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Herbivory, litter and soil disturbance as determinants of vegetation dynamics during early old-field succession under set-aside

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Abstract Early-successional old fields are a major component of the European landscape. While a range of factors governing vegetation development in old fields has been identified, empirical and theoretical studies have tended to concentrate on plant competition as the dominant driving force behind succession. We studied the influence of three little researched, yet inter-related, factors on the early stages of an old-field succession: litter cover, soil disturbance and herbivory. Physical and chemical techniques were used to exclude large vertebrates and insects from experimental plots. These treatments had little effect on plant recruitment. A litter-removal experiment, nested within the exclusion treatments, revealed a significant inhibition of forb seedling germination by litter cover. However, the majority of seedlings died during the first month following emergence, whether or not litter was removed. A second experiment, involving the factorial combination of mollusc exclusion and soil disturbance, revealed that the response to disturbance was dependent on life-history characteristics of the plants. However, the dominant factor regulating community composition was seedling herbivory by molluscs. Molluscs caused high rates of forb seedling mortality and promoted the transition from a forb-dominated, to a grass-dominated community. Herbivory is often assumed to influence plant community dynamics through effects on competitive interactions. However, direct effects of herbivory, on the survival of seedlings, may be a significant factor structuring plant communities in ruderal, or other annual dominated systems.

Keywords Disturbance · Mollusc · Slug · Vegetation dynamics

Introduction

The introduction in 1988 of the European Set-Aside Scheme brought a major change in agricultural land use, which resulted in early-successional old fields becoming a substantial component of European agricultural landscapes (Floyd 1992). Study of the mechanisms of early secondary succession is, therefore, highly relevant to our understanding of vegetation dynamics in agricultural landscapes. Research into successional systems has identified numerous processes that may govern vegetation dynamics (Pickett et al. 1987). These include the properties of plants themselves (e.g. life-history characteristics), interspecific interactions between plants (e.g. competition), and those involving third parties (e.g. herbivory; Glenn-Lewin and van der Maarel 1992). Experimental work is required in order to identify which of these processes is governing vegetation dynamics in a particular successional system (Pickett et al. 1987).

Direct evidence, such as that reported by Gross and Werner (1982), reveals that certain life-history traits, such as an ability to establish in the shade, may govern the colonisation and persistence of species in successional seres. Gross and Werner's work showed that large seeded biennial species were able to persist longer, as the proportion of bare ground decreased, by virtue of their ability to germinate under cover. Their results indicated that litter, or vegetation accumulation, may be an important determinant of early secondary succession. Other studies have shown that litter has an important influence on community structure in successional seres (Facelli

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and Facelli 1993). Multiple mechanisms, including allelopathy (Bosy and Reader 1995), light interception (Facelli and Pickett 1991) and the facilitation of seed predators (Facelli 1994) may be involved in the effect of litter on seedling establishment. Thus, site pre-emption by plants, by virtue of their living, or dead, tissues is an important mechanism whereby the germination of some species is inhibited. Consequently, disturbance of vegetation, litter or soil in successional communities tends to promote persistence of those annual and ruderal species inhibited by cover (Goldberg and Gross 1988; Gibson 1989; Milton et al.1997).

A less studied determinant of successional dynamics is herbivory (Pickett et al. 1987, but see Brown and Southwood 1987). The effects of vertebrate herbivores on plant communities are well known (see Hairston 1989 and references therein) and studies on the role of insect herbivory suggest that this too may alter the direction or rate of succession (Brown and Gange 1992). However, in a large-scale manipulative experiment, at the same site as the current study, neither large vertebrates nor insect herbivores were found to have a significant effect on early successional dynamics (Wilby 1996). The role of invertebrates other than insects, such as molluscs, is less clear (but see Rees and Brown 1992).

This study aimed to demonstrate how herbivores, litter cover and soil disturbance interactively affect early old-field succession. Plant communities in pioneer and early-successional seres are usually dominated by monocarpic species, whose persistence is dependent on recruitment from seed. We therefore explored, in two manipulative experiments, how the above factors affect recruitment of plant species and whether these effects explain observed vegetation dynamics during the first 3 years of secondary succession.

Materials and methods

The experimental site was a 0.6 ha set-aside area in Buckinghamshire, UK (Grid Reference SP 898 304) with sandy, clay, loam soil of pH 5.5. The field was left fallow in late summer 1992, following a harvest of wheat. The site was allowed to regenerate naturally, but mown each year between 15 July and 15 August, as required by the European Set-aside Scheme. Thus, references to year in this study refer to set-aside years commencing in autumn. The immediate area surrounding the study site consisted predominantly of cereal fields separated by hedgerows and interspersed with areas of pasture and set-aside.

Effects of litter removal on forb recruitment

A litter removal experiment was superimposed upon an existing experiment comprising a factorial combination of insect and large vertebrate exclusion (for full details see Wilby 1996). The exclusion experiment consisted of five replicate experimental blocks, positioned at random coordinates, within the site. Each block (8×8 m) comprised the four exclusion combinations (large-vertebrate exclusion, insect exclusion, insect and large vertebrate exclusion and untreated control) which were randomly assigned to 3×3 m plots arranged in a square with 2 m walkways between plots.

The litter removal experiment commenced in autumn at the beginning of the second year of set-aside. Two adjacent 50×50 cm subplots were defined in one corner of each plot of the aforementioned exclusion experiment. One of the 50×50 cm subplots was raked to remove all vegetation and litter; the other was left as an undisturbed control. The presence of forbs in the subplots was recorded 1 week after disturbance and at approximately 3-week intervals through the autumn, and again the following spring. Recording involved identification and counting of forb seedlings, and estimation of the percentage cover of all grass species (as it was impossible to distinguish individual plants) in the central 25×25 cm of each disturbed and undisturbed area.

Two permanent 1×1 m quadrats, demarcated in diagonally opposite corners of each untreated control plot of the exclusion experiment, were used to monitor the background vegetation dynamics at the site. These quadrats were used to estimate, visually, the percentage cover of each plant species in each of 25, 20×20 cm cells. A simple scale (1: <5% cover, 2: 5–50% cover and, 3: >50% cover) was used. Vegetation was recorded four times each year: late April/early May (pre-treatment sample in year 1), mid-June, late July and late September/early October (post-cut sample).

The activity of molluscs was quantified using pitfall traps, an effective method for trapping slugs (Melbourne et al. 1997; Griffiths et al. 1998). Trapping was undertaken in October, April and June of the second year, and October and April the following year. Each trap (9 cm diameter) contained ca. 50 cm^3 ethylene glycol (50%) as a preservative. Two such traps were set in each plot. The traps were opened for 3 days on each recording occasion. Molluscs caught in the traps were identified and counted.

Effects of soil disturbance and mollusc exclusion on recruitment

In autumn of the third year of set-aside, an experiment was established involving a factorial combination of soil disturbance and mollusc exclusion (two factors, each with two levels, applied and not applied). In the disturbance treatment, all above-ground vegetation was removed and the soil was turned to a depth of 10 cm. The molluscicide (Mifaslug, Farmer Crop Chemicals, active ingredient: 6% w/w metaldehyde) was applied at the recommended agricultural rate (ca. 3 g m^{-2}) at 4-week intervals. This molluscicide has been shown to have no significant effect on the germination and early growth of the common forb species present on the site (Wilby 1996).

Ten replicate blocks were positioned randomly within an area adjacent to the main exclusion experiment. Each block contained four 1×1 m plots, to which the treatment combinations (untreated control, molluscicide, disturbed and molluscicide + disturbed) were randomly assigned. The treatment plots were positioned at the corner of a 5×5 m area so that the minimum distance between plots was 3 m. This distance was assessed adequate to isolate the effects of mollusc exclusion on each treated plot, preventing interference between adjacent treated and untreated plots (Wilby 1996). The few forbs already established in undisturbed areas were marked following the first treatment. Subsequently, forbs were recorded at approximately 4-week intervals, until May of the third year. Monitoring was restricted to a central 50×50 cm quadrat in each plot. On each sample date, the presence of all forb and grass species rooted in 25, 10×10 cm cells of each quadrat was recorded, and the species richness calculated (total number of species present in each quadrat). Additionally, on the first recording occasion, the number of seedlings of each forb species was recorded for each quadrat.

Data analysis

Data were analysed using generalised linear models (GLIM 3.77 Royal Statistical Society, London). In the insect and large-vertebrate exclusion experiment, mean absolute cover values were calculated for each plant species in each quadrat:

$$\frac{\sum_{i=1}^{3} fi.mi}{25} \tag{1}$$

where i = the cover category (1, 2, or 3), f_i = the count of subcells of the cover category and m_i = the mid-point of the cover category (2.5, 27.5 and 75 respectively). Absolute cover values for the life-history categories: annual forbs, annual grasses, monocarpic perennial forbs, polycarpic perennial forbs, and perennial grasses, were calculated as the sum of absolute values of the constituent species. Means were taken across the two quadrats in each plot, before analysis with a normal error structure and identity link function.

The litter removal experiment was analysed in two stages. Firstly, the undisturbed and disturbed plots were examined separately with respect to the large vertebrate and insect exclusion design (factorial analysis of deviance, two factors, each with two levels). Poisson errors with a log link function were used. Secondly, the means of the undisturbed and disturbed areas for each block were analysed, specifying a normal error structure with identity link function.

In the soil disturbance and mollusc exclusion experiment, factorial analyses of deviance (two factors, each with two levels) were employed. The total number of forb seedlings was analysed using a Poisson error structure and log link function. The proportions of cells occupied were analysed using a binomial error structure and logit link function and species richness data were examined separately using a Poisson error structure and log link function.

In all analyses, hypothesis tests were based on omission of terms from the full model. Where appropriate, block was included in the model as a random factor. The adequacy of the model was checked by inspection of residual plots and overdispersion in the Poison and binomial analyses was corrected by empirical estimation of the scale factor (Crawley 1993).

Results

Vegetation dynamics and mollusc activity

The total number of vascular plant species recorded on the site declined through the study from 43 in year 1 to 37 and 31 in years 2 and 3 respectively. Five species colonised the experimental plots in the second season, but only one of these persisted into the third year [*Arrhenatherum elatius* (L.) P. Beauv.]. There were major changes in composition of the untreated control plots between the first and second growing seasons (Fig. 1). Annual forbs and annual grasses dominated the first season. The annual grasses were a major component of the vegetation throughout the study, proportional cover reaching 40–60% in each year, although their proportional cover fell considerably between generations. Whereas, cover of annual forbs fell to zero in the autumn of first season, recovering only slightly in autumn of the second year, and remained a minor constituent of the total cover for the duration of the study. The perennial grasses increased during the first year and thereafter maintained a relatively high proportional cover, though their absolute cover was less than 25% throughout the study. The proportional cover of monocarpic perennial forbs peaked in the second season, whereas that of polycarpic perennial forbs increased gradually during the study period.

There was no significant effect of the insect and large-vertebrate exclusion on mollusc activity. Across the treatments as a whole, mean mollusc activity (measured as molluscs caught per trap per day) increased from 2.1±0.3 (SEM) in autumn of the first year to 7.0±0.5 (SEM) in April of the second year, but declined abruptly to 0.2±0.1 (SEM) by June. Mollusc activity recovered slightly to 2.3 ±0.2 (SEM) in autumn of the second year, but reached only 2.1±0.3 (SEM) in April of the third year. The majority of molluscs belonged to a single genus, *Deroceras*: 99%, 85% and 45% (October, April and July year 2, respectively), and 33% and 86% (October and April year 3, respecively).

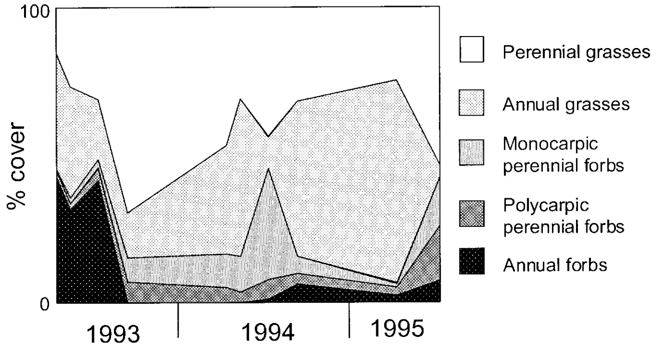

Fig. 1 Composition of vegetation, in untreated control plots, in terms of proportional cover of five life-history categories during the first 3 years of vegetation development on set-aside land

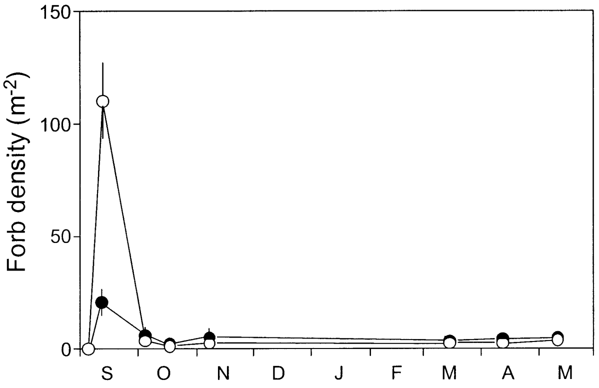

Fig. 2 Forb density in subplots from which surface litter had been removed (*open circles*) compared with subplots where surface litter remained (*solid circles*) for the second year of set-aside (September to May). Combined data for all insect and large vertebrate exclusion plots are shown

Effects of litter removal on forb recruitment

The density of forb seedlings was highest 1 week after the start of the litter removal experiment. There was no significant effect of either insect or large-vertebrate exclusion on the number of forb seedlings on this date. However, the disturbance treatment had a highly significant effect on the number of forb seedlings ($F_{1,4}$=292.6, P<0.001) with 107 m^{-2} ±16 (SEM) in disturbed plots, compared with 20 m^{-2}±6 (SEM) in undisturbed plots (Fig. 2). By October, there was no longer a significant difference between the disturbance treatments with 3.2 forbs m^{-2} ±2.4 (SEM) in disturbed and 5.6 forbs m^{-2}

±3.7 (SEM) undisturbed plots. Following the early autumn decline, seedling density remained relatively constant through to the final sample in May of the second year. At the end of the study, there were 4.8 forbs m^{-2} ±2.9 (SEM) in disturbed plots and 4.0 forbs m^{-2} ±2.6 (SEM) in undisturbed plots. During the period of high forb mortality in September, total live grass cover was less than 15% in disturbed areas and less than 20% in undisturbed areas, suggesting that competitive effects of the grasses were unlikely to have caused the high forb mortality.

Effects of soil disturbance and mollusc exclusion on recruitment

Both the soil disturbance and the mollusc-exclusion treatments had a significantly positive effect on the number of forb seedlings 4 weeks after the start of the experiment. The factorial analysis of deviance revealed no statistically significant interaction between the mollusc and disturbance treatments, indicating that the treatment had an additive effect on log-seedling density (a log link-function was used in the analysis). However, both main effects were highly significant. Molluscicide treatment increased mean forb density from 53.6 m^{-2} ±5.2 (SEM) in untreated plots, to 219.6 m^{-2} ±20.8 (SEM) in treated plots (χ^2_1=48.4, P<0.001), and the mean forb density in undisturbed plots was 240.0 m^{-2} ±21.2 (SEM) compared with only 33.0 m^{-2} ±8.0 (SEM) in disturbed plots (χ^2_1=29.5, P<0.001).

As in the litter removal experiment, high mortality of seedlings was observed during the early autumn period, but was less extensive under mollusc exclusion (Fig. 3). From December onwards, the frequency of forbs was relatively stable in all treatments. On the final recording date (May, third year), there were significant main effects of disturbance (χ^2_1=11.64, P<0.001) and mollusc exclusion (χ^2_1=8.87, P<0.01) on the proportion of subcells of the quadrat occupied by a forb. Again, no significant interaction between treatments was found.

The disturbance and mollusc-exclusion treatments also affected the species richness of the quadrats. Four weeks after the initial treatment, the disturbed plots were significantly more species rich (χ^2_1=5.92, P<0.05) than the undisturbed plots (Fig. 4), while molluscicide had no significant effect. By the final recording date, the response of species richness to the treatments had switched (Fig. 4), there was a significant main effect of molluscicide (χ^2_1=5.52, P<0.05), but not of disturbance. This switch in significance can be attributed to a loss in species richness of the plots that were disturbed but not treated with molluscicide. All other treatment combinations maintained approximately equal species richness throughout the experiment. Hence, the increased species richness caused by soil disturbance persisted only where molluscs were excluded.

Frequency histograms of the forb species under the four treatment combinations highlight individual species responses to the mollusc-exclusion and soil disturbance treatments (Fig. 5). In the undisturbed plots, the community was dominated by four grass species (*Bromus commutatus* Schrader, *Poa trivialis* L., *Anisantha sterilis* (L.) Nevski, and *Agrostis gigantia* Roth.). However, where molluscs were excluded, a number of forb species (*Stellaria media* (L.), *Capsella bursa-pastoris* (L.) Medicus, *Epilobium ciliatum* Raf. and *Galium aparine* L.) were present at low frequency. These species were absent where molluscs were at natural densities. In the disturbed plots, there was less dominance exhibited by the grass species mentioned above. *Poa annua* L. and the volunteer cereals (including *Triticum aestivum* L. and *Avena sativa* L.) were more frequent in the disturbed than in the undisturbed plots. Where molluscs were excluded in addition to disturbance, *Tripleurospermum inodorum* (L.), *S. media*, *S. asper* and *Cirsium vulgare* (Savi) Ten. also attained high frequency.

The response of grasses to molluscicide treatment was assessed in the disturbed plots only. One grass species,

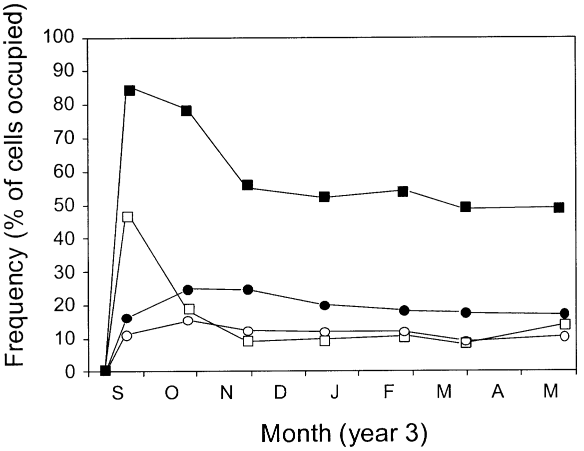

Fig. 3 The frequency of seedling forbs under the treatments: untreated control (*hollow circles*); molluscicide (*solid circles*); disturbance (*hollow squares*); molluscicide and disturbance (*solid squares*). Frequency refers to the proportion of 10×10 cm cells of the 50×50 cm quadrats containing one or more forb

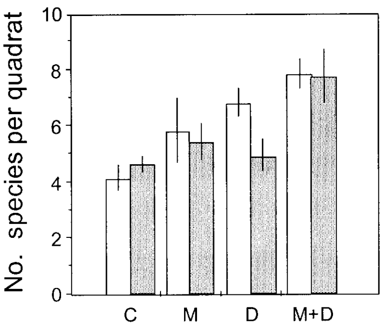

Fig. 4 The mean species richness of the treatment quadrats (0.25 m^2): *C* untreated control; *D* disturbed; *M* molluscicide; *M+D* molluscicide and disturbed, 4 weeks after the start of treatment and (*open bars*) on the final recording date (*shaded bars*). *Error bars* are ± 1 SE

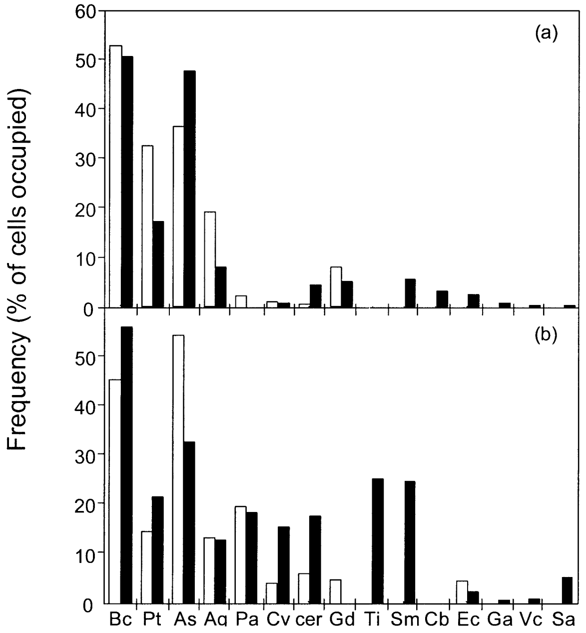

Fig. 5 The frequency of the species recorded during the soil disturbance and mollusc exclusion experiment in **a** undisturbed plots and **b** disturbed plots. *Open bars* represent plots without molluscicide, *shaded bars* represent those plots treated with molluscicide. The species are labelled: (*Bc*) *Bromus commutatus*; (*Pt*) *Poa trivialis*; (*As*) *Anisantha sterilis*; (*Ag*) *Agrostis gigantia*; (*Pa*) *Poa annua*; (*Cv*) *Cirsium vulgare;* (*cer*) volunteer cereals; (*Gd*) *Geranium dissectum* L.; (*Ti*) *Tripleurospermum inodorum*; (*Sm*) *Stellaria media*; (*Cb*) *Capsella bursa-pastoris*; (*Ec*) *Epilobium ciliatum*; (*Ga*) *Galium aparine*; (*Vc*) *Veronica chamaedrys*; (*Sa*) *Sonchus asper*

A. sterilis, showed a significant molluscicide effect with reduced frequency in treated quadrats. This grass occurred in 54% of untreated cells compared with 34% of treated cells (χ^2_1=5.55, $P<0.05$).

Discussion

The observed vegetation changes, characterised by a reduction in cover of pioneer annual species and an increase in the cover of perennials as succession proceeded (Fig. 1), are typical of those often recorded in early secondary succession (Davidson 1993) and in naturally regenerating set-aside (Ford et al. 1992). The most dramatic change in community composition during the study was the abrupt decline in annual-forb cover between the first and second growing seasons, which is also a common feature of set-aside seres (Fisher et al. 1992). If we assume that the peak in monocarpic-perennial cover in the second year resulted from maturation of seedlings that germinated in the first year, it appears that there was an almost complete failure of forb recruitment from seed in the second year. Our experiments helped elucidate which mechanisms accounted for these major changes in vegetation composition.

The absence of any insect or large-vertebrate exclusion effect in the litter removal experiment (and see Wilby 1996) suggests that the impacts of these herbivores on seed production, pre- and post-dispersal seed survival, germination and seedling survival, did not limit forb recruitment. This contrasts with other studies on set-aside have shown that large vertebrate herbivores, in particular rabbits (*Oryctolagus cuniculus*), have a major effect on plant community composition (Diaz 1999, 2000). Rabbits were rarely observed at our study site, although there were abundant pheasants (*Phasianus colchicus*) (Wilby 1996), which have been shown to be effective seedling predators in English grassland (McKendrick 1995). Here, however, we had no evidence that seedling recruitment was affected by seedling predation by pheasants.

The litter removal experiment revealed that litter limited forb germination, as litter removal resulted in a 5-fold increase in the density of forb seedlings. A number of studies have shown that grass litter inhibits the germination of old-field and grassland forbs, and may limit forb populations in old-field systems (Hulbert 1969; Watt 1974; Facelli and Pickett 1991; Facelli and Facelli 1993; Bosy and Reader 1995). Although litter inhibited forb germination, it was not the factor limiting forb establishment at the site, as the vast majority of the seedlings died shortly after emergence in both litter-removal and control plots.

High rates of mortality are normally observed in the early stages of seedling growth (Watkinson 1986) and competition from neighbours is generally considered the most common cause (Fenner 1985). However, it is very unlikely that competition was the primary cause of seedling mortality in the litter removal experiment as the vegetation was relatively sparse. The relatively high density of molluscs during the litter removal experiment, and frequent observations of their trails in the experimental areas, led to the hypothesis that mollusc herbivory was limiting forb recruitment. Failure of seedling establishment may also have been caused by physical (flat, exposed surface) or chemical (e.g. the presence of allelopathic chemicals leached from the plant litter, see Bosy and Reader 1995) properties of the soil surface layers. The hypotheses that some property of the undisturbed soil and mollusc herbivory limited seedling recruitment were tested in the soil disturbance and mollusc exclusion experiment.

Regulation of forb recruitment by seedling predation by molluscs was confirmed. Whereas soil disturbance promoted germination of forbs, as had litter removal in the previous season, the molluscicide treatment promoted the survival of seedlings. This had important ramifications for the species richness and composition of the community. In the following flowering season (May of the third year), both soil disturbance and mollusc-exclusion plots had an increased frequency of forbs (Fig. 3), while the mollusc-exclusion plots also had higher species richness than the untreated plots (Fig. 4). The experimental evidence for the effect of molluscs is supported by a comparison of mollusc activity and annual forb cover. Failure of annual forb recruitment in autumn and spring of the second year coincided with very high mollusc activity, and the reappearance of annual forbs in summer of the second year was coincident with a dramatic reduction in mollusc activity. Previous work has highlighted, with certain exceptions (e.g. cyanogenic legumes, see Hulme 1994), that molluscs feed preferentially on forbs rather than grasses (Grime et al. 1968; Pallant 1969, 1972; Cates and Orians 1975) and on seedlings rather than mature plants (Barker 1989; Hanley et al. 1995a, b; Fenner et al. 1999). The combination of mollusc preferences for young seedlings, and their selectivity between taxa, explains the effect of mollusc herbivory on plant species composition in the experiments reported here. In addition, there was evidence for more subtle indirect effects via competitive interactions between plant species. In the soil disturbance and mollusc exclusion experiment, cover of the annual grass, *A. sterilis*, was higher in disturbed plots that were also treated with molluscicide. This suggests competitive release of the *A. sterilis* following removal of forb seedlings by molluscs.

Exclusion of invertebrate herbivores has previously been shown to increase species richness in successional communities (Gange and Brown 1991). This effect was attributed to the fact that the excluded insect herbivores fed preferentially on the competitively dominant perennial grasses. In contrast, we suggest that the reverse effect occurred in this study. Mollusc herbivory reduced species richness, as the preferred species were the competitively subordinate forbs. We suggest that herbivory by molluscs may commonly be an important factor governing species composition on set-aside arable land. Slugs are serious pests of wheat, although they prefer to feed on broad-leaved weeds (Cook et al. 1997). Set-aside in the vicinity of wheat, or on land previously cultivated for wheat production, may, therefore, be expected to harbour high densities of slugs. Mollusc herbivory may also have wider significance, outside set-aside, as they have been shown limit forb seedling recruitment (Edwards and Crawley 1999) and to determine species composition (Hanley et al. 1996) in grasslands in the United Kingdom, and to limit the distribution of a perennial herb in European montane grasslands (Bruelheide and Scheidel 1999). Thus, the influence of seedling herbivory by molluscs may not be restricted to the early stages of succession, but extend to other systems where disturbance results in forb recruitment from seed being an important process governing species composition. For example, Diaz (1999) showed that in the presence of rabbits, long-term set-aside may remain relatively forb-rich into the eighth year of set-aside, and Hill and Silvertown (1997) showed that molluscs control establishment of seedlings in grassland gaps caused by sheep grazing.

Further insights into the interaction of disturbance and seedling herbivory can be gained by examining the responses of individual species to our experimental treatments. Species responses fall into three categories reflecting the relative importance of herbivory and microsite availability in constraining plant recruitment (see Fig. 5). Volunteer cereals and *S. media* occurred where molluscs were excluded, whether or not the sward was disturbed. Herbivory was clearly the major constraint on the recruitment of these species. Unlike other forb species in the study, *S. media* has been shown to germinate equally well in the dark as in the light (Grime et al. 1988), and therefore does not necessarily require gap conditions to establish. Previous studies have shown *S. media* to be a dominant autumn-germinating species through existing vegetation and litter (Brown and Gange 1989). However, this study showed that the seedlings of *S. media* are very susceptible to mollusc predation. Cereals are relatively large-seeded grasses, and seedling performance during establishment is positively correlated with seed size (Crawley 1997). However, artificial selection for large seed size in cereals has rendered them irresistible to seed predators, particularly molluscs (Wilby 1996). This result is consistent with a hump-shaped response of fitness against seed size caused by the attractiveness of very large seeds to seed predators (Leishman and Westoby 1994).

Other species, such as *P. annua* and *C. vulgare*, responded primarily to disturbance, indicating that the availability of recruitment microsites limited their recruitment. Neither of these species was eliminated from plots where molluscs were present, although the frequency of *C. vulgare* was much higher when molluscs were excluded. *C. vulgare* seeds are relatively large (ca. 3 mg), and the pattern of response here indicates that large seed size may confer tolerance to herbivory in the seedling stages (see Armstrong and Westoby 1993), as well as better performance in closed swards (Crawley 1997).

Finally, a third group of species, including *T. inodorum*, *V. chamaedrys* and *S. asper*, exhibited microsite-limited establishment, and strong regulation by herbivory. These species required low mollusc activity and disturbance to establish.

It appears from these results that interspecific trade-offs between tolerance to closed sites with thick litter cover, and probably colonisation ability, have a marked impact on the relative frequency of species establishment during the early years of secondary succession. The experiments also highlight the importance of seedling herbivory in regulating plant establishment. Large seed size may confer tolerance to seedling herbivory, as well as susceptibility to seed predators. We suggest that complex, three-way interspecific trade-offs, among colonisation ability, and tolerance to shade and herbivory, may be instrumental in governing species replacement during the early, annual-dominated stages of secondary succession, and generally, in governing species composition in annual-dominated systems.

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