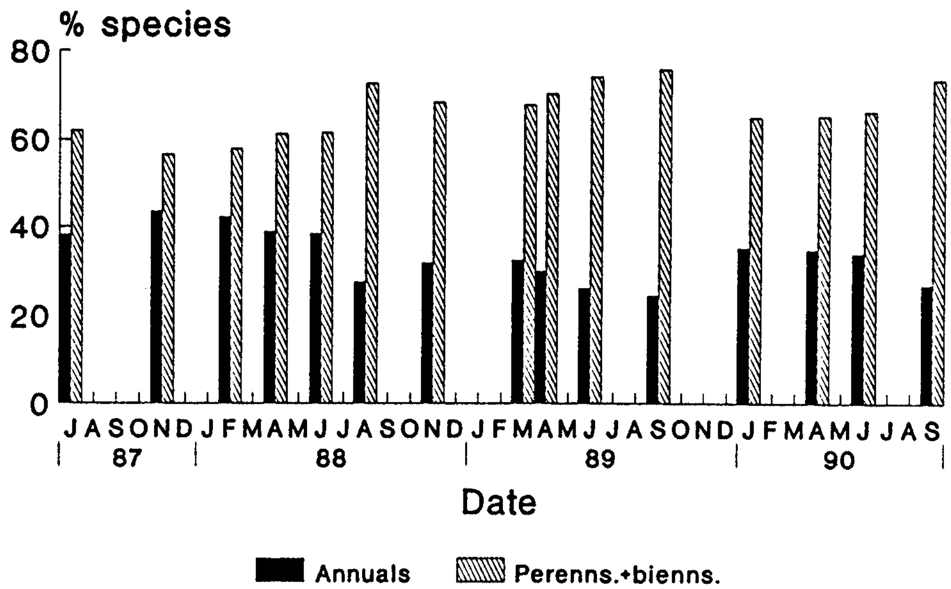
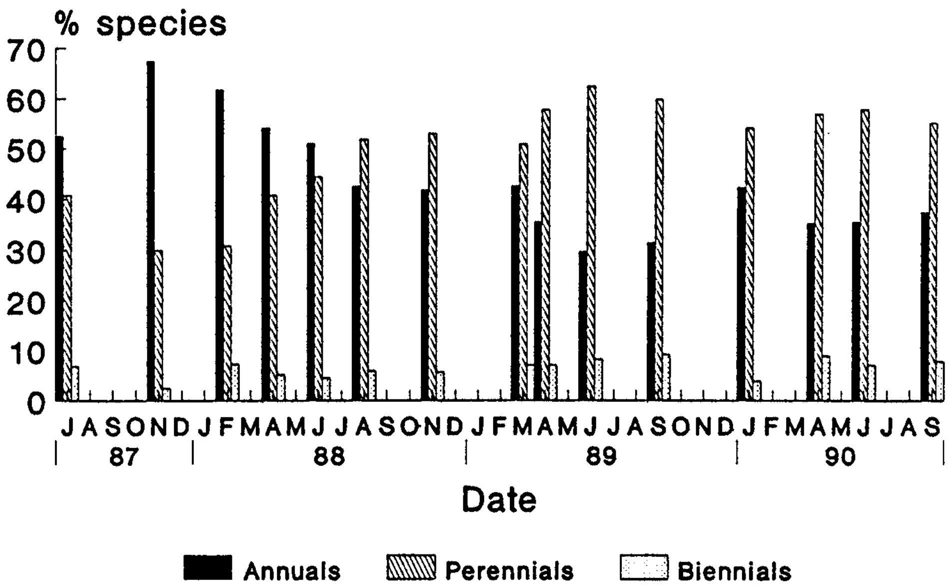


Figure 3.5 Percentage of annual, perennial and biennial species on
(a) the new margins



(b) the old margins

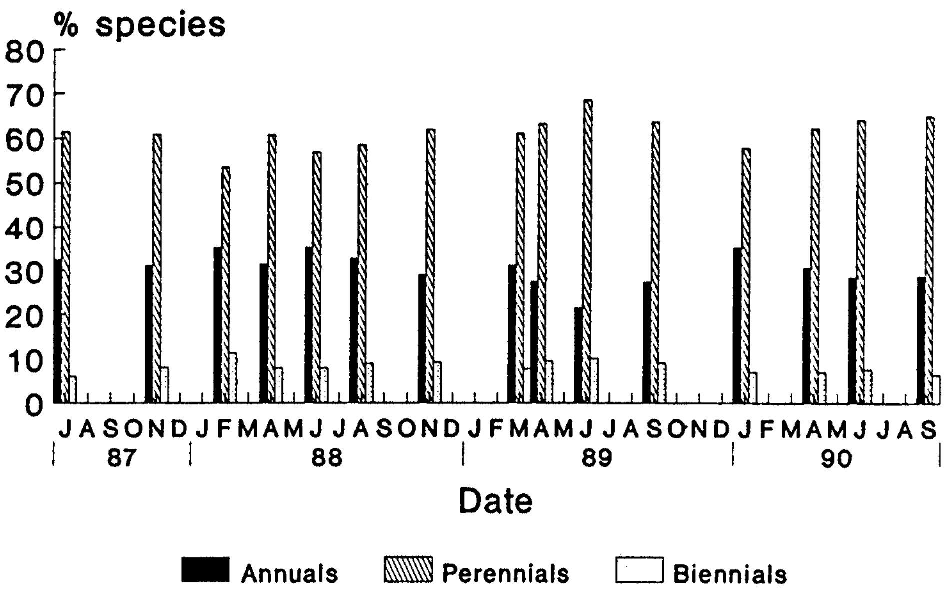
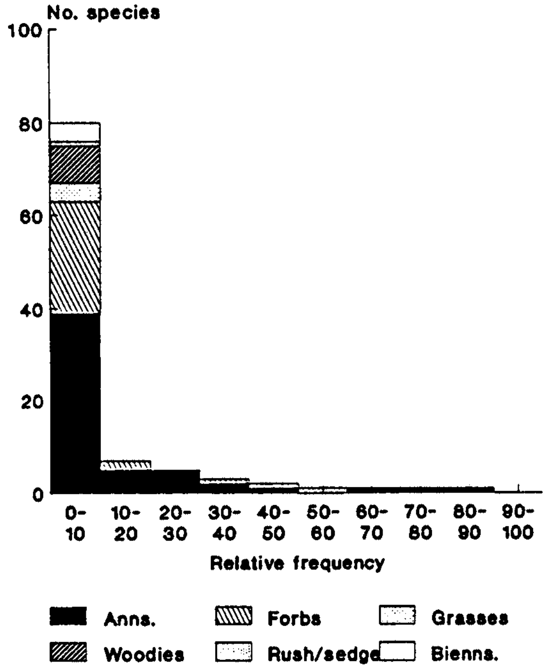
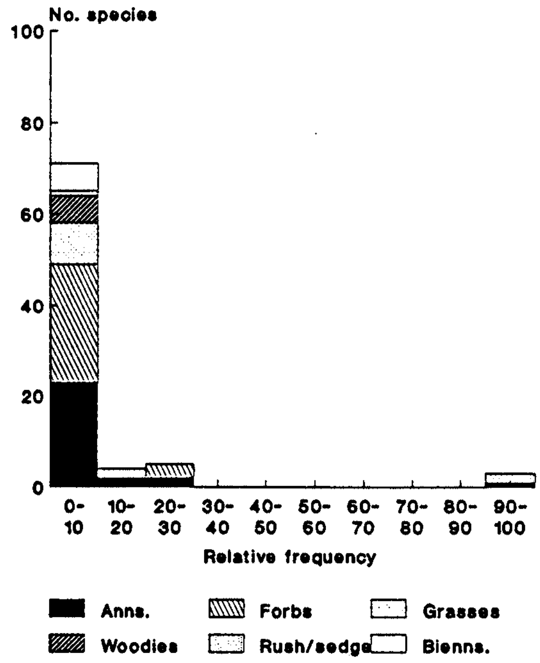


Figure 3.6 Relative frequency of species on the new margins

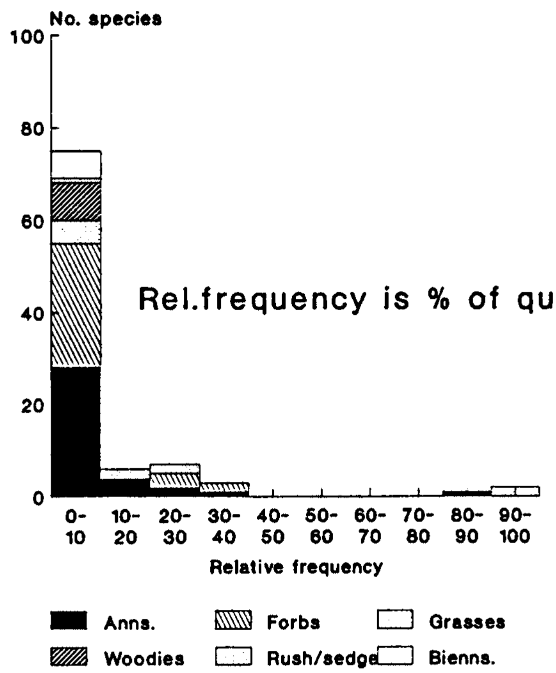
(a) June 1988



(b) June 1989



(c) June 1990

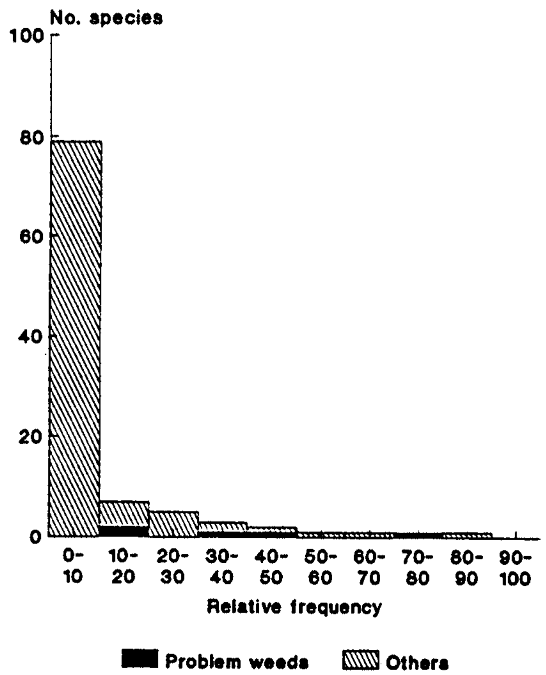


Grasses, forbs, rushes/sedges and woody species all refer only to perennial species

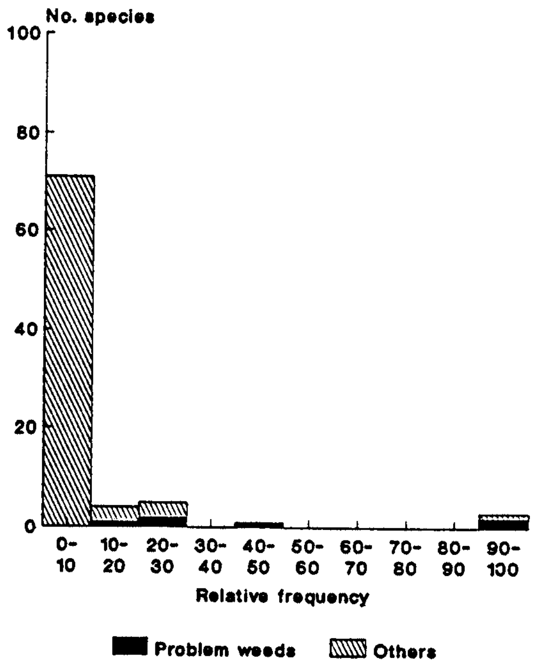
Rel.frequency is % of quadrat cells in which spp. occurred

Figure 3.7 Relative frequency of problem weeds: new margins

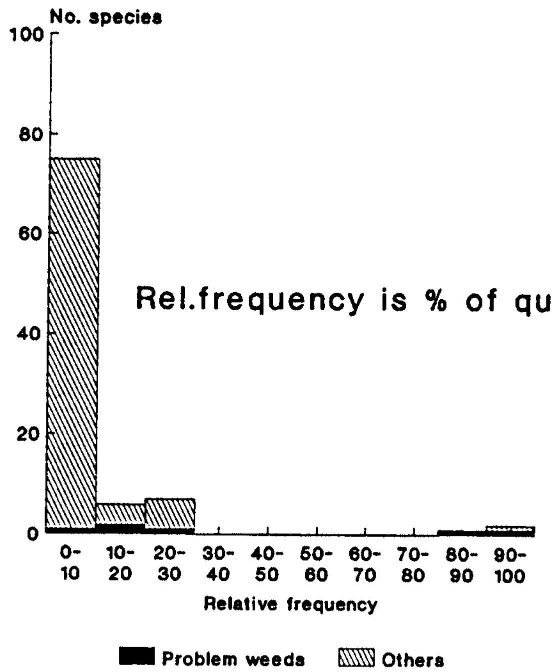
(a) June 1988



(b) June 1989

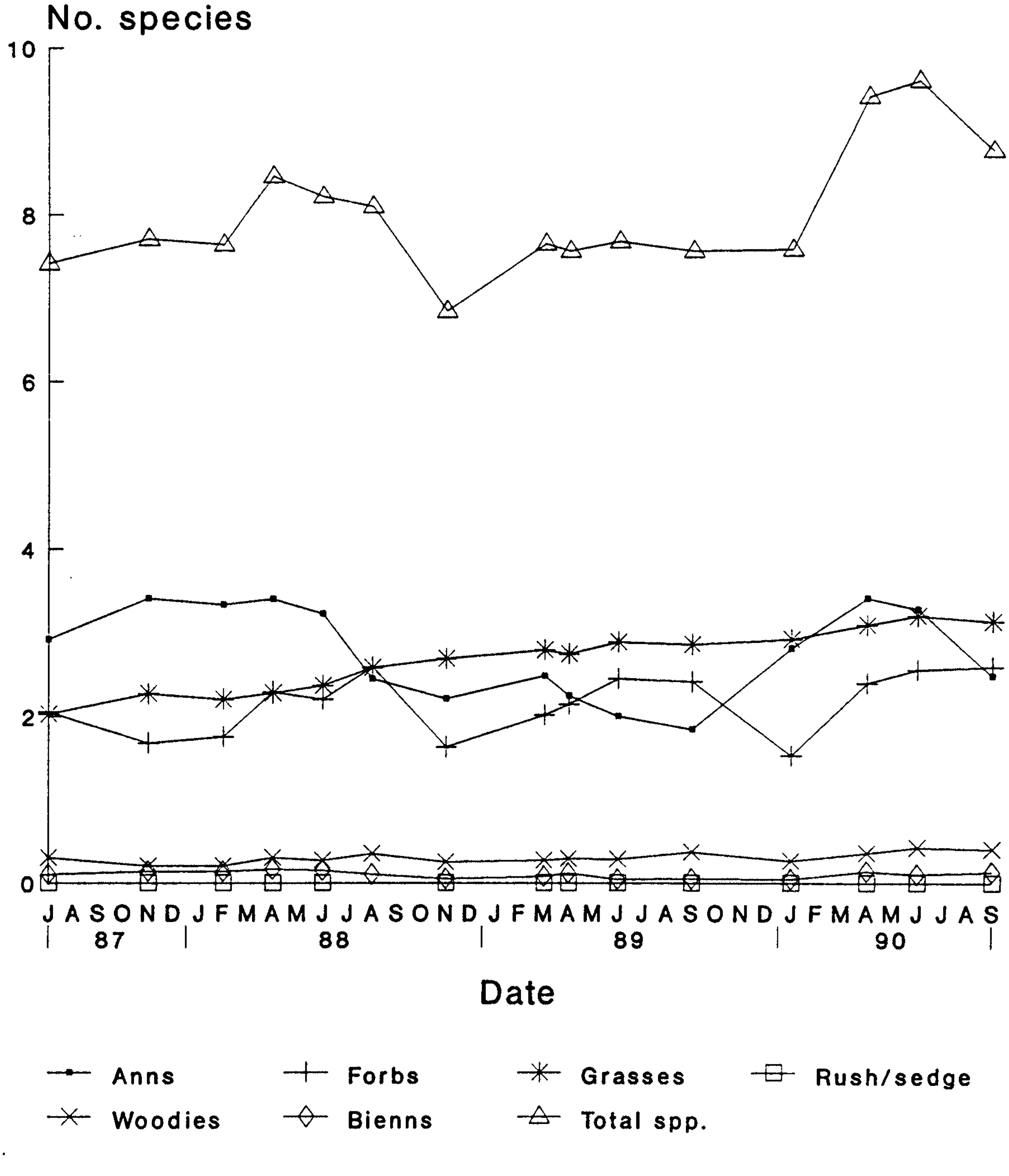


(c) June 1990



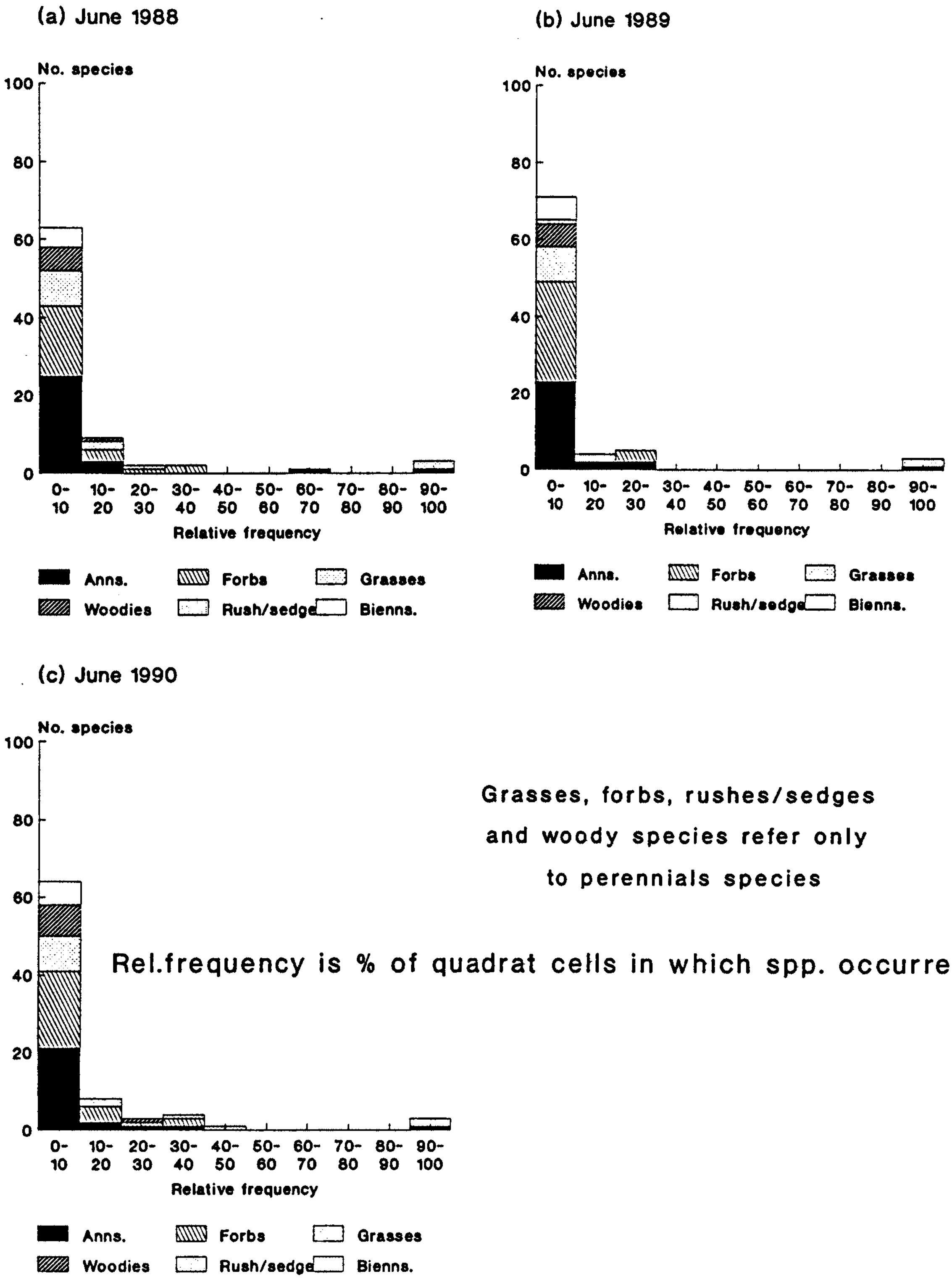
Rel.frequency is % of quadrat cells in which spp. occurred

Figure 3.8 Numbers of species on old margins, divided by life-history type (Data are means per 0.5x1m quadrat)



Grasses, forbs, rushes/sedges and woody species refer only to perennials

Figure 3.9 Relative frequency of species on the old margins

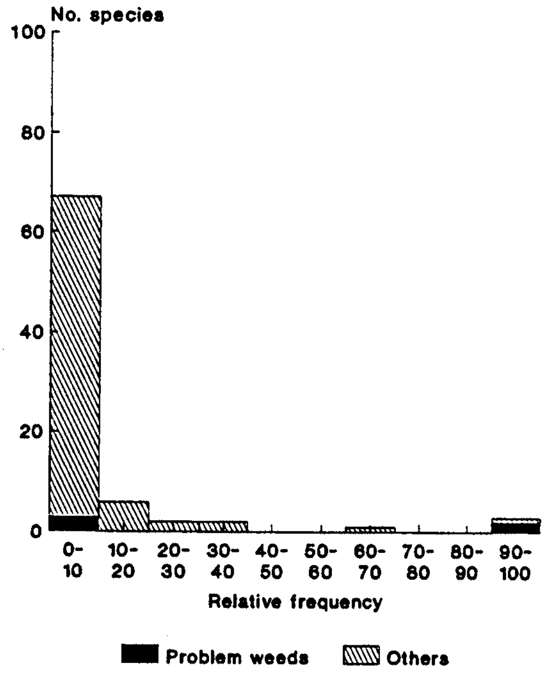


Grasses, forbs, rushes/sedges and woody species refer only to perennials species

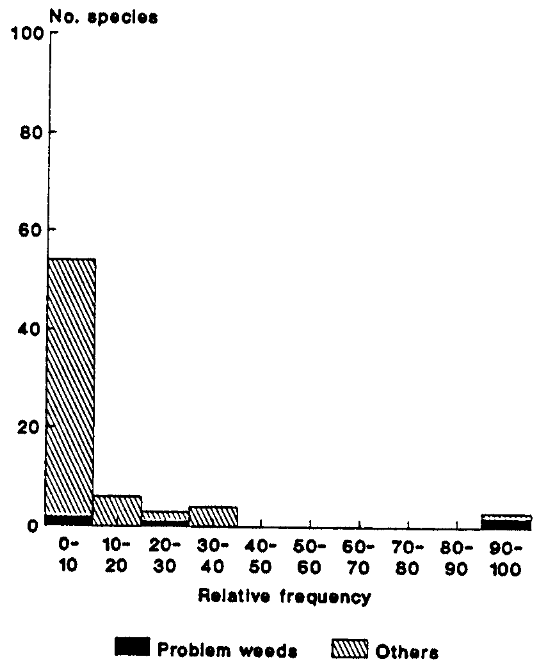
Rel.frequency is % of quadrat cells in which spp. occurred

Figure 3.10 Relative frequency of problem weeds: old margin

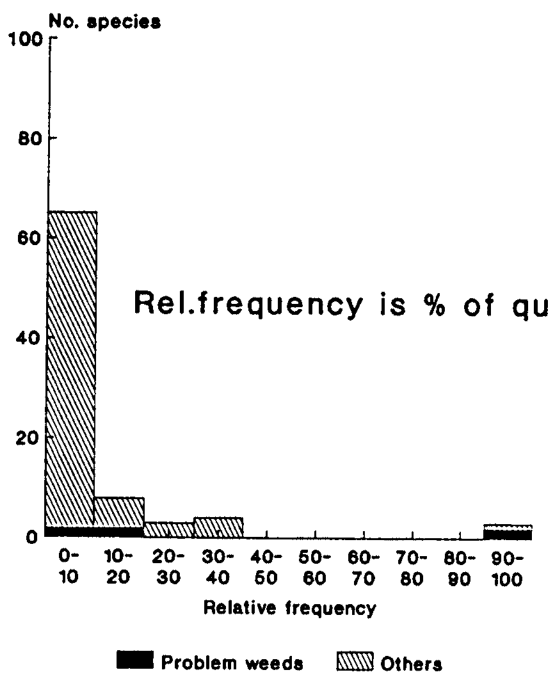
(a) June 1988



(b) June 1989

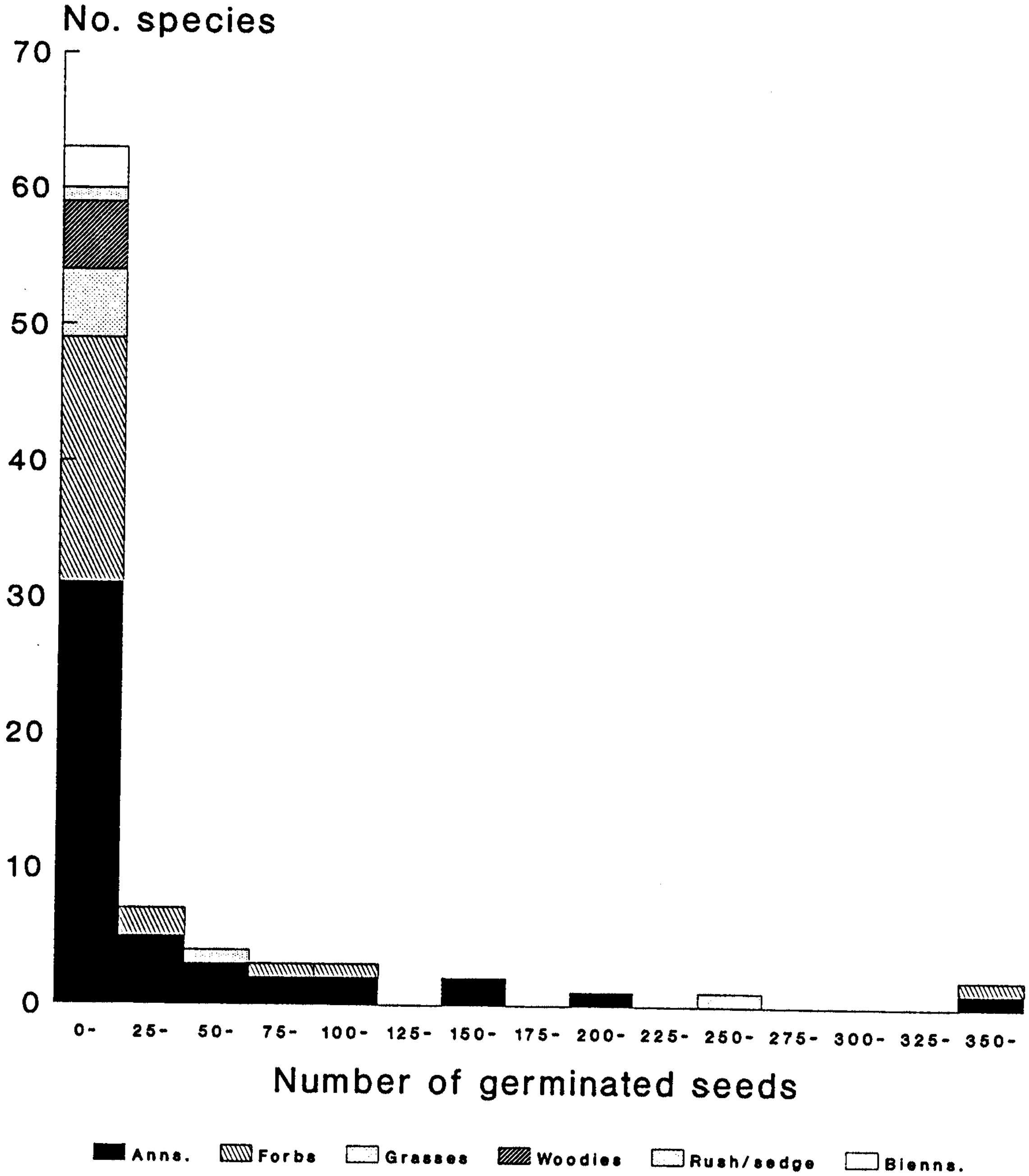


(c) June 1990



Rel.frequency is % of quadrat cells in which spp. occurred

Figure 3.11 Relative frequency of species in the seed bank



Grasses, forbs, rushes/sedges and woody species all refer only to perennial species

4 THE EFFECTS OF MANAGEMENT ON PLANT SPECIES RICHNESS AND DIVERSITY

4.1 Introduction

In this chapter we consider the effects of our experimental treatments on the development of two conventional criteria of nature conservation value; plant species richness and diversity. Temporal trends in the numbers and life-history characteristics of colonising species are considered independently of treatment effects in Chapter 3. All species in the permanent quadrats were last monitored in September 1990, by which time the summer-only cutting regime had been through three complete cycles and the spring/summer and spring/autumn regimes through two complete cycles (Chapter 2.2.3). This is a relatively short period in which to detect the effects of treatment on plant species abundance. Monitoring of percentage cover would have given more rapid results by detecting proximate effects of mowing on plant size. However, our monitoring method, of recording rooted presence, gives a more accurate measure of real changes in population size.

We consider the effects of sowing, mowing and spraying on species number in swards on both the new and the old field margins. In sown swards the numbers of species are likely to be determined, to a greater or lesser extent, by the numbers of species sown. For these swards we examine the relative numbers of sown and naturally-regenerating species and the ways in which mowing affected these two components.

Mowing might be expected to influence species richness by several mechanisms. First, it affects seed production. Amongst the species that reproduce predominantly by seed, the extent to which this influences population size the following season will vary, depending largely on the extent to which the size and longevity of their seed bank buffers annual fluctuations in seed return. We tested the prediction that amongst our treatments that were cut twice a year, species richness would be higher in the spring and autumn-cut treatment, which allows seed return, than in the spring and summer-cut treatment.

Secondly, mowing influences the competitiveness of the sward. It is well established that mowing, like grazing, can promote the development of diversity by selecting for slow-growing species of low stature at the expense of more competitive species that are better able to utilise high soil nutrient status. We therefore tested the prediction that species richness would be higher in treatments that were cut than in those that were uncut, and also higher in those that were cut twice than in those that were cut once. This relationship between mowing and the development of diversity can be accentuated if the removal of cut material also brings about progressive reductions in soil nutrient status. We therefore tested the prediction that species richness would be higher in the spring and summer-cut treatment from which the hay was removed than in that on which it was left lying.

Thirdly, mowing is likely to influence seed germination through its effects on sward density. Many species require light gaps in which to germinate and establish. We therefore predicted that swards which were more open during peak periods for germination and establishment would have most species. We found that our autumn-cutting regime left swards more open and gappy throughout the winter than swards which were left uncut at this time. This was particularly conspicuous at the end of the first year of fallow, in 1988, when removal of a large biomass of tall, predominantly annual species, in late September exposed substantial areas of bare ground. This effect of mowing leads to the same prediction as that for its effects on seed input, that species richness will be higher in spring and autumn than in spring and summer cut swards. For species richness, it is unlikely that we would be able to distinguish between these two causal factors, either or both of which may be important for individual species. We discuss these possibilities again for individual species in the unsown and sown components of the swards in Chapters 5 and 6 respectively.

Sowing, mowing and spraying might be expected to affect the annual and the perennial components of the swards to different extents. Although in semi-natural grassland annuals are usually a minor component of the sward, in secondary successional situations they are initially the dominant element (see Chapter 3). Although annuals, by definition, rely completely on annual regeneration from seed, while many perennials can persist and multiply for many years without reproducing by seed, the relative effects of removal of seed production in the two groups are difficult to predict. Many annual species are buffered from the effects of annual failures in seed return by large banks of long-lived seeds whereas the seeds of many species of grassland perennials are short-lived. Mowing might also have differential effects on annuals and perennials through its effects on the availability of suitable gaps for germination. Annual species tend to require larger gaps than perennials and so might be expected to be more affected by autumn cutting. We therefore tested the effects of sowing and mowing on annual and perennial species separately.

Annual spraying with broad spectrum herbicides is likely to select for annual species at the expense of perennials. The more effective the kill the more this is likely to be the case. The species composition of the annual community might be expected to change from year to year, depending on the species most effectively controlled before seeding the previous season, with species with the largest, longest-lived seed banks forming the most consistent elements. We used a planned comparison to compare the effects of spraying with those of leaving swards uncut, and unplanned comparisons to compare them with all other regimes. These comparisons were made for species richness and for diversity of all species, and of annuals and perennials separately.

The implications of the relative contributions of annual and perennial species to the richness and diversity of the sward are important. If some treatments result in the development of more species rich and diverse swards than others, the importance to nature conservation of this finding depends on the relative extents to which the effect is on the annual and the perennial components of the sward. In the context of the general aim of developing species-rich, weed-free, predominantly perennial swards, a sward in which the 'additional' diversity is contributed by perennials is of more value than that in which it is contributed by annuals.

4.2 Results

4.2.1 ALL SPECIES

The new margins

Species richness In the new margin the predominant effect of treatment on the numbers of species present was that of sowing (Table 4.1). We sowed 23 species (Chapter 2.2.2) and from April 1988, one month after sowing, until our last measurement in September 1990, this resulted in very significantly higher numbers of species in sown than in unsown treatments. At all monitoring rounds all sown treatments had more species than all unsown treatments although the magnitude of the difference was such that there was always overlap in the confidence intervals for some sown and unsown treatments. This is illustrated by the treatment means for June 1990 in Table 4.2.

Mowing first had a significant effect on species number in November 1988 when there were significantly more species in treatments cut in spring and autumn than in those cut in spring and summer. From this date onwards, the spring and autumn-cut treatments on both unsown and sown swards, had most species although the comparison with the spring and summer cut treatment was only significant on two dates (Table 4.1). Overall, the effect of cutting first became significant in June 1989 and was subsequently significant in January and June in 1990. The uncut treatment on unsown swards had least species by November 1988 and remained the most species-poor treatment at all subsequent dates. From the same time, on sown swards, the uncut treatment always had less species than treatments cut twice but the numbers of species were always slightly above or below those in the treatment cut once. We could not detect any significant differences in numbers of species between swards cut twice and those cut once or between swards cut in spring and summer in which the hay was removed and those in which it was left lying.

The sprayed plots were first treated in 1989, prior to which they were exactly equivalent to unsown, uncut plots (see Chapter 2.2.3). These two treatments never differed significantly from one another either before or after the spray treatment commenced (Table 4.1), having together the lowest species numbers of all treatments (e.g. see Table 4.2).

Species diversity The pattern of development of significant treatment effects on diversity and on the rank orders of the mean diversity indices for the different treatments was very similar to that for species richness alone. Diversity indices were calculated as both Simpson's Index (Table 4.3) and the Shannon-Weiner function (analyses not presented).

The old margins

Species richness Sowing had much less influence on numbers of species in the old than the new margins (Table 4.4). The sown treatments first had significantly more species than unsown treatments in April 1989, the second year of fallow. Even at this time some unsown treatments had more species than some sown treatments. The difference between sown and unsown treatments was significant at most, but not all, subsequent dates but the mean species number in all sown treatments did not exceed that in all of the unsown treatments until June and September in 1990 (means for June 1990 are presented in Table 4.5).

Mowing also had less effect on the species richness of the old than the new margin swards. The mean species number in uncut treatments was less than that in cut treatments on both sown and unsown swards at most monitoring rounds from June 1989 onwards although this difference was significant only in September 1989 (Table 4.4). No other consistent patterns developed either in the significance of the planned comparisons or in the rank orders of the treatment means. The spring and autumn cut treatment did not develop higher species numbers than other treatments as on the new margins and, in November 1988, it had significantly less species than the spring and summer cut treatments. It is difficult to interpret with confidence the differences between the treatments cut once and those cut twice because the differences within blocks resulted in some isolated significant differences from November 1987 onwards, before the treatments were in place. Where, as in this case, there is evidence that the results are affected by patchy conditions at the outset of the experiment, further analyses are required to distinguish between any treatment effects and this source of background variability. In this report we attach confidence only to significant effects which form part of a consistent pattern over time.

As on the new margins, the numbers of species on the sprayed treatment never differed significantly from those on the uncut treatment, either before or after the spraying commenced in 1989.

Diversity Analyses of diversity indices for the old margins gave almost the same rank orders of means as those of species richness and less of the differences between means were significant (data not presented). Because of the similarity in the conclusions that can be drawn from analyses of species richness and diversity indices for the plants species, we have presented only the analyses for species richness in the remainder of this chapter.

Summary Plant species richness and diversity in the new field margins were improved substantially by sowing but could also be manipulated by mowing, even over a three year period. Both leaving swards uncut and annual spraying with glyphosate rapidly resulted in swards that were poorer in species than mown swards. Over this time period we could not detect differences between swards mown once and those mown twice, nor between those in which the hay was left and those from which it was removed. However, the timing of mowing rapidly became important, with swards mown in autumn having more species than those mown in summer.

Management of the old margin swards by sowing and mowing had much less effect on species number. Sowing started to become important only in the third year. There was some evidence that mowing resulted in higher numbers of species than leaving swards unmown but this effect was also slower to have effect than on the new margins. None of our other cutting regimes appeared to affect the species richness of the old margin swards during this period.

Spraying annually with glyphosate for two seasons did not reduce the numbers of species significantly below those on plots which were left unmanaged. Both were relatively species poor.

4.2.2 THE SOWN AND UNSOWN COMPONENTS OF SOWN SWARDS

The new margins Most of the species comprising the sown swards were components of the seed mixture. By 1990 between 63 and 68% of the species recorded in June 1990 were sown (Table 4.6). It was shown above that these swards had significantly more species in total than the unsown swards but the numbers of unsown species that they accommodated were substantially lower than in the unsown swards. The sown species were thus effective in excluding natural colonists.

Our mowing regimes influenced the numbers of species in both the unsown and the sown components of the sown swards. Tables 4.7 and 4.8 show the development of significant effects on both of these components. Only forbaceous sown species were monitored in 1991 and 1992 (see Chapter 2.2.5) and so the results presented for these years must be interpreted with caution.

In contrast to the effect detected for all species, using both sown and unsown swards (Section 4.2.1 above), the overall effect of cutting on the numbers of sown species on sown swards alone was never significant. However, planned comparisons between individual treatments or combinations of treatments, did reveal some significant effects of the mowing regimes. Amongst both the sown and unsown species, the treatments that were uncut, or cut once, usually had less species than those cut twice (see below) but the rank orders of these two treatments varied (e.g. see June 1990 data, Table 4.6). They differed significantly only amongst the unsown component in January 1990, when the uncut swards had least species.

Treatments cut twice had more sown species than those cut once from September 1989 onwards, although this difference was not significant on all dates (Table 4.7). This contrast was also significant on some dates between November 1988 and March 1989 for the unsown component of the swards, although after this period the treatment cut once did not have consistently less unsown species than those cut twice (Table 4.8). The appearance of this effect in November 1988, when no treatment had been cut twice (see Chapter 2.2.3), and its disappearance by late 1989, suggests that it may have been an artefact resulting from differences within blocks. It cannot be interpreted with confidence until further analyses have been undertaken to examine this possibility.

Cutting in spring and autumn resulted in higher numbers of species than cutting in spring and summer in both the unsown and sown components of the sward. Amongst the unsown species this effect first became significant in June 1988 and was significant again in June 1990 (Table 4.6). On all subsequent dates the spring and autumn cut treatment had more species than any other treatment. This effect was present but less marked amongst the sown species. The spring and autumn cut treatment had more sown species than all other treatments on all dates from April 1989 onwards. However, contrast between the spring+autumn and spring+summer cut treatments approached significance in June 1989

(P=0.068) and was significant only in June 1992, when only the forbaceous species were recorded.

The old margins We were unable to detect any consistent effects of mowing on the numbers of sown or unsown species in the old margins of the sown plots (Tables 4.9 and 4.10). Our failure to detect the overall effect of mowing, shown in Section 4.2.1 for the analyses of all treatments and species, is likely to be due to the smaller number of treatments, and sample species, used in these analyses (Table 4.11). The significant differences detected between treatments cut once and those cut twice in the winter of 1988/89 are likely to have resulted from the same problems discussed above for the new margins.

Summary The frequency of mowing appeared to be less important in influencing the species richness of the sown than of the naturally regenerating swards. There was no evidence that there were more sown species in cut than in uncut swards, although there was some evidence that there were more unsown species. We are unable to draw reliable conclusions about the relative effects of cutting once and twice on the numbers of sown and unsown species until further analyses have been carried out. The dominant effect of mowing on both the sown and unsown components of the sown swards was of its timing, with swards cut in autumn supporting more species than those cut in summer.

4.2.3 ANNUAL AND PERENNIAL SPECIES

The new margins

Annuals Overall, the numbers of annual species recorded were very significantly reduced by sowing from very soon after the sown sward established (Tables 4.12 and 4.13). All sown treatments had lower mean numbers of annual species than all unsown treatments from November 1988 onwards, and in June and September 1990 all sown treatments differed significantly from all unsown treatments (unplanned comparisons).

The numbers of annual species were lower in uncut than in cut treatments, although this effect was significant on only two dates. This trend was established by June 1989, when uncut treatments had lower numbers of annual species than most but not all cut treatments on both unsown and sown swards. At all subsequent dates uncut treatments had lower numbers of annuals than other treatments on either one or both swards types. Treatments cut twice had significantly less annuals than those cut once on several dates in 1989. However, this result should be treated with caution because the effect disappeared completely by 1990. It is likely that this effect is the same artifact as that reported above (4.2.2) and requires further analysis to remove possible effects of background variation within blocks.

Treatments cut in spring and autumn had significantly higher numbers of annual species from those cut in spring and summer only in June 1990. On this date, this effect was largely attributable to the sown treatments: the numbers of annuals in these two treatments in unsown plots did not differ significantly from each other (unplanned tests). On other dates this effect was not apparent even in the rank orders of the treatment means.

The sprayed treatment had significantly more annual species than the uncut treatment in September 1990, three months after spray was applied. On this date it also had significantly more annual species than all other treatments. It also had high numbers of species in September 1989, after the first spray application, although the effect was not significant. This effect disappeared in the intervening period, in spring and summer 1990.

Perennials The analyses presented in this section are for unsown perennial species in both the sown and unsown swards. Since all but one of the sown species were perennials, equivalent results for them are presented in the analyses sown species (Section 4.2.2 above, Table 4.7).

Sowing reduced significantly the numbers of unsown perennial species in the new margins from November 1988 onwards (Table 4.14). Overall, uncut treatments had less perennial species than cut treatments on all dates from November 1989 onwards although this effect was significant on only two dates. There were no differences in the numbers of perennials between treatments cut once and those cut twice, nor were there any significant differences between treatments in which the hay was left lying and those from which it was removed. Cutting in spring and autumn resulted in significantly higher numbers of perennials than cutting in spring and summer in November 1988. Amongst both sown and unsown swards spring and autumn-cut treatments had more species than all other treatments on most subsequent dates.

Spraying resulted in significantly lower numbers of perennial species than in the uncut treatment in September 1990. At this time there were less perennial species in the sprayed treatment than in all other treatments on unsown swards. On all previous dates the numbers of species in the sprayed treatments did not differ significantly from those in the uncut treatment.

The old margins

Annuals Numbers of annual species in the old margins were low (Table 4.15) and with such a small sample size we were unable to detect any effects of our treatments. Although these low numbers suggest that annuals are an irrelevant criterion in the management of the old margin sward, we show in Chapter 5 that some species of pernicious annual weeds can be very abundant there.

Sowing had no significant effects on the numbers of annuals and the single significant result from cutting in September 1990, in which treatments cut once had more species than those cut twice, was not part of a trend and may be an artefact of the low numbers available for analysis (Table 4.16).

Perennials The numbers of perennial species in the old margins were very similar to the total numbers of species (Section 4.2.1 above) because the numbers of annuals were so low. There were no consistent trends in their numbers and there were rarely any significant differences between any of the treatment means (e.g. Table 4.17). Sowing had no significant effects on the numbers of unsown species of perennials. The single significant effect of mowing in January in 1990, when spring and autumn-cut treatments appeared to have significantly less species than those cut in spring and summer was not part of a trend (e.g. see June data in Table 4.15). This effect is likely to have resulted from the relatively low detectability of perennials in mid-winter being exacerbated by the autumn cut. This removed dead stems which, in other treatments, provided an additional means of detection and identification.

Summary Although sown swards on the new margins had more species in total, they accommodated significantly less unsown annual and perennial species than unsown swards. Treatments that were mown had more annual and perennial species than those left unmanaged. We are unable to draw reliable conclusions about the relative effects of mowing once or twice until additional analyses have been completed. The timing of mowing appeared to be a more important influence on the numbers of perennial than on annual species. Cutting in autumn resulted in higher frequencies of perennials from an early stage but only affected annuals in 1990. Although spraying resulted in similar numbers of species overall to the uncut treatment, the numbers of annual species in the sprayed treatment were significantly higher than in the uncut treatment and the numbers of perennial species significantly lower.

4.3 Discussion

4.3.1 CONCLUSIONS AND PRACTICAL IMPLICATIONS

Over a three year period sowing wild flower seed mixtures on fallowed arable field margins can create swards that are richer in species than allowing natural regeneration, as long as a sufficiently rich mixture is used. Sowing effectively side-steps secondary succession. These sown swards were highly competitive and accommodated significantly fewer species that regenerated naturally from the local flora than were found in unsown swards. This may be seen as an advantage if the species that are excluded include pernicious weeds. We show in Chapter 5 that sown swards are an extremely effective means of controlling both annual and perennial pernicious weeds. Conversely, it may be seen as a disadvantage if desirable elements from the local flora are excluded. Thus where a diverse and attractive flora is available to colonise extended field margins (see Chapter 3), sowing a seed mixture is likely to prevent it from doing so. However, in many intensively farmed areas of lowland England, the potential for establishment of swards that are both relatively species rich and acceptable to farmers is low. In these areas sowing seed mixtures is likely to be the only viable means of creating satisfactory swards.

Whilst our relatively complex seed mixture resulted in higher diversities than developed in naturally regenerating swards, it is equally likely that relatively simple mixtures could result in lower numbers of plant species than in naturally regenerating swards. Any seed mixture that includes grass species that form a dense sward base are likely to exclude a high proportion of naturally regenerating species. Thus, seed mixtures should be seen as a management tool for manipulating plant species richness. In Chapter 5 we discuss their use as management tool for weed control and in Chapters 8 to 10 as a means of manipulating invertebrate diversity.

Species richness in fallowed field margins can also be manipulated by mowing. Leaving swards unmanaged (with fertiliser and herbicides excluded, Chapter 2.2.2) and spraying annually with glyphosate both resulted in swards that were poorer in species than those that were mown. However, spraying was a much less desirable management tool than doing nothing for two reasons. First, it was more expensive and, second, the sprayed sward comprised significantly more annuals and less perennials than the unmanaged swards. Spraying effectively re-creates a first year successional sward each year and so removes the possibility of natural biological control of weedy annuals by competition from perennials. In Chapter 5 we show that although some of the perennials that were controlled by spraying were pernicious weeds, many of the annuals that proliferated were also problem species.

Although we could not detect any reliable differences between the numbers of species in swards cut once and those cut twice, it should not be assumed that cutting twice has no advantages over a single cut. Further analyses are needed to remove within-block variance resulting from patchy starting conditions before this effect can be fully evaluated. The relative cost implications of cutting once or twice a year make it important that this possibility is fully explored. While it is not yet established whether it is important in determining plant species richness, we show in Chapters 5 and 6 that it can be important in influencing the abundance of particular plant species.

The timing of mowing rapidly became an important influence on the numbers of species present. Mowing in autumn resulted in significantly higher numbers of species than mowing in summer in both sown and unsown swards. We suggested in the introduction (4.1) that this effect could result from higher seed production in swards left uncut in summer, from improved germination and establishment opportunities or from a combination of the two. We discuss the relative importance of these two possibilities in determining the abundance of key species in Chapters 5 and 6.

We suggested in the introduction that the nature conservation importance of management regimes that promote the development of diversity must depend partly on the 'value' of the additional species and that autumn cutting might be expected to promote annuals rather than perennials, which are more 'valuable' in this context (4.1). We found, however, that autumn cutting promoted numbers of perennial more than of annual species. It also promoted species richness of both the sown and the unsown components of sown swards. It therefore appears to be a valuable technique in developing species rich, perennial-dominated swards on fallowed arable land. We show in Chapter 5, however, that whilst it may not increase the total numbers of annual species in can result in substantial increases in the abundance of particular annual species, including pernicious weeds.

We were unable to detect any significant differences in the numbers of species in swards in which the cut material was collected and those on which it was left lying. It is generally assumed that the removal of cut material is advantageous for nature conservation management because it reduces fertility and is consequently likely to promote diversity. It presents problems on field margins because many farmers do not have cutting machinery that removes clippings. In the light of these practical difficulties and of our results, it would be difficult to make a strong case for the need to remove cut material. However, there are three reasons for caution in suggesting that it is not a useful management technique. First, in highly productive swards, which are common on arable soils, the large biomass of cut material can result in die-back of the underlying sward. Second, although we could not detect effects of the removal of cut material on the numbers of species, we show in Chapter 5 that it can decrease the abundance of several species of pernicious weeds. Finally, reduction in soil nutrient status by removal of cut material might be expected to be a very slow process, the effect of which would be unlikely to be apparent within the three-year timescale of our monitoring. Further years of species richness data, together with soil sampling, are needed if this effect is to be properly evaluated. Despite the importance of its implications for management, no rigorous experimental data exist on changes in soil nutrient status and the ways in which it can be affected by sward management, in contemporary, ex-arable soils. Our experiment provides an ideal facility for evaluating these factors.

Whilst sowing and some mowing regimes had rapid and significant effects on the numbers of plant species in the early successional swards on the field margins, they were relatively ineffective and much slower to change the numbers of species in the established swards on the old field margins. This has important implications for management. It suggests that in the short-term, the expense and effort of sowing or mowing established field margins will appear to be wasted. We discuss the reasons for the slow establishment of the sown species in the old field margins in more detail in Chapter 6. It is likely, however, that these regimes will have greater effects on the numbers of species in these swards over longer periods of time.

Much of the rapid response of the new margin swards to sowing and mowing resulted from effects on the establishment of species from seed in the relatively open, early-successional communities. Manipulation of species richness in more established swards is likely to be a longer-term process because it must involve both fewer opportunities for the establishment of new species and changes in the persistence of already established perennials. The changes in the size of plants and eventual extinctions that contribute to changes in species number recorded in a given area are difficult to detect on short timescales. We need to continue to monitor species richness to evaluate whether sowing and mowing are useful conservation management tools for established field margin vegetation and whether the same regimes that are beneficial in early successional swards are also the most effective at later stages. The implications of this are as important for the longer-term management of the new margins as they are for the management of old field margins.

4.3.2 FUTURE ANALYSES

The next analytical step that is planned for the data presented in this chapter is a re-analysis that takes account of differences in starting conditions that may affect differentially the plots within blocks of the experiment. We have seen above that this relatively small-scale patchiness in the distribution of plant species can occasionally give rise to anomalous significant treatment effects and, equally, can mask real treatment effects.

4.3.3 FUTURE MONITORING

We have suggested that monitoring of numbers of plant species richness should be continued because it is likely that the effects and effectiveness of management that we have detected in the first three years after fallowing are likely to differ from those that are appropriate from manipulating the very different process that determine species number in more established swards. If the establishment of extended field margins is seen as a medium to long term investment for nature conservation and for the farmer, it is important that advice can also be provided on appropriate management techniques for established swards. However, we have also argued that changes in diversity resulting from differential management of more established swards are likely to be slower than those in new swards. This suggests that a single monitoring round every two or three years could now supply adequate information on this subject. It is also important that the soil nutrient status of contrasting treatments is measured and compared with that in the existing field edge. This need only be done once.

4.3.4 IMPLICATIONS FOR SET-ASIDE MANAGEMENT

All of our conclusions on the effects of sowing and mowing on species richness are as applicable to whole field set-aside as to field margin management. The numbers of species colonising are likely to differ between the edges and centres of fields (see Chapter 3.3) but the relative effects of management on their numbers are not.

Table 4.1 Numbers of species in the new margin 1987-1990
Summary of significance of differences for selected comparisons

		07/ 87	11/ 87	02/ 88	04/ 88	06/ 88	08/ 88	11/ 88	03/ 89	04/ 89	06/ 89	09/ 89	01/ 90	04/ 90	06/ 90	09/ 90
from 2-way ANOVA:	d.f															
BLOCK effect	5,45	***	***	***	***	***	***	***	***	***	***	*	***	**	***	***
TREAT effect	9,45	ns	ns	ns	***	***	***	***	***	***	***	***	***	***	***	***
Planned contrasts:																
Remove v leave hay	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Spray v uncut	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
from 3-way ANOVA:																
SOWING effect	1,35	ns	ns	ns	***	***	***	***	***	***	***	***	***	***	***	***
CUTTING effect	3,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	**	ns	*	ns	*	ns
INTERACTION	3,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned contrasts:																
Cut v uncut	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	**	ns	ns	ns
Cut once v twice	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Cut sp + su v sp + au	1,35	ns	ns	ns	ns	ns	ns	*	ns	ns	*	ns	ns	ns	ns	ns

Table 4.2 Mean[2] numbers of species in the new margins in June 1990

Treatment	No. species (/0.25m²)	Sig.[1] diffs.
Sown - cut in spring & autumn	18.0	a
Sown - cut in spring & summer	15.0	a b
Sown - not cut	14.7	a b
Sown - cut in summer only	14.0	a b c
Not sown - cut in spring & autumn	13.0	b c
Not sown - cut in spring & summer	12.4	b c
Not sown - cut in summer	12.2	b c
Not sown - cut spring & summer, hay left	11.6	b c
Not sown - not cut	11.2	b c
Not sown - sprayed	10.4	c

Treatment effect: $F_{(9,45)} = 4.86$, $P < 0.001$

[1] Means with the same letter are not significantly different (Tukey's Test)

[2] Means are back-transformed from log-transformed data

Table 4.3 Plant species diversity (Simpson's Index) in the new margin 1987-1990
Summary of significance of differences for selected comparisons

		07/ 87	11/ 87	02/ 88	04/ 88	06/ 88	08/ 88	11/ 88	03/ 89	04/ 89	06/ 89	09/ 89	01/ 90	04/ 90	06/ 90	09/ 90
from 2-way ANOVA:	d.f															
BLOCK effect	5,45	***	***	***	***	***	***	***	***	***	**	*	***	**	***	***
TREAT effect	9,45	ns	ns	ns	***	***	***	***	***	***	***	***	***	***	***	***
Planned contrasts:																
Remove v leave hay	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Spray v uncut	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
from 3-way ANOVA:																
SOWING effect	1,35	ns	ns	ns	***	***	***	***	***	***	***	***	***	***	***	***
CUTTING effect	3,35	ns	ns	ns	ns	ns	ns	*	ns	ns	**	ns	ns	ns	*	ns
INTERACTION	3,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned contrasts:																
Cut v uncut	1,35	ns	ns	*	ns	ns	ns	ns	ns	ns	*	*	**	ns	*	*
Cut once v twice	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns
Cut sp+su v sp+au	1,35	ns	ns	ns	ns	ns	ns	**	ns	ns	ns	ns	ns	ns	*	ns

Table 4.4 Numbers of species in the old margin 1987-1990
Summary of significance of differences for selected comparisons

		07/ 87	11/ 87	02/ 88	04/ 88	06/ 88	08/ 88	11/ 88	03/ 89	04/ 89	06/ 89	09/ 89	01/ 90	04/ 90	06/ 90	09/ 90
from 2-way ANOVA:	d.f															
BLOCK effect	5,45	***	***	***	***	***	***	***	***	***	***	***	***	***	***	*
TREAT effect	9,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
Planned contrasts:																
Remove v leave hay	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Spray v uncut	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
from 3-way ANOVA:																
SOWING effect	1,35	ns	ns	ns	ns	ns	ns	ns	ns	**	**	ns	*	ns	ns	*
CUTTING effect	3,35	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	*	*	ns	ns	ns
INTERACTION	3,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned contrasts:																
Cut v uncut	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns
Cut once v twice	1,35	ns	*	ns	*	ns	*	ns	**	*	ns	*	*	ns	ns	ns
Cut sp+su v sp+au	1,35	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns

Table 4.5 Mean numbers of species in the old margins in June 1990

Treatment	No. species (/0.25m²)	Sig.[1] diffs.
Sown - cut in summer only	12.8	a
Sown - cut in spring & autumn	11.0	a
Sown - cut in spring and summer	10.9	a
Sown - not cut	10.4	a
Not sown - cut in summer	10.3	a
Not sown - cut in spring & summer	9.9	a
Not sown - cut in spring and autumn	9.7	a
Not sown - sprayed	9.4	a
Not sown - not cut	8.9	a
Not sown - cut spring and summer, hay left	8.9	a

Treatment effect: $F_{(9,46)} = 1.02$, ns

[1] Means with the same letter are not significantly different (Tukey's Test)

[2] Means are back-transformed from log-transformed data

Table 4.6 Mean[2] numbers of sown and unsown species in the new margins in June 1990

Treatment	No. sown (/0.25m²)	Sig.[1] diffs.	No. unsown (/0.25m²)	
Sown - cut in spring and autumn	11.15	a	6.66	a
Sown - cut in spring and summer	9.93	a	4.73	b
Sown - not cut	9.90	a	4.73	b
Sown - cut in summer	9.35	a	4.60	b

[1] Means with the same letter are not significantly different (Tukey's Test)

[2] Means are back-transformed from log-transformed data

Note that the treatments are ranked in descending order of magnitude for the perennial but not the annual species

Table 4.7 Numbers of sown species in sown treatments in the new margin 1987-1992
Summary of significance of differences for selected comparisons

		06/88	08/88	11/88	03/89	04/89	06/89	09/89	01/90	04/90	06/90	09/90	07/91	07/92
from 2-way ANOVA:	d.f													
BLOCK effect	5,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
TREAT effect	3,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
Planned comparisons:														
cut v uncut	1,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
cut once v twice	1,15	ns	ns	ns	ns	ns	ns	*	*	ns	ns	*	ns	**
cut sp+su v sp+au	1,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*

Table 4.8 Numbers of unsown species in sown treatments in the new margin 1987-1990
Summary of significance of differences for selected comparisons

		06/88	08/88	11/88	03/89	04/89	06/89	09/89	01/90	04/90	06/90	09/90
from 2-way ANOVA:	d.f											
BLOCK effect	5,15	*	ns	*	ns	*	**	ns	**	**	***	ns
TREAT effect	3,15	ns	ns	ns	ns	ns	*	ns	**	ns	*	ns
Planned comparisons:												
cut v uncut	1,15	ns	ns	ns	ns	ns	ns	ns	**	ns	ns	ns
cut once v twice	1,15	ns	ns	*	ns	*	**	ns	ns	ns	ns	ns
cut sp+su v sp+au	1,15	ns	ns	ns	ns	ns	*	ns	ns	ns	**	ns

Table 4.9 Numbers of sown species in sown treatments in the old margin 1987-1990
Summary of significance of differences for selected comparisons

		06/ 88	08/ 88	11/ 88	03/ 89	04/ 89	06/ 89	09/ 89	01/ 90	04/ 90	06/ 90	09/ 90
from 2-way ANOVA:	d.f											
BLOCK effect	5,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
TREAT effect	3,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned comparisons:												
cut v uncut	1,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
cut once v twice	1,15	*	ns	ns	**	ns	ns	ns	ns	ns	ns	ns
cut sp+su v sp+au	1,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 4.10 Numbers of unsown species in sown treatments in the old margin 1987-1990
Summary of significance of differences for selected comparisons

		06/ 88	08/ 88	11/ 88	03/ 89	04/ 89	06/ 89	09/ 89	01/ 90	04/ 90	06/ 90	09/ 90
from 2-way ANOVA:	d.f											
BLOCK effect	5,15	**	*	*	ns	ns	*	*	*	*	*	ns
TREAT effect	3,15	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns
Planned comparisons:												
cut v uncut	1,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
cut once v twice	1,15	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns
cut sp + su v sp + au	1,15	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 4.11 Mean[2] numbers of sown and unsown species in the old margins in June 1990

Treatment	No. sown ($/0.25m^2$)	Sig.[1] diffs.	No. unsown ($/0.25m^2$)	
Sown - cut in summer	2.76	a	9.52	a
Sown - cut in spring and summer	1.79	a	9.08	a
Sown - cut in spring and autumn	2.13	a	8.76	a
Sown - uncut	1.95	a	8.43	a

[1] Means with the same letter are not significantly different (Tukey's Test)

[2] Means are back-transformed from log-transformed data

Note that the treatments are ranked in descending order of magnitude for the unsown but not the sown species

Table 4.12 Numbers of annual species in the new margin 1987-1990
Summary of significance of differences for selected comparisons

		07/ 87	11/ 87	02/ 88	04/ 88	06/ 88	08/ 88	11/ 88	03/ 89	04/ 89	06/ 89	09/ 89	01/ 90	04/ 90	06/ 90	09/ 90
from 2-way ANOVA:	d.f															
BLOCK effect	5,45	***	***	***	***	***	***	***	***	*	ns	ns	***	**	ns	***
TREAT effect	9,45	ns	ns	ns	ns	ns	**	***	***	***	***	***	***	***	***	***
Planned contrasts:																
Remove v leave hay	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Spray v uncut	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**
from 3-way ANOVA:																
SOWING effect	1,35	ns	ns	ns	*	ns	***	***	***	***	***	***	***	***	***	***
CUTTING effect	3,35	ns	ns	ns	ns	ns	ns	*	ns	ns	*	ns	ns	ns	ns	*
INTERACTION	3,35	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned contrasts:																
Cut v uncut	1,35	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	*
Cut once v twice	1,35	ns	ns	ns	ns	ns	ns	*	ns	*	*	ns	ns	ns	ns	ns
Cut sp+su v sp+au	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns

Table 4.13 Mean[2] numbers of annual and perennial species in the new margins in June 1990

Treatment	No. annuals (/0.25m²)	Sig.[1] diffs.	No. perennials (/0.25m²)	
Unsown - cut in spring & autumn	5.10	a	7.30	a
Unsown - cut in summer only	5.29	a	6.55	a b
Unsown - uncut	4.29	a b	6.35	a b
Unsown - cut in spring & summer, hay left	5.13	a	6.28	a b
Unsown - cut in spring and summer	5.28	a	6.01	a b c
Unsown - sprayed	4.64	a b	5.65	a b c
Sown - cut in spring and autumn	2.14	b c	4.36	b c d
Sown - cut in spring and summer	0.69	c	3.99	c d
Sown - not cut	1.09	c	3.57	d
Sown - cut in summer	1.23	c	3.20	d

[1] Means with the same letter are not significantly different (Tukey's Test)

[2] Means are back-transformed from log-transformed data

Note that the treatments are ranked in descending order of magnitude for the perennial but not the annual species

Table 4.14 Numbers of perennial species in the new margin 1987-1990
Summary of significance of differences for selected comparisons

		07/ 87	11/ 87	02/ 88	04/ 88	06/ 88	08/ 88	11/ 88	03/ 89	04/ 89	06/ 89	09/ 89	01/ 90	04/ 90	06/ 90	09/ 90
from 2-way ANOVA:	d.f															
BLOCK effect	5,45	***	*	**	***	***	***	***	***	***	***	***	***	***	***	***
TREAT effect	9,45	ns	ns	ns	ns	ns	ns	***	*	ns	***	***	***	***	***	***
Planned contrasts:																
Remove v leave hay	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Spray v uncut	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
from 3-way ANOVA:																
SOWING effect	1,35	ns	ns	ns	ns	ns	ns	***	**	**	*	***	***	***	***	***
CUTTING effect	3,35	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	**	ns	ns	ns
INTERACTION	3,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned contrasts:																
Cut v uncut	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	**	ns	ns	ns
Cut once v twice	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Cut sp + su v sp + au	1,35	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	ns	ns

Table 4.15 Mean[2] numbers of annual and perennial species in the old margins in June 1990

Treatment	No. annuals ($/0.25m^2$)	Sig.[1] diffs.	No. perennials ($/0.25m^2$)	
Unsown - cut in spring & autumn	3.75	a	6.81	a
Unsown - cut in summer only	2.84	a	6.61	a
Sown - cut in spring and summer	2.51	a	6.47	a
Sown - cut in summer only	2.91	a	6.41	a
Sown - cut in spring and autumn	2.39	a	6.28	a
Sown - uncut	2.27	a	6.03	a
Unsown - sprayed	3.14	a	5.99	a
Unsown - cut in spring and summer	3.75	a	5.93	a
Unsown - not cut	2.78	a	5.93	a
Unsown - cut in spring & summer, hay left	3.34	a	5.42	a

[1] Means with the same letter are not significantly different (Tukey's Test)

[2] Means are back-transformed from log-transformed data

Note that the treatments are ranked in descending order of magnitude for the perennial but not the annual species

Table 4.16 Numbers of annual species in the old margin 1987-1990
Summary of significance of differences for selected comparisons

		07/87	11/87	02/88	04/88	06/88	08/88	11/88	03/89	04/89	06/89	09/89	01/90	04/90	06/90	09/90
from 2-way ANOVA:	d.f															
BLOCK effect	5,45	***	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	*	**	ns	ns
TREAT effect	9,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned contrasts:																
Remove v leave hay	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Spray v uncut	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
from 3-way ANOVA:																
SOWING effect	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CUTTING effect	3,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
INTERACTION	3,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned contrasts:																
Cut v uncut	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Cut once v twice	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
Cut sp+su v sp+au	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Table 4.17 Numbers of perennial species in the old margin 1987-1990
Summary of significance of differences for selected comparisons

		07/ 87	11/ 87	02/ 88	04/ 88	06/ 88	08/ 88	11/ 88	03/ 89	04/ 89	06/ 89	09/ 89	01/ 90	04/ 90	06/ 90	09/ 90
from 2-way ANOVA:	d.f															
BLOCK effect	5,45	***	***	***	***	***	***	***	***	***	***	***	***	***	***	***
TREAT effect	9,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned contrasts:																
Remove v leave hay	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Spray v uncut	1,45	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
from 3-way ANOVA:																
SOWING effect	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CUTTING effect	3,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns
INTERACTION	3,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Planned contrasts:																
Cut v uncut	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Cut once v twice	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Cut sp+su v sp+au	1,35	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	*	ns	ns	ns