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Effects of seed mixture and management on beetle assemblages of arable field margins

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Abstract

Beetle assemblages and their response to plant community composition and architectural structure were monitored from 2002 to 2006 within arable field margins. Field margins were sown with either tussock grass and forbs, fine grass and forbs or grass only seed mixtures. After an establishment year, field margins were managed using standard sward cuts, scarification, or graminicide application. For predatory beetles, overall density was greatest where tussock grasses were included within the seed mixtures, while the densities of phytophagous beetles were greatest where forbs were present. Unexpectedly, species rarefaction curves suggested that phytophagous beetle species richness was greatest where field margins were established using a grass only seed mixture. The structure of the beetle assemblages, i.e., the relative abundances of individual species, was largely dependent on seed mixture, although margin management also played an important role. The results suggest that field margins established using seed mixtures containing tussock grasses and forbs would be expected to provide the greatest resources for beetles, at least at local scales. However, the use of a single standardised seed mixture for margin establishment would result in a homogenisation of beetle assemblages at a regional scale.

Keywords: Coleoptera; Cutting; Forbs; Grasses; Graminicide; Scarification

1. Introduction

Greater public awareness of declining farmland biodiversity has increased political impetus within the EU to develop new approaches to the management of arable land (Donald, 1998; Ovenden et al., 1998). This has been realised in part though the development of agri-environmental schemes that provide financial incentives to farmers to manage their land in ways perceived as being sensitive to native wildlife (Ovenden et al., 1998). Field margins represent one of the most widely adopted and well known of the agri-environmental scheme prescriptions, both within the UK and across Northern Europe (Marshall and Moonen, 2002; Critchley et al., 2006). Field margins are compatible with modern agricultural practices and have been shown to be beneficial for both invertebrates (Marshall and Moonen, 2002; Meek et al., 2002; Woodcock et al., 2005) and birds (e.g., Vickery et al., 2002). Such sown margins have been established in many European countries, for example, as part of England's 'Entry Level Schemes' (ELS) (DEFRA, 2005) or Switzerland 'Ecological Compensation Areas' (ECA) (Knop et al., 2006). However, the absence of forbs within many such seed mixtures has raised questions about their value for numerous invertebrate taxa, including the pollinators (Meek et al., 2002; Critchley et al., 2006; Carvell et al., 2007) and phytophagous insects in general (Asteraki et al., 2004; Woodcock et al., 2005, 2007a).

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For this reason, there is an increased awareness that the use of seed mixtures containing forbs may be of considerable value for native invertebrate biodiversity (Woodcock et al., 2005; Critchley et al., 2006; Carvell et al., 2007).

This study investigates the impact of establishing seed mixtures and subsequent margin management on a key component of farmland biodiversity, the beetles. The prediction that the inclusion of a forbs component into seed mixtures increases the density, species density and rarefied species richness of the beetles was tested using a 5-year data set. Both seed mixture and management were also predicted to play a key role in defining the structure of beetle assemblages over the life of the margins.

2. Methods

In September 2001, 45 non-cropped field margin plots were sown on each of three UK farms. The underlying soil types for these farms were chalk (High Mowthorpe, Yorkshire, 55:08:55 N, 0:49:39 W), sand (Gleadthorpe, Nottinghamshire, 53:13:28 N, 1:06:45 W) and clay (Boxworth, Cambridgeshire, 52:15:10 N, 0:01:54 W). Each farm contained five replicate blocks of nine experimental plots. Three plots were randomly selected from each block and sown with one of three seed mixtures: (1) grass only (GO); (2) tussock grass and forbs (TG); (3) fine grass and forbs seed mixture (FG). A general description of these seed mixtures and typical farm management has been given by Woodcock et al. (2005). In all cases experimental plots were 25 m × 5 m and separated from adjacent plots by 5 m buffer zones. The long edge of experimental plots ran adjacent to and parallel with the hedgerow. To promote the establishment of sown species all plots were cut in July 2002 to a height of 10–15 cm; cuttings were left *in situ*. Crop management was based on a 4-year rotation, with 2 years of winter wheat, 1 year of winter barley and a break crop of potatoes, oil seed rape or beans. All experimental blocks adjoined crops that were started at the same stage of the rotation in 2002.

In 2003, three management practices were superimposed over the three seed mixtures to create a randomised three × three factorial design within each replicate block. The three management practices were: (1) cutting vegetation to 10–15 cm to reduce the competitive dominance of fast growing species and control arable weeds; (2) application of Fusilade Max Trade Mark graminicide (Fuazifop-*p*-butyl) at a rate of 0.8 l ha^{-1} to reduce the dominance of susceptible grass species; (3) scarification of 60% of the soil surface to increase sward heterogeneity and promote further establishment from seed. Margin management was applied in May of each year, from 2003 to 2006.

2.1. Plant and invertebrate assessments

Plant assessments were made in June 2002, 2003, 2004 and 2006 using 10 randomly positioned 0.5 m × 0.5 m quadrats in each experimental plot. Neither plant nor invertebrate samples were taken in 2005. Plants were identified to species and assigned a percentage cover score according to an 8-point scale, where: 1 = <1%; 2 = 1.1–5%; 3 = 5.1–10%; 4 = 10.1–20%; 5 = 20.1–40%; 6 = 40.1–60%; 7 = 60.1–80%; 8 = 80.1–100%. Percentage cover of bare ground was also recorded. Mean plot percentage cover was derived from the 10 quadrats using the mid-points of the eight percentage ranges.

At the same time, vertical drop pins were used to assess the architectural complexity of the sward. This was assessed for all plant species within the sward and separately for the tussock grasses, e.g., *Dactylis glomerata* L. The method used ten equally spaced 3 mm diameter pins lowered vertically through the sward (Woodcock et al., 2007a,b). The number of contacts of each pin with either all vegetation structures or just those of the tussock grasses was recorded at 5 cm intervals. This provided stratified information on the vertical distribution of plant structures within the sward. Sampling was repeated four times at randomly chosen points in each plot (equivalent to 40 pins), and the total number of contacts for a particular interval was recorded for each vegetation component. A modified version of the Shannon-Wiener index, commonly used to measure diversity in species assemblages (Krebs, 1999), was used to condense information from the drop pin frames into a single parameter reflecting changes in vertical sward architectural complexity:

$$H' = \sum p_i \cdot \log_2 p_i$$

where H' is the index of sward architectural complexity; p_i is the proportion of the total number of contacts with the drop pin in a particular plot at each height interval i. This produced diversity measures of sward architecture for the entire sward (H'_{All}) and the tussock grasses (H'_{Tussock}).

A Vortis (Burkard Ltd., UK) suction sampler was used to sample beetle assemblages within the field margin plots during June and September of 2002, 2003, 2004 and 2006. Each sample comprised 75 suctions over a fixed area (equivalent to 1.45 m^2), each of duration 10 s and this was repeated for each sampling date. Individual suction samples encompassed the full height of the vegetation within each plot, rather than only sampling insects on the ground. Suction sampling was undertaken between 10.00 and −16.00 h on dry days only. As sampling only occurred during daylight hours, beetles that dispersed from the field margins during the day, but utilised these areas at night, would not have been sampled. Weevils (Curculionoidea), leaf-beetles (Chrysomelidae), ground beetles (Carabidae) and ladybirds (Coccinellidae) were identified to species. Rove beetles (Staphylinidae) from the chalk soil farm were also identified to species (excluding the Aleocharinae), and were included in the farm specific ordination analyses described below. Nomenclature follows Strejcek (1993), Luff (2007), Morris (2003) and Lott (2007).

2.2. Statistical analyses

The following analyses are based on summed density (total abundance m^{-2}) and species density (species richness m^{-2}) of the beetles. These values are derived for individual experimental plots for each year, and were based on summed June and September sampling dates. As management was not implemented until 2003, subsequent analyses have excluded the 2002 sample year. The responses of density and species density to seed mixture and management were analysed using a temporal split-plot ANOVA. Predatory and phytophagous beetles were treated separately, their categorisation into these feeding functional groups following the methodologies described by Woodcock et al. (2007a). For each farm, a single average value of density and species density was calculated for the nine treatment levels of the three × three factorial design, each based on the five replicates per farm (*pers. comm.* T. Sparks). At the whole plot level the ANOVA tested the effects of farm (3 levels), seed mixture (3 levels), management (3 levels) and seed mixture × management. These whole plot factors were tested against the error term of farm × seed mixture × management. The temporal split-plot explanatory variables were year (3 levels), year × seed mixture, year × management and year × seed mixture × management. Analyses were carried out in SAS 9.01. The *post hoc* comparisons of means presented on graphs were performed using the CONTRAST statement within SAS. This analysis was restricted to those beetle groups identified from all farms.

Species density has been identified as an important parameter when comparing the conservation value of different treatments as it provided a direct assessment of the number of species per unit area (Gotelli and Colwell, 2001). However, if different treatments were to support different densities of beetles, then the plots with the greatest number of individuals would be expected to contain more species. To account for this bias EstimateS 8.0 (Colwell, 2005) was used to compute individual-based rarefaction curves based on the 'random placement' curves approach of Coleman (1981). From this rarefied species richness values were calculated that assumed a constant sampling effort of 20 individuals. These were calculated for each experimental treatment, for each farm and year based on data derived from the five replicate experimental plots on each farm (Gotelli and Colwell, 2001; Colwell, 2005). The rarefied species richness values were then compared using the split-plot ANOVA approach described above.

The multivariate ordination, redundancy analysis (RDA), was used to assess changes over time in beetle assemblage structure in response to seed mixture, management, plant community structure and sward architecture. Separate RDA analyses were performed for each soil type reflecting the need to account high levels of variation in beetle species composition between farms. The choice of this linear ordination method was based on short gradient lengths determined from preliminary detrended correspondence analyses (DCA). For each farm, the RDA analysis included all 45 experimental plots. For the chalk soil farm rove beetles were included in the RDA analysis. Abundances of individual species were summed for each year and $\log_{10}$ transformed. Singleton species were excluded.

Following ter Braak and Šmilauer (2003) temporal changes in beetle assemblage structure were tested within the RDA based on interactions of environmental variables with year (e.g., Env.Var. × 2003, Env.Var. × 2004 and Env.Var. × 2006). Sample year (2003, 2004 and 2006) and replicate block were included as covariables, with the latter used as a blocking factor. Individual sample years were treated as a temporal split-plot within the analysis, and samples were permuted freely at the whole plot level only. In all cases, significance was tested for each interaction individually using Monte Carlo permutation tests of both canonical axes under a reduced model (1000 permutations). The RDA analysis was divided into two sections, the first focused on the effects of the seed mixture and management treatments. This was done by performing four main analyses, although each of these may comprise tests of multiple interactions. The tests were: (1) the overall effect of year × seed mixture (e.g., 2003 × TG, 2003 × GO, 2003 × FG, . . ., etc.); (2) the overall effect of year × management (e.g., 2003 × Cutting, 2003 × Scarification, 2003 × Graminicide, . . ., etc.); (3) the overall effect of all year × seed mixture × management interactions; (4) individual effects of seed mixture × management interactions (e.g., TG with scarification × year, . . ., etc.). The treatment effects were coded individually by nominal environmental variables.

The second part of the RDA analysis considered the effect of the continuous measures of the plant community and sward architecture on beetle assemblage structure. Each environmental variable was tested as an interaction with year, as described above. Continuous environmental variables were: (1) overall sward architecture (H_{all}); (2) tussock grass architecture ($H_{tussock}$); (3) percentage bare ground (%Bare); (4) grass diversity (Grass H'); (5) Forbs diversity (Forbs H'). All diversity measures used the Shannon-Wiener index. The RDA analysis was carried out using CANOCO 4.5. The establishment year (2002) has been included as supplementary data to provide a reference point for changes in beetle assemblage structure.

3. Results

Between 2002 and 2006 a total of 25,565 Carabidae, Coccinellidae, Chrysomelidae and Curculionoidea were collected from all farms (chalk soil = 10,801; clay soil = 7341; sand soil = 7423), representing 248 species. Eighty-two species were found at all three farms, although there was often large between farm variations in individual species abundance. The sandy soil farm supported the

Table 1
Temporal split-plot ANOVA assessing the effects of seed mixtures (Seed), margin management (Man.) and sample year (Year) on the abundance (Abund. m^{-2}), species density (m^{-2}) and rarefied species richness (assuming a sampling effort of 20 individuals) of the phytophagous and predatory beetles

Source	DF	Phytophagous beetles			Predatory beetles		
		Density (m^{-2})	Species density (m^{-2})	Rarefied species richness	Density (m^{-2})	Species density (m^{-2})	Rarefied species richness
Whole plot factors							
Seed	2	7.77**	0.21 ns	8.91**	11.2**	5.27*	0.56 ns
Man.	2	0.33 ns	1.90 ns	1.35 ns	3.58 ns	4.75*	2.42 ns
Seed × Man.	4	0.08 ns	0.73 ns	0.38 ns	0.02 ns	0.64 ns	0.58 ns
Farm	2	6.82**	8.87**	20.9***	5.49*	27.9***	45.2***
Error (Year × Seed Man.)	16						
Temporal split-plot factors							
Year	2	9.07***	13.5***	17.1***	7.52**	0.59 ns	1.32 ns
Year × Seed	4	1.53 ns	0.79 ns	1.59 ns	0.42 ns	1.67 ns	0.83 ns
Year × Man.	4	0.12 ns	0.71 ns	0.12 ns	0.63 ns	1.41 ns	0.49 ns
Year × Seed × Man.	8	0.08 ns	0.27 ns	0.63 ns	0.63 ns	0.79 ns	1.49 ns
Error	36						
Corrected total	80						
R^2		0.71	0.84	0.84	0.85	0.74	0.75

'×', Interaction effect; DF, degreed freedom; ns, $p > 0.05$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

largest number of species (species richness (SR) = 170), followed by the chalk (SR = 131) and clay (SR = 130) soil farms. For the chalk soil farm, the identification of the Staphylinidae added a further 11,418 individuals from 62 species.

The seed mixture used to establish the field margins had a significant effect on the density of both the predatory and phytophagous beetles (Table 1). Highest densities of the phytophagous beetles were found in seed mixtures that contained a sown forbs component, e.g., FG and TG, while the densities of predatory beetles were highest in the tussock grass dominated GO and TG. Predatory beetle species density was highest in the tussock grass containing seed mixtures, while management by scarification also resulted in significantly higher levels of species density (Fig. 1). However, neither seed mixture nor management had a significant effect on the species density of the phytophagous beetles. Unexpectedly, rarefied species richness was highest for the phytophagous beetles where the field margins had been established using the GO seed mixture, rather than those seed mixes that contained a forbs component (Fig. 2). In contrast, the rarefied species richness of the predatory beetles showed no response to seed mixture. Neither the phytophagous nor predatory beetles showed a significant difference in rarefied species richness between the three margin management practices.

In addition to the main seed mixture and management effects described above, year also had a significant effect on phytophagous beetle density, species density and rarefied species richness, all of which increased from 2003 to 2006. Only predatory beetle density differed significantly between years, however, in contrast to the phytophagous beetles, this peaked in 2004 and declined thereafter. With the exception

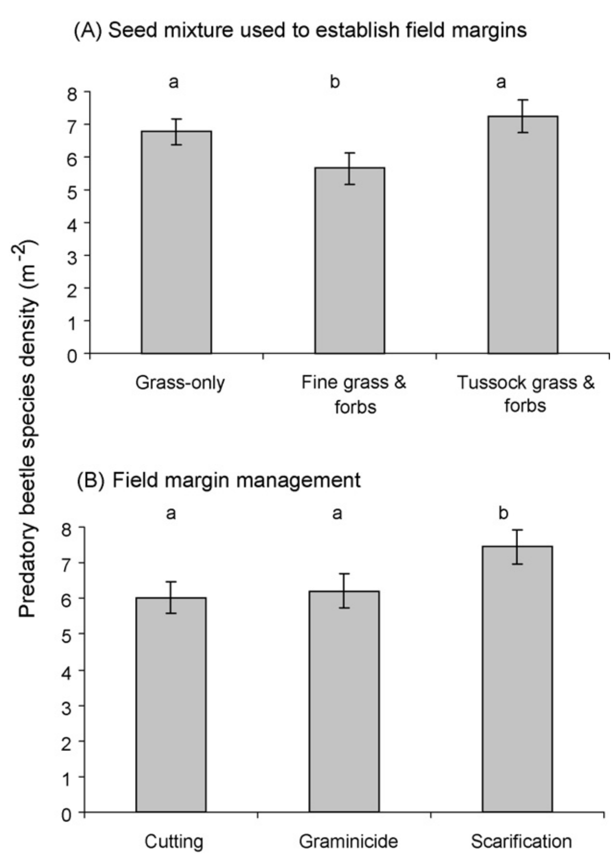

Fig. 1. Predatory beetle species density m^{-2} (±S.E.) in response to (A) the seed mixtures used to establish the field margins, and (B) the three-margin management practices. Where seed mixtures do not share the same letter they differ significantly ($p < 0.05$).

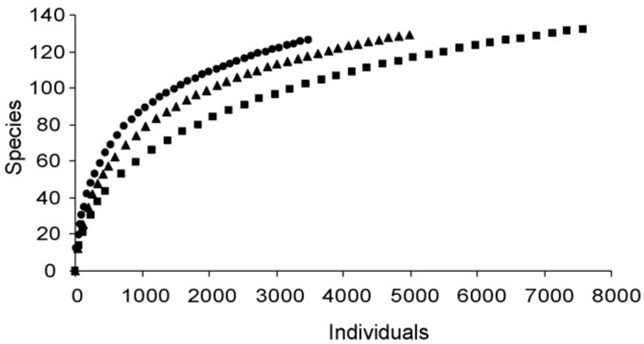

Fig. 2. Individual-based rarefaction curves based on the Coleman method (Coleman, 1981) and calculated for all experimental plots from all years. Species richness values represent the means of repeated re-sampling of all pooled individuals for the three seed mixtures across all sites and years. Rarefaction curves are (●) grass only margins; (▲) fine grass and forbs; (■) tussock grass and forbs. Note, for clarity only a sub-set of the 135 data points for each seed mix have been included.

of significant between farm differences, no other significant responses of density, species density and rarefied species richness were found to the interaction effects of seed mixture, management and year for either the predatory and phytophagous beetles (Table 1).

Responses of beetle assemblage structure to seed mixture, management, sward architecture and measures of plant community structure showed clear similarities for all three-soil types. Overall, all three farms showed the same significant responses to the interaction of year with seed mix, management and seed mix × management. Considering each of the nine seed mixture × management terms individually, there were between soil type differences in the responses of the beetle assemblages (Table 2). For example, on chalk soils distinct beetle assemblages were associated with all nine levels of the seed mixture × management interactions with year (Fig. 3). On sandy soils, the interaction between seed mixture and scarification had a significant effect on beetle assemblage structure only where the field margins had been established using the TG seed mixture (Fig. 4). On the clay soil farm, differences in assemblage structure were found only for the FG margins managed with either scarification or graminicide, or the GO margins with cutting or graminicide (Fig. 5). There were no significant effects of management interactions with the TG seed mixture for this soil type.

Between farm patterns in the succession of beetle assemblage structure from 2003 to 2006 showed consistent patterns between soil types (Figs. 3–5). Typically, the three different seed mixtures used to establish the field margins resulted in successional changes in beetle assemblages that diverged from each other. For both the clay and sandy soil farms, seed mixture was, therefore, the principal factor driving divergence in beetle assemblage structure over the 4-year period. Sward management had small effects on the successional patterns of divergence in assemblage structure compared to seed mixture. The exception to this was at the chalk soil farm where scarification resulted in relatively high levels of divergence in beetle assemblage structure over the 4-year period (Fig. 3).

Table 2
Results for redundancy analysis of beetle assemblage responses to establishing seed mixture, margin management and the floristic composition and architectural structure of the field margins

Environmental interaction	Chalk soil farm	Sand soil farm	Clay soil farm
Treatment effects			
Seed mixture × Year	$F = 4.06^{***}$ (18.1%)	$F = 2.16^{***}$ (9.5%)	$F = 2.79^{***}$ (11.9%)
Management × Year	$F = 2.46^{***}$ (10.7%)	$F = 0.99^{*}$ (4.5%)	$F = 1.33^{*}$ (6.06%)
Seed mixture × Management × Year	$F = 2.45^{***}$ (35.7%)	$F = 1.65^{***}$ (20.2%)	$F = 1.54^{***}$ (25.7%)
Tests for individual seed mixture × management interactions			
TG and Cutting × Year	$F = 1.36^{*}$	$F = 1.14^{**}$	$F = 1.28$ ns
TG and Scarification × Year	$F = 2.05^{***}$	$F = 1.20^{**}$	$F = 1.00$ ns
TG and Graminicide × Year	$F = 1.40^{***}$	$F = 1.16^{**}$	$F = 1.21$ ns
FG and Cutting × Year	$F = 2.57^{***}$	$F = 1.13^{*}$	$F = 1.02$ ns
FG and Scarification × Year	$F = 2.03^{***}$	$F = 0.94$ ns	$F = 2.24^{***}$
FG and Graminicide × Year	$F = 2.75^{***}$	$F = 1.52^{***}$	$F = 1.40^{*}$
GO and Cutting × Year	$F = 1.94^{***}$	$F = 1.15^{*}$	$F = 1.85^{***}$
GO and Scarification × Year	$F = 1.84^{***}$	$F = 0.76$ ns	$F = 1.29$ ns
GO and Graminicide × Year	$F = 1.95^{***}$	$F = 1.15^{*}$	$F = 1.46^{*}$
Continuous environmental effects			
Architecture H'_{All} × Year	$F = 3.32^{***}$ (7.2%)	$F = 2.03^{***}$ (4.5%)	$F = 2.00^{**}$ (4.5%)
Architecture H'_{Tussock} × Year	$F = 4.91^{***}$ (10.3%)	$F = 1.83^{***}$ (4.2%)	$F = 2.73^{***}$ (6.1%)
% Bare ground × Year	$F = 3.12^{***}$ (6.8%)	$F = 2.17^{***}$ (4.8%)	$F = 1.67^{***}$ (3.8%)
Grass diversity (H') × Year	$F = 4.77^{***}$ (10.0%)	$F = 1.58^{***}$ (3.6%)	$F = 1.26$ ns
Forbs diversity (H') × Year	$F = 3.61^{***}$ (7.8%)	$F = 1.08$ ns	$F = 1.84^{**}$ (4.1%)
Overall model	$F = 2.12^{***}$ (47.4%)	$F = 1.52^{**}$ (33.9%)	$F = 1.63^{**}$ (26.7%)

All significances were tested using Monte Carlo permutation tests (1000 permutations) of both canonical axes, where 'F' is the F-statistic of this test. See Section 2 for environmental variable abbreviations. '×', Interaction effect; DF, degreed freedom. The variance in the species data explained by each fixed effect parameter is given in parentheses. ns, $p > 0.05$; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

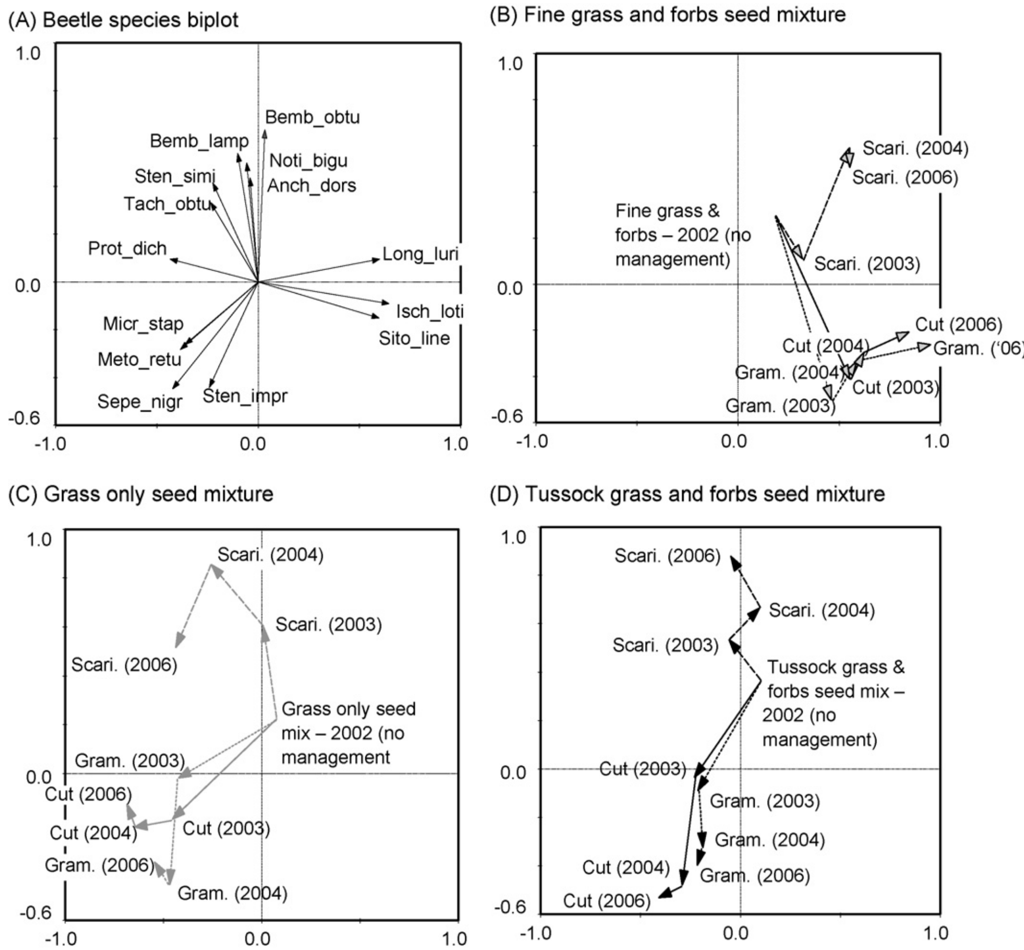

Fig. 3. Ordination diagrams of the RDA for years 2003–2005 based on the beetle assemblages from the chalk soil farm only. Biplots are: (A) a beetle species scatter plot, where beetle species name abbreviations represent the first four letters of the generic and specific names; (B) the temporal interaction between sample year and the management treatments for the fine grass and forbs seed mixture only; (C) the temporal interaction between sample year and the management treatments for the grass only seed mixture only and (D) the temporal interaction between sample year and the management treatments for the tussock grass and forbs seed mixture only. The change with time of the beetle assemblages is emphasized by the connection of the centroids of the year × treatment interaction with arrows, from the 2003 × treatment (start of first arrow) to the 2004 × treatment (end of first arrow) to the 2006 × treatment (end of second arrow). Centroids of transformed plot scores for the three seed mixtures in 2002 have been included in the RDA model as supplementary farms only. These had no effect on the overall model (which is based on 2003–2006 data only) and have been included to provide a reference point for the successional trajectories in response to the management treatments. Only selected species with the best fits to the first two axes of the ordination have been shown. Carabidae: Anch_dors = *Agonum dorsale*; Amar_aene = *Amara aenea*; Bemb_obtu = *Bembidion obtusum*; Bemb_lamp = *B. lampros*; Deme_atri = *Demetrias atricapillus*; Drom_line = *Dromius linearis*; Noti_aqua = *Notiophilus aquaticus*; Noti_bigu = *N. biguttatus*; Synt_fove = *Syntomus foveatus*. Coccinellidae: Rhyz_litu = *Rhyzobius litura*; Tytt_sede = *Tytthaspis sedecimpunctata*. Chrysomelidae: Asio_ferr = *Asiorestia ferruginea*; Cass_rubi = *Cassida rubiginosa*; Long_luri = *Longitarsus luridus*; Long_mela = *L. melanocephalus*; Long_prat = *L. pratensis*; Spha_test = *Sphaeroderma testaceum*. Apionidae: Cera_onop = *Ceratapion onopordi*; Eutr_vici = *Eutrichapion viciae*; Isch_loti = *Ischnopterapion loti*; Prot_dich = *Protapion dichroum*. Curculionidae: Rhin_cast = *Rhinoncus castor*; Sito_line = *Sitona lineatus*; Tric_trog = *Trichosirocalus troglodytes*; Tych_pici = *Tychius picirostris*. Staphylinidae: Ste_impr = *Stenus impressus*; Ste_simi = *S. similis*; Sepe_nigr = *Sepedophilus nigripennis*; Meto_retu = *Metopsia retusa*; Micr_stap = *Micropeplus staphylinoides*; Tach_obtu = *Tachyporus obtusus*.

Independent of soil type, sward architectural complexity (both overall and of the tussock grasses alone) caused changes in the structure of the beetle assemblages. Percentage cover of bare ground was also important in structuring assemblages on all soil types. Other measures of species composition of the plant communities within the field margin also influenced beetle assemblage structure, though the farms varied in the nature of the response. The diversity of grass species within the margin plots influenced beetle assemblage structure at the chalk and sandy soil farms, while that of forbs influenced assemblage structure on the chalk and clay soils only. Typically, the variance in the species data explained by the interaction between year and the continuous environmental variables was low, and rarely exceeded 10.0%. Overall, the significant interactions between year and seed mixture, management, plant community structure and sward architecture explained 51.1%, 36.7% and 32.5% of the variance in the beetle data for the chalk, sand and clay soil farms, respectively (Table 2).

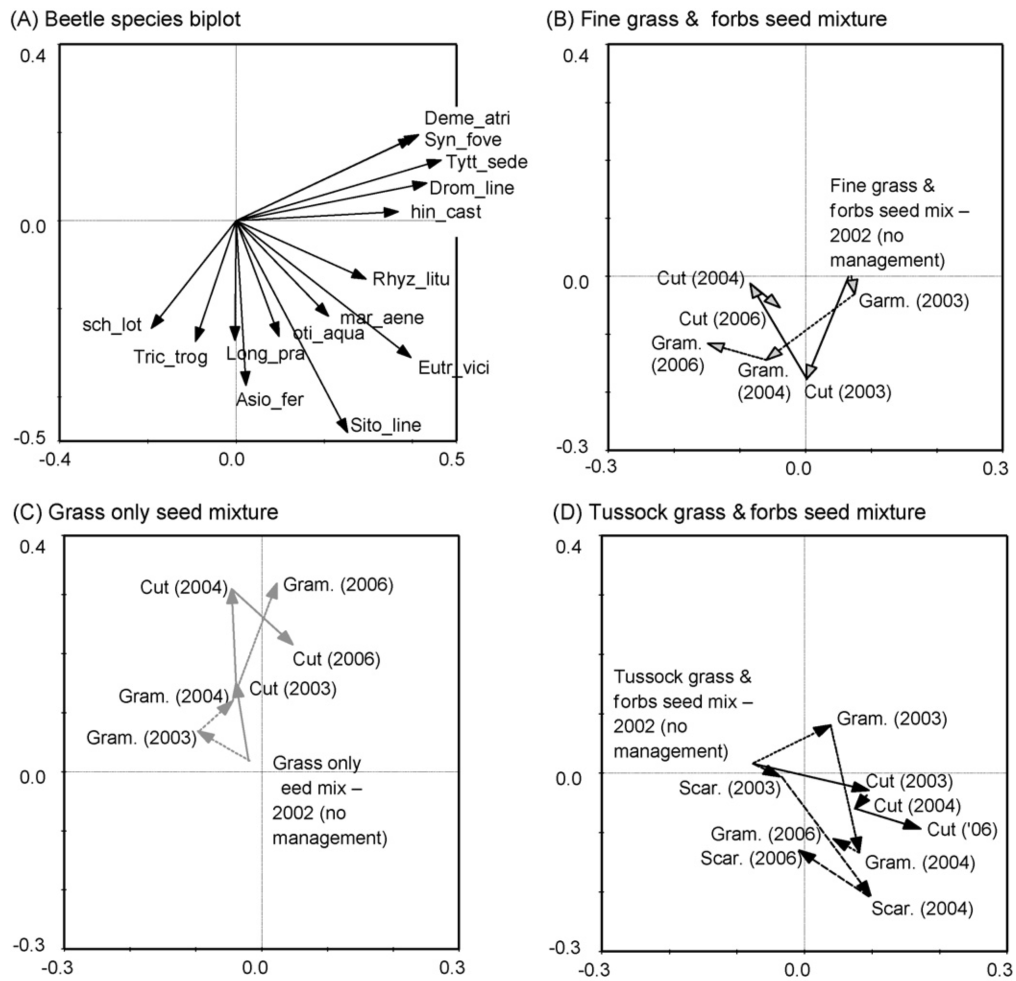

Fig. 4. Ordination diagrams of the RDA for years 2003–2005 based on the beetle assemblages from the sandy soil farm only. Explanations for these biplots follow those described in the caption for Fig. 3.

4. Discussion

Higher densities of predatory beetles were found in plots sown with a tussock grass component, while a forbs component was important in providing a quality forage resource for phytophagous species. How the two feeding functional groups responded to the seed mixtures reflected fundamental differences in their habitat requirements, namely the availability of an architecturally complex sward for the predatory beetles (Sotherton, 1995; Woodcock et al., 2007b) and the need for specific host plants for the phytophagous species (Asteraki et al., 2004; Woodcock et al., 2005).

For the phytophagous beetles the importance of a forbs component to the sward was only apparent when considering the density of this feeding group. This reflected the importance of a few species of the plant family Fabaceae, which supported high densities of the most numerically dominant species of phytophagous beetle. For example, *Trifolium* spp. supported large numbers of the common weevils within the genus *Sitona*. For the phytophagous beetles in general, forbs, rather than grasses, represented the dominant host plants (Bullock, 1992).

Independent of the importance of forbs within seed mixtures as a means of increasing densities of phytophagous beetles, this component of the field margin flora had no significant effect on the density of species. However, when individual-based rarefaction curves were used to compare species richness more species of phytophagous beetles were associated with the grass only seed mixture. This suggested that the inclusion of forbs within the seed mixtures was of no importance in increasing overall species richness, but rather only benefited a numerically dominant sub-component of the phytophagous beetle fauna.

While the architectural complexity of the sward would have some importance for phytophagous beetles (Woodcock et al., 2007b), the presence of tussock grasses was of greatest importance for the predatory taxa, specifically the ground beetles. The architectural complexity of the sward also played an important role in structuring the assemblages of both the predatory and phytophagous beetles.

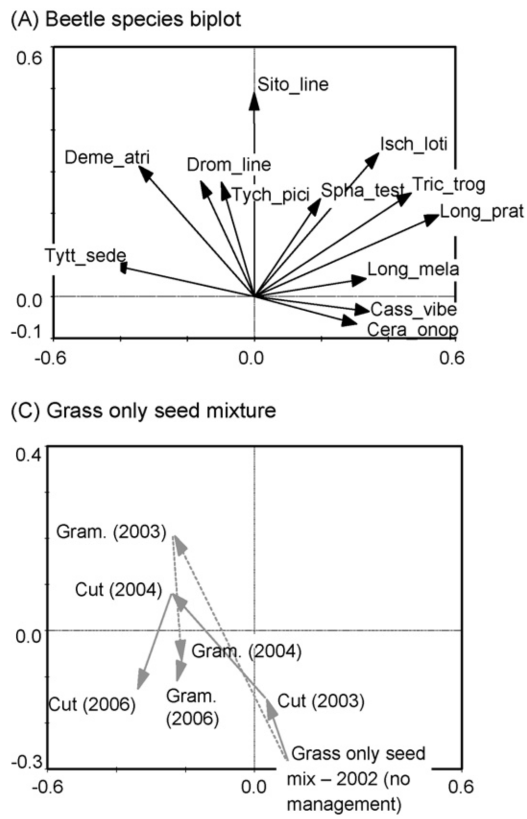

Fig. 5. Ordination diagrams of the RDA for years 2003–2005 based on the beetle assemblages from the clay soil farm only. Explanations for these biplots follow those described in the caption for Fig. 3. Note, as the interaction between management and the tussock grass seed mixture had no significant effect on beetle assemblage structure this biplot has been excluded.

The importance of field margin management was observed chiefly in terms of its effect on beetle assemblage structure, rather than its impact on beetle density, species density or rarefied species richness. However, the effect of margin management was to a large extent superimposed over that of seed mixture, which was the principal factor-driving diversification in the structure of the beetle assemblages. Typically, each seed mixture supported a characteristic beetle assemblage, from which margin management resulted in subtle patterns of differentiation in beetle assemblages over time. The greater influence of seed mixture, compared to management, underlies the key factors on which the beetles depend, namely host plant abundance and sward architectural complexity (Asteraki et al., 2004; Woodcock et al., 2005, 2007a). Although the three management practices did impact on the structure of the floral communities, their effects remained relatively minor compared to that of seed mixture. The only exception to this trend was on the chalk soil farm, where scarification tended to result in a convergence of the beetle assemblages, independent of seed mixture. At this farm, scarification played an important role in the establishment of non-sown components of the field margins, and it is thought that the convergence of beetle assemblages represents a response to these unsown species.

The greater association of predatory beetles with field margins that had been scarified is counterintuitive as one of the main consequences of scarification was to disturb the sward. Indeed, scarification had a large negative impact on the overall density of grasses found within the field margins. However, for many of the tussock grasses, it seems that regeneration from disturbed tussocks was possible even when 60% of the soil surface was scarified. Scarification allowed plots to retain enough sward architectural complexity to maintain populations of predatory beetles that were dependent on the tussock grasses. In addition to this, scarification also opened up the sward, and so increased the availability of bare ground.

In conclusion, both seed mixture and subsequent management had important implications for structuring beetle assemblages in arable field margins. There was also evidence for recommending the tussock grasses and forbs seed mixture, particularly if the aims of margin establishment were to increase densities of beetles of both feeding functional groups. However, the use of a standard seed mixture during the establishment of the majority of field margins would be expected to have a detrimental impact on beetle assemblages by homogenising these habitats at a regional scale.

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