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Spatial patterns in seed bank and vegetation of semi-natural mountain meadows

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Abstract

Soil seed bank composition and vegetative spatial patterns were studied in four mountain meadow communities in the Broto Valley (N. Spain), in order to analyse the differences that might exists between the two life forms. Soil and vegetation samples were taken at 1 m intervals from 10 m × 10 m quadrats in each meadow in one-year study. The spatial distribution of species was analysed along with the calculation of an autocorrelation coefficient which takes account of the relative position of samples: (Moran's *I*). The results indicate that the abundance of the majority of the species in the seed bank and in the vegetation are randomly distributed, the percentage of species with a clumped distribution only exceeds 35% in the vegetation of one meadow and none of the taxa identified showed a uniform spatial organisation. The species that were distributed in the seed bank in a clumped pattern in more than one meadow were those of the pioneer species (*Anagallis arvensis, Centaurium erythraea*, *Lamium purpureum* and *Stellaria media*). All of these formed long-term persistent seed banks but were absent in the established vegetation in these meadows. According to the results, there exist not only differences between the spatial distribution of the species present in the same community, but also, that some species change their pattern of distribution according to the life form and to the grassland type in which they are found.

Introduction

Species composition of soil seed banks is affected by the historical composition of the established vegetation, by the seed longevity and regeneration strategies of individual species and by environmental factors influencing seed persistence in the soil (Harper 1977). The pool of "germinable" seeds and the actual vegetation are dynamically linked, and their spatio-temporal patterns can be expected to be interdependent (Parker et al. 1989).

Mountain meadows in the Spanish Pyrenees are associated with traditional agricultural management regimes and are an example of diverse plant communities (Fillat et al. 1999). There are also complex relationships between species richness and the type and the timing of grazing, cutting and fertiliser applications in these meadows. Grazing disturbs grassland structure, creating gaps in the sward suitable for seed germination (Peart 1989). Seed sources include; soil seed bank, seed dispersing naturally from adjacent habitats, dispersal by domestic livestock and farm machinery or introduction by farmyard manure (Smith et al. 2002). Cutting promotes clonal growth of species (Herben et al. 1995) and also increases the competition for light, space and nutrients that affects the spatial organisation within the community (Grace and Tilman 1990; Skálová et al. 1999).

These patterns of distribution in the herbaceous communities on a small scale have been considered in detail by various authors (Schenkeveld and Verkaar 1984; Thompson 1986; Bigwood and Inouye 1988; Lavorel et al. 1991; Chocarro et al. 1994; Herben et al. 1995; Rebollo et al. 2001; Shaukat and Siddiqui 2004) and have important ecological implications. Seed predation or competition among seedlings can result in an increasing mortality if seeds are clustered, whereas a uniform spatial pattern minimises mortality (Bigwood and Inouye 1988). In other situations, the grouped distribution could be more appropriate: such as rapid colonisation of some disturbance, in order to take advantage of the occurrence of small micro-sites suitable for germination (Peart 1989; Rusch 1992), or for example, to take advantage of the physical collective force that occurs when the seedlings emerge from dry clay soils (Harper 1977).

Spatial autocorrelation (Moran's *I*) is a geostatistical method which detects clusters by examining the change that occurs in the degree of correlation between paired density measurements when the physical distance between the location of points is measured (Sokal and Oden 1978; Legendre and Fortin 1989). This index has been used as an estimate of the spatial distribution of the species in different vegetative communities, in the seed bank of soils (Dessaint 1991; Dessaint et al. 1991; Butler and Chazdon 1998; Shaukat and Siddiqui 2004) and in above ground vegetation (Herben et al. 1995; Fortin 1999; Skálová et al. 1999).

The aims of the present study were to investigate the spatial distribution models in soil seed banks and in the above ground vegetation in four mountain meadows communities, analysing the differences that might exist between the two life forms.

Methods

Study site

Four meadows were studied in the locality of Fragen (Broto Valley) in the Spanish Pyrenees, found between U.T.M. coordinates 2721–4722 and 734–735, 42° 36′50″ latitude N, 0° 8′25″ longitude W. Pastures in Fragen have a patchwork appearance, the meadows are terraced on the *Flysch* (alternate layers of calcareous sandstone and clay cement) slopes, separated by either stone walls or rows of trees to denote individual ownership of each field. These meadows lie between 800 and 1600 m.a.s.l. The mean annual rainfall of the area is 1262 mm and the average annual temperature 9.2 °C. Each one of the four meadows is characterised by different systems of agricultural management in the study area:

(1) *Intensive irrigated (II)* meadow, 975 m.a.s.l., area of 1.85 ha, facing south east. The soil texture is clay loam. This area was cut twice (June and August) and grazed in spring and autumn (each occasion, 30 cattle for only 4 days). Cattle slurry was spread annually (30–35 t ha^{-1}) and NPK fertiliser (7:14:20) was applied every second year at 150 kg ha^{-1} were applied. The site had been converted from cereals to grassland 50 years ago.

(2) *Intensive cut (IC)* non-irrigated meadow, 1130 m.a.s.l. facing south with loam soil texture. The 1.38 ha area was cut in mid July and grazed in spring and autumn (each occasion, 30 cattle for only 2–3 days). Fertiliser application and conversion being as for meadow (1).

(3) *Extensive cut (EC)* meadow is on an alluvial terrace, 1030 m.a.s.l. facing south with loam soil texture. The 0.9 ha area was cut once in July and grazed twice a year, in spring and autumn (each occasion, 15 cows for 4–5 days). Farmyard manure was applied at 21 t ha^{-1} annually, in addition 150 kg ha^{-1} of 7:14:20 fertiliser was applied every 3 years. This site had been converted to grassland 30 years ago.

(4) *Extensive uncut (EU)* meadow, 1200 m.a.s.l. facing south with sandy loam soil texture. The 0.1 ha was grazed in spring (5 cattle for 1 day) and autumn (5 cattle for 1 day). No fertiliser was

applied. This site had been converted to grassland 20 years ago.

Soil seed bank sampling

The seed bank study was carried out at the end of winter of 1994. Cylindrical soil samples (3.5 cm in diameter and 20 cm in length) were obtained at 1 m intervals to complete a total of 100 samples evenly distributed to form a matrix of 10×10 m over the area of the four meadows. The total volume of soil sampled for each field was 19,242 cm^3.

The 100 samples from each meadow were processed individually. Estimates of seed bank composition were obtained by controlled environment germination of previously concentrated samples (Barralis and Chadoeuf 1980; Ter Heerdt et al. 1996, Thompson et al. 1997), carried out in a germination chamber. Methodological aspects of the reduction of the samples, the physical conditions, the time of germination and the identification of seedlings are described more fully in Reiné et al. (2004). Seed and species numbers per sample were used to estimate the seed bank composition, and the relative abundance of species.

Vegetation sampling

The above ground vegetation was sampled in June 1994, this coincided with the maturity of the plant community and used the same experimental design as for seed bank sampling. 100 vegetative samples, with a surface area of 25 cm^2 per sample were collected in each one of the meadows, forming a 10×10 m matrix each sample 1 m apart. Subsequently the species of each sample were identified and separated in the laboratory. These were dried in an oven at 60 °C for 48 h and the relative abundance of each species was expressed in grams of dry matter per sample. Species names follow those of Tutin et al. (1964–1980).

Ecological attributes

Meadow species were assigned to types of seed dispersal (“anemochorous”, “autochorous” and “zoochorous”), and to types of life form (“hemicryptofhyte”, “geophyte”, “therophyte” and “chamaephyte”) according to Grime et al. (1988). The classification of the species in seed bank types (“transient”, “short-term persistent” and “long-term persistent”) was assessed using the dichotomous key of Thompson et al. (1997) (Appendix 1).

Spatial statistics

In order to analyse the spatial distribution Moran’s index of autocorrelation (I) was used (Sokal and Oden 1978), calculated by the formula:

$$I = \frac{N\Sigma_i\Sigma_j w_{ij}(Y_i - Y_m)(Y_j - Y_m)}{W\Sigma_i(Y_i - Y_m)^2}$$

where: N = number of points sampled, Y_m = mean value, Y_i = value of the variable at point i, Y_j = value of the variable at point j, w_{ij} = value of connection between two points, W = sum of all values of connection.

The value of the index I varies between −1 and 1, and approximates to zero when there is no tendency in the spatial distribution model. This demonstrates the absence of autocorrelation and suggests a distribution due to chance. A positive value of I signifies that the variable measured in i and j varies in the same direction, indicating that similar values tend to occur together (clumped distribution). A negative value of I indicates that the variable measured at two neighbouring points i and j vary in opposite directions with no shared tendencies (Dessaint 1991). The coefficients of autocorrelation are compared to the null hypothesis such that the estimated value I doesn’t differ from the expected value $E(I) = -1/(N-1)$, following the statistical method proposed by Sokal and Oden (1978).

The values w_{ij} vary according to the position and the distance of the points i and j in the net designed for sampling. In this experiment the values w_{ij} were chosen according to the *king’s pattern definition* (Sokal and Oden 1978) (Figure 1). Two points are connected with $w_{ij} = 1.00$, when their neighbours of either row or column, and with $w_{ij} = 0.71$ if only the diagonal joins them (8 neighbours per point according to the movement of the king in chess). If they are not connected, they are assigned the value $w_{ij} = 0.00$. The index

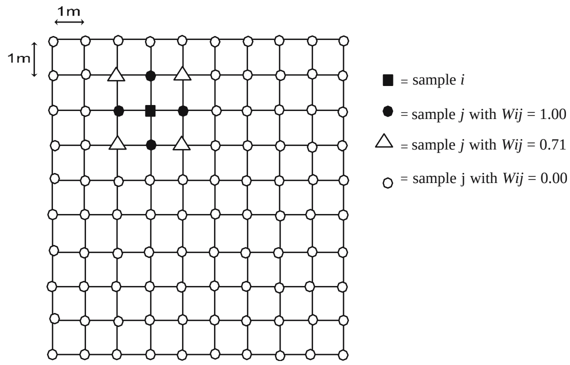

Figure 1. Sampling grid and connection values (w_{ij}) of Moran's Index of Autocorrelation (I).

and its significance were calculated using the programme Idrisi 4.0 (Eastman 1992).

Indices of autocorrelation were assessed for both seed bank and vegetation samples. In the first case, in the seed bank, with the number of seed of each identified species and in the second case, in the above ground vegetation, with the number of grams of dry matter of each species.

Results

Appendix 1 shows the taxonomic composition for both the seed bank and the established vegetation of the four meadows. Species with less than 5 seeds in the seed bank, or less than 5 grams of dry matter in the established vegetation were not included in the results, as they are below the level of significance in the calculation of autocorrelation. For a complete list of the recorded species including the mean number of seeds per square meter soil and the frequencies of plant species found in the vegetation see Reiné et al. (2004).

Table 1 shows the autocorrelation of the abundance of the different species and their significance according to the Moran's index (*I*). It can be seen that the greater majority of species do not show significant autocorrelation, and therefore show a random distribution. The percentage of species with a clumped distribution was in all the cases less than 42% (Figure 2). None of the analysed taxa demonstrated uniform spatial distributions (significant negative values of Moran's index).

The taxa that were clumped in more than one of the meadows were: *Anagallis arvensis, Centaurium erythraea*, *Lamium purpureum* and *Stellaria media* in the seed bank, and *Achillea millefolium* and *Poa pratensis* in the above ground vegetation. In any given meadow no individual species demonstrated clumped distribution in both the soil seed bank and the above ground vegetation at the same time. Referring to distinct communities, *Plantago lanceolata* showed grouped distribution in the seed bank in the *extensive cut* meadow, and the same grouped distribution in the vegetation but in a different meadow; the *extensive uncut*.

Discussion

The use of Moran's index to estimate the type of spatial distribution of species showed a clear predominance of species randomly distributed, both in the seed bank and in the vegetation of the four meadows. The spatial pattern of seeds in and on the soil is the result of the dispersal process (Harper 1977). When the dispersion is by autochory it could be expected that seeds are generally grouped around the mother plant. In this case the distribution only depends on the quantity of seeds produced, and of the spatial heterogeneity of parent plants in the field, not forgetting the persistence of seeds deposited in previous years in the seed bank (Dessaint et al 1991; Shaukat and Siddiqui 2004). In other types of dispersion the shape and size of the seeds and the activity of dispersal agents (wind, water and animals) must be taken into account. 48% of the plants in the four meadows studied were autochorous, 36% were zoochorous and 15% were anemonochorous. According to these percentages the grouped distribution seems to have had a major influence on these results.

It is common to assign a clumped distribution to the majority of the identified species in the seed bank when using adjustments to theoretical models (Poisson, Negative Binomial) or when comparing means and variance estimates (Lloyd's index, Morisita's index) (Bigwood and Inouye 1988; Rush 1992; Dessaint 1991; Dessaint et al. 1991; Shaukat and Siddiqui 2004), although there are exceptions (Thompson 1986). In general these procedures are very sensitive to the sample size and to total number of samples, therefore the use in these cases of technical

Table 1. Values of Moran's Index of Autocorrelation (I) and their significance for the identified species in the seed bank and in the vegetation of the four meadows: intensive irrigated (II), intensive cut (IC), extensive cut (EC) and extensive uncut (EU) ($n = 100$; $^{**}p < 0.01$; $^{*}p < 0.05$; n.s. – $p > 0.05$).

Species	Moran's index (I) Seed Bank				Aboveground Vegetation			
	II	IC	EC	EU	II	IC	EC	EU
Achillea millefolium	–	–	–	–	–	0.07 n.s.	0.09*	0.10**
Agrimonia eupatoria	–	–	–	0.09 n.s.	–	–	–	–
Agrostis capillaris	0.03 n.s.	0.07 n.s.	0.10*	−0.01 n.s.	–	–	–	–
Ajuga reptans	–	–	−0.05 n.s.	0.01 n.s.	–	–	–	–
Anagallis arvensis	–	–	0.09**	0.09*	–	–	–	–
Anthoxanthum odoratum	–	0.01 n.s.	–	–	–	–	–	–
Arenaria serpyllifolia	0.11*	–	0.01 n.s	−0.01 n.s.	–	–	–	–
Arrhenatherum elatius	–	–	–	–	−0.04 n.s.	0.24**	0.06**	–
Atriplex patula	–	−0.03 n.s.	0.15**	−0.02 n.s.	–	–	–	–
Bellis perennis	−0.03 n.s.	–	–	−0.01 n.s.	–	–	–	–
Brachypodium pinnatum	–	–	–	–	–	–	–	0.21**
Bromus erectus	–	–	–	–	–	–	–	0.10*
Bromus hordeaceus	–	–	–	–	–	0.03 n.s.	0.07**	–
Carex caryophyllea	–	–	–	−0.01 n.s.	–	–	–	0.23**
Centaurea nigra	–	–	–	–	−0.02 n.s.	–	−0.01 n.s.	–
Centaurea scabiosa	–	–	–	–	–	–	–	0.09**
Centaurium erythraea	–	–	0.15**	0.14**	–	–	–	–
Cerastium fontanum	−0.10 n.s.	−0.06 n.s.	−0.02 n.s.	−0.04 n.s.	–	–	–	–
Clinopodium vulgare	0.05 n.s.	–	–	–	–	–	–	–
Crepis capillaris	–	–	–	0.03	–	–	–	–
Cynosurus cristatus	–	–	–	–	0.05 n.s.	0.07 n.s.	–	–
Dactylis glomerata	−0.03 n.s.	−0.01 n.s.	–	–	0.01 n.s.	0.04 n.s.	0.02 n.s.	–
Daucus carota	−0.03 n.s.	−0.05 n.s.	0.04 n.s.	−0.05 n.s.	–	–	–	−0.02 n.s.
Eryngium campestre	–	–	–	–	–	–	–	−0.01 n.s.
Festuca pratensis	–	–	–	–	−0.03 n.s.	0.05 n.s.	−0.07 n.s.	−0.04 n.s.
Festuca rubra	–	–	–	0.10**	−0.01 n.s.	–	–	0.02 n.s.
Galium verum	–	–	0.07 n.s.	−0.04 n.s.	–	–	–	–
Genista scorpius	–	–	–	–	–	–	–	−0.01 n.s.
Geranium rotundifolium	–	–	0.04 n.s.	–	–	–	–	–
Hieracium pilosella	–	–	–	0.02 n.s.	–	–	–	–
Holcus lanatus	−0.08 n.s.	−0.03 n.s.	0.04 n.s.	0.01 n.s.	−0.06 n.s.	−0.03 n.s.	−0.03 n.s.	–
Hypericum perforatum	–	–	0.23**	0.02 n.s.	–	–	–	–
Juncus bufonius	–	–	–	−0.05 n.s.	–	–	–	–
Juncus effusus	0.06 n.s.	0.21**	–	–	–	–	–	–
Juncus inflexus	−0.02 n.s.	–	–	–	–	–	–	–
Lamium purpureum	0.23**	0.02 n.s.	0.06 n.s.	0.14**	–	–	–	–
Leontodon hispidus	–	–	–	0.03 n.s.	–	–	–	–
Leucanthemum vulgare	0.10*	–	0.03 n.s.	0.02 n.s.	–	–	–	–
Linum bienne	–	–	–	–	–	–	–	−0.01 n.s.
Lolium perenne	–	–	–	–	–	0.20**	−0.03 n.s.	–
Lotus corniculatus	–	–	–	–	–	0.05 n.s.	0.03 n.s.	0.18**
Medicago lupulina	−0.06 n.s.	0.02 n.s.	0.11*	−0.01 n.s.	–	–	–	–
Onobrychis viciifolia	–	–	–	–	–	–	−0.02 n.s.	–
Ononis spinosa	–	–	–	–	–	–	–	0.08 n.s.
Origanum vulgare	–	−0.01 n.s.	–	–	–	–	–	–
Picris hieracioides	–	–	−0.03 n.s.	–	–	–	−0.01 n.s.	–
Plantago lanceolata	0.06 n.s.	–	0.23**	0.09 n.s.	0.01 n.s.	−0.01 n.s.	−0.01 n.s.	0.26**
Plantago major	–	–	0.13**	0.09 n.s.	–	–	–	0.04 n.s.
Plantago media	–	–	0.05 n.s.	0.06 n.s.	–	–	–	–

Table 1. Continued

Species	Moran's index (I) Seed Bank				Aboveground Vegetation			
	II	IC	EC	EU	II	IC	EC	EU
Poa pratensis	0.08 n.s.	0.07 n.s.	0.02 n.s.	–	0.24**	0.09*	0.09*	−0.01 n.s.
Poa trivialis	–	0.19**	–	–	–	–	–	–
Polygonum aviculare	–	–	–	−0.04 n.s.	–	–	–	–
Potentilla erecta	–	–	–	0.04 n.s.	–	–	–	–
Potentilla reptans	–	–	−0.01 n.s.	0.18**	–	–	–	0.06 n.s.
Prunella laciniata	–	–	0.05 n.s.	−0.04 n.s.	–	–	–	–
Ranunculus acris	–	–	–	–	−0.01 n.s.	–	–	–
Ranunculus bulbosus	0.02 n.s.	0.03 n.s.	0.04 n.s.	−0.07 n.s.	–	–	–	–
Rumex acetosa	–	–	0.03 n.s.	–	–	–	–	–
Sanguisorba minor	–	–	–	−0.02 n.s.	–	–	–	0.03 n.s.
Seseli montanum	–	–	–	−0.04 n.s.	–	–	–	−0.02
Stellaria media	−0.01 n.s.	−0.01 n.s.	0.24**	0.16**	–	–	–	–
Taraxacum officinale	–	−0.02 n.s.	–	0.04 n.s.	–	0.10*	0.03 n.s.	–
Thymus serpyllum	–	–	–	−0.05 n.s.	–	–	–	–
Tragopogon pratensis	–	–	–	–	–	−0.04 n.s.	−0.02 n.s.	–
Trifolium pratense	−0.08 n.s.	−0.08 n.s.	0.01 n.s.	−0.04 n.s.	0.13**	−0.05 n.s.	0.06 n.s.	–
Trifolium repens	0.04 n.s.	−0.01 n.s.	0.01 n.s.	–	0.08 n.s.	0.20**	0.05 n.s.	–
Trisetum flavescens	–	–	–	–	−0.05 n.s.	−0.04 n.s.	0.04 n.s.	–
Urtica dioica	–	−0.01 n.s.	–	–	–	–	–	–
Valerianella dentata	–	–	0.08 n.s.	0.24**	–	–	–	–
Verbena officinalis	–	0.05 n.s.	0.20**	–	–	–	–	–
Veronica chamaedrys	–	–	–	−0.03 n.s.	–	–	–	–
Veronica officinalis	–	–	–	−0.03 n.s.	–	–	–	–
Vicia sativa	–	–	−0.09 n.s.	−0.01 n.s.	–	–	0.03 n.s.	–
Viola versicolor	0.04 n.s.	–	–	–	–	–	–	–

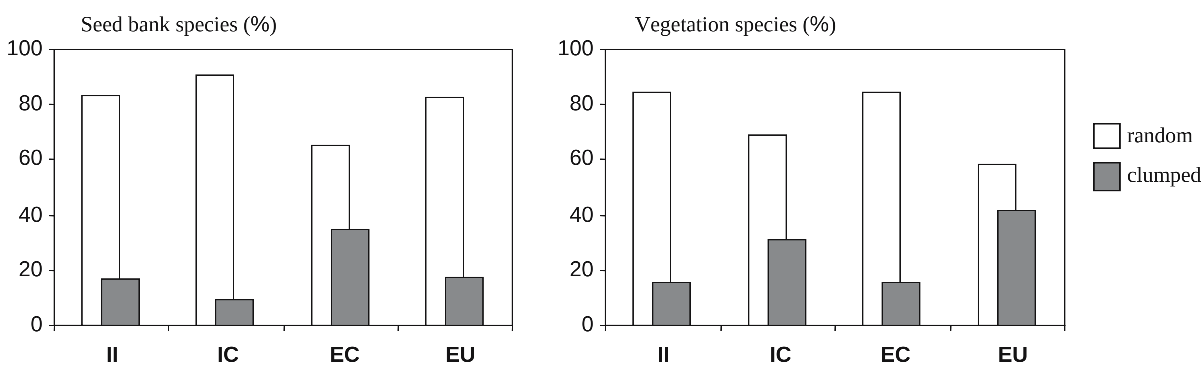

Figure 2. Percentages of species with clumped and random distribution in the seed bank and in the vegetation in the four meadows investigated: intensive irrigated (II), intensive cut (IC), extensive cut (EC) and extensive uncut (EU).

geostatistics is preferable (Albrecht and Forster 1996). In fact, the results obtained from Moran's index usually reduce the number of species with clumped distribution in the seed bank (Dessaint 1991; Dessaint et al. 1991). Autocorrelation is a more demanding method because it determines the aggregation based only at the physical location of each sample point.

The positive I values for species imply that the scale of pattern is greater than the distance between two adjacent soil cores (1 m). Possible grouped distributions existing at smaller distances remain hidden. However it is believed that the chosen distance was ideal since this gives a good relationship between the size of the groups and the total surface sampled by 100 points, this area is capable of showing the spatial differences of the distribution of species in these Pyrennean meadows (Chocarro et al. 1994). The sensitivity of Moran's *I* spatial autocorrelation coefficient depends only on this sampling scale resolution, as reported by Fortin (1999).

The use of similar designs and analyses for the sampling of both the vegetation and seed bank allows comparison of their spatial organisations. Due to both biotic and abiotic factors, different patterns are seen between species within one community and between communities that differ in the composition of their vegetation (Schenkeveld and Verkaar 1984; Thompson 1986; Lavorel et al. 1991). Studies undertaken in old field communities have shown that there is a natural connection between the grouping of species within the seed bank with that of the established vegetation (Bigwood and Inouye 1988; Lavorel et al. 1991) and when this connection does not occur, it is due to some abiotic factors controlling their spatial distribution (Lavorel et al. 1991). Nevertheless, in permanent pastures it is more difficult to determine the relationship between the distribution of species in the seed bank to that of in the above ground vegetation (Schenkeveld and Verkaar 1984). The distribution of the established vegetation is affected by the form of growth of the species (clonal growth, or in a basal rosette) (Herben et al. 1995) and by canopy competition (Skálová et al. 1999). In the seed bank, the model of distribution of the species is by means of the already mentioned processes of dispersion and incorporation into the soil (Harper 1977).

Anagallis arvensis, Centaurium erythraea, *Lamium purpureum*, and *Stellaria media* were the species that showed a clumped distribution in the seed bank in more than one plant community. These therophyte species, none of which are present in the above ground vegetation of the meadows, have distinct modes of seed dispersion and also all form long-term persistent seed banks (Thompson et al. 1997). This tendency differs from that pointed out by Schenkeveld and Verkaar (1984) who noted that the species forming transient seed banks had clumped spatial distributions, quite different to those forming long-term persistent seed banks, which have a more homogenous spatial distribution.

Finally it is worth emphasising that the total percentage of taxa with random or grouped spatial organisation hardly vary across all the different meadows in the trial. However, differences in the distribution of certain species were detected in some instances. For example, *Stellaria media* in the intensive managed meadows (*intensive irrigated* and *intensive cut*) showed a random distribution in the seed bank, whereas in the extensively managed fields (*extensive cut* and *extensive uncut*) it showed a clumped distribution. *Poa pratensis* was found with a clumped distribution in all the meadows in the above ground vegetation except in the *extensive uncut* (the most extensively managed) where it demonstrated a random distribution. According to these results not only are there differences between the spatial distribution of species in the same environment (Thompson 1986), but also the same species seem to change their distribution pattern according to the type of herbaceous community in which they are found.

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Appendix 1

Seed bank and plant species composition in the vegetation of four meadows: intensive irrigated (II), intensive cut (IC), extensive cut (EC) and extensive uncut (EU).

Species	Seed Bank (seeds 9.62 cm^{-2})				Vegetation (g dry matter 25 cm^{-2})				Seed dispersal type	Life form type	Seed bank type
	II	IC	EC	EU	II	IC	EC	EU			
Achillea millefolium	–	–	–	–	–	8.42	12.98	6.41	ane	hem	trans
Agrimonia eupatoria	–	–	–	34	–	–	–	–	zoo	hem	long
Agrostis capillaries	23	76	14	5	–	–	–	–	aut	hem	long

Appendix 1. Continued

Species	Seed Bank (seeds 9.62 cm^{-2})				Vegetation (g dry matter 25 cm^{-2})				Seed dispersal type	Life form type	Seed bank type
	II	IC	EC	EU	II	IC	EC	EU			
Ajuga reptans	–	–	4	5	–	–	–	–	zoo	hem	long
Anagallis arvensis	–	–	6	10	–	–	–	–	aut	ther	long
Anthoxanthum odoratum	–	25	–	–	–	–	–	–	zoo	hem	trans
Arenaria serpyllifolia	7	–	5	14	–	–	–	–	ane	ther	long
Arrhenatherum elatius	–	–	–	–	51.18	51.99	98.28	–	zoo	hem	trans
Atriplex patula	–	7	15	7	–	–	–	–	aut	ther	long
Bellis perennis	6	–	–	12	–	–	–	–	aut	hem	short
Brachypodium pinnatum	–	–	–	–	–	–	–	54.89	aut	hem	trans
Bromus erectus	–	–	–	–	–	–	–	7.57	zoo	hem	trans
Bromus hordeaceus	–	–	–	–	–	9.97	12.9	–	zoo	ther	trans
Carex caryophyllea	–	–	–	18	–	–	–	5.42	aut	hem	long
Centaurea nigra	–	–	–	–	20.96	–	21.61	–	aut	hem	trans
Centaurea scabiosa	–	–	–	–	–	–	–	7.12	aut	hem	trans
Centaurium erythraea	–	–	8	12	–	–	–	–	ane	ther	long
Cerastium fontanum	7	12	7	6	–	–	–	–	aut	cham	long
Clinopodium vulgare	31	–	–	–	–	–	–	–	aut	hem	short
Crepis capillaris	–	–	–	16	–	–	–	–	ane	ther	short
Cynosurus cristatus	–	–	–	–	15.28	10.05	–	–	aut	hem	trans
Dactylis glomerata	12	18	–	–	128.68	163.66	52.45	–	aut	hem	short
Daucus carota	30	12	48	46	–	–	–	6.39	zoo	hem	short
Eryngium campestre	–	–	–	–	–	–	–	7.04	zoo	ther	trans
Festuca pratensis	–	–	–	–	69.82	34.23	35.86	5.07	zoo	hem	trans
Festuca rubra	–	–	–	11	10.88	–	–	6.64	zoo	hem	trans
Galium verum	–	–	32	50	–	–	–	–	zoo	hem	short
Genista scorpius	–	–	–	–	–	–	–	11.81	aut	cham	trans
Geranium rotundifolium	–	–	14	–	–	–	–	–	zoo	ther	long
Hieracium pilosella	–	–	–	9	–	–	–	–	ane	hem	short
Holcus lanatus	12	42	85	17	56.41	48.83	64.36	–	aut	hem	short
Hypericum perforatum	–	–	14	25	–	–	–	–	ane	hem	long
Juncus bufonius	–	–	–	7	–	–	–	–	zoo	ther	long
Juncus effusus	5	10	–	–	–	–	–	–	zoo	hem	long
Juncus inflexus	8	–	–	–	–	–	–	–	zoo	hem	long
Lamium purpureum	172	60	20	13	–	–	–	–	zoo	ther	long
Leontodon hispidus	–	–	–	11	–	–	–	–	ane	hem	trans
Leucanthemum vulgare	71	–	6	13	–	–	–	–	aut	hem	long
Linum bienne	–	–	–	–	–	–	–	5.22	aut	hem	long
Lolium perenne	–	–	–	–	–	66.33	6.86	–	aut	hem	trans
Lotus corniculatus	–	–	–	–	–	42.84	50.8	46.00	aut	hem	trans
Medicago lupulina	14	54	224	34	–	–	–	–	aut	ther	long
Onobrychis viciifolia	–	–	–	–	–	–	8.64	–	zoo	hem	trans
Ononis spinosa	–	–	–	–	–	–	–	9.23	aut	cham	trans
Origanum vulgare	–	14	–	–	–	–	–	–	aut	hem	long
Picris hieracioides	–	–	5	–	–	–	10.76	–	ane	hem	trans
Plantago lanceolata	98	–	102	101	29.01	12.09	56.8	11.07	zoo	hem	short
Plantago major	–	–	53	4182	–	–	–	9.07	zoo	hem	short
Plantago media	–	–	36	95	–	–	–	–	zoo	hem	short
Poa pratensis	15	52	39	–	8.47	40.73	20.1	5.11	aut	hem	short
Poa trivialis	–	19	–	–	–	–	–	–	aut	hem	short
Polygonum aviculare	–	–	–	13	–	–	–	–	aut	ther	long
Potentilla erecta	–	–	–	11	–	–	–	–	aut	hem	long
Potentilla reptans	–	–	6	53	–	–	–	5.05	aut	hem	short
Prunella laciniata	–	–	23	46	–	–	–	–	zoo	hem	long
Ranunculus acris	–	–	–	–	10.84	–	–	–	zoo	hem	trans
Ranunculus bulbosus	20	26	10	10	–	–	–	–	zoo	geo	long

Appendix 1. Continued

Species	Seed Bank (seeds 9.62 cm^{-2})				Vegetation (g dry matter 25 cm^{-2})				Seed dispersal type	Life form type	Seed bank type
	II	IC	EC	EU	II	IC	EC	EU			
Rumex acetosa	–	–	17	–	–	–	–	–	ane	hem	trans
Sanguisorba minor	–	–	–	42	–	–	–	5.44	aut	hem	short
Seseli montanum	–	–	–	9	–	–	–	7.50	aut	hem	short
Stellaria media	35	36	156	175	–	–	–	–	aut	ther	long
Taraxacum officinale	–	11	–	8	–	23.54	23.62	–	ane	hem	long
Thymus serpyllum	–	–	–	7	–	–	–	–	aut	cham	long
Tragopogon pratensis	–	–	–	–	–	11.98	6.41	–	ane	hem	trans
Trifolium pratense	12	6	20	6	28.68	21.33	33.83	–	zoo	hem	long
Trifolium repens	23	23	11	–	22.03	49.4	59.63	–	zoo	hem	long
Trisetum flavescens	–	–	–	–	25.81	26.59	25.67	–	zoo	hem	trans
Urtica dioica	–	17	–	–	–	–	–	–	zoo	hem	long
Valerianella dentata	–	–	10	30	–	–	–	–	aut	ther	long
Verbena officinalis	–	9	557	–	–	–	–	–	aut	hem	long
Veronica chamaedrys	–	–	–	7	–	–	–	–	aut	cham	short
Veronica officinalis	–	–	–	15	–	–	–	–	aut	cham	short
Vicia sativa	–	–	19	6	–	–	27.91	–	aut	ther	trans
Viola versicolor	5	–	–	–	–	–	–	–	aut	hem	long

Species with less than 5 seeds in the seed bank or less than 5 g of dry matter in the above ground vegetation do not appear in the results (Seed dispersal type: *ane* anemochorous, *aut* autochorous, *zoo* zoochorous; Life form type: *hem* hemicryptofhyte, *geo* geophyte, *ther* therophyte, *cham* chamaephyte; Seed bank type: *trans* transient, *short* short-term persistent, *long* long-term persistent).

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