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Gap colonization as a source of grassland community change: effects of gap size and grazing on the rate and mode of colonization by different species

J. M. Bullock, B. Clear Hill, J. Silvertown and M. Sutton

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Grazers may bring about vegetation change in pastures through effects on the creation and colonization of gaps. The natural colonization of three sizes of artificial gap in a species-poor, fertile pasture was monitored in an experiment in which two seasons of sheep grazing were applied, each at two levels: spring (grazed or ungrazed) and summer (hard or light grazed). The experiment had a 2×2 factorial design with two blocks in eight paddocks. Gap filling was slow; after 50 weeks the ramet density of the smallest gaps was 71% of that of the surrounding sward. Seedling establishment was the dominant mode of colonization, accounting for 59% of colonizing ramets. The remaining colonists were from clonal ingrowth. Smaller gaps filled fastest, having higher clonal ramet densities than the larger gaps.

Gap size had complex effects on seedling colonization. Over the whole gap area there was a non-significant trend for increased densities of seed-derived plants in smaller gaps, but in just the central area of the gap, increased gap size increased the density and size of seed-derived plants. There were no spring grazing or grazing treatment × gap size interactions. Harder summer grazing did not affect gap filling rates but it decreased seedling densities and increased clonal ramet densities, possibly by reducing flowering.

Species differed in gap colonization ability, measured by the change in a species' frequency between the surrounding sward and the colonized gap. Species also differed significantly in the ratio of seed-derived to clonal colonizing ramets, ranging from almost complete clonal colonizers to almost complete seedling colonizers. Species with a higher proportion of colonizing ramets derived from seed had higher colonization abilities than more clonal species. Increased gap size increased the frequencies of some species and decreased those of others. Both spring and summer grazing treatments affected the frequencies in the gaps of some species. There were no interaction effects of gap size and grazing treatment on gap species composition. Treatment effects on species with high proportions of seed-derived ramets were due only to effects on the frequencies of seed derived ramets and treatment effects on more clonal species were due to effects on the frequencies of clonal ramets.

These results show that grazing may bring about vegetation change by its effects on the rate of gap creation because colonized gaps have different species frequencies to the closed sward. However, these gap effects are complex; the frequencies of some common species were decreased in gaps but those of other common species were increased, and most rarer species were decreased in gaps. Gap size and grazing treatment effects show that the effects of gap creation on vegetation change will be dependent on the sizes of gaps created.

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Vegetation with a closed canopy tends to be resistant to colonization by new plants. It is widely appreciated that for this reason the formation and colonization of canopy gaps holds the key to understanding forest dynamics (e.g. Brokaw 1985, Denslow 1987). This point is equally valid, though less widely appreciated, for grasslands (Silvertown and Smith 1988a). By contrast with forest vegetation where most gap colonists are of seed origin, colonists of canopy gaps in perennial grasslands can be of seed or clonal origin. To date, most studies of grassland gaps have concentrated on the colonization of relatively large gaps (>100 mm diameter) by seedlings. In North American prairies, oldfields and other grasslands such gaps are created by fossorial mammals (Platt 1975, Platt and Weiss 1977, Rapp and Rabinowitz 1985, Goldberg 1987, Goldberg and Gross 1988, Peart 1989, Hobbs and Mooney 1991). Seedling colonization of gaps has also been studied in infertile, calcareous European grasslands (Silvertown 1981, Silvertown and Wilkin 1983, Rusch 1988, Hillier 1990, Ryser 1993). Except in the extreme climatic conditions of the alpine zone (Ryser 1993), these studies report that gaps favoured seedling recruitment.

Plant species often occur with different relative frequencies in recently colonized gaps than in the surrounding vegetation (Davis and Cantlon 1969, Platt and Weiss 1977, Rusch 1988, Hillier 1990, Martinsen et al. 1990; but see Rapp and Rabinowitz 1985). This is evidence that gap colonization is potentially an important source of vegetation change in grasslands and that changes in the rate of gap creation, for example caused by excluding fossorial mammals (Hobbs and Mooney 1991), can cause changes in grassland community composition. Since many of the species of perennial grasslands are capable of clonal growth as well as sexual reproduction, the relative abilities of different species to colonize gaps by these two modes may be one of the most important variables affecting how the creation of gaps influences species composition. For example, one might expect clonal growth to be a more effective mode of colonization of small gaps, while seed colonization should be more effective in large ones. Because most studies address only one of these modes of colonization our ability to predict how the creation of gaps will influence grassland composition is still limited. Since vertebrate grazing is the main cause of small canopy gaps in mesic perennial grasslands, the potential interaction between grazing intensity and colonization mode must also be addressed.

Previous work at our field site, which is located in fertile, lowland grassland in southern England, has shown that alterations to both the season and intensity of sheep grazing has brought about changes in plant species composition (Bullock et al. 1994a) and that heavier grazing increases the frequency of canopy gaps (Silvertown and Smith 1988b). In this study we compare how perennial grassland species colonize small, experimentally created gaps by seed and by clonal growth and how this is affected by gap size and by experimentally controlled grazing by sheep. The combination of these effects is used to predict compositional change.

Methods

Site description and grazing treatments

Our experiments were carried out inside a long-term sheep grazing experiment which was set up at Little Wittenham Nature Reserve in Oxfordshire, England (Lat 15°37'N, Long 1°10'W) in 1986 (Treweek 1990). Arable cultivation of the site last occurred in the 1940s and subsequently the site was seeded with an agricultural grass mix and managed with sheep grazing and fertilizer application. All application of agrochemicals ceased in 1984. The sward is species poor and dominated by the grasses *Lolium perenne* and *Agrostis stolonifera* (Bullock et al. 1994a), most closely resembling an MG7 community in the British National Vegetation Classification (Rodwell 1992).

Sheep grazing treatments were applied individually to 50 m × 50 m enclosures (paddocks) in two seasons: 'spring' (21 March–21 May) and 'summer' (21 May–1 November). Within each season there were two levels of grazing. In spring, paddocks were either ungrazed or grazed by two Suffolk × Mule ewes per paddock and in summer the sward height was maintained at either 3 cm or 9 cm height by weekly measurement of the sward height followed by adjustment of the stocking rate. The grazing experiment was fully factorial with a 2 × 2 structure and two randomized blocks. All paddocks were grazed during winter (1 November–21 March) by two ewes per paddock.

Colonization of experimental gaps

Gaps were created in three sizes using circular cutters of either 3 cm, 6 cm or 9 cm diameter. Gaps of these sizes are found naturally at Little Wittenham (Silvertown and Smith 1988b). Within each gap all plants were removed and shoot bases and rhizomes were dug out. This prevented regeneration of plants from fragments and was intended to replicate the situation where grazing has killed all the plants in the gap area. Gap creation was carried out with the minimum soil removal or disturbance possible. There were no observable differences among the paddocks in the characteristics (e.g. soil surface or the sharpness of the gap boundary) of these created gaps. Eight gaps of each size were randomly allocated at evenly spaced intervals along three transects placed 10 m apart in each of the eight paddocks. To reduce edge effects a 10-m strip around the perimeter of each paddock was avoided. At the beginning of the experiment all ramets in a 2-cm wide annulus bordering each gap were identified and counted. Here and subsequently 'ramet' refers to the rooted tiller of a grass or the rooted shoot of a dicot, regardless of its clonal or seed origin.

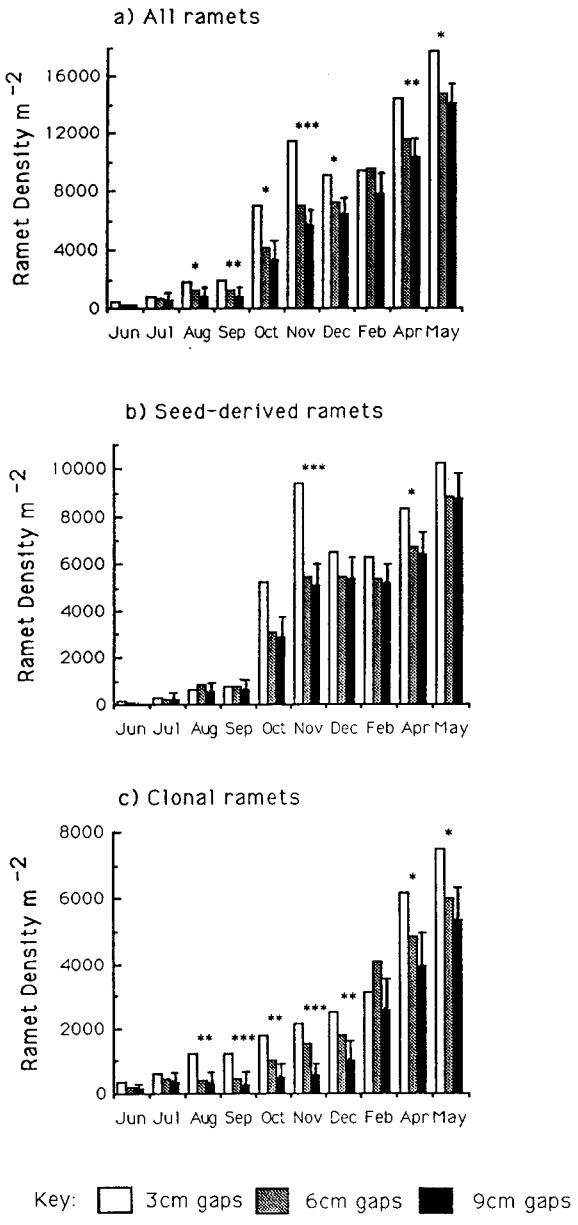

Fig. 1. Gap size effects on colonization. The mean density of ramets in each gap size at each census pooled over the grazing treatments. The standard errors of the differences of the means are shown. The significances of the differences between the sizes, as determined by split-plot ANOVA, are shown for each census. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Experimental gaps were created inside the grazing experiment at the end of May 1991. This date was chosen because it fell a few weeks after the end of the winter grazing period and therefore coincided with the time of maximum natural gap density. The mean monthly precipitation and temperatures over the period June 1991 – May 1992 were similar to the long term averages from a weather station 12 km from Little Wittenham (monthly averages June 1991 – May 1992: precipitation = 48.7 mm; daily minimum temperature = 6.1°C; daily maximum temperature = 15.2°C. These are 97%, 105% and 110% of the averages for 1951–1992). Each gap was censused two weeks after creation and every two weeks subsequently until early December and then in early February 1992, early April and early May. The final censuses took place 50 weeks after the gaps were created. At each census the original gap boundary was delineated using a circular wire quadrat of appropriate diameter which was placed over the gap using a fixed marker to position it precisely. All ramets that rooted in gaps were identified and their mode of invasion (from seed or by clonal growth) was noted. Seedlings were easily distinguished from clonal ramets; in many cases the seed was visible as was the connection of the clonal ramet to the parent or stolon. In order to compare equal areas in gaps of different diameter the quadrats used for the two larger gap sizes (6 cm and 9 cm diameter) were divided into two zones: a 3-cm diameter core and an annulus (1.5 cm or 3 cm wide) around the core. Ramets occurring in the different zones were recorded separately. Seedlings of the grasses *Poa annua, P. trivialis* and *P. pratense* could not be distinguished and were therefore lumped as *Poa* spp. (nomenclature follows Clapham et al. 1987). When it first appeared the base of a seedling was marked with acrylic poster paint so that it could be identified as a seed-derived plant at later censuses. The paint did not damage the seedling. Seed-derived ramets were further divided into the primary ramet of a seedling and the secondary ramets produced by these primary ramets.

Analysis

Analysis was performed on selected censuses, chosen to represent intervals approximately a calendar month apart, with a hiatus caused by bad weather in January 1992 and in March 1992.

Grazing, colonization mode and gap size

At each chosen census three variables were calculated for each gap size, averaged across the eight gaps of the same size in each paddock: 1. total ramet density per gap, 2. density of seed-derived ramets per gap, 3. density of clonally derived ramets per gap. In addition, these three variables were calculated for just the 3-cm diameter core of 6-cm and 9-cm diameter gaps. Main and interaction effects of grazing treatment and gap size on these variables were determined separately for each census by split-plot ANOVA with blocks and grazing treatments on the upper stratum and gap size on the lower stratum. When significant gap size effects were found means of the three sizes were compared using the standard errors of the differences of the means. For the final census alone gap size and grazing treatment effects on the densities of primary and secondary seed-derived ramets, and the pro-

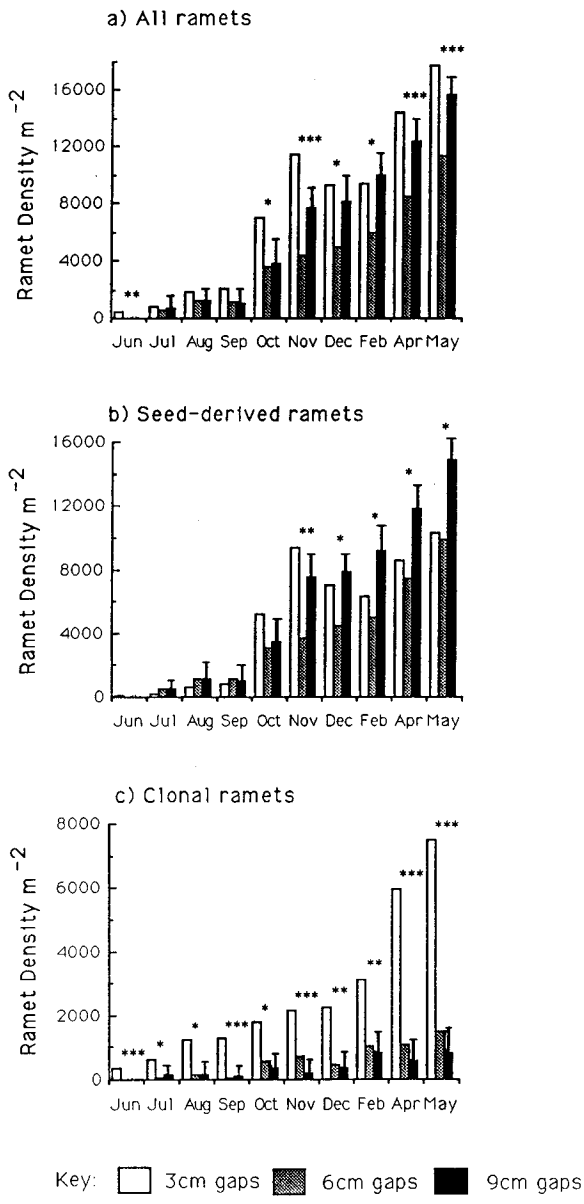

Fig. 2. Gap size effects on colonization of the core zones. The mean density of ramets in the inner zone of each gap size at each census pooled over the grazing treatments. The standard errors of the differences of the means are shown. The significances of the differences between the sizes, as determined by split-plot ANOVA, are shown for each census. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

portion of seed-derived ramets that were secondary were determined by split-plot ANOVA.

Differences among species

Twelve taxa were analysed: the ten commonest species (all grasses), a category of 'other grasses' containing the less common species and a category containing all the dicot species as a group. All the taxa are referred to as 'species' for convenience. For each species in each gap size × paddock combination we calculated: 1. Total frequency – total ramets belonging to the species as a proportion of all ramets, 2. Seed-derived frequency – seed-derived ramets belonging to the species as a proportion of all seed-derived ramets, 3. Clonal frequency – clonally derived ramets belonging to the species as a proportion of all clonally derived ramets, 4. Border frequency – the proportion of all ramets recorded in the border that belonged to the species. Main effects of gap size, grazing treatment and their interaction on frequencies 1–4 were calculated by ANOVA on arcsine transformed values using a split-plot design with gap size on the lower stratum.

Results

Grazing, colonization mode and gap size

The densities of seed-derived, clonal and total ramets generally increased over time in gaps of all three sizes (whole gap areas; Fig. 1). After August ramet densities were almost always higher in the 3-cm gaps than larger ones, mainly because densities of clonal colonists were significantly higher in smaller gaps (Fig. 1c), with few significant effects on seed-derived ramets (Fig. 1b). Ramet densities were only rarely significantly higher in the 6-cm gaps than in the 9-cm ones. The final ratio of seed-derived to all ramets had an overall mean value of 0.59 and was unaffected by gap size (split-plot ANOVA of arcsine transformed data; results not shown). The final densities in the 3-cm gaps (mean = 17672 ramets m^{-2}) were still significantly less than the ramet densities in the 2-cm gap borders determined at the start of the experiment (mean = 24766 ramets m^{-2}) (paired t-test using each gap as a sample; $t = 3.92$, $p < 0.001$, d.f. = 63).

Ramet densities in the core zones revealed a more complex picture. Although clonal ramets were at much higher densities at all censuses in 3-cm gaps than in the 3-cm cores of larger gaps (Fig. 2c), seed-derived ramets were at significantly higher densities in the core of 9-cm gaps than in smaller ones from February through to the final census in May (Fig. 2b). In cores the ratio of secondary ramets derived from seed to primary ones was higher in 9-cm gaps because of the greater density of secondary, seed-derived ramets in this gap size (Table 1).

Summer but not spring grazing treatment affected densities of the different ramet types at monthly censuses. In general densities of seed-derived ramets were significantly higher under light (9 cm sward height) than under heavier grazing (3 cm sward height) (Fig. 3b), while the reverse was the case for densities of clonal ramets (Fig. 3c). At most censuses these effects cancelled each other out, and total ramet densities were not significantly different under the two grazing treatments (Fig. 3a). Monthly censuses showed no significant interactions be-

Table 1. The effects of gap size on the densities at the final census of the two types of seed-derived ramets, primary and secondary, and on the proportion of seed-derived ramets that were secondary. Results are shown for colonization of the whole gap and of the inner zone. The standard errors of the differences of the means and the ANOVA F-values are shown. Significances: * = p < 0.05, ** = p < 0.01, *** = p < 0.001.

		Gap size (cm)			SE	$F_{2,8}$
		3	6	9		
Whole gap	Primary ramets (m^{-2})	6235	5155	4790	824	1.66
	Secondary ramets (m^{-2})	4022	3671	3971	376	0.51
	Proportion of secondary ramets	0.395	0.456	0.064	0.464	0.69
Inner zone	Primary ramets (m^{-2})	6235	6154	7847	752	3.08
	Secondary ramets (m^{-2})	4022	3684	7029	722	13.31**
	Proportion of secondary ramets	0.395	0.368	0.469	0.034	4.58*

tween summer and spring grazing (results not shown), and the few significant gap size × grazing treatment interactions were not more common than expected by chance (results not shown). Summer grazing effects on the colonization of the cores were the same as effects on colonization of the whole gap and are not presented. There were no summer grazing effects in the final census on the proportion of seed-derived ramets that were secondary ($F = 1.36$, NS).

Differences among species

ANOVAs of the border frequencies of each of the 12 species showed only one effect of grazing treatment (summer × spring effect on *Lolium perenne*, $F_{1,3} = 13.3$, $p < 0.05$) and no effects of gap size or gap size × grazing treatment interactions.

Species tended to colonize gaps with a density relative to their average density in the gap borders (Fig. 4). Spearman rank correlation showed significant similarities in the rank order of species in the gaps compared to that in the borders ($Rs = 0.867$, $p < 0.001$, d.f. = 11). An index of colonization ability was calculated for each of the 12 species by dividing the total frequency in the gap by the border frequency. This was calculated for each paddock by summing the density of a species over all the gaps in the paddock. The species differed significantly in this colonization index (Kruskal Wallis using paddocks as samples; $H = 65.09$, $p < 0.001$, d.f. = 11) (Table 2). Two of the rarest border grasses *Cynosurus cristatus* and *Bromus mollis* had the highest average colonization indices and *Festuca rubra* had the lowest (0.40). The proportion of ramets of a species that were seed-derived varied significantly among the species (Kruskal Wallis using paddocks as samples by summing the density of a species over all the gaps in the paddock; $H = 73.88$, $p < 0.001$, d.f. = 11) (Table 2). *Bromus mollis* had the highest average proportion (0.953) and *Agrostis stolonifera* had the lowest (0.023) (Table 2). There was a significant positive correlation between this proportion and the colonization index of species (Spearman rank correlation $Rs = 0.70$, $p < 0.05$, d.f. = 11).

Split-plot ANOVAs on arcsine transformed total frequencies (density of all ramets of the species/total ramet density of all species) of colonizing ramets of each species showed that most (9/12 spp.) were affected by gap size, and a smaller number (5/12 spp.) by one or both grazing treatments (Table 3). Frequencies significantly decreased with increasing gap size in six species (*Alopecurus pratensis, Dactylis glomerata, Festuca rubra, Lolium perenne* and *Phleum pratense*) but significantly increased with gap size in four species (*Agrostis stolonifera, Bromus mollis, Cynosurus cristatus* and *Hordeum secalinum*). Harder summer grazing significantly increased the total frequencies of *Festuca rubra* and *Hordeum secalinum* and decreased the frequency of *Agrostis stolonifera*. Spring grazing significantly increased the frequencies of *Cynosurus cristatus* and *Phleum pratense* and decreased the frequency of *Agrostis stolonifera*. These grazing effects on total frequencies were mirrored by effects on the seed-derived frequencies in four species (*Bromus mollis, Cynosurus cristatus, Hordeum secalinum* and *Lolium perenne*) (Table 4). In *Agrostis stolonifera, Dactylis glomerata, Festuca rubra* and *Phleum pratense* the grazing effects on clonal frequencies mirrored those on total frequencies except for the effects on total frequencies of summer and spring grazing on *Agrostis stolonifera* and gap size on *Phleum pratense* (Table 5), where no significant effects on clonal frequency were found. Both seed and clonal frequencies of *Alopecurus pratensis* were decreased by increased gap size. There were only a few cases of significant grazing effects on seed-derived or clonal frequencies different from those on total frequencies (Tables 3, 4, 5). There were no significant effects on any of the measures of species' frequencies of interactions between summer × spring grazing or between gap size × grazing treatment (results not shown).

Discussion

Grazing, colonization mode and gap size

Over the 50 weeks of the experiment, ramet densities rose from zero to over 16 000 m^{-2} in 3-cm gaps and to over

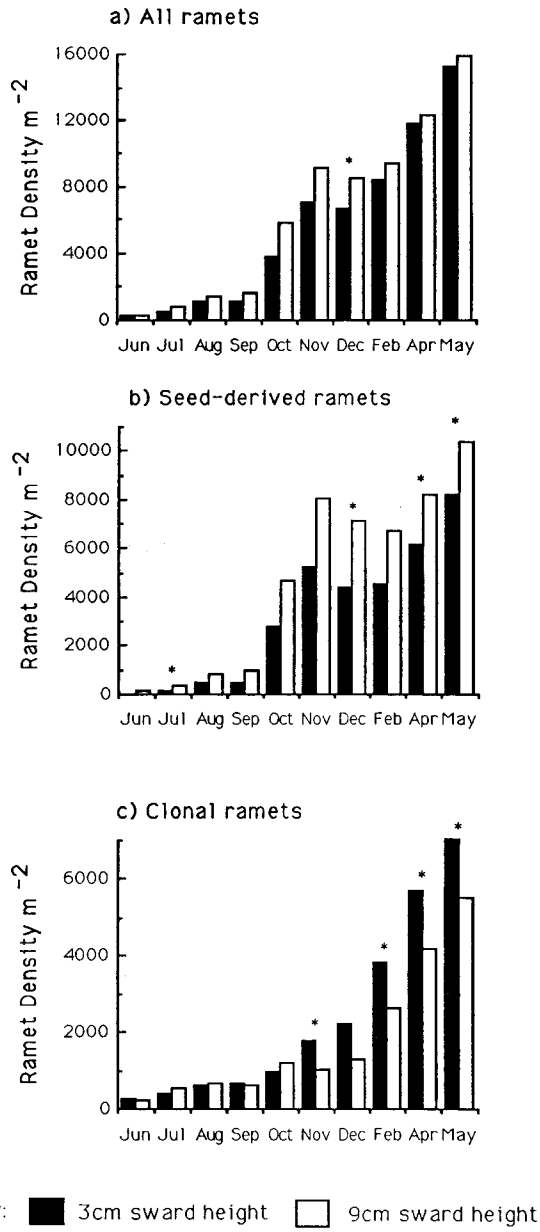

Fig. 3. The main effects of grazing in summer to 3 cm vs grazing to 9 cm sward height on mean ramet density pooled over all gap sizes. The significances of the grazing effects, as determined by ANOVA, are shown for each census. * = $p < 0.05$.

14 000 m^{-2} in larger ones (Fig. 1a), though even the higher of these densities was still only 71% of the initial tiller densities measured in gap borders. The only comparable study of gap filling, in a USA old field, found closure rates of a similar magnitude with gaps of between 10–20 cm diameter taking between 1–2 yr to fill (Goldberg and Gross 1988).

The size of a gap affected how and by which species it was filled. Small gaps were colonized more rapidly than

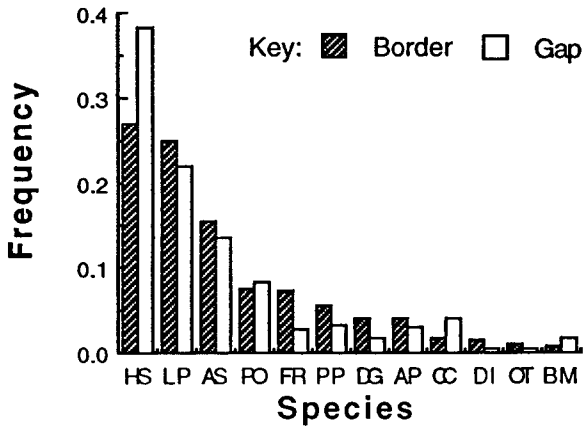

Fig. 4. The average frequency distributions of species in the border zones and in the gaps calculated by averaging densities over all replicates, gap sizes and paddocks. HS = *Hordeum secalinum*, LP = *Lolium perenne*, AS = *Agrostis stolonifera*, PO = *Poa* spp., FR = *Festuca rubra*, PP = *Phleum pratense*, DG = *Dactylis glomerata*, AP = *Alopecurus pratensis*, CC = *Cynosurus cristatus*, DI = Dicot species, OT = Other grass species, BM = *Bromus mollis*.

larger ones (Fig. 1a). This would be expected from their greater ratio of gap circumference to gap area, which decreases the average distance of colonizable space from the source of colonists by seed or clonal growth on the gap boundary. Greater clonal growth into smaller gaps was mostly responsible for this difference (Fig. 1c), although seedling colonists also had transitorily significant effects in the same direction in autumn and spring (Nov. and Apr., Fig. 1b). The lesser effect on seedling densities was probably due to the presence of a seedbank the density of which should not be affected by gap size. A comparison of how colonization occurred over the whole gap area with how it occurred in just the 3-cm cores of gaps demonstrates a remarkable difference between the

Table 2. The index of colonization ability and the proportion of seed-derived colonizing tillers for each species averaged over the eight paddocks. The value for each paddock is derived from the sum of densities over all replicates of all gap sizes.

Species	Mean index of colonization ability	Mean proportion of seed-derived colonizing tillers
Cynosurus cristatus	2.435	0.942
Bromus mollis	2.372	0.953
Hordeum secalinum	1.403	0.891
Poa spp.	1.162	0.335
Lolium perenne	0.890	0.625
Agrostis stolonifera	0.886	0.023
Alopecurus pratensis	0.789	0.330
Phleum pratense	0.623	0.281
Other grasses	0.598	0.416
Dicots	0.565	0.540
Dactylis glomerata	0.475	0.071
Festuca rubra	0.401	0.027

Table 3. The effects of gap size, summer grazing treatment and spring grazing treatment on the relative frequency of all colonizing ramets for each species. The results of split-plot ANOVAs on arcsine transformed frequencies are shown with the back-transformed means. Treatment effects on total ramet densities are also shown. The significance of the F-values are: *** = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$.

Species	Gap size (cm)				Summer grazing			Spring grazing		
	3	6	9	$F_{2,8}$	3 cm	9 cm	$F_{1,3}$	+	−	$F_{1,3}$
Agrostis stolonifera	0.098	0.156	0.166	10.14**	0.163	0.116	30.85*	0.167	0.112	45.12**
Alopecurus pratensis	0.065	0.015	0.009	17.64**	0.024	0.035	1.96	0.025	0.034	2.10
Bromus mollis	0.010	0.018	0.029	6.96*	0.024	0.014	1.72	0.017	0.021	0.79
Cynosurus cristatus	0.027	0.041	0.054	7.86*	0.040	0.042	0.01	0.023	0.059	10.53*
Dactylis glomerata	0.034	0.011	0.008	6.83*	0.019	0.017	0.25	0.013	0.022	2.58
Festuca rubra	0.049	0.024	0.009	6.68*	0.016	0.039	10.94*	0.022	0.033	3.47
Hordeum secalinum	0.315	0.384	0.443	4.65*	0.333	0.428	11.85*	0.395	0.366	0.96
Lolium perenne	0.274	0.216	0.168	16.96**	0.250	0.189	4.37	0.213	0.226	0.35
Phleum pratense	0.038	0.041	0.021	4.45*	0.033	0.033	0.01	0.022	0.045	10.71*
Poa spp.	0.086	0.087	0.077	0.63	0.089	0.078	0.22	0.093	0.073	0.76
Other grasses	0.002	0.003	0.010	1.00	0.005	0.005	0.82	0.006	0.004	0.29
Dicots	0.003	0.004	0.007	1.61	0.005	0.004	0.09	0.005	0.004	0.54
Ramet density (m^{-2})	17724	14843	14128	6.86*	15241	15889	0.63	15857	15273	0.51

centre and the periphery of gaps. Cores of 9-cm gaps had the highest densities of seed-derived ramets (Fig. 2b), while 3-cm gaps had the highest densities of clonal ramets (Fig. 2c). At the final census there were significantly more secondary ramets of seed origin in the cores of 9-cm gaps than in the cores of smaller gaps, indicating better growth of seedling colonists in the cores of 9-cm gaps (Table 1). The net consequence of these contrasting modes of colonization in gaps of different size was a bimodal distribution of core ramet densities with gap size from November through to May (Fig. 2a). When densities were averaged over whole gap areas the bimodality disappeared (Fig. 1a), but its existence in the cores suggests that we should not necessarily expect the density of colonists or the frequencies of different species colonizing to vary unidirectionally with gap size.

The relative contributions of seedling establishment and clonal growth to gap colonization have been little studied in grasslands. Rabinowitz and Rapp (1985) found that excluding clonal colonization of artificial gaps in a prairie had no effect on seedling colonization and hypothesised that there was little interaction between these two types of colonists. However, studies on an analogous community of subtidal epifauna by Kay and Keough (1981) and Keough (1984) found a decreased ratio of clonal to planktonic colonists in larger gaps because the slower colonization of clonal animals into larger gaps allowed planktonic larvae to settle and establish. If the gap creation event was not severe (e.g. trampling) and left live stolons and rhizomes in the gap area then clonal colonization might be more important than in this experiment.

Table 4. The effects of gap size and grazing treatments on the relative frequency of seed-derived ramets belonging to each species. The results of split-plot ANOVAs on arcsine transformed frequencies are shown with the back-transformed means. Treatment effects on total ramet densities are also shown at the bottom of the table. The significance of the F-values are: *** = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$.

Species	Gap size (cm)				Summer grazing			Spring grazing		
	3	6	9	$F_{2,8}$	3 cm	9 cm	$F_{1,3}$	+	−	$F_{1,3}$
Agrostis stolonifera	0.008	0.002	0.004	1.64	0.005	0.004	0.02	0.006	0.004	0.36
Alopecurus pratensis	0.040	0.010	0.002	18.90**	0.007	0.027	10.72*	0.013	0.021	2.33
Bromus mollis	0.010	0.031	0.044	12.16**	0.036	0.021	7.41	0.025	0.032	4.69
Cynosurus cristatus	0.043	0.062	0.083	5.11*	0.065	0.060	0.13	0.039	0.086	10.86*
Dactylis glomerata	0.004	0.002	0.002	0.06	0.003	0.003	0.11	0.002	0.004	0.30
Festuca rubra	0	0.004	0.003	1.11	0.001	0.004	1.09	0.002	0.003	0.06
Hordeum secalinum	0.490	0.526	0.653	26.0***	0.524	0.622	10.31*	0.611	0.535	3.72
Lolium perenne	0.330	0.240	0.155	20.6***	0.288	0.196	10.48*	0.242	0.242	0.05
Phleum pratense	0.018	0.021	0.010	0.95	0.017	0.016	0.17	0.009	0.024	2.46
Poa spp.	0.049	0.046	0.042	0.34	0.049	0.042	2.09	0.048	0.043	2.97
Other grasses	0.004	0.001	0.001	0.93	0.001	0.004	3.23	0.002	0.002	0.56
Dicots	0.005	0.005	0.002	0.68	0.006	0.002	0.78	0.003	0.005	0.14
Ramet density (m^{-2})	10257	8826	8761	2.48	8195	10368	11.37*	9083	9480	0.38

Table 5. The effects of gap size and grazing treatments on the relative frequency of clonal ramets belonging to each species. The results of split-plot ANOVAs on arcsine transformed frequencies are shown with the back-transformed means. Treatment effects on total clonal ramet densities are also shown at the bottom of the table. The significance of the F-values are: *** = $p < 0.05$, ** = $p < 0.01$, * = $p < 0.001$.

Species	Gap size (cm)				Summer grazing			Spring grazing		
	3	6	9	$F_{2,8}$	3 cm	9 cm	$F_{1,3}$	+	−	$F_{1,3}$
Agrostis stolonifera	0.207	0.377	0.463	16.79**	0.358	0.340	0.14	0.390	0.308	3.15
Alopecurus pratensis	0.092	0.022	0.016	11.95**	0.039	0.048	1.20	0.035	0.053	1.90
Bromus mollis	0.007	0.001	0	0.62	0.005	0	1.40	0.001	0.004	0.20
Cynosurus cristatus	0.010	0.007	0.004	0.11	0.005	0.010	0.03	0.001	0.013	1.68
Dactylis glomerata	0.074	0.030	0.017	5.28*	0.038	0.043	1.15	0.027	0.054	4.56
Festuca rubra	0.123	0.052	0.021	9.82**	0.032	0.098	20.80*	0.050	0.080	6.35
Hordeum secalinum	0.078	0.095	0.087	0.20	0.109	0.064	11.07*	0.098	0.075	3.43
Lolium perenne	0.214	0.193	0.187	1.01	0.220	0.177	2.65	0.190	0.260	0.56
Phleum pratense	0.063	0.067	0.039	1.16	0.051	0.061	0.98	0.037	0.076	15.06*
Poa spp.	0.130	0.150	0.132	1.19	0.130	0.144	0.01	0.150	0.124	0.29
Other grasses	0	0.006	0.019	2.05	0.008	0.008	0.08	0.009	0.007	0.25
Dicots	0.001	0.001	0.015	8.57**	0.003	0.008	0.83	0.009	0.003	3.66
Ramet density (m^{-2})	7467	6017	5366	6.11*	7046	5521	14.51*	6774	5793	6.01

Of the possible effects of grazing treatment or interactions among grazing treatments and gap size on ramet densities at each census only the summer grazing treatment had significant effects (non-significant results are not shown). Summer grazing treatment had no effect on the overall rate of colonization (Fig. 3a) but harder grazing increased the density of clonal ramets (Fig. 3c) and decreased the seed-derived ramet density (Fig. 3b). These effects may be due to harder summer grazing decreasing the seed production of the dominant grasses by removal of infloresences (Bullock et al. 1994a) and increasing grass tiller turnover rates (Bullock et al. 1994b). O'Connor (1991) found that cattle grazing increased seedling emergence and survival in gaps in savanna due to the build-up of litter in gaps in ungrazed areas. The removal of vegetation overhanging gaps may increase seedling emergence and survival (e.g. de Hullu and Gimingham 1984) and thus grazing may increase seedling colonization. Grazing effects on gap filling may be complex and require further study.

Differences among species

The rank order of the frequencies of species colonizing gaps was similar to that in the border vegetation (Fig. 4) because ramets colonized from there and because seedling colonists came almost exclusively from the local seed rain rather than from a persistent seed bank (Bullock et al. 1994a). Within these constraints however, colonizing species did show significant differences in frequency between the border and the gap. The best colonizers were those species invading by seed (Table 2) and these seedlings ultimately comprised the majority of ramets (59%) that colonized gaps. Among the best colonizers was the annual grass *Bromus mollis* but the perennials *Hordeum secalinum* and *Cynosurus cristatus* had similar colonization abilities and also relied on seeds (Table 2). The notable exception to the relationship between colonizing ability and seedling recruitment was *Agrostis stolonifera* which colonized much more frequently than other species with low seedling recruitment. *A. stolonifera* may be contrasted with *Lolium perenne* which had virtually the same colonization index but much higher seedling recruitment (Table 2). In a comparative study of the tiller dynamics of these two species at Little Wittenham we found that *A. stolonifera* was more stoloniferous, had faster tiller turnover, responded more rapidly to weather and to local changes in density and had much lower flower and seed production than *L. perenne* (Bullock et al. 1994b). Despite these differences these two species had similar colonizing abilities.

Gap size, summer grazing treatment and spring grazing treatment all significantly affected the species composition of colonized gaps (Table 3). Where gap size or grazing treatment affected the total ramet frequency of a species this was generally due to treatment effects on only one mode of colonization. For the four species with the highest proportion of seed-derived ramets in their colonizing ramets (*Bromus mollis, Cynosurus cristatus, Hordeum secalinum, Lolium perenne*) only colonization by seedlings was affected by treatments (Table 4) and for the four species with the lowest seed-derived proportions (*Agrostis stolonifera, Dactylis glomerata, Festuca rubra, Phleum pratense*) only clonal colonization was affected (Table 5). *Alopecurus pratensis* was intermediate in the proportion of seed-derived ramets and both seed-derived and clonal ramet colonizing frequencies were affected by treatments (Tables 4 and 5). Although species divided reasonably clearly into 'seed-colonizers' and 'clonal-colonizers' there was no uniformity in the *direction* in which treatments influenced species within each group. For example larger gaps and lighter grazing both significantly increased frequencies of seed-derived ramets in *Hordeum*,

secalinum while the same treatments significantly reduced the frequencies of seed-derived ramets in *Lolium perenne* (Table 4).

Clonal species may differ in the rate of ramet production, internode lengths and the branching angle of internodes (Bell and Tomlinson 1980). There is also evidence that clonal plants can show plasticity in response to increased resource levels, such as gaps (Sutherland and Stillman 1988) and that species may differ in this 'foraging' ability (de Kroon and Knops 1990). *Agrostis stolonifera* and the commonest of our dicots, *Trifolium repens*, are both stoloniferous and so it may be significant that *A. stolonifera* and the dicots were the only taxa to have higher clonal frequencies in the larger gaps (Table 5). This suggests that, whereas the clonal spread of most species into the larger gaps was constrained by their short internodes, these stoloniferous species could reach and colonize the centres of the large gaps. The stoloniferous habit of *Agrostis* also explains its high colonization ability in relation to its very low proportion of seed-derived ramets.

The differing gap colonization abilities of the different species indicate that changing the density and size of gaps in the sward should change its species composition. Silvertown and Smith (1988b) found that winter grazing and harder summer grazing both increased gap densities at Little Wittenham and the present results suggest how these grazing treatments should alter the vegetation, although so far the changes we have monitored have been slow and small (Bullock et al. 1994a). Of the four commonest species, *Lolium perenne* and *Agrostis stolonifera* should be decreased but *Hordeum secalinum* and *Poa* spp. should be increased by increased gap densities (Table 2). Of the rarer species, only two, *Bromus mollis* and *Cynosurus cristatus*, should increase with gap density (Table 2). Grazing creates a range of gap sizes (Silvertown and Smith 1988b) and this experiment showed that, because species colonization abilities are differentially affected by gap size (Table 3), any attempt to predict how changing grazing management will alter vegetation composition must consider the distribution of gap sizes created.

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References

Bell, A. D. and Tomlinson, P. B. 1980. Adaptive architecture in rhizomatous plants. – Bot. J. Linn. Soc. 80: 125–160.

Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure in tropical forests. – In: Pickett, S. T. A. and White, P. S. (eds), Natural disturbance: the patch dynamics perspective. Academic Press, Orlando, FL, pp. 53–69.

Bullock, J. M., Clear Hill, B., Dale, M. P. and Silvertown, J. 1994a. An experimental study of vegetation change due to grazing in a species-poor grassland and the role of seedling recruitment into gaps. – J. Appl. Ecol. 31: 493–507.

– , Clear Hill, B. and Silvertown, J. 1994b. Comparative tiller dynamics and community change: two grasses in a grazing experiment. – J. Ecol. 82: 331–340.

Clapham, A. R., Tutin, T. G. and Moore, D. M. 1987. Flora of the British Isles, 3rd edn. – Cambridge Univ. Press, Cambridge.

Davis, R. M. and Cantlon, J. E. 1969. Effect of size of area open to colonization on species composition in early old-field succession. – Bull. Torrey Bot. Club 96: 660–673.

de Hullu, E. and Gimingham, C. H. 1984. Germination and establishment of seedlings in different phases of the *Calluna* life cycle in a Scottish heathland. – Vegetatio 58: 115–121.

de Kroon, H. and Knops, J. 1990. Habitat exploration through morphological plasticity in two chalk grassland perennials. – Oikos 59: 39–49.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. – Annu. Rev. Ecol. Syst. 18: 431–451.

Goldberg, D. E. 1987. Seedling colonization of experimental gaps in two old field communities. – Bull. Torrey Bot. Club 114: 139–148.

– and Gross, K. L. 1988. Disturbance regimes of midsuccessional old fields. – Ecology 69: 1677–1688.

Hillier, S. H. 1990. Gaps, seed banks and plant species diversity in calcareous grasslands. – In: Hillier, S. H., Walton, D. W. H. and Wells, D. A. (eds), Calcareous grasslands – ecology and management. Bluntisham Books, Huntingdon, pp. 57–67.

Hobbs, R. J. and Mooney, H. A. 1991. Effects of rainfall and gopher disturbance on serpentine annual grassland dynamics. – Ecology 72: 59–68.

Kay, A. M. and Keough, M. J. 1981. Occupation of patches in the epifaunal communities on pier pilings and the bivalve *Pinna bicolor* at Edithburgh, South Australia. – Oecologia 48: 123–130.

Keough, M. J. 1984. Effects of patch size on the abundance of sessile marine invertebrates. – Ecology 65: 423–437.

Martinsen, G. D., Cushman, J. H. and Whitman, T. G. 1990. Impact of pocket gopher disturbance on plant species diversity in a shortgrass prairie community. – Oecologia 83: 132–138.

O'Connor, T. G. 1991. Patch colonization in a savanna grassland. – J. Veg. Sci. 2: 245–254.

Peart, D. R. 1989. Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds and grazing on colonization. – J. Ecol. 77: 267–289.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall grass prairie. – Ecol. Monogr. 45: 285–305.

– and Weiss, I. M. 1977. Resource partitioning and competition within a guild of fugitive prairie plants. – Am. Nat. 111: 479–513.

Rabinowitz, D. and Rapp, J. K. 1985. Colonization and establishment of Missouri prairie plants on artificial soil disturbances. II. Detecting small-scale plant-to-plant interactions and separating disturbance from resource provision. – Am. J. Bot. 72: 1629–1634.

Rapp, J. K. and Rabinowitz, D. 1985. Colonization and establishment of Missouri prairie plants on artificial soil disturbances. I. Dynamics of forb and graminoid seedlings and shoots. – Am. J. Bot. 72: 1618–1628.

Rodwell, J. S. (ed.) 1992. British plant communities, volume 3. Grasslands and montane communities. – Cambridge Univ. Press, Cambridge.

Rusch, G. 1988. Reproductive regeneration in grazed and ungrazed limestone grassland communities on Öland. Preliminary results. – Acta Phytogeogr. Suec. 76: 113–123.

Ryser, P. 1993. Influences of neighbouring plants on seedling

establishment in limestone grassland. – J. Veg. Sci. 4: 195–202.
Silvertown, J. 1981. Micro-spatial heterogeneity and seedling demography in species rich grassland. – New Phytol. 88: 117–125.
– and Wilkin, F. R. 1983. An experimental test of the role of micro-spatial heterogeneity in the co-existence of congeneric plants. – Biol. J. Linn. Soc. 19: 1–8.
– and Smith, B. A. 1988a. Gaps in the canopy: the missing dimension in vegetation dynamics. – Vegetatio 77: 56–60.
– and Smith, B. A. 1988b. Mapping the microenvironment for seed germination in the field. – Ann. Bot. 63: 163–167.
Sutherland, W. J. and Stillman, R. A. 1988. The foraging tactics of plants. – Oikos 52: 239–244.
Treweek, J. R. 1990. The ecology of sheep grazing: Its use in nature conservation management of lowland neutral grassland. – D. Phil. Oxon.