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Early plant succession on former arable land

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Abstract

Since 1988, the removal of land from arable production under the set-aside scheme has formed a significant part of EU agricultural policy primarily aimed at reducing food surpluses. Set-aside can also offer a number of environmental benefits, particularly as a wildlife resource. The rate and type of vegetation development on set-aside will determine the overall conservation value. Management will often seek to accelerate or decelerate the successional process to produce a particular species assemblage that is either annual or perennial dominated. This study examined models of early succession on an area removed from an experimental arable rotation at Silwood Park, UK and considered the interaction between early-colonizing annual species and later-colonizing perennial species by using plant removal and addition experiments. Removal of all annual species had no effect on perennial performance during the two years of the experiment. The removal of perennial species increased annual recruitment in the first year, but had no effect in the second. Consequently, at natural densities, there is only a weak net interaction between annuals and perennials and they are considered to be tolerant of one another. Enhancement of annuals by the addition of *Poa annua* and *Capsella bursa-pastoris* by seeds to plots delayed perennial recruitment in the first year of the experiment, but had no effect on perennial performance in the second. Facilitation by early-colonizers as a mechanism of species replacement was thus discounted. Perennial establishment was significantly increased in both years of the experiment following addition of *Holcus lanatus* and *Trifolium repens* by seed. Exclusion of insect herbivores by chemical insecticides did not alter the underlying tolerance-based successional mechanism. With regard to set-aside management for conservation purposes, the experiment confirmed that planting later-colonizing species will accelerate succession, but increasing the abundance of annuals will not retard succession. © 1998 Elsevier Science B.V. All rights reserved.

Keywords: Set aside; Plant succession; Plant communities; Species diversity; Insect herbivores

1. Introduction

Since 1988, the introduction of the set-aside scheme as a means of controlling grain supply within the European Union has removed many hectares of arable land from production (Floyd, 1992). The scheme has evolved from initial participation on a voluntary basis and is now an integral part of EU agricultural policy (Renshaw, 1994). Abandoning arable fields from production, (even on a temporary basis as is the case with rotational set aside), allows the colonization of both cultivated (volunteers) and non-cultivated plant species. The colonization process often follows a typical

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pattern of continuing species replacement. Early-colonizing species are typically annual plants and these are eventually replaced by later-colonizing perennial dominated communities (Brown, 1991; Corbet, 1995)

Why this sequence of succession should occur has been widely debated among ecologists and several theories explaining the actual mechanisms of species replacement have been proposed (see Miles, 1987; Peet, 1992 for reviews). Current opinion as to the underlying mechanisms of succession remains influenced by three alternative hypotheses originally proposed by Connell and Slatyer (1977) and are referred to as the models of facilitation, tolerance and inhibition (Pickett et al., 1987a, b; Glenn-Lewin and Van Der Maarel, 1992; Begon et al., 1996). Connell and Slatyer (1977) (hereafter referred to as C and S) describe invading species as either early- or late-colonizers by virtue of their life history and the interaction between the two determines the model that operates within a sere at any one time. The facilitation model states that only early-colonizing species can occupy an open site and following establishment, they subsequently change the immediate environment to provide favourable conditions for late-colonizing species. For the model of tolerance, both early- and late-colonizers can establish on an open site, but early-colonizers have no effect on later-colonizers. Early-colonizers eventually die and are eliminated, but further invasion can only take place by species tolerant to the environmental conditions provided by the current species assemblage. The inhibition model specifies that both early- and late-colonizers can invade an open site. Further invasion by any other species cannot take place until the initial colonist is killed or damaged and thus release resources.

In addition to their proposals C and S (1977) also provide details of how their models may be tested by assessing the result of species addition or removal on experimental communities. Most research efforts have focused on the selective removal of individual plants or complete life-history groupings of early- or late-colonizers and have shown a range of outcomes generally supporting the tolerance or inhibition models (Pinder, 1975; Allen and Forman, 1976; Hils and Vankat, 1982; Armesto and Pickett, 1986).

The C and S models have importance with regard to succession on set-aside because the pattern of species colonization and replacement is significant in addressing the overall management objectives. From an economic point of view, the farmer will wish to minimise the number of damaging annual weeds (which can be defined as early-colonizers according to C and S terminology) and prevent further additions to the seed bank if the land is to be returned to agricultural production (Burch, 1996). Furthermore, to enhance the environmental benefits of set-aside in terms of habitat creation and the minimization of nutrient leaching, the farmer may also wish to increase rapidly the proportion of perennial plants (late-colonizers) and thus accelerate succession (Firbank et al., 1993; Corbet, 1995). It is also possible to envisage scenarios where it is desirable to encourage and maintain the early-colonizing annual weeds for example, as an indirect and direct food source for birds (Sears, 1992; Wilson et al., 1995). By determining the exact nature of the interaction between early- and late-colonizers, the most appropriate C and S model(s) can be applied to succession on set aside and be used to support management decisions.

At Silwood Park, secondary succession following ploughing and abandonment has been studied since 1977 (Southwood et al., 1979; Brown and Southwood, 1987; Brown et al., 1988) and there is a predictable pattern of vegetation change following disturbance. Early-colonizing species predominantly comprise annual forbs and the most commonly recorded species include *Capsella bursa-pastoris*, *Spergula arvensis* and *Tripleurospermum inodurum* and the annual grass *Poa annua*. Within two to three years, the annual vegetation is replaced by perennial forbs, typically *Plantago major* and *Trifolium pratense* and perennial grasses such as *Holcus lanatus*. The exact mechanism by which early succession proceeds has not been fully investigated, but the study has indicated that there are significant interactions between individuals of each life history grouping which strongly influence community composition and thus the rate and direction of succession at least in the medium term (Brown and Gange, 1989a). Insect herbivory has also been demonstrated to be a particular determinant of community structure during early succession within experimental plots at Silwood Park, by altering the strengths of competitive interactions between life history groupings. Foliar feeding insects reduce early-colonizing species diversity and performance by allowing increased perennial grass (late-colonizer) growth (Brown and Gange, 1989a). The implications of insect herbivory on the Connell and Slatyer models of succession are potentially wide and have rarely been tested by field experimentation.

Consequently, this study investigates the mechanisms of early succession on newly created former arable land and establishes whether the models of facilitation, tolerance and/or inhibition provide appropriate descriptions of species turnover. A field experiment was established that allowed comparison on a plant by plant basis of naturally developing communities with experimental communities from which either annuals (early-colonizers) or perennials (late-colonizers) had been removed from plots, or key annual and perennial species had been introduced by seed. Introduced species were chosen by virtue of their role as the main representatives of early successional communities within earlier studies (see Brown and Southwood, 1987, for description). The role of insect herbivores on the composition and structure of manipulated communities was evaluated by the use of chemical exclusion on additionally replicated plots.

2. Materials and methods

2.1. Experimental site

The experimental site is situated at Silwood Park (National Grid reference 4194 4691) on soil derived from Bagshot sands and gravel of Eocene Bracklesham beds (pH 4–5) and occupied a 494 m^2 area. Until 1986, the site formed part of a small scale, experimental arable rotation of field beans (*Phaeseolus vulgaris*), Brussels sprouts (*Brassica oleracea*) and Spring wheat (*Triticum aestivum*) and is surrounded by acidic grassland and woodland. The purpose of the arable area was to enable the study of pest management practices requiring complex manipulations that could not easily be performed in commercial crops. Consequently, inputs to the arable area depended upon whatever study was being undertaken at the time. Rabbits were excluded from the entire experimental area by means of a close-mesh wire fence. A broad spectrum, non-residual herbicide, glyphosate (Roundup), was applied in the autumn of 1987 at a rate of 1.8 kg ha^{-1} active ingredient to kill existing vegetation and cereal volunteers. The site was subsequently harrowed and hand-raked during April of 1988 to remove any remaining tussocks of vegetation and to provide a fine litter for natural colonization by plants. Consequently, for the purposes of this experiment, succession of vegetation would proceed from the seedbank and immigrant propagules only.

2.2. Experimental design

There were six experimental treatments in total; one serving as a control, three involving the manipulation of annual plant species and two involving the manipulation of perennial plant species. Table 1 summaries all the treatments. For the ‘natural succession’ treatment, vegetation was allowed to colonize within 20 cm^2 (0.04 m^2) plots, located within larger 1.5 m^2 (2.25 m^2) plots without further interference and served as a control.

Natural colonization of vegetation was supplemented by the hand sowing of 25 seeds of each of the annual grass *Poa annua*, and the annual forb *Capsella bursa-pastoris* (early-colonizers), into plots for the ‘add annuals’ treatment. (The density of seeds selected for species additions was based on earlier glasshouse experiments that are not reported here). Conversely, either all colonizing annual plants were initially removed for the ‘remove all annuals’ treatment or

Table 1
Summary of treatments applied in the field experiment

Treatment	Summary of action
Natural succession	Vegetation allowed to colonise naturally following disturbance.
Add annuals	Colonization supplemented by the addition of 25 seeds of annuals *Poa annua* and *Capsella bursa-pastoris*.
Remove annuals	All annual species removed from plots on germination.
Remove 1/2 annuals	Half the annual plants removed randomly from plots initially, followed by removal of half new annual colonists after each monitoring occasion.
Add perennials	Colonization supplemented by the addition of 25 seeds of annuals *Holcus lanatus* and *Trifolium pratense*.
Remove perennials	All perennial species removed from plots on germination.

half were removed by random selection for the 'remove 1/2 annuals' treatment. If monitoring (see Section 2.3 for details) revealed new colonization, then further removals were carried out in a similar manner. For the 'add perennials' treatment 25 seeds of the perennial grass *Holcus lanatus* and 25 seeds of the perennial forb *Trifolium pratense* (later-colonizers) were again hand sown into plots in a comparable manner as described previously. Similarly all initial and subsequent colonizing perennial vegetation was removed for the 'remove perennials' treatment. The plot size for treatments was chosen because it allowed detailed monitoring of succession as a plant by plant replacement process and permitted accurate identification and assessment of the density of individual plants in the first year of the experiment. All the 20 cm square treatment plots were located within larger 1.5 m^2 plots in which vegetation was allowed to naturally colonize and serve as a buffer zone.

Ten replicates of the six treatments were applied to plots arranged in five randomised blocks. In order to carry out the second part of the experiment, investigating the effect of chemical exclusion of insect herbivores during early succession, all treatments were replicated a further ten times and assigned to additional plots within the five randomised blocks. Each block thus contained twelve treatment combinations and there were one hundred and twenty experimental plots in total.

2.3. Experimental procedure

The experiment began at the end of April 1988, immediately following the final raking of the site. At this time, all the seeds for the addition treatments were sown and the initial removals were performed. Monitoring of the plots initially took place during mid-May of 1988 and then at two-weekly intervals until October 1988 to provide a total of twelve samples. During the first year of the experiment, the colonization of vegetation was sparse enough to allow identification and recording of each individual plant present within plots, on each sample date. For the two treatments that required complete removal of vegetation, seedlings were carefully extracted with the minimum of interference to other non-target individuals immediately before recording. However, in the case of the 'remove 1/2 annuals' treatment, half of newly recruited annual seedlings were randomly extracted following recording and comparison with the previous sample data.

Treatment combinations requiring the exclusion of insects were treated with chemical insecticides before the appearance of any vegetation at the end of April 1988 until October 1989. Dimethoate-40, a contact and systemic foliar insecticide, was applied fortnightly as sprays at the manufacturers recommended application rate of 340 g ha^{-1}. In addition, Dursban-5G (active ingredient chloropyrifos), a soil insecticide, was applied monthly at a rate of 1 kg ha^{-1} as granular formulation. Mifaslug (active ingredient metaldehyde), a mollusicide, was also applied on a monthly basis to all plots or more frequently when molluscs were observed to be active. Dimethoate-40, Dursban-5G and Mifaslug have been shown to exert no direct effects on plant growth or performance (V.K. Brown and A.C. Gange, unpublished results).

In the second year of the experiment (1989), it was not physically possible to assess individual plants because growth was predominantly vegetative and an alternative method to sample plant cover was employed using point quadrat pins. Plant species in subplots were monitored monthly from May to September 1989 by placing at random five linear (3 mm diameter and 1 m length) point quadrat pins in each plot. Each pin was divided into 5 cm height intervals and the number of touches of each living plant species at each height interval was recorded. This allowed detailed assessment of the total touches or cover abundance of a particular species or life history grouping. The technique has been widely used in the study of succession at Silwood Park (Brown and Gange, 1989a, b). No further removals of annual vegetation were made from the 'remove 1/2 annuals' treatment in the second year but plots continued to be sampled.

2.4. Analysis

Data for each species were pooled to provide general information on plant life history groupings (either annual or perennial) which were considered to be of more importance in understanding general mechanisms of succession than the individual performance of a single species. Information was thus available on the species richness and number of individual plants (1988) and plant cover abundance (1989) for each life history category within each plot.

Analysis focused on the effects of the following factors: vegetation manipulation, change of vegetation over time, exclusion of insects and their corresponding interactions. Because the same plots were continually assessed, differences in plant performance for the various treatments were determined using multivariate repeated measures analysis of variance (RM MANOVA) (O'Brien and Kaiser, 1985; Gurevitch and Chester, 1986; Von Ende, 1993) with sample date as the repeated measures factor. Separate repeated measures analyses were performed for each of the two years of the experiment. A priori comparison of treatment means on individual dates were made using contrast analysis with sequential Bonferroni corrections at an α-level of $p<0.05$ or 0.01 (Rice, 1989).

3. Results

3.1. General vegetation composition and species richness

Substantial germination throughout the whole of the site had occurred by the time the first sample was taken during mid-May of 1988. In total, 27 species of annuals and 13 species of perennial were recorded over the two years of the experiment, including species introduced as part of manipulation treatments (Table 2). Within 'natural succession' plots in the absence of insecticides (control), the most frequently recorded species in the first year were annuals (maximum mean number of annual species per plot=8.6) and the annual forb *Spergula arvensis* was the most common (Fig. 1(a)). Perennial species were generally poorly represented and only one individual of *Cirsium arvense*, *Plantago major* or *Sonchus arvensis* was

Table 2
Annual and perennial species recorded on the experimental site during 1988 and 1989

Annual forb	Annual grass	Perennial forb	Perennial grass
Anagallis arvensis	*Poa annua*	*Cirsium arvense*	*Elymus repens*
Aphanes arvensis		*Epilobium montanum*	*Agrostis stolonifera*
Atriplex patula		*Medicago lupilina*	*Holcus lanatus*
Bilderdykia convolvulus		*Plantago major*	*Lolium perenne*
Capsella bursa-pastoris		*Ranunculus repens*	
Chenopodium album		*Rumex acetosella*	
Chenopodium rudrum		*Sonchus arvensis*	
Conyza canadensis		*Trifolium pratense*	
Gallinsoga parviflora		*Trifolium repens*	
Gnaphalium uglinosum			
Papaver rhoeas			
Polygonum aviculare			
Polygonum lapathifolium			
Polygonum persicaria			
Raphanus raphanistrum			
Senecio vulgaris			
Sisymbrium officinale			
Sonchus asper			
Sonchus oleraceus			
Spergula arvensis			
Stellaria media			
Tripleurospermum inodurum			
Veronica arvensis			
Veronica persica			
Vicia cracca			
Vicia hirsuta			

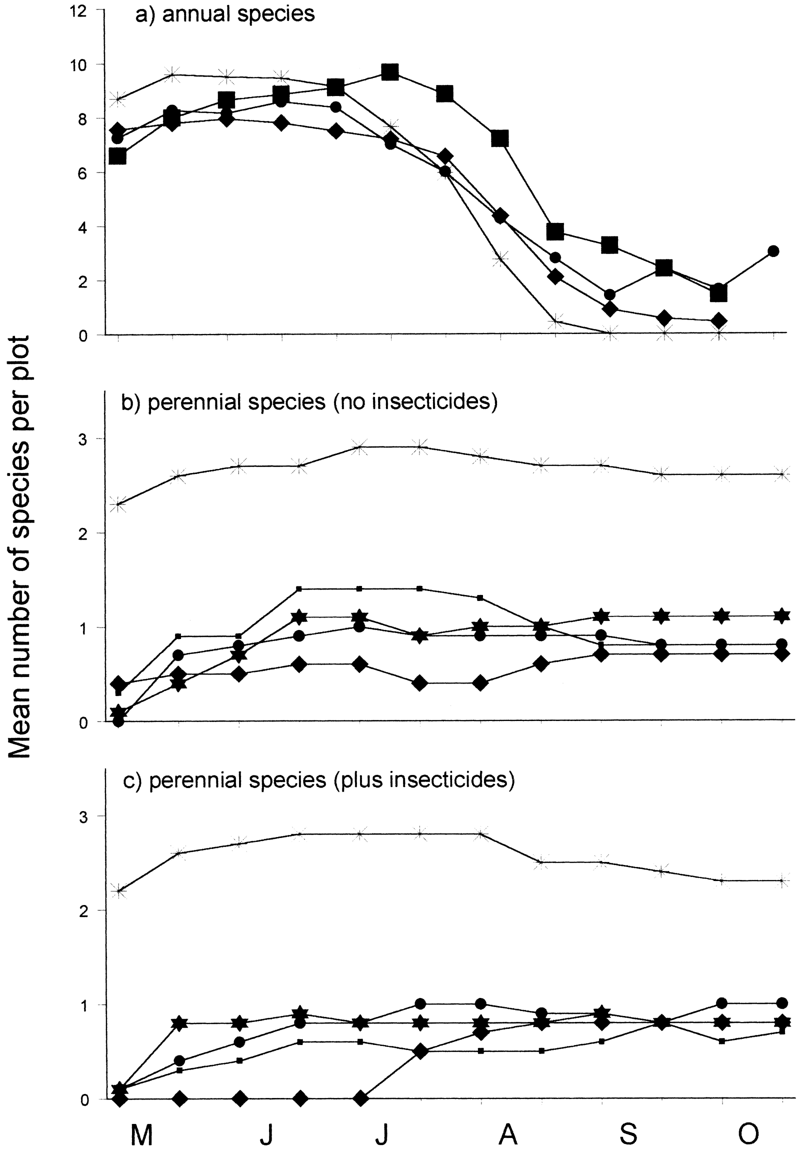

Fig. 1. Mean number of (a) annual (SE±0.84) and (b) and (c) perennial species (SE±0.55) per plot for 'natural succession' (●), 'add annuals (◆), 'remove 1/2 annuals'(■), 'remove annuals'(✶), 'remove perennials' (■) and 'add perennials' (✳) treatments in 1988.

present within each 'natural succession' treatment plot (Fig. 1(b)). Number of individual annual plants generally declined over time from an initial mean density of 30.3 plants per plot following colonization, almost to extinction (mean=2.4 plants per plot) by the end of the first year's sampling in mid-October 1988 (Fig. 3(a)). In contrast, mean perennial density remained low and constant (maximum mean=2.4 plants per plot) (Fig. 3(g)). However, by the end of 1989, the situation had reversed and plots were dominated by two perennial species, typically *Agrostis stolonifera* and *Plantago major* (Fig. 2(c) and Fig. 4(g)). Annual species were subsequently eliminated (Fig. 2(a) and Fig. 4(a)).

The vegetation manipulations had significant effects on annual and perennial species richness in

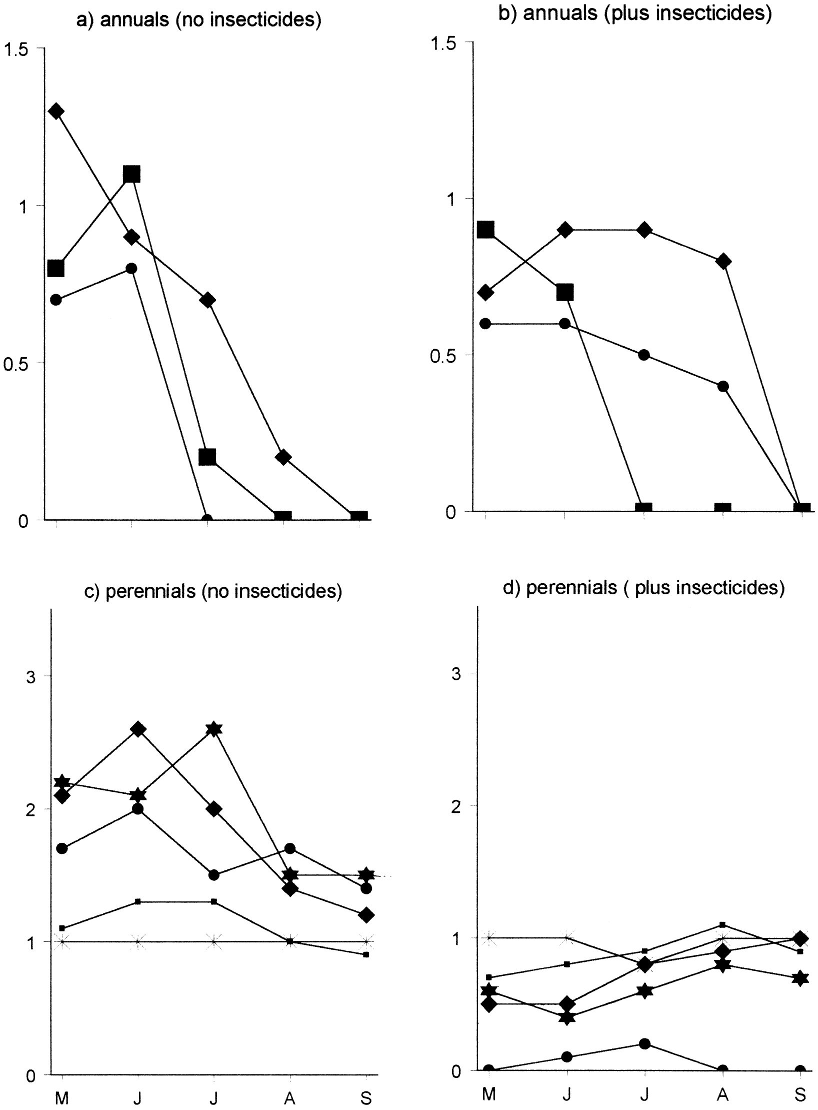

Fig. 2. Mean number of (a) and (b) annual (SE±0.12) and (c) and (d) perennial species (SE±0.26) per plot for 'natural succession' (●), 'add annuals (◆), 'remove 1/2 annuals'(■), 'remove annuals' (✶), 'remove perennials' (■) and 'add perennials' (✳) treatments in 1989.

both years of the experiment, often forming a complex three-way interaction with sampling date and chemical insecticide application (Tables 3 and 4). In some cases, differences between treatments were not immediately evident but became more apparent as the succession proceeded and the community developed. Attention is focused on treatment differences that were consistent over groups of consecutive sampling dates.

Despite successful recruitment, the addition of annual species *Poa* and *Capsella* to plots under the 'add annuals' treatment did not significantly increase the overall mean annual species richness on any of the sample dates in 1988 or 1989 when compared with the 'natural succession' control (Fig. 1(a) and Fig. 2(a)). Likewise, the mean number of perennial species present was not significantly altered during sample dates from mid-May to early-September following annual

Table 3
Three-way MANOVA results with Date (Dt) as the repeated measures factor for the effects of treatment (Tr) and chemical exclusion of insects (Ins) on annual and perennial vegetation in 1988

Source		DF	Number of annual species			Number of individual species			Number of perennial species			Number of individual perennial plants		
			F	P		F	P		F	P		F	P	
Treatment (Tr)		5	188.72	<0.001		73.19	<0.001		62.95	<0.001		54.84	<0.001	
Insecticide (Ins)		1	0.51	0.478		0.004	0.945		2.39	0.125		0.560	0.456	
Tr×Ins		5	0.26	0.934		1.92	0.096		0.57	0.720		0.029	0.999	
Error		108	—	—		—	—		—	—		—	—	
	DF numerator	DF denominator	Wilks' Lambda	F	P	Wilks' Lambda	F	P	Wilks' Lambda	F	P	Wilks' Lambda	F	P
Date (Dt)	11	98	0.038	220.80	<0.001	0.061	137.02	<0.001	0.488	9.33	<0.001	0.787	2.40	0.011
Tr×Dt	55	457	0.272	9.70	<0.001	0.041	8.30	<0.001	0.412	1.76	0.001	0.470	1.47	0.196
Ins×Dt	11	98	0.913	0.84	0.603	0.845	1.63	0.101	0.851	1.56	0.122	0.767	2.71	0.004
Trs×Ins×Dt	55	457	0.601	0.94	0.597	0.380	1.93	<0.001	0.483	1.42	0.032	0.447	1.58	0.007

Table 4
Three-way MANOVA results with Date (Dt) as the repeated measures factor for the effects of treatment (Tr) and chemical exclusion of insects (Ins) on annual and perennial vegetation in 1989

Source		DF	Number of annual species			Annual cover abundance			Number of perennial species			Perennial cover abundance		
			F	P		F	P		F	P		F	P	
Treatment (Tr)		5	31.29	<0.001		26.22	<0.001		32.74	<0.001		62.96	<0.001	
Insecticide (Ins)		1	16.25	<0.001		2.98	0.087		112.97	<0.001		0.356	0.552	
Tr×Ins		5	2.64	0.027		2.79	0.021		18.22	<0.001		0.747	0.590	
Error		108	—	—		—	—		—	—		—		—
	DF numerator	DF denomenator	Wilks' Lambda	F	P	Wilks' Lambda	F	P	Wilks' Lambda	F	P	Wilks' Lambda	F	P
Date (Dt)	4	105	0.387	41.58	<0.001	0.504	25.82	<0.001	0.901	2.60	0.040	0.433	34.32	<0.001
Tr×Dt	20	349	0.319	7.19	<0.001	0.418	5.25	<0.001	0.817	1.10	0.350	0.394	5.66	<0.001
Ins×Dt	4	105	0.855	4.45	0.002	0.924	2.15	0.080	0.792	6.91	0.001	0.958	1.14	0.342
Trs×Ins×Dt	20	349	0.620	2.70	0.001	0.778	1.37	0.132	0.701	1.98	0.008	0.629	2.62	0.002

addition in 1988 or 1989 (Fig. 1(b) and Fig. 2(c)). Sowing of *Trifolium* and *Holcus* in the 'add perennials' treatment resulted in rapid establishment in 1988 and elimination of all annual species by early-September. The sown species continued to dominate the community throughout 1989 (Fig. 2(c)).

Removal of perennials significantly increased mean annual species richness between 25–41% over five consecutive sample dates from late-July to late-September in 1988 (contrast analyses; lowest $F_{1,108}$=7.46, $p<0.05$) (Fig. 1(a)). However, by 1989 there was no significant difference in mean annual species richness between 'natural succession' and 'remove perennial' plots. Annual removal had no effect on perennial species richness in 1988 or 1989 (Fig. 1(b) and Fig. 2(c)).

3.2. *Effects of vegetation manipulation on abundance*

Experimental manipulation of the early successional vegetation also had a significant effect on annual and perennial recruitment and establishment over both years of the experiment and again formed a three-way interaction with both sample date and the exclusion of insects by chemical insecticides (Tables 3 and 4). In 1988, the addition of the annual plants, *Capsella* and *Poa*, resulted in a significant increase in the recruitment of both species to produce mean annual plant densities 20–35% greater than the 'natural succession' control over five consecutive sampling dates from mid-June to mid-August (contrast analyses; lowest $F_{1,108}$=3.94, $p<0.05$) (Fig. 3(b)). The increase continued into 1989 with a significantly greater mean annual covers of 51 and 56% recorded in May and June, but there was no overall increase in annual persistence time when compared with the 'natural succession' control (contrast analyses; lowest $F_{1,108}$=42.36, $p<0.01$) (Fig. 4(b)). Mean germination and establishment of perennials, although intrinsically low, was affected by the addition of annual plants in 1988. In the 'natural succession' treatment, perennial plants were present from late-May onwards, but were not recorded until late-July for the add annuals treatment (Fig. 3(g) and (h)). By the second year there was no difference in perennial cover or persistence between 'natural succession' and 'add annual treatments' (Fig. 4(g) and (h)). The rapid recruitment of *Trifolium* and *Holcus* within the 'add perennials' treatment provided the highest mean perennial densities recorded in the experiment and resulted in the early elimination of all annual plants by July in 1988, when compared with the 'natural succession' control (Fig. 3(e) and (k)).

The complete removal of annual plants did not have a significant influence on perennial establishment in 1988. Although mean perennial number per plot was generally greater, the increase was not significant when compared with the 'natural succession' control treatment. There was also no significant effect on mean perennial density by applying the 'remove 1/2 annuals' treatment (Fig. 3(i) and (j)). Perennial density was unaffected by either treatment in 1989 (Fig. 4(i) and (j)). Perennial plant removal significantly increased the mean recruitment of annual plants by 24–64% over six consecutive sampling dates from mid-June to late-August during 1988 (contrast analyses; lowest $F_{1,108}$=6.38, $p<0.05$) (Fig. 3(f)). This trend was extended into 1989, but the difference in mean annual cover compared with the 'natural succession' control was not significant and the annual persistence time was not increased (Fig. 4(f)).

3.3. *Effects of insect herbivory*

Applying chemical insecticides to the vegetation had a number of effects on plant recruitment and species richness, depending upon treatment. For the 'natural succession' control, herbivore exclusion resulted in a significant increase in the number of individual annual plants (20–46%) over five consecutive sampling dates from late June to late August in 1988 (contrast analyses; lowest $F_{1,108}$=3.94, $p<0.05$) (Fig. 3(a)). Mean perennial numbers were not significantly higher in untreated natural succession control plots over the same period (Fig. 3(g)). Annual and perennial species richness were unaffected by insecticide application within natural succession plots over any sample dates in 1988. In 1989, mean annual cover was significantly greater in June by 71% within insecticide treated plots compared with untreated natural succession controls (contrast analysis, lowest $F_{1,108}$=7.85, $p<0.05$). In addition, annual persistence was also extended into July and August (Fig. 4(a)). Insecticide application had no significant effect on mean perennial cover within the 'natural succession'

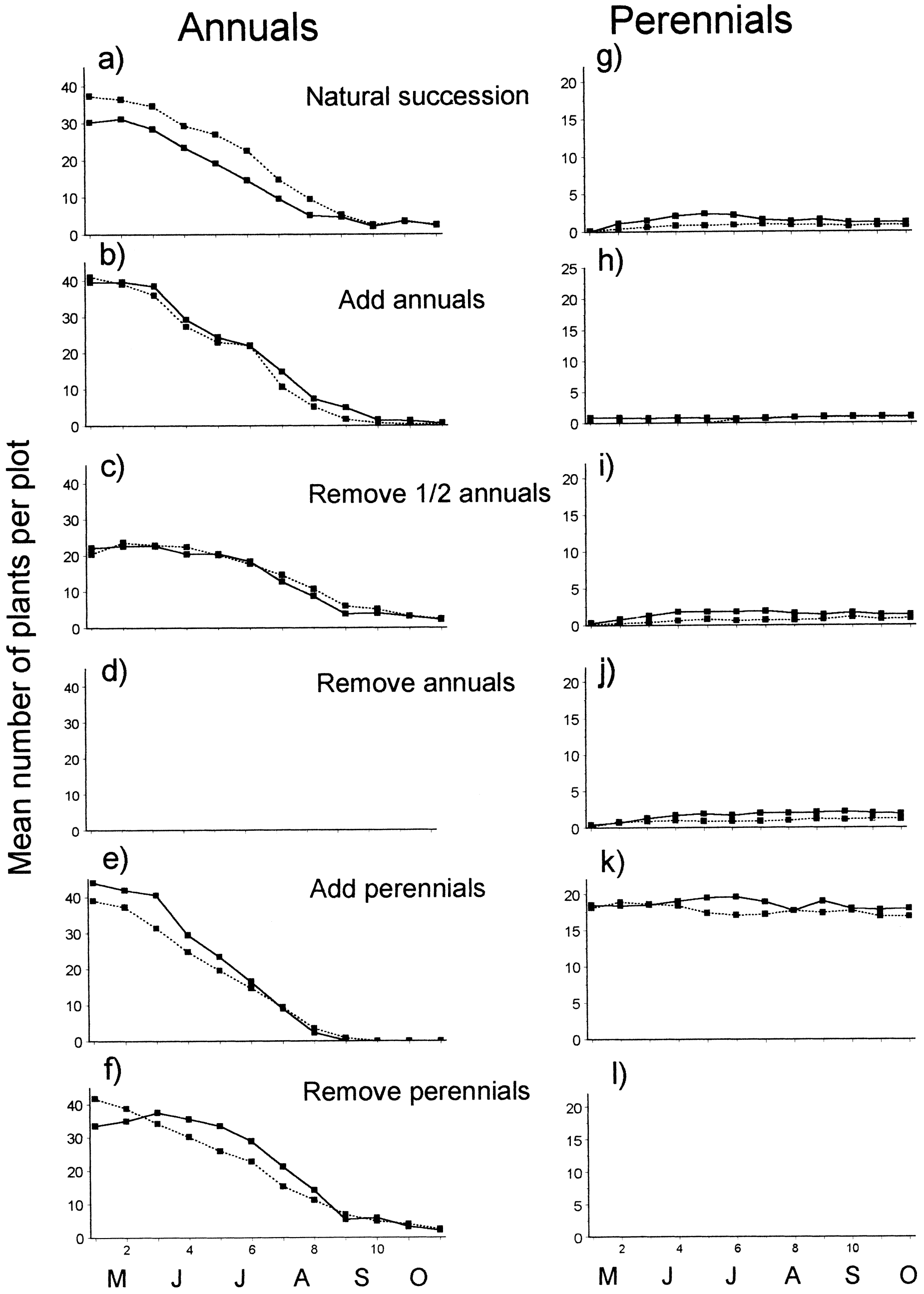

Fig. 3. Changes in annual (SE±4.19) and perennial (SE±4.68) density with (dashed line) and without (solid line) insecticide applications in 1988 for various treatments.

plots in 1989, but mean perennial species richness was significantly reduced by 87–100% over all sampling dates (contrast analyses, lowest $F_{1,108}=26.00$, $p<0.01$) in treated plots (Fig. 2(c) and (d)).

Insecticide application to 'add annuals' treatment plots, did not enhance annual recruitment or establishment in 1988. For the most part, mean annual plant densities were similar to untreated plots except for

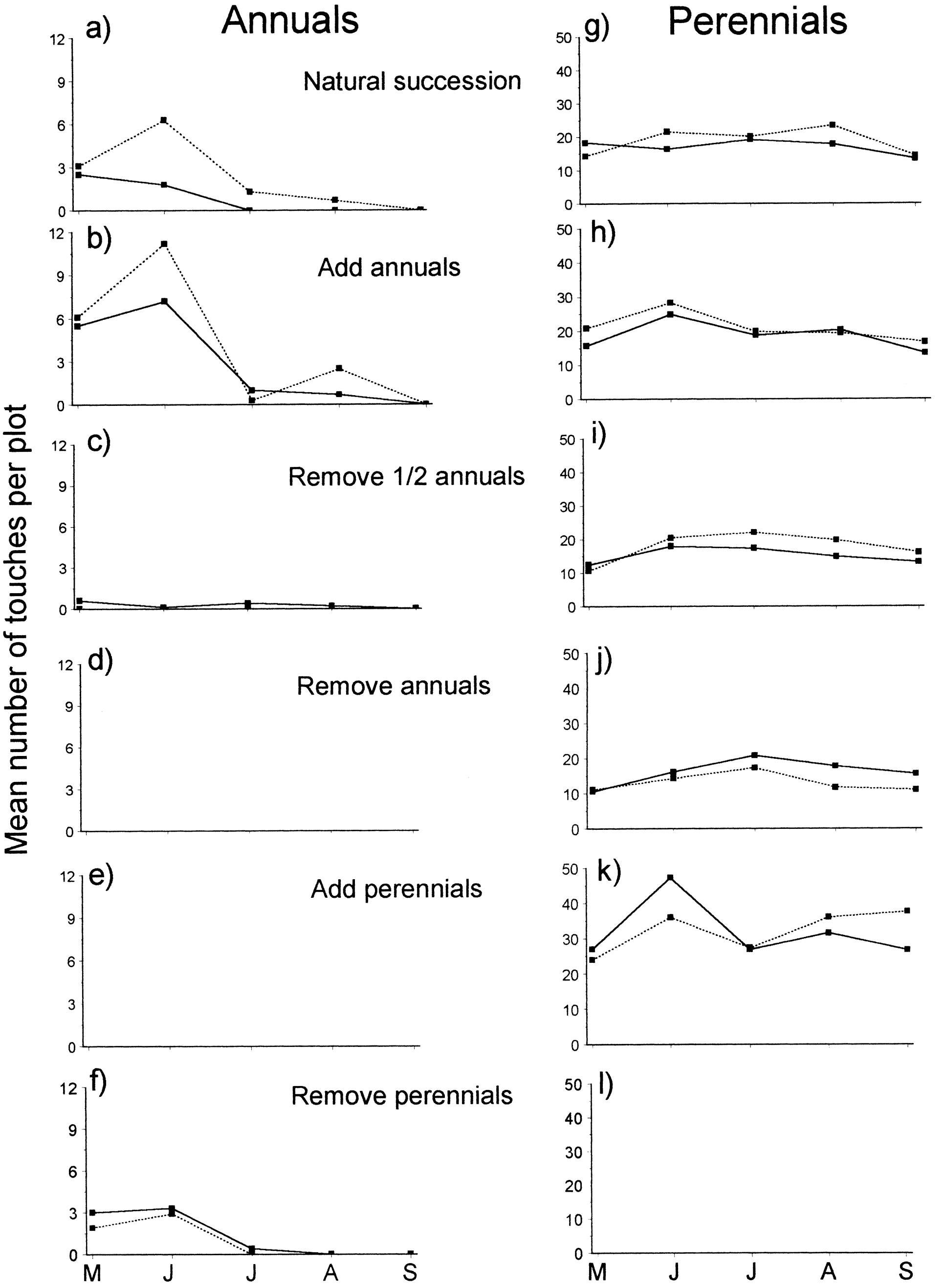

Fig. 4. Changes in (a) annual (SE±0.79) and (b) perennial (SE±3.96) cover adbundance with (dashed line) and without (solid line) insecticide applications in 1988 for various treatments.

three sample dates in late July/early August, where mean annual numbers were significantly lower by 28–64% (contrast analyses, lowest $F_{1,108}$=5.71, p<0.05) (Fig. 3(b)). There was no effect on annual species richness over any of the sample dates. Mean perennial density in the 'add annuals' treatment was unaffected by insecticide applications. In 1989, mean annual cover was unaffected by application of insecticide within 'add annuals' plots. There was no effect of insecticide application on mean annual species richness (Fig. 2(a) and (b)). Mean perennial cover within the 'add annuals' treatment was unaffected by insecticide applications, but perennial species richness was significantly reduced from May to August between 35–80% (contrast analyses, lowest $F_{1,108}=7.34$, $p<0.05$) (Fig. 2(c) and (d)).

Insecticide applications within the 'remove annuals' treatment had no effect on perennial density or species richness in 1988 over any sample dates. There was also no effect of insecticides on perennial cover in 1989. However, insecticide application significantly reduced perennial species richness by 47–81% over all sample dates within 'remove annuals' plots in year 1989 (Contrast analyses, lowest $F_{1,108}=14.38$, $p<0.05$) (Fig. 2(c) and (d)). In the 'remove perennials' treatment, the application of insecticides resulted in a significant decrease of 21–28% in the mean number of annual plants over four consecutive sample dates from mid-July to late August in 1988 (contrast analyses, lowest $F_{1,108}=5.19$, $p<0.05$) (Fig. 3(f)). In 1989, there was no significant effect of insecticides on annual cover or species richness.

4. Discussion

During the first year of the experiment, the pattern of colonization within 'natural succession' plots was typical of that observed in studies at Silwood Park when succession is allowed to proceed from seed only (Brown, 1985; Brown and Gange, 1989a). Initial colonists are predominantly annual and the majority of these species are functionally classified as ruderal (Grime et al., 1990). Germination of annual species is generally synchronous (within two weeks of disturbance) and competition for resources between neighbouring annual plants is intense. The resulting high level of mortality causes a reduction in annual density between each consecutive sample date. The low densities of perennial species observed in the first year could be attributed to sampling error as a result of the small plot size used in the experiment. Evidence from other studies on succession at Silwood Park on the same soil type using a larger plot size suggests that this is unlikely to be the case. Perennials species on natural succession plots typically account for less than 10% of the total vegetation cover in the first year of succession (Brown and Gange, 1989a), or are virtually absent (Brown and Gange, 1992). These results are consistent with the levels of perennial abundance described in the current study. The developing flora was typical of that regenerating on set-aside in England. Rew et al. (1992) and Wilson (1992) sampled a range of sites of similar age and report found a comparable species diversity and composition of vegetation to that observed in the experiment.

By the second year, most annual species were replaced by a competitive-ruderal *Agrostis stolonifera* (Grime et al., 1990) dominated perennial stand that had regenerated from vegetative *A. stolonifera* fragments present within the soil during the autumn. None of the perennial species that initially developed from seed during the first year of the experiment became dominant during the second year, suggesting that colonization from a vegetative source is more important than the seedbank composition during early secondary succession. Based on observation only, the underlying dynamics of the succession is an expression of the life histories of propagules within the soil or an example of the 'initial floristic composition' model (Egler, 1954).

As a test of the facilitation model, increasing the number or biomass of early-colonizing annual species should produce an improvement in perennial (later-colonizer) performance. Conversely, a corresponding reduction in annual presence would be expected to reduce perennial performance. Adding annual seed did result in an increase in annual density when compared with the 'natural succession' control, indicating that annual populations within 'natural succession' plots are initially seed and not microsite limited. However, it is not possible to attribute the increase in annual plant density to an overall increase in annual biomass because no measurements were taken, but the increased annual persistence into the second year would support this conclusion. Because perennial establishment was delayed within 'add annuals' plots in the first year and there was no improvement in perennial species diversity, density or cover abundance following the complete or partial removal of annuals, any facilitatory effects can be discounted. Over the timescale involved within the experiment, it is difficult to envisage how the facilitation model could be supported during early succession on former arable land. Following abandonment, the high fertility levels arising from agricultural inputs and open biological space allow colonization by a wide range of species which do not require modification of the initial environmental conditions by specialist species.

The lack of response by perennial species to annual removal does provide strong evidence for the tolerance model. However, there is no suggestion of non-interacting life histories originally indicated by Connell and Slatyer, because interspecific competition between annuals and perennials on early succession sites is well documented (Miller and Werner, 1987). Despite their relative paucity (approximately one individual per plot), perennial species appear to exert a major competitive influence on the annual community as observed by an increase in annual recruitment following perennial removal during the first year. Improvements in annual subdominant species performance has been reported in several old-field selective removal experiments in the USA (Allen and Forman, 1976; Gross, 1980; Armesto and Pickett, 1986). Surprisingly, in this experiment, the improvement was relatively short-lived and there was only minimal annual colonization in the second year, despite plots remaining free of perennial competitors. Additional disturbance is probably necessary to stimulate further germination of annual plants as many buried annual seeds respond to light in order to break dormancy and resume the cycle (Pickett and White, 1985; Baskin and Baskin, 1989). This does provide a mechanism by which species turnover within the successional sequence is a result of contrasting life-histories and not species interactions. Pickett et al. (1987a) modified the definition of the original C and S (1977) paper and termed this neutral meshing of life-histories ‘passive tolerance’. This type of succession can also be interpreted as the ‘gradient in time’ model proposed by Peet (1992) where the sequence of species replacement is a function of chance and life-history adaptation.

Further evidence for the model of tolerance is provided by the ability of the sown later-colonizing perennial species *H. lanatus* and *T. pratense* to establish in the presence of annuals. This also suggests that perennial seeds within the seedbank are either relatively few in number, possibly as result of predation (Hulme, 1994) or are unable to break dormancy despite conditions that are favourable (Fenner, 1985; Baskin and Baskin, 1989). Asymmetric competition for resources between annual and perennial plant species appears to be the mechanism through which the succession proceeds and this occurs at relatively low perennial densities and can be considered as ‘active tolerance’ (Pickett et al., 1987a). The superior long term competitive ability of many perennial species arises from their well developed root systems (Crawley, 1997) and ability to endure lower levels of resource than annuals (Goldberg, 1990). There was no evidence for the inhibition of perennials by annuals at natural densities.

Herbivores lower the fitness of individual plants and thus can affect the rate and direction of succession (Davidson, 1993), very often by altering competitive interactions between individual community members (Edwards and Gilman, 1987). Although no assessment of the levels of herbivory on the site vegetation were made in the experiment, detailed studies of the composition and role of the herbivore fauna on nearby sites of the same successional age have been undertaken at Silwood Park. Regular sampling of an early successional site by Edwards-Jones and Brown (1993) demonstrated that above-ground insect herbivores belonged to three major groups; Heteroptera (25 species), Cicadellidae (20 species) and Curculionedea (38 species). In contrast, the subterranean insect fauna is predominantly composed of larvae of Tipulidae, Noctuidae, Curculionidae and Scarabaeidae (Brown and Gange, 1989a).

Reducing insect herbivory within the field experiment had mixed results. For some treatment combinations, annual and/or perennial performance is reduced, and in others it is enhanced. Applying insecticides to ’natural succession’ plots increased annual recruitment and establishment over both years when compared with untreated controls, thus suggesting that natural levels of insect herbivory can enhance succession. This observation has also been reported in other studies of succession at Silwood Park. Brown and Gange (1989a) used insecticides to exclude below-and above-ground herbivores, either separately or in combination. All three treatments significantly enhanced annual species performance, but the effects were greatest when insecticides were applied in combination. In the current study, perennial density or cover were unaffected by insecticides within ’natural succession' plots, but the already low perennial species diversity within the second year was further reduced, possibly as a result of competition arising from the increased annual presence. However, perennial species richness within the 'remove-annuals' treatment was also significantly reduced following insecticide application, suggesting that improvements in perennial performance as a result of the reduction in herbivore load, prevent recruitment of further perennial species and thus lower diversity. A corresponding increase in perennial cover abundance may have been expected, but this is not apparent. It is possible that observed improvements in overall perennial performance could be mediated through an increase in root production, but no assessments were made in the experiment. Other studies have reported an improvement in perennial performance and diversity within natural communities following insecticide applications, particularly those which exclude below-ground herbivores (Brown and Gange, 1989b). Although the current experiment demonstrates that the major effects of herbivory can influence the perennial (late-colonizer) species diversity, perennial numbers or cover are generally unaffected. Consequently, the underlying successional mechanism remains the same and the tolerance model continues to provide the best description of the pattern of early community development on former agricultural land.

The operation of the tolerance model of succession on ex-arable land has two implications for set-aside management. The first is that it is very difficult to maintain an annual dominated community for a period longer than a year without there being some form of disturbance at intervals. Generally, the simple removal of the more competitive perennial vegetation will not significantly extend the period of annual dominance. However, there were no annual species considered to be extremely competitive present on the site, such as Barren brome (*Bromus sterilis*) or cleavers (*Galium aparine*) (Grime et al., 1990) which may have persisted for longer. Secondly, the establishment of late-colonizing perennial species is independent of the previous vegetation type and there is no facilitatory pre-requisite. By supplementing the natural availability of representative seeds within the seedbank, succession can be artificially accelerated to a later seral stage. Because seed species diversity is often impoverished on former agricultural land following many years of cultivation and herbicide application (Ford, 1996; Wilson, 1994) then additional seed introduction will be necessary for enhanced perennial based habitat creation schemes on set aside.

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