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**Effects of seed addition on beetle assemblages during the re-creation
of species-rich lowland hay meadows.**

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Abstract

1. Species-rich lowland hay meadows are of conservation importance for both plants and invertebrates, however, they have declined in area across Europe as a result of conversion to other land uses and management intensification. The re-creation of these grasslands on ex-arable land provides a valuable approach to increasing the extent and conservation value of this threatened habitat.
2. Over a three-year period a replicated block design was used to test whether introducing seeds promoted the re-creation of both plant and phytophagous beetle assemblages typical of a target hay meadow. Seeds were harvested from local hay meadows, and applied to experimental plots in the form of either green hay or brush harvesting seeds.
3. Green hay spreading achieved the greatest success in re-creating plant and phytophagous beetle assemblages. While re-creation success increased over time for both taxa, for the phytophagous beetles the greatest increase in re-creation success relative to the establishment year also occurred where green hay was applied. We also considered the phytophagous beetles in terms of functional traits that describe host plant specificity, larval feeding location and dispersal. Phytophagous beetle functional trait composition was most similar to the target hay meadow assemblage where some form of seed addition was used, i.e. hay spreading or brush harvested seeds.
4. This study identified the importance of introducing target plant species as a mechanism to promote the re-creation of phytophagous beetle communities. Seed addition methods (e.g. green hay spreading) are crucial to successful hay meadow re-creation.

Key words: arable reversion, brush harvesting, Chrysomelidae, Curculionidae, functional traits, hay spreading, mesotrophic grasslands.

Introduction

For plant communities in the UK, as little as 1-2 % of remaining grassland is considered to be of conservation importance (Blackstock *et al.*, 1999). These grasslands are important not only plants, but also for many invertebrates (e.g. Wallis De Vries *et al.*, 2002; Walker *et al.*, 2004; Edwards *et al.*, 2007; Woodcock *et al.*, 2008). The loss of species-rich grassland has largely been the result of management intensification (e.g. inorganic fertilizers, herbicides) or conversion to other land uses, such as arable agriculture (Duffey *et al.*, 1974; Blackstock *et al.*, 1999; Wallis De Vries *et al.*, 2002). The re-establishment of such grasslands on ex-arable land (re-creation) or within existing agriculturally improved swards (restoration / grassland enhancement) is a potentially important mechanism for the conservation of both grassland plants and invertebrates (Bakker & Berendse, 1999; Willems, 2001; Woodcock *et al.*, 2010b). This study investigates the re-creation of species-rich lowland hay-meadows, a type of mesotrophic grasslands.

The re-creation of grasslands on ex-arable land is limited by factors including soil fertility, dispersal limitation and the intensity of long term grazing and cutting management regimes (Bakker & Berendse, 1999; Willems, 2001; Walker *et al.*, 2004; Edwards *et al.*, 2007). Of these, the failure of plants to colonise represents a crucial limiting process during the early stages of habitat re-creation (Bakker & Berendse, 1999; Willems, 2001; Pywell *et al.*, 2003; Walker *et al.*, 2004; Edwards *et al.*, 2007;

Woodcock *et al.*, 2008). Management designed to overcome dispersal limitation is particularly important where there are few nearby fragments of species-rich grassland from which species can colonise (Bakker & Berendse, 1999; Blackstock *et al.*, 1999). For plants, management used to overcome dispersal limitation typically involves the direct transfer of seeds, either from commercially grown stocks or from seeds harvested from existing species-rich grasslands (Manchester *et al.*, 1998; Bakker & Berendse, 1999; Willems, 2001; Pywell *et al.*, 2003; Walker *et al.*, 2004; Edwards *et al.*, 2007; Woodcock *et al.*, 2008). Seeds collected from existing local species-rich grasslands, particularly when they are local, will contain a wide array of species that are likely to be adapted to local environmental conditions (Jones & Hayes, 1999; Edwards *et al.*, 2007). Seeds can be collected from local grasslands using a variety of methods, including hand collection, brush harvesting (Edwards *et al.*, 2007; Woodcock *et al.*, 2008) or as a component of green hay (Manchester *et al.*, 1998; Edwards *et al.*, 2007; Woodcock *et al.*, 2008). Of these, green hay spread onto re-creation sites is one of the most widely available methods to most farmers.

Re-creation success for invertebrates is likely to be ultimately dependent on replicating plant communities typical of the target grassland type (Woodcock *et al.*, 2008; Woodcock *et al.*, 2010b). This is particularly important for phytophagous invertebrates that depend on the establishment of their specific host plants (Mortimer *et al.*, 1998; Wallis De Vries *et al.*, 2002; Pöyry *et al.*, 2004; Woodcock *et al.*, 2010a). Dispersal limitation also affects invertebrate assemblages during re-creation (Watts & Didham, 2006; Woodcock *et al.*, 2010a; Woodcock *et al.*, 2010b). As for plants, colonisation will be from a local species pool. However, this species pool may not be typical of the target grassland type, particularly in landscapes that contain very little species-rich grassland (Young *et al.*, 2001; Woodcock *et al.*, 2010b). Methods to

overcome this problem have been developed (e.g. turf translocation), however, they are typically prohibitively expensive and require specialist machinery (Snazell & Clarke, 2000). As a result their uptake has been limited. There may also exist contrasting responses to management between plants and invertebrates (Woodcock *et al.*, 2010a). For example, the control of competitively dominant pernicious weeds during grasslands re-creation may depend on regular sward cuts (Crofts & Jefferson, 1999) that could negatively impact on invertebrate assemblages (Morris, 2000).

This study aims to experimentally test whether seed addition promoted the re-creation of species-rich lowland hay meadow assemblages (both plants and phytophagous beetles) on ex-arable land. We use phytophagous beetles as a model system as they are a major component of both the total abundance and species-richness of grassland invertebrates, and represent a direct link between the plants and higher trophic level via their specific host plant associations (Woodcock *et al.*, 2008; Woodcock *et al.*, 2010b). We predict that: 1) successful re-creation of the phytophagous beetle assemblages would be directly linked to the re-creation of the plant assemblages via seed addition used to overcome plant dispersal limitations; 2) As re-creation of the phytophagous beetle assemblages will be limited by natural immigration, colonising species will not necessarily be typical of the target grassland (Young *et al.*, 2001). However, the re-created plant communities will provide the same niches for colonising phytophagous beetles. We therefore predict that re-creation of phytophagous beetle assemblages in terms of functional traits will have greater success than that seen for species composition alone (Fukami *et al.*, 2005).

Methods

Study site and experimental design

The experiment was established in 2000 at Little Sprays Farm, East Sussex, UK (50°56'28" N, 0°24'41" E). This site had previously been used for arable agriculture, although historically would have been covered by species-rich lowland hay meadows. The target grassland and the site from which all seeds were collected was Coach Road, East Sussex, UK (Lat: 50° 55' 27" N; Lon: 0° 23' 51" E). This site is a species-rich lowland hay meadow, classified as a *Cynosurus cristatus* – *Centaurea nigra* MG5 grassland (Rodwell, 1992). This grassland type is the principal type of unimproved lowland mesotrophic grassland in England and is of conservation importance as c. 5,000 ha remain in its pure form (Blackstock et al., 1999).

The experiment was structured as a randomised complete block design testing the effects of a single main treatment with four factor levels. This treatment was 'seed addition' sourced from a local species-rich lowland hay meadow, and comprised of: 1) control, with no seed addition, so that colonisation was from the seed bank or from natural colonisation only; 2) green hay spreading at a low application rate; 3) green hay spreading at a high application rate; 4) brush harvested seeds applied at a high rate. All seeds were collected from the Coach Road site. For the hay spreading treatments, hay was cut using a forage harvester during July 2000 and was subsequently applied directly to the plots using a manure spreader. Brush harvested seeds were collected using machinery that utilises rotating brushes to strip seeds from the sward. This removes the need to harvest the bulk of the foliage, as is the case with hay cutting. Brush harvested seeds were air-dried, cleaned and broadcast onto the plots in July 2000. For both hay spreading and brush harvesting, the low application

rate comprised the addition of material from one unit area of the donor site to three times the area on the experimental site, whilst the high rate comprised a 1:1 ratio. These four treatment levels were replicated within four blocks giving a total of 16 plots. Each experimental plot was 10×10 m and was separated from adjacent plots by 5 m. Experimental treatments were applied in 2000, and not in subsequent years. The experimental plots were subsequently managed as a hay meadow: late July hay cut, aftermath sheep grazing ($1.5 - 2.5$ livestock units ha^{-1}) between late July and late October density of. The year 2000 was treated as an establishment year, with botanical and phytophagous beetle assemblage sampling beginning in 2001.

Plant sampling

For each experimental plot, the botanical composition was recorded during late May to early June for the years 2001 to 2003. Ten 0.5×0.5 m quadrats were randomly positioned within each plot, excluding a 1 m buffer area around the edge. In each quadrat the presence or absence of each vascular plant species was recorded, and then summed across the 10 quadrats to provide a score ranging from zero to ten. This method is suited to determining the occurrence of potentially patchily-distributed species at low frequency in the sward. Following the above method 15 randomly positioned sets of 10 quadrats were also placed in the lowland hay meadow at Coach Road during 2001. Each quadrat was separated by at least 15 m.

Phytophagous beetle sampling

Phytophagous beetle sampling was simultaneously carried out for the same three years from 2001 to 2003. During each year, experimental plots were sampled three times (May, July and September). Sampling was performed using a Vortis suction sampler (Burkhard Ltd, Rickmansworth, UK). On each sampling occasion, the Vortis sampler was placed in 15 positions, located randomly within the plot area. For each of these 15 positions the Vortis was held in place for 10 seconds. The total area sampled per plot for each sampling date was 0.3m². Suction sampling is a quantitative method suitable for the collection of adult invertebrates inhabiting short grassland swards (Brook et al., 2008). All phytophagous beetle counts were summed within an individual plot for individual years. Samples were also taken at the Coach Road species-rich lowland hay meadow. Fifteen samples were made at this site in May, July and September 2001. Each sample was separated by at least 10 m, matching the inter-sample distances used at the experimental site. Leaf beetles (Chrysomelidae) and weevils (Apionidae and Curculionidae) were identified to species.

Functional traits of phytophagous beetle assemblages

Functional traits broadly define assemblages in terms of what they do, rather than on the basis of their evolutionary history (Petchey & Gaston, 2006). For each phytophagous beetle species a total of 4 traits were recorded reflecting host plant specialisation (4 trait levels), dispersal (4 trait levels) and larval feeding location (4 trait levels). Details of these traits are given in Table 1. Traits were determined either from existing published sources or by direct measurement (e.g. Hoffman, 1950-58;

Woodcock *et al.*, 2010b). For each experimental plot, weighted mean trait values (mT) for each of the 12 functional trait levels were calculated as:

$$(Eq. 1) \quad mT = \frac{\sum_{i=1}^s n_i \cdot x_i}{\sum_{i=1}^s n_i}$$

Where n_i is the abundance of each species (s) in a sample and x_i is the trait value.

This approach allowed an assessment of the degree of success achieved in re-creating a functionally similar assemblage to that of the target grassland.

Assessing re-creation success

Assemblage re-creation is poorly defined by species-richness alone, as this does not reflect compositional differences. Following Woodcock *et al* (2008), re-creation was considered successful if the same species with the same relative abundances as those found within the target lowland hay meadow site were established. In this case the Coach Road site was used as the ‘target grassland’ for re-creation success. Re-creation success for the plants, phytophagous beetles and weighed mean functional traits was calculated as the Euclidean distance between the assemblages of the experimental plots and those of the target grassland. Euclidean distance was defined as:

$$(Eq. 2) \quad ED_{jk} = \sqrt{\sum_{i=1}^s (x_{ij} - x_{ik})^2}$$

Where: ED_{jk} = Euclidean distance between samples j and k ; x_{ij} = number of individuals / percentage cover of species i in sample j ; x_{ik} = number of individuals / percentage cover of species i in sample k ; s = total number of species. There is an inverse relationship between the Euclidean distance and similarity.

Data analysis

For each response variable an ANOVA was used to assess responses to seed addition, years since the start of re-creation and the interaction between these two factors. Block was included as a random factor in all analyses. As repeated measures were taken from each experimental plot, year and its interaction with seed addition were treated as split-plots over time. Therefore, all assessments of the significance of seed addition were tested against the error term seed addition \times block. Model simplification was by deletion of the least significant effects, although where part of significant interactions non-significant ($p < 0.05$) terms were retained. Where appropriate, *post hoc* Tukey's tests were performed to determine where treatment means were significantly different. Phytophagous beetle re-creation success (expressed as Euclidean distance) in the final year of re-creation (2003) was also correlated with the re-creation success of the plants using linear regression. Plant re-creation success was included as both a single term and as a first order polynomial. All analyses were carried out in SAS 9.01.

As Euclidean distance depends on the scale of the values from which it is derived, changes in similarity to the target grassland for the plants, phytophagous beetles and weighted mean traits were not directly comparable. To account for this the change in Euclidean distance between the control and that of the most successful seed addition treatment (i.e. the most similar to the target grassland) were expressed as a percentage of the Euclidean distance from the target grassland to that of the control plots. This allowed direct comparisons of the relative re-creation success of taxonomic similarity (plants and phytophagous beetles) and functional trait similarity (phytophagous beetle weighted mean traits).

Results

During the four year period from 2001 – 2003 a total of 2,933 phytophagous beetles were sampled (experimental plots 1,329; target grassland = 1,604). This represented 38 species of weevils and 23 species of leaf beetles. Of the phytophagous beetles 23 species were found only in the target grassland, and as such failed to become established during re-creation. Within the experimental site 90 % of the abundance of phytophagous beetles was composed of six species, with the most abundant species being *Longitarsis pratensis* (Panzer) (Chrysomelidae). For the 84 species of plants recorded from both experimental and target grassland sites, only 15 failed to become established during re-creation.

Success in re-creating species assemblages

For the plants re-creation success was greatest where seed addition had been used, with the highest success achieved where green hay was applied at the high application rate (Fig. 1a). This response reflects a significant effect of the seed addition treatment on the Euclidean distance of the plant assemblages from the target grassland (Table 2). Re-creation success for the plants also increased over time, although how re-creation success changed over time did not differ between the seed addition treatments. This was explained by a significant effect of year, and a non-significant effect of the interaction between year and seed addition. After three years, re-creation success for the plant assemblages was 17.5 % greater where green hay was applied (high application rate) than was achieved by the control.

For the phytophagous beetles re-creation success was significantly influenced by seed addition, year and the interaction between these two factors (Table 2). The general pattern of success seen for the plants was repeated for the phytophagous beetles, in that greatest success was achieved where seed addition was used in the form of green hay. However, it did not matter whether green hay was applied at the high or low application rate (Fig. 2). In contrast to the plants, the interaction between year and seed addition showed that changes in re-creation success for the phytophagous beetles differed over time between treatments (Fig. 2). Specifically re-creation success for the control did not change over time. For the other seed addition treatments, there was a distinct increase in re-creation success with years following the start of re-creation, albeit marginally non-significant for brush harvesting. The use of green hay spreading between 2001 and 2003, at either application rate, resulted in re-creation of a phytophagous beetle assemblage most similar to the target meadow assemblage. The use of green hay at a high rate of application represented a 16.6 % increase in re-creation success relative to the control. The increase in re-creation

success over this time period was greater than that seen for either the low application rate of green hay or brush harvesting.

There was a significant positive correlation between the re-creation success of the phytophagous beetles and that of the plants in the final year of re-creation (2003) ($F_{1,14}=10.6$, $p<0.01$, Fig 3), although the polynomial term (plant re-creation success \times plant re-creation success) was not significant ($F_{1,13}=0.89$, $p>0.05$).

Effects of re-creation on functional traits

The similarity of the weighted mean functional traits of the phytophagous beetles to the target grassland responded significantly to both seed addition treatment and the number of years since the start of re-creation (Table 2). In general trait similarity increased with the number of years since re-creation began, although there was no interaction between year and the seed addition treatment. While the success in re-creating phytophagous beetle functional traits was always greater where seed addition had been used, there was no significant difference between brush harvesting or green hay spreading at either application rate (Fig. 1b). For the phytophagous beetle functional traits the use of brush harvesting (the best seed addition method) resulted in a 37.3 % increase in re-creation success relative to the control.

Discussion

The positive relationship between successful re-creation of plant and phytophagous beetle assemblages supports our first prediction by demonstrating the dependency of the phytophagous beetles on specific host plants (Pöyry *et al.*, 2004;

Woodcock *et al.*, 2008; Woodcock *et al.*, 2010b). This relationship shows the importance of successful establishment of the target plant assemblage for subsequent re-creation of the associated insect assemblage. The establishment of specific host plants is likely to be only one aspect needed for the colonisation and persistence of invertebrates during grassland re-creation. Other factors include cutting and grazing regimes (Pöyry *et al.*, 2005; Woodcock *et al.*, 2006), patch quality (Krauss *et al.*, 2005), local microclimate (Davis *et al.*, 2002; Perner & Malt, 2003) and landscape structure (Woodcock *et al.*, 2010b). In contrast, generalist predatory invertebrates may have a lower dependence on establishment of the plant assemblage during re-creation (Woodcock *et al.*, 2006). Even without specific host plants dependencies, predatory invertebrates may still require the presence of plants that provide key architectural characteristics within the sward, i.e. tussock forming grasses (Morris, 2000).

The addition of seeds consistently increased the success in replicating both the plant and phytophagous beetle assemblages. The use of green hay spreading was superior to the alternative method of brush harvesting. In part, this may be the result of a mulching effect of the hay that reduces the establishment of pernicious weeds typical of the target grassland during the initial years of re-creation (Cummings *et al.*, 2005; Liira *et al.*, 2009). Higher application rates of hay spreading resulted in greater success in replicating the plant assemblage, and while not statistically significant, there was an indication that this also benefited the phytophagous beetle assemblage. While both hay spreading application rates are likely to have introduced a broadly similar flora, rarer and more patchily distributed plants within the donor grassland may have been more likely to be introduced at high application rates (Manchester *et al.*, 1998; Pywell *et al.*, 2003; Edwards *et al.*, 2007).

While success in replicating the plant assemblage increased over time (years since initiation of re-creation), there was no evidence this was modified by seed addition treatment. For the phytophagous beetles, re-creation success showed a distinct increase in the third year after the start of re-creation for all seed addition treatments, although this was greatest where green hay spreading was used. Such a temporal increase in re-creation success has been reported in other studies for invertebrate assemblages (Davis *et al.*, 2003; Wassenaar *et al.*, 2005; Woodcock *et al.*, 2008). This apparent time lag before a jump in re-creation success occurred for the phytophagous beetles may indicate some level of colonisation limitation, whereby establishment of species by natural immigration takes several years (Grimbacher & Catterall, 2007; Woodcock *et al.*, 2010a; Woodcock *et al.*, 2010b). This contrasts with the use of hay spreading for the plants, which actively introduces seeds in the first year and so reduces, at least initially, dispersal limitation (Manchester *et al.*, 1998; Jones *et al.*, 1999; Edwards *et al.*, 2007; Woodcock *et al.*, 2008). It should be remembered that the temporal changes in re-creation success presented here have been over a three year period. Over much longer time scales colonisation limitation for invertebrates may well be ultimately overcome (Grimbacher & Catterall, 2007), although possible over decades (Woodcock *et al.*, 2006).

It is possible that some phytophagous beetles were introduced with green hay, similar to the way seeds were introduced (Wagner, 2004). However, insects are far more fragile than seeds. The subsequent use of a manure spreader to apply the green hay would have resulted in considerable levels of mortality in the phytophagous beetle. In addition, those plant species introduced as part of green hay would have taken a time to germinate. Phytophagous beetles transferred within the green hay would have arrived before their specific host plants had become established. The

importance of green hay as a mechanism for introducing phytophagous beetles is therefore likely to have been limited. Biases may also exist in colonisation rates of the phytophagous beetles associated with life history traits that act to limit their long-term persistence in some plant communities (Woodcock *et al.*, 2010a).

In agreement with the second prediction, after three years of re-creation management the similarity of the functional traits of the phytophagous beetles to the target grassland was greater where seed addition management had been used. Overall, success in re-creating these functional traits was greater than that achieved in replicating the phytophagous beetle species assemblages. This may be an artefact linked with describing an entire assemblage on the basis of a restricted number of traits. However, where the surrounding species pool of phytophagous beetles is not representative of target grassland, colonisation may be from species showing limited taxonomic affiliation with that target grassland (Young *et al.*, 2001). Such species may still serve similar functional roles within the grassland (Woodcock *et al.*, 2010a; Woodcock *et al.*, 2010b). If this occurs it has potentially significant implication for re-creation, as such functionally equivalent assemblages may show a high degree of resilience to being replaced by species typical of the target grassland (Young *et al.*, 2001; Woodcock *et al.*, 2006). This could result in the establishment of alternative stable states and so fundamentally limit the success of re-creation (Holling, 1973; Bakker & Berendse, 1999; Young *et al.*, 2001). If such a scenario occurred it could justify targeting sites intended for re-creation within landscapes containing existing high proportions of source populations, i.e. existing areas of species-rich grassland (Woodcock *et al.*, 2010b). Such an approach would, however, have the disadvantage of creating a regional bias in where re-creation occurs, with landscapes containing little extant species-rich grassland being effectively ignored.

Conclusions

Ideally promoting successful re-creation is dependent on differentiating between the merits of alternative management practices (Bakker & Berendse, 1999; Pöyry *et al.*, 2004; Walker *et al.*, 2004). While a considerable level of success has been achieved in re-creating grassland plants, this has not always been the case for invertebrates (Walker *et al.*, 2004; Wassenaar *et al.*, 2005; Woodcock *et al.*, 2006). While plants ultimately define grassland type (Rodwell, 1992; Blackstock *et al.*, 1999), the multi-trophic nature of these habitat means that the identification of best management practices should take other taxa into account (Pöyry *et al.*, 2004; Woodcock *et al.*, 2010b). The present study has identified that convergence in best management practice occurs between the plants and phytophagous beetles, highlighting the importance of using green hay spreading to introduce target plants during re-creation. By extension, re-creation of lowland hay meadows that relies simply on natural colonisation is unlikely to be effective, at least over short periods of under five years.

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Tables

Functional trait	Trait classifications
Host specificity	1) Monophagous, feeding on one host 2) Oligophagous, feeding within a single plant genera 3) Oligophagous, feeding within several plant genera of the same family 4) Polyphagous, feeding on multiple plant families
Dispersal	1) Fully developed wings 2) Absent or reduced wing size 3) Polymorphic in wing size 4) Individual species mass (g)
Larval feeding location	1) Feeding on roots 2) Feeding within stems 3) Feeding on plant inflorescences / seed heads 3) General foliage feeder

Table 1. List of functional traits classified for each of phytophagous beetle species.

With the exception of the continuous measure body mass, all traits were binary, with 0 indicating the absence of a trait, and 1 if it is present.

Response variable	Seed addition	Year	Seed addition × year
<i>Assemblage re-creation success</i>			
Plant similarity to target grassland	$F_{3,9} = 63.3^{***}$	$F_{3,30} = 20.4^{***}$	ns
Beetle similarity to beetle grassland	$F_{3,9} = 8.06^{**}$	$F_{3,24} = 23.6^{***}$	$F_{9,24} = 7.50^*$
<i>Beetle functional trait</i>			
Trait similarity to target grassland	$F_{3,9} = 4.87^*$	$F_{3,30} = 47.5^{***}$	ns

ns = non-significant ($p > 0.05$); ** = $p < 0.01$; *** = $p < 0.001$. †

Table 2. The effects of re-creation management by seed addition on plant and phytophagous beetle similarity to target species-rich hay meadow grasslands and the trait similarity of the phytophagous beetle assemblages to the same target grassland. Non-significant terms that are part of a significant interaction are retained in the model (†)

Figure captions

Fig. 1. Euclidean distance of plant assemblages (a) and weighted mean traits of phytophagous beetles (b) to a target lowland hay meadow in response to seed addition management during arable reversion. Where: Control = no seed addition; Hay = seed addition by green hay spreading at either a low (low) or high (high) application rate; Brush = brush harvested seeds. Based on *post hoc* Tukey's tests means that share the same letter do not differ significantly ($p>0.05$).

Fig. 2. Euclidean distance of phytophagous beetle assemblages to a target lowland hay meadow in response to seed addition management over a three year period. Where: Control = no seed addition; Hay = seed addition by green hay spreading at either a low (low) or high (high) application rate; Brush = brush harvested seeds. Based on *post hoc* Tukey's tests means that share the same letter do not differ significantly ($p>0.05$).

Fig.3. Regression between the Euclidean distance from target lowland hay meadow community for the phytophagous beetles and plants. This relationship is for the final year of restoration monitoring (2003) only.

Fig. 1

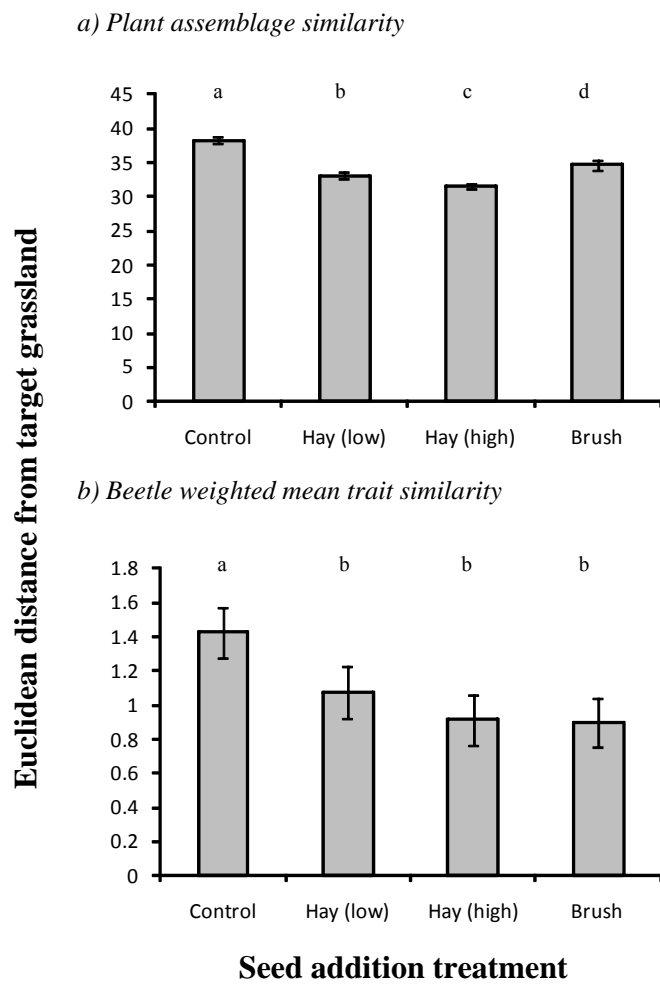


Fig. 2

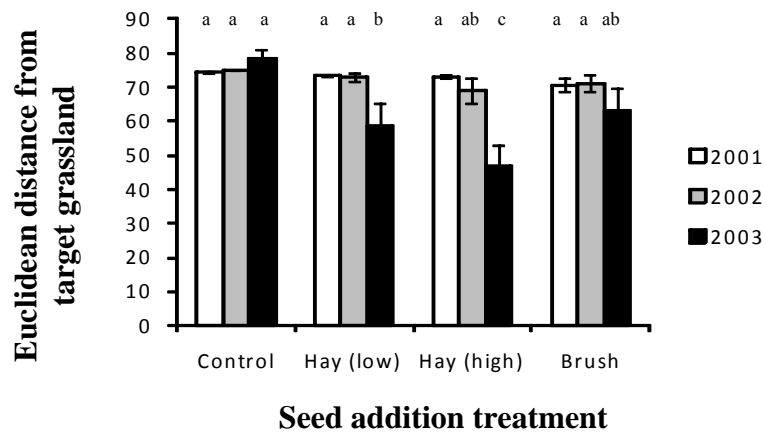


Fig. 3

