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1 **The implications of seed rain and seed bank patterns for plant succession at the edges of**  
2 **abandoned fields in Mediterranean landscapes**

3  
4 Elise Buisson<sup>a\*</sup>, Thierry Dutoit<sup>b</sup>, Franck Torre<sup>a</sup>, Christine Römermann<sup>c</sup>, Peter Poschlod<sup>c</sup>

5  
6 *<sup>a</sup> Paul Cézanne University, UMR/CNRS 6116 IMEP, FST Saint Jérôme, case 461, 13397*  
7 *Marseille Cedex 20, France*

8 *<sup>b</sup> UMR INRA-UAPV 406 Ecologie des Invertébrés, Université d'Avignon, site Agroparc,*  
9 *Domaine Saint-Paul, 84914, Avignon, France*

10 *<sup>c</sup> University of Regensburg, Institute of Botany, Universitätsstrasse 31, 93051 Regensburg,*  
11 *Germany*

12  
13  
14  
15 \* Corresponding author      Ph. +33.4.42.90.84.86  
16                                              Fax. +33.4.42.90.84.48  
17                                              e-mail: elise.buisson@univ.u-3mrs.fr  
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23

24 **Abstract**

25 Some environmental variables and above-ground vegetation, seed rain, ant-borne seeds and  
26 seed banks were studied on three abandoned fields, at the margins between these fields and a  
27 remnant patch of a native steppe vegetation of a high value for nature and species  
28 conservation. While the fields were the same size, were adjacent to the same patch of  
29 remnant steppe and were cultivated with the same crop, site-specific environmental variables  
30 contributed to 23% of the vegetation patterns; each site was characterised by its unique  
31 historical trajectory and thus, by a particular set of species. Distance from boundaries  
32 contributed to 10% of the vegetation patterns. Species characterising the surrounding steppe  
33 were found close to boundaries; species characterising abandoned fields were found further  
34 away. Winter seed banks and summer deep seed bank did not contribute much to either effect  
35 and were characterised by species dating back from past cultivation. Conversely, summer  
36 surface seed bank greatly contributed to (83%) the differences in species composition  
37 between the three fields. Seed rain contributed to differences in species composition between  
38 fields (91%) and distance (76%). Ant-borne seeds largely contributed to the differences  
39 between fields (87%). The colonisation of steppe species on field margins occurs mainly  
40 through seed rain and is very slow and incomplete. In a semi-arid fragmented open-  
41 landscape, patches of native vegetation do not play a great role in colonisation processes, and  
42 itinerant sheep grazing is insufficient to initiate recovery.

43

44 *Keywords:* ants; dry grassland; mosaic of herbaceous communities; seed bank; seed rain;  
45 steppe

## 46 **1. Introduction**

47 While many studies on grazing, mowing and burning regimes have been carried out to plan  
48 conservation management for individual grasslands (Hillier et al., 1990; Poschlod and  
49 WallisDeVries, 2002), only few studies plan for long-term management within fragmented  
50 open-landscapes and studies on secondary succession and edges have yet to be relevant to  
51 long-term management. Studies focusing on edges assessed either the influence of  
52 agriculture-related factors on field-margin vegetation (Kleijn et al., 1997) or the influence of  
53 field-margin vegetation on crops (Dutoit et al., 1999; Von Arx et al., 2002).

54 Investigating colonisation processes at edges of abandoned fields is important (Wilson  
55 and Aebischer, 1995) because the field potential to recover via long-term seed bank or long-  
56 distance seed rain has often been found to be relatively low in Northern Europe (Graham and  
57 Hutchings, 1988; Hutchings and Booth, 1996a; Kalamees and Zobel, 2002). Studying edges  
58 is even more important in dry climates, where drought induces conditions that dramatically  
59 slow down successional processes (Blondel and Aronson, 1999). Results may have important  
60 conservation implications, particularly in the Mediterranean basin where grasslands harbour  
61 a high proportion of endangered taxa (Médail and Quézel, 1999).

62  
63 The hypothesis of this research was that remnant patches of vegetation are a source  
64 of seeds for the colonisation of abandoned fields either by seed rain or ant dispersal. The  
65 aims of the present study were (1) to describe the colonisation processes on abandoned field  
66 margins over a complete growing season in order to determine how steppe vegetation re-  
67 establishes at the margins between abandoned fields and a remnant patch of steppe in order  
68 (2) to provide information for the long-term management of abandoned fields.

## 69 **2. Methods**

### 70 *2.1. Study area*

71  
72 The study was carried out in the plain of La Crau, located ~50 km north-west of Marseille in  
73 south-eastern France. The steppe vegetation of the plain evolved with: 1) a dry  
74 Mediterranean climate; 2) a shallow soil (<400 mm) and an impermeable bedrock; 3)  
75 itinerant sheep grazing since 3000 BP (Buisson and Dutoit, 2004). The steppe vegetation is  
76 dominated by the stress-tolerant species *Brachypodium retusum* and *Thymus vulgaris*, which  
77 represent ~50% of the biomass, and is composed of a great diversity of annual species  
78 (Buisson and Dutoit, in press). The remnant central patch of steppe was fragmented by row  
79 crop and melon cultivations between 1965 and 1985, after which all patches of steppe and  
80 fields were grazed by itinerant sheep from February to June.

81 Three abandoned fields (A, B, C) were selected on the sheepfold of Peau de Meau  
82 (43°33'E 4°50'N, elevation 10m), in the centre of the plain. All fields were adjacent to one  
83 same remnant patch of undisturbed steppe (D) in order to avoid confounding changes in the  
84 floristic composition on the margins of abandoned fields with differences due to species  
85 composition of steppe patches (Römermann et al., 2005). However, fields had varied  
86 cultivation periods, dates of abandonment and locations given in Table 1.

### 87 *2.2. Sampling*

88  
89 On each studied field (A, B, C), three transects (1, 2, 3) were set out perpendicular to the  
90 field boundary. Each transect started at the boundary and stretched towards the centre of  
91 abandoned fields and measured 10 m because the visible gradient of the typical steppe  
92 perennial species *T. vulgaris* % cover never exceeded 10 m. The three transects per field  
93 were laid 10 m apart because most herbaceous species do not disperse by wind over more

94 than a few meters (Verkaar et al., 1983), especially in the plain were vegetation grow very  
95 low. Collection points were set 1 m apart along the transects starting at the field edge (point  
96 0) between steppe and fields (0 to 10 m; 11 samples). All data were collected in 2001, a year  
97 with an average climate.

98 Above-ground vegetation was recorded in 10 sub-quadrats of 40 × 40 cm at each  
99 sampling point totalling 990 sub-quadrats, in May 2001. *T. vulgaris* and *B. retusum* % cover,  
100 as well as stones, vegetation and bare ground % cover were visually estimated by one  
101 observer in each quadrat. All other species were sampled in each quadrat using the  
102 presence/absence method. To avoid disturbing the vegetation, other sampling was taken on  
103 the other side of the transects.

104 200g of soil was taken at sampling points 0, 5 and 10 m along each transect in  
105 February 2001 (27 samples total). Samples were dried and sieved through a 200 µm mesh  
106 sieve. Total nitrogen was measured using the Kjeldahl method, phosphorus using the Olsen  
107 method and total carbon using the Anne method (Baize, 2000). The concentrations of  
108 calcium, potassium and magnesium available to plants were measured using the  
109 Shollenberger and Dreibelbis method (Baize, 2000). The soil pH was also measured in H<sub>2</sub>O  
110 (Baize, 2000).

111 The persistent seed bank, seeds that persist in the seed bank >1year, (Thompson et al.,  
112 1997) was sampled in February 2001 before the input of fresh seeds and after the  
113 germination of most seeds in the fall and winter. To deduce the transient seed bank, the  
114 summer seed bank, seeds that persist in the seed bank <1year, (Thompson et al., 1997), was  
115 sampled at the beginning of July 2001 after seeds were shed. Cores could not be taken  
116 because the soil was extremely rocky. For each sampling point, two 500 cm<sup>3</sup> containers were  
117 filled, one for the 0-10 cm depth and one for the >10 cm depth (198 samples for summer and  
118 198 for winter seed bank). The volume of soil sampled was 1500 cm<sup>3</sup>/soil layer/field/distance  
119 from the boundary; the volume recommended by Bakker et al. (1996) was 1200 cm<sup>3</sup>. The 396  
120 samples of soil seed bank were set to germinate using the standard procedure recommended  
121 by Ter Heerdt et al. (1997). Soil samples were washed with water on sieves of 4 mm and 200  
122 µm mesh sizes to reduce bulk and clay. The concentrated soil was spread in a thin layer in  
123 trays filled with 20mm of vermiculite and topped with medical compresses of 100 µm mesh  
124 size. Trays were watered every day from below. Emerged seedlings were identified, counted  
125 and removed weekly.

126 Seed rain was sampled from April 15<sup>th</sup> to October 15<sup>th</sup> 2001. Sticky traps, made of  
127 paper filters coated with grease and placed in 140 mm diameter Petri dishes (Hutchings and  
128 Booth, 1996a), were fixed with pegs at all sampling points along the transects. Sticky papers  
129 were changed every two weeks (1287 traps total). Seeds were identified to the species or  
130 genus level under a dissecting microscope using a reference collection.

131 To assess ant seed dispersal from the steppe to the abandoned fields, ant pitfall traps  
132 were set out at all sampling points along the transects. These traps, consisting of 50 mm  
133 diameter × 100 mm high containers, were filled with a non-attractive liquid of 50% glycol to  
134 conserve seeds and reduce evaporation, 49% water, 1% acetic acid to act as an anti-fungic  
135 and a few drops of tensioactive detergent to make the ants sink. Traps were changed every  
136 two weeks from April 15<sup>th</sup> to October 15<sup>th</sup> 2001 (1287 traps total). Seeds were identified to  
137 the species or genus level and harvesting ants (*Messor barbarus* and *Messor sanctus*) were  
138 identified and counted.

139

### 140 2.3. Data analyses

141 Multivariate analyses were used to study simultaneously the complex relationships among  
142 species, and between the species and their environment. A partial canonical correspondence  
143 analysis pCCA (Ter Braak, 1987) was used to determine 1) the relationship between the  
144 above-ground vegetation and a set of environmental variables once the impact of distance  
145 variables was statistically removed; and 2) the relationship above-ground vegetation and the  
146 distance from boundaries once the impact of the environmental variables was statistically  
147 removed (McIntyre and Lavorel, 1994). The above-ground vegetation data and some  
148 environmental variables (pH, P<sub>2</sub>O<sub>5</sub>, C:N, K<sub>2</sub>O and % cover of vegetation) were used at points  
149 0, 5 and 10 m from boundary.

150 To identify which of the six data-sets best contributed to the composition of the  
151 above-ground vegetation, a K-sets principal component analysis was used (K-sets PCA,  
152 Pagès and Escofier, 1994). Classical multivariate approaches consider alternatively: i) as  
153 many separate PCAs as there are data-sets, but the interpretation is doubtful as it is based on  
154 empirical comparisons of separate analyses; ii) a unique overall PCA of all six data-sets,  
155 although some may weigh more than others in the analysis. A K-sets PCA allowed us to  
156 analyse all six data-sets by weighting differently each variable so that they played a balanced  
157 role in the analysis. Separate PCAs were first conducted for each data-set and then the  
158 inverse of the first eigenvalue was used as a weighting coefficient for the global K-PCA  
159 analysis (Pagès and Escofier, 1994). Computations for the pCCA and the K-sets PCA were  
160 performed using ADE4 software (Thioulouse et al., 1997)

161 To explain plant distribution at field margins, the means per distance (n=9 transects)  
162 were calculated for (1) soil variables (2) total and steppe-only species richness and density of  
163 above-ground vegetation, seed rain, seeds in ant-traps, summer and winter surface and deep  
164 seed banks. Data were directly compared or log<sub>10</sub> transformed (Sokal and Rohlf, 1998)  
165 before being compared with one-way ANOVAs (Statistica software, version 6.0), followed  
166 by post-hoc tests (Least Significant Difference). Non-parametric multiple comparisons by  
167 STP tests (Simultaneous Test Procedure, based on Mann-Whitney U test, Sokal and Rohlf,  
168 1998) were performed on non-normal data.

169

### 170 3. Results

171 The total number of species found in the vegetation, seed bank, seed rain and ant-traps are  
172 given for each field in Table 2. All the species found during this study are listed in the  
173 Appendix and their frequency of occurrence in each of the various types of data are recorded.

174 The partial CCA showed that the environmental variables alone explained 23% of the  
175 variance of the above-ground vegetation matrix (no figure). The partial CCA also showed  
176 that distances from sampling points to boundary contributed to 10% of the above-ground  
177 vegetation matrix (Fig. 1). This distance effect showed that points close to the boundary were  
178 associated with species such as *Asphodelus ayardii*, *B. retusum*, *Filago pyramidata*, *Linaria*  
179 *arvensis* and *T. vulgaris*, whereas points far from the boundary were associated with species  
180 such as *Calamintha nepeta*, *Lepidium graminifolium*, *Rumex pulcher* and *Cynoglossum*  
181 *officinale* (Fig. 1). Non-parametric multiple comparisons by STP tests confirmed that *T.*  
182 *vulgaris* % cover was significantly higher at 0, 1 and 2 m from boundaries than at 10 m  
183 (U=34.7  $p<0.001$ ); and phosphorus contents significantly increased with the distance from  
184 boundaries (U=11.7  $p<0.001$ ).

185 Axis 1 of the K-sets PCA was correlated with the first principal components of all  
186 seven matrices and particularly with above-ground vegetation (89%), seed rain (91%), ant-  
187 borne seed (87%) and summer surface seed bank (83%) matrices (Fig. 2), showing

188 correlation between these variables. This axis (6%) separated abandoned field A, associated  
189 with species, such as *Bromus* sp., *Diplotaxis tenuifolia*, *Polycarpon tetraphyllum* and *Vulpia*  
190 sp., from abandoned field C points associated with species, such as *Aegilops* sp., *Bellis*  
191 *sylvestris*, *Carthamus lanatus* and *Senecio vulgaris*. Abandoned field B points were grouped  
192 between A and C. A site effect was thus observable not only on above-ground vegetation but  
193 also on most of the types of data studied except on winter seed bank. Axis 2 of the K-sets  
194 PCA was particularly correlated with the second components of above-ground vegetation  
195 (80%) and seed rain (76%) matrices (Fig. 2). This axis (4%) separated the points close to the  
196 boundary from the points far from the boundary. Points close to the boundary were  
197 associated with species, such as *Erodium cicutarium*, *Euphorbia exigua*, *Galium* sp. and *P.*  
198 *tetraphyllum* for both matrices as well as *Linum trigynum*, *Sideritis romana* and *T vulgaris* in  
199 the vegetation and *Brachyposium distachyon* and *Plantago bellardii* in the seed rain (Fig. 3).  
200 Points far from the boundary were associated with species, such as *Conyza* sp. in the  
201 vegetation and *Lobularia maritima* in the seed rain (Fig. 3).

202 ANOVA showed that steppe species richness of above-ground vegetation and steppe  
203 species richness of seed rain were significantly higher at 0, 1, 2, and 3 m as well as 4 m for  
204 vegetation than at 7 to 10 m from boundaries (respectively  $F=9.5$  and  $F=6.1$ ,  $P<0.001$  and  
205 LSD test  $P<0.05$ ).

206

#### 207 4. Discussion

208 Independently from the site effect and from the differences in species number found on each  
209 field (Table 2) which are well-known phenomena (Buisson and Dutoit, 2004), original  
210 patterns were observed which were comparable on the three field margins. The composition  
211 of above-ground vegetation changed with distance from boundary: there were more steppe  
212 species close to boundaries and more arable weed species and mesophilous species further  
213 away. Soil pH and soil concentrations in phosphorus increased with distance from boundary  
214 because more fertiliser was applied on the fields than on the field margins that were less  
215 deeply ploughed. Grime et al. (1987) and Gough and Marrs (1990) have shown that ruderal  
216 species out-compete dry grassland species when phosphorus is in excess. Although a  
217 phosphorus gradient existed on the field margins in this study, Buisson and Dutoit (2004)  
218 have shown that concentrations observed in La Crau were not high enough on field margins  
219 (mean phosphorus = 0.019g/kg) to explain the degree of vegetation change (Janssens et al.,  
220 1998).

221 On field margins, the deep seed bank mainly consisted of arable weed species  
222 (*Kickxia elatine* and *Portulaca oleracea*), ruderal and nitrophilous species (*Calamintha*  
223 *nepeta*, *L. maritima*, *Polygonum aviculare*, *S. vulgaris*, *Solanum nigrum*) dating back to  
224 melon cultivation. The surface seed bank consisted not only of recently established steppe  
225 species (seed bank <1 year), but also of the species cited above, some of which (e.g. *P.*  
226 *oleracea* and *S. nigrum*) have not been found in above ground vegetation since the  
227 abandonment of melon cultivation because favourable conditions no longer exist (ploughing,  
228 fertiliser, irrigation etc.). Re-establishment of steppe species from seed bank appeared to be  
229 minimal, as most steppe species were shown to have a transient seed bank (see also  
230 Römermann et al., 2005), although margins offered better environmental conditions for  
231 stress-tolerant steppe species than the middle of the fields.

232 The stress-tolerant steppe species now growing on field margins, but absent in the  
233 seed bank, came from seed rain or ant-borne seeds. Seed dispersal by ants on the margins,  
234 while worth noting (about 10000 seeds and 10000 ants trapped throughout the study), was  
235 probably limited to small distances, as observed by Harrington and Driver (1995). Seed rain

236 thus contributed to most steppe species colonisation. Even sampled over a complete  
237 fructification and dispersal season, seed rain and seed dispersal by ants did not suffice for the  
238 re-establishment of steppe species on the fields since only a few steppe species were found  
239 on margins while typical steppe species such as *Stipa capillata*, *A. ayardii*, *Plantago*  
240 *holosteum*, *Hyssopus canescens*, and *Fumana procumbens* were not. These results contrast  
241 strongly with Etienne et al.'s (1998) assessment of potential steppe vegetation re-  
242 establishment in La Crau and with results found in north-western Europe (Gibson and  
243 Brown, 1992).

244  
245 The results of this study under Mediterranean climate show that the role of the seed  
246 bank in the re-establishment of former steppe on abandoned fields is minimal and thus  
247 corroborate those found elsewhere (Graham and Hutchings, 1988; Hutchings and Booth,  
248 1996a). While in many landscapes, remnant patches of native vegetation have a positive role  
249 on the secondary succession of abandoned fields, in a Mediterranean fragmented open-  
250 landscape, remnant patches of steppe adjacent to abandoned fields do not seem to have much  
251 of a role in the colonisation processes of steppe species as seed dispersal by wind or ants is  
252 limited.

253 Plant and insect dispersal in fragmented landscape has been studied in open  
254 landscapes and it has been concluded that livestock (Poschlod et al., 1998) are an excellent  
255 vector to disperse seeds between plots by epizoochory and endozoochory (Fischer et al.,  
256 1996) in Northern Europe. The steppe of La Crau and abandoned fields are grazed by  
257 itinerant sheep and their daily ranging patterns could easily be planned so that they graze on  
258 the steppe first, then on fields, in order to disperse steppe-species seeds and insects onto  
259 fields. However, grasshoppers thrive and most plants set seeds in summer (Bourrelly et al.,  
260 1983) when all flocks are in transhumance in the Alps. Also, Fischer et al. (1996) have  
261 shown that most of the seeds dispersed came from plants bigger than 80 cm high and Dutoit  
262 et al. (2003) have shown that, in a Mediterranean area where sheep graze year around, sheep  
263 were not a good vector of rare arable weeds. In La Crau, most dicotyledons grow rather small  
264 and have small and smooth seeds resembling those of rare arable weeds. Therefore, although  
265 sheep grazing is required to maintain steppe vegetation (Fabre and Pluinage, 1998), it is not  
266 sufficient for the long-term management of abandoned fields.

267 The long-term conservation of the steppe has to include a plan to re-connect the larger  
268 patches of steppe. Future experiments should focus on sowing seeds or transplanting nurse  
269 species. This management tool has been used to enhance species richness of grasslands in  
270 northern Europe. Its success depends on the seeds sown (Hutchings and Booth, 1996b), on  
271 facilitation processes between transplanted nurse species and others native species (Pywell et  
272 al., 2002) or on concurrent vegetation management (Warren et al., 2001).

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383

384 **Appendix**

385 Total frequency of occurrence (%) of species in all three fields in the vegetation (990  
 386 quadrats of 40 × 40 cm), in the 1287 seed rain traps, in the 1287 ant traps and in the various  
 387 seed banks Nomenclature according to Kerguélen (1999).

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Species	Typical steppe vegetation (Römhann et al. 2005)	Above-ground vegetation	Seed rain	Ant-borne- seeds	Summer surface seed bank	Summer deep seed bank	Winter surface seed bank	Winter deep seed bank
<i>Aegilops ovata</i> L.	X	98.4	0.9	0.3	0.4			
<i>Aira cupaniana</i> Guss.	X	98.2	0.1	0.4	1.3			
<i>Anagallis arvensis</i> L.		32.1			5.2	30.6	12.0	20.1
<i>Anagallis foemina</i> Miller		50			3.8		36.2	10.0
<i>Anagallis</i> sp.				100.0				
<i>Asperula cynanchica</i> L.	X	100.0						
<i>Asphodelus ayardii</i> L.	X	100.0						
<i>Asterolinon linum-stellatum</i> (L.) Duby in DC.	X	96.6	3.0	0.4				
<i>Avena barbata</i> Link	X	98.8	0.7	0.4	0.1	<0.05		
<i>Bellis sylvestris</i> Cirillo	X	99.3	0.5	0.2				
<i>Brachypodium distachyon</i> (L.) P. Beauv.	X	37.7	9.4	2.5	50.0	0.4		
<i>Brachypodium retusum</i> (Pers.) P. Beauv.	X	100.0						
<i>Bromus hordeaceus</i> L. subsp. hordeaceus		87.8	2.0	0.5	9.5	0.2		
<i>Bromus intermedius</i> Guss.		85.1	8.8	1.4	4.3	0.4		
<i>Bromus madritensis</i> L.		84.6	1.4	8.1	5.9			
<i>Bromus rubens</i> L.		78.7	6.6	0.6	14.0	0.1		
<i>Bromus</i> sp.							50.00	50.00
<i>Calamintha nepeta</i> (L.) Savi		91.4		<0.05	5.2	0.7	2.1	0.4
<i>Carduus nigrescens</i> Vill.		58.6	9.9	25.7	5.8			
<i>Carduus tenuiflorus</i> Curtis		99.7	0.18	0.02	0.1			
<i>Carex</i> sp.								100.0
<i>Carlina corymbosa</i> L.	X	100.0						
<i>Carlina lanata</i> L.	X	99.8	0.1	0.1				
<i>Carthamus lanatus</i> L.	X	99.99	0.01					
<i>Catapodium rigidum</i> (L.) C.E. Hubbard in Dony	X	90.1	0.9	0.2	8.8	<0.05		
<i>Cerastium glomeratum</i> Thuill.	X	98.6			1.4			
<i>Cerastium</i> sp.				13.6			86.40	0.00
<i>Chenopodium album</i> L.					11.4	22.7	20.45	45.45
<i>Convolvulus cantabrica</i> L.		100.0						
<i>Conyza</i> sp.		54.4	0.2	0.6	26.5	5.5	10.53	2.27
<i>Crepis foetida</i> L.	X	100.0						
<i>Crepis sancta</i> (L.) Bornm.	X	100.0						
<i>Crepis</i> sp.			29.3	31.3	26.3	13.1		
<i>Cynoglossum officinale</i> L.		92.6	7.4					
<i>Dactylis glomerata</i> L.	X	90.4	5.06	0.3	3.8	0.4	<0.05	0.01
<i>Daucus carota</i> L.	X	100.0						
<i>Diplotaxis tenuifolia</i> (L.) DC.		98.4	0.1		0.4	0.2	0.7	0.2
<i>Erodium cicutarium</i> (L.) L'Hérit. in Aiton		99.0	0.4	0.3	0.3			
<i>Eryngium campestre</i> L.	X	99.8	0.1	0.1	<0.05			
<i>Euphorbia cyparissias</i> L.	X	99.8	0.1	0.1				
<i>Euphorbia exigua</i> L.	X	98.8	0.8	0.3	0.1	<0.05		
<i>Euphorbia seguieriana</i> Necker		100.0						
<i>Evax pygmaea</i> (L.) Brot.	X	99.8		0.2				
<i>Filago pyramidata</i> L.	X	99.7					0.15	0.15
<i>Filago</i> sp.			98.9	1.1				
<i>Galactites elegans</i> (All.) Soldano		98.3	0.1	1.3	0.3			
<i>Galium murale</i> (L.) All.	X	99.3	0.2		0.5			
<i>Galium parisiense</i> L. / <i>G. pumilum</i> Murray	X	97.3	1.7	0.4	0.4	0.1	0.1	<0.05
<i>Gastridium ventricosum</i> (Gouan) Schinz & Thell.	X	93.8	3.5	0.4	2.3			
<i>Geranium molle</i> L.	X	95.1	1.3	0.5	3.0	0.1		
<i>Hedypnois cretica</i> (L.) Dum.-Cours.		98.23	0.01	0.23	1.4	<0.05		<0.05
<i>Hordeum murinum</i> L.		96.1	1.9	0.3	1.7	<0.05		
<i>Hypochaeris glabra</i> L.	X	97.1	1.9	0.6	0.4			
<i>Juncus bufonius</i> L.							50.0	50.0

<i>Juncus subnodulosus</i> Schrank							50.0	50.0
<i>Kickxia elatine</i> (L.) Dumort.				14.3	48.2		23.2	14.3
<i>Lepidium graminifolium</i> L.		97.9	0.2	0.1			1.6	0.2
<i>Linaria arvensis</i> (L.) Desf.	X	99.9	0.1					
<i>Linum strictum</i> L.	X	98.5	1.3	0.2				
<i>Linum trigynum</i> L.		100.0						
<i>Lobularia maritima</i> (L.) Desv.		91.1	0.3	0.2	5.5	0.5	1.6	0.8
<i>Logfia gallica</i> (L.) Cosson & Germain	X	97.0	1.7	0.1	0.9		0.2	0.1
<i>Lolium perenne</i> L.		100.0						
<i>Lolium rigidum</i> Gaudin		100.0						
<i>Lolium</i> sp.			22.5	2.3	75.0	0.2		
<i>Marrubium vulgare</i> L.		100.0						
<i>Medicago minima</i> (L.) L.	X	99.7	0.3					
<i>Medicago praecox</i> DC.		100.0						
<i>Medicago rigidula</i> (L.) All.		99.8	0.2					
<i>Melica ciliata</i> L.		37.1	36.0	24.1	1.9	0.9		
<i>Neatostema apulum</i> (L.) I.M. Johnston		100.0						
<i>Onopordum illyricum</i> L.		98.1		1.9				
<i>Panicum capillare</i> L.	X						100.0	
<i>Petrorhagia prolifera</i> (L.) P.W. Ball & Heywood		99.6	0.3	0.1				
<i>Phleum pratense</i> L.		87.3	1.1	3.7	7.9			
<i>Plantago bellardii</i> All.	X	72.5	27.2	0.3				
<i>Plantago lagopus</i> L.		92.8	0.2		5.8	1.2		
<i>Poa annua</i> L.				34.8	40.6	4.9	14.8	4.9
<i>Polycarpon tetraphyllum</i> (L.) L.		95.0	2.8	0.4	0.2	<0.05	1.3	0.3
<i>Polygonum aviculare</i> L.					69.2	23.1	7.7	
<i>Portulaca oleracea</i> L.					6.8	44.1	19.6	29.5
<i>Potentilla</i> sp.					100.0			
<i>Psilurus incurvus</i> (Gouan) Schinz & Thell.			54.9	25.5		18.7	0.9	
<i>Ranunculus paludosus</i> Poiret					100.0			
<i>Reichardia picroides</i> (L.) Roth	X	100.0						
<i>Reseda</i> sp.		100.0						
<i>Rostraria cristata</i> (L.) Tzvelev	X	92.8	2.8	1.1	3.0	0.3		
<i>Rumex pulcher</i> L.		99.9	0.1					
<i>Sagina apetala</i> Ard.	X	83.3			16.7			
<i>Salvia verbenaca</i> L.	X	99.8		<0.05	0.2		<0.05	
<i>Samolus valerandi</i> L.							100.0	
<i>Sanguisorba minor</i> Scop.	X	99.8			0.2			
<i>Scirpus</i> sp.							39.9	60.1
<i>Senecio vulgaris</i> L.		13.1			75.0	2.2	8.4	1.3
<i>Sherardia arvensis</i> L.	X	99.98		0.02				
<i>Sideritis romana</i> L.	X	98.0	<0.05	0.2	1.6	0.2		
<i>Silene gallica</i> L.	X	95.4	4.6					
<i>Solanum nigrum</i> L.				0.6	8.1	14.2	24.4	52.7
<i>Sonchus asper</i> (L.) Hill		95.4	1.4	0.2	3.0			
<i>Stipa capillata</i> L.	X				100.0			
<i>Taeniatherum caput-medusae</i> (L.) Nevski	X	99.0	0.3	0.5	0.2			
<i>Thymus vulgaris</i> L.	X	93.0	1.1	0.5	4.6	0.3	0.4	0.1
<i>Torilis nodosa</i> (L.) Gaertner		100.0						
<i>Trifolium campestre</i> Schreber in Sturm	X	95.5		0.2	4.3			
<i>Trifolium glomeratum</i> L.	X	95.8	0.02	0.2	2.5	0.48	0.3	0.7
<i>Trifolium scabrum</i> L.		99.48	<0.05	0.08	0.2	0.1		0.1
<i>Trifolium</i> sp.		97.8	0.2		1.6	0.40		
<i>Trifolium stellatum</i> L.	X	98.6	0.1	0.6	0.7			
<i>Trifolium subterraneum</i> L.		100.0						
<i>Trifolium suffocatum</i> L.		93.3	0.2	1.5	4.6	0.3		0.1
<i>Trigonella monspeliaca</i> L.	X	97.1	0.1	0.4	2.2	0.2		
<i>Typha latifolia</i> L.							72.2	27.8
<i>Verbascum sinuatum</i> L.		100.0						
<i>Verbena officinalis</i> L.					12.8	18.0	43.6	25.6
<i>Veronica arvensis</i> L.		96.1	0.2	<0.05	3.3	<0.05	0.3	<0.05
<i>Vulpia</i> sp.		61.4	6.3	1.3	30.3	0.7	<0.05	

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392 Table 1. Cultivation history of the three abandoned fields A, B, C and the steppe on the  
 393 sheepfold of Peau de Meau. After abandonment, grazing occurred on all fields, as on the  
 394 steppe, by itinerant sheep from February to June.

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Sites	Type of cultivation	Duration of cultivation & year of abandonment	Field location
Field A 5 ha	Melons (small tunnels) Cereals and alfalfa	1 year in 1971 1 year in 1972	N-NW of the steppe patch (D)
Field B 5 ha	Cereals and alfalfa Melons (small tunnels) Cereals and alfalfa	from 1960 to 1966 1 year in 1971 1 year in 1972	W of the steppe patch (D)
Field C 5 ha	Melons (small tunnels) Cereals and alfalfa Melons, courgettes, aubergines, peppers (large tunnels)	1 year in 1968 1 year in 1969 from 1979 to 1984	W-SW of the steppe patch (D)
Steppe D 6500 ha	Not cultivated	na	na

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399 Table 2. Species and germination or seed number of abandoned field A, B and C in the  
 400 vegetation, soil seed bank, seed rain and ant-borne seeds.  
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	A	B	C	Total
Vegetation (33 sampling points / field)				
Species number in the vegetation	63	66	83	94
Soil seed bank (198 soil samples / season)				
Species number in summer seed bank	58	54	58	73
Seedling number in summer seed bank	7562	7292	4684	19538
Species number in winter seed bank	27	28	21	39
Seedling number in winter seed bank	691	375	497	1563
Seed rain (1287 traps)				
Number of taxa	52	62	65	76
Seed number	20880	13802	8019	42701
Ant-borne seeds (1287 traps)				
Number of taxa	46	49	61	69
Seed number	4402	3140	2414	10588

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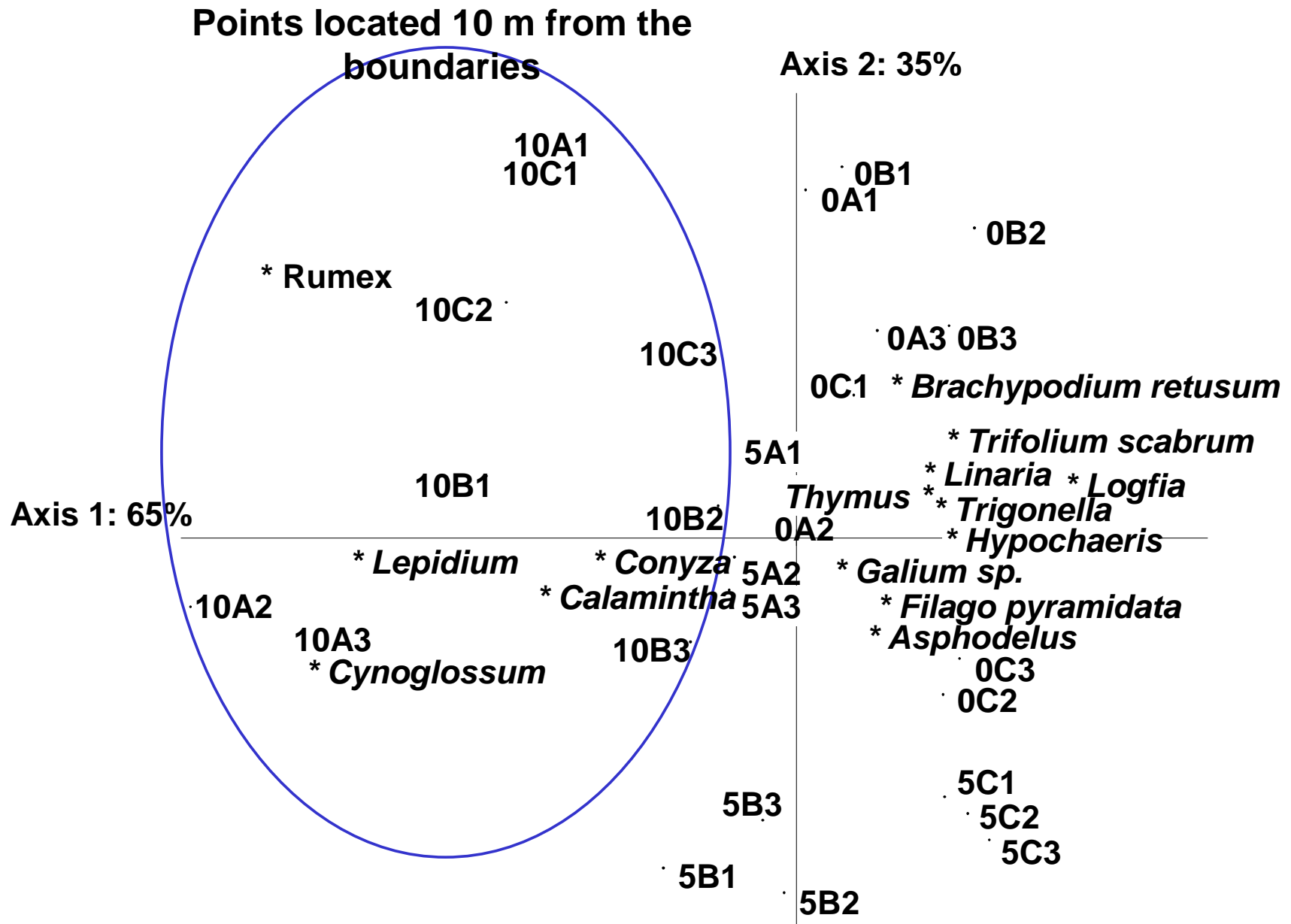


Fig. 1. Partial CCA performed on distance and vegetation variables once the impact of environmental variables was statistically removed. All sampling points are shown. Point abbreviations: first number = distance to boundary (0 to 10 m); letter = field A, B or C; second number = transect number (1, 2 or 3). Only the species with high contributions are shown. The nine sampling points far from the boundaries are circled.



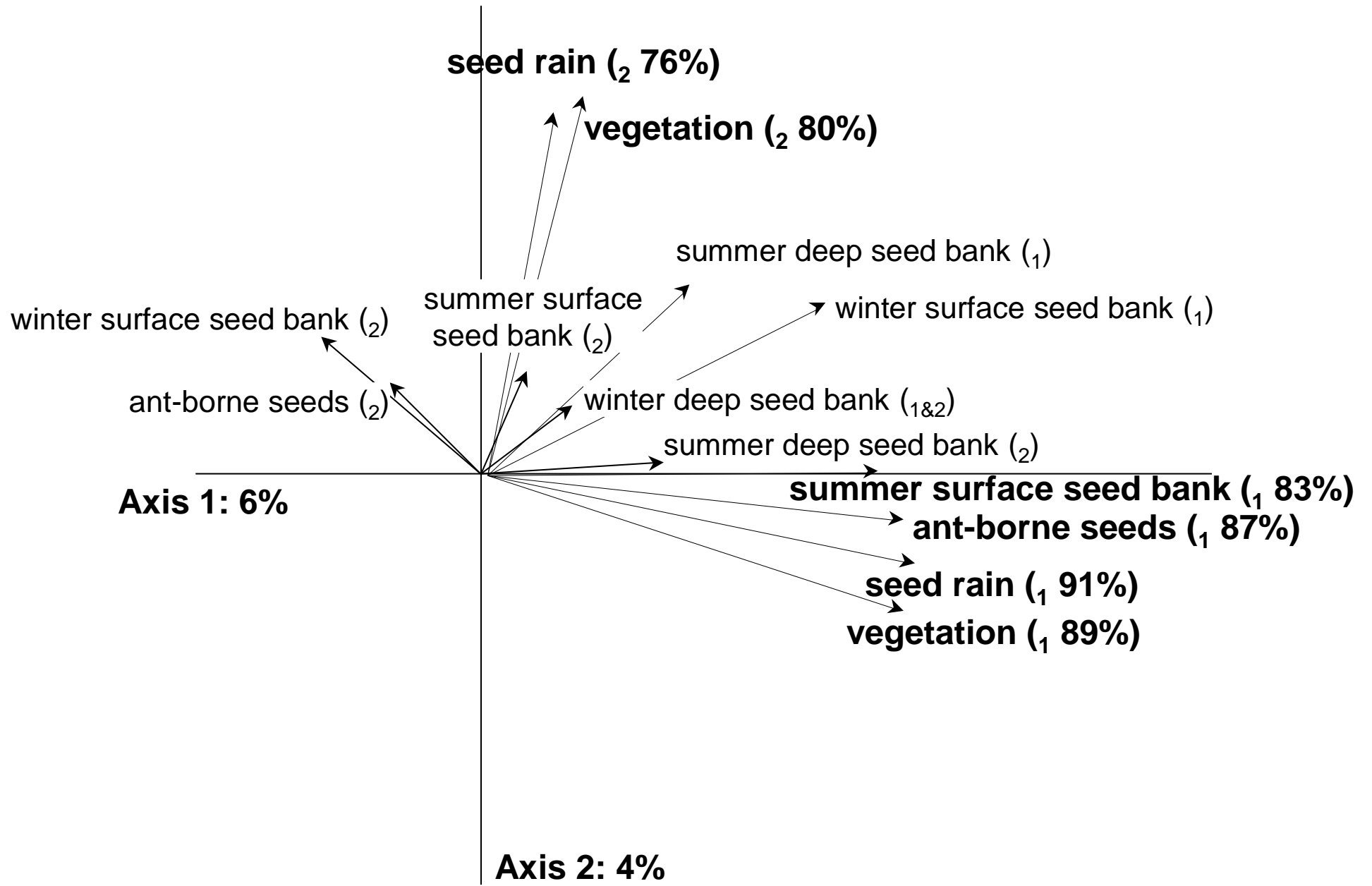


Fig. 2. Projection of the first two principal components of the separate analysis of each of the seven matrices onto the K-set PCA best plane. Sets with the highest contributions to axes 1 or 2 are written in bold and their contribution written in brackets.

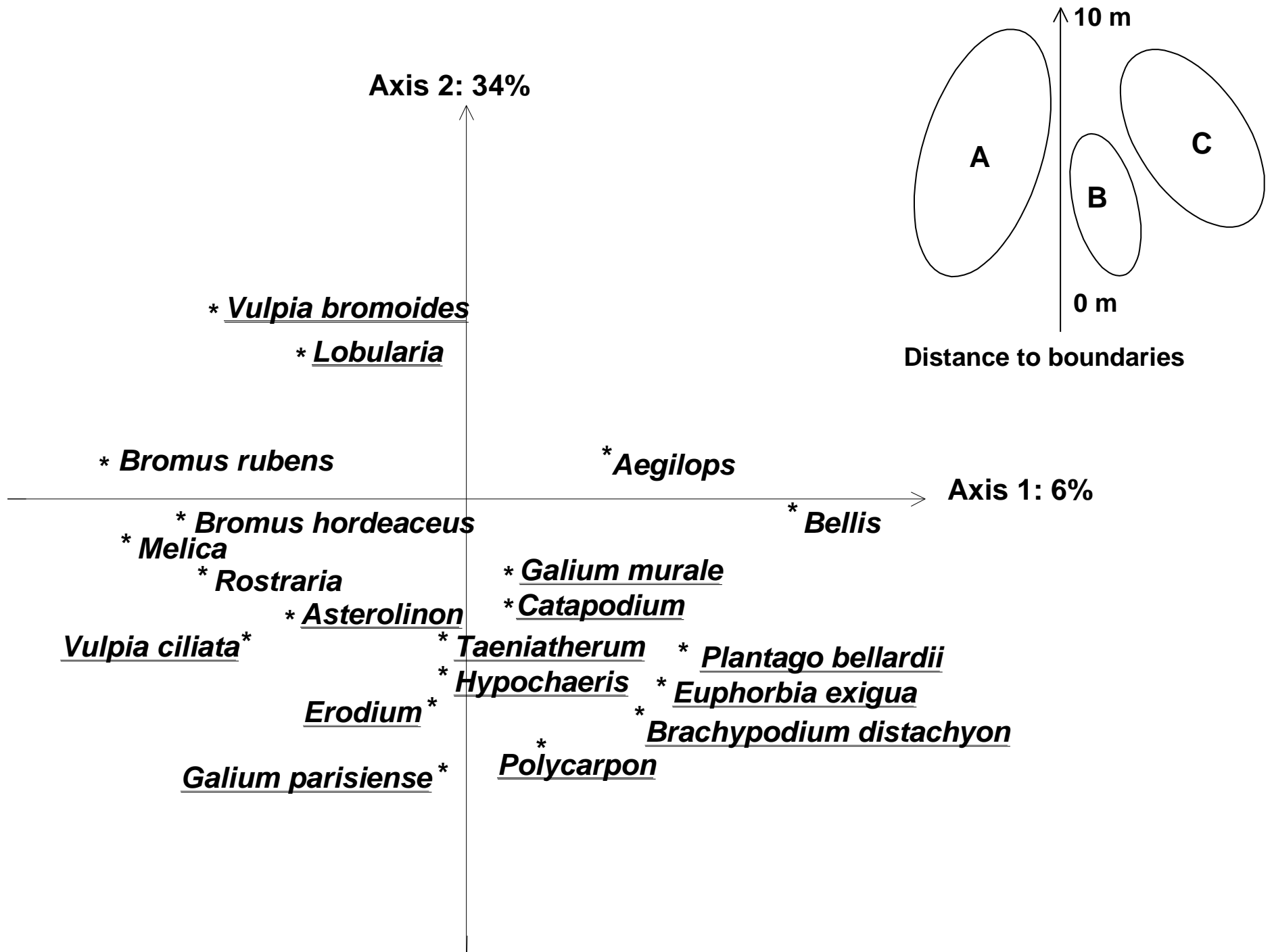


Fig. 3. Factor map of species in the seed rain only, resulting from the K-set PCA. Only species with the highest contributions to axes 1 or 2 are written. Underlined species contribute to axis 2. The K-set PCA map of sampling points is schematized on the top right corner.