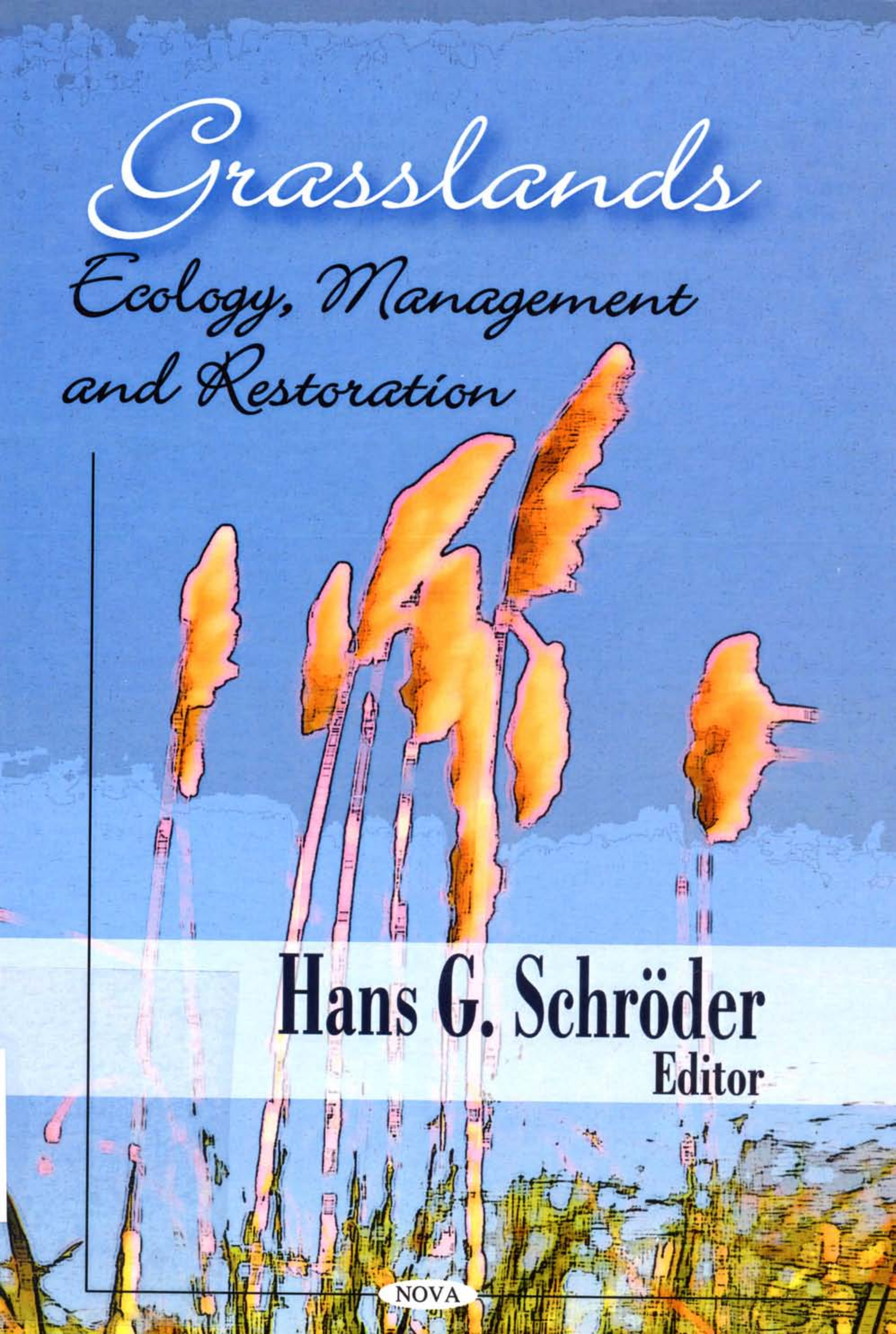

Grasslands

Ecology, Management and Restoration

Hans G. Schröder
Editor

NOVA

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Chapter 4

ON THE ROLE OF SOIL SEED BANK OF RICH PASTURE COMMUNITIES IN A FRAGMENTED SUBMEDITERRANEAN LANDSCAPE

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ABSTRACT

Here we report the main trends observed in the soil seed bank of some species-rich pastures located near Vic (NE Spain), evaluating the relationship between soil seed bank and standing vegetation in two contrasting communities (xerophilous pasture and mesoxerophilous grassland), and the potential role of the soil bank in community regeneration. We analyzed 140 soil samples via germination tests and direct observation. The total seed pool (including soil seed bank and standing vegetation) was characterized in terms of morpho-functional traits.

The soil seed content was high and showed strong seasonal variation. We found 12,178.8 to 785.7 seeds m^{-2} in the germination tests, and 6,909.1 to 4,882.5 seeds m^{-2} through direct observation. The shallow soil horizon contained much higher densities and species richness than the deep horizon, and higher relative frequencies of elongated or appended seeds. In both communities, 35-45% of the species richness in the soil seed bank corresponded to opportunists, which were rarely found in the established vegetation. In contrast, half of the taxa in the aboveground xerophilous pasture and two-thirds in the mesoxerophilous grassland were not found in the soil bank.

The persistent seeds in the soil bank belonged to a few taxa, mainly not found or rare in the established vegetation. Most of the main species of this vegetation, such as dominant grasses and abundant sub-shrubs, were poorly represented in the soil seed bank.

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These trends indicate the limited role of this bank in the regeneration of the communities studied, particularly in the mesoxerophilous grassland. The changes in land use occurred during the last half century have strongly increased the fragmentation of semi-natural plant communities, and impair the conservation of plant diversity of this species-rich landscape.

Keywords: biodiversity decline, community ecology, habitat fragmentation, grasslands, landscape ecology, seed persistence, seed traits, xerophilous pastures

1. INTRODUCTION

Soil seed banks are important components of terrestrial ecosystems, being crucial vegetation drivers after perturbation events and in annual regeneration. Their composition and dynamics are highly evident in therophytic communities, found in dry areas or subject to frequent disturbance (Recasens et al., 1991; Lyaruu and Backéus, 1999; Caballero et al., 2003; Mayor et al., 2003; Reiné et al. 2004). On the contrary, the relationship between soil seed bank and standing vegetation is more obscure where resprouting perennials are dominant (Thompson and Grime, 1979; Leck et al., 1989). Thus, the crucial role played by soil seed banks in maintaining the biodiversity of vegetation over space and time is related to the particular constrictions and perturbation dynamics of each habitat (Fenner and Thompson, 2005). Besides the theoretical interest in this relationship, there are also implications for ecological restoration (Bekker et al., 1997; Willems and Bik, 1998; Lyaruu and Backéus, 1999).

Grime and co-workers have developed a promising approach based on seed features, concerning vegetation dynamics (Grime et al., 1981; Thompson, 1993). According to their methods and focus, the analysis of a few 'soft' morpho-functional seed traits allows one to predict for each taxa the chances of dispersal, persistence and germination. Various studies have shown that these predictions work well enough at least in temperate and Mediterranean floras (Thompson et al., 1993; Cerabolini et al., 2003; Peco et al., 2003). Thus, this approach may assist in understanding the role the soil seed bank plays in shaping standing vegetation, according to the capacities and limitations of the different morphotypes.

A good deal of information on species composition, distribution and the main habitat descriptors in Mediterranean and submediterranean vegetation has been obtained (Rivas-Martínez et al., 2002, and references therein). However, only a few studies have targeted functional aspects, while those devoted to regeneration functions are scarce. Moreover, most of these studies deal with sclerophyllous forests, whereas scrubs and pastures remain much less investigated (but see Russi et al., 1992; Peco et al., 1998a; Guàrdia et al., 2000; etc.), despite the diversification and species richness of these communities. In the Plana de Vic area, a wide range of species-rich pasture communities stand out against a farmed landscape, forming heterogeneous mosaics on the slopes of a number of small hills (Casas and Ninot, 1994, 1995). These hilly surfaces represent noticeable biodiversity headquarters, with very low connectiveness among them (Figure 1). Traditionally, sheep flocks maintained these pastures exploited, also acting as diaspore vectors among the pastures and between pasture areas, fallows and other marginal lands (Poschold and Bonn, 1998).

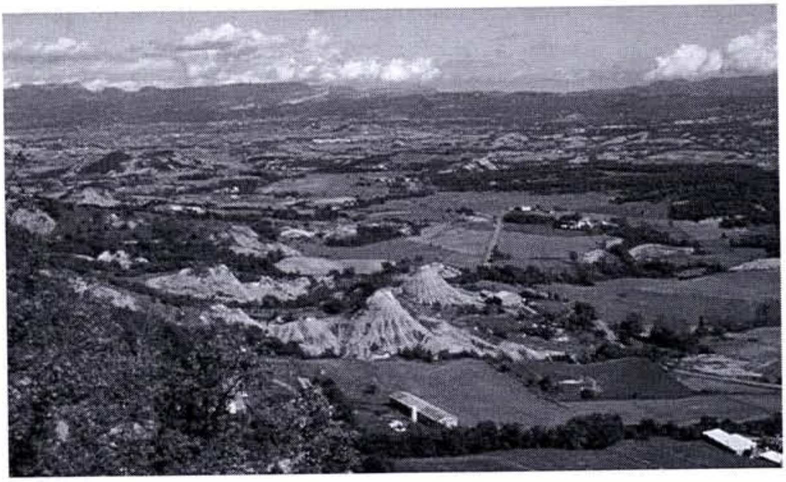


Figure 1. General view of Plana de Vic, with scattered hills (strongly eroded on South facing slopes) over the farmed plateau.

However, the abandonment of these activities, in tandem with farming intensification during the past half century has increased the actual fragmentation of the pasture units, furthering their encroachment and impoverishment (Casas, 2001).

The aim of this paper is to provide an analysis of the soil seed bank of these pastures, which on the whole are a good example of a seminatural, species-rich landscape. We have selected the two most extensive communities, which moreover show contrasting site conditions, species composition, and functional structure. The analysis included comparisons between standing vegetation and soil seed bank, between communities, and between seasons, on the basis of species composition, functional and ecological plant groups, and seed traits. Specifically, we wanted to evaluate (i) the size and the dynamics of the soil seed bank in these transitional pastures, (ii) the appropriateness of this ecological compartment in community regeneration, and (iii) the functional differences between the two communities studied in terms of soil seed bank. Scientific interest in these aspects has increased along with awareness of the ongoing biodiversity impoverishment in most seminatural landscapes, since knowledge of the structure and dynamics of soil seed banks is a key foundation for restoration management (Bekker et al., 1997; Willems and Bik, 1998).

2. MATERIALS AND METHODS

2.1. The Area and the Communities Studied

This study deals with the pastures situated on several small hills located in the Plana de Vic basin (Catalonia, Spain; 41° 53' N, 2° 15' E; Figure 2), lying between the Mediterranean, Catalanidic mountains south- and eastwards, and the pre-Pyrenean ranges northwards. The main outcrops are flat, lime rich, Tertiary rocks, chiefly Eocene marls. The macroclimate is submediterranean axeromeric (Bolòs and Vigo, 1984), a transition type between Mediterranean and montane (Pyrenean). The mean annual temperature in Vic lies between 12 and 13 °C and the annual rainfall normally ranges from 650 to 750 mm (Figure 2).

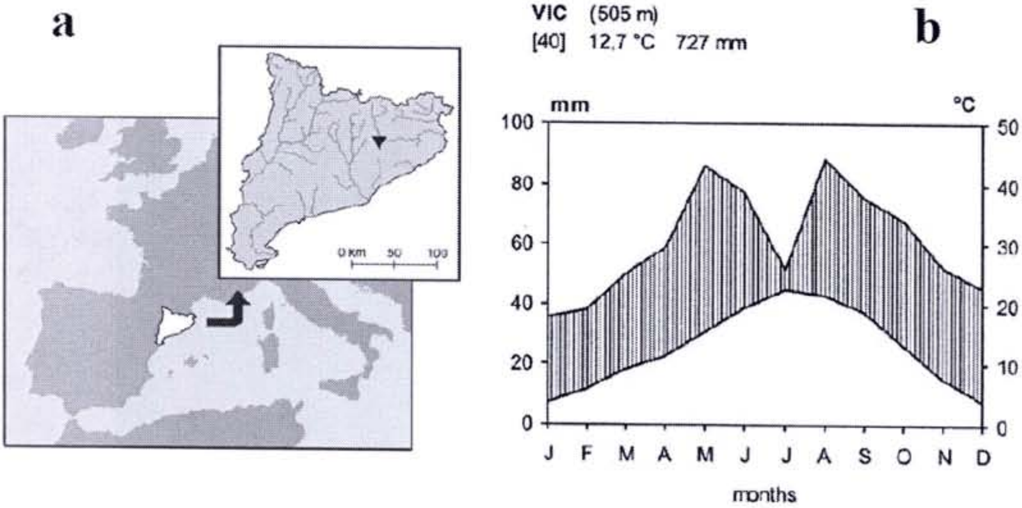


Figure 2. Location of the area studied (a), and climatic diagram of Vic, corresponding to a submediterranean climate with a continental tendency (b).

The vegetation is mainly mesoxerophilous, with xerophilous Mediterranean communities being restricted to drier habitats, such as the south facing slopes and rocky shelves. The hills and the peripheral slopes around Vic stand out from the intensively farmed surrounding plains, and are the main location of varied mosaics of semi-natural communities (Figure 3).

Figure 3. Hill slope bearing a complex mosaic of semi-natural vegetation: *Quercus pubescens* stands, diverse xerophilous pastures and eroded surfaces with sparse vegetation (badlands).

The climax vegetation is a deciduous, mesoxerophilous oak forest (*Buxo sempervirentis-Quercetum pubescentis* Br.-Bl. 1932), which remains on a few gently sloping sites. Deforested slopes, on any aspect and with soils ranging from well preserved to highly eroded, are prime locations for a wide variety of pasture communities (Figure 4).

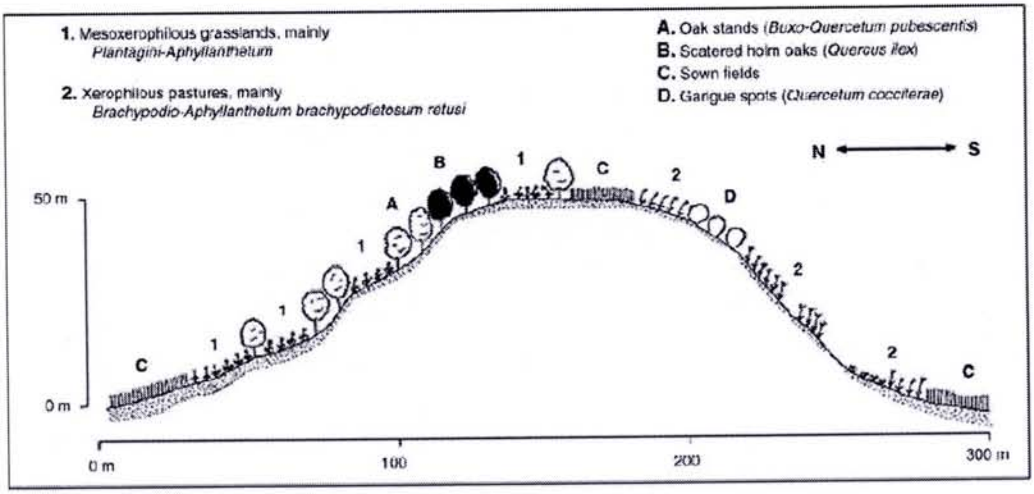


Figure 4. Cross-section of a hill in the area studied, with semi-natural plant communities surrounded by farmland.

Depending on each precise habitat, plant communities include varying percentages of Mediterranean species (xerophilous plants, more abundant in drier environments), Medio-European species (mesophilous plants, more abundant in milder environments), and pluriregional species (ubiquituous plants, widespread).

Most of the pasture surfaces correspond to calcicole perennial communities, from xerophilous to mesophilous. Excluding the extremes of this range, we selected two pasture communities showing contrasting ecological conditions, structure and phenology (Table 1), which are rather extensive in the current landscape (Casas and Ninot, 1994). These communities are:

- *Brachypodio-Aphyllanthetum* O. Bolòs (1956) 1967 *brachypodietosum retusi* O. Bolòs (1959) 1960. Irregular pastures dominated by the chamaephytic, xerophilous grass *Brachypodium retusum*, bearing some dwarf shrubs, therophytes and small patches of bare soil (Figure 5). They develop on south facing slopes with stony, eroded soil.
- *Plantagini-Aphyllanthetum* O. Bolòs (1948) 1956. Dense grasslands dominated by *Aphyllanthes monspeliensis* (Liliaceae) and various mesoxerophilous graminoids, such as *Brachypodium phoenicoides* (Figure 6). They cover deep, stable soils occurring on north facing or intermediate slopes.

2.2. Field Sampling

The two communities were sampled at two sites (Malla and Montrodon) representative of the relief discussed above. In the resulting 4 plots (2 communities x 2 sites) we recorded the standing vegetation in terms of phytosociological relevés (complete lists of the plant taxa found in 20 m^2 areas, with evaluation of cover/abundance), and completed them with additional taxa occurring in pasture adjacent to the plots. Nomenclature and taxonomy of taxa follows Bolòs et al. (2005) from sampling to here onwards.

Table 1. Main aspects of the communities studied (summarised from Casas, Ninot 1994). Percentages of life forms and phytogeographic types refer both to species number and to relative cover, respectively.

	Plantagini-Aphyllanthetum	*Brachypodio-Aphyllanthetum brachypodietosum retusi*
Life forms (%)	Hemicryptophytes: 60 / 78 Chamaephytes: 20 / 20 Geophytes: 5 / 2 Therophytes: 13 / <1	Hemicryptophytes: 47 / 50 Chamaephytes: 31 / 47 Geophytes: 3 / <1 Therophytes: 19 / 3
Dominant species (mean cover)	Brachypodium phoenicoides*: 64* *Avenula pratensis*: 35 *Aphyllanthes monspeliensis*: 32 *Carex caryophyllea*: 11 *Plantago media*: 11	Brachypodium retusum*: 68* *Thymus vulgaris*: 30 *Koeleria vallesiana*: 17 *Teucrium polium*: 13 *Aphyllanthes monspeliensis*: 12
Aspect, slope (°)	N (any), 4	S (SW-SE), 17
Topographic situation	Toeslopes, gentle slopes	Abrupt slopes
Cover (%)	99	89
Phytogeographic types (%)	Mediterranean: 28 / 53 Medio-European: 44 / 34 Pluriregional: 28 / 13	Mediterranean: 56 / 78 Medio-European: 21 / 16 Pluriregional: 23 / 6

Figure 5. Stand of the xerophilous pasture (*Brachypodio-Aphyllanthetum*) on a dry slope, showing typical patchy structure and dominance of *Brachypodium retusum* and dwarf shrubs (*Santolina chamaecyparissus, Teucrium polium,* etc.).

Figure 6. Aspect of the mesoxerophilous grassland (*Plantagini-Aphyllanthetum*) in fulll bloom of *Aphyllanthes monspeliensis.*

We collected 10 soil samples from each plot using a steel cylinder, 5.5 mm in diameter, knocked 10-12 cm into the soil. Each cylindrical sample (core) was cut into two samples (0 to 5 cm and 5 to 10-12 cm deep) representing shallow and deep soil horizons, respectively, as in other studies addressing soil seed banks (Thompson, 1993). Thus, for each sampling date we obtained 80 samples, which were laid out to dry for 15 days or more in the laboratory, to prevent both germination and loss of viability.

Soil sampling took place three times during the year, with the aim of obtaining data related to the three basic seasonal states of the soil seed bank in temperate regions, following Thompson and Grime (1979): at the end of spring, when the seeds in the soil correspond to the persistent bank; at the end of summer, when the currently produced seeds have been incorporated; and in winter, after the autumn germinating species may have left the soil bank. Samples were collected in February, at the end of June and in September (October) of 2000. Moreover, we took an extra set of samples in June of 1999 (5 cores per plot, total 40 samples), to provide some estimate of the inter-annual variability of the persistent bank.

2.3. Laboratory Analyses

Given the difficulties and constraints involved when analysing the composition of soil seed banks (Gross, 1990; Recasens et al., 1991; Russi et al., 1992), we used two complementary methods. From each set of samples, one-half (40 samples: i.e., 5 samples from each plot and depth) was laid out to germinate in the greenhouse, and the other half was hand sorted to separate and identify seeds. It is known that direct observation of soil samples involves the inventorying of non-viable seeds, and may neglect a number of cryptic seeds (small, irregular, brown). On the other hand, germination tests can result in under-estimates, because this procedure may miss a number of species with special germination requirements, or with dormancy mechanisms (Grime et al., 1981; Gross, 1990).

In this paper, what we call seed corresponds more precisely to the diaspore or dispersule: i.e., the seed of a legume, the entire fruit of a compositae, or the fruit with the concealing lemma and palea of a grass.

2.3.1. Hand Sorting and Visual Observation

The soil samples were washed and hand screened through a column of sieves decreasing in mesh width (1, 0.5 and 0.2 mm) resulting in three sub-samples per sample. The material retained in each sieve contained diverse plant materials (debris, seeds) and mineral particles (aggregates, sand); these were particularly abundant in the medium and finest sieves. The three sub-samples obtained from each sample were maintained separately to facilitate their handling; this gave 120 sub-samples per sampling date.

The sorting and identification of the seeds was done under a stereoscopic microscope, at 10-40X magnification. Seeds showing evidence of damage (broken cover, anomalous appearance) were rejected. Identification was supported by illustrations or descriptions of seeds (Hanf 1982; Jávorka-Csapody, 1991; Bolòs and Vigo, 1984-2001; Castroviejo et al., 1996-2004; etc.) and by comparison with herbarium samples or by seeds collected *ad hoc*.

Sorting the sub-samples retained in the 0.2 mm sieve proved a very hard task, and yielded almost no seeds. Thus, we laid a selection of these samples in a culture chamber with standard spring conditions (14 light hours at 25 °C and 10 dark hours at 15 °C), watered with a 10^{-3}M giberelic solution. Seedling emergence obtained after one month was less than 1 per sub-sample, and none coincided with the few species found in the pastures with diaspores smaller than 0.2 mm (*Blackstonia perfoliata*, *Hypericum perforatum*, *Helichrysum stoechas* and *Sedum sediforme*, and Orchidaceae). Consequently, given the time needed and the almost sterile results expected, we abandoned the exhaustive sorting of these samples, basing this part of the study on the remaining 80 samples retained in the 1 mm and 0.5 mm sieves.

2.3.2. Germination

For this treatment the 5 samples from each plot, depth and date were pooled, and then used as a single soil sample. Each of these samples was spread out in a 40 x 60 cm container, forming a layer a few mm deep, on a standard substrate made of peat, mica and perlite. The containers were laid on greenhouse tables, sprayed with water daily, and protected with a fine net to avoid contamination by new seeds.

The samples obtained were cultivated for 6 months, from November, 2000, to April, 2001. During this period the seedlings were identified as soon as possible, recorded, and removed to avoid interference with other possible germinations. The identification of seedlings was done by means of comparison with herbarium material, when available, or with the help of some specific studies (Hanf, 1982; Jávorka-Csapody, 1991). Seedlings that were not easily identified were grown on in small containers until identification was possible.

2.3.3. Morpho-Functional Analysis

This analysis addressed the seeds of the entire taxa pool of the pastures; i.e., taxa found in the standing vegetation of the plots studied and taxa found only in the soil seed bank, which produced a list of 95 taxa. The analysis is based on the classification of diaspores given by Grime et al. (1981), and refers to their general morphology, surface and appendages. We introduced small modifications to the given categories (Table 2), consisting of the union of certain traits not clearly differentiated, and also in the omission of a few not occurring in our local Flora. In addition, the attribute 'teeth and hairs' was moved into the group of appendages. We also measured length, width and thickness of the seeds, averaged from 5 samples, following Thompson (1993).

Table 2. Classification of diaspores into categories relating to general morphology, appendages and surface (slightly modified after Grime et al. 1981)

Morphology	Appendages	Surface
1. Spherical, or nearly so 2. Ovoid, rhomboidal, turbinate 3. Trigonous or triquetrous 4. Lenticular, reniform or subulate 5. Cylindrical or ligulate 6. Clavate 7. Winged 8. Tadpole-shaped 9. Conical	1. Absent 2. Straight awn(s) or spine(s) 3. Hygroscopic awn or spine 4. Persistent pappus or calyx 5. Large hook(s) or barbed spine(s) 6. Elaiosome 7. Wing 8. Antrorse hairs or teeth	1. Smooth 2. Rugose, muricate, tuberculate or reticulate 3. Striate 4. Hairy 5. Striate and hairy 6. Mucilaginous

In the classification of the diaspores, we took into account previous studies dealing with the morphology and function of seeds (Grime et al., 1981; Hanf, 1982; Jávorka-Csapody, 1991) and also standard floras (Bolòs and Vigo, 1984-2001; Castroviejo et al., 1996-2004). For taxa not included in those studies, or for data not recorded previously, we examined a number of seeds from samples available in the Herbarium of the University of Barcelona (BCN), or obtained from the field. We omitted from our analysis a few species, namely the Orchidaceae since, due to the very small size and specific germination requirements or their seeds, they would not be detected in germination tests, or by hand sorting.

3. RESULTS

3.1. Seed Density and Species Richness in the Soil Bank

The soil seed content varied noticeably throughout the year (Table 3), this being more evident in the germination study (values ranging from 12,178.8 to 785.7 seeds m^{-2}) than via direct observation (values between 6,909.1 and 4,882.5 seeds m^{-2}). In seasonal terms, the densities obtained in 2000 followed the expected dynamics, with the lowest values occurring in spring, when the soil would contain only the persistent seeds. But the densities found in the spring of 1999 were surprisingly high, according to germination tests. The differences in seed density between soil horizons revealed by visual observation also followed the expected pattern (Thompson, 1993); i.e., the topsoil was much richer (Table 4).

Table 3. Seed densities (number of seeds m-2 and standard deviation) found in the sites Malla (Ma) and Montrodon (Mo) for the two pasture types, Plantagini-Aphyllanthetum (P-A) and Brachypodio-Aphyllanthetum (B-A), and the four sample dates, using direct observation (obs.) and germination tests (germ.)

	Ma, P-A	Ma, B-A	Mo, P-A	Mo, B-A	Means
June 1999					
obs.	11,867	2,267	-	6,720	6,951 ± 4,404
germ.	13,400	18,000	-	9,360	13,587 ± 4,323
total	12,633	10,133	-	8,040	10,269 ± 5,469
February 2000					
obs.	6,482	8,081	6,061	2,441	5,766 ± 2,382
germ.	2,525	2,240	3,283	1,179	2,306 ± 871
total	4,504	5,161	4,672	1,810	4,037 ± 2,485
June 2000					
obs.	4,293	3,788	5,556	5,809	4,862 ± 975
germ.	-	926	337	1,094	786 ± 398
total	4,293	2,357	2,946	3,451	3,115 ± 2,297
September 2000					
obs.	5,303	2,525	4,883	8,418	5,282 ± 2,422
germ.	1,599	589	926	10,439	3,388 ± 4,719
total	3,451	1,557	2,904	9,428	4,335 ± 3,617

Table 4. Mean seed densities (seeds m^{-2} and standard deviation) found for the four sample dates, the two soil horizons and the two communities, using direct observation (obs.) and germination tests (germ.). P-A, *Plantagini-Aphyllanthetum*; B-A, *Brachypodio-Aphyllanthetum*

	shallow	deep	P-A	B-A
obs.	4,799 ± 200	782 ± 78	6,081 ± 445	5,149 ± 399
germ.	1,972 ± 584	1,639 ± 655	2,469 ± 1 362	4,438 ± 2,228
total	3,385 ± 1,999	1,210 ± 606	4,275 ± 2,554	4,794 ± 503

However, differences based on germination tests were smaller, although this was mainly due to the high germination rates attained in deep samples collected in the spring of 1999.

The total species number found visually in the soil samples was slightly lower than that from germination tests (41 and 45, respectively), although the amount of seeds was clearly higher in the former method (946 compared to 574, across all samples). The established vegetation of *Plantagini-Aphyllanthetum* at the two sites included 70 species of vascular plants, whereas in the corresponding soil samples we found only 55 species (of which 7 could not be identified); 26 species were found in both the soil bank and the established vegetation. As for *Brachypodio-Aphyllanthetum,* the vegetation consisted of 52 species while soil sampling yielded 46 species (of which 4 could not be identified); in this case, 25 species were found in both. It is interesting to point out that although the relevés of *Plantagini-*

Aphyllanthetum included almost 40% more species than that of *Brachypodio-Aphyllanthetum*, the species richness found in each soil seed bank was similar.

With regards species frequencies, we found noticeable differences between the observation and the germination methods (Table 5). Whereas the 10 species recorded most often by visual observation were frequently found, or even dominant, in the established vegetation (e.g. *Aphyllanthes mospeliensis*, *Brachypodium retusum*, *Thymus vulgaris*, *Carex caryophyllea* and *Dichanthium ischaeumum*), the germination method yielded more uneven results. Among the taxa most recorded by this method, some were only sparsely found in the established vegetation (*Blackstonia perfoliata* or *Centaurium pulchellum*) or were even absent (*Capsella bursa-pastoris, Sorghum halepense* and *Conyza sumatrensis*), while a few were either frequently found or abundant in the relevés (*Thymus vulgaris* or *Brachypodium retusum*). Some of the most abundant species in the vegetation, mainly in *Plantagini-Aphyllanthetum,* appeared very sparsely in the germination tests (such as *Aphyllanthes mospeliensis* or *Brachypodium phoenicoides*).

Table 5. Taxa most frequently found in the soil seed bank of the two associations, based on germination and observation, expressed as the mean of seeds per sample and the percentage vs. the numbers of seeds found

Plantagini-Aphyllanthetum	Seeds/ sample	%	Brachypodio-Aphyllanthetum	Seeds/ Sample	%
Aphyllanthes monspeliensis	2.79	20.78	*Brachypodium phoenicoides*	1.36	11.81
Linum tenuifolium subsp. *milletii*	1.90	14.11	*Plantago lanceolata*	1.34	11.70
Helianthemum sp.	0.88	6.51	*Blackstonia perfoliata*	0.91	7.91
Centaurium pulchellum	0.81	6.05	*Euphorbia flavicoma* subsp. *flavicoma*	0.83	7.22
Carex caryophyllea	0.56	4.19	*Linum tenuifolium* subsp. *milletii*	0.82	7.11
Ononis pusilla	0.46	3.41	*Dichanthium ischaemum*	0.82	7.11
Coronilla minima subsp. *minima*	0.44	3.26	*Capsella bursa-pastoris*	0.55	4.82
Potentilla neumaniana	0.44	3.26	*Thymus vulgaris*	0.49	4.24
Thymus vulgaris	0.44	3.26	*Coris monspeliensis*	0.42	3.67
Helianthemum oleandicum subsp. *italicum*	0.44	3.15	*Helianthemum oleandicum* subsp. *italicum*	0.36	3.00
sp. 1	0.42	3.10	*Convolvulus cantabrica*	0.36	3.10
Blackstonia perfoliata	0.38	2.79	*Aphyllanthes monspeliensis*	0.34	2.98
Ranunculus bulbosus	0.31	2.33	*Teucrium* sp.	0.33	2.87
sp. 2	0.23	1.71	*Lavandula* sp.	0.32	2.75
Teucrium sp.	0.23	1.71	*sp.* 1	0.30	2.64
TOTAL	13.14		TOTAL	11.47	

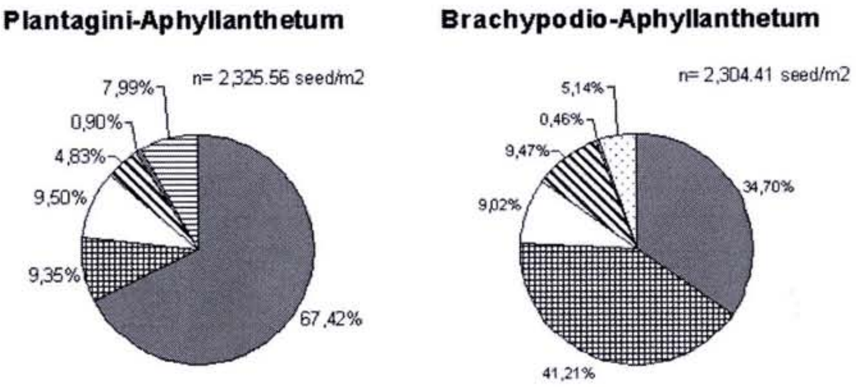
3.2. Life Forms, Families and Ecological Groups

In the visual observation of soil samples, the relative frequencies of life forms showed small variability among communities, depths and sampling dates, in terms of the numbers of taxa identified. Hemicryptophytes and chamaephytes were the main groups (25-35% and 45-60%, respectively), whereas therophytes accounted for about 15%. In contrast, when these frequencies were based on seed numbers, the soil seed bank reflected better the distinct life-form spectra of each community. That is, chamaephytes were more abundant than hemicryptophytes in the xerophilous *Brachypodio-Aphyllanthetum* (more than 45%, versus 35%); and hemicryptophytes surpassed chamaephytes in the mesoxerophilous *Plantagini-Aphyllanthetum* (65%, versus 50%). Other life forms were represented by less than 5% of the seeds. If soil depth is taken into account, chamaephytes were more frequent in the shallow horizon of the samples, decreasing to around 30% in the deep horizon, compared to the other main group, hemicryptophytes. As to sampling dates, variations in percentages did not show clear patterns, except for the frequency of therophytes in spring of 1999, which exceeded 10% of the seeds, following the expected trend whereby short-lived species show a relative increase in the persistent soil bank.

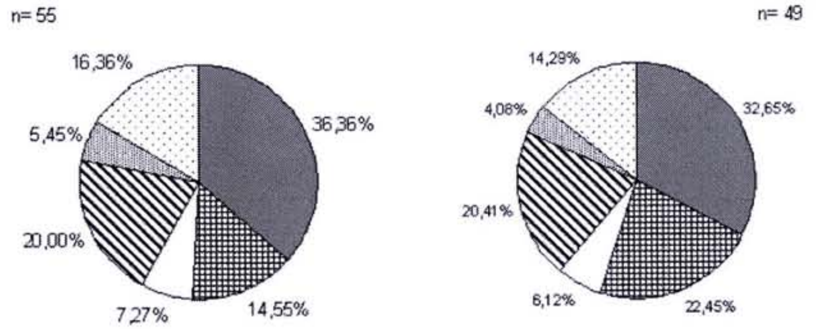
The germination analysis yielded generally higher percentages of therophytes (45% in spring 2000, and in all the deep soil samples), as well as greater differences between sampling dates (40-50% in the spring versus less than 25% in the winter and autumn). Therophytes also stood out in the deep soil horizon, accounting for 45% of the taxa identified, versus less than 35% of chamaephytes.

The main plant families (compositae, grasses, legumes) were found in the seed bank in proportions similar to those occurring in the vegetation, although the germination analysis yielded some irregularities. Grasses were more frequent in the xerophilous pasture than in the mesoxerophilous grassland (15-20% and 5-10%, respectively), and were mainly concentrated in the shallow soil horizon, which would corroborate the feeble contribution of this group to seed regeneration in dense grasslands, as well as their generally low presence in persistent banks. Legumes were more frequent in the observation analysis than after cultivation, probably due in part to generalised requirements for dormancy breaking in this family (Russi et al., 1992). On the other hand, compositae germinated easily, their frequency being higher in the germination test than via observation.

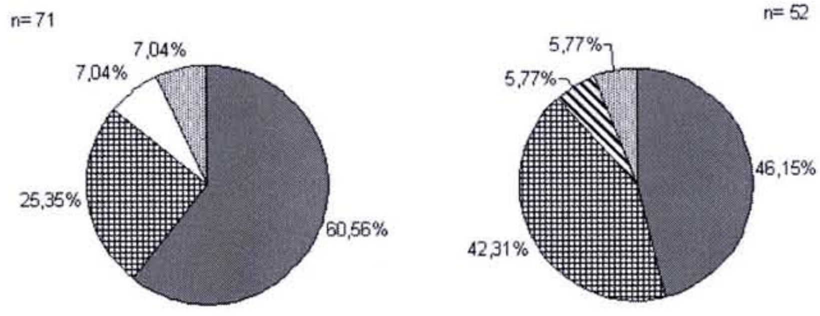
Overall the main phytosociological group represented was the order *Rosmarinetalia* s.l. (2,034.44 seeds m^{-2}, average of plots and sampling dates), a syntaxon characterized by mesoxerophilous, slow-growing perennials. Caespitose herbs like *Aphyllanthes monspeliensis, Carex humilis* and *Potentilla neumanniana*, and sub-shrubs like *Coris monspeliensis, Helianthemum oelandicum* and *Linum tenuifolium* were the core of this ecological group (Figure 7). The second most dominant group (1,120.91 seeds m^{-2}) was the class *Thero-Brachypodietea*, characterized by therophytes (*Linum strictum, Odontites lutea*) and xerophilous perennials (*Botriochloa ischaemum, Brachypodium retusum, Thymus vulgaris*) that are more adapted to Mediterranean conditions and partly to perturbation. Such adaptation implies a more 'ruderal' character, since greater soil moisture irregularities cause more seasonal variation in standing biomass (Grime 2001). The other groups were less well represented (average densities lower than 400 seeds m^{-2}), that of low shrubs (*Dorycnium pentaphyllum, Genista scorpius*) being the lowest (27.1 seeds m^{-2}).



Frequency of seeds in the soil seed bank



Frequency of taxa in the soil seed bank



Frequency of taxa in the stablished vegetation

Figure 7. Contribution of ecological groups to the species pool in the pastures studied, the mesoxerophilous grassland *Plantagini-Aphyllanthetum* (left column) and the xerophilous pasture *Brachypodio-Aphyllanthetum* (right column), by means of the percentage of seeds found in the soil samples (top), the percentage of taxa in the soil samples (middle), and the percentage of taxa in the standing vegetation (bottom).

In the mesoxerophilous grassland (*Plantagini-Aphyllanthetum*), the dominance of *Rosmarinetalia* seeds was even higher, accounting for one-third of the total species, but nearly 70% of seeds. Here, the hygrophilous opportunists were the second most dominant group (220.98 seeds m^{-2}), though consisting of only 4 species. Samples from the xerophilous pasture (*Brachypodio-Aphyllanthetum*) contained the most seeds of *Thero-Brachypodietea*: 22.45% of the species found in the soil bank and more than 40% of the total amount of seeds. The *Rosmarinetalia* taxa were also well represented (16 taxa, 32.65%). The hygrophilous opportunists and the ruderals showed moderate seed densities (more than 200 m^{-2}), the latter ecological group (ruderals) being more frequent here than in the mesoxerophilous grassland.

3.3. Morpho-Functional Trends in the Seed Pool

The established vegetation of the two communities showed very similar spectra of seed types. Percentages of the different morphologies varied by less than 10% (the maximum corresponded to trigonous diaspores, close to 25% in *Brachypodio-Aphyllanthetum* and nearly 35% in *Plantagini-Aphyllanthetum*). The absence of appendages was dominant, slightly higher than 60% in both communities, whereas in the other categories only small differences appeared. Awns, spines and pappus were slightly more abundant in *Brachypodio-Aphyllanthetum*, while diaspores with teeth, antrorse hairs or hygroscopic spines were more numerous in *Plantagini-Aphyllanthetum*. With regards to seed surface, the two communities were similar, with 50% of smooth seeds in both (Figure 8).

Most of the species identified visually from the soil samples had more or less compact seeds (from spherical to reniform) with smooth surfaces; only a few had pappus or appendages (Figure 4). The same trends occurred across the sampling periods, the two communities, and the two soil depths. When taking into account the number of seeds, the spring samplings yielded higher percentages of compact seeds, mainly ovoid, and also of seeds without appendages; these seeds were also more abundant in the deep soil horizon than in the shallow horizon. In general, cylindrical or ligulate seeds (mainly of grasses) showed higher percentages in terms of number of seeds rather than number of species.

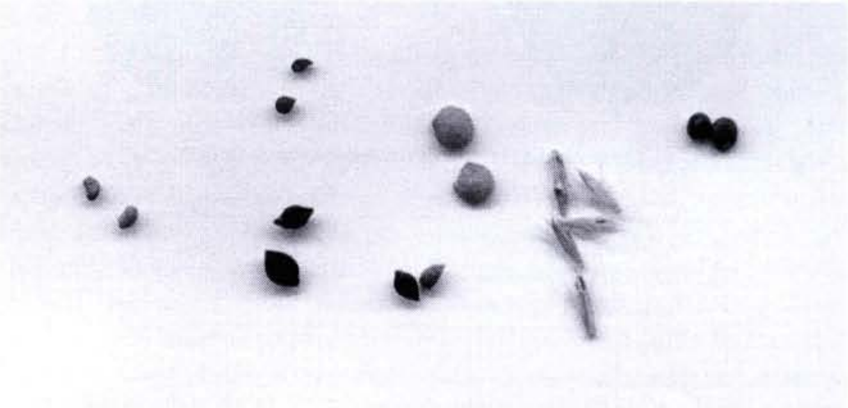


Figure 8. Some representative seeds from the pastures (from 1.8 to 5.6 mm in length).

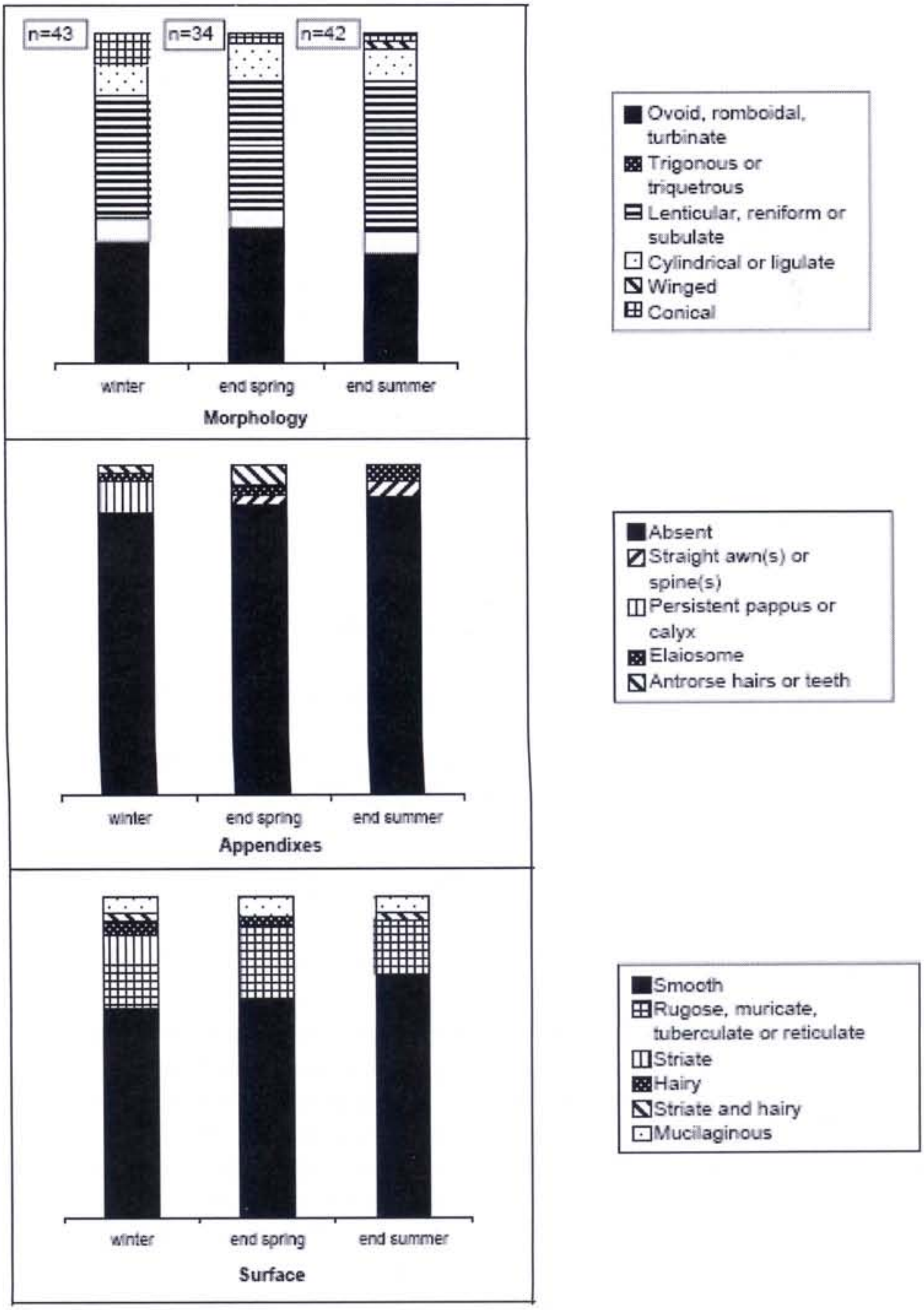


Figure 9. Morpho-functional spectra (percents on each vertical bar) of the seeds found in the soil bank, in terms of general morphology, appendages and surface. Seasonal dynamics is evident as changing percentages (*n* stands for number of taxa).

The morphological spectrum of the germinated seeds was slightly different from that of seeds found visually (Figure 9). There was a noticeable decrease in lenticular or reniform seeds (almost 20% lower) and an increase in conical diaspores (including achenes with pappus) and, less pronounced, of ovoid seeds.

As for differences between depths, species with lenticular or reniform seeds were more abundant in the deep horizon, which would result in better persistence of these types. On the contrary, seeds with appendages were clearly more frequent near the soil surface, as previously hypothesised (Grime et al., 1981). Species with conical seeds (including seeds with pappus) occurred in both horizons with similar percentages, but the number of these seeds was clearly lower in the deep horizon.

Differences between established flora and soil seed bank were more noticeable than that between the two communities. Isometric types (rounded, ovoid, rhomboidal, turbinate, lenticular, reniform or subulate) were more dominant in the soil bank (almost 75% of the total species found) than in the vegetation (less than 65%). The absence of appendages was slightly more frequent in the soil bank (about 70%) than in the vegetation (65%), but the different types of appendages showed similar percentages in soil and vegetation. As for surface types, smooth diaspores were more abundant in the soil seed bank (almost 70% of species) than in the vegetation (less than 55%), where striate or hairy seeds were more frequent.

4. DISCUSSION

4.1. Soil Seed Bank and Standing Vegetation Face to Face

The size of the soil seed bank of the pastures studied is similar to those of other temperate pasture communities (Leck et. al., 1989; Reiné et al., 2004; Bisteau and Mahy, 2005), but clearly lower than those corresponding to dryer open communities, such as gypsophilous scrubs of central Spain (Caballero et al., 2003) or semiarid Syrian pastures (Russi et al., 1992). This would corroborate the contention that the role played by the soil seed bank is clearly less crucial in the perennial, mesoxerophilous pastures of Vic than in therophytic, xerophilous pastures and low scrubs, which are subject to strong seasonal dynamics (Guàrdia et al., 1998).

Following a general trend in perennial pastures (Thompson, 1989), some of the most abundant species in the communities studied appeared very sparsely in the soil bank. Such impoverishment could have been enhanced by the low grazing levels in the pastures studied (Milberg, 1995; Handlová and Münzbergová, 2006). This fact, and the occurrence in the soil seed bank of opportunists rarely found in the established vegetation, resulted in relatively low similarity between the two ecosystem compartments. The Sørensen index (Sørensen, 1948) was 0.4407 in *Plantagini-Aphyllanthetum* and to 0.5319 in *Brachypodio-Aphyllanthetum*. These figures should actually be even lower, since the seeds not identified in the visual observation were not included in the ratio; in fact they probably do not correspond to any of the established species. Higher similarities have been found in communities subjected to severe constraints, such as badlands vegetation in the Pyrenees (Guàrdia et al., 2000) or salt catchments (Gul and Weber, 2001). However, these values are higher than those obtained by Lyaruu and Backéus (1999) in semiarid pastures, and similar to the autumn values calculated by Peco et al. (1998b) for Mediterranean pastures in the Iberian Sistema Central. Such values reveal the impaired potential of the soil seed bank in perennial, dense pastures for community regeneration after severe disturbance.

In both communities, species richness was lower in the soil seed bank than in the standing vegetation. In general, the higher numbers of seeds without appendages and of more or less compact seeds did not compensate for the lack of or weak representation of other seed types. Therophytes showed higher frequencies in the soil bank than in the standing vegetation, a trend more clearly apparent in the germination analysis. Moreover, they reached the highest frequencies in those samples more representative of the persistent bank (spring, and deep soil horizon), a tendency already found in previous studies (Milberg and Hanson, 1993). This fact was less obvious in our visual observation, reflecting the difficulty in detecting the small seeds of most annuals (*Blackstonia perfoliata*, *Centaurium pulchellum*, *Capsella bursa-pastoris*, *Cardamine hirsuta*, etc.). On the other hand, the fairly high percentage of therophytes in the mesoxerophilous *Plantagini-Aphyllanthetum* may be evidence of the greater role taken in the soil bank by the persistent taxa, compared with that of the transient taxa. This is consistent with the observations made by Peco et al. (1998b), who pointed out the prevalence of persistent seeds in the soil bank of ungrazed pastures.

4.2. Space and Time Heterogeneity in the Soil Seed Bank

The seasonal dynamics in the soil seed bank of the pastures studied was apparent from several points of view. Spring samples included lower taxa richness, lower seed densities, higher frequency of therophytes, and higher proportion of compact morphotypes (rounded, ovoid, lenticular) without appendages. This is consistent with the expected seasonal dynamics, in which the soil seed bank becomes impoverished in spring, while the resulting persistent species become more proportionally represented (Thompson and Grime, 1979).

However, inter-annual heterogeneity seems to be higher than seasonal variations, at least with regards to seed densities. This trend seems to become common towards Mediterranean and arid pastures (Coffin and Lauenroth, 1989; Russi et al., 1992; Peco et al., 1998a). Occasional high spring densities, like that obtained from germination of the 1999 samples, might be due to good emergence rates in persistent seeds accumulated in the soil over several years (Grime et al., 1981).

The differences between shallow and deep soil horizons proved to be the highest found in our study, since both density and species richness were clearly higher in the superficial samples. Moreover, ornamented seeds (with appendages, hairs, awns, etc.) and heterometric seeds (conical, clavate, winged) were clearly more frequent near the surface as well. These results are consistent with the hypothesis of Grime et al. (1981), in the sense that compact seeds without appendages become more easily buried, and thus are dominant in the persistent soil banks. Hairy or striate diaspores showed no differences between the two horizons, which suggests these traits have little effect on the chances of the seeds reaching deep soil horizons.

A number of lenticular or reniform seeds were from papilionaceae, which are known to produce very persistent seeds with strong testae and, consequently, are more prone to forming part of the persistent soil seed bank (Grime et al., 1981). On the other hand, the impoverishment of conical seeds (mainly of compositae) in the deep horizon is consistent with this group being mainly transient (Leck et al., 1989). A similar trend may be deduced for the dominant grasses of the pastures studied, based on their diaspore morphology (including awns and lemmas). Thus, persistent seeds in the soil bank are confined to a few taxa in the pastures, as found in various studies (Fenner and Thompson, 2005, and references herein; but see Bossuyt et al., 2007). This demonstrates the limited role of these soil banks in regeneration at the community level, compared to other processes (resprouting, immigration).

4.3. Differences between the Two Communities Studied

The higher seed content shown by germination tests in *Brachypodio-Aphyllanthetum* is consistent with the Mediterranean character of this community, made of high proportions of annuals and dwarf shrubs producing large numbers of seeds (Casas and Ninot, 1994). This is partly because the small gaps and the low intensity disturbance typical of this xerophilous pasture create more opportunities for annuals, which may occur sparsely here and there. Also, the more stressful conditions of this community would slow down plant succession (Casas, 2001; Figure 10), and allow most non-dominant species (small chamaephytes, sparse forbs, therophytes) to persist and contribute to the soil seed bank. This may explain the higher similarity between soil bank and standing vegetation in *Brachypodio-Aphyllanthetum*.

The ongoing pasture abandonment had stronger effects in *Plantagini-Aphyllanthetum*. There, the increasingly dominant grasses (especially *Avenula pratensis* and *Brachypodium phoenicoides*) and some encroachment of shrubs would inhibit the flowering and fruiting of the typical pasture species (Figure 11), as found in various studies (Poschold et al., 1998; Willems and Bik, 1998). The higher seed content in *Plantagini-Aphyllanthetum* revealed by some visual analyses could be partially due to the higher proportion of non-viable seeds included, since seed ageing (without germination) would be enhanced under these conditions.

Figure 10. Even under low grazing pressure, the xerophilous pasture keeps most of its typical irregular structure and species richness.

Figure 11. Pasture abandonment in *Plantagini-Aphyllanthetum* involves densification of dominant grasses (top) and encroachment of shrubs and *Quercus pubescens* (bottom), which lead to species loss via declining of typical pasture plants.

Seeds without appendages and more or less compact were more frequent in the soil bank of this grassland. These and other features indicate a more persistent bank, i.e. *Plantagini-Aphyllanthetum* is more sensitivite to the effects of grazing abandonment. Thus, the potential for regeneration from the soil seed bank in this grassland is lower, compared with that of *Brachypodio-Aphyllanthetum.*

4.4. Declining Biodiversity

The pastures studied include high species richness both within each community (areas of a few square meters harbour 30-40 species) and between communities (a mosaic of 3 different communities may include 50-75 species). The number of species in a whole hill may reach two hundreds, most of them from pastures and others from forests, thickets, rocky areas and ruderal sites (Casas and Ninot, 1994, 1995).

Differences between hills are noticeable, mainly where they include different rock outcrops. These rich systems are semi-natural, small landscape patches standing out from a matrix of farmed land, where vegetation consists of relatively poor flora, very distinct than that secluded in the hills (Figure 12). In landscapes like that of Plana de Vic, pastures include high species percentages from local floras (25-33 %), and together with neighbouring habitats (shrubs, forest clearings, rocky places) may account for 48-53 % of species richness (Ninot and Ferré, 2008) at the landscape level.

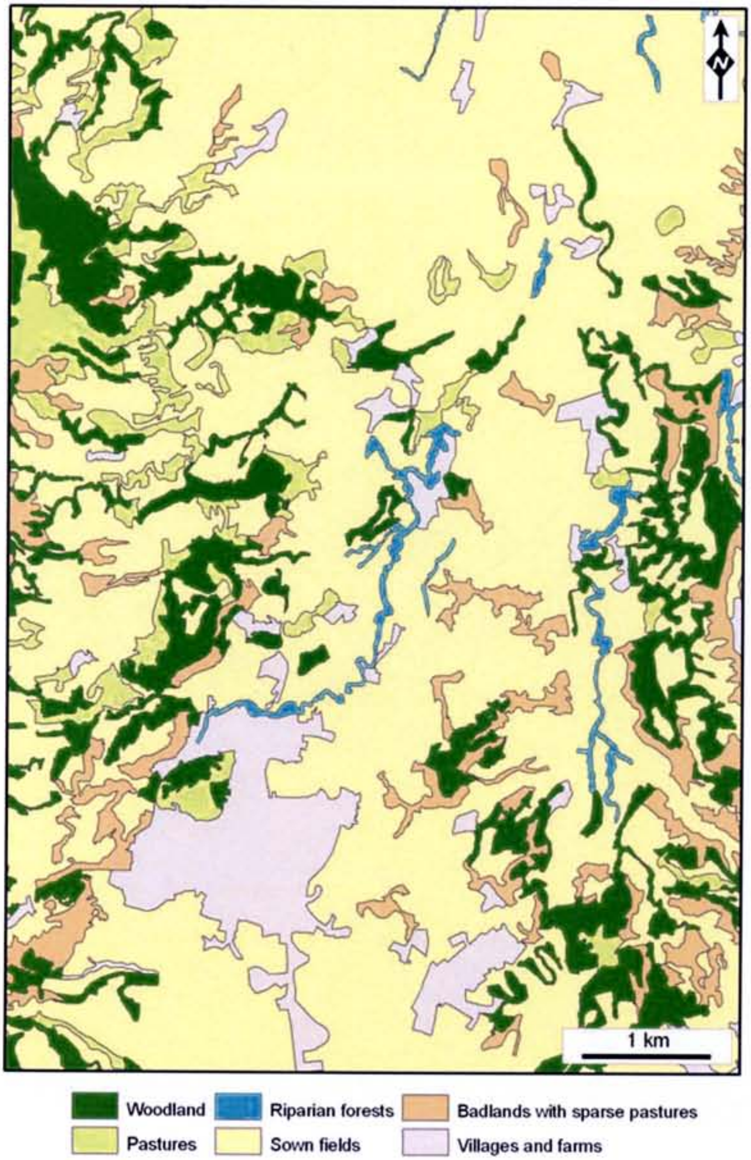


Figure 12. Simplified vegetation map in one example from Plana de Vic, which shows the fragmented structure of semi-natural hills (rangeland = pastures + badlands) on the agricultural matrix.

The traditional land use of Plana de Vic and similar areas involved rotation of crops and fallows and livestock ranging extensively. Small sheep and goat flocks took some profit from fallows, marginal areas and hills (pastures, open woodland, eroded slopes), and manured fields. In parallel, they acted as diaspore vectors between all these habitats, both via endo- and epizoochory, together with other domestic animals. Given the poor dissemination ability of most of the pasture species, these processes carried out most of the seed flow between different hills (Poschold and Bonn, 1998). During the last half century, farming intensification has reduced crop rotation and almost avoided fallow areas. The use of chemical fertilizers and the specialization in farming practices has almost eliminated sheep ranging; the few remaining flocks are much more sedentary than decades ago. These changes in land use have strongly increased the fragmentation of the semi-natural plant communities of the hills (Figure 13).

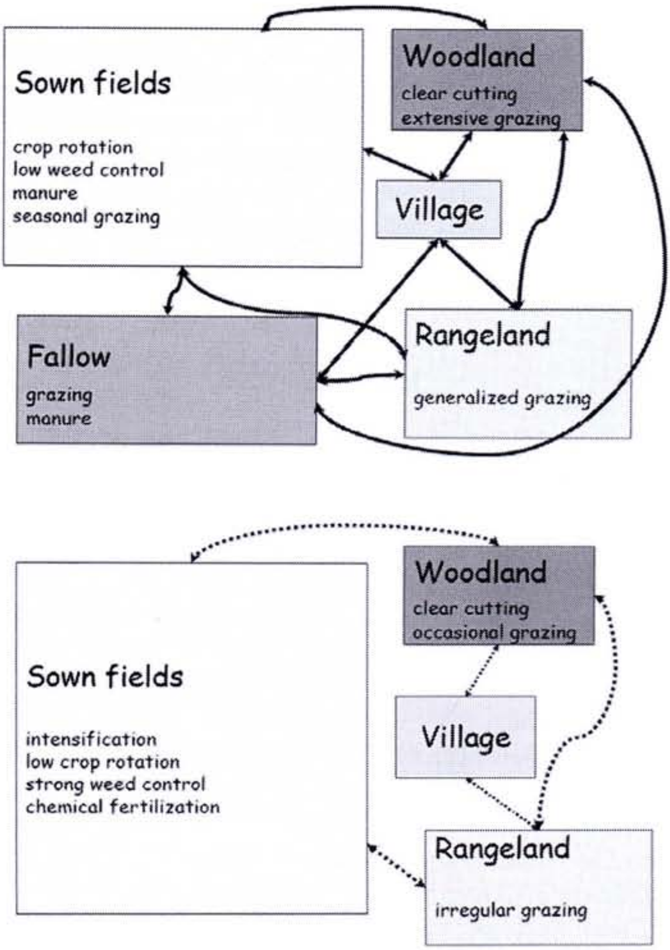


Figure 13. Scheme of landscape structure and seeds flow in traditional (top) and present (bottom) land use. Besides field intensification and vanishing of fallow, seed transfer between distinct habitats via livestock and other processes has changed from diverse and active to few and scarce.

Wind maintains seed flow between populations for anemochorous plants, such as a number of ruderals and opportunists. Other ruderals and therophytes with persistent seeds keep good regeneration potential in the soil seed banks following occasional colonization and seed production. But most of perennial pasture species remain strongly secluded as small populations in some of the hills. Low seed production due to ongoing pasture densification and encroachment, and poor dispersal ability make the less common of these species prone to local extinction. Therefore, present landscape functioning impairs the conservation of plant diversity of this species-rich landscape, and biodiversity restoring is not very promising if soil bank is the main seed source, given the low potential of this ecosystem compartment (Poschold et al., 1998; Willems and Bik, 1998; Bisteau and Mahy, 2005; Rosef, 2008)

CONCLUSION

In semi-natural pastures of Plana de Vic, most of the main species in the stablished vegetation are poorly represented in the soil seed bank, but are able to thrive or e dominate via vegetative persistence and expansion. The changes in land use occurred during the last half century have promoted species impoverishment at stand scale, and fragmentation of semi-natural plant communities at landscape scale. This, together with the low dissemination ability of most pasture species and the limited role of the soil seed bank, impair the conservation or recovery of plant diversity of this species-rich landscape.

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