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Environmental and management factors determining weed species composition and diversity in France

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ABSTRACT

Multivariate analysis of data from approximately 700 arable fields from France was carried out to partition the respective importance of environmental factors *versus* management practices on weed species richness and composition. Overall, canonical correspondence analysis indicated that the major variations in species composition between fields were associated with human management factors; (1) the current crop type and (2) the preceding crop type. Three main weed communities were identified according to sowing season: winter, spring and summer-sown crops. The third most important gradient was associated with soil pH and soil texture to a lesser degree, resulting in highly contrasting weed communities on basic clay soils against those on acidic sandy soils. The influence of climate and geographical region was less pronounced and identified mainly through relationships with precipitation and longitude. Within individual crop types, the effect of other management practices became more prominent. Species richness is dependant on factors other than, or in addition to those influencing species composition, like those describing landscape organisation and/or tillage depth. Species richness (α-diversity) and community composition (β-diversity) had, for example, contrasting relationship to altitude: 300–450 m altitude giving high species richness but low species turnover. The variations observed in this large scale data set help to identify the agricultural practices which have had the most significant impact on the loss of species diversity in arable fields in recent decades.

1. Introduction

A major objective of most weed community ecology studies has been to identify patterns of species composition and distribution and to interpret these patterns in relation to known or presumed gradients in the environment. Factors found to act on the build up of weed communities include abiotic factors such as climate or soil properties (Andreasen et al., 1991), biotic factors such as competition from the crop (Caussanel, 1989) or other weed species, agricultural practices (Dale et al., 1992) and landscape heterogeneity (Weibull et al., 2003; Roschewitz et al., 2005; Boutin et al., 2008). While the main principles governing weed vegetation and its ecology are generally known, the large number of factors involved and their interactions have strongly limited attempts to measure the relative importance of each factor on either community composition or diversity (Pysek and Leps, 1991). However, some studies have attempted to rank the relative importance of several factors in different situations (Andersson and Milberg, 1998; Hallgren et al., 1999; Lososova et al., 2004). This approach was also the underlying objective of the phytosociological classification of vegetation which took place in the early 1930s.

In pioneering weed studies, phytosociologists made a fundamental distinction between the weed communities developing in cereals (*Secalietalia* Br.-Bl. 1936) and those developing in root crops (*Chenopodietalia* Br.-Bl. 1936) (Braun-Blanquet et al., 1936). Soil type was then established as a second order criterion to split the observed diversity within these crop types. Finally, within a particular soil type, broad scale regional differences were identified as the third gradient differentiating communities, with those from Mediterranean regions contrasting most with weed communities from northern regions. The most important factor differentiating between communities was thus one under human control. In the more recent work by Hüppe and Hofmeister (1990), weed vegetation of Central Europe is split into '*Papaveretalia rhoeadis* (Hüppe and Hofmeister, 1990)' from basic soils and

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'*Sperguletalia arvensis* (Hüppe and Hofmeister, 1990)' from acidic soils. For these authors, the fundamental differentiating factor is environmental, not under human control. A number of multivariate analyses on weed community composition support the conclusion that environmental gradients play the key role in weed vegetation composition (Thomas and Dale, 1991; Dale et al., 1992; Andersson and Milberg, 1998; Lososova et al., 2004). On the other hand, management practices, especially crop types (i.e. summer *versus* winter crops, Hallgren et al., 1999), crop succession or tillage systems (Loudyi et al., 1995) have been recognized to explain the majority of variations in weed species composition over vast regions covering a large range of soil conditions. The lack of consensus on the relative importance of environmental against human controlled factors on weed community composition may however result from differences in the scale at which studies have been carried out, as well as the level of information on management practices included in the analysis. Here, one of our aims is to evaluate the effect of scale on the relative importance given to potential explanatory factors.

While community ecology is becoming more commonly applied to weed science, analyses of large data set of weed flora coupled with environmental and management variables are still seldom undertaken. To our knowledge, only three studies have been conducted over more than 500 fields in the last 15 years (Dale et al., 1992; Hallgren et al., 1999; Lososova et al., 2004), all of which respond to varying sampling strategies or contrast in the number and kind of factors considered. For West European weed vegetation, including Atlantic and Mediterranean areas, modern multivariate analysis has not to date been carried out on large data sets with the purpose of determining the relative importance of factors influencing the assemblage of weed communities, thus leaving only early empirical phytosociological theories (Braun-Blanquet et al., 1936; Le Maignan, 1981; Bardat et al., 2004) to classify weed community assemblages.

This paper analyses a large data set coupling weed flora and 14 agro-ecological factors collected between 2002 and 2004 on 694 arable fields across France. Our objectives were (1) to test the relationships between broad-scale environment gradients and management practices and weed species composition and diversity, (2) to rank the relative importance of each factor on species composition at a range of scales from the largest sample (all regions and all crops) to more restricted sub-samples and finally, (3) to see whether the same factors were involved in different measures of weed community richness and diversity.

2. Materials and methods

2.1. Weed survey

The 'Biovigilance Flore' framework, a weed survey set up in France in 2002 was designed to measure the impact of new innovations in agricultural land (Fried et al., 2007). The survey was carried out across a large number of fields (269 in 2002, 602 in 2003 and 798 in 2004) chosen to represent the diversity of cultural practices and environmental conditions present in arable fields in France. Apart from mountainous (Alp, Massif Central, Pyrenees) and Mediterranean areas where annual crops are poorly represented, the plots were regularly distributed across France (Fig. 1).

In each arable field, an area of approximately 2000 m^2 (50 m × 40 m) subject to normal field management practices was surveyed, positioned at least 20 m from field boundaries to avoid field edge effects (Marshall and Arnold, 1995). An equivalent control plot was located in an unsprayed area adjacent to the survey area. Surveys were performed by two or more trained persons walking across the survey area for a minimum of 20 min, recording all species observed until no more new species were found. The abundance of each species was estimated using six abundance classes as developed in Barralis (1976). This method takes into account the number of individuals per m^2, using the following scale intervals: '+' found once in the 2000 m^2 area; '1' less than 1 individual/m^2; '2' 1–2 individual/m^2; '3' 3–20 individuals/m^2; '4' 21–50 individuals/m^2; '5' more than 50 individuals/m^2. In each field, surveys were conducted twice (N1, N2) in each year in both the sprayed and control plot areas. The N1 survey took place 30–40 days after crop sowing, therefore survey date varied according to crop species. The N2 survey took place in spring (between the end of March and the beginning of April) for winter-sown crops, and in summer (around the beginning of July) for spring- and summer-sown crops. This second survey was generally made after herbicide treatments. Consequently the two sampling dates made it possible to account for seasonal variations in weed populations (i.e. weeds associated with both autumn and spring cropping patterns) as well as differences before and after post-emergence chemical weed control.

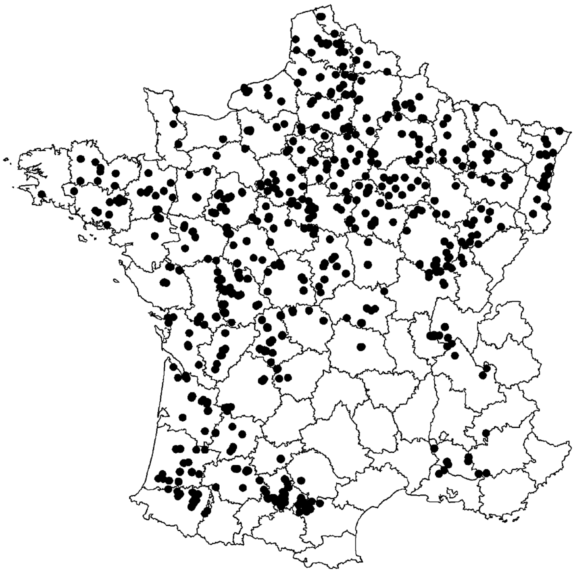

Fig. 1. Distribution of the 694 sampling plots across France. At this scale individual points may, in some cases, represent a number of plots.

A few plant records determined only at the genus level were discarded from the analysis while other taxa known to be inconsistently identified at seedling stage were grouped at the genus level: *Valerianella* spp., *Lolium* spp., *Vicia* spp., *Bromus* spp., *Cerastium* spp., *Rubus* spp., *Crepis* spp., *Allium* spp., *Carex* spp. and *Sedum* spp.

2.2. Explanatory variables

Farmers were asked about the surveyed crop and preceding crop, the kind, number and maximum depth of tillage operations, the date of sowing and the kind, number and dose of herbicides used. Due to a huge diversity of responses on herbicide practices and only little explanatory weight at the studied scale (data not shown), the direct impact of herbicides will not be examined further in the present study but will be discussed as supplementary information. In order to analyse the effects of broad-scale environmental gradients, crop successions and tillage systems, we pooled the data from all four samples available for each field (i.e. the N1 and N2 surveys carried out in both the sprayed and the unsprayed control plot) to produce one list of weed species per year for each field. In total five management variables were

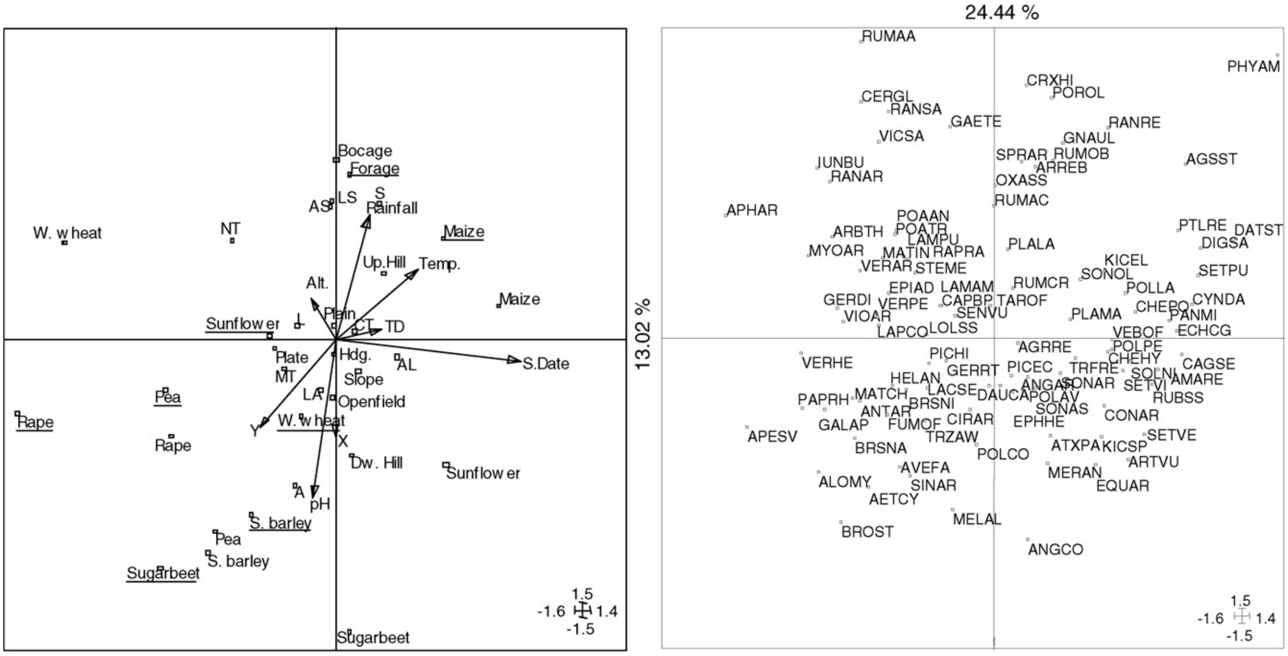

Fig. 2. Plots showing the results of canonical correspondence analysis (CCA) investigating the impacts of a range of environmental and management variables (plot 1) on weed communities (plot 2). Variables included in plot 1 are as follows: S. Date: sowing date; W. wheat: winter wheat; Rape: oilseed rape, (underlined crop names indicate that the crop was a preceding crop); NT: no-tillage; MT: minimum tillage; CT: conventional tillage; Hdg.: fields surrounded by hedges; Bocage: fields surrounded by hedges and meadows. A: clay; AL: clay loam; AS: sandy clay; L: silt loam; LS: silty clay; S: sandy loam and sand. The arrows indicate the direction and magnitude of responses. In plot 2 species codes refer to Bayer codes (Bayer, 1992) which are provided in Supplementary file. Species with low weight (frequencies of occurrence <5%) are not shown.

included in the analysis (as shown in brackets below). The variable 'Crop' (1) included maize (*Zea mays* L.), oilseed rape (*Brassica napus* L.), pea (*Pisum sativum* L.), spring barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), soyabean (*Glycine max* (L.) Merr.), sugar beet (*Beta vulgaris* L.), sunflower (*Helianthus annus* L.), common winter and durum wheat (*Triticum aestivum* L. and *T. durum* Desf.). The variable 'Preceding crop' (2) included all the above and one additional crop type: forage crops, comprising either of lucerne (*Medicago sativa* L.) or a rye-grass (*Lolium* spp.)/red clover (*Trifolium pratense* L.) mix. Tillage system (3) distinguished between three kinds of tillage systems: no-tillage (NT, i.e. implementing direct drilling), minimum tillage (MT) which consists in only chiselling the soil and conventional tillage (CT) including tilling the soil with mouldboard plough followed by one or more harrow and/or cover-crops passage(s). Tillage depth (4) and sowing date (5) comprised the final two management variables.

Environmental variables included in the analysis (nine in total—as shown in brackets below) were grouped into a number of categories; (a) soil conditions incorporating soil pH (1) and soil texture (2) in seven classes; clay, clay loam, sandy clay, silt loam, silty clay, sandy loam and sand, (b) climatic conditions as represented by mean temperature (3) and annual rainfall (4), obtained from 30 years METEO-France climatic data by the AURELHY method of interpolation (Benichou and Lebreton, 1987), (c) geographic position as given by the site longitude (*X*)(5), latitude (*Y*)(6) and altitude (*Z*)(7), (d) local agricultural land context around the field (landscape)(8) in three coarse landscape types; intensive open-field area, field surrounded (at least partly) by hedges and field included in mixed-cropping–breeding systems with hedges and both arable fields and meadows around, referred to in the following text by its French name 'bocage' and (e) local field topography (9) which was split into four classes: (i) plain or plate, (ii) at the bottom of hillside, (iii) on the top of hillside and (iv) on a slope.

Preliminary work in which we conducted separate analysis for each of the years (2002, 2003 and 2004) revealed very similar results across years for both weed composition and diversity (data not shown). Therefore in order to increase the robustness and generality of the results, data from all 3 years were analyzed together. The final analysis included 694 samples across the 2002–2004 period, after eliminating all observations with missing environmental data to improve statistical robustness.

2.3. Data analysis

First, we submitted the whole data set (694 sampled fields, 153 weed species observed in more than 1% of the surveyed fields and 14 explanatory variables) to canonical correspondence analysis (CCA; ter Braak, 1986) performed under 'R' Software (Ihaca and Gentleman, 1996) as implemented into the ade4 library (Thioulouse et al., 1997). Following the methodology of Lososova et al. (2004), we then tested for both gross and net effects of each of the 14 explanatory variables on species composition. Separate CCAs with a single explanatory variable were used to test gross effects. The effect of a particular variable after partitioning out the effect shared with the other explanatory variables (i.e. net effect) was tested using partial CCAs (pCCA), each with a single explanatory variable and the other 13 variables used as covariates. In each case, significances were tested by 1000 permutation tests. We used the ratio of a particular canonical eigenvalue over the sum of all eigenvalues (total inertia) as a rough measure of the proportion of variation explained by each factor, respectively. To further explore the hierarchy of factors and evaluate the possible influence of the study scale, we performed several successive analyses in which we separately examined subsets of samples nested within the variation of the main factor which had been previously shown to be influencing weed species composition.

The effect of each of the 14 variables on species richness (α-diversity) was tested using ANOVA. A principal component analysis (PCA) was also performed to account for correlations between variables when determining which of the 14 variables would best correlate with total species richness. In order to assess patterns of β-diversity (i.e. the mean difference in weed species composition between samples) along the different gradients identified, we calculated β-diversity as mean Jaccard dissimilarity between all pairs of surveys ($1 - J$, where J is Jaccard similarity index; see Koleff et al., 2003). For quantitative variables, we partitioned the data set into either four or five parts according to practical significance along the gradients.

3. Results

3.1. Factors affecting weed composition

The variation of weed species composition across the whole data set was detected using CCA (Fig. 2). The first axis explained 24.4% of the variation and corresponded to differences between winter and spring crop types. The species associated with winter-sown crops were: *Aphanes arvensis*, *Veronica hederifolia*, *Papaver rhoeas*, *Myosotis arvensis*, *Juncus bufonius*, *Alopecurus myosuroides* and *Galium aparine*. Those associated with summer crops were: *Amaranthus retroflexus*, *Echinochloa crus-galli*, *Calystegia sepium*, *Cynodon dactylon*, *Setaria pumila*, *Digitaria sanguinalis* and *Datura stramonium*. The second axis explained 13.0% of total variation and was associated with a trophic gradient between acidic sandy soils of precipitation-rich areas to basic soils of drier areas. *Reseda phyteuma*, *Anagallis foemina*, *Bromus sterilis* and *Ammi majus* were associated with basic and clay rich-soils, and *Rumex acetosella*, *Phytolacca americana*, *Portulacca oleracea* and *Ranunculus sardous* were associated with acidic sandy soils. The third axis (8.2%) was mainly associated with a latitudinal-temperature gradient from Mediterranean to continental climates (not added in Fig. 2 for simplicity). The species typically associated with warm climates were *Legousia speculum-veneris*, *Anthemis arvensis* and *Reseda phyteuma* whilst *Galeopsis tetrahit*, *Gnaphalium uliginosum*, *Matricaria perforata* were associated with colder and more northern regions. Together, the 14 variables explained 34.75% of the total variation in species data.

According to permutation tests, 9 out of 14 variables were significantly linked to the species composition of the community (Table 1). The amount of variation in species data explained by the net effects of particular variables, as detected by partial CCAs (Table 1), was highest for crop and decreased first through preceding crop and soil pH, second through other major environmental variables (rainfall, soil texture, latitude and altitude) and was lowest for a third group of variables including both environmental and management variables (longitude, landscape and sowing date). Topography, tillage & temperature did not explain significant variations in species composition. Species ranks along the main gradients identified are summarized in Table 2.

3.2. Winter- and summer-sown crop subsets

As the main factor affecting weed community composition in the complete data set was crop type and particularly the division between winter- and summer-sown crops represented along CCA axis 1, a second analysis for each of these two sub-samples was performed independently (Table 1). In winter-sown crops, the main factors associated with CCA axes 1, 2 and 3 were respectively: the soil pH-precipitation gradient (14.6% of total variation), the latitudinal-temperature gradient (9.6%) and thirdly, differences between crop type in terms of sowing date (8.8%). The net effect, however, remained higher for the two management variables crop type ($0.087/0.253 = 0.35$) and preceding crop (0.29) than for the environmental gradients of soil pH (0.21) or longitude (0.24). In summer-sown crops, only two significant gradients were detected: the first gradient included the influence of latitude, temperature and preceding crop (17.5% of total variations) contrasting thermophilous species observed in maize grown in a monoculture

Table 1

Gross and net effect of tested variables on weed community composition in surveyed fields

Factors	Complete data set			Winter-sown crop			Summer-sown crop			Winter wheat			Maize		
	Gross effect	Net effect	*P*	Gross effect	Net effect	*P*	Gross effect	Net effect	*P*	Gross effect	Net effect	*P*	Gross effect	Net effect	*P*
Management practices															
Crop	0.89	0.18	***	0.59	0.35	**	0.35	0.24	***	–	–	–	–	–	–
Preceding crop	0.38	0.12	***	0.40	0.29	***	0.57	0.21	**	0.36	0.17		0.56	0.22	*
Sowing date	0.84	0.06	*	0.44	0.21		0.32	0.14	*	0.37	0.24		0.36	0.16	*
Tillage system	0.14	0.07		0.38	0.21		0.23	0.14		0.40	0.17		0.26	0.17	
Tillage depth	0.14	0.06		0.27	0.19		0.19	0.12		0.27	0.19	*	0.22	0.14	
Broad-scale environmental gradients															
Soil conditions															
Soil pH	0.37	0.11	***	0.64	0.21	***	0.58	0.20	***	0.65	0.21	**	0.60	0.21	***
Soil texture	0.20	0.10	**	0.42	0.25		0.32	0.20		0.44	0.21		0.31	0.22	
Climatic conditions															
Rainfall	0.29	0.10	***	0.55	0.18		0.49	0.23	***	0.51	0.17		0.51	0.25	***
Temperature	0.42	0.05		0.57	0.15		0.72	0.11		0.64	0.15		0.80	0.12	
Geographical position															
Latitude	0.24	0.09	**	0.61	0.17		0.59	0.13		0.65	0.16		0.66	0.13	
Longitude	0.40	0.07	***	0.41	0.24	***	0.45	0.22	***	0.48	0.28	**	0.52	0.24	***
Altitude	0.22	0.08	***	0.45	0.15		0.51	0.17	**	0.42	0.15		0.56	0.16	
Local environmental conditions															
Topography	0.09	0.07		0.26	0.20		0.19	0.14		0.26	0.17		0.19	0.15	
Landscape	0.20	0.07	*	0.45	0.19		0.32	0.16	*	0.41	0.17		0.32	0.16	*
All explanatory variables	0.35	0.35	***	0.25	0.25	***	0.22	0.22	***	0.25	0.25	**	0.23	0.23	***

Gross effect was calculated using separate CCAs each with one explanatory variable. Net effect was estimated with partial CCAs performed using one of the explanatory variables with the other 13 as covariables. Gross and net effect are estimated as the ratio between a particular eigenvalue and the sum of all eigenvalues. *P*-values associated with permutation tests on pCCA are as follows: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2
Species with highest fit in partial CCAs and their respective scores along ordination axis 1

Crop			Soil pH			Altitude			Longitude		
Species	Axis 1 score	Fit	Species	Axis 1 score	Fit	Species	Axis 1 score	Fit	Species	Axis 1 score	Fit
O. rape											
			Acidic pH			Low altitudes (≈10 m)			West		
Chenopodium hybridum	−0.85	0.019	*Arenaria serpyllifolia*	−1.65	0.010	*Xanthium strumarium*	−0.79	0.007	*Lithospermum arvense*	−0.98	0.009
Thlaspi arvense	−0.79	0.006	*Spergula arvensis*	−0.38	0.008	*Erophila verna*	−0.78	0.007	*Veronica polita*	−0.49	0.006
Sonchus arvensis	−0.45	0.013	*Polygonum lapathifolium*	−0.37	0.018	*Phytolacca americana*	−0.65	0.009	*Kicksia elatine*	−0.48	0.007
Geranium dissectum	−0.44	0.038	*Ranunculus sardous*	−0.34	0.010	*Centaurea cyanus*	−0.56	0.005	*Gnaphalium uliginosum*	−0.48	0.007
Mercurialis annua	−0.31	0.029	*Oxalis fontana*	−0.32	0.008	*Datura stramonium*	−0.37	0.013	*Oxalis fontana*	−0.48	0.012
Maize											
Echinochloa crus-galli	−0.20	0.014	*Rumex obtusifolius*	−0.30	0.015	*Aethusa cynapium*	−0.37	0.006	*Chenopodium hybridum*	−0.40	0.007
Polygonum persicaria	−0.19	0.018	*Chenopodium polyspermum*	−0.28	0.010	*Sonchus oleraceus*	−0.24	0.006	*Avena fatua*	−0.39	0.006
Chenopodium album	−0.18	0.021	*Datura stramonium*	−0.26	0.010	*Polygonum lapathifolium*	−0.20	0.006	*Setaria viridis*	−0.27	0.008
Amaranthus retroflexus	−0.14	0.007	*Echinochloa crus–galli*	−0.15	0.012	*Capsella bursa-pastoris*	0.16	0.011	*Rumex obtusifolius*	−0.25	0.009
S. barley											
Polygonum aviculare	0.13	0.011	*Polygonum persicaria*	−0.15	0.014	*Poa annua*	0.16	0.010	*Datura stramonium*	−0.17	0.005
Poa annua	0.15	0.018	*Veronica hederifolia*	0.16	0.009	*Cerastium glomeratum*	0.19	0.006	*Capsella bursa-pastoris*	−0.09	0.008
Veronica persica	0.20	0.014	*Fallopia convolvulus*	0.20	0.012	*Rubus spp.*	0.26	0.009	*Solanum nigrum*	0.03	0.007
Papaver rhoeas	0.23	0.010	*Convolvulus arvensis*	0.22	0.018	*Chenopodium polyspermum*	0.27	0.009	*Anagallis arvensis*	0.17	0.019
Viola arvensis	0.24	0.023	*Setaria viridis*	0.25	0.018	*Matricaria inodora*	0.29	0.007	*Setaria verticillata*	0.28	0.007
Alopecurus myosuroides	0.25	0.009	*Sinapis arvensis*	0.28	0.013	*Vicia sativa*	0.32	0.013	*Lactuca serriola*	0.36	0.013
Fallopia convolvulus	0.26	0.019	*Avena fatua*	0.37	0.009	*Oxalis fontana*	0.41	0.008	*Sorghum halepense*	0.37	0.007
W. wheat											
Aphanes arvensis	0.32	0.011	*Mercurialis annua*	0.39	0.039	*Poa trivialis*	0.58	0.009	*Panicum milliaceum*	0.39	0.007
Myosotis arvensis	0.41	0.015	*Ammi majus*	0.45	0.008	*Rumex acetosella*	0.65	0.009	*Anthemis arvensis*	0.57	0.013
Veronica hederifolia	0.45	0.033	*Aethusa cynapium*	0.47	0.010	*Digitaria ischaemum*	0.79	0.007	*Legousia speculum-veneris*	1.25	0.028
Legousia speculum-veneris	0.67	0.006	*Reseda phyteuma*	0.82	0.008	*Holcus mollis*	0.82	0.009	*Reseda phyteuma*	1.74	0.034
			Basic pH			High altitudes (≈450 m)			East		

Each column represents a separate partial CCA in which crop, soil pH, altitude and longitude were used sequentially, one at a time, as the explanatory variable while the effects of the other variables were subtracted by entering them as co-variables.

Table 3
Influence of management practices and environmental gradients on species richness

Variables	F	R^2
Landscape	$F_{2,606} = 49.71^{**}$	0.126
Tillage depth	$F_{4,694} = 22.66^{**}$	0.116
Sowing date	$F_{4,694} = 12.92^{**}$	0.070
Altitude	$F_{4,694} = 12.34^{**}$	0.067
Preceding crop	$F_{7,648} = 12.08^{**}$	0.066
Total rainfall	$F_{4,694} = 11.59^{**}$	0.063
pH	$F_{4,694} = 11.27^{**}$	0.061
Soil texture	$F_{6,676} = 11.24$	0.061
Crop	$F_{6,693} = 8.581^{**}$	0.070
Topography	$F_{4,665} = 7.268^{**}$	0.040
Tillage system	$F_{2,693} = 6.512^{*}$	0.019
Temperature	$F_{4,694} = 1.075$	0.009
Longitude	$F_{4,694} = 0.646$	0.004
Latitude	$F_{4,694} = 0$	0

P-values associated with one-way ANOVA are given with the following scale: $^{*}P < 0.05$, $^{**}P < 0.001$.

to species occurring in maize grown in a rotation with winter cereals or forage crops. The second gradient mainly represented the effects of soil pH and precipitation (13.0%) but also contrasted cropping systems including rotations with forage crops within a 'bocage' landscape to those including cereals in rotations within other landscape types. For summer-sown crops, the management variable crop type (0.24) only slightly outweighed the two broad-scale environmental gradients of longitude (0.22) and annual rainfall (0.23).

As crop type was still found to be the main factor affecting weed community composition for both winter-sown and, to a lesser degree, summer-sown subsets, a third analysis was performed for the two major crop types of these subsets, winter wheat and maize, respectively. The main gradients identified on CCA axes did not differ from those observed on the whole dataset as given in Table 1. In addition, at the scale of a given crop type, gradients associated

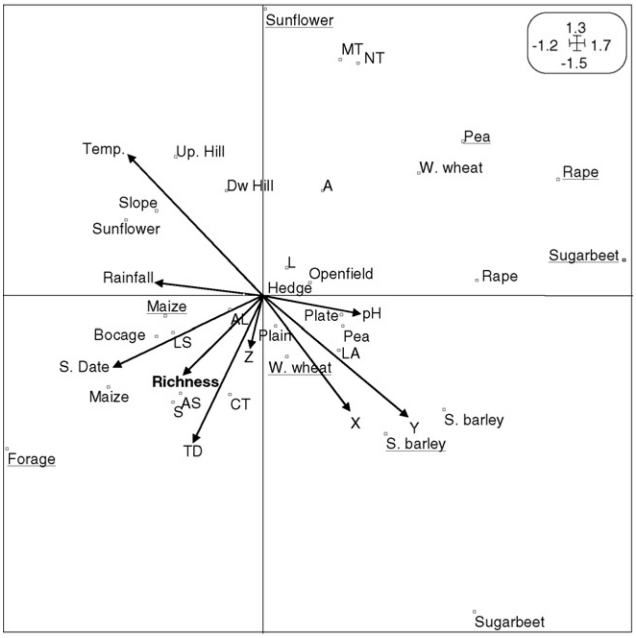

Fig. 3. Principal components analysis plot showing the correlations between species richness and environmental gradients and management practices. Abbreviations are as used in Fig. 2.

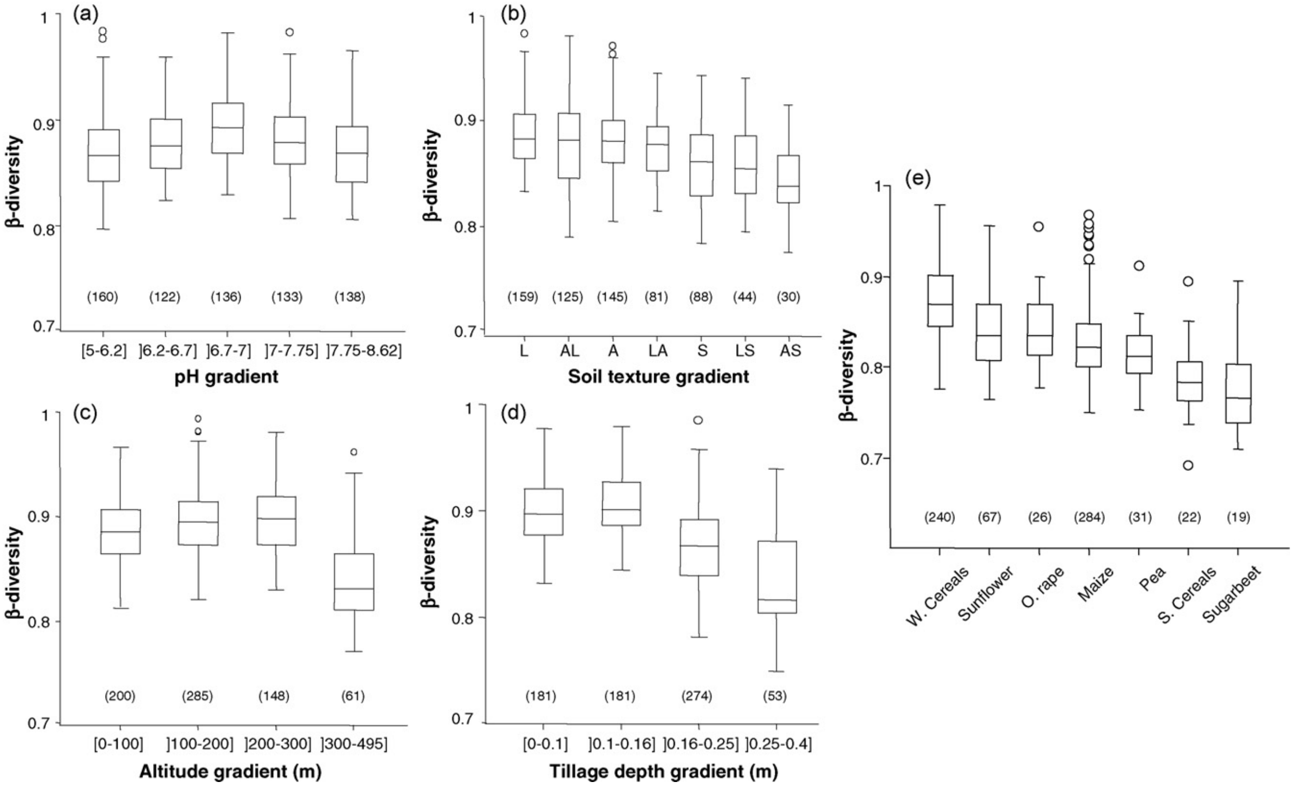

Fig. 4. β-Diversity (measured using mean pairwise Jaccard dissimilarity index) in relation to; (a) pH, (b) soil texture, (c) altitude, (d) tillage depth and (e) crop type. On the *X*-axis, samples were grouped according to practical significance along the gradients. For categorical variables, groups of samples were ordered from maximal to minimal β-diversity. For soil texture, abbreviations are as used in Fig. 2. Boxes represent interquartile ranges, containing 50% of values; the line across boxes is the median values; the whiskers are drawn from the top of the box up to the largest data point less than 1.5 times the box height from the box (the "upper inner fence"), and similarly below the box. Values outside the inner fences are shown as circles. Numbers in brackets refer to the number of samples in each group.

with management practices that were not detected at larger scales either became significant, e.g. tillage depths in winter wheat (Monte-Carlo permutation test, $P = 0.05$), or increased their significance, e.g. effects of sowing date in winter wheat (net effect rising from 0.21 to 0.24).

3.3. Species richness and β-diversity

Landscape had the greatest influence on species richness (Table 3). Fields situated in a 'bocage' landscape or 'landscapes including hedges' harbouring significantly more species than fields from open-field areas (15.2 ± 0.9, 15.0 ± 0.6 and 11.0 ± 0.4, respectively). The number of species per field was also greatly influenced by tillage depths with greater diversity in deeply tilled fields compared to fields where superficial or no tillage was applied. Sowing date and preceding crop were the two other variables under human control that affect species diversity. There were significant differences between summer-sown crops as represented by maize and sunflower containing 14.8 ± 0.5 and 13.2 ± 1.2 species per field, respectively, compared to 10.1 ± 0.4 in winter wheat. Crops following forage crops harbouring almost twice the overall mean species richness (22.7 ± 2.4 compared to 12.7 species) while at the opposite extreme, crops following sugarbeet were very poor (6.9 ± 0.8). Species richness was also associated to some environmental gradients with an increasing number of species per field at higher altitude and under higher annual rainfall as well as on acidic soils and sandy textures. PCA (Fig. 3) showed that the maximum number of species per field was observed in fields with deeply tilled soil, sandy (either sandy clay, sandy loam or sand) soils, acidic pH conditions, late sown crops and relatively high altitudes.

Conversely, Jaccard dissimilarity values for β-diversity (where values closer to 1 represented higher β-diversity) indicated that β-diversity decreased at high altitude (above 300 m), under extreme pH (acid or basic), or in sandy soils (Fig. 4). Higher β-diversities were also found in winter cereals compared to spring cereals or sugarbeet and under no-tillage systems (Fig. 4). Other variables showed no clear pattern although significant differences of β-diversity were detected between categories.

4. Discussion

The present analysis aimed to identify the main factors affecting weed species composition and diversity in order to rank the relative importance of environmental *versus* management factors as explanatory variables. High explanatory weight attached to management factors would open up possibilities for cropping systems with reduced impacts on weed diversity. It would also pinpoint the agricultural practices with the highest negative impact on species diversity under different environmental conditions. Conversely, high weightings of environmental variables would suggest that any strategy aimed at enhancing weed communities would gain from targeting a geographic area of defined interest rather than exploring management options.

4.1. The effect of crop type

Crop type had the most significant influence on species composition although it had a low impact on species richness. Three main weed community types were identified according to sowing season; (a) winter-sown crops (winter cereals and oilseed rape), (b) spring-sown crops (spring cereals, pea and sugarbeet) and (c) summer-sown crops (maize, sunflower and soyabean). The pCCA showed that even when partitioning out effects of other possibly correlated variables (e.g. sowing date), crop type remained the most significant factor. This indicates that in addition to sowing date, crop type is likely to affect other variables known to vary with crop type such as main herbicide families and fertilization regimes (Andersson and Milberg, 1998). In addition to crop-specific management practices, we might also expect that each crop would result in different ecological conditions for weeds with regard to light conditions or growth phenology (Hallgren et al., 1999).

The results observed here contrast with other recent weed community analysis which showed the role of management practices to be minimal, highlighting instead the importance of geographical variability on weed vegetation (Hüppe and Hofmeister, 1990; Thomas and Dale, 1991; Dale et al., 1992; Salonen, 1993; Lososova et al., 2004). This potential discrepancy between studies could result from differences in sampling methods between the studied datasets (e.g. the extent of the cropping systems under study, the areas studied – although many weed species have extensive distributions – and the breadth of environmental gradients considered) or may rely upon decisions made in the data analysis. In the present analysis, the sampling method has been defined in order to be able to answer agronomical questions (surveys in sprayed and unsprayed control plot, plots of identical size to allow comparisons between fields). This differs from the traditional methods of the phytosociologists that are more centred on the vegetation per se (for example, plot size should vary according to the species-area relationships to capture the whole community). It should also be kept in mind that the consideration of data from unsprayed control plots resulting in an 'artificial weed composition' clearly distinguishable from that in the plots under normal agricultural practice may contribute to differences between this and other studies. Additionally, the pooling of samples from different seasons (N1 and N2 surveys) may have increased the effect of 'Crop type' at the expense of seasonal variation.

The potential effect of decisions made in the data analysis can be illustrated using the study of Lososova et al. (2004), where the variable defined as 'Crop' referred to the two broad groupings 'Cereals' and 'Root Crops', thereby including in each category crops sown at very different times of the year and mixing perennial and annual crops within the same categories. Applying this classification rule on our data set, we found that the effect of crop type dropped from 0.31 to 0.05 in terms of gross effect and from 0.06 to 0.03 in terms of net effect. A number of the studies cited above only examined spring-seeded crops (Thomas and Dale, 1991; Dale et al., 1992; Salonen, 1993). Our embedded scale analyses clearly showed that homogenizing crop type tended to increase the weight attached to regional variables: see, for example the evolution of the net effects of longitude in Table 1. However, even when we split the analysis among crop types sown in (a) winter or (b) summer, crop type still explained the largest variations in species composition. Long-term studies covering a 50-year period (Hallgren et al., 1999; Lososova et al., 2004) which included time as a variable revealed that important changes have occurred in the composition of weed communities associated with specific crop types. Based on the comparison between the data set analyzed in this paper and a former survey performed in the 1970s, we showed that the spectrum of the most common weeds found in oilseed rape shifted from winter wheat specialist species in the 1970s to oilseed rape specialist species in the 2000s (Fried and Reboud, 2007). Such a major shift in weed community composition over time would thus reduce the importance of crop type when analysing long-term datasets. This specific example strongly suggests that herbicide use should be considered when trying to capture changes in weed communities over time. The shift in active ingredients used in herbicides for certain crops in the past 30 years had dramatically affected weed communities as shown in sunflower (Fried et al., in press).

4.2. The effect of broad-scale environmental gradients

Broad-scale environmental gradients explained large variations in weed species composition, particularly within a given crop type, while their relative importance on species richness was much lower. Soil pH was the main broad-scale environmental gradient differentiating between weed communities within different crop types on the basis of the presence of calcifuge or calcicole species. As found in other studies covering Central Europe (Hüppe and Hofmeister, 1990; Ries, 1992; Mucina, 1993), the pH gradient was found to co-vary with a gradient of annual rainfall, with the main discontinuity in ecological conditions occurring between the weed vegetation of basic soils in drier areas *versus* that of more acidic soils in precipitation-rich areas. While this gradient is of established significance and therefore predictable, the significance of the longitudinal gradient at a range of scales, was less expected. Longitude was the main factor affecting weed community composition in both winter wheat and in maize (in addition to soil pH or total rainfall, respectively). A previous study focusing on oilseed rape weed communities (Fried and Reboud, 2007) showed that such a gradient is likely to be associated with low winter minimum temperatures thereby discriminating between frost-susceptible and frost-tolerant species in oilseed rape. In this crop type, species such as *Mercurialis annua* or *Chenopodium album* only develop in the Atlantic (warmer) regions of France.

Finally, our data set also highlight an increase in species richness with Altitude, in sandy and very acidic soils. Higher numbers of species per field at higher altitudes (ranging from 300 to 495 m) are probably a side effect of lower agricultural intensity in upland areas as previously suggested by Lososova et al. (2004). The mean number of herbicide treatments in fields above 300 m altitude is indeed significantly lower (1.21 ± 0.05 S.E.; min: 0, max: 2) than that of fields at lower altitudes (mean 1.59 ± 0.03 S.E.; min: 0, max: 6). More generally, we may expect more extensive agricultural practices under marginal environmental conditions (e.g. poor sandy and/or acidic soils).

Importantly we found that β-diversity showed the opposite pattern, i.e. it was reduced at higher altitudes, on soils with extreme acid or basic pH and on sandy soils. As these conditions were found in different areas, this would suggest that the same set of species were found on these more extreme conditions irrespective of the region or cropping systems under consideration (e.g. on very acid soils, *Gnaphalium uliginosum*, *Spergula arvensis* and *Galeopsis tetrahit* were found together in geographically distinct regions such as Franche-Comté, Limousin or Aquitain or in different crop types, i.e. winter wheat or maize).

4.3. The effect of management practices and local environment

When considered at the largest global scale, the impacts of both management practices and local landscape environment on weed species composition are limited, while, conversely, these variables were found to be highly correlated with species richness at this scale. Species richness was 33% higher in fields located in diversified landscapes surrounded by hedges and meadows than in field located in open areas. This result is in agreement with the studies of Gabriel et al. (2005) and Roschewitz et al. (2005) showing that increased landscape complexity enhances species diversity in arable fields. Further studies may be able to partition this increase between a direct influence of hedges (acting as potential refuges for weed populations or to increase isolation between fields) and the indirect influence of other (extensive) management practices usually associated with these landscape types as in Boutin et al. (2008).

The study also revealed that tillage depth had more influence on species richness than tillage system with the lowest species richness observed in superficially tilled soils (Table 3). According to the literature, the impact of tillage system on species richness remains under debate with cases where reduced tillage was found to increase diversity (Mas and Verdu, 2003; Sosnoskie et al., 2006) and others where the impact of reduced tillage on diversity was found to depend upon other management practices such as crop rotation (Stevenson et al., 1997; Legère et al., 2005). This indicates that the precise effect of reduced tillage should therefore be explored for specific crop types in relation to herbicide use, application rates, active ingredients and timing of applications. Finally, we found that management practices had a more significant effect on weed species composition at the finest scale, i.e. for a particular crop type than at the broad scale (Table 1, tillage depth or sowing date in winter wheat).

4.4. Managing weed species composition and diversity

Our study showed that weed community composition and species richness are not generally correlated with the same sets of environmental factors and management practices although both are largely influenced by crop type and/or preceding crop. We believe that, without subsidies, farmers are unlikely to manage in such a way as to encourage diversity of weed communities on their land. Higher weed diversity could however be perceived positively. For example, a species-rich weed community, within threshold limits, may favour diversity at other trophic levels (e.g. birds and insects of conservation values (De Snoo, 1999). Moreover, species-rich communities would help to contain pest outbreaks by maintaining populations of predators and parasites. Conversely, composition may remain of greater direct significance for farmers as the presence of some weed species may have serious implications for management (Legère et al., 2005). The overriding importance of the variables ‘Crop’ and ‘Preceding crop’ on species composition, with different sets of species associated with particular cropping practices, suggests that farmers could induce important shifts in their weed flora by simply altering their choice of crops and rotational practices. A complex rotation would aid weed control as the resulting communities would not contain dominant (noxious) species. On the other hand, a varied crop rotation could be favourable to species that can grow under a large range of cropping conditions, thus resulting in weed communities rich in generalist species (i.e. species with the most central position in CCA plot on Fig. 2).

In general, fields harbouring species-rich communities are correlated with (i) marginal environmental conditions, i.e. fields located on slope and poor sandy soils rather than in fields located at the bottom of hills on fertile clay soils and (ii) in mid-altitudinal areas where the landscape includes hedges and meadows and forage crops in the rotation. Fields of this type are often part of a mixed-cropping-breeding system that is dependant on both animal and crop production and uses extensive practices compared to more intensive cereal-based cropping systems.

If we assume that the diversity of spatial patterns covered in this study may be representative of changes in agricultural practices over time, it is possible to highlight some of the factors which may have been involved in the maintenance or loss of species diversity in the recent past. Thus, landscape simplification including; the loss of hedges, simplification of crop rotations, abandonment of forage crops and increasing soil nutrient richness are likely to be among the factors which have had the greatest impact on the decline of weed species richness within agrosystems. Agri-environmental schemes aimed at addressing losses in plant diversity in agricultural land should therefore favour the maintenance of mixed farming practices as the whole farm management system (including landscape management) appears to enhance species richness.

5. Conclusion

Statistical analyses of a large data set covering a 1000-km south-to-north and west-to-east transect through France, confirmed, clarified and broadened our knowledge of weed species communities. Firstly, the study indicated the primary importance of crop type in differentiating between weed communities. Contrary to early phytosociologist's systems and other recent studies, the effect of crop type was not related to differences in management practices between cereals and root crops, but rather to sowing dates, with three important periods of soil disturbance: autumn–winter, spring and summer. By applying nested scale approaches, the study indicated that crop type and preceding crop, i.e. factors under human control, better discriminate between weed communities than any broad-scale environment gradient. Our study also reinforced previous findings indicating complex relationships between weed communities and a gradient combining the effects of soil pH and total rainfall. Finally, our study showed the importance of landscape diversity on local weed species richness.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2008.05.003.

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