- CHAPTER 5 -

THE VALUE OF SOIL SEED BANKS IN THE RESTORATION OF AGRICULTURALLY IMPROVED GRASSLAND

Newly-formed earthworks frequently cause the sudden growth of wild plants which have never before been observed in the district. Hence, however careful we may be to destroy weeds in one crop, we shall assuredly have some fresh species with the next, as well as fresh plants of the same, in consequence of dormant seeds having been brought within the power of growth by newly stirring soil.

Buckman Prof. (1855) On agricultural weeds. *Journal of the Royal Agricultural Society of England* **16**: 359-381.

SUMMARY

1. There is increasing research into the importance of soil seed banks in habitat management and restoration ecology, not only in terms of the part soil seed banks play in the maintenance of grassland diversity, but also the value of viable soil seed in restoring grassland from neglect or disturbance. Populations of species deleted from the above ground vegetation by intensive agricultural may survive as dispersules in the soil, and for restoration these communities may be an important element in encouraging diversification. Knowledge of the persistent soil seed bank enables the restorationist to decide whether the *in-situ* seed pool is an asset in re-establishing lost species, a neutral component, or even a liability.

2. An experiment was carried out to investigate the restoration potential of the viable seed present within the soils of the experimental grassland plots described in **Chapters 2** & **3**. Estimation using direct germination was used, consisting of taking cores of soil of known volume, spreading the soil out on a bed of a suitable medium in pots, and maintaining conditions favourable to seed germination. The seedlings are then identified and counted as they emerge. The soil samples were collected during each of the four seasons: autumn (October 1994); winter (January 1995); spring (May 1995); and summer (August 1995).

3. A total of 16,173 seedlings were recorded, comprised of 69 species. Of this species total, 16 (23%) were grasses and 53 (77%) forbs. Although forbs dominated the soil seed bank in terms of species richness, grasses predominated in terms of numbers. When presented in terms of seedling abundance grasses amounted to 12,908 (79%) and forbs 3,265 (21%). *Ranunculus acris* and *R. bulbosus* were the most abundant forb species.

4. A gradient of seed bank similarity from Plot 1 to Plot 4 was apparent. However there was little difference between Plots 2 to 4. The seed bank of Plot 4 had only 34% similarity with the reference community, and Plot 1 even less at 12%, indicating that a large proportion of species found in Plot 5 are of low abundance or missing from the agriculturally improved grasslands. The results do show the usual discrepancy between the above-ground vegetation and the respective soil seed banks of all the plots as far as relative species abundance. However, in terms of species composition alone, for Plots 1-4 this discrepancy was much reduced. Only Plot 5 had a high dissimilarity for both species composition and species-abundance (70%).

5. For the total seed bank size, significant positive correlations were with soil phosphorus and potassium, as well as with sward height/phytomass. The very significant negative relationship between total soil seed and subplot number reflected the predicted gradient of grassland improvement. Multiple linear stepwise regression confirmed that productivity as measured by sward height, soil phosphorus and potassium were the most significant factors explaining total seed bank size.

6. Seed bank diversity seemed to be at its highest during January and lowest during August. In August the dominance of the most abundant species is exacerbated by summer seed production. By January, most of the transient *Lolium* seed has germinated or died, and overall species abundances are at their lowest also due to germination and mortality factors, leading to greater evenness and higher diversity. Overall, there was a marginally greater abundance of seedling emergence from the upper 5-cm of the soil horizon than the lower 5-cm. Totalised for all plots, 59.6% of the seedlings came from the top 5-cm and 40.6% from the lower.

7. Plot 4, the least improved grassland, only had a seed bank similarity with Plot 5 of 34%, indicating agricultural improvement seems to alter seed banks irrevocably. The results suggest that any vegetation developed from the seed bank, other than from Plot 5, will be dominated by perennial grass species, and specifically by *Poa trivialis*, *Holcus lanatus* and *Agrostis stolonifera*. Furthermore, the evidence indicates that activating seed banks after agricultural improvement will establish a vegetation matrix at most neutral in character.

Keywords: agriculturally improved, seed bank, restoration, direct germination, emergence, similarity, above-ground vegetation, seasonality, activation, neutral.

INTRODUCTION

Much of the work by plant ecologists concerning seed banks and agricultural systems has revolved around the negative part dormant viable seeds in the soil play as a reservoir for 'weed' regeneration (e.g. Chippindale & Milton 1934; Champness & Morris 1948; Jalloq 1975; Roberts 1981; Roberts & Neilson 1981; Howe & Chancellor 1983; Froud-Williams *et al* 1984; Williams 1984; Williams 1985; Warwick 1984; Chancellor 1986; Hill *et al* 1989). However, as nature conservation becomes an ever more established form of land use, there is increasing research interest into the importance of soil seed banks in habitat management and restoration ecology (Johnson & Bradshaw 1979; Jefferson & Usher 1987; Granström 1988; van der Valk & Verhoeven 1988; van der Valk & Pederson 1989; McDonald 1993; Aerts *et al* 1995; McDonald *et al* 1996; Thompson *et al* 1997; Bekker *et al* 1998; Bakker & Berendse 1999; Smith *et al* 2002). For example, a significant number of researchers have focused on evaluating the dynamics of the soil seed banks under grasslands with respect to comparing the above-ground and below-ground species compositions (Rabinowitz 1981; Thompson 1986; Henderson *et al* 1988; Rice 1989; Kitajima & Tilman 1996; Kirkham & Kent 1997; Eriksson & Eriksson 1997; Davies & Waite 1998; Morgan 1998; Edwards & Crawley 1999), the part soil seed banks play in the maintenance of grassland diversity (Hillier 1990; Bullock *et al* 1994; Fowler 1994; Rusch & Fernádez-Palacios 1995; Willems 1996; Willems & van Nieuwstadt 1996; Bekker *et al* 1997; Bakker & Berendse 1999; Smith *et al* 2002), as well as assessment of the value of viable soil seed in restoring grassland from neglect or disturbance (Graham & Hutchings 1988a; Berendse *et al* 1992; Bakker *et al* 1996; McDonald *et al* 1996; Dutoit & Alard 1995; Davies & Waite 1998; Willems & Bik 1998; Hopkins *et al* 1999; Losvik 1999).

Agricultural 'improvement' of grassland clearly alters the above ground vegetation through ploughing, reseeding and fertiliser application (Rodwell 1992; Hopkins *et al* 1995). However, despite the above ground changes in vegetation, there can be a continuity of species composition laid down as seed within the mineral soil (Rabinowitz 1981; Thompson 1986; Henderson *et al* 1988; Thompson 1993; Davies & Waite 1998). Thus, it is possible that populations of species deleted from the above ground vegetation by intensive agricultural operations survive as soil seed banks (Hutchings & Booth 1996a; Bekker *et al* 1997; Willems & Bik 1997). Most of the few agriculturally 'desirable' grasses used in intensive agriculture, such as *Lolium perenne* and *Phleum pratense*, do not have long-term persistent seed banks (Thomspon & Grime 1979; Fenner 1985; Howe & Chancellor 1983; Grime *et al* 1988; Thompson *et al* 1997). This is in marked contrast to many of the agriculturally unwanted ones such as *Holcus lanatus*, *Poa annua* and *Agrostis* spp., which can be present in considerable numbers in the soil for decades, despite being virtually absent from the above-ground vegetation of newly agriculturally improved grassland (Grime 1981; Grime *et al* 1988; Thompson *et al* 1994; Thompson *et al* 1997; Rice 1989). It has been noted by researchers and farmers alike that the deterioration of improved swards i.e. ingress of non-sown species, is significantly facilitated by recrudescent 'weeds' regenerating from buried seed opportunely germinating and establishing when the soil is disturbed through stock trampling and machinery operations for example (Roberts 1981; Williams 1984; Howe & Snaydon 1986; Berendse *et al* 1992; Davies 1997).

For conservation restoration, the presence of seed from the pre-agricultural improvement communities may be an important element in encouraging diversification and /or rehabilitating desirable vegetation (Wilson 1994; Thompson *et al* 1997; Mitchell *et al* 1998; Willems & Bik 1998). Knowledge of the persistent soil seed bank enables the restorationist to decide whether the *in-situ* seed pool is an asset in re-establishing lost species, a neutral component, or even a liability (Fenner 1985; van der Valk & Pederson 1989; Davies & Waite 1998; Smith *et al* 2002). It has been noted in a number of studies that many indicator or target species of diverse grassland do not have long-term persistent soil seed banks (Hodgson & Colasanti 1995; Tallowin *et al* 1995; Hutchings & Booth 1996a; McDonald *et al* 1996; Willems & van Nieuwstadt 1996). The perennial forb species that are the most important component of old, species-rich swards usually persist as mature vegetative individuals, rather than dispersing in time by producing long dormant soil seed reserves (Grubb 1976; Thompson 1987; McDonald *et al* 1996; Davies & Waite 1998). Studies have shown that even annual and biennial components of old unimproved meadow grassland rarely seem to have persistent soil seed banks (van Hulst *et al* 1987; McDonald *et al* 1996; Thompson *et al* 1997). Thus, the seed bank of old swards may only contain a few graminoid species, and perhaps some immigrant weed species. Species-rich grasslands, which have been converted to high productivity agricultural swards, may inherit components of the former seed bank, though much of the evidence does suggest that even if target species do survive agricultural improvement as persistent seed in the soil, the depletion rate of these reserves will increase markedly, and the potential for restoration will diminish with each year (Hutchings & Booth 1996a; Bekker *et al* 1997). However, the evidence is still ambiguous, suggesting that further work needs to be undertaken to divulge whether, for grassland restoration after agricultural improvement, regeneration from the soil seed bank is a positive, neutral or negative factor. Consequently, this chapter is concerned with investigating the potential of the viable seed present within the soils of the experimental grassland plots described in **Chapters 2 & 3** for the restoration of conservation value to these species-depauperated swards (van der Valk & Pederson 1989). In addition, an attempt was made to quantify seasonality in seed bank populations in order to understand propagule flux as well as prediction of optimal timing for seed bank stimulation (Thompson & Grime 1979; Thompson 1993; Losvik 1999).

METHODS

The method used for sampling the viable seed in the mineral soil in each treatment subplot followed the standard seedling emergence procedure as used by many researchers (Thompson & Grime 1979; Donelan & Thompson 1980; Roberts 1981; Brown & Oosterhuis 1981: Brown & Warr 1992; Hutchings & Booth, 1996; Davies & Waite 1998). Direct germination (Gross 1990) basically consists of taking cores of soil of known volume, spreading the soil out on a bed of a suitable medium in pots or trays, and maintaining conditions favourable to seed germination. The seedlings can then be identified and counted as they emerge (Fenner 1985).

It is apparent from previous research that it can be difficult to obtain statistically adequate estimates of total buried seed densities from this method (Major & Pyott 1966; Hutchings 1986). However, as with the seminal work of Thompson & Grime (1979), and subsequent studies such as Davies and Waite (1998), the aim of this seed bank study was to quantify the ‘readily-germinable’ or ‘available’ component of the seed bank rather than total soil seed numbers (Roberts 1981; Fenner 1985; Hutchings 1986). Brown and Warr (1992) state that as long as appropriate conditions for germination are provided, the above general method of investigation produces good estimates of the seed bank with respect to species composition. However, Forcella (1984) found that in order to determine the number of species present in the seed bank of a grassland ley community, the combined surface area of replicate samples from any one treatment should be about 1000-cm^2. Within this precept, an effort was made to maximize the number of samples collected within practical means (Roberts 1981; Thompson 1993). Gross (1990) estimated that 15 to 20 sampling locations are sufficient to determine the number of species present in the seed bank (in an arable field). Extrapolating from these basic parameters, within each of the 13 subplots, 20 soil samples were extracted. The total area collected from each subplot was 565.5-cm^2, and total soil volume 4523.9-cm^3. Though, not essentially adequate for Forcella's estimations, these dimensions do exceed those recommended by Hayashi & Numata (1971) as necessary for the detection of most species present in grassland seed banks.

One of the main aims of this study was the quantification of seasonality in seed bank germination dynamics (Hutchings 1986). In order to analyse these seasonal differences in the composition of the viable seed found in the soil of the experimental grassland plots it was necessary to take this into account in the sampling procedure (Thompson & Grime 1979). The soil samples were therefore collected during each of the four seasons: autumn (October 1994); winter (January 1995); spring (May 1995); and summer (August 1995). The August and October samples were expected to contain a high proportion of seed of species, which primarily form *transient* seed banks (Thompson and Grime 1979; Thompson 1993). In comparison, the samples taken in January and May were expected to contain a higher proportion of seed of species, which exhibit at least short-term persistent soil seed banks (Thompson 1993). Within each 20-m x 30-m subplot (including plot 5), 20 randomly selected sampling positions were located using random-walk co-ordinates generated by computer. Cores were gathered using a steel bulb planter (diameter 6-cm), which was worked into the ground by hand. The planter was then pulled from the ground and the soil core pushed out by hand, and placed in individual polythene bags. The cores were 8-cm long, and 226.2-cm^3 in volume, though the absolute volume of mineral soil did vary with the proportion of stones and other extraneous material such as roots. A variation of the Thompson and Grime (1979) method was used to promote seed germination. Each sample was air-dried to reduce possible soil predators and pathogens that were present, and then sieved through a griddle with 5-mm mesh. This removed the stones, shoots and roots, as well as breaking down the lumps to increase the surface area for germination. The prepared soil was then placed on a bed of coconut fibre compost in a 9-cm pot. It was necessary to spread the soil to an even depth. However, the soil layer often exceeded this depth, and was on average between 15-mm and 20-mm. Because most seed is released from enforced dormancy after exposure to light (Fenner 1985; Hutchings 1986), the soil was later recrumbled to expose as much of the soil as possible to full light conditions in an effort to ensure as complete a germination as possible. Ten control pots of pure coconut fibre were also included to test for airborne seeds, which might enter the greenhouse. The twenty pots per subplot were then put in Empot trays and placed on the floor of an unheated polytunnel. Metaldehyde slug pellets had to be used around the pots to prevent predation by molluscs, especially *Deroceras* spp., *Arion* spp., *Cepaea* spp., and *Helix aspersa*.

The method used by Thompson and Grime for optimal seed germination required the use of carefully controlled greenhouse conditions, such as 16 hours of light at 20 ^{o}C and 8 hours of dark at 15 ^{o}C. Because of limited facilities, it was not possible to conduct such strict regimes. Consequently, samples were placed in an unheated polytunnel and kept moist by regular watering. Obviously, throughout the seasonal study periods there were significant variations in ambient polytunnel temperature. Though this made it impossible to determine critical temperature regimes for species germination, it did mean that the seeds, in general, were exposed to widely fluctuating temperatures, and these conditions more closely mimic the natural conditions that aid the breaking of seed dormancy (Fenner 1985). This was the preferred method used by Brown & Oosterhuis (1981).

Surveillance of the soil samples was undertaken at regular intervals. As the seed germinated, the seedlings were identified and then removed. Species that were not easily identifiable from an early growth stage were removed and grown on in 9-cm pots until they were mature enough to be identified. In order to make identification of the grass species seedlings easier, seed of known species origin was sown onto compost in pots in order to act as voucher specimens for comparison. Due to practical limitations, the soil samples were kept for approximately 4 months, even though the majority of the available seed probably had germinated within the first 4 weeks (Thompson & Grime 1979; Graham & Hutchings 1988a). Compared to many other studies (Roberts, 1981), this germination test period was quite short. However, this period was considered long enough in order to evaluate the extent of the germinable part of the seed bank (*sensu* Thompson & Grime

1979), and estimate potential restoration worth (van der Valk & Pederson 1989; Davies & Waite 1998).

Distribution of the viable seed with soil depth

In May 1995, along with the full set of soil samples from each subplot, a further 5 cores per subplot were taken in order to test whether differences in seed populations occurred with soil depth (Williams 1984; Granström 1988; Thompson *et al* 1997). These samples were taken at greater depth than the other cores (10-cm), and divided in half i.e. separation of the top 5-cm and the bottom 5-cm of soil. These sections were then prepared as for the other soil cores and spread over compost in separate 9-cm pots.

Data analysis

Apart from the basic quantification of the readily germinable seed banks from the soil of each of the subplots, the two main important aspects of the work were to compare the similarity between above ground vegetation composition and that of the species below ground in the soil seed bank, and seasonality in seed bank composition. Most of the analyses were undertaken using cluster analysis and Detrended Correspondence Analysis in order to assess similarities between the datasets (Kent & Coker 1992). Both techniques were performed using the computer program *Multi- Variate Statistical Package ver 3.0* (Kovach 1998). The clustering method used was UPGMA centroid similarity analysis, the results presented as both matrices and dendrograms (Kovach 1998). The DCA results are presented as scatterplots. Canonical Correspondence Analysis was also applied to the total seed bank dataset and environmental soil variables (nitrogen, phosphorus, potassium, organic matter & pH), and presented as a biplot with vectors for the environmental data (ter Braak 1987). Species rank-abundance plots (Ludwig & Reynolds 1988; Magurran 1988) were used to examine the seasonal changes in seed bank dominance and diversity. Calculating Shannon's diversity indices for the same data further elucidated this aspect. Correlations between seed bank size and environmental gradients were examined using Pearson Correlation Coefficient (r) (two-tailed), and least-squares linear regression (Norušis 1998).

RESULTS

Combining all seedling counts from all of the four seasonal surveys, a total of 16,173 seedlings were recorded, comprised of 69 species. Of this species total, 16 (23%) were grasses (including *Carex flacca*) and 53 (77%) forbs. However, when presented in terms of seedling abundance, the hierarchy is reversed, with grasses amounting to 12,908 (79%) and forbs 3,265 (21%) (see **Figure 5.01a**). The proportion of forb to grass seedlings was approximately 4:1, with grass seedling emergence peaking in subplots 1-3, with forbs remaining relatively constant. Only for subplot 13, the species-rich sward, are forb seedlings more numerous than grasses. A breakdown of the proportion of forb to grass species along the subplot gradient (**Figure 5.01b**) shows a far less consistent pattern than for seedling numbers. For the three analysis strata, the trend is essentially linear, with species numbers comparatively unvarying along the gradient. The species composition is seen to change but the species number remains relatively constant, again, apart from Subplot 13. The top 20 most common species emerging from the soil samples are shown in **Table 5.01**.

Figure 5.01 Grand totals for **a)** seedlings and **b)** species counts for all subplots, for all seasons; counts split into forbs and grasses (including *Carex flacca*) to show relative proportions.

a) **b)**

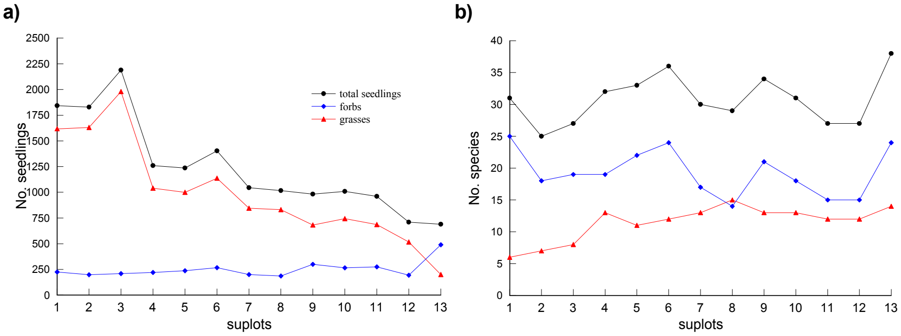


Table 5.01 Top 20 most abundant seedling species recorded from all soil samples.

Seedling species	Total counts for each species	As percentage of grand total of all seedlings
Poa trivialis	5682	35.1
Poa annua	1889	11.7
Holcus lanatus	1789	11.1
Lolium perenne	1417	8.8
Agrostis stolonifera	1234	7.6
Ranunculus bulbosus	485	3.0
Ranunculus acris	332	2.0
Urtica dioica	323	1.9
Dactylis glomerata	307	1.8
Arrhenatherum elatius	253	1.5
Leucanthemum vulgare	238	1.4
Taraxacum officinale	196	1.2
Trifolium repens	168	1.0
Cerastium fontanum	143	0.8
Festuca arundinacea	140	0.8
Bromus hordeaceus	103	0.6

Polygonum aviculare	96	0.5
Rumex obtusifolius	89	0.5
Cynosurus cristatus	80	0.4
Festuca rubra	79	0.4

Although forbs dominate the soil seed bank in terms of species richness, grasses predominate in terms of numbers, as also found by Edwards & Crawley (1999). The first five places are grass species, the first three of which are considered to be components of the long-term persistent soil seed bank (Thompson 1993). *Lolium perenne* was prominent, though generally considered a transient seed bank former (Grime 1981; Grime *et al* 1988). The huge numbers of seed generated during the summer, germinating in the August and October sampling periods, may explain this result. *Ranunculus acris* and *R. bulbosus* are the most important forb species in terms of germination from the mineral soil. Sarukhán (1974) suggests that neither species forms a long-term persistent seed bank, however Grime *et al* (1988) indicate that there may be greater capacity for persistence in the soil than Sarukhán predicts.

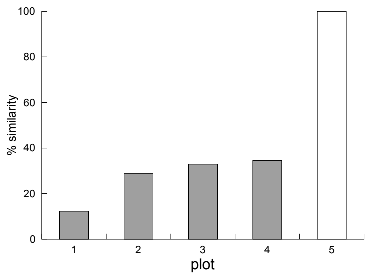
Air-borne seed contamination was recorded for *Epilobium* spp. and *Salix* spp. Seven *Epilobium ciliatum* and one *Salix cinerea* seedling grew from the compost-only-control pots, from July 1995, therefore prompting some doubts concerning the origins of the seed germinating from the soil samples. These may have generated from around the polytunnel area, though *Epilobium ciliatum* continued to germinate from soil samples taken from other times of the year.

Because the viable soil seed was censused in 1994-5 before the management treatments could be expected to have had a major impact on vegetation dynamics of the experimental subplot structure, seed bank analysis was applied to the *a priori* plot-by-plot basis of the study i.e. the gradient of agricultural improvement from Plot 1 to Plot 5. **Table 5.02** presents the half-matrix results of similarity (UPMGA - centroid) cluster analysis (Kovach 1998) applied to totalised abundances of all seed bank species from the four seasons of data collection. In addition, **Figure 9.02** graphically demonstrates the total plot seed bank similarity with the reference seed bank population (White & Walker 1997).

Table 5.02 Similarity half-matrix comparing plots.

Similarity matrix					
	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5
Plot 1	100				
Plot 2	63.636	100			
Plot 3	32.882	53.413	100		
Plot 4	24.012	46.78	74.657	100	
Plot 5	12.312	28.708	32.961	34.556	100

Figure 5.02 graphically shows the percentage similarity of each plot with the reference community (Plot 5).



Clearly there is a gradient of similarity from Plot 1 to Plot 4. However there is little change in similarity between Plots 2 to 4, and the seed bank of Plot 4 has only a 34% similarity with the reference community, indicating that a large proportion of species found in Plot 5 are of low abundance or missing from the agriculturally improved grasslands. **Table 5.03** provides a more detailed account of the species composition of the seed banks of each of the agriculturally improved plots in relation to Plot 5, the reference community. According to Hodgson *et al* (1995) 27.5% of the recorded species are transient; 14.5% short-term persistent; and 58% long-term persistent seed bank formers. The *desirability* of each species was determined by noting its inclusion or not in commercial wildflower meadow seed mixtures (van der Valk & Pederson 1989). Although included in many seed mixtures, most grasses were viewed as neutral unless restricted to unproductive grasslands.

Table 5.03 Restoration value of soil seed banks of each improved plot in relation to the seed bank of the restoration reference community Plot 5.

Species	**Seed Bank**[1]	**Plot 5**	Plot 1	Plot 2	Plot 3	Plot 4
Achillea millefolium	1			#*		

Agrostis stolonifera	3	~	~	~	~	~
Alopecurus pratensis	1			#	#	#
Anagallis arvensis	3		#			#
Arrhenatherum elatius	1	~	~	~	~	~
Bellis perennis	2	~	~	~	~	~
Briza media	1	*				
Bromus hordeaceus	1			#	#	#
Capsella bursa-pastoris	3		#	#		
Carex flacca	3	*				
Centaurea nigra	2	*			*	*
Cerastium fontanum	3	~	~	~	~	~
Chenopodium album	3		#		#	
Cirsium arvense	3		# (-)	# (-)	# (-)	# (-)
Cirsium vulgare	2		# (-)	# (-)	# (-)	# (-)
Coronopus didymus	3		#			
Cynosurus cristatus	1	*		*	*	*
Dactylis glomerata	1	~	~	~	~	~
Elytrigia repens	3		#	#	#	#
Epilobium hisurtum	3		#	#		#
Epilobium spp.	3	~	~	~	~	~
Euphorbia helioscopia	3		#	#		
Festuca arundinacea	1	~	~	~	~	~
Festuca rubra	1	~	~	~	~	~
Fumaria officinalis	3		#			
Geranium dissectum	2			#	#	#
Helictotrichon pubescens	1	*				
Heracleum sphondylium	1				#	#
Holcus lanatus	3	~	~	~	~	~
Hypochoeris radicata	2	*			*	
Knautia arvensis	1	*				
Lamium purpureum	3		#	#		
Leontodon hispidus	2	*		*		
Leucanthemum vulgare	3	*	*	*	*	*
Linum catharticum	3	*				
Lolium perenne	1	~	~	~	~	~
Lotus corniculatus	3	*				
Phleum pratense	3			#	#	#
Pimpinella saxifraga	1	*				
Plantago lanceolata	3	*		*		*
Plantago major	3		#	#	#	#
Plantago media	2	*		*	*	*
Poa annua	3	~	~	~	~	~
Poa trivialis	3	~	~	~	~	~
Polygonum aviculare	3		#	#		#
Primula veris	1			# *		
Prunella vulgaris	3	*				
Ranunculus acris	2					*
Ranunculus bulbosus	3	*	*	*	*	*
Ranunculus ficaria	1				*	*
Rumex acetosa	2			~	~	~
Rumex obtusifolius	3		# (-)	# (-)	# (-)	# (-)
Salix spp.	1			~	~	~
Salvia verbenaca	1		# *			
Sambucus nigra	3	~	~	~	~	
Sanguisorba minor	3	*	*	*		
Senecio jacobea	3			# (-)		
Senecio vulgaris	3	~	~	~	~	~
Sinapis arvensis	3		#			
Solanum nigrum	3		#	#		
Sonchus asper	3	~	~	~	~	~
Stellaria media	3	~	~		~	~
Taraxacum officinale	2	~	~	~	~	~
Trifolium pratense	3	*		*	*	*
Trifolium repens	3	~		~	~	~
Trisetum flavescens	1	*				
Urtica dioica	3	**(-)**	(-)	(-)	(-)	(-)
Veronica persica	3		#			
Veronica serpyllifolia	3			#*		#*

***** = positive seed bank component: also found in the reference community (Plot 5)
~ = neutral seed bank component: also found in the reference community (Plot 5)
(-) = negative seed bank component: also found in the reference community (Plot 5)
= neutral seed bank component: not found in the reference community (Plot 5)
 # * or **# (-)** = positive or negative seed bank components: not found in reference community (Plot 5)
Where symbols in red, seed probably derived from initial implants rather than *natural* occurrence
Seed Bank[1] = classification determined by Hodgson *et al* (1995): 1=transient; 2=short-term persistent; 3=long-term persistent

Clearly not all the species of Plot 5 are specific to unimproved species-rich grassland, thus those that are considered to be specifically 'positive', 'neutral' or 'negative' restoration components are annotated a such. As identified by the cluster analysis (**Figure 5.04**), it is clear that the soil seed bank of the improved plots contains few species in common with the reference community. Of those species that are in common, few are specifically desirable restoration components, and are only broadly classifiable as desirable such as *Cynosurus cristatus* and *Ranunculus bulbous*

Figure 5.03 Average soil seed bank persistence score (Hodgson *et al* 1995)

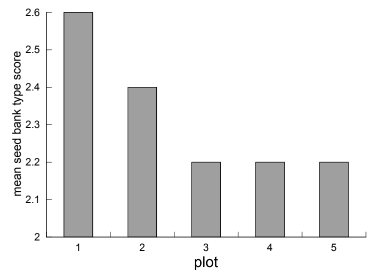
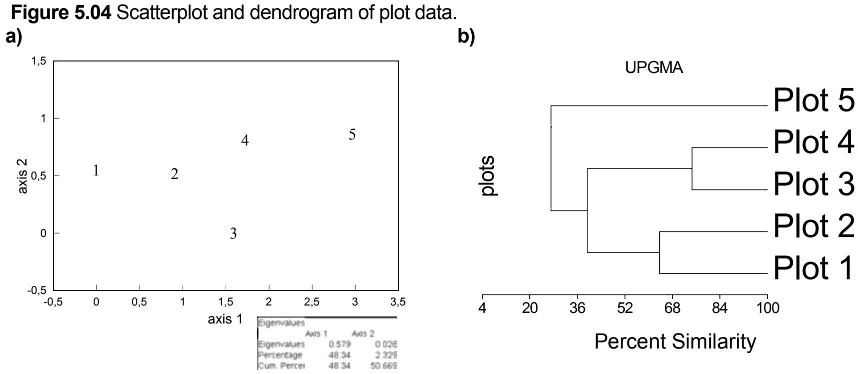


Figure 5.04a is a scattergram of the results of Detrended Correspondence Analysis of the total plot-by-plot seed bank data. The Plots are clearly separated along axis-1, with the linear trend following the projected sequence from Plot 1 through to Plot 5. This gradient can be explained generally in terms of the decline in more ruderal species; the proportion of grass seedling abundance to forbs; and the changes in species composition with vegetation succession. There is little dispersion along axis-2, though Plot 3 is clearly offset from the other Plots. This deviation is probably due to the much higher abundances of *Holcus lanatus* and *Ranunculus bulbosus* emerging from the soil samples of Plot 3 compared to the other

Figure 5.04 Scatterplot and dendrogram of plot data.



Plots. The dendrogram of **Figure 5.04b** represents the results of % similarity cluster analysis of the same data set, and offers a similar sequence of plot delineation as the DCA. The linkage between Plots 1 and 2 shows the strong association between the two must improved grassland communities in terms of soil seed bank. The linkage between Plots 3 and 4 establishes this dichotomy. As **Table 5.02** shows, there is limited similarity between Plot 5 and the others. The dendrogram illustrates this fact as the primary node of division is between Plot 5 and the other Plots at 27% similarity.

Correlations with soil fertility and productivity

Table 5.04 presents the results of Pearson Correlation Coefficient (*r*) results for the total and seasonal subplot soil seed bank results, and a range of soil fertility and sward productivity parameters. Sward productivity was measured using a weighted disk method (Frame 1981) (see **Chapter 4**). For the total seed bank inventory, the notable very significant positive correlations are with soil phosphorus and potassium concentrations (see **Figure 5.05**), as well as with sward height/phytomass (see **Figure 5.05c**). These results indicate that soil seed abundance is positively related to these macronutrients, which in turn correlates with sward productivity i.e. the greater the sward productivity, the greater the seed input (especially grass seed) into the soil reservoir.

Table 5.04 Correlations between total subplot soil seed bank size and productivity factors.

		Total Seed	OM	PH	K	P	N	Sward Height 1994	Sward Height 1995	Subplot	No. Species
Total Seed	Pearson Correlation	1.000	-.366	.063	.858**	.871**	-.437	.916**	.167	-.893**	-.344

** Correlation is significant at the 0.01 level (2-tailed).

The very significant negative relationship between total soil seed and subplot number (see **Figure 5.05a**) reflects the predicted gradient of grassland improvement, with highest seed productivity related to the lowest numbered but most improved subplots (Subplots 1-3), and lowest soil seed input related to highest subplot numbers (especially Subplot 13). This same correlation pattern is essentially repeated for the October and August soil seed bank surveys. However for the January and May inventories there is more variability. For the January results there is a significant negative correlation with total soil nitrogen levels, and non-significant correlations with phosphorus, sward height and subplot. Similarly, for the May inventory, there is again a significant negative correlation with total soil nitrogen, though the other parameters are significantly positively correlated.

Table 5.05 Results of stepwise linear regression for seed bank explanatory variables.

Variables Entered/Removed

Model	Variables Entered	Variables Removed	Method
1	SWARD94	.	Stepwise (Criteria: Probability-of-F-to-enter <= .050, Probability-of-F-to-remove >= .100).

a Dependent Variable: TOTLSEED

Model Summary

Model	R	R Square	Adjusted R Square	Std. Error of the Estimate
1	.916	.839	.824	191.7384

a Predictors: (Constant), SWARD94

ANOVA

Model		Sum of Squares	df	Mean Square	F	Sig.
1	Regression	2102979.050	1	2102979.050	57.203	.000
	Residual	404399.873	11	36763.625		
	Total	2507378.923	12			

a Predictors: (Constant), SWARD94
b Dependent Variable: TOTLSEED

Coefficients

		Unstandardized Coefficients		Standardized Coefficients	t	Sig.
Model		B	Std. Error	Beta		
1	(Constant)	-273.731	207.608		-1.318	.214
	SWARD94	53.346	7.053	.916	7.563	.000

a Dependent Variable: TOTLSEED

Multiple linear stepwise regression (**Table 5.05**) confirmed that productivity as measured by Sward Height (see **Chapter 4**) in 1994 was the most significant factor in explaining total seed bank size. All variables (NPK, Ph, OM, Subplot, Species No., Sward 1995 & Sward 1994) accounted for 99.1% prediction.

Figure 5.05 Scatterplots with fitted linear regression curves illustrating the main significant correlation relationships. Figure 5.05d column chart shows seed bank total per subplot.

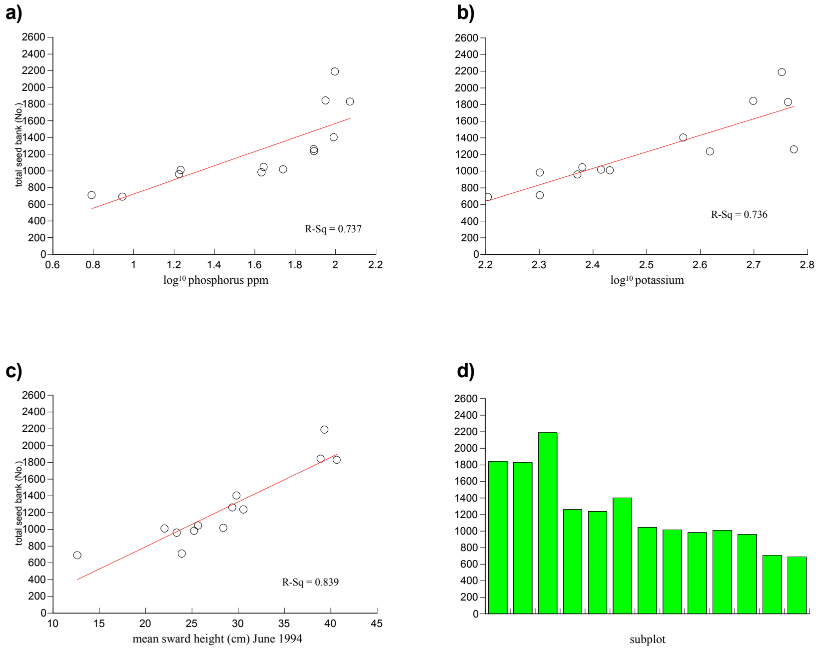
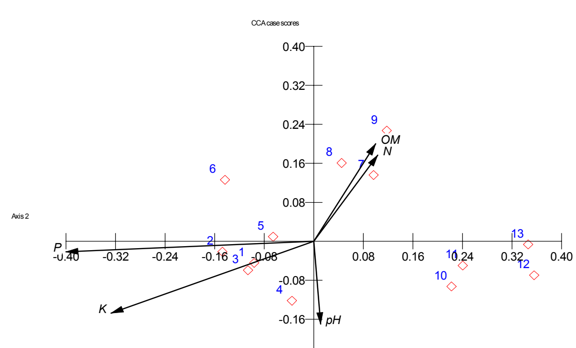


Figure 5.06 Biplot of CCA results for seed bank and environmental data (vectors).



	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.024	0.01	0	0
Percentage	68.75	28.012	0.489	0.01
Cum. Percentage	68.75	96.762	97.251	97.261
Cum.Constr.Percentage	70.686	99.487	99.99	100
Spec.-env. correlations	0.99	0.979	0.936	0.968

In view of the highly significant correlations between P and K and total subplot seed bank abundances, Canonical Correspondence Analysis was applied, and the results presented in **Figure 5.06**. The strength of the P and K influence is clearly defined by the length of the vectors, and particularly for phosphorus, showing a linear response along axis-1. The subplots with the most species-rich soil seed banks (and above ground vegetation) are clearly clustered in opposition to the strong P vector, and K vector to a lesser degree, whereas the subplots with the least species-rich seed banks are more allied with P and K soil concentrations, probably reflecting the highly dominant grass component. Markedly, the subplots of plot 3 (subplots 7-9) are allied with the correspondent variables of nitrogen and organic matter, strongly suggesting that the seed bank composition of these subplots is significantly influenced by these nutrient factors e.g. *Holcus lanatus* abundance.

Comparisons with above ground vegetation

Table 5.06 shows the results from a % similarity (UPMGA - centroid) cluster analysis (Kovach 1998) composed in order to compare the above ground vegetation and viable soil seed bank vegetation. The most pertinent results are the similarities between Plot5

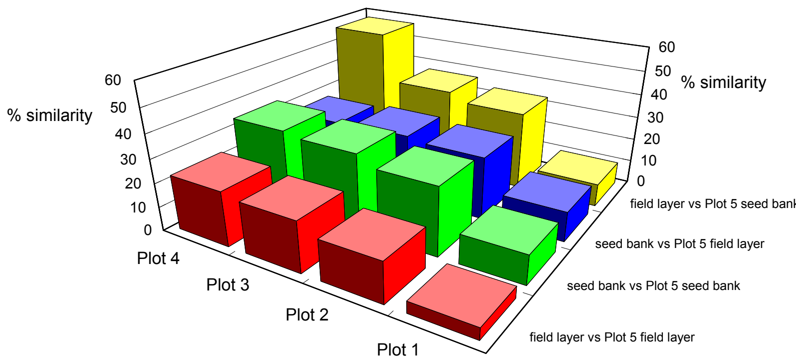
Table 5.06 Similarity half-matrix: comparison between field layer vegetation as determined by % cover abundance (1994) and soil seed bank composition, calculated on a Plot by Plot basis. Fly = field layer; SB = soil seed bank

Similarity matrix

	Plot 1 Fly	Plot 2 Fly	Plot 3 Fly	Plot 4 Fly	Plot 5 Fly	Plot 1 SB	Plot 2 SB	Plot 3 SB	Plot 4 SB	Plot 5 SB
P1ot 1 Fly	100									
Plot 2 Fly	40.5	100								
Plot 3 Fly	18.1	49.1	100							

Plot 4 Fly	11.1	50.4	66.1	100						
Plot 5 Fly	4.8	16.8	21.2	22.9	100					
Plot 1 SB	41.3	27.4	15.2	9.6	2.9	100				
Plot 2 SB	41.1	47.7	37.6	33.1	10.5	63.6	100			
Plot 3 SB	27.8	31.2	35.6	36.6	9.7	32.8	52.6	100		
Plot 4 SB	22.7	37.5	43.3	57.1	11.0	24.0	46.7	73.8	100	
Plot 5 SB	12.6	26.4	27.9	26.6	29.6	12.3	28.7	32.9	34.5	100

Figure 5.07 illustration of % similarity of Plots 1-4 seed banks and field layers with reference community (Plot 5) seed bank and field layer.



the reference community and the other four plots. Most notably, as would be predicted, Plot 1 has the consistently lowest similarity with both the Plot 5 field layer and seed bank. There is also relatively little discrimination between Plots 2-4 and the floristic aspects of Plot 5, apart from the Plot 4 field layer has a curiously high similarity with Plot 5s seed bank. These results are also represented in the form of a dendrogram (**Figure 5.08a**). In order to broaden the scrutiny, Detrended Correspondence Analysis was applied to the same data set, and plotted as a scattergram **Figure 5.08b**. The most significant aspect of these results is the clear polarities between both seed banks and field layers of Plot 1 and Plot 5. In the DCA **Figure 5.08b** there is a clear separation along axis-1, with field layer and seed bank of Plot 1 distributed to the left of the graph and field layer and seed bank of Plot 5 located to the right. However, there is also a significant separation of all data along axis-2. Most seed bank studies indicate that the seed bank vegetation differs markedly from the above-ground vegetation (Thompson 1986; Eriksson & Eriksson 1997), and this distribution exhibits the same basic division, with all seed bank datasets located in the upper half of the chart and the field layer data-sets in the lower half. The major divisions in the dendrogram (**Figure 5.08a**) are between Plot 1 and Plot 5 both in terms of field layer and seed bank. Thus, the seed bank of Plot 5, the species-rich sward, seems to have more in common with the above ground vegetation of the same plot than the seed banks of the four agriculturally improved plots. This indicates that for restoration purposes, once species-rich grassland is modified by agricultural improvement, the restorative potential of the seed bank is also irreparably damaged.

Figure 5.08 Multivariate comparisons of seed bank flora (seedling number) with field layer (% cover-abundance): **a)** cluster analysis dendrogram; **b)** DCA scattergram.

a) **b)**

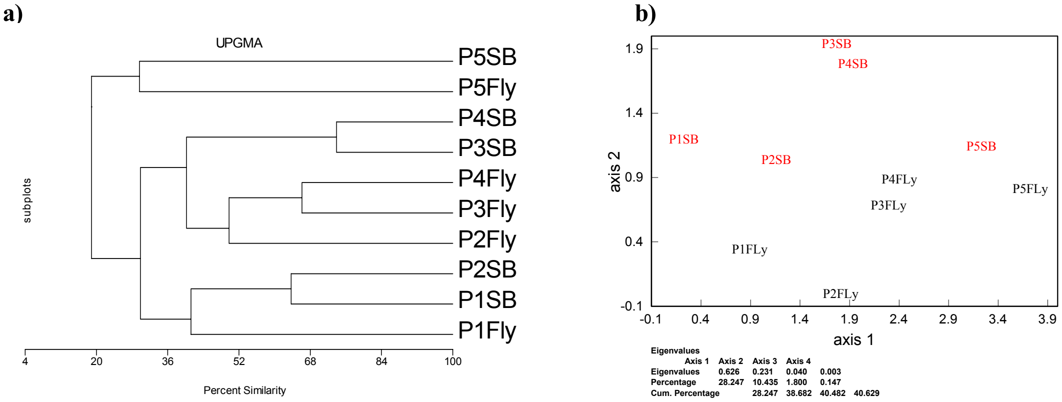


Table 5.07 Comparisons of seed bank with field layer flora. Unlike **Table 5.06**, a contrast is made between % similarity cluster scores for pure species composition comparisons, with the scores above for species occurrence including abundance weightings. The species only scores were calculated by giving species found in both seed bank and field layer the same abundances.

% Similarity	Species only (same abundances)	Species + actual abundances
Plot 1	73.7	41.3
Plot 2	93.2	47.7
Plot 3	96.5	35.6
Plot 4	91.8	57.1
Plot 5	29.6	29.6

While **Table 5.06** shows that there is a clear discrepancy of 40-70% dissimilarity between plot field layer and seed bank vegetation, by down-weighting the importance of relative abundance in the analysis, perhaps a clearer comparison between species compositions can be made. **Table 5.07** gives the % similarity scores for field layer vs. seed bank both in terms of species similarity and species-abundance similarity. The discrepancies so clear in the abundance calculations seem to become minimal for Plots 2-4 in the abundance down-weighted analysis. Plot 1 still shows some degree of differentiation with 26% dissimilarity, however Plot 5 demonstrates exactly the same high discrepancy for both analyses. The direct interpretation from these results is that for Plots 1-4, whilst the abundances of the different species show clear differentials, the species compositions of the seed bank and field layer floras are very similar. That is except for Plot 5, which shows dissimilarity more typical of older grassland (Thompson 1986).

Table 5.08 Species recorded in seed banks but not in field layers

Anagallis arvensis	*Salvia verbenaca*
Capsella bursa-pastoris	*Salix* spp.
Chenopodium album	*Sambucus nigra*
Coronopus didymus	*Senecio vulgaris*

Epilobium hirsutum	*Sinapis arvensis*
Epilobium spp.	*Solanum nigrum*
Fumaria officinalis	*Stellaria media*
Lamium purpureum	*Veronica persica*
Plantago major	*Veronica serpyllifolia*
Polygonum vulgare	

Red = probably contaminants

A number of species found in the total seed bank inventory were not found in any of the grassland subplots. These are listed below in **Table 5.08**. Nearly all of these species were recorded from the soil samples of Plot 1 – the MG7 *Lolium perenne* ley grassland. Most are usually described as arable weeds or ruderals, and known to produce long-term persistent seed banks. These species, while not usually present in the dense sward of the intensively managed agricultural grassland, can germinate spontaneously as a consequence of soil disturbances from grazing animals (e.g. hoof scuffs and skids), but most consistently when the ley is regularly destroyed, ploughed and re-seeded. Otherwise, the *Epilobium* spp. and *Salix* spp. were either dispersed by wind into the soils of the experimental grassland plots, or airborne contaminants of the germination treatments. *Sambucus nigra* was probably vectored through bird droppings, and *Salvia verbenaca* seed came from transplants, which had set seed prior to insertion in the spring of 1994.

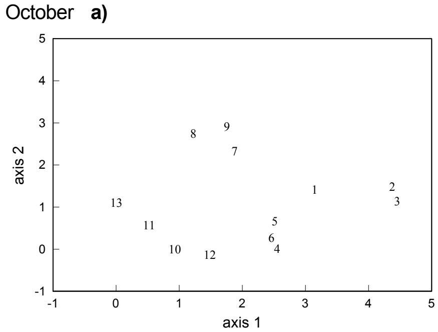
Seasonal differences in seedling emergence

Seasonality, or phenology of soil seed bank composition is an important factor influencing the relative abundance of the above-ground vegetation. As Thompson & Grime (1979) first quantified and Thompson (1993) abridged, viable seed within the soil can be broadly separated into transient, short-term persistent; and long-term persistent. For habitat restoration purposes it is of paramount importance to identify which components of the soil seed bank at any one point of the year will be transient or permanent features of vegetation regeneration after historical or contemporary perturbation events. This research complies with this approach as soil samples were taken at points during each of the four seasons. The results of these seasonal seedling emergence tests are analysed with DCA on a subplot basis (**Figure 5.09**) and a species basis (**Figure 5.10**). The subplot results indicate how the seed bank totality evolves during the year. The species results suggest the degree to which the abundances of different species alter their hierarchies in the annual cycle. Probably most attention should be paid to the May results, which should represent the persistent seed component of the soil (Thompson & Grime 1979), and thus be most indicative of the restorative potential of the seed bank.

The distribution of the subplots along axis-1 in **Figure 5.09** maintains a basic constancy with regard to the *a priori* gradient of improvement (see **Chapter 2**). Thus throughout the year, Subplot 5 is a constant to the left of the graphs and the subplots of Plot 1, in particularly Subplot 3, are constants to the right. The subplots of Plots 3 and 4 were the most variable in position along axis-1 throughout the seasons. The order of subplot positions clearly alters with the season, though the scattergram patterns for October and August seem to be similar, as do those of January and May. This emphasises the fact that October and August soil samples had a larger component of grass seed, particularly the transient *Lolium perenne*, and overall higher grass seed abundance. By January and May, overall seed abundance had declined due to predation, pathogens, germination etc, and the remaining seed were persistent seed bank formers. Pattern in the y-axis is most distinct between the subplots of Plot 3, and subplots of Plot 4, which form a distinct gradient, especially in samples taken from January and May.

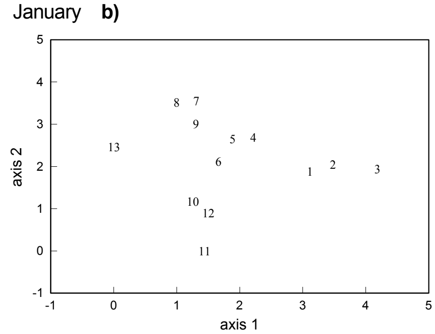
Figure 5.09 Detrended Correspondence Analyses of seasonal subplot seed bank data. Experimental subplots are numbered 1–13.

October **a)**



Eigenvalues	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.523	0.153	0.033	0.015
Percentage	36.742	10.774	2.308	1.041
Cum. Perce	36.742	47.516	49.824	50.865

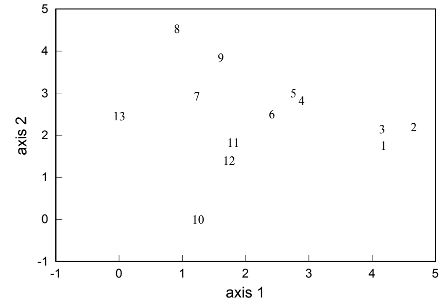
January **b)**



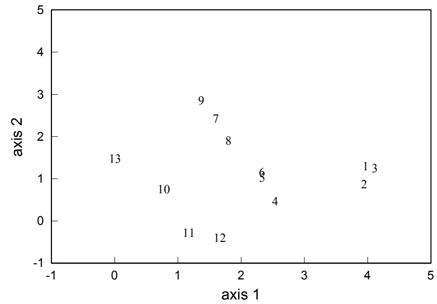
Eigenvalues	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.622	0.21	0.074	0.046
Percentage	30.48	10.298	3.63	2.265
Cum. Perce	30.48	40.777	44.408	46.673

May **c)**

August **d)**



Eigenvalues	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.632	0.147	0.082	0.036
Percentage	34.594	8.051	4.462	1.992
Cum. Perce	34.594	42.644	47.107	49.099



Eigenvalues	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.501	0.11	0.037	0.031
Percentage	35.501	7.764	2.632	2.216
Cum. Perce	35.501	43.264	45.896	48.113

Table 5.09 shows rankings of the 20 most abundant species for each of the seasonal censuses. What is most notable is the consistent dominance of *Poa trivialis* throughout the year maintained by very large persistent populations, compared to *Lolium*, which fluxes with annual seed production. Seed bank diversity seems to be at its highest during January and lowest during August. In August the dominance of the most abundant species is exacerbated by summer seed production. By January, most of the transient *Lolium* seed has germinated or died, and overall species abundances are at their lowest also due to germination and mortality factors, leading to greater evenness and higher diversity. These fluxes in seasonal abundance are also displayed in **Figure 5.10**. The patterns follow a similar linear trend to that of the subplot graphs. The arable weed species found the mostly in Plot 1 soils are clustered mainly to the right of axis-1 in all of the seasonal datasets. Species mostly found in the soils of species-rich Plot 5 are noticeably clustered to the left of axis-1.

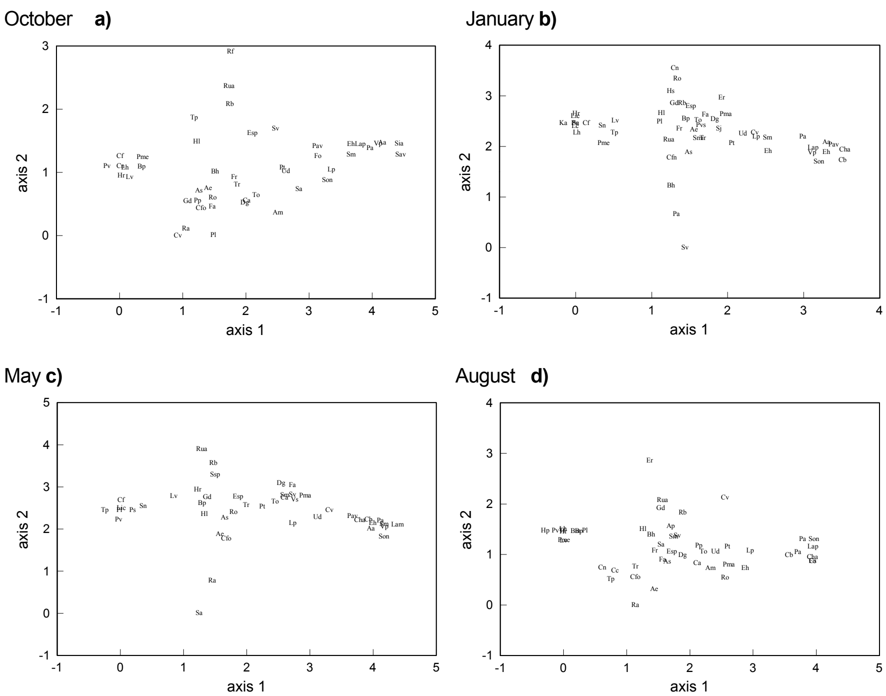
Table 5.09 Rank of the top 20 must abundant species (omitting Plot 5) from seasonal inventories. Also given are Simpson's *D* (dominance) index and Shannon *H'* (diversity) index.

October 1994	January 1995	May 1995	August 1995
2031 *Poa trivialis*	566 *Poa annua*	793 *Poa trivialis*	2484 *Poa trivialis*
897 *Lolium perenne*	393 *Poa trivialis*	689 *Poa annua*	602 *Holcus lanatus*
724 *Holcus lanatus*	293 *Agrostis stolonifera*	242 *Agrostis stolonifera*	351 *Lolium perenne*
345 *Agrostis stolonifera*	275 *Holcus lanatus*	125 *Holcus lanatus*	349 *Poa annua*
291 *Ranunculus bulbosus*	117 *Ranunculus acris*	76 *Lolium perenne*	313 *Agrostis stolonifera*
284 *Poa annua*	109 *Urtica dioica*	64 *Ranunculus acris*	125 *Ranunculus bulbosus*
175 *Dactylis glomerata*	86 *Lolium perenne*	56 *Ranunculus bulbosus*	114 *Ranunculus acris*
117 *Festuca arundinacea*	71 *Dactylis glomerata*	56 *Trifolium repens*	86 *Urtica dioica*
103 *Arrhenatherum elatius*	49 *Trifolium repens*	49 *Leucanthemum vulgare*	79 *Arrhenatherum elatius*
83 *Taraxacum officinale*	35 *Chenopodium album*	43 *Urtica dioica*	75 *Cynosurus cristatus*
78 *Urtica dioica*	34 *Polygonum aviculare*	35 *Arrhenatherum elatius*	58 *Epilobium spp.*
51 *Festuca rubra*	34 *Taraxacum officinale*	35 *Plantago major*	53 *Sonchus asper*
49 *Cerastium fontanum*	26 *Plantago major*	30 *Taraxacum officinale*	52 *Bromus hordeaceus*
48 *Rumex acetosa*	22 *Cerastium fontanum*	28 *Dactylis glomerata*	38 *Dactylis glomerata*
46 *Bromus hordeaceus*	21 *Arrhenatherum elatius*	27 *Geranium dissectum*	37 *Cerastium fontanum*

37 *Ranunculus acris*	18 *Rumex obtusifolius*	26 *Cerastium fontanum*	33 *Rumex obtusifolius*
36 *Trifolium repens*	16 *Capsella bursa-pastoris*	20 *Rumex obtusifolius*	30 *Taraxacum officinale*
23 *Lamium purpureum*	14 *Lamium purpureum*	19 *Anagallis arvensis*	26 *Trifolium repens*
23 *Leucanthemum vulgare*	12 *Rumex acetosa*	17 *Chenopodium album*	23 *Geranium dissectum*
19 *Ranunculus ficaria*	11 *Leucanthemum vulgare*	15 *Lamium purpureum*	19 *Festuca rubra*

	Index	Evenness	(calculated from total seed inventories rather than above abridged versions)					
D	0.814	0.833	0.871	0.891	0.810	0.831	0.733	0.750
H'	2.235	0.594	2.523	0.659	2.241	0.612	2.053	0.542

Figure 5.10 Detrended Correspondence Analyses of seasonal species seed bank data. Species abbreviations are given below[1]:



The January and May species patterns show a more compressed linearity along axis-1 compared to the autumn and summer data sets. Certainly the species forming the central cluster are more tightly clustered. This is probably representative of the diminution of soil

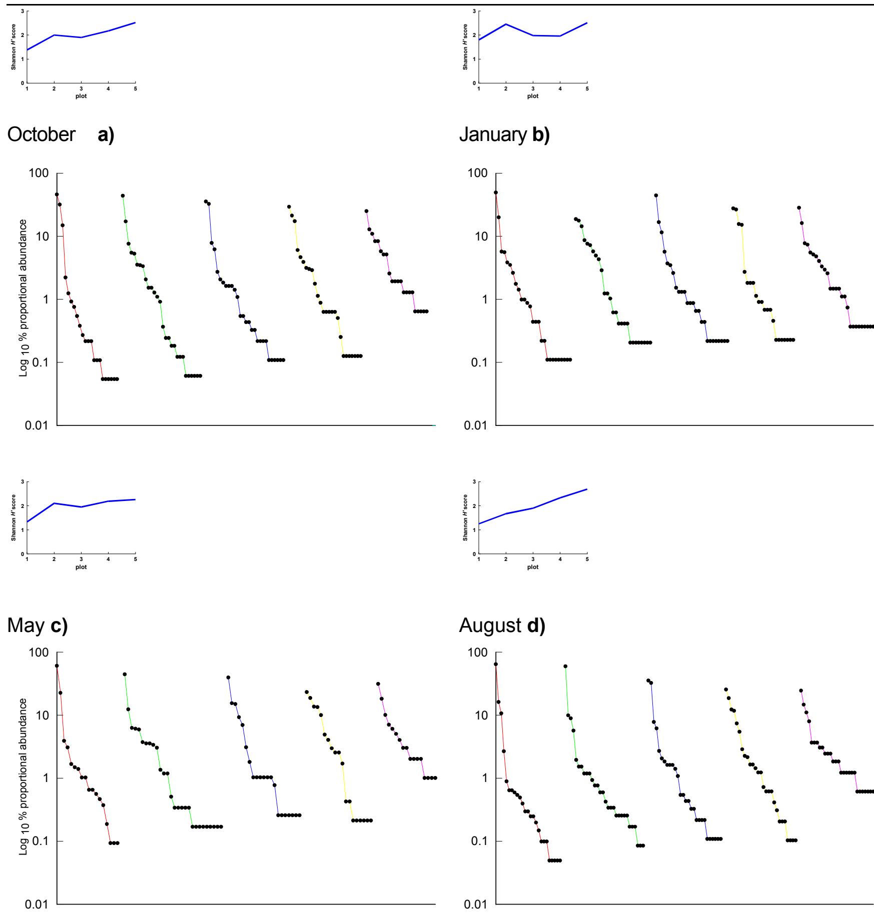
1

Achillea millefolium	Am	*Elytrigia repens*	Er	*Lotus corniculatus*	Lc	*Sanguisorba minor*	Smi
Agrostis stolonifera	As	*Epilobium hirsutum*	Eh	*Pimpinella saxifraga*	Ps	*Sambucus nigra*	Sn
Alopecurus pratensis	Ap	*Epilobium spp.*	Esp	*Phleum pratense*	Pp	*Senecio jacobea*	Sj
Anagallis arvensis	Aa	*Euphorbia heliscopia*	Eh	*Plantago lanceolata*	Pl	*Senecio vulgaris*	Sv
Arrhenatherum elatius	Ae	*Festuca arundinacea*	Fa	*Plantago major*	Pm	*Sinapis arvensis*	Sia
Bellis perennis	Bp	*Festuca rubra*	Fr	*Plantago media*	Pme	*Solanum nigrum*	San
Briza media	Bm	*Fumaria officinalis*	Fo	*Poa annua*	Pa	*Sonchus asper*	Sa
Bromus hordeaceus	Bh	*Geranium dissectum*	Gd	*Poa trivialis*	Pt	*Stellaria media*	Sm
Capsella bursa-pastoris	Cb	*Helictotrichon pubescens*	Hp	*Polygonum vulgare*	Pav	*Taraxacum officinale*	To
Carex flacca	Cf	*Heracleum sphondylium*	Hs	*Primula veris*	Pvs	*Trifolium pratense*	Tp
Centaurea nigra	Cn	*Holcus lanatus*	Hl	*Prunella vulgaris*	Pv	*Trifolium repens*	Tr
Cerastium fontanum	Cfo	*Hypochoeris radicata*	Hr	*Ranunculus acris*	Ra	*Trisetum flavescens*	Tf
Chenopodium album	Cha	*Knautia arvensis*	Ka	*Ranunculus bulbosus*	Rb	*Urtica dioica*	Ud
Cirsium arvense	Ca	*Lamium purpureum*	Lap	*Ranunculus ficaria*	Rf	*Veronica persica*	Vp
Cirsium vulgaris	Cv	*Leontodon hispidus*	Lh	*Rumex acetosa*	Rua	*Veronica serpyllifolia*	Vs
Coronopus didymus	Cd	*Leucanthemum vulgare*	Lv	*Rumex obtusifolius*	Ro		
Cynosurus cristatus	Cc	*Linum catharticum*	Lic	*Salvia verbenaca*	Sav		
Dactylis glomerata	Dg	*Lolium perenne*	Lp	*Salix spp.*	Ssp		

seed abundance for all species in this winter-spring period, leading to a less dispersed pattern.

Figure 5.11 demonstrates the changes in soil seed bank dominance-diversity over the four seasons. The curves of Plots 1 and 2 seem to show the most variability throughout the year. The October and August soil samples demonstrate greater dominance due to the high, but relatively ephemeral input of grass seed, particularly from the transient *Lolium perenne*. In comparison, the curves for January and May seem to even out, indicating the effect of dominant persistent, and consistent seed bank formers throughout the plot gradient, such as *Poa* spp., *Holcus lanatus* and *Agrostis stolonifera*. Not surprisingly, the species-rich reference community confounds the trend somewhat by having a seed bank against the general trend with a significantly lesser graminoid component, and far more dominant forb species, thus lessening the overall dominance spectrum by grass species (excluding *Carex flacca*). The overall pattern is amplified by the calculation of Shannon index scores, which are added as inset graphs. The diversity scores for October, and particularly August, show a definite gradient of seed bank diversity along the *a priori* gradient. Many of these species, especially the most *restoration* desirable components, are, however, transient seed bank formers. During January and especially May, the Shannon index curves are flatter, indicating that the persistent seed bank of the plots are far more similar than the transient components. The extrapolation is that the long-term restoration potential of the soil seed banks of the less improved grasslands is little different to the most eutrophied and disturbed grasslands.

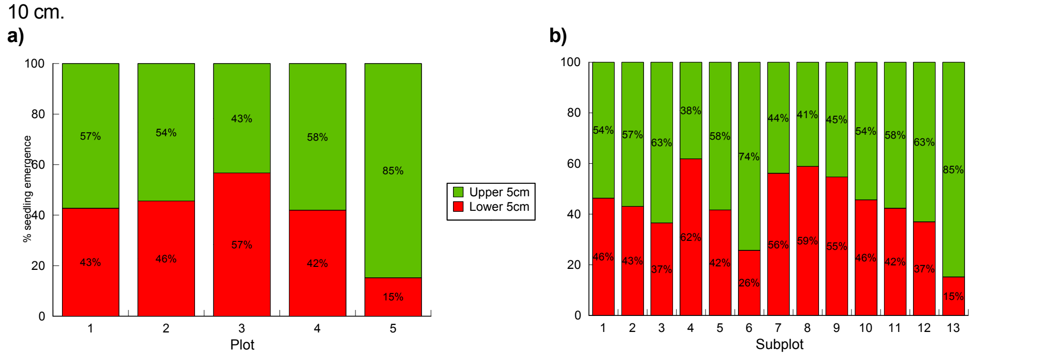
Figures 5.11 Rank-abundance curves for seasonal seed bank data, including inset graphs showing Shannon index (*H'*) scores.



Abundance of viable soil seed with soil depth

Overall, there was a marginally greater abundance of seedling emergence from the upper 5-cm of the soil horizon than the lower 5-cm. Totalised for all plots, 59.6% of the seedlings came from the top 5-cm and 40.6% from the lower. If Plot 5 is excluded, the difference is even less marked with 42.4% versus 37.6%.

Figure 5.12 Stack graphs showing the proportions of seedling emergence form soil samples taken at two depths: 0-5 cm & 5-10 cm.



This seems to indicate that seed is incorporated relatively evenly through the soil profile, perhaps attributed to the high levels of invertebrate activity, especially worms. **Figure 5.12a** exhibits this relationship as a stack graph. Only Plot 5 shows a significant proportion of the soil seed to be accumulated in the upper 5 cm of the profile, though this is probably due to the thin soils in this grassland, with the lower 5 cm made up mainly of 'cornbrash' stones than mineral soil. **Figure 5.12b** shows that there is some within-plot variability as far as soil seed abundance with soil depth, most notably with Plot 2, where the proportion of upper 5 cm soil seed varied between 38 - 78%.

Figure 5.13 Same data as for **Figure 5.12** but also showing proportions of forbs and graminoids with soil depth.

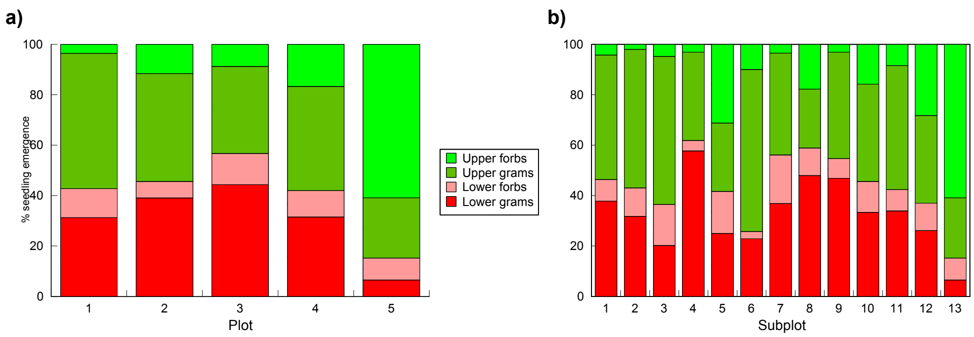


Figure 5.13 show the same data as for the previous two graphs, but with the data from the two soil layers split into forbs and graminoids. Apart from Plot 5, grass seed abundance dominates the seed banks of both upper and lower profiles. Forbs are particularly poorly represented in the upper 5-cm of soil in Plot 1, in dramatic contrast to Plot 5 where forbs are dominant.

DISCUSSION

Agricultural improvement and soil seed banks

Clearly, management operations involved in agricultural improvement of grasslands impoverish both the field layer and the soil seed bank to a degree which makes the deleterious changes difficult to reverse, thus requiring long-term restoration commitment (Gibson 1998). As Newbould (1989) advises, the soil "seed bank cannot be relied on as intensive farming practices using fertiliser and pesticide spray seem to eliminate all but the arable weeds from the seed bank." The work of Smith et al (2002) also suggest that agricultural intensification exaggerates the relationship between seed banks and vegetation such that there is a net loss of species with short-lived seed banks. Much research evidence suggests that regular ploughing and reseeding of swards encourages the development of seed banks of weeds of cultivation (Howe & Chancellor 1983; Graham & Hutchings 1988a; 1988b; Milberg 1995; Hutchings & Booth 1996). Plot 1, for example, is a medium-term ley grassland (7-10 year resowing cycle), and the seed bank contains a significant number of species such as *Anagallis arvensis*, *Capsella bursa-pastoris*, *Chenopodium album* and *Veronica persica*, which are annuals commonly found in frequently disturbed habitats such as arable plough-fields (Wilson 1994; Aerts *et al* 1995). Graham and Hutchings (1988a) concluded that the soil seed bank of a chalk grassland ley contained very few species typical of the previous unimproved species-rich vegetation, many of which produce only transient soil seed banks. Thus, the seed bank was more of a hindrance to restoration than help, as it was composed of arable weed species, which could be released from dormancy after disturbance, only to dominate regeneration at the expense of desirable calcicolous perennial species.

The significant correlations of seed bank volume with phosphorus, potassium and phytomass identify one of the consequences of intensive applications of P and K (in association with nitrogen), that is to selectively increase phytomass production and regeneration above that of non-target species. Thus, the productive, dominant grasses are stimulated by P and K applications into producing high quantities of seed, which are incorporated into the mineral soil. Although for the transient seed bank grasses such as *Lolium perenne* this is largely recorded as a post harvest pulse, long-term persistent seed bank species such as *Poa trivialis* continue to top-up already abundant soil reserves. More complicated relationships between soil seed bank and grassland are seen to develop as the above-/below-ground system ages i.e. from the period of last major disturbance. The significant negative correlations between total nitrogen and seed bank volume in the January and May censuses, for example, indicate that the organic nitrogen peak from subplots 6-10, and particularly Plot 3, apparently sustains a lower persistent soil seed bank volume. This may be accounted for by the indication that by January and May most of the transient component has probably either germinated or suffered mortality. This significant correlation may be a function of the fact that Plot 1, having been a short-term ley, has low soil organic nitrogen, but high P and K which encourages very high seed abundances in the soil of *Poa trivalis* and *Poa annua*, both of which are long-term persistent seed bank formers (Williams 1985). Conversely, higher organic nitrogen seems to demote *Poa* spp.

dominance, and promote *Holcus lanatus*, as evinced by **Table 5.10** (Grime 1988; Hodgson *et al* 1995; Kitajima & Tilman 1996).

Table 5.10 Correlations between dominant seed bank species and total soil nitrogen.

	Poa annua	*Poa trivialis*	*Holcus lanatus*	Total nitrogen
Poa annua	1	0.77**	-0.51	-0.60*
Poa trivialis	0.77**	1	-0.64*	-0.37
Holcus lanatus	-0.51	-0.64*	1	0.74**
Total nitrogen	-0.60*	-0.37	0.74**	1

Correlation is significant at the 0.01 level (2-tailed).
Correlation is significant at the 0.05 level (2-tailed).

Some of the results of Bullock *et al* (1994) are reflected in this study. They found that natural grassland diversification 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 filled up with the prevailing species. They concluded that the seed bank was an insignificant factor in seedling recruitment either because it was depauperate or that the seed that was present in the soil was just not reaching the surface and germinating. The results of the present study show that there is quite a large persistent seed bank in grassland soil similar to the area of Bullock *et al*'s research. Unfortunately for diversification purposes, grasses again dominate the seed banks of this suite of grasslands, though in differing proportions to the above-ground vegetation. *Poa* spp., *Holcus lanatus* and *Agrostis stolonifera* are the most influential species in that they form large soil reserves and have long-term persistence. These species, while differing in relative abundances along the plot gradient, are found in consistently high numbers in all but Plot 5. Therefore, it may be fair to postulate that these species will be pre-dominant in colonising either natural or artificial gaps created in the sward (Snaydon & Howe 1986; McDonald 1993; Arnthórsdóttir 1994; Bullock *et al* 1995). This particular aspect is studied in more detail in **Chapter 6**.

In terms of the comparative characteristics of the suite of seed banks, this research has shown that the *a priori* gradient of agricultural improvement, as initially observed for the above-ground vegetation, is also evident in the soil seed bank (Davies *et al* 1999). Of particular interest to restoration is the similarity of the improved grasslands to the reference community, Plot 5, as the greater the similarity, the greater the potential for using the seed bank for recruitment of desirable species. However, it is clear that with even Plot 4 only having 35% similarity with Plot 5, this potential seems limited (Bekker 2000). Agricultural improvement has altered the seed bank irrevocably. Seemingly, there is no useful 'memory' (Bakker *et al* 1996) or 'palimpsest' (Davies & Waite 1998) of relict species to draw on, and the species occurring in Plot 5 are either of low abundance or missing from the soils of the other plots. However, Ward & Jennings (1990) found that some species, often short-lived, e.g. *Linum catharticum*, which have generally been lost from ungrazed grassland undergoing succession for 14 years, could still be present in the seed bank. Such species, however, do not seem able to survive agricultural improvement in the same way. *Linum catharticum* is abundant in both above-ground and seed bank vegetation in Plot 5, but is absent from the vegetation and seed bank of the rest of the plots, where it is possible to suppose it occurred prior to improvement.

The abundance of germinable seed with soil depth does not seem to be an important parameter in restoration terms for these improved grasslands. The average mineral soil depth of all the grasslands is less than 20-cm. In contrast to the findings of Williams (1984) and Hutchings and Booth (1996), the top 10-cm of soil surveyed in this research, as examined in two equal parts, revealed that the top 5-cm of soil did not, overall, have significantly higher abundances of seed than the lower 5-cm. As this was the May inventory, when seed persistence is best evaluated, this result may be more indicative of evenness of persistent seed incorporation into the soil rather than total distribution. However, that seed seems to be incorporated relatively evenly throughout the soil profile may be due to high invertebrate activity (Thompson 1987; Thompson *et al* 1994). Only Plot 5 shows a marked differential in both seed abundance with depth, and forb versus graminoid components.

Desirable and undesirable seed bank components

Van der Valk & Pederson (1989) state that vegetation management based on the utilization of seed banks will only be successful when:

- The seeds of the required/preferred species are present in the seed bank.
- The seeds of unwanted species are not present or at least uncommon.
- Conditions suitable for germination for preferred species can be established and maintained.

On this basis, the description presented in **Table 5.03** of the plot-by-plot seed bank composition in terms of 'desirability', is worth further scrutiny in order to assess whether any useful restoration components are present in the agricultural improved soils. The advantageous species found in the soils of Plots 1-4 (omitting species clearly of implant origin) include: *Achillea millefolium*; *Hypochoeris radicata*; *Leucanthemum vulgare*; *Plantago lanceolata*; *Ranunculus acris*; *Ranunculus bulbosus*; *Ranunculus ficaria*; *Trifolium pratense*; and *Veronica serpyllifolia*. *Cynosurus cristatus*, though a common grass, can probably be added to this list as it plays such a key part in the definition of MG5 unimproved meadow grassland (Rodwell 1992). Nearly all of these species were found in the seed bank of the reference community, however none could be said to be indicators of species-rich grassland (Wells *et al* 1976; Gibson 1998). *R. acris* and *R. bulbosus*, *L. vulgare* and *C. cristatus* were of high enough abundances to occur in **Table 5.01.** However, seed dispersed from the newly planted implants most likely elevated the *Leucanthemum vulgare* counts beyond the pre-experiment abundance. Few desirable species are long-term persistent such as *Carex flacca, Linum catharticum* and *Prunella vulgaris*, and these do not seem able to survive, or persist long enough in sufficient abundance to postdate agricultural improvements such as have been applied to Plot 4.

The only negative species occurring in the seed bank of Plot 5 was *Urtica dioica*. Although other undesirables occurred in the improved grasslands, only *U. dioica* and *Rumex obtusifolius* attained abundances adequate to cause restoration concerns. Between the positive and negative species, the large majority of seed bank species can be considered of neutral restoration character. Thus, disturbances created specifically to encouraging positive seed bank regeneration from the seed bank seems to carry the high probability that either negative species or neutral grasses of high abundance will quickly take advantage of the gaps and necessarily, little α-diversity increments will be generated (Magurran 1988) (also see **Chapter 6**).

Matching above ground vegetation with seed bank composition

The results for species-abundance comparisons do partially show the often-quoted discrepancy between the above-ground vegetation and the respective soil seed banks (Williams 1984; Thompson 1986; Fowler 1994). The average for Plots 1-4 was 45% similarity between vegetation strata. Also, there was less than 50% carry over in seed bank similarity between each plot along the sequence, and the Plot 1 and Plot 5 seed banks only had 12% in common. However, as presented in **Table 5.07**, with abundances down-weighted to emphasise % similarities in species composition, only Plots 1 and 5 show significant differentials between field layer and seed bank. For Plots 2-4, in terms of species composition, above- and below-ground vegetations are very similar, with domination by a few grass species. Most of the variation was in the proportional contributions of each of these species to the overall soil seed reserve. The discrepancy for Plot 1 in above- and below-ground vegetation is largely to do with the arable weeds with long-term persistent seed banks, which regenerate when the ley grassland is ploughed again. For Plot 5 the discrepancy in terms of both species composition and species-abundances conforms to the frequent evaluation for semi-natural, species-rich grasslands (Dutoit & Alard 1995; McDonald *et al* 1996; Bekker *et al* 1998). The corollary of this data is that the potential of the respective plot seed banks to act as recruitment sources for re-establishing the grasslands if they were neglected, highly disturbed, fertilised, or destroyed through herbicide application, seems limited (Kirkham & Kent 1997; van Duren *et al* 1998; Stampfli & Zeiter 1999). As Bekker *et al* (2000) comment on the seed banks of their wet and dry Dutch meadow study sites: "Because of the low similarity (46-50%) between the vegetation and the seed bank, we propose that changes in the seed bank… follow, rather than cause, changes in the vegetation." Similarly, in this study, as for Plot 5 there is only a 30% similarity between above- and below-ground plant communities, it seems unlikely just from using this statistic that the above-ground vegetation could successfully regenerate even from the seed bank of the same community. As highlighted many times, a large percentage of the most important constituents of species-rich grassland do not produce long-term or even short-term persistent seed banks (Bakker *et al* 1996: Davies & Waite 1998; Bekker *et al* 2000). Notable absences from the seed bank inventory of the reference community, but found in the field layer, are *Agrimonia eupatoria*, *Cirsium acaule*, *Polygala vulgare*, and *Pilosella officinarum*. **Table 5.05** and **Figure 5.12** perhaps summarise some of the most significant restoration aspects of the respective seed banks. Though with certain caveats (see **Chapter 4**), grassland Plot 5 is the restoration target community, which informs much of the research project. As noted above, similarities with this reference grassland in terms of field layer and seed bank composition/abundance and the other four plots should give a considerable idea as to relative restoration potential. Not surprisingly Plot 1 seems to have very little in common with Plot 5 and suggests an intractable dissimilarity for restoration purposes. The seed banks of Plots 2-4 have a rising gradient of similarity with the Plot 5 seed bank, though in fact the seed banks are more similar than the field layer vegetation. This is supported by Smith *et al* (2002) who also affirm that species composition of meadow soil seed banks is often relatively uniform. Notably, the comparisons between Plots 2-4 field layer and the Plot 5 seed bank shows the highest similarities. However, because the seed bank of Plot 5 is markedly dissimilar to the Plot 5 field layer, the relationship seen here has probably most to do with the thread of restoration-unimportant generalists - often grass species - which are components of the majority of mesotrophic grasslands except those most disturbed by agricultural improvement (e.g. *Arrhenatherum elatius, Festuca spp. Holcus lanatus, Dactylis glomerata, Plantago lanceolata, Poa* spp., *Taraxacum officinale* and *Trifolium pratense*) (McDondald 1993; Wells 1995; Gibson 1998). However, Chapman and Younger (1994) do considered such "unsown" volunteer species to be an important contribution to the overall diversity of newly created grasslands.

Seasonality in the seed bank resource

The clear finding from the seasonal seed bank surveys is that soil seed banks do differ noticeably throughout the annual cycle, especially in relation to seed rain and the seasonality of germination and dormancy (Hutchings 1986; Lavorel *et al* 1994). This is primarily a function of the strategies employed by each species, i.e. whether a seed is predominantly transient (germinate or perish), or has the capacity for longer-term dormancy to take advantage of temporal opportunities to avoid the potentially dominating effects of competition from established plants (Roberts 1986; Thompson & Grime 1979; Thompson *et al* 1997) The polarities between the seed banks of the subplots of Plot 1 and Plot 5 are maintained throughout the four seasons. However, the variability in seasonal distribution of the subplots indicates how species abundances, in particular vary, throughout the year (see **Figure 5.09**). The seasonal seed bank species DCA scatterplots (**Figure 5.10**) emphasise the polarity between those arable weed species, which characterise Plot 1, and the few notable seed bank species that characterise Plot 5. The greatest flux, and seasonality of species occurs amongst more generalist species. As the rank-abundance/Shannon diversity curves indicate, the persistent seed components, germinating from the January and May soils, show the least diversity. However, it is necessarily this component, which should be of highest restoration interest, that is, the species that may persist beyond agricultural perturbations and act as a restoration catalyst. The special long-term restoration value of most of these species is, unfortunately, questionable. The May inventories are probably the key to the overall seed bank value, as many researchers suggest that the only species recorded at this time of year are those that mostly form persistent seed banks (Roberts 1986; Hillier 1990; van Duren *et al* 1998). For example, *Briza media*, *Helictotrichon pubescens*, *Centaurea nigra*, *Plantago media*, *Knautia arvensis*, and *Leontodon hispidus*, are present at other times of year in the soil of Plot 5, but their absence in the May samples, suggests they are all transient or short-term persistent components. For Plot 4, the May survey indicates, not only are the useful transient species not detected (*Cynosurus cristatus*, *Helictotrichon pubsecens*, *Lathyrus pratensis*), as would be expected, but known persistent seed bank formers *Leucanthemum vulgare*, *Ranunculus bulbosus* and *Trifolium pratense* (Hodgson *et al* 1995) are also not recorded. The seasonal seed bank surveys strongly indicate that there is considerable annual flux of viable soil seed, and most of the desirable species are transient (Roberts 1986). The restorationist therefore has to work with the persistent components, which are most prominent in soil samples from May. However, because viable soil seed shows marked seasonal variations, this can be utilised in two ways. Firstly, if the whole sward is to be removed and resown with a species-rich seed mix, a seasonal seed bank survey will show which times of year are best to attain optimal seed bank recruitment. Secondly, if the aim is retain the extant sward and attempting diversification with techniques such as seasonal gap creation, this knowledge is useful to predict what seed bank species might establish in the gaps, and in what abundance, at different times of the year (Hillier 1990; Arnthórsdóttir 1994; Bullock *et al* 1995; Kirkham & Tallowin 1995; Tallowin *et al* 1995). In practice this may mean avoiding periods when there is highest dominance - typically of grass species - and lowest diversity, or conversely to target the seasons with the lowest dominance and highest diversity for restoration works (see **Table 5.09**) (Magurran 1988; Fowler 1994; Lavorel 1994; Kitajima & Tilman 1996).

Restoration potential: concluding remarks

A common grassland restoration aim is to increase the abundance and diversity of forbs in relation to grasses (Mountford *et al* 1993; Mountford *et al* 1994; Smith *et al* 1997). Specific to this Chapter is the quantification of the value of the soil seed bank to this process. While Thompson (1993) states: "the seed bank is a major determinant of the rate and direction or recovery of vegetation from disturbance, and is of vital importance to attempts to restore degraded or neglected vegetation", it is prudent, as van der Valk & Pederson (1989 suggest, "to establish the composition of seed bank prior to the initiation of any management plan that presupposes its existence". This is necessary as much to identify negative characteristics as positive ones (van Duren *et al* 1998). For instance, the seed banks of the agriculturally improved grasslands studied in this research do not seem to be a particularly valuable element in restoring grassland to a pre-improvement condition. Smith *et al* (2002) also determined that seed banks of upland hay meadows were, "not likely to be important as a source of propagules for diversifying the vegetation." The seed banks are dominated by most of the same grasses that dominate the vegetation, and contain very few desirable species. This is chiefly because the desirable, target species, as a whole, do not form persistent, viable seed stores in the soil (Bakker *et al* 1996; van Duren *et al* 1998; Davies & Waite 1998; Mitchley *et al* 1998; Morgan 1998). Even the seed bank of Plot 5, the reference community, is limited in its restoration potential, a characteristic reinforced by the May survey. This suggests that sward diversification can only be achieved through immigration (Bekker *et al* 2000) and/or artificial means such as inoculation (van der Valk & Verhoeven 1988; Bobbink & Willems 1993; Jones & Hayes 1999). As Milberg (1995) confirms, "few species can be recruited from the seed bank when restoring grassland vegetation abandoned for several years. For a successful restoration, species might have to be naturally, or artificially introduced."

If the swards of each of the plots were stripped off to reveal the mineral soil, the results of this research provide an indication as to what vegetation would regenerate from the activated seed bank (van der Valk & Pederson 1989). However, Bullock *et al* (1994) observed that re-vegetation after disturbances in perennial grasslands is often dominated by regrowth from vegetative parts rather than by seedlings. Even with this caveat in mind it would still seem reasonable to suggest that regeneration composition and abundance would be also highly influenced by the seed bank once large populations of viable soil seed are revealed to germination stimuli.

Table 5.11 Rank of seed bank species with more that 1% abundance in seed banks of each plot.

Plot 1		Plot 2		Plot 3		Plot 4		Plot 5	
% abundance		% abundance		% abundance		% abundance		% abundance	
43.90	*Poa trivialis*	45.60	*Poa trivialis*	34.72	*Holcus lanatus*	26.22	*Holcus lanatus*	22.31	*Leucanthemum vulgare*
29.05	*Poa annua*	11.18	*Lolium perenne*	26.57	*Poa trivialis*	18.53	*Poa trivialis*	11.30	*Linum catharticum*
15.30	*Lolium perenne*	8.97	*Agrostis stolonifera*	9.78	*Ranunculus bulbosus*	16.40	*Agrostis stolonifera*	9.13	*Holcus lanatus*
3.07	*Urtica dioica*	5.33	*Dactylis glomerata*	9.55	*Agrostis stolonifera*	8.16	*Ranunculus acris*	6.95	*Poa trivialis*
		4.48	*Ranunculus bulbosus*	2.26	*Rumex acetosa*	5.55	*Ranunculus bulbosus*	6.08	*Prunella vulgaris*
		3.64	*Poa annua*	1.54	*Dactylis glomerata*	3.18	*Arrhenatherum elatius*	5.94	*Agrostis stolonifera*
		3.02	*Taraxacum officinale*	1.47	*Lolium perenne*	2.33	*Cynosurus cristatus*	5.07	*Bellis perennis*
		2.46	*Trifolium repens*	1.41	*Bromus hordeaceus*	2.10	*Cerastium fontanum*	3.91	*Trifolium pratense*
		2.38	*Arrhenatherum elatius*	1.28	*Geranium dissectum*	1.79	*Trifolium repens*	2.89	*Taraxacum officinale*
		1.84	*Urtica dioica*	1.11	*Urtica dioica*	1.66	*Festuca arundinacea*	2.46	*Plantago lanceolata*
		1.79	*Plantago major*	1.05	*Arrhenatherum elatius*	1.62	*Bromus hordeaceus*	2.17	*Arrhenatherum elatius*
		1.59	*Festuca arundinacea*	1.01	*Poa annua*	1.59	*Polygonum aviculare*	2.17	*Carex flacca*
		1.20	*Holcus lanatus*			1.15	*Geranium dissectum*	2.02	*Hypochoeris adicata*
		1.12	*Festuca rubra*			1.05	*Dactylis glomerata*	1.88	*Leontodon hispidus*
								1.88	*Sambucus nigra*
								1.59	*Ranunculus bulbosus*
								1.30	*Cerastium fontanum*
								1.15	*Plantago media*
								1.15	*Urtica dioica*
								1.01	*Lolium perenne*
								1.01	*Sonchus asper*
Shannon index	evenness								
1.13	0.815	1.89	0.715	1.71	0.687	2.07	0.785	2.62	0.860

The summary presented in **Table 5.11** can be used as a tentative indicator of the contribution of seed bank species to vegetation regeneration after effective removal of the above-ground vegetation, such as through herbicide application or turf stripping (Williams 1984; van der Valk & Pederson 1989). The Shannon index scores are given to show the diversity levels expected from seed bank only sward regeneration. The suggestion is that any vegetation developed from the seed bank, other than for Plot 5, will be dominated by perennial grass species, and specifically by *Poa trivialis*, *Holcus lanatus* and *Agrostis stolonifera*. The only forbs of general regeneration note are *Ranunculus acris* and *R. bulbosus*. The evidence indicates that the post-disturbance vegetation matrix developed from the seed bank would be essentially neutral in character, though seasonal differences may alter relative abundances. Other key grass species of these grasslands such as *Lolium perenne*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca* spp. and *Cynosurus cristatus* do not seem to have long-term persistent soil seed stores (Rice 1989). These species regenerate in gaps through their seed rain, whereas species such as *Holcus lanatus*, *Agrostis stolonifera* and *Poa* spp., which do form seed banks, can recruit seedlings from both the seed rain and seed bank, and have vigorous vegetative reproduction and foraging strategies such as the production of stolons and rhizomes (Grime *et al* 1988; Bullock *et al* 1994; Tallowin *et al* 1995). These species are capable of achieving rapid dominance after disturbance, thus producing a competitive environment, which may exclude opportunities for further species to arise from the seed bank or seed rain (van Duren *et al* 1998). It is the rapidity and dominance of establishment of these key species, which may dictate succession after disturbance, and affect establishment success of artificial seed inoculations of more desirable species (see **Chapter 10**). One way of altering the domination of seed input by a few productive grasses is through management, particularly grazing and cutting (Bakker *et al* 1980; Tallowin *et al* 1995). Bullock *et al* (1994) showed grazing to affect seed production and proposed this as an added mechanism with which to effect desirable vegetation change i.e. by decreasing the seed production of the dominant grasses, and also to increase the forb proportion in the seed rain. However, it is clear that these changes are going to remain relatively minimal while the soil fertility is high and the grasses are still able to dominate.

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