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

Elise Buisson, Thierry Dutoit, F. Torre, C. Romermann, P. Poschlod

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

Elise Buisson[a*], Thierry Dutoit[b], Franck Torre[a], Christine Römermann[c], Peter Poschlod[c]

[a] Paul Cézanne University, UMR/CNRS 6116 IMEP, FST Saint Jérôme, case 461, 13397 Marseille Cedex 20, France
[b] UMR INRA-UAPV 406 Ecologie des Invertébrés, Université d'Avignon, site Agroparc, Domaine Saint-Paul, 84914, Avignon, France
[c] University of Regensburg, Institute of Botany, Universitätsstrasse 31, 93051 Regensburg, Germany

* Corresponding author Ph. +33.4.42.90.84.86
Fax. +33.4.42.90.84.48
e-mail: elise.buisson@univ.u-3mrs.fr

Abstract

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

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

1. Introduction

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

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

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

2. Methods

2.1. Study area

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

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

2.2. Sampling

On each studied field (A, B, C), three transects (1, 2, 3) were set out perpendicular to the field boundary. Each transect started at the boundary and stretched towards the centre of abandoned fields and measured 10 m because the visible gradient of the typical steppe perennial species *T. vulgaris* % cover never exceeded 10 m. The three transects per field were laid 10 m apart because most herbaceous species do not disperse by wind over more than a few meters (Verkaar et al., 1983), especially in the plain were vegetation grow very low. Collection points were set 1 m apart along the transects starting at the field edge (point 0) between steppe and fields (0 to 10 m; 11 samples). All data were collected in 2001, a year with an average climate.

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

200g of soil was taken at sampling points 0, 5 and 10 m along each transect in February 2001 (27 samples total). Samples were dried and sieved through a 200 µm mesh sieve. Total nitrogen was measured using the Kjeldahl method, phosphorus using the Olsen method and total carbon using the Anne method (Baize, 2000). The concentrations of calcium, potassium and magnesium available to plants were measured using the Shollenberger and Dreibelbis method (Baize, 2000). The soil pH was also measured in H_2O (Baize, 2000).

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

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

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

2.3. Data analyses

Multivariate analyses were used to study simultaneously the complex relationships among species, and between the species and their environment. A partial canonical correspondence analysis pCCA (Ter Braak, 1987) was used to determine 1) the relationship between the above-ground vegetation and a set of environmental variables once the impact of distance variables was statistically removed; and 2) the relationship above-ground vegetation and the distance from boundaries once the impact of the environmental variables was statistically removed (McIntyre and Lavorel, 1994). The above-ground vegetation data and some environmental variables (pH, P_2O_5, C:N, K_2O and % cover of vegetation) were used at points 0, 5 and 10 m from boundary.

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

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

3. Results

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

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

Axis 1 of the K-sets PCA was correlated with the first principal components of all seven matrices and particularly with above-ground vegetation (89%), seed rain (91%), ant-borne seed (87%) and summer surface seed bank (83%) matrices (Fig. 2), showing correlation between these variables. This axis (6%) separated abandoned field A, associated with species, such as *Bromus* sp., *Diplotaxis tenuifolia*, *Polycarpon tetraphyllum* and *Vulpia* sp., from abandoned field C points associated with species, such as *Aegilops* sp., *Bellis sylvestris*, *Carthamus lanatus* and *Senecio vulgaris*. Abandoned field B points were grouped between A and C. A site effect was thus observable not only on above-ground vegetation but also on most of the types of data studied except on winter seed bank. Axis 2 of the K-sets PCA was particularly correlated with the second components of above-ground vegetation (80%) and seed rain (76%) matrices (Fig. 2). This axis (4%) separated the points close to the boundary from the points far from the boundary. Points close to the boundary were associated with species, such as *Erodium cicutarium, Euphorbia exigua, Galium* sp. and *P. tetraphyllum* for both matrices as well as *Linum trigynum, Sideritis romana* and *T vulgaris* in the vegetation and *Brachyposium distachyon* and *Plantago bellardii* in the seed rain (Fig. 3). Points far from the boundary were associated with species, such as *Conyza* sp. in the vegetation and *Lobularia maritima* in the seed rain (Fig. 3).

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

4. Discussion

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

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

The stress-tolerant steppe species now growing on field margins, but absent in the seed bank, came from seed rain or ant-borne seeds. Seed dispersal by ants on the margins, while worth noting (about 10000 seeds and 10000 ants trapped throughout the study), was probably limited to small distances, as observed by Harrington and Driver (1995). Seed rain thus contributed to most steppe species colonisation. Even sampled over a complete fructification and dispersal season, seed rain and seed dispersal by ants did not suffice for the re-establishment of steppe species on the fields since only a few steppe species were found on margins while typical steppe species such as *Stipa capillata, A. ayardii, Plantago holosteum, Hyssopus canescens,* and *Fumana procumbens* were not. These results contrast strongly with Etienne et al.'s (1998) assessment of potential steppe vegetation re-establishment in La Crau and with results found in north-western Europe (Gibson and Brown, 1992).

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

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

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

Acknowledgements

This study was financed with a grant from "Ministère du Développement Durable et de l'Ecologie", program 'Espaces Protégés'. We acknowledge the CEEP Ecomusée de Crau, Mr Bernhardt, Fadda, Gerbaud, and Mrs Bottone, Rolando, and Trivelly for technical support and field assistance, as well as Mr Hayes and Mrs Sweetko for proof reading the manuscript. We also thank several anonymous reviewers for helpful comments on the manuscript.

References

Baize, D., 2000. Guide des analyses en pédologie. INRA, Paris.
Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., Thompson., K., 1996. Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45, 461-490.
Blondel, J., Aronson, J., 1999. Biology and Wildlife of the Mediterranean Region. Oxford University Press, Oxford.
Bourrelly, M., Borel, L., Devaux, J.P., Louis-Palluel, J., Archiloque, A., 1983. Dynamique annuelle et production primaire nette de l'écosystème steppique de Crau. Biologie-Ecologie méditerranéenne 10, 55-82.
Buisson, E., Dutoit, T., 2004. Colonisation by native species of abandoned farmland adjacent to a remnant patch of Mediterranean steppe. Plant Ecology 174, 371-384.
Buisson, E., Dutoit, T., in press. Creation of the Natural Reserve of La Crau: implications for the creation and management of protected areas. Journal of Environmental Management.
Dutoit, T., Gerbaud, E., Ourcival, J.M., 1999. Field boundary effects on soil seed banks and weed vegetation distribution in an arable field without weed control (Vaucluse, France). Agronomie, Agriculture and Environnement 19, 579-590.
Dutoit, T., Jäger, M., Gerbaud, E., Poschlod, P., 2003. Rôles des ovins dans le transport de graines d'espèces messicoles: le cas d'une exploitation agricole du Parc Naturel Régional du Luberon. Courrier scientifique du Parc régional du Luberon 7, 68-75.
Etienne, M., Aronson, J., Le Floc'h, E., 1998. Abandoned lands and land use conflicts in southern France. Piloting ecosystem trajectories and redesigning outmoded landscapes in the 21st century. In: Rundel, P.W., Montenegro, G., Jaksic, F. (Eds), Landscape degradation and biodiversity in Mediterranean-type ecosystems. Ecological Studies Series n°136. Springer, Berlin, pp. 127-140.
Fabre, P., Pluvinage, J., 1998. Intégration des mesures agri-environnementales aux systèmes d'élevage ovin de la Crau. In: CEEP Ecomusée de Crau (Eds), Patrimoine nature et pratiques pastorales en Crau. Saint-Martin de Crau, France, pp. 100-113.
Fischer, S.F., Poschlod, P., Beinlich, B., 1996. Experimental studies on the dispersal of plants and animals on sheep in calcareous grasslands. Journal of Applied Ecology 33, 1206-1222.
Gibson, C.W.D., Brown, V.K., 1992. Grazing and vegetation change: deflected or modified succession? Journal of Applied Ecology 29, 120-131.
Gough, M.W., Marrs, R.H., 1990. A comparison of soil fertility between semi-natural and agricultural plant communities: implications for the creation of species-rich grasslands on abandoned agricultural land. Biological Conservation 51, 83- 96.
Graham, D. J., Hutchings, M.J., 1988. A field investigation of germination from the seed bank of a chalk grassland ley established on former arable land. Journal of Applied Ecology 25, 253-263.
Grime, J.P., MacKey, J.M.L, Hillier, S.H., Read, D.J., 1987. Floristic diversity in a model system using experimental microcosms. Nature 328, 420-422.
Harrington, G.N., Driver, M.A., 1995. The effect of fire and ants on the seed-bank of a shrub in a semi-arid grassland. Australian Journal of Ecology 20, 238-247.
Hillier, S.H., Walton, D.W.H., Wells, D.A., 1990. Calcareous grassland: ecology and management. Bluntisham Books, Bluntisham.

Hutchings, M.J., Booth, K.D., 1996a. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. I. The potential roles of the seed bank and the seed rain. Journal of Applied Ecology 33, 1171-1181.

Hutchings, M.J., Booth, K.D., 1996b. Studies on the feasibility of re-creating chalk grassland vegetation on ex-arable land. II. Germination and early survivorship of seedlings under different management regimes. Journal of Applied Ecology 33, 1182-1190.

Janssens, F., Peeters, A., Tallowin, J.R.B., Bakker, J.P., Bekker, R.M., Fillat, F., Oomes, M.J.M., 1998. Relationship between soil chemical factors and grassland diversity. Plant and Soil 202, 69-78.

Kalamees, R., Zobel, M., 2002. The role of the seed bank in gap regeneration in a calcareous grassland community. Ecology 83, 1017-1025.

Kerguélen, M., 1999. Index synonymique de la flore de France. [pages html]. INRA Dijon. http://www.dijon.inra.fr/flore-france/ [October 1999 ; last checked in September 2005].

Kleijn, D., Joenje, W., Kropff, M.J., 1997. Patterns in species composition of arable field boundary vegetation. Acta Bot. Neerl. 46, 175-192.

McIntyre, S., Lavorel, S., 1994. How environmental and disturbance factors influence species composition in temperate Australian grasslands. Journal of Vegetation Science 8, 521-531.

Médail, F., Quézel, P., 1999. Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities. Conservation Biology, 13, 1510-1513.

Pagès, J., Escofier, B., 1994. Multiple factor analysis (AFMULT package). Computational Statistics and Data Analysis 18, 121-140.

Poschlod, P., Kiefer, S., Tränkle, U., Fisher, S., Bonn, S., 1998. Plant species richness in calcareous grasslands as affected by dispersability in space and time. Applied Vegetation Science 1, 75-90.

Poschlod, P., WallisDeVries, M.F., 2002. The historical and socio-economic perspective of calcareous grasslands-lessons from the distant and recent past. Biological Conservation 104, 361- 376.

Pywell, R. F., Bullock, J.M., Hopkins, A., Walker, K.J., Sparks, T.H., Burke, M.J.W., Peel, S., 2002. Restoration of species-rich grassland on arable land: assessing the limiting processes using a multi-site experiment. Journal of Applied of Ecology 39, 294-309.

Römermann, C., Dutoit, T., Poschlod, P., Buisson, E., 2005. Influence of former cultivation on the unique Mediterranean steppe of France and consequences for conservation management. Biological Conservation 121, 21-33

Sokal, R. R., Rohlf, F.J., 1998. Biometry: the principles and practice of statistics in biological research. 3rd edition, W. H. Freeman Company, New York.

Ter Braak, C.J.F., 1987. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetatio 69, 69-77.

Ter Heerdt, G.N.J., Verweij, G.L., Bekker, R.M., Bakker, J.P., 1997. An improved method for seed-bank analysis: seedling emergence after removing the soil by sieving. Functional Ecology 10, 144-151.

Thioulouse, J., Chessel, D., Dolédec, S., Olivier, J.M., 1997. ADE-4: a multivariate analysis and graphical display software. Statistics and Computing 7, 75-83.

Thompson, K., J. Bakker, and R. Bekker. 1997. The soil seed bank of North West Europe: methodology, density and longevity. Cambridge University Press, Cambridge.

Verkaar, H.J., Schenkeveld, A.J., Van De Klashorst, M.P., 1983. On the ecology of short lived forbs in chalk grasslands: dispersal of seeds. New Phytologist 95, 335-344.

Von Arx, G., Bosshard, A., Dietz, H., 2002. Land-use intensity and border structures as determinants of vegetation diversity in an agricultural area. Bulletin of the Geobotanical Institute ETH 68, 3-15.
Warren, J., Christal, A., Wilson, F., 2001. Effects of sowing and management on vegetation succession during grassland habitat restoration. Agriculture, Ecosystems and Environment 1909, 1-10.
Wilson, P.J., Aebischer, N.J., 1995. The distribution of dicotyledonous arable weeds in relation to distance from the field edge. Journal of Applied Ecology 32, 295-310.

Appendix

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

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

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

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

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

Table 2. Species and germination or seed number of abandoned field A, B and C in the vegetation, soil seed bank, seed rain and ant-borne seeds.

	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

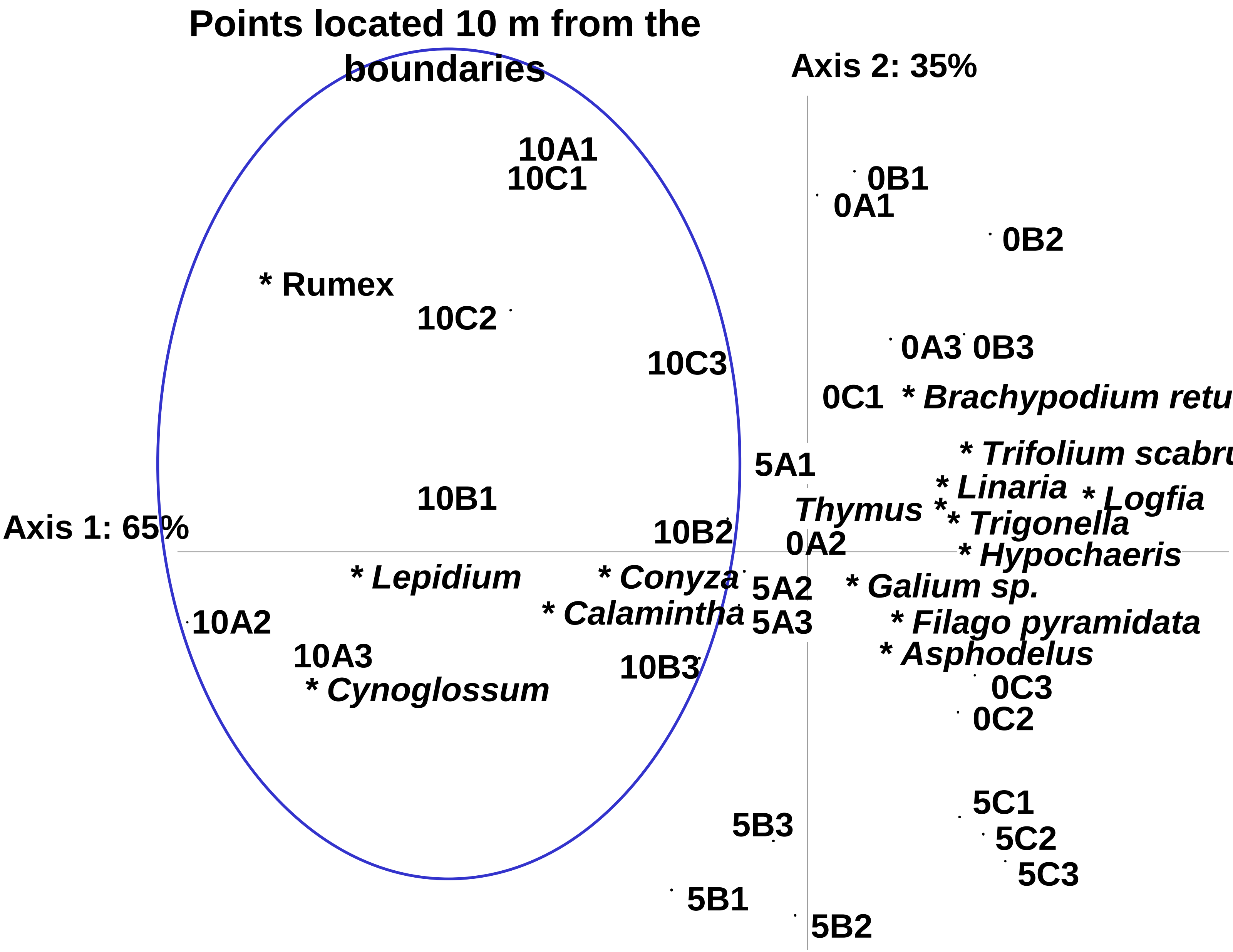

Fig. 1. Partial CCA performed on distance and vegetation variables once the impact of environmental variables was statistically removed. All sampling points are shown. Point abbreviations: first number = distance to boundary (0 to 10 m); letter = field A, B or C; second number = transect number (1, 2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

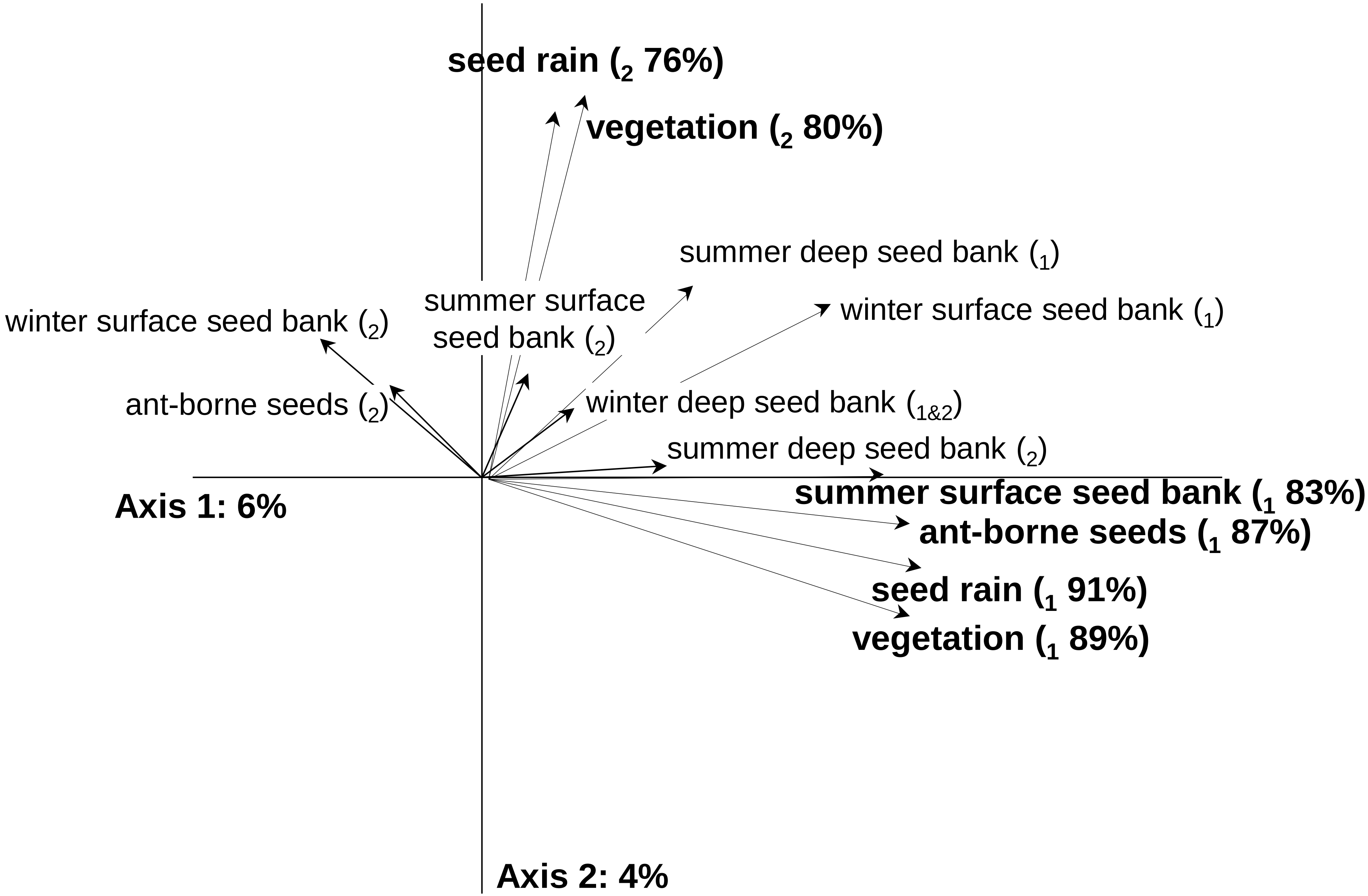

Fig. 2. Projection of the first two principal components of the separate analysis of each of the seven matrices onto the K-set PCA best plane. Sets with the highest contributions to axes 1 or 2 are written in bold and their contribution written in brackets.

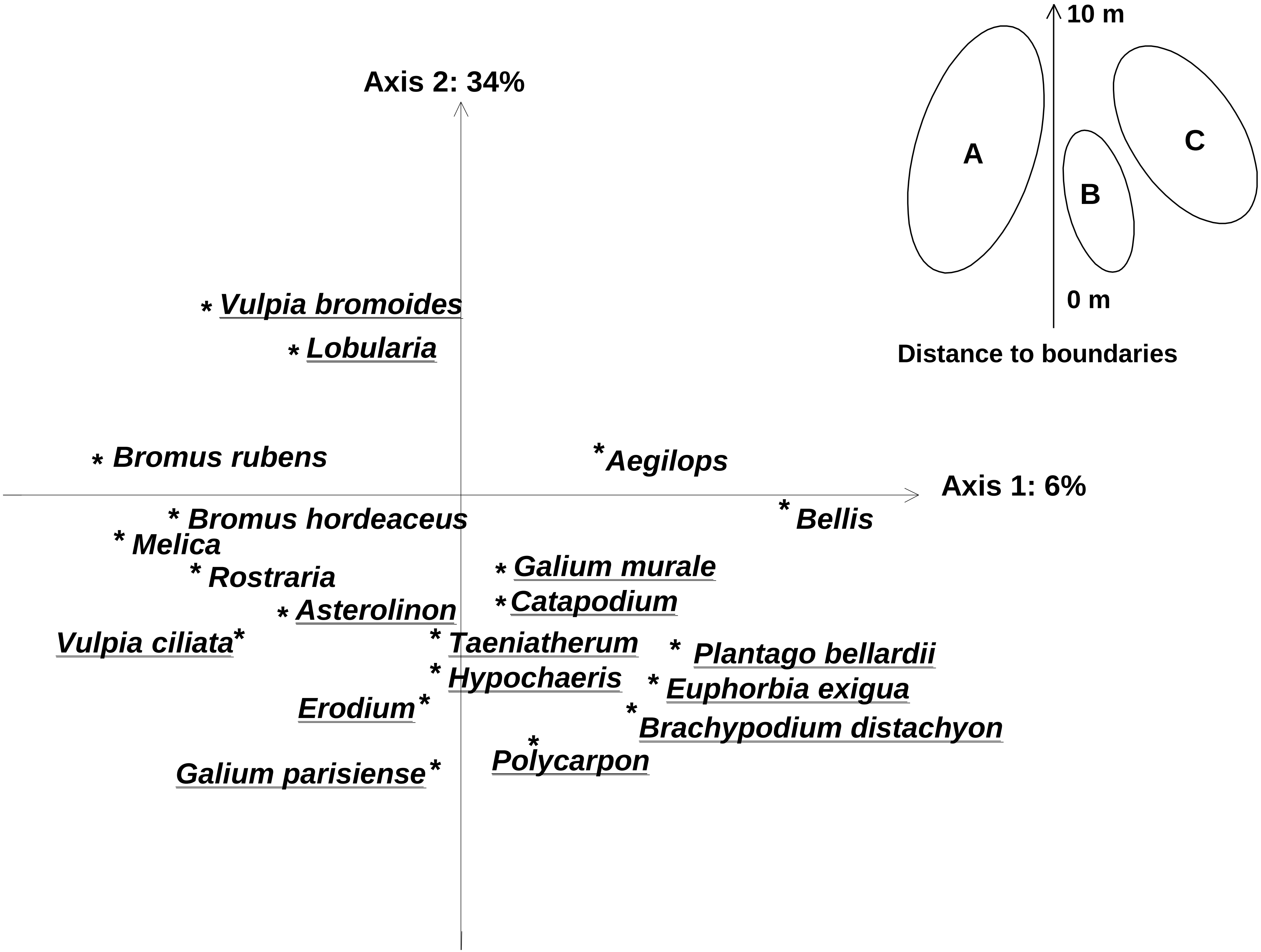

Fig. 3. Factor map of species in the seed rain only, resulting from the K-set PCA. Only species with the highest contributions to axes 1 or 2 are written. Underlined species contribute to axis 2. The K-set PCA map of sampling points is schematized on the top right corner.