Community assembly from the local species pool: an experimental study using congeneric species pairs

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Summary

1 Vegetation–environment relationships are well understood at the geographical scale, but it is still not clear what role chance and historical contigency play in the assembly of communities from the local species pool. We addressed this question experimentally by comparing the performance of congeneric species introduced into a grassland community.

2 We used the National Vegetation Classification and distribution maps to define the local pool of grassland species suited to our experimental site. From this we selected five pairs of congeneric species. One member of each pair was native to the experimental site ('present' species) and one member was represented in the local species pool but absent from the community ('absent' species).

3 If community assembly processes are deterministic, then absent species should underperform present congeners. Any other result would imply that chance, dispersal limitation or historical contingency plays a role in community assembly. Our experimental arrangement allowed us to assess the consistency of comparisons across different grazing treatment combinations.

4 Two field experiments were undertaken. The first investigated the effects of dispersal limitation by introducing seed of congeners and monitoring performance. The second investigated the survival of congeners introduced as small plants at the early stages of growth in 'plugs'. A laboratory germination test and a combined analysis of both field experiments were also undertaken.

5 Some species showed markedly different responses from their congeners in the two field experiments. Overall, the present species did not consistently perform better than their absent congeners. This indicates that the study community bears the strong imprint of dispersal limitation or other historical factors, a finding consistent with results previously obtained for the same community using a trait-based model.

6 We conclude that the accuracy of predictions about community composition will be limited by the success with which factors such as propagule dispersal and differential effects of seed predation and herbivory can be modelled. We predict the circumstances under which modelling of community assembly is most likely to be successful.

Key-words: *Cirsium*, community assembly, dispersal limitation, *Leontodon*, *Galium*, grassland, grazing, *Rumex*, transplants, *Trifolium*

Journal of Ecology (2002) **90**, 385–393

Introduction

The assembly of communities from the species pool is a central theme in ecology (Cody & Diamond 1975; Drake 1990; Keddy 1992; Weiher & Keddy 1999), but is this process sufficiently deterministic to be predictable? If so, naturally present species should outperform congeners introduced from the local species pool. Equal or better performance of species naturally absent from the community would imply a major role for chance, dispersal limitation or historical contingency.

Eriksson (1993) produced a simple model for the process of community assembly whereby all species

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within the species pool are equally likely to invade, or to be excluded from, a community. However, provided there is a non-zero extinction rate, there will always be fewer species in the community than in the species pool, the ratio of the two numbers being determined by the colonization and extinction rates. Under this null model, community composition cannot be predicted because it represents a random selection from a group of equally suitable inhabitants.

Inability to predict the outcome of an ecological process reflects 'disorderliness' (Fowler 1990), which at the community level may be influenced by the stochastic nature of factors such as seed dispersal. Small seed mass and seed dispersal by vertebrates, for example, were associated with invasiveness in the woody species studied by Rejmanek & Richardson (1996).

Assembly of the community studied here has previously been investigated using a trait-based model (Tofts & Silvertown 2000a). That model correctly predicted the presence of most species that were actually found in the community, but it also gave several absent species a high probability of occurrence. This may have resulted from imperfections in the model, but some absences may be caused by dispersal limitation or historical contingencies that were not included in the model. We test this possibility here by comparing the success of species native to the site with that of naturally absent congeners that were experimentally introduced. Because management treatments may affect the relative performance of species (cf. Vesk & Westoby 2001), we tested for species–grazing interactions in experiments performed under four grazing treatment combinations.

Comparisons were made at the key life history stages when species are most likely to be filtered out of a community – during propagule dispersal (dispersal limitation, see e.g. Herrera 1991; Primack & Miao 1992; Ackerman *et al*. 1996; Tilman 1997; Turnbull *et al*. 2000), and during the early stages of seedling growth (e.g. Fenner 1987; Herrera 1991; Oliviera Silva 1992; Hanley *et al*. 1995).

Methods

SITE

The fieldwork was undertaken within a grazing experiment conducted between 1986 and 1998 at Little Wittenham Nature Reserve, Oxfordshire (grid reference SU568924). Until 1982 the site had been treated with mineral fertilizer in a similar way to most grasslands across lowland England. The soils are well-drained calcareous silty rendzinas of the Wantage 1 Association (Soil Survey of England and Wales 1983), with a mean *p*H of 7.5 and a high residual fertility (Watt *et al*. 1996).

Eight 50×50 m paddocks were organized factorially into two complete blocks of four, with one of two levels of grazing in both winter (November 1 to March 20) and summer (May 21 to October 31).

In winter, paddocks were either grazed by two sheep or ungrazed. In summer, sheep numbers were manipulated to maintain a sward of 3 or 9 cm average height (details in Treweek 1990; Bullock *et al*. 1994). All paddocks were also grazed by two sheep each in the spring (March 21–May 20).

SELECTION OF THE STUDY SPECIES

Information from Rodwell (1992) was used to identify the local species pool as in Tofts & Silvertown (2000a) and Tofts (1998). We identified grassland communities for which the conditions (soil depth, *p*H, etc.) at the study site were suitable and included in the local species pool all component species that occurred within a 50×50 km square centred on the site. These, together with a few species added on the basis of additional published information (Tofts & Silvertown 2000a), contributed approximately 150 species, excluding graminoids, to the species pool. Five suitable pairs of congeners from four dicot families were selected (Table 1). Determining the reasons for the scarcity of such species in species-poor grasslands is of both ecological and conservation interest.

Table 1 Congeneric pairs: numbers of plugs planted per paddock, date of plug planting and recording date

Species	Number planted per paddock	Date planted	Date recorded
Galium aparine	40	25 March 1996	6 June 1996
*Galium verum	40		
Trifolium pratense	45	21 April 1997	3 July 1997
*Trifolium dubium	45		
Rumex crispus	40	24 April 1996	13 March 1997
*Rumex obtusifolius	40		
Cirsium vulgare	15	3 July 1996	13 March 1997
*Cirsium eriophorum	41 (Block 1), 29 (Block 2)		
Leontodon autumnalis	15	6 July 1996	13 March 1997
*Leontodon hispidus	45		

*, Species did not occur naturally at the study site.

LABORATORY EXPERIMENTS

Each of the five species pairs was germinated in a growth cabinet at a constant temperature of 20 °C in both dark (blackened Petri dish) and light (100 µmol m^{-2} s^{-1}) conditions. *Trifolium* seeds were lightly scarified. The pappus of *Cirsium* and *Leontodon* and perianth segments of *Rumex* were removed from the fruits. Fifty seeds were placed on filter paper placed in a Petri dish. Two replicates of each species/treatment combination were used. The experiment was analysed as a completely randomized 2 × 2 factorial design to detect differences between congeners.

FIELD EXPERIMENTS

Germination: seed experiments

Two sub-blocks of 28 paired plots (one planted and one control) were located at random in four rows of seven on a 1 m grid within each paddock, subject to the constraints that they avoided a 10 m strip around the edge and two permanent quadrats in the centre. The 10 species were allocated to plots at random, and the selection of planted vs. control and gap vs. sward (see below) was also randomized. Eight 'extra' plots per block were provided in case replanting was required. Control plots were used to estimate the amount of germination occurring naturally. We analysed the average results of the two blocks within each paddock.

Sowing was undertaken in autumn 1996 (17 October–14 November). Seeds were sown into both sward and bare ground (gap) created by spraying 33 cm diameter circular patches with glyphosate on 31 August 1996 and removing dead vegetation 6 weeks later. The soil was disturbed as little as possible, producing an area of bare ground similar to that which occurs naturally at the site as a result of flattened molehills. Each congeneric pair was sown over 1 or 2 consecutive days, the seeds being treated (pappus removal, etc.) as described above. For each species, 100 (150 in the case of *Leontodon*) seeds per plot were mixed with 5 cm^3 of fine sand and sprinkled evenly within a circle of 22 cm diameter, centred on the larger 33 cm diameter gap in the case of the gap treatment. Each control plot was 'sown' with the 5 cm^3 of sand alone. Plots were then lightly watered to help the seed make contact with the ground.

For *Cirsium*, very heavy seed predation by small mammals was observed. This part of the experiment was therefore repeated. Four extra pairs of plots in each sub-block were used, selected at random. In each, 81 seeds of either *Cirsium vulgare* or *Cirsium eriophorum* were planted into the soil with forceps to a depth of approximately 5 mm, on a 9 × 9 grid at 2 cm spacing.

Seed plots were monitored at approximately 7–14-day intervals, and every newly emerged seedling was marked with a small dot of acrylic paint until mid-May 1997, after which no further emergence was noted. After germination, seedlings were allowed to grow to the stage where two true-leaf pairs were formed (or, in the case of *Galium*, two whorls of leaves) before removal from the plot to avoid excessive interference with the other seedlings. The number of seeds germinating and the number reaching the two true-leaf pair (or two-leaf whorl) stage were recorded for each plot, and numbers in the control plots subtracted to allow for natural germination. Only *C. vulgare* germinated in the control plots.

The experiment is a factorial split-plot design. The data were therefore analysed using a split-plot multivariate analysis of variance (MANOVA; Krzanowski 1988) owing to the expected positive correlation between the number of seeds germinating and the number reaching two true-leaf pairs or whorls.

Survivorship: plug experiment

Plants of the five congeneric pairs were grown in 40 mm (depth) × 28 mm (width at top) × 20 mm (width at bottom) 'plugs' of John Innes No. 1 compost. They were kept out of doors until planting, and were watered as required. There were unequal numbers of plugs for some pairs of species (Table 1) as a result of variability in germination and constraints on seed availability.

Plugs were planted into the sward of the eight paddocks in congeneric pairs once the plants had reached the two true-leaf pairs or leaf-whorl stage of development. Planting locations were chosen randomly (subject to the same constraints as in the seed experiment), 20 cm apart (40 cm in the case of *Cirsium*) in two rows 20 cm (or 40 cm in the case of *Cirsium*) apart. Each plug was pressed firmly into a hole of similar size cut from the soil using a sharp metal tube. Plugs were watered as required during the first month of establishment. The proportion of plants of each species surviving to a particular time (Table 1) was compared with the proportion of surviving plants of its congener under the four grazing treatment combinations. Some species (e.g. both *Rumex* spp.) showed a slower decline in numbers than others (e.g. *Galium aparine*), so each congeneric pair was analysed using data from the monitoring visit at which approximately half the total number of planted congeners was still alive. In cases where one of the congeners was an annual species, the analysis was performed on data gathered before any individuals of the annual had died following seed set. This retained a sufficiently large number of individuals for analysis and allowed adequate time for treatments to take effect.

A generalized linear model with logit link function (McCullagh & Nelder 1989; Dobson 1990) was fitted to the data.

A COMBINED ANALYSIS

In some cases, one species of a pair performed best during the seed experiment, and the other performed best during the plug experiment. We therefore estimated

overall survival probabilities by multiplying the survival probabilities produced by these two field experiments (here termed P_1 and P_2) to obtain the overall probability (or compound probability, here termed P_{comp}) of survival from seed planting to the end of the second experiment.

Where the relative performance of congeners depended on the experimental treatment (i.e. where there was a significant species × treatment interaction for either field experiment), separate calculations were undertaken for those treatment combinations. Overall survival probabilities for congeners were compared by calculating the ratio (the 'P ratio') of P_{comp} for the species occurring naturally at the site ('present' species) divided by P_{comp} for the species not naturally present ('absent' species). A ratio >1 indicates that the present species outperformed its absent congener, and a ratio <1 indicates the reverse. Statistical significance of any departures from unity was assessed by bootstrapping (Manly 1991) based on observed values for P_1 and P_2. If, for example, P_1 was estimated as 0.3 from a sample size of 800 seeds, and P_2 was estimated as 0.5 from a sample size of 120 plugs, two samples were randomly drawn from binomial distributions with $P = 0.3$, $n = 800$ and $P = 0.5$, $n = 120$, respectively. The P_1, P_2 and P_{comp} values were obtained for both congeners from the randomization, and the P ratio calculated. The significance of the departures from the hypothesized value of 1 was assessed against the distribution of the P ratio obtained from 10 000 randomizations.

Where there was a gap effect, the same P_2 values were used in both cases because the effect of gaps was investigated only in the seed experiment.

Results

GALIUM

In the laboratory, no difference was found in germination between *G. aparine* (present) and *Galium verum* (absent) in either light or dark conditions (Table 2).

Field germination showed two significant interactions (Table 3). In the absence of winter grazing, *G. verum* outperformed *G. aparine* (mean number germinating = 48.8 per plot, mean number reaching two leaf whorls = 27.8 per plot vs. 24.6 and 14.4, respectively), but the reverse occurred in winter-grazed paddocks (mean number germinating = 33.1 per plot, mean number reaching two leaf whorls = 13.9 per plot vs. 38.1 and 22.5, respectively). In the sward, *G. verum* outperformed *G. aparine* (mean number germinating = 44.4 per plot, mean number reaching two leaf whorls = 22.3 vs. 25.0 and 14.4, respectively), but the situation was reversed in gaps (mean number germinating = 37.5 per plot, mean number reaching two leaf whorls = 16.4 vs. 37.8 and 22.5, respectively).

Plug survival showed a significant species × winter grazing interaction (Table 4). *Galium verum* outperformed *G. aparine* under all conditions. Winter grazing improved the survival of both species, but led to a greater improvement in the case of *G. verum* (winter ungrazed: 43.1% survival for *G. aparine* vs. 68.1% for *G. verum*; winter grazed: 59.4% survival for *G. aparine* vs. 93.8% for *G. verum*).

Overall (Table 5), *G. verum* (absent) outperformed *G. aparine* (present) in the two cases where the difference was statistically significant.

TRIFOLIUM

Laboratory germination in *Trifolium dubium* (absent) was significantly greater than in *Trifolium pratense* (present). Light and dark treatments had no effect (Table 2).

Field germination showed a significant species effect, with *T. dubium* germinating and surviving significantly better than *T. pratense* (mean number germinating = 17.4 per plot; mean number reaching two true leaves = 3.4 per plot vs. 1.5 and 0.1, respectively; Table 3).

Plug survival showed three significant main effects (Table 4). Under winter grazing, plants showed better survival compared with the ungrazed treatment (76.4% vs. 63.1%, respectively). Summer grazing to 9 cm improved survival compared with 3 cm grazing (73.1% vs. 66.4%, respectively). *Trifolium pratense* showed better survival in this experiment than *T. dubium* (75.6% vs. 63.9%, respectively).

Table 2 Mean percentage laboratory germination for the five pairs of congeners in darkness and in light

Species	Dark germination (%)	Light germination (%)
Galium aparine	56[a]	72[a]
Galium verum	77[a]	84[a]
Trifolium pratense	78[a]	85[a]
Trifolium dubium	95[b]	96[b]
Rumex crispus	94[a]	96[a]
Rumex obtusifolius	76[c]	89[d]
Cirsium vulgare	93[a]	85[a]
Cirsium eriophorum	93[a]	85[a]
Leontodon autumnalis	1[a]	2[a]
Leontodon hispidus	80[b]	83[b]

Figures with the same superscript *within each congeneric group* do not differ significantly from one another.

Table 3 MANOVA of germination and early seedling survival (seed experiment)

Level	Grazing and gap treatment	Wilk's λ				
		Galium	*Trifolium*	*Rumex*	*Cirsium*	*Leontodon*
Main plot	Block	0.4901	0.8114	0.6055	0.5354	0.2815
	Summer (S)	0.7584	0.4805	0.6126	0.4960	0.0278*
	Winter (W)	0.5177	0.8901	0.5971	0.7751	0.1047
	S × W	0.5379	0.6577	0.4909	0.5399	0.0407*
Subplot	Gap (G)	0.9215	0.6672	0.3765**	0.0832***	0.0204***
	Species (Sp)	0.7668	0.2331***	0.5135*	0.0639***	0.0637***
	G × Sp	0.5335*	0.6998	0.6803	0.1062***	0.0204***
	S × G	0.6304	0.7507	0.9116	0.4929*	0.9074
	S × Sp	0.7300	0.8116	0.8255	0.5749*	0.5627*
	W × G	0.6540	0.9850	0.7739	0.9954	0.7831
	W × Sp	0.4189**	0.8806	0.9999	0.7059	0.7511
	W × S × G	0.8548	0.8748	0.9841	0.6730	0.6495
	W × S × Sp	0.5806	0.8941	0.9835	0.6234	0.6496
	W × G × Sp	0.9666	0.8689	0.9589	0.8234	0.7831
	S × G × Sp	0.6731	0.7784	0.8907	0.5418*	0.9074
	W × S × Sp × G	0.6580	0.9546	0.9735	0.7500	0.6495

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Values lacking asterisks are not statistically significant.

Table 4 Analysis of deviance of seedling survival (plug experiment)

Grazing treatment	Deviance				
	Galium	*Trifolium*	*Rumex*	*Cirsium*	*Leontodon*
Winter (W)	31.69***	15.25***	0.79	4.44*	2.41
Summer (S)	1.65	3.88*	4.78*	19.98***	5.25*
Species (Sp)	68.36***	11.98***	18.63***	6.20*	3.08
Block	2.38	1.35	27.21***	1.55	34.28***
W × S	1.89	0.01	0.39	4.53*	11.32***
W × Sp	9.61**	3.61	0.71	6.96**	2.44
S × Sp	2.71	2.31	3.20	0.10	0.53
W × S × Sp	0.07	0.36	0.05	0.17	0.15

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Values lacking asterisks are not statistically significant.

Table 5 Combined analysis: germination and survival

Treatment	*Galium*	*Trifolium*	*Rumex*	*Cirsium*	*Leontodon*
All combined		0.0438***			0.000***
Winter grazing absent	0.328***			0.523**	
Winter grazing present	1.027			0.382***	
Summer grazing 3 cm			1.778***		
Summer grazing 9 cm			1.381*		
Gap absent	0.3605***				
Gap present	0.870				
Summer grazing 3 cm, gap absent				0.218***	
Summer grazing 3 cm, gap present				0.549*	
Summer grazing 9 cm, gap absent				0.343***	
Summer grazing 9 cm, gap present				0.579***	

Numbers >1 indicate that the species naturally present outperforms its congener overall. Numbers <1 indicate the reverse.
*, $P < 0.05$; **, $P < 0.01$; ***, indicates $P < 0.001$. Values lacking asterisks are not statistically significant.
Blank cells indicate that the congeners (columns) showed no interaction with that treatment (row). See Methods for further explanation.

Overall (Table 5), *T. dubium* (absent) performed significantly better overall than *T. pratense* (present).

FUMEX

Laboratory germination of *Rumex crispus* (present) showed significantly better germination than did *Rumex obtusifolius* (absent) in both light and dark treatments. Only *R. obtusifolius* was affected differently by light and dark treatments (Table 2), with greater germination evident under the light treatment.

Field germination showed significant effects of gap and species (Table 3). Both species performed better in gaps than in the sward (mean germination =

25.8 vs. 4.5 per plot, mean number reaching two true leaves = 9.3 vs. 0.8 per plot). More individuals of *R. obtusifolius* were found to germinate compared with *R. crispus* (20.8 vs. 9.5), although this difference disappeared at the two true-leaf stage when no significant differences remained between the species (univariate ANOVA not presented here).

Plug survival showed three significant main effects (Table 4). Summer grazing to 9 cm improved survival compared with 3 cm grazing (64.7% vs. 56.3%, respectively). A greater proportion of plugs survived in block 1 compared with block 2 (70.3% vs. 50.6%, respectively). *Rumex crispus* outperformed *R. obtusifolius* (68.8% survival vs. 52.2%, respectively).

Overall (Table 5), *R. crispus* (present) performed significantly better than *R. obtusifolius* (absent) in both combinations analysed.

CIRSIUM

No significant difference was found in laboratory germination for *C. vulgare* (present) and *C. eriophorum* (absent) in either light or dark conditions (Table 2).

Field germination showed a significant three-way interaction of gap, species and summer grazing (Table 3). *Cirsium eriophorum* generally outperformed *C. vulgare* in terms of both number germinating and number reaching two true leaves. The situation was reversed, however, in gaps subject to 3 cm summer grazing. Performance in gaps for both species always exceeded that in the sward, although the extent to which gaps were beneficial depended on the levels of other experimental treatments.

Plug survival showed a significant winter × summer grazing interaction (Table 4). Winter grazing showed little effect following a 9 cm summer grazing regime (44.0% survival, winter ungrazed vs. 46.0% survival, winter grazed), but showed differing effects after a 3 cm summer grazing regime (15.0% survival, winter ungrazed vs. 33% survival, winter grazed). A species effect in the form of an interaction with winter grazing was observed (*C. eriophorum*, 22.1% survival, winter ungrazed vs. 39.3% survival, winter grazed; *C. vulgare*, 46.7% survival, winter ungrazed vs. 40% survival, winter grazed).

Overall (Table 5), *C. eriophorum* (absent) showed a significantly better performance than *C. vulgare* (present) in all six combinations.

LEONTODON

In the laboratory, *Leontodon autumnalis* (present) germinated less than *Leontodon hispidus* (absent) in both treatments (Table 2).

Field germination showed a significant species effect. No individuals of *L. autumnalis* were recorded (Table 3), a result consistent with the laboratory experiment. Two significant species interactions (species × gap and species × summer grazing) occurred because numbers of *L. hispidus* differed under different gap and summer grazing regimes, while numbers of *L. autumnalis* remained constant at zero. Mean results for *Leontodon* are therefore averaged over non-significant treatments for *L. hispidus* alone. Significant summer- and winter grazing effects were observed in the form of an interaction, and a significant gap main effect was recorded. Numbers of *L. hispidus* plants germinating and surviving to two true leaves were significantly greater in the sward than gap treatments (mean number of seeds germinating = 44.2 per plot, mean number reaching two true leaves = 29.6 per plot, vs. 17.2 and 13.6, respectively). In the absence of winter grazing the performance of *L. hispidus* was broadly similar under both summer grazing regimes (mean number germinating = 26.2 per plot, mean number reaching two true leaves = 18.6 per plot for 3 cm summer grazing vs. 24.6 and 12.6, respectively, for 9 cm summer grazing). In the presence of winter grazing, the effects of summer grazing were markedly different (mean number germinating = 22.2 per plot, mean number reaching two true leaves = 16.6 per plot for 3 cm summer grazing vs. 49.8 and 38.8, respectively, for 9 cm summer grazing).

Plug survival showed a significant block effect (Table 4), with a greater proportion of plants surviving in block 1 than in block 2 (63.8% vs. 37.5%, respectively). No species effect was observed. There was a significant summer × winter interaction (when summer grazed to 9 cm: 66.7% survival, winter ungrazed vs. 45% survival, winter grazed; when summer grazed to 3 cm: 41.7% survival, winter ungrazed vs. 49.2% survival, winter grazed).

Overall, the very significantly better performance by *L. hispidus* resulted from the lack of germination in *L. autumnalis* (Table 5). The conclusion remains unaltered if the value of P_1 for *L. autumnalis* is replaced by 0.02, the laboratory germination probability obtained under light. If it is assumed that the germination rate and survival to two true leaves is normally similar in both *Leontodon* species, the plug experiment reported here suggests that the overall performance of the two species would be similar.

Discussion

Species naturally present within our study community did not perform consistently better than their absent congeners. In fact, out of the 12 different overall assessments (Table 5), the advantage was with the naturally present congener in only two cases (both *Rumex*). This indicates that the community bears the strong imprint of dispersal limitation or historical contingency, as has been argued by others elsewhere (e.g. Primack & Miao 1992; Tilman 1997). We first consider the extent to which the statistically significant differences between congeners were predictable on the basis of plant traits, life-history stages and observations made during the course of the study. We then discuss the implications of our results for predicting community assembly.

CAUSES OF DIFFERENCES BETWEEN CONGENERIC SPECIES

Higher germination and survivorship of *G. verum* seedlings in the sward and of *G. aparine* in the gaps is consistent with other published information. *Galium aparine* often occurs in open conditions, unlike *G. verum* which mainly grows in established grasslands (Rodwell 1992, 2000). During the experiments, it appeared that *G. verum* suffered a greater amount of slug damage than *G. aparine* in the gap treatments. This may be a result of the thinner and smoother stems of *G. verum* (cf. Westerbergh & Nyberg 1995, who showed glabrous plants of *Silene dioica* to be preferentially grazed by slugs at both the seedling and adult stage). The reason for the species × winter grazing interaction affecting germination and the two-leaf whorl stage is unclear. The coarser winter ungrazed sward may offer protection for *G. verum* during the very early stages, with the more open winter grazed sward benefiting *G. aparine*. This explanation would be consistent with the effect caused by gaps, but it is noteworthy that the beneficial effects of no winter grazing on *G. verum* were reversed in the plug experiment. Here the interaction appears to be caused indirectly through the effects on sward structure rather than through grazing damage, because the plugs were planted at the very end of the winter grazing period. *Galium aparine* grows more rapidly than *G. verum* and it is likely that it suffered less from the competitive effects of the winter ungrazed sward.

Trifolium dubium showed slightly better germination in the laboratory than *T. pratense*, but the great difference in performance between the two species (over a 10-fold increase in numbers germinating and 30-fold increase in numbers reaching the two true-leaf stage) suggests that seed viability was not the primary cause. During fieldwork, many seeds of *T. pratense* were seen to have been cracked open, apparently by small mammals, but none of the *T. dubium* seeds appeared to suffer in this way. It therefore seems likely that differential seed predation contributed to the difference in species performance, with the larger seeds of *T. pratense* perhaps being the reason why they were favoured by granivores. Substantial effects of seed predation have been shown in some other studies (Hulme 1994). The reason for the better performance of *T. pratense* in plugs is not certain, but its more robust habit may confer an advantage in closed swards.

Some slug damage to *Rumex* seedlings was noted, and *R. obtusifolius* was found to germinate more quickly than *R. crispus* (R.T., unpublished results), coinciding with a greater period of slug activity. Slug herbivory may therefore have accounted for the disproportionate losses of *R. obtusifolius*, although the reason for the reversal of germination success between the laboratory and field studies in the two species is unclear. The reason for the better performance of *R. crispus* compared with *R. obtusifolius* in the plug

experiment is also not clear, but is consistent with a study by Hongo (1989) (see below).

It is noteworthy that *C. eriophorum* outperformed *C. vulgare* under all circumstances in the germination experiment except in gaps subject to 3 cm summer grazing, particularly given that *C. vulgare* occurs naturally in considerable abundance in many of the paddocks. *Cirsium eriophorum* has substantially bigger seeds than *C. vulgare*, and this may have accounted for its generally superior performance, especially in the non-gap treatments (cf. Armstrong & Westoby 1993; Westoby *et al.* 1996). This contrasted with the finding for the *Trifolium* congeners, but to avoid small mammal predation the *Cirsium* seeds were planted into the soil rather than scattered on top of it. The better performance of *C. vulgare* shortly after germination under close summer grazing in gaps may have resulted from the more prostrate leaves evading defoliation more successfully (Tofts 1999; Tofts & Silvertown 2000b). The species × winter grazing interaction seen in the plug experiment may have arisen as a result of the lower growth rate of *C. eriophorum* (Tofts & Silvertown 2000b) making it more susceptible to competition from the winter ungrazed sward.

The better performance of *L. hispidus* compared with *L. autumnalis* was due to the low germination of *L. autumnalis* seed.

Overall, although only five species pairs from four families were investigated, there appears to be no general pattern in the causes of species being present or absent from the community.

IMPLICATIONS FOR COMMUNITY ASSEMBLY

Our experiments were undertaken over a comparatively short period, but we examined two different life-history stages and a range of grazing treatments, giving the results relevance over a broad range of circumstances. Other evidence also supports temporal extrapolation of our results. Although the grazing experiment was abandoned in 1998, the site continues to be managed as grassland under a combined cutting and grazing regime, and a visit to the site in 2000 revealed that the experimentally introduced species *G. verum* and *C. eriophorum* were still present. Both species out-performed their congener that was naturally present in the community. In the case of *Rumex*, our results are in agreement with those of a 4-year transplant of the same two species by Hongo (1989). With regard to *T. dubium*, the experiment was of sufficient length to show that this species could flower and set seed within the grazing experiment.

The results of the field experiments are in broad agreement with the trait-based model reported by Tofts & Silvertown (2000a), which predicted that a number of absent species 'should' be present. In that study, four of the naturally absent congeners examined here were predicted to have a more than even ($P > 0.6$) chance of occurring within the study site, and this predicted

chance of occurrence was similar for the congener which was in fact present. The exception to this was *Cirsium*, where *C. eriophorum* was given a low predicted probability of occurrence ($P = 0.16$) compared with *C. vulgare* ($P = 0.68$). This low predicted probability of occurrence resulted, however, from the comparative scarcity of *C. eriophorum* (and presumed strong dispersal limitation) that was overcome by the planting experiments adopted here.

Several of the results from the field experiments were predictable on the basis of what is known about the ecology of the study species. An example of this is the better performance of *G. aparine* in gaps, and *G. verum* in the closed sward reflected in the differences in relative frequencies in a wide range of communities (Rodwell 1992, 2000). In this and similar cases, it would be possible to construct a model that takes the ecological information into account, and such a model is likely to be of general applicability. We also identified likely causes for the results of several other field experiments, such as seed predation adversely affecting the performance of *T. pratense*, and slug herbivory adversely affecting *R. obtusifolius*. Here, however, it is much more difficult to incorporate the results into a model of community assembly because it is not clear beforehand whether the causal factors will be operating in any particular case. The explanation for some other sets of results such as the better performance of *R. crispus* compared with *R. obtusifolius* is not clear. This range of findings is probably indicative of the sorts of factors that will limit the predictability of community assembly more generally.

Our results suggest that the accuracy of predictions about community assembly is likely to be limited by the accuracy with which events such as propagule dispersal and seed predation can be modelled, and the actual community arising or developing under a particular set of environmental conditions is probably only one of many possible ones. Based on these considerations, circumstances under which models are most likely to provide useful predictions include those where (i) the environment is comparatively predictable; (ii) the appearance of microsites suitable for germination is reliable and can be quantified; (iii) there is a steady and predictable source of propagules; (iv) the species in the species pool differ considerably in their ability to flourish under the environmental conditions being considered; and (v) the species in the species pool possess a wide range of different traits that are amenable to analysis. Predictions about communities over large areas may also be more reliable than those relating to small areas, because small-scale factors such as localized disturbance and seed predation are likely to be the least predictable. But even under controlled conditions, a strong stochastic component may be evident (Weiher & Keddy 1995). One of the key challenges is therefore to identify levels of predictability in community assembly (species, life form, functional group, etc.) that are achievable under different sets of environmental conditions.

References

Ackerman, J.D., Sabat, A. & Zimmerman, J.K. (1996) Seedling establishment in an epiphytic orchid: an experimental study of seed limitation. *Oecologia*, **106**, 192–198.

Armstrong, D.P. & Westoby, M. (1993) Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrasts. *Ecology*, **74**, 1092–1100.

Bullock, J.M., Clear Hill, B., Dale, M.P. & Silvertown, J. (1994) An experimental study of the effects of sheep grazing on vegetation change in a species-poor grassland and the role of seedling recruitment into gaps. *Journal of Applied Ecology*, **31**, 493–507.

Cody, M.L. & Diamond, J.M. (1975) *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, MA, USA.

Dobson, A.J. (1990) *An Introduction to Generalized Linear Models*. Chapman & Hall, London.

Drake, J.A. (1990) Communities as assembled structures: do rules govern pattern? *Trends in Ecology and Evolution*, **5**, 159–164.

Eriksson, O. (1993) The species-pool hypothesis and plant community diversity. *Oikos*, **68**, 371–374.

Fenner, M. (1987) Seedlings. *New Phytologist*, **106**, 35–47.

Fowler, N.L. (1990) Disorderliness in plant communities: comparisons, causes and consequences. *Perspectives on Plant Competition* (eds J. B. Grace & D. Tilman), pp. 29–306. Academic Press, Orlando.

Hanley, M.E., Fenner, M. & Edwards, P.J. (1995) An experimental field study of the effects of mollusc grazing on seedling recruitment and survival in grassland. *Journal of Ecology*, **83**, 621–627.

Herrera, J. (1991) Herbivory, seed dispersal, and the distribution of a ruderal plant living in a natural habitat. *Oikos*, **62**, 209–215.

Hongo, A. (1989) Transplant survival of *Rumex obtusifolius* L. and *Rumex crispus* L. in three old reseeded grasslands. *Weed Research*, **29**, 13–19.

Hulme, P.E. (1994) Post dispersal seed predation in grassland – its magnitude and sources of variation. *Journal of Ecology*, **82**, 645–652.

Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, **3**, 157–164.

Krzanowski, W.J. (1988) *Principles of Multivariate Analysis*. Clarendon Press, Oxford.

Manly, B.F.G. (1991) *Randomization and Monte Carlo Methods in Biology*. Chapman & Hall, London.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*. Chapman & Hall, London.

Oliviera Silva, M.T. (1992) Effects of mollusc grazing on the development of grassland species. *Journal of Vegetation Science*, **3**, 267–270.

Primack, R.B. & Miao, S.L. (1992) Dispersal can limit local plant distribution. *Conservation Biology*, **6**, 513–519.

Rejmanek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.

Rodwell, J.S., ed. (1992) *British Plant Communities, Vol. 3. Grasslands and Montane Communities*. Cambridge University Press, Cambridge, UK.

Rodwell, J.S., ed. (2000) *British Plant Communities, Vol. 5. Maritime Communities and Vegetation of Open Habitats*. Cambridge University Press, Cambridge, UK.

Soil Survey of England and Wales (1983) *Soils of South East England*, 1:250 000 map and legend. Rothamsted Experimental Station, Harpenden, UK.

Tilman, D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81–92.

Tofts, R. (1998) Assembly of a grassland plant community. PhD thesis, Open University, Milton Keynes, UK.

Tofts, R. (1999) Biological Flora of the British Isles. *Cirsium eriophorum. Journal of Ecology*, **87**, 529–542.

Tofts, R. & Silvertown, J. (2000a) A phylogenetic approach to community assembly from a local species pool. *Proceedings of the Royal Society, B*, **267**, 363–369.

Tofts, R. & Silvertown, J. (2000b) Niche differences and their relation to species' traits in *Cirsium vulgare* and *Cirsium eriophorum. Folia Geobotanica*, **35**, 231–240.

Treweek, J.R. (1990) The ecology of sheep grazing: its use in nature conservation management of lowland neutral grassland. PhD thesis, Keble College, Oxford, UK.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, **88**, 225–238.

Vesk, P.A. & Westoby, M. (2001) Predicting plant species' responses to grazing. *Journal of Applied Ecology*, **38**, 897–909.

Watt, T.A., Treweek, J.R. & Woolmer, F.S. (1996) An experimental study of the impact of seasonal sheep grazing on formerly fertilized grassland. *Journal of Vegetation Science*, **7**, 535–542.

Weiher, E. & Keddy, P.A. (1995) The assembly of experimental wetland plant communities. *Oikos*, **73**, 323–335.

Weiher, E. & Keddy, P.A., eds (1999) *Ecological Assembly Rules*. Cambridge University Press, Cambridge, UK.

Westerbergh, A. & Nyberg, A. (1995) Selective grazing of hairless *Silene dioica* plants by land gastropods. *Oikos*, **73**, 289–298.

Westoby, M., Leishman, M. & Lord, J. (1996) Comparative ecology of seed size and dispersal. *Philosophical Transactions of the Royal Society of London, B*, **351**, 1309–1318.