



## - CHAPTER 6 -

### OCCLUSION OF ARTIFICIAL GAPS WITH RESPECT TO SWARD DIVERSIFICATION

There are two schools of thought [in grassland management], the one considering that, as 'nature never cheated', the best species would be found under natural conditions; and the other taking the directly opposite view, as expressed by Carruthers in 1890, that the best plants from the farmer's point of view were those which gave least attention to their own life cycle, thereby being able to produce a greater amount of nutritive matter for the animal. He thus argued that the successful farmer was he who was able to fight nature most satisfactorily.

**Jones M. G.** (1933) Grassland management and its influence on the sward: I. factors influencing the growth of pasture plants. *Empire Journal of Experimental Agriculture* **1**: 43-57.

#### SUMMARY

1. Gap creation and gradual vegetation in-fill may be an important conservation management tool in maintaining species diversity where livestock grazing is inappropriate, unavailable or unreliable. The process of gap recolonisation may be manipulated to increase indigenous diversity in depauperated grasslands. This Chapter is an investigation into the colonisation of a range of artificial gap treatments created in the suite of agriculturally improved swards described elsewhere in the thesis.

2. The present study was accommodated within the experimental design used for implant inoculation described in **Chapter 7**. Principally there were two treatments, 15-cm diameter (177-cm<sup>2</sup>) gaps, and 30-cm diameter (707-cm<sup>2</sup>) gaps, ten of each type randomly allocated across each subplot. The gaps were created using the non-selective herbicide. Six randomly allocated gaps 3 x 15-cm diameter and 3 x 30-cm diameter in each subplot were dug to a depth of 15-cm and back-filled with compost. This allowed the analysis of gap occlusion from two different processes: seed rain input and seed bank (no sterile soil in-fill); and seed rain without the inclusion of propagules from the seed bank (sterile soil in-fill). In all, 240 gaps were created in the 12 subplots, amounting to 120 x 15-cm diameter gaps, and 120 x 30-cm diameter gaps. Of these, 36 x 30-cm and 36 x 15-cm gaps were in-filled with compost. Gap occlusion censuses to record % bare ground and vegetation cover were carried out in June and October 1997, and March 1998

3. Only 28% species occupying gaps were graminoids as opposed to 72% forb species. However, in terms of abundance the 28% of grass species accounted for 48% of infill abundance. *Poa* spp. were the most frequent components of gap infill, followed by *Geranium dissectum*, *Trifolium repens*, *Lolium perenne*, and *Agrostis stolonifera*. Mosses were also more abundant in the gaps.

4. By the end of the study, there was significantly less bare ground in the more improved Plots 1 and 2 compared to the other two plots, and significantly less bare ground remaining even between Plot 3 and Plot 4. Thus the rank order of occlusion rate Plot1>Plot2>Plot3>Plot4, essentially following the improvement gradient. There were no significant differences between the average bare ground remaining in March 1998 between the two (totalised) gap sizes i.e. the levels were statistically even though the gap areas were markedly different. The compost (non-seed bank) gaps occluded at similar rates to that of non-compost gaps (seed bank & seed rain). Soil phosphorus, soil potassium, peak phytomass and sward height were significantly negatively correlated with percentage bare ground. However, size of soil seed bank was the most significant explanatory variable in gap occlusion.

5. The dominant components in gap occlusion seem to be grasses and *Trifolium repens*, species with particularly flexible regeneration strategies. Also, gap infill was comprised of greater cover of annuals and bryophytes (mosses). Therefore, gap vegetation does seem to form a discrete type in comparison to the surrounding field-layer. In addition, gap vegetation demonstrated a surprising uniformity throughout the grassland plots.

6. Because artificial gaps, even relatively large ones, seem to be re-filled chiefly by dominant field-layer species, significant gains in overall diversity are probably minimal. Under productive conditions, artificial gaps seem to have limited positive influence due to their transitory nature. To have significant restoration value, the created gaps may have to be larger than 30-cm in diameter, though such extensive gap creation would then begin to compromise the integrity of the extant sward.

**Keywords:** artificial gap, creation, occlusion, regeneration, agriculturally improved, soil seed rain, seed bank, bare ground, infill, field-layer, gap vegetation.

#### INTRODUCTION

**M**any researchers have shown that gaps are an important dynamic in the change in relative abundance of component species within vegetation (Grubb 1977; Fenner

1978; Fenner 1985; Goldberg & Werner 1983; Hutchings 1983; Waite 1984; Rabinowitz & Rapp 1985; Silvertown & Smith 1988; Thórhallsdóttir 1990; Wu & Levin 1994; Morgan 1997; Ehrlén & van Groenendael 1998). Pertinent to the present research is the role gaps play in grassland ecology, and more particularly, grassland diversity (Grubb 1977; Gibson *et al* 1987; Mahdi & Law 1987; Coffin & Launenroth 1988; Smith & Rushton 1994; Bullock *et al* 1994, 1995; Burke & Grime 1996; Edwards & Crawley 1999). As gaps arise in grassland vegetation they are recolonised both vegetatively and/or by the establishment of new plants from the soil seed bank or seed rain (Rabinowitz & Rapp 1985; Arnthórsdóttir 1994; Bullock *et al* 1995; Rusch & Fernández-Palacios 1995; McLellan *et al* 1997). The process of gap creation and gradual vegetation in-fill is considered by a number of researchers to be an important conservation management tool in maintaining species diversity (Grubb 1977; Hillier 1990; Mitchley 1994; Gilbert & Anderson 1998; Losvik 1999). Gaps in vegetation can be created by *natural* means through livestock grazing and trampling, animal digging, ramet death, as well as through climatic disturbances such as drought or flooding (Gibson *et al* 1987; Parish & Turkington 1990a; 1990b; Smith & Rushton 1994; Edwards & Crawley 1999). However, where livestock grazing is inappropriate, unavailable or unreliable, creation of regeneration gaps by artificial means may be a technique for aiding diversity. Thus, the process of gap recolonisation may be manipulated to increase indigenous diversity in depauperated grasslands, such as swards which have been left derelict (Crofts 1999), or impoverished by agricultural improvement (Tallowin *et al* 1995; Pywell *et al* 1997; Davies *et al* 1999). Hillier (1990), for instance, suggests that artificial gap creation is a technique that can be usefully employed in the management of calcareous grassland to encourage plant species diversity. Artificial gap creation may also enhance the inoculation of depauperate grasslands with diaspores and implants (Bisgrove 1988; Bisgrove & Dixie 1994; Boyce 1994; Morgan 1997; Davies *et al* 1999). Hopkins *et al* (1999) showed that turf removal before sowing was the only treatment that significantly reduced herbage production, and had the greatest effect on increasing botanical diversity (a mean of 28 species per site compared to 15 for the control 2 years after sowing).

This paper is an investigation into the colonisation of a range of artificial gap treatments created in the suite of agriculturally improved swards described elsewhere in the thesis (principally **Chapters 2 & 3**). The process of artificial gap recolonisation is important both

with respect to the efficacy of the creation of competition-free zones to increase implant establishment success (Wells *et al* 1989; Davies *et al* 1999), but also the diversification potential of the gap itself (Hillier 1990).

## METHODS

The present study was accommodated within the experimental design used for implant inoculation described in **Chapter 7** (Davies *et al* 1999). After three years of surveillance of each individual implant throughout the four plots (12 subplots), approximately 80% were assessed as ‘deceased’. Thus approximately 2,900 implantation positions were possibly vacant for other uses. Consequently, the artificial gaps were created in grid positions where individual implants had been identified as missing, and presumed dead, for two growing seasons. Because of the limited experimental space, and the imperative to evaluate the dynamics of artificial vegetation gap closure in a systematic way, these vacant gaps were deemed acceptable for utilisation for the present research. Overall, this design strategy also provided the structure for easily relocating and monitoring created gaps as evinced by the efficacy of the **Chapter 7** experimental set-up.

The vacant grid points were identified and pooled for each subplot in March 1997. Principally there were two treatments, 15-cm diameter (177-cm<sup>2</sup>) gaps, and 30-cm diameter (707-cm<sup>2</sup>) gaps, ten of each type randomly allocated across each subplot. These gap sizes are larger than the 10-cm herbicide band width commonly applied using slot-seeding machinery (Wells *et al* 1989; Luscombe & Scott 1994). The gaps were created, as for the transplant and sowing positions, using the non-selective herbicide glyphosate (Arnthórsdóttir 1994; McLellan *et al* 1997), and 30-cm and 15-cm diameter stencils. Thus, a total of twenty gaps were created in each subplot in mid March 1997 (Arnthórsdóttir 1994). The herbicide treated vegetation had died by early April, and the remains of the vegetation began to decompose down to mineral soil by late May. Six randomly allocated gaps 3 x 15-cm diameter and 3 x 30-cm diameter in each subplot were dug to a depth of 15-cm and back-filled with John Innes No. 3 loam based compost. This allowed the analysis of gap occlusion from two different processes: seed rain input and seed bank (no sterile soil in-fill); and seed rain without the inclusion of propagules from the seed bank (sterile soil in-fill) (Bullock *et al.* 1994). Thus, in all, 240 gaps were created in the 12

subplots, amounting to 120 x 15-cm diameter gaps, and 120 x 30-cm diameter gaps. Of these, 36 x 30-cm and 36 x 15-cm gaps were in-filled with compost.

In order to make rapid assessments of species frequency, relative abundance, and total extent of vegetation in-fill compared to bare ground, circular grid ‘quadrats’ were used stratified into a grid of square recording points (Chalmers & Parker 1989). These survey frames were created out of the same plastic stencils as the herbicide treatment stencils, with wire grids composed of 14-mm squares (487 squares for the 30-cm quadrat, and 113 squares for the 15-cm quadrat). Because the quadrats were circular and the grids square, only complete squares were counted for effective equilibration. In the centre of each quadrat a steel pin was fixed in order to provide a stand. In order to accurately relocate the monitoring position, an 8-cm section of 20-mm diameter rigid blue plastic piping was knocked-in to ground level in the centre of each gap. This provided a socket for placing the quadrat and also a means of accurately relocating the centre of the gap for repeated surveys. In order to quantify relative abundance, the quadrat was placed in the socket and the numbers of squares occupied by each species were counted. The percentage cover was then calculated by dividing the number of occupied and unoccupied squares by the total number of squares in the quadrat grid. Bryophyte species were not differentiated to species but recorded generically as “moss”. The extent of bare ground was calculated in the same way as for the vegetation. The experiment was effectively conducted from March 1997 to March 1998, with gap occlusion surveys carried out in June 1997, October 1997, and March 1998. The June 1997 census records differentiated between seedling and vegetative regeneration. However, for the purposes of the present chapter, particularly in order to limit the amount of data analysis bulk, only the results from the final census conducted in March 1998 will be presented. This data does not distinguish between gap regeneration strategies, other than that inferred by comparative ecological accounts (Grime *et al* 1988). Abundances are based on percentage species cover.

#### **Data analysis**

Data were analysed at both subplot and plot scales. For some forms of analysis both data scales were used, while for others it was deemed that a single scale illustrated the information in the most coherent way. The degrees of gap occlusion were principally

quantified by calculating the percentage of quadrat squares occupied respectively by bare ground and plant regeneration. Pie charts were used as the principal technique for describing the experimental results, along with error bar graphs (Norušis 1998). In order to strictly apply statistical tests, the abundance percentages were arcsine transformed before analysis (Fowler *et al* 1998). One-way Analysis of Variance tests were applied to the data to assess whether sample means of the main gap occluding dependent variables (bare ground, graminoids, forb and moss percentage abundances) were significantly different for each of the main artificial gap treatment types among the four plots (Green *et al* 1997). A number of different approaches were taken to more closely compare significant characteristics of the occluding vegetation. The Shannon index ( $H'$ ) and species-richness ( $s$ ) were used to broadly compare the vegetation diversities across the subplot sequence (Magurran 1988). Detrended Correspondence Analysis ordination and UPGMA percentage similarity cluster analysis were applied to the data to assess the similarities between the compositions of the occluding vegetation for both subplot and plot scales (Kent & Coker 1992). Least-squares linear regression, in combination with the Pearson correlation coefficient ( $r$ ) (two-tailed) were used to examine the relationships between the respective gap occlusion results and key environmental variables (Norušis 1998). Stepwise multiple linear regression was conducted in order to directly compare the predictive validity of all the key environmental variables on gap infill rates i.e. percentage bare ground (Green *et al* 1997). All statistical analyses were conducted using SPSS ver 9.0 (SPSS 1998) and MVSP ver 3.0 (Kovach 1998).

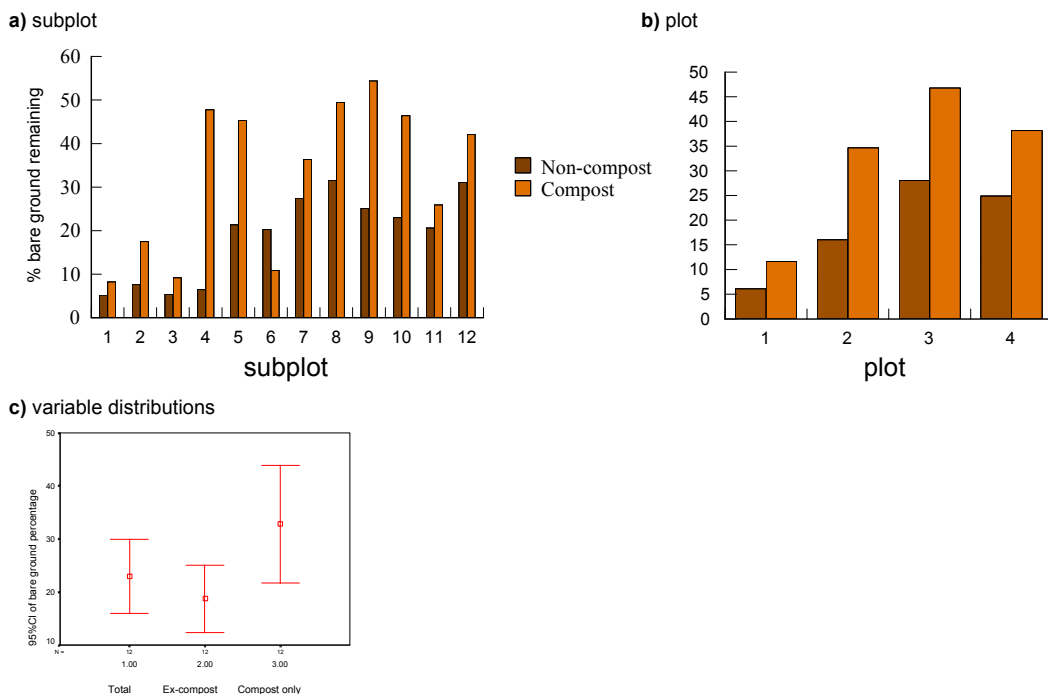
## RESULTS

### Components of gap occlusion: totals

The main component of this research was the comparison of levels of gap occlusion between gap treatments and the subplot/plot gradient. The charts of **Figure 6.01** compare the total percentage cover of bare ground remaining in compost and non-compost gaps after one year in the final census conducted in March 1998. The results of one-way ANOVA (Norušis 1998) indicate that there is a significant occlusion differential between the main treatment types: non-compost (seed bank & seed rain); and compost (seed rain only) ( $F_{1,22} = 5.863$ ;  $P = 0.024$ ). This suggests that the seed bank is a significant source of recruitment for gap regeneration, as removal results in a slower rate of infill. However,

there are certain caveats associated with the compost (seed rain only) treatment, which will be addressed in the discussion.

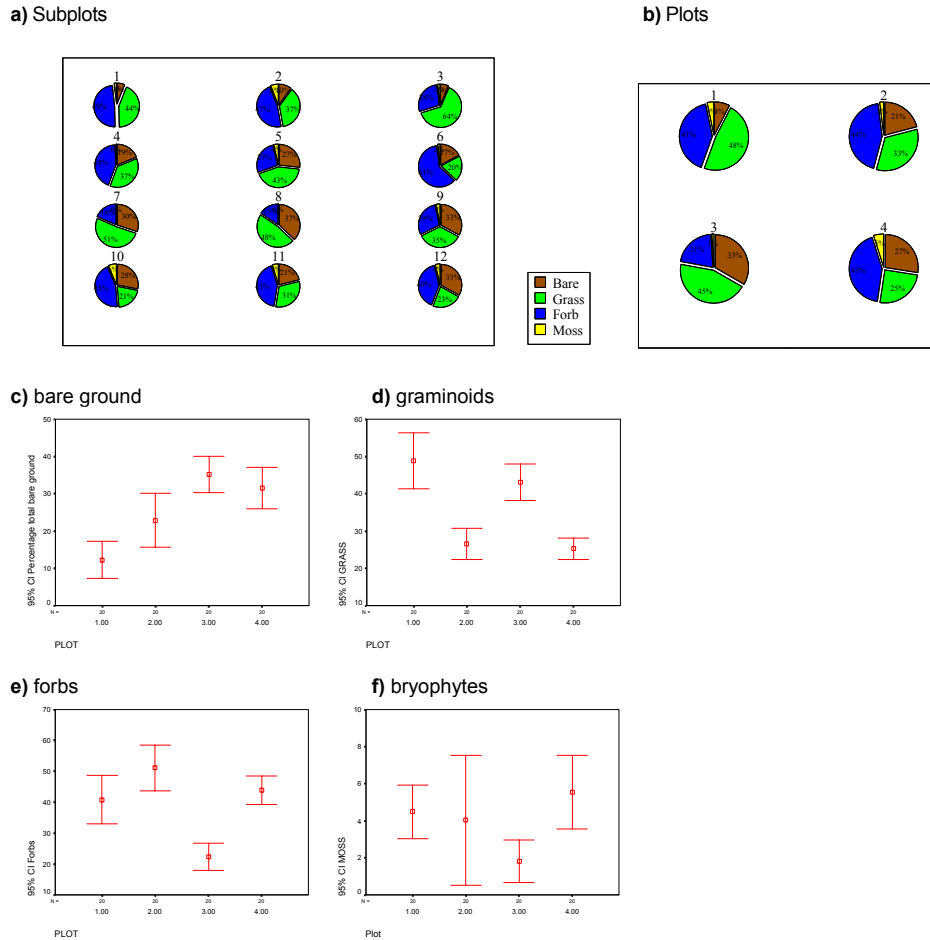
**Figure 6.01** Percentages of *total* non-compost gap bare ground compared to *total* compost gap bare ground.



**Figure 6.02** shows the proportion of total bare ground, as well as the totals for the three main functional plant categories: grasses; forbs; and bryophytes (Joshi *et al* 2000). When analysed by one-way ANOVA on a plot basis for percentage bare ground, there is a highly significant difference between plots ( $F_{3,76} = 13.716$ ;  $P = 0.000$ ), particularly between (discriminated by Tukey HSD) Plots 1 & 2/3/4, and Plots 2 & 3. This strongly indicates that gap occlusion was most consistently rapid in the swards of Plot 1. Comparison of total grass percentage cover between plots shows a highly significant difference between means ( $F_{3,76} = 23.474$ ;  $P = 0.000$ ), with significant comparisons between Plots 1 & 2/4, Plots 2 & 3, and Plots 3 & 4. Plots 1 and 3 therefore have a statistically greater proportion of grass infill. Forb percentage cover also demonstrates a very significant difference across the Plots ( $F_{3,76} = 16.669$ ;  $P = 0.000$ ), with Tukey HSD showing significant differences between Plots 1 & 3, Plots 2 & 3, and Plots 3 & 4. However, when the relative abundances of the graminoid and forb categories were compared within plot, only Plot 1 had a significant (negative) correlation ( $r = -0.891$ ;  $P = 0.000$ ) indicating that in the other plots, neither grass nor forbs seem to be obviously usurping the colonisable space at the expense of the other. There was no significant

difference of bryophyte percentage cover between plots ( $F_{3,76} = 2.177$ ;  $P = 0.098$ ) at the end of the experiment.

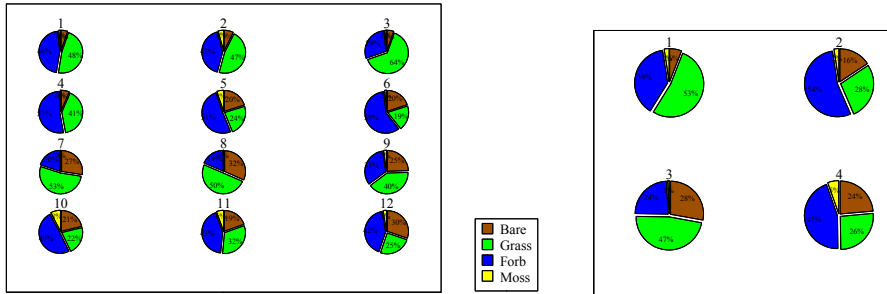
**Figure 6.02** Totals – charts showing features of combined treatment data (averages across substrate and gap size treatment) at end of the experiment March 1998, with divisions showing percentage cover for bare ground, grass, forbs and bryophytes (moss). Graphs c-e are error-bar summaries showing distribution of variables.



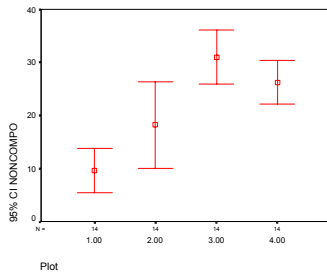
The results from the primary gap treatments i.e. non-compost and compost, are presented in **Figures 6.03** and **6.04**. **Figure 6.03** shows the different proportions of functional plant types for all non-compost gaps. Analysis by one-way ANOVA indicates that there was a significant difference in remaining bare ground between the plots ( $F_{3,52} = 13.091$ ;  $P = 0.000$ ). Post hoc analysis by Tukey HSD shows that the essential differences were between Plots 1 & 3/4, and Plots 2 & 3).

**Figure 6.03** Relative proportions of gap occluding parameters for functional plant types (+ bare ground) for all non-compost gaps only.

**a) Subplots** **b) Plots**



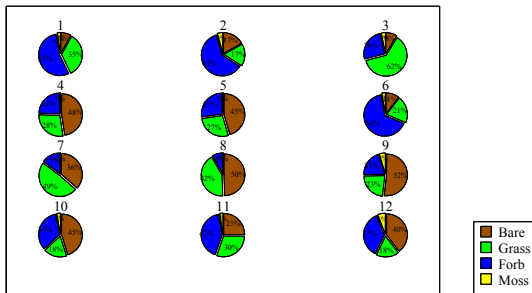
c) variable distributions



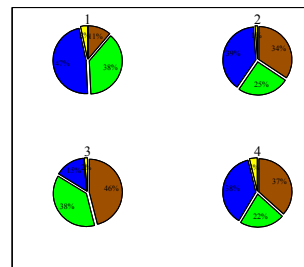
Similarly, **Figure 6.04** illustrates the relative proportions of gap occluding parameters, though for compost-only gap treatments. One-way ANOVA analysis comparing the colonisation of the four plots in terms of the compost gaps, shows that there was a significant difference between plots ( $F_{3,20} = 8.256; P = 0.001$ ). Post hoc analysis with Tukey HSD indicates that the significant differentials are between Plots 1 & 3/4, and Plots 2 & 3/4. Thus, Plots 2 and 3 seem to have significantly faster occlusion than Plots 3 and 4 in compost gaps.

**Figure 6.04** Relative proportions of gap occluding parameters for functional plant types (+ bare ground) for all compost gaps only.

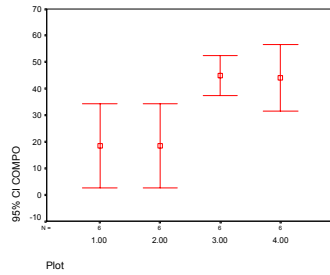
a) Subplot



c) Plot



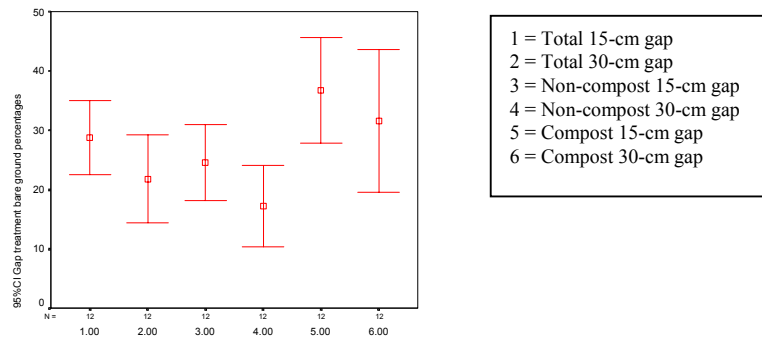
c) variable distributions



### Gap size and occlusion speed

The second tier of this area of research was to evaluate the effect artificial gap size has on occlusion and gap composition. There were no significant differences between the average bare ground remaining in March 1998 between the two (totalised) gap sizes ( $t_{22} = 1.603$ ;  $P = 0.123$ ) i.e. the levels were statistically even though the gap areas were markedly different. However, the results of one-way ANOVA suggest that there were significant differences between mean bare ground remaining between gap treatments ( $F_{5,66} = 3.533$ ;  $P = 0.007$ ), and specifically between 30-cm non-compost and 15-cm compost only gap types (**Figure 6.05**). In comparison with remaining bare ground, analysis of the proportions of vegetational gap infill across treatment types indicates that there were no significant differences in proportions of grass and forb species colonising the gap treatment types ( $F_{3,47} = 1.063$ ,  $P = 0.374$ ).

**Figure 6.05** Summary of occlusion levels - mean bare ground percentages for totals and discrete treatments including 95% confidence limits.

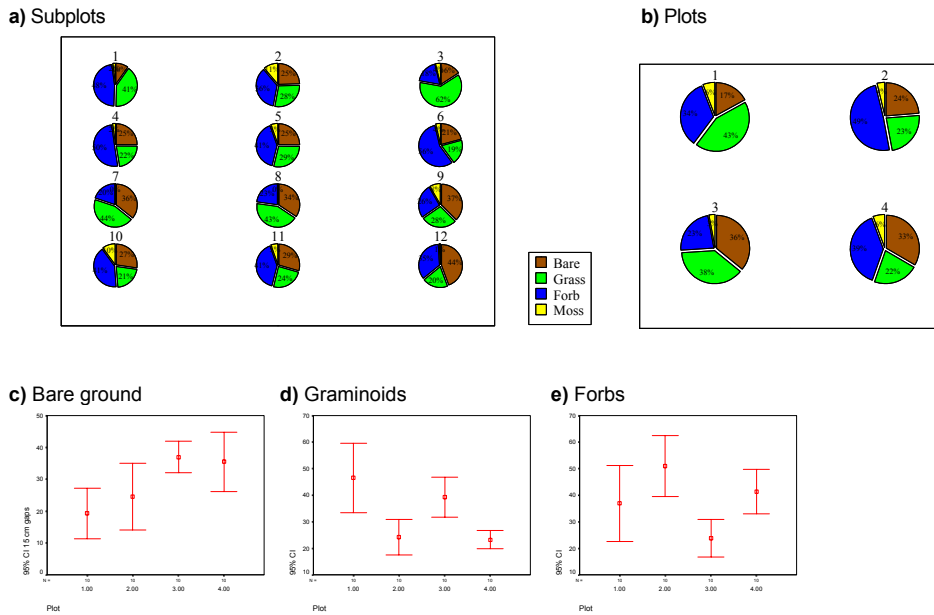


- 1 = Total 15-cm gap
- 2 = Total 30-cm gap
- 3 = Non-compost 15-cm gap
- 4 = Non-compost 30-cm gap
- 5 = Compost 15-cm gap
- 6 = Compost 30-cm gap

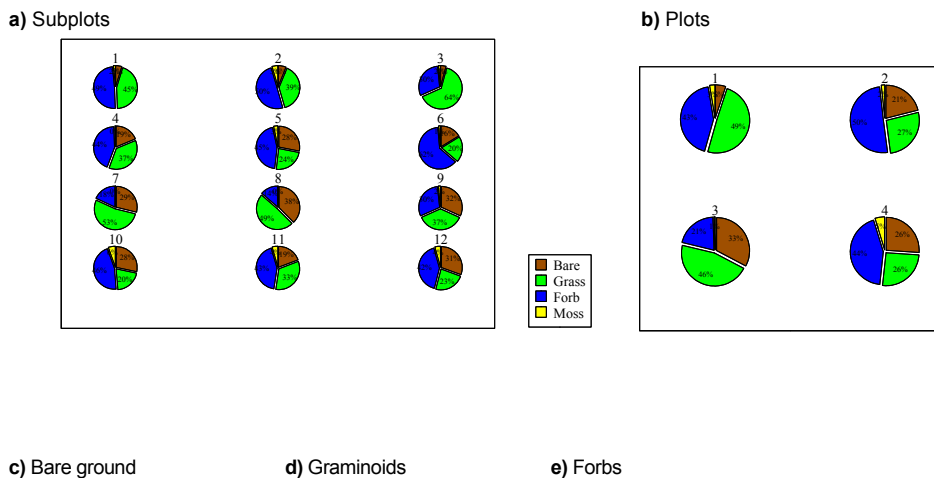
**Figure 6.06** illustrates the occlusion parameters for the total data for all 15-cm gaps. In comparison, **Figure 6.07** shows the final census results for total 30-cm gaps. One-way ANOVA results indicate a significant difference of bare ground availability after one year of vegetation regeneration for all 15-cm gaps between plots ( $F_{3,36} = 5.304$ ;  $P = 0.004$ ). Tukey HSD shows that the significant differences were between Plot 1 and Plots 3/4, whereby the occlusion speed for Plot 1 was highest. For graminoids in 15-cm gaps, significant relations are between 1 and 2/4, 2 and 3, 3 and 4 ( $F_{3,36} = 9.471$ ;  $P = 0.000$ : using

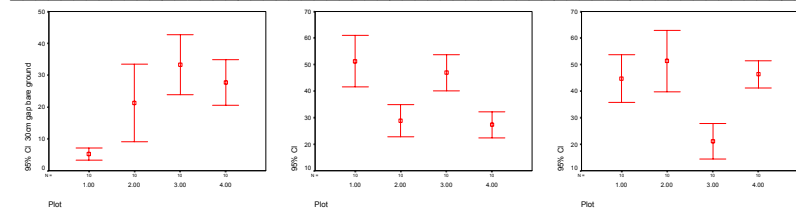
Tukey HSD), indicating that Plots 1 and 3 had proportionately much greater grass infill than Plots 2 and 4. For forb species there is also a significant difference between Plots 2 and 3 ( $F_{3,36} = 5.663$ ;  $P=0.003$ ; using Tukey HSD). The same pattern, though even more statistically significant, was shown for total 30-cm gaps ( $F_{3,36} = 10.289$ ;  $P = 0.000$ ) indicating significant differences between Plot 1 and plots 2/3. For graminoids and 30-cm gaps, the significant relationships ( $F_{3,36} = 15.492$ ;  $P = 0.000$ : Tukey HSD) were between Plots 1 & 2/4, Plot 2 & 3, and Plot 3 & 4, and for forbs ( $F_{3,36} = 13.021$ ;  $P=0.000$ ) Plot 1 & 3, Plot 2 & 3, and Plot 3 & 4

**Figure 6.06** Occlusion levels for all 15-cm gaps combined. Charts a) and b) show percentages of infill parameters; c)-e) show data distributions of the key infill parameters.



**Figure 6.07** Occlusion levels for all 30-cm gaps combined. Charts a) and b) show percentages of infill parameters; c)-e) show data distributions of the key infill parameters.

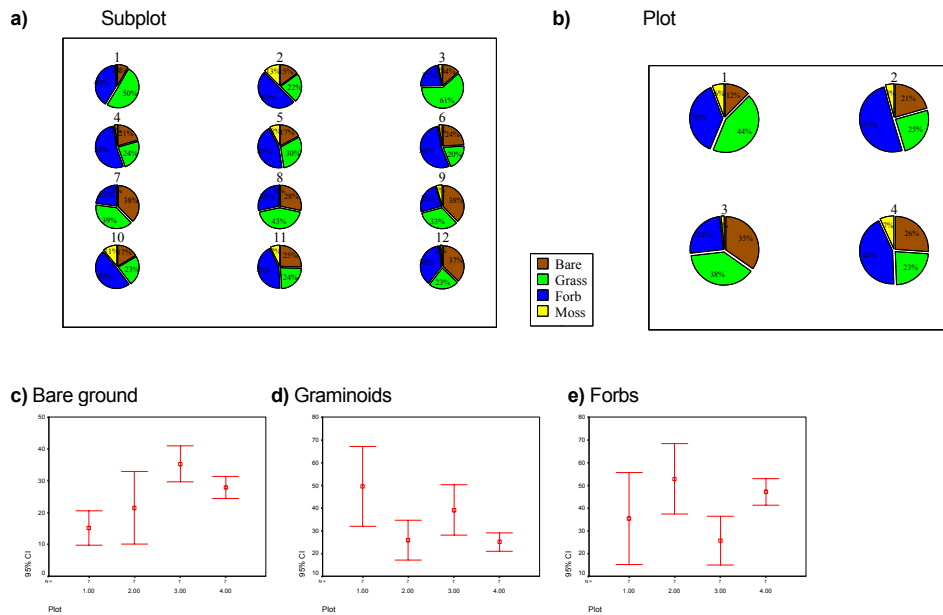




*Non-compost gaps only*

In order to evaluate the effects of the treatment types in more detail, analysis was applied separately to compost and non-compost gaps. **Figure 6.08** summarizes the results for 15-cm non-compost gaps. One-way ANOVA clearly demonstrates that there were significant differences between the remaining bare ground in March 1998 between Plots ( $F_{3,24} = 8.713$ ;  $P = 0.000$ ). Plot 1 again stands out as having gaps with the highest infill, and also the highest percentage of graminoid revegetation ( $F_{3,24} = 6.229$ ;  $P = 0.003$ ; using Tukey HSD, Plots1 & 2/4). However for forb infill percentages, the only significant difference was between Plot 2 & 3 ( $F_{3,24} = 4.377$ ;  $P = 0.014$ ; Tukey HSD).

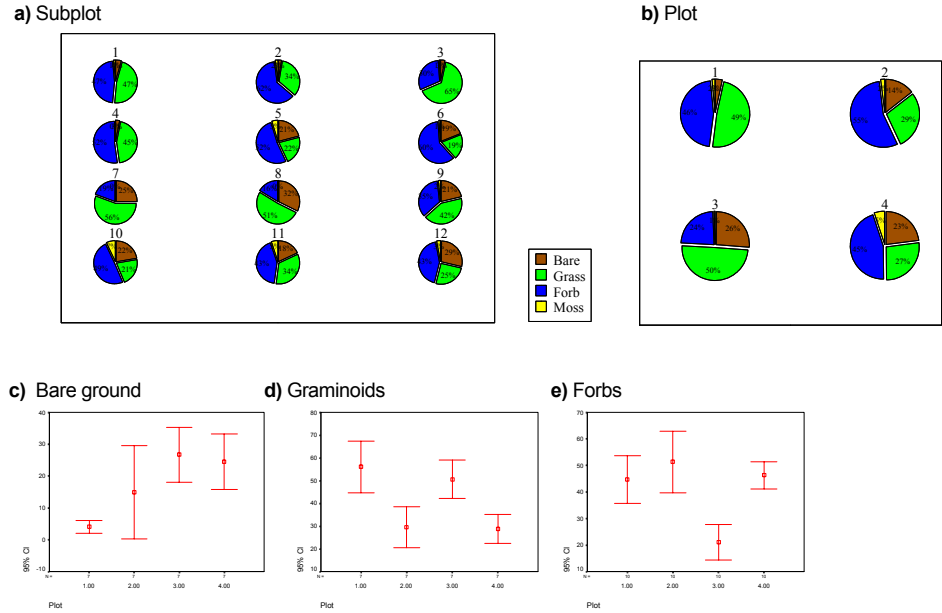
**Figure 6.08.** Occlusion levels for all 15-cm non-compost gaps. Charts **a)** and **b)** show percentages of infill parameters; **c)-e)** show data distributions of the key infill parameters.



For 30-cm non-compost gaps (**Figure 6.09**) the same relationships between plots for remaining bare ground are also apparent ( $F_{3,24} = 6.966$ ;  $P = 0.002$ ). However there were even stronger differentials between plots as far as proportional graminoid infill ( $F_{3,24} = 14.954$ ;  $P = 0.000$ ), with significant multiple comparisons for Plots 1 & 2/4, 2 & 3, 3 & 4.

As far as forb species, there are also significant relationships between Plot 1 & 3, Plot 2 & 3, and Plot 3 & 4 ( $F_{3,24} = 10.984$ ;  $P = 0.000$ ; Tukey HSD).

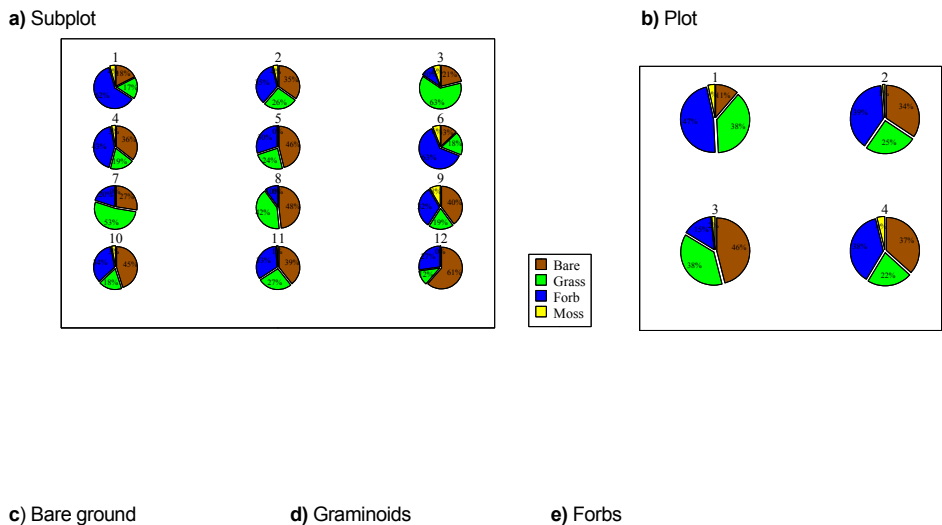
**Figure 6.09** Occlusion levels for all 30-cm non-compost gaps. Charts **a)** and **b)** show percentages of infill parameters; **c)-e)** show data distributions of the key infill parameters.

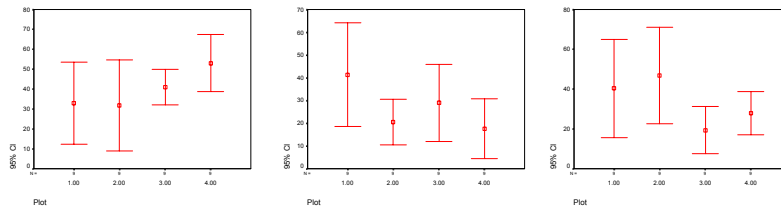


*Gaps: compost only*

**Figure 6.10** shows the proportions of the occlusion parameters for 15-cm compost gaps. The results are non-significant, not only between plots for bare ground ( $F_{3,32} = 1.665$ ;  $P = 0.194$ ), but for graminoids ( $F_{3,32} = 2.235$ ;  $P = 0.103$ ), and also forbs ( $F_{3,32} = 2.207$ ;  $P = 0.106$ ).

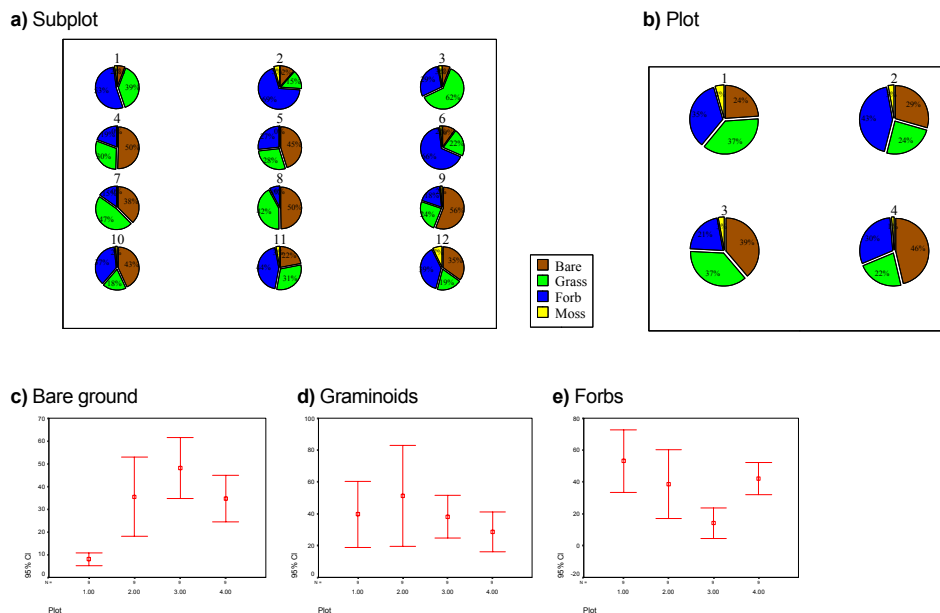
**Figure 6.10** Occlusion levels for all 15-cm compost gaps. Charts **a)** and **b)** show percentages of infill parameters; **c)-e)** show data distributions of the key infill parameters.





In comparison, there were significant relationships for 30-cm compost gaps for bare ground across plots ( $F_{3,32} = 10.127$ ;  $P = 0.000$ ) with significant multiple comparisons between Plots 1 & 2/3/4, and differences between plots for forb proportionate infill ( $F_{3,32} = 5.487$ ;  $P = 0.004$ ; Tukey HSD Plots 1 & 3, 3 & 4). The differentials between graminoids proportions, were, however, non-significant ( $F_{3,32} = 1.017$ ;  $P = 0.398$ ).

**Figure 6.11** Occlusion levels for all 30-cm compost gaps. Charts a) and b) show percentages of infill parameters; c)-e) show data distributions of the key infill parameters.



### Characteristics of colonising vegetation

When species are collated into functional groups (graminoids; non-legumes; legumes; bryophytes), there are no significant differences in abundances between the four plots ( $F_{3,12} = 0.933$ ;  $P = 0.573$ ). **Table 6.01** presents summary data for all species recorded in the form of frequency-abundance in the final census (March 1998). The total ranking for combined vascular plant plot data shows that only 28% species occupying gaps were graminoids as opposed to 72% forb species. However, on the basis of percentage frequency the 28% of grass species accounted for 48% of infill abundance, and forbs 52%. *Poa* spp. (mainly *Poa trivialis*) were the most widespread components of gap infill, followed by *Geranium*

*dissectum*, *Trifolium repens*, *Lolium perenne*, and *Agrostis stolonifera*. Interestingly, these species seem to be broadly different in their regeneration strategies, and this aspect will be further looked at in the discussion.

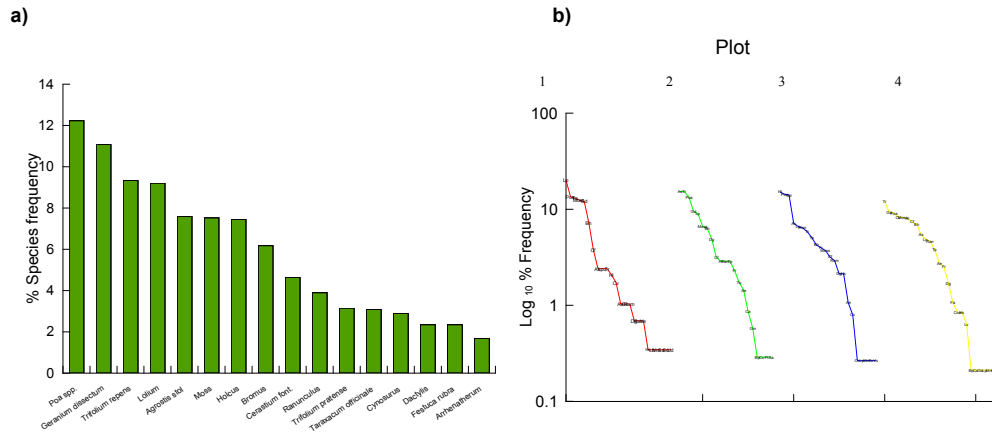
**Table 6.01** Percentage frequencies of species regenerating in artificial gaps. These results are calculated from data pooled from all gap treatments from the final survey conducted in March 1998.

	Plot 1	Plot 2	Plot 3	Plot 4	Ranked Total	
<i>Agrostis stolonifera</i>	2.41	15.27	7.16	5.49	12.23	<i>Poa</i> spp.
<i>Arrhenatherum elatius</i>	1.03	1.44	1.06	2.74	11.08	<i>Geranium dissectum</i>
<i>Bellis perennis</i>	0	0.29	0	0.21	9.34	<i>Trifolium repens</i>
<i>Bromus hordeaceus</i>	7.22	6.34	4.24	6.97	9.20	<i>Lolium perenne</i>
Bryophytes	12.37	6.63	3.71	8.24	7.59	<i>Agrostis stolonifera</i>
<i>Cerastium fontanum</i>	3.78	3.17	3.18	7.39	7.52	Bryophytes
<i>Cirsium arvense</i>	0	0.86	0	0.21	7.45	<i>Holcus lanatus</i>
<i>Cirsium vulgare</i>	1.72	0	0.26	0	6.18	<i>Bromus hordeaceus</i>
<i>Convolvulus arvensis</i>	0	0	0	0.84	4.63	<i>Cerastium fontanum</i>
<i>Crepis capillaris</i>	1.03	0	0	0	3.89	<i>Ranunculus</i> spp.
<i>Cynosurus cristatus</i>	0	0.28	0.79	8.24	3.15	<i>Trifolium pratense</i>
<i>Dactylis glomerata</i>	0.68	4.89	2.12	1.69	3.09	<i>Taraxacum officinale</i>
<i>Festuca arundinacea</i>	0	0	0	1.05	2.88	<i>Cynosurus cristatus</i>
<i>Festuca rubra</i>	0	2.30	3.97	2.53	2.35	<i>Dactylis glomerata</i>
<i>Galium aparine</i>	0	0	0	0.21	2.35	<i>Festuca rubra</i>
<i>Geranium dissectum</i>	12.02	9.51	14.05	9.30	1.68	<i>Arrhenatherum elatius</i>
<i>Geranium molle</i>	0	0.57	0	0	0.94	<i>Rumex</i> spp.
<i>Heracleum sphondylium</i>	0.34	0	2.12	0.84	0.87	<i>Heracleum sphondylium</i>
<i>Holcus lanatus</i>	2.06	2.88	15.11	8.03	0.47	<i>Lamium purpureum</i>
<i>Lamium purpureum</i>	2.40	0	0	0	0.40	<i>Cirsium vulgare</i>
<i>Lathyrus pratensis</i>	0	0	0.26	0.21	0.33	<i>Festuca arundinacea</i>
<i>Leontodon hispidus</i>	0.34	0	0	0	0.26	<i>Cirsium arvense</i>
<i>Leucanthemum vulgare</i>	0	0	0	0.63	0.26	<i>Convolvulus</i>
<i>Lolium perenne</i>	19.93	8.93	6.63	4.86	0.20	<i>Crepis capillaris</i>
<i>Malva moschata</i>	0.34	0	0.26	0.21	0.20	<i>Leucanthemum vulgare</i>
<i>Plantago lanceolata</i>	0	0.28	0	0	0.20	<i>Malva moschata</i>
<i>Poa</i> spp.	13.40	13.25	14.32	9.09	0.20	<i>Vicia sativa</i>
<i>Prunella vulgaris</i>	0	0	0	0.21	0.13	<i>Bellis perennis</i>
<i>Ranunculus</i> spp.	0.68	2.88	6.36	4.65	0.13	<i>Geranium molle</i>
<i>Rumex</i> spp.	1.03	0	2.91	0	0.13	<i>Lathyrus pratensis</i>
<i>Sonchus asper</i>	0.34	0.28	0	0	0.13	<i>Sonchus asper</i>
<i>Sonchus oleraceus</i>	0.34	0	0	0	0.06	<i>Galium aparine</i>
<i>Taraxacum officinale</i>	13.05	1.72	0.26	0.21	0.06	<i>Leontodon hispidus</i>
<i>Trifolium pratense</i>	0	2.88	5.03	3.80	0.06	<i>Plantago lanceolata</i>
<i>Trifolium repens</i>	2.40	15.27	5.83	12.05	0.06	<i>Prunella vulgaris</i>
<i>Urtica dioica</i>	0.34	0	0	0	0.06	<i>Sonchus oleraceus</i>
<i>Vicia sativa</i>	0.68	0	0.26	0	0.06	<i>Urtica dioica</i>
<b>Rankings for top ten</b>	<b>Plot 1</b>	<b>Plot 2</b>	<b>Plot 3</b>	<b>Plot 4</b>		
<i>Poa</i> spp.	2	3	2	3		
<i>Geranium dissectum</i>	5	4	3	2		
<i>Trifolium repens</i>	10	2	3	1		
<i>Lolium perenne</i>	1	5	5	10		
<i>Agrostis stolonifera</i>	8	1	4	9		
Bryophytes	4	6	11	5		
<i>Holcus lanatus</i>	11	10	1	6		
<i>Bromus hordeaceus</i>	6	7	9	8		
<i>Cerastium fontanum</i>	7	9	12	7		
<i>Ranunculus</i> spp.	17	11	6	11		

Although individual species frequencies varied across Plots, **Figure 6.12 a)** depicts the ranked abundance of the main occluding species across the subplots as listed in **Table 6.01**. **Figure 6.12 b)** describes the frequency data in the form of rank-abundance curves for the four plots. The graph shows clear diversity curve separation from Plot 1

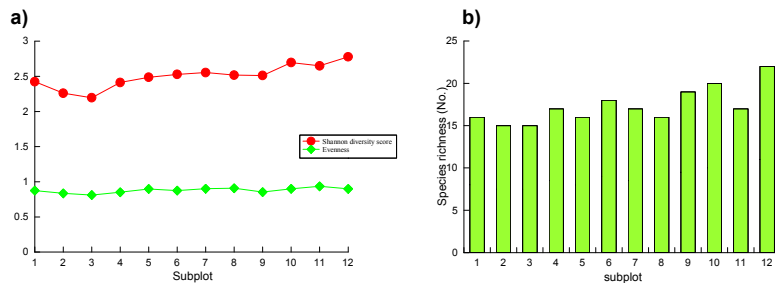
to Plot 4, with Plot 1 presenting a log series type curve, whereas from Plots 2-4 the curve approaches further to log normal with a more even distribution, indicating greater species-richness (Magurran 1988).

**Figure 6.12** Charts showing a) total (combined plots) species frequency; b) rank-abundance curves indicating diversity profiles for the four plots.



This contrasts with the information calculated from the Shannon Diversity score ( $H'$ ), which indicates a minimal increment of species-diversity across the subplots, though the curve does follow the usual gradient from Subplot 1 to Subplot 12. There is a similar configuration for species-richness, again with little change through the subplots, but a definite upward gradient (**Figure 6.13**).

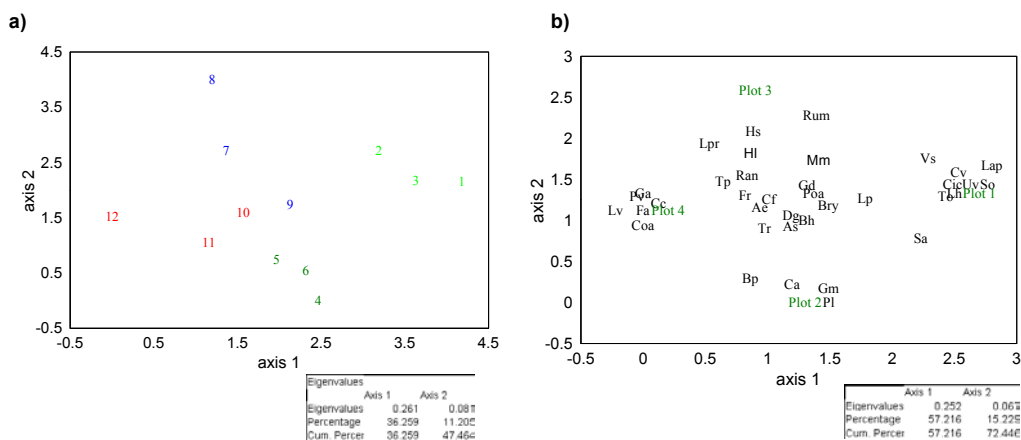
**Figure 6.13** Diversity characteristics for subplot gaps (combined): a) Shannon diversity scores; b) species richness scores.



When Detrended Correspondence Analysis is applied to the subplot vegetation data, it is clear from the scattergram (**Figure 6.14a**) that the spread of subplots along axis-1 generally follows the gradient of improvement from most improved on the left, and least to the right. The subplots are also loosely clustered in their plot groupings, suggesting that the gap occluding vegetation has similar within-plot homogeneity to the field-layer vegetation. The jointplot of **Figure 6.14b** provides an indication as to which species define the gap-

occluding vegetation for each grassland. The data markers for each plot are coupled with discrete species clusters. Thus, the gap vegetation of plot is typified by annual arable weed species not found in the other grassland gaps; the infill of the gaps in Plot 2 are associated particularly with *Cirsium arvense* and *Plantago lanceolata*; gaps of Plot 3 are least defined, though associated most closely with *Holcus lanatus* and *Rumex* species; and the gaps of Plot 4 are typified by *Cynosurus cristatus*, *Festuca arundinacea*, *Convolvulus arvensis*, and *Leucanthemum vulgare*. The majority of species are clustered in the centre of the chart, and not allied with specific plots. These are the species which make up the bulk of gap infill for all plots, such as *Poa* spp., *Trifolium repens* and *Agrostis stolonifera*.

**Figure 6.14** Scattergrams of results from Detrended Correspondence Analysis for a) subplots; b) gap species frequency. Species abbreviations are given below<sup>1</sup>.



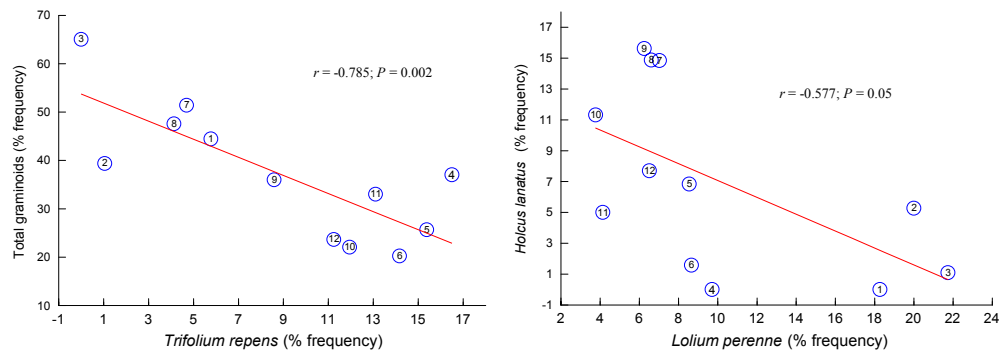
As noted above, there are certain species which dominant in gap occlusion vegetation throughout the grasslands. However, there are variations in the levels of dominance of these species between plots. To highlight these variations **Figure 6.15a** displays the relationship between the *Trifolium repens* and graminoid species. Clearly, there is a highly significant negative relationship between total frequency-abundance of *Trifolium repens* and the frequency-abundance of the grasses.

**Figure 6.15** Relationships between a) *Trifolium repens* and grass species; b) *Lolium perenne* and *Holcus lanatus*. Numbers within marker circles indicate subplot.

a) b)

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<i>Agrostis stolonifera</i>	As	<i>Festuca rubra</i>	Fr	<i>Poa</i> spp.	Poa
<i>Arrhenatherum elatius</i>	Ae	<i>Galium aparine</i>	Ga	<i>Prunella vulgaris</i>	Pv
<i>Bellis perennis</i>	Bp	<i>Geranium dissectum</i>	Gd	<i>Ranunculus</i> spp.	Ra
<i>Bromus hordeaceus</i>	Bh	<i>Geranium molle</i>	Gm	<i>Rumex</i> spp.	Rum
Bryophytes	Bry	<i>Heracleum sphondylium</i>	Hs	<i>Sonchus asper</i>	Sa
<i>Cerastium fontanum</i>	Cf	<i>Holcus lanatus</i>	Hl	<i>Sonchus oleraceus</i>	So
<i>Cirsium arvense</i>	Ca	<i>Lamium purpureum</i>	Lap	<i>Taraxacum officinale</i>	To
<i>Cirsium vulgare</i>	Cv	<i>Lathyrus pratensis</i>	Lpr	<i>Trifolium pratense</i>	Tp
<i>Convolvulus arvensis</i>	Coa	<i>Leontodon hispidus</i>	Lh	<i>Trifolium repens</i>	Tr
<i>Crepis capillaris</i>	Cic	<i>Leucanthemum vulgare</i>	Lv	<i>Urtica dioica</i>	Ud
<i>Cynosurus cristatus</i>	Cc	<i>Lolium perenne</i>	Lp	<i>Vicia sativa</i>	Vs
<i>Dactylis glomerata</i>	Dg	<i>Malva moschata</i>	Mm		
<i>Festuca arundinacea</i>	Fa	<i>Plantago lanceolata</i>	Pl		

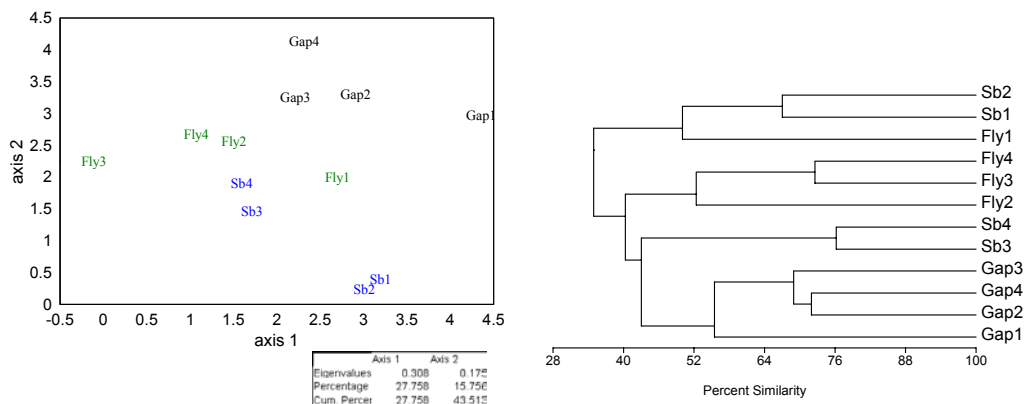


**Figure 6.15b** shows the relationship between *Lolium perenne* and *Holcus lanatus* across the subplot gradient. Again, there is a significant negative relationship between the two species, with *Lolium* replaced by *Holcus* through the sequence. Both analyses fit with the inferences from **Figure 6.14b** where *Lolium* is located more to the right of axis-1, and *Holcus* more to the left, following the improvement gradient, also related to disturbance levels. Two other species' abundances particularly stand out as influenced by artificial gap creation. Observations of *Geranium dissectum* abundances seemed to indicate that this species was more abundant in artificial gaps than the general intact sward. This is borne out by comparison of the means for both gap and field-layer vegetation, which shows that there is a highly significant difference ( $t_{22} = 4.232$ ;  $P = 0.000$ ). Equally, the other *naturally* abundant annual in the grasslands *Bromus hordeaceus* was also significantly more abundant in artificial gaps than the extant swards ( $t_{22} = 3.332$ ;  $P = 0.003$ ).

**Figure 6.16a** displays the results of a DCA comparison between gap vegetation, the intact field-layer vegetation, and soil seed bank of each plot. Perhaps surprisingly, there is apparently a clear separation of gap vegetation from field-layer and seed bank. This suggests that gap vegetation is a discrete vegetation type, and has more affinity with the gap vegetation of other plots than with the field-layer and seed banks from which it is derived. This finding is reinforced in the cluster analysis where gap vegetation as a whole has only approximately 40% similarity with the other plant communities.

**Figure 6.16** Results from comparisons between gap, field-layer and seed bank vegetation: a) is a scattergram of plot data; b) is a dendrogram of cluster analysis for the same dataset. Gap=gap vegetation; Fly=field-layer; Sb=seed bank. Accompanying numbers refer to plot.

a) b)



The species rankings in **Table 6.02** identify where the gap vegetation differs in species composition/abundance. While all the plant communities are a high constancy of *Poa* spp., *Agrostis stolonifera*, *Lolium perenne* and *Holcus lanatus* in common, the major departure in the gap vegetation is the high abundance of the annuals *Geranium dissectum* and *Bromus hordeaceus*, along with *Cerastium fontanum*, all three of which have far lower rankings in both field-layer and seed bank. Also of particular note is the far greater dominance of *Trifolium repens* in the artificial gaps, and bryophyte vegetation is far more abundant than in the swards as a whole where it was ranked only 20<sup>th</sup> in the 1998 field-layer census.

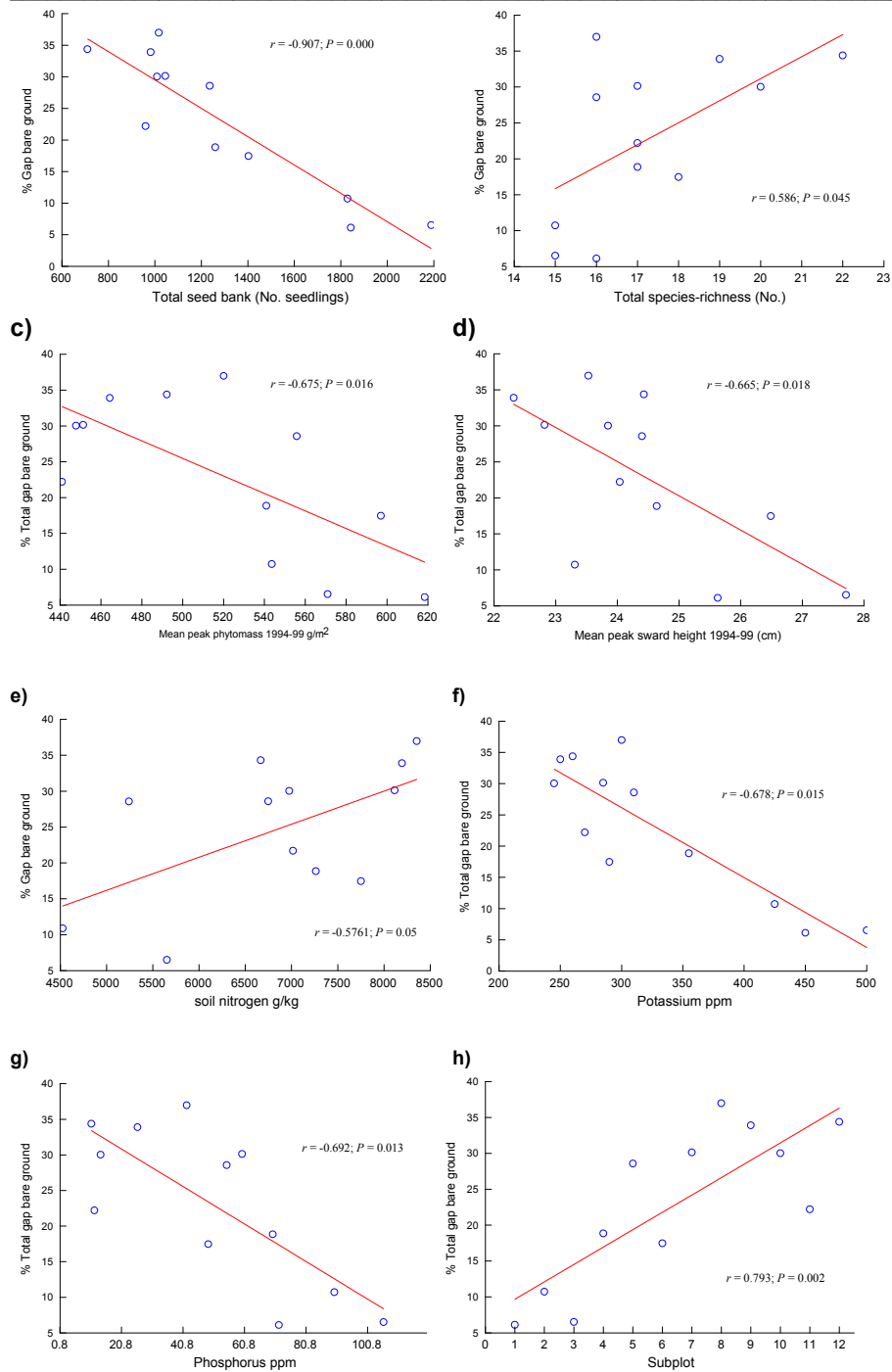
**Table 6.02** Ranking of ten most abundant species recorded from field-layer, gap vegetation and soil seed bank.

Field-layer	Gap vegetation	Seed bank
<i>Lolium perenne</i>	<i>Poa</i> spp.	<i>Poa trivialis</i>
<i>Holcus lanatus</i>	<i>Geranium dissectum</i>	<i>Holcus lanatus</i>
<i>Poa trivialis</i> .	<i>Trifolium repens</i>	<i>Agrostis stolonifera</i>
<i>Arrhenatherum elatius</i>	<i>Lolium perenne</i>	<i>Lolium perenne</i>
<i>Festuca rubra</i>	<i>Agrostis stolonifera</i>	<i>Poa annua</i>
<i>Dactylis glomerata</i>	Bryophytes	<i>Ranunculus bulbosus</i>
<i>Agrostis stolonifera</i>	<i>Holcus lanatus</i>	<b><i>Ranunculus acris</i></b>
<i>Trifolium repens</i>	<i>Bromus hordeaceus</i>	<i>Dactylis glomerata</i>
<i>Festuca arundinacea</i>	<i>Cerastium fontanum</i>	<i>Urtica dioica</i>
<i>Convolvulus arvensis</i>	<i>Ranunculus</i> spp.	<i>Arrhenatherum elatius</i>

### Relationships between gap occlusion vegetation and environmental parameters

In order to assess the effect of environmental influences on the rate of gap occlusion, comparisons were made between the percentage of bare ground remaining after one year and the main environmental variables measured throughout the research. The significant relationships are presented in **Figure 6.17**.

**Figure 6.17** Relationships between percentage gap occlusion and significant environmental variables.  
a) b)



The one of the fundamental features of improved grasslands is the elevated nutrient status of the soil. Therefore, it is not surprising that soil phosphorus and potassium are apparently significant positive factors in the rapidity of gap infill, though less clear why nitrogen should seem to reduce gap occlusion. The usual corollaries of unnaturally high nutrient supply are enhanced peak phytomass and sward height, which are also implicated in gap

occlusion rate, showing significant negative relationships. However, size of soil seed bank is apparently the most significant variable in the occlusion of artificial gaps, indicating that the grasslands with the largest soil seed banks have the most rapid gap occlusion. To determine the importance of eight key variables in explaining the amount of vegetative gap occlusion, stepwise variable selection multiple linear regression was applied, which is the most commonly used method for model building (Norušis 1998). The results of the analysis are presented in **Table 6.04**. The regression output has only one model, and this is comprised of the constant and the explanatory variable TOTSEEDB (total soil seed bank size), which explains 82.3% of the observed variability in the levels of gap occlusion. Except for seed bank size, all other variables are excluded; strongly suggesting that soil seed bank size is the best predictor for rate of gap occlusion. However, it must be noted that the seed bank size estimate also includes a large proportion of seed from transient seed bank species such as *Lolium perenne*, and thus must also be indicative of the volume of seed rain as well (Edwards & Crawley 1999).

**Table 6.04** Results of stepwise multiple linear regression for gap occlusion (remaining bare ground) and environmental variables. AVSWHGT=AVERAGE SWARD HEIGHT 1994-99; AVPHYTO=AVERAGE PEAK PHYTOMASS 1994-99; DIVERSITY=FIELD LAYER DIVERSITY H' INDEX; P2000=SOIL PHOSPHORUS 2000; K2000=SOIL POTASSIUM 2000; N98=SOIL NITROGEN 1998.

Variables Entered/Removed						
Model	Variables Entered	Method				
1	TOTSEEDB	Stepwise				
a Dependent Variable: GAP98						
Model Summary						
Model	R	R Square	Adjusted R Square	Std. Error of the Estimate		
1	.907	.823	.805	4.8549		
a Predictors: (Constant), TOTSEEDB						
ANOVA						
Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	1095.457	1	1095.457	46.476	.000
	Residual	235.704	10	23.570		
	Total	1331.161	11			
a Predictors: (Constant), TOTSEEDB b Dependent Variable: GAP98						
Coefficients						
Model	Unstandardized Coefficients		Standardized Coefficients		t Sig.	
		B	Std. Error	Beta		
1	(Constant)	51.947	4.473		11.614	.000
	TOTSEEDB	-2.244E-02	.003	-.907	-6.817	.000
a Dependent Variable: GAP98						
Excluded Variables						
Model		Beta In	t Sig.	Partial Correlation	Collinearity Statistics Tolerance	
1	SUBPLOT	-.013	-.045 .965	-.015	.230	
	AVSWHGT	-.143	-.810 .439	-.261	.591	
	AVPHYTO	-.036	-.176 .864	-.058	.473	
	DIVERS98	-.310	-.916 .383	-.292	.157	
	P2000	.3041	.044 .324	.329	.207	
	K2000	-.089	-.207 .841	-.069	.106	
N98.2281.227.251.379.488						

## DISCUSSION

### Primary gap occlusion factors

The principal dynamic measured in this research was the amount of bare ground remaining in the herbicide gaps after approximately one year of exposure to natural vegetation infill factors such as recruitment from seed rain, seed bank and vegetative spread. The proportion of bare ground may be considered an indicator of the receptivity of the sward to immigration and invasion, as it is colonisable space, and the length of time it stays open may well increase the probability of recruitment of species with more limited powers of dispersal (Bakker *et al* 1980; Hillier 1984). In turn this may contribute at a restoration level by increasing the opportunities for *natural* grassland diversification (Wells *et al* 1989; Hiller 1990; Willems 1996).

Overall, the results are consistent with observations made in **Chapter 7** concerning the value of artificial competition-free gaps in implant establishment. It was noted that spray gaps seem to occlude very rapidly in productive grasslands, the inference being, that they are therefore of limited value in reducing neighbour competition except under particular parameters (Parish *et al* 1989; Tallowin *et al* 1995). Regeneration gaps, therefore, seem to be a rare commodity in agriculturally improved grasslands, and most particularly in intensively managed grassland, where the occurrence of bare ground is often seen as a failure of management as it can allow the ingress of non-sown species (Williams 1984; Crofts 1999). The present research quantifies this observation in that there was significantly less bare ground in the more improved Plots 1 and 2 compared to the other two plots, and significantly less bare ground remaining even between Plot 1 and Plot 2. Thus the rank order of occlusion rate Plot1>Plot2>Plot3>Plot4, essentially follows the improvement gradient (see **Figure 6.17f**) as described by phytomass productivity measurements and soil chemical analyses (see **Chapter 4**). In fact, the correlations established between percentage bare ground and environmental/vegetation parameters implicitly illustrates these relationships (**Figures 6.17a-e**). Soil phosphorus, soil potassium, peak phytomass and sward height were significantly negatively correlated with percentage bare ground. Soil phosphorus seems to be the key controlling factor in the productivity of these grasslands (Davies *et al* 1999). As shown in **Chapter 4**, sward height and phytomass are positively correlated with P levels. It is important also, to emphasise the relationship

between P and seed bank size as studied in **Chapter 5 (Table 5.04)**, where it is shown that there was a very significant relationship between these two variables. This fact conflates with the present gap occlusion research where there is a very significant correlation between percentage bare ground and seed bank size (**Figure 6.17a**). This is underscored by the results of the linear multiple regression (**Table 6.04**) which identifies seed bank size as the best predictor of gap occlusion rate. In this context, the term ‘seed bank’ is a total that includes data from all the seed bank censuses, and comprises everything from short-term transient to long-term permanent viable seed residing in the soil (Thompson & Grime 1979; Thompson 1993; Bekker *et al* 2000). It can therefore be viewed as both an estimate of resident soil seed as well as an indicator of the volume of seed rain. Indeed, the fact that the compost (non-seed bank) gaps occluded at similar rate to that of non-compost gaps (seed bank & seed rain) suggests that, as with Bullock *et al* (1994), the vast majority of recruitment was from seed rain. Thus, the results propose that the most productive plots also produce the most propagules - mostly from dominant grass species – which rapidly fill in any gaps that are created and negate attempts to encourage diversification. Surprisingly, soil nitrogen was positively related to percentage bare ground. This is rather a confounding result, however, the soil N measured is largely a function of percentage soil organic matter, which is relatively immobile and inaccessible (Brady & Weil 1999). Thus, this result is possibly a product of the polarising strength of the relationship between the subplots of Plot 1 with very low N (previously ploughed regularly), and little remaining bare ground, and the subplots of Plot 3 (not ploughed within living memory) with high N and relatively high bare gap space remaining. However Kitajima & Tilman (1996) found that suppression of seed germination rather than limitation of the availability of the seeds in the soil or seedling survivorship was the primary mechanism of lower colonization rates in higher N grassland plots.

When graminoid percentage abundance is correlated with percentage gap bare ground the resulting significant negative relationship ( $r = -0.740$ ;  $P = 0.006$ ) strongly indicates that grass dominance is the *prime mover* in gap infill. And while overall percentage gap vegetation abundance does not correlate with phytomass measurements, % graminoid occlusion is significantly positively related with phytomass samples taken in June 1997 ( $r = 0.639$ ;  $P = 0.025$ ). The evidence suggests that productive conditions favouring a few dominant closed-turf grass species (Fenner 1978) can effectively preclude diverse

graminoid and forb regeneration in *comparatively large* artificial gaps (Rapp & Rabinowitz 1985; Silvertown & Smith 1988; McLellan *et al* 1997). Parish *et al* (1989) found that for most species in their artificial sward, the threshold gap diameter for seedling establishment was generally >20-cm. The 10-cm diameter turf divots created in their study were only suitable for species encroachment rather than germination Britton *et al* (2000) also found that small gaps in heathland were largely occluded by lateral growth. Thus, the difficulty comes in allocating influence to the main regeneration mechanisms. Reviewing the data at a plot level shows that the gaps of Plots 1 and 3 had significantly more grass occlusion than that of Plots 2 and 4. Surprisingly perhaps, these results do not correlate with the respective graminoid percentage of the extant field layer. This is also reflected in the results for forb infill, for which gaps in Plots 1 and 3 also had significantly less relative forb infill than Plots 2 and 4. While the *bulk* categories of grams and forbs show core interactions, a species-focussed approach identifies the grasses *Lolium perenne* and *Holcus lanatus* (see **Figure 6.15a**), and the forb *Trifolium repens* (**Figure 6.15b**) as the gap occlusion phytometers. *Lolium perenne* does not produce a persistent soil seed bank, and has limited potential for lateral vegetative spread (Grime *et al* 1988), therefore its ability to maintain dominance relies largely on increasing seed rain through productivity enhancement under conditions of elevated soil fertility. *Holcus lanatus*, however, is a dominant of soils of lower fertility, and is able to monopolise free ground-space through seed bank, seed rain, and vegetative expansion (Arnthórsdóttir 1994). Under the moderate productivity conditions of the research grasslands, the only forb species able to compete, in gap regenerative terms with the grass species, is *Trifolium repens*, with its own N-producing capability, thus suggesting further analysis may require splitting the forb functional type into legumes and non-legumes (Hector *et al* 1999). The results are typified by comparing the vegetation occlusion of the plot sequence in terms of these core species. The gaps of Plot 1, for instance, are specifically dominated by *Lolium perenne*, while the gaps of Plot 3 are primarily occluded by *Holcus lanatus*. In contrast, the definitive gap infill of Plots 2 and 4 was *Trifolium repens*. However, the link between the gap occlusion parameters of Plots 1 and 3, and Plots 2 and 4 are only supported by these species, and subordinate species composition is significantly different.

#### Significance of gap size and soil treatment on occlusion

It would seem a logical presumption that 15-cm gaps as a whole would occlude faster than 30-cm gaps. The 15-cm gaps have a greater ratio of circumference to area, which decreases the average dispersal distance for colonisation (Britton *et al* 2000). In addition, the 30-cm gaps have four times the amount of ground to be re-vegetated. Bullock *et al* (1995), although using gaps of only 3- to 9-cm diameter, found that smaller gaps occluded faster due to higher clonal ramet densities, as did Miles (1974) and Coffin & Launenroth (1988). However, in this study, there were no significant differences for the combined totals (from all plots) for the two gaps sizes within treatments (see **Figure 6.05**). Burke & Grime (1996) also observed that large gaps did not encourage a greater invasion potential compared to smaller gaps, though stating that this was probably because of the: “differences in the destructive effects of gap creation on the indigenous vegetation as opposed to any direct effects through differences in the regenerative opportunities that they provide.” Overall then, both 15-cm and 30-cm gaps seemed to occlude equally rapidly. As was suggested from the results of **Chapter 7**, the rate of gap infill around transplants was only weakly conditioned by gap size, and only then within specific parameters such as soil fertility and aboveground phytomass. The only significant result in terms of gap-size comparisons was between soil treatments, with non-compost 30-cm gaps and compost 15-cm gaps showing a significant difference in bare ground, though surprisingly not between 30-cm non-compost and 30-cm compost gaps. The indication is that in these productive swards, gap size, when at 30-cm diameter or under does not differentially affect the rate of occlusion. As already mentioned, other factors such as soil fertility, phytomass and sward species composition override that of gap size in terms of recolonising space after disturbance. Fenner (1985) also notes that although larger gaps have enhanced features over smaller gaps such as reduced competition (McLellan *et al* 1987), increased irradiance and diurnal fluctuations in superficial soil temperature (Bakker *et al* 1980), the greater shelter and humidity (Goldberg 1987; Britton *et al* 2000) of smaller gaps may equalise the relative colonisation benefits.

While gap treatments as a whole show little significance, comparing only the *totals* data, however, masks what are significant results between plots, within treatment types. When combined data for all 15-cm gaps (non-compost + compost) are compared across plots, a new pattern emerges. The 15-cm gaps of Plot 1 had significantly less bare ground than Plots 3 & 4. Similarly, there was significantly less bare ground in the 30-cm gaps in Plot 1

than Plots 2 & 3. As already stated, the proportions of the functional plant types within the occluding vegetation were also different across the plots. While no significant results were found for the totalised data between gap sizes, within gap size, patterns emerge, with graminoids significantly more abundant in Plots 1 and 3, and forbs more abundant in Plots 2 and 4. It was evident that 30-cm gaps amplified these differences (e.g. one-way ANOVA:  $F_{3,36} = 15.492$  for 30-cm as opposed to  $F_{3,36} = 9.471$  for 15-cm gaps).

Soil treatment type had its most significant effect at the total combined level, whereby the comparison between all non-compost and all compost gaps showed that compost gaps occluded more slowly. The obvious inference from this result is that the soil seed bank, which was removed in the compost gaps, is a significant addition to the rate of gap infill rather than just seed rain alone. Both non-compost gap sizes follow the same general pattern described for the *totals* for each size i.e. Plot 1 was remarkable for having both the least bare ground and most graminoid infill, in contrast to Plot 4. However, there were no significant differences between 15-cm compost gaps across the plots, though 30-cm compost gaps did show a very significant difference between Plots for both bare ground and forb infill, but not graminoid infill. For Plot 1 the 30-cm compost gaps had more than double the bare ground than for 15-cm compost gaps and nearly 7 times that of 30-cm non-compost gaps. This discrepancy is probably due to the 30-cm compost gaps being a focus for animal disturbance. Rabbits in particular found these large gaps conspicuous and easy to dig, and thus their activities, along with foxes and corvids, conspired to significantly hinder occlusion. Although a ‘natural’ component of the ecology of the grasslands (Bakker *et al* 1980; Goldberg 1987), the compost experiment was partly invalidated by this factor.

#### **Characteristics of gap colonising vegetation**

The multivariate analyses seem to suggest that “gap” vegetation differs both in species composition and species abundance in comparison to the surrounding field-layer. In addition, the gap vegetation demonstrated a surprising uniformity throughout the grassland plots. Characteristically, gap vegetation comprised of greater cover of annuals, bryophytes, and *Trifolium repens*. The annuals *Geranium dissectum* and *Bromus hordeaceus* were significantly more abundant in gaps than fieldlayer. Both do not produce persistent seed banks (Grime *et al* 1988), and are therefore *de facto* seed-colonisers (Bullock *et al* 1995). The creation of gaps consequently seems to be very advantageous for these two species, providing suitable competition-free regeneration sites (Grubb 1977).

Bullock *et al* (1994) also identified *G. dissectum* as a gap dependent species, along with *Cerastium fontanum*. *C. fontanum* was also more abundant in the gaps than in the field layer in this study (see **Table 6.01**). Five other annuals were exclusively recorded in gaps. *Crepis capillaris*, *Geranium molle* and *Lamium purpureum* established in the gaps of Plot 1, while *Sonchus asper*, *Sonchus oleraceus* and *Cirsium vulgare* also exploited gaps in other plots. Otherwise, perennial species were the most abundant gap species, and *Lolium perenne*, *Holcus lanatus* and *Trifolium repens* most indicative of differences between plots. Where *T. repens* is a dominant in the sward of Plots 2, its vegetative regeneration via stoloniferous clonal extension, aggressively occludes sward openings (Arnthórsdóttir 1994; Boyce 1994). Bullock *et al* (1994) suggest that *T. repens* does respond positively to disturbance; it is primarily a clonal-coloniser and actively forages for readily colonisable space (Thórhallsdóttir 1990; Hutchings & Kroon 1994). *Lolium perenne*, as apparent to most dairy farmers, can infill sward gaps through copious seed rain (Bullock *et al* 1995) where it is kept dominant through fertiliser input (Boyce 1994). Once fertiliser inputs cease, this research shows that *Lolium* is replaced in these swards by *Holcus lanatus*, *Agrostis stolonifera*, and the ubiquitous *Poa trivialis*. All three species have flexible regeneration strategies (Grime *et al* 1988; Bullock *et al* 1995), and they are able to effectively exploit gaps through vegetative expansion, seed rain and persistent seed banks. For species such as *Dactylis glomerata*, *Cynosurus cristatus*, *Ranunculus acris*, and *Taraxacum officinale* without long-term persistent seed banks and limited lateral expansion, there is probably more reliance on recruitment facilitated purely by the natural formation of microsites (Roberts 1986; Grime *et al* 1988; Parish *et al* 1989).

An intriguing finding was the much higher abundance of bryophytes in gap vegetation than the field-layer. Virtanen *et al* (2000) found that total bryophyte biomass decreased with increasing vascular plant biomass in the Park Grass Experiment. Certainly Willis (1963) and Boorman & Fuller (1982) observed that after fertiliser applications, the stimulated vascular species markedly suppressed the once abundant bryophyte layer. Taking the converse approach, Bakker *et al* (1983) found that inhibition of dominant vascular grassland species through heavy grazing encouraged moss expansion. Clearly then, the bryophyte layer can be largely eliminated under productive grassland conditions, though certain common species can exploit the seasonal phases i.e. excluded under peak phytomass, but regenerate in the spring and autumn (Al-Mufti *et al* 1977). Within this

context, the high abundance of bryophytes in the artificial gap vegetation may be explained by the elimination of the tall, domineering species, which promotes a brief flourish of moss colonisation and expansion before the gaps are saturated once again by vascular species.

At the subplot scale, using a number of analytical approaches, generally the vegetation follows the gradient of improvement, or at least shows a marked slope of difference along the numbered scheme from 1 to 12. Species diversity (see **Figure 6.13b**), for instance increases along the gradient with the gaps of Plot 12 having the highest  $H'$  index value. Ordination of the same data using DCA also indicates a general linearity in vegetation along axis-1, with the subplots of Plot 1 and subplots of Plot 4 most opposed. This tends to indicate that the species which dominate each sward also define the characteristics of the gap vegetation structure within each sward. This obvious contention can only be assessed by directly comparing the field layer vegetation with the gap vegetation across the improvement gradient. The results of this aspect show that the gap vegetation, although conforming to the lines of the gradient, does not specifically conflate with the field layer vegetation data (see **Figures 6.16a & 6.16b**). This may be attributable to the survey methods, that is, point-quadrat cover estimates were used for the field layer surveys, and frequency-abundance for the gap surveys. However, taking differing methodologies into account, there is scope for direct contrast (Kent & Coker 1992). Comparing the total field layer species abundance results from 1998 to the total gap abundance data, there was only a 54.6% similarity. The maximum similarity between gap vegetation and field layer for the plots was 57.6% for Plot 2. This differential must reflect the processes of sward maturation after disturbance, whereby even after a year of development the gaps have vegetation composition significantly divergent from the surrounding undisturbed field layer. All grasslands are subject to forms of localised disturbance, and thus while the sward as a whole is complete when described in broad terms, localised disturbances result in patches which are regressions to immature states, thus allowing age-state diversity and constant re-assembly of species combinations (Hillier 1990; Wu & Levin 1994). However, because the dominant species are also the main recolonisers, under productive conditions in particular, any differentials between gap and field-layer communities will rapidly disappear once full competitive inter-specific interactions resume (Edwards & Crawley 1999).

#### **Value of artificial gap creation in grassland diversification**

While there is general conservation interest in the value of artificial gap creation for grassland diversification, there is relatively little research to underpin the development of this technique as a practicable conservation tool (Wells *et al* 1989; Hillier 1990; Tallwin *et al* 1995; Kirkham & Kent 1997; Hopkins *et al* 1999; Losvik 1999). Natural regeneration niches, colonisation gaps, safe sites etc are seemingly essential for maintaining grassland diversity, to allow maintenance of populations, and vegetational development (Grubb 1977; Bakker *et al* 1980). Typical conservation management of grasslands such as cutting, and most particularly grazing, directly and indirectly create regeneration gaps (Bakker *et al* 1980; Bullock *et al* 1994; Bullock *et al* 1995; Crofts & Grayson 1999). Under these circumstances, however intentional, regeneration gaps are a by-product of management, and their formation can only be regulated imprecisely through cutting or grazing pressure (Anderson 1995; Bullock *et al* 1995; Jefferson 1999). Creating artificial gaps seems on the surface, therefore, to be a useful approach to ensure less competitive, colonisable space is available to subdominants and immigrant species to diversify swards. This is particularly so when trying to restore diversity to grasslands post-agricultural improvement, where the canopy is closed and sward resistant to immigration (Fenner 1978; Bullock *et al* 1995; Burke & Grime 1996).

In this study, gap diversity as measured by the Shannon index ( $H'$ ) was consistently higher than that of the related surrounding field layer. This may seem a positive outcome for the technique; however, the result is possibly a product of not quite comparing like-with-like, as cover-abundance estimates were made for the field layer censuses and frequency-abundance measurements for the gap vegetation. There was also a very significant relationship between field-layer diversity and gap diversity ( $r = 0.880$ ;  $P = 0.000$ ), showing both series follow the subplot gradient. Although the ordinations and cluster analyses indicate that gap and field layer vegetation were notably different in composition, this correlation and comparison of rank abundances, suggests that the hierarchy of species dominance in the field-layer also controls the organization of gap occlusion. Bekker *et al* (2000) state that the seed banks of improved grasslands tend to *follow* changes in the above-ground vegetation rather than cause change, and Bullock *et al* (1994) also found that natural diversification of agriculturally depauperated swards is hampered by the domination of the seed bank and seed rain by the dominant grasses. This means that when regeneration gaps are formed, they are rapidly occluded by the dominant grass species

(Kirkham & Kent 1997). Tallowin *et al* (1995) established that creation of gaps in the established vegetation of previously fertilized MG 5 meadow plots did not promote any long-term enhancement in species-richness/recruitment. Considering the strong relationship between gap occlusion and seed bank in the present study, it may also hold that gaps are also dependent on the specific vegetation dynamics rather than being genuinely catalytic factors (Britton *et al* 2000). Artificial gaps, even relatively large ones, seem to be re-filled chiefly by the dominant species, mostly grasses, and therefore significant gains in overall diversity are probably minimal. This is a logical scenario since the dominant species also dominate the main forms of regeneration – seed rain, soil seed bank and vegetative - and while over the period of a year the vegetation formed in the gaps differs from the intact swards, as the gap vegetation matures and integrates with the surrounding matrix, homogenisation seems to take place.

The gaps used in this research were larger than the vast majority of those, which would naturally occur in grasslands (Fenner 1978; Silvertown & Smith 1988). It may seem logical, or rather, intuitive, that greater gap area should encourage greater diversity in vegetation regeneration because of the larger colonisable space, increased dispersal target area, and reduced competitive environment (Burke & Grime 1996; Britton *et al* 2000). However comparing the Shannon diversity index for 15-cm and 30-cm diameter gaps across the twelve subplots, there was no significant difference ( $t_{22} = 0.346$ ;  $P = 0.733$ ). Although the greater levels of rabbit disturbance in 30-cm gaps may have influenced this result, within these parameters, the evidence suggests that colonisation diversity is not significantly influenced by gap size at these relatively large, coarse scales (Mahdi & Law 1987). It cannot be discounted that to have significant restoration value, the created gaps may have to be larger than 30-cm in diameter (Edwards & Crawley 1999), though such extensive gap creation would then begin to compromise the integrity of the extant sward. Also, failure of the technique may be due to the features of herbicide gaps, which are regular in form, and do not directly reduce soil fertility, or may actually increase local soil fertility through mineralisation (Hopkins *et al* 1999). It is worth noting that that gaps caused by the death of individuals or groups due to injury and pathogens do not necessarily alter soil fertility. It is possible that important micro-scale subtleties of natural regeneration gap formation may be beyond re-creation with herbicide (Bonis *et al* 1997). Fenner (1984) comments that gap qualities such as size may be species specific and therefore restoration

using gap creation requires fine-tuning (Mahdi & Law 1987). Goldberg (1987) also states that gaps may reduce seedling mortality through greater irradiance, but conversely increase mortality through reduced soil moisture. Alternative methods for artificial gap creation are turf scaling, or turf + topsoil removal, the evidence suggesting that they may produce longer-term results (Hopkins *et al* 1999). Certainly both these methods reduce soil fertility - crucially phosphorus - through export, and thus have immediate potential over herbicide. This may prevent rapid infill, and create more stressed conditions promoting less dominance, and thus present access to a broader range of colonisers. The drawbacks are that turf removals take much more effort to create, and may also contradict any positive aspects of the seed bank composition. And Rapp & Rabinowitz (1985) found that graminoid shoots were more abundant in scaled gaps than in controls the first year, due to the edge effect of cutting roots and rhizomes and stimulating new growth.

For the restorationist, ‘broadband’ artificial gap creation seems to present a *swings-and-roundabouts* situation. In terms of ‘narrowband’ restoration worth, perhaps a species-specific approach is necessary. Only six species recorded in the gap experiment can be considered strictly ‘desirable’ (see **Chapter 5**). These are *Lathyrus pratensis*, *Leontodon hispidus*, *Leucanthemum vulgare*, *Malva moschata*, *Prunella vulgaris* and *Trifolium pratense*. *L. pratensis* was not strictly a gap coloniser as regeneration was probably mostly derived from extant perennating rhizomes (Grime *et al* 1988) which were unaffected by the herbicide application. The only desirable non-introduced species to profit from the herbicide gaps were *Trifolium pratense*, which is *naturally*<sup>2</sup> present in Plots 2-4, and *Leucanthemum vulgare*, which is naturally, present in Plot 4. Importantly, *Leontodon hispidus*, *Malva moschata* and *Prunella vulgaris* were recorded in the gaps. These are purely introduced species through inoculation, and it is perhaps encouraging that the gaps facilitated their regeneration. However, *Leontodon hispidus* and *Prunella vulgaris* only occurred in gaps of Subplot 1 and Subplot 12 respectively. More positively, *M. moschata* occurred in gaps of three subplots. Perhaps this presages a more beneficial role for artificial gaps once soil fertility is depleted and sward productivity declines. However this advent is confounded by difficulty in establishing *cause and effect*. Under productive conditions, artificial gaps seem to have limited positive influence due to their transitory nature. Yet once grassland productivity has been reduced through long-term conservation

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<sup>2</sup> Though probably included in the sward renovation seed mixture of 1965.

management, regeneration gaps become naturally more abundant, and intervention through artificial gap creation becomes essentially superfluous (Tallowin *et al* 1995; Burke & Grime 1996).

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