

A functional analysis of large-scale temporal shifts from 1970 to 2000 in weed assemblages of sunflower crops in France

Fried, G.^{1,2,3}; Chauvel, B.^{1,4} & Reboud, X.^{1*}

¹INRA, UMR 1210 Biologie et Gestion des Adventices, INRA/ENESAD/UB, BP 86510, F-21065 Dijon CEDEX, France;

²Present address: LNPV, Laboratoire National de la Protection des Végétaux, F-34000 Montpellier, France;

³E-mail fried@supagro.inra.fr; ⁴E-mail chauvel@dijon.inra.fr;

*Corresponding author; Fax +33 380693222; E-mail reboud@dijon.inra.fr

Abstract

Questions: What are the relationships between weed species traits and their change in distribution over a 30-year period? What does it tell us about factors that have driven shifts in the composition of weed communities?

Location: France.

Methods: We analysed the links between change in the status of weed species in sunflower crops (decreasing or increasing) and a set of 17 traits using data sets collected in the 1970s and the 2000s, respectively. We analysed the contribution of traits to explain changes in the status of species both individually and in a multivariate way by mean of a clustering of species into functional groups.

Results: 69% of the most widespread species had significantly changed their frequency rank status over the last 30 years. Nearly two thirds of the increasing species belonged to a single functional group, out of the five groups identified in this analysis. Overall, the weed flora occurring in sunflower crops has specialised since the 1970s in favour of 'sunflower mimicking' functional groups: increasing species were more nitrophilous, more heliophilous, less sensitive to sunflower herbicides and shared a rapid summer life cycle.

Conclusions: The individual trait approach gave some indication as to the environmental factors likely to have caused the shift in sunflower weed communities. The functional group approach seemed to outperform direct trait comparisons as it accounted for major traits combinations i.e. cases where a species has a number of favourable traits, but is severely disadvantaged by the possession of one or a few deleterious traits.

Keywords: Agricultural practice; Diachronic survey; *Helianthus annuus*; Multiple correspondence analysis; Plant functional type; Species temporal turnover; Trait-based approach; Vegetation monitoring.

Nomenclature: Jauzein (1995).

Abbreviations: MCA = Multiple Correspondence Analysis; IV = Indicator Value.

Introduction

The clearing of large areas of natural habitat for cultivation has increased the distribution of open, disturbed habitats and enabled a broad range of species presenting biological characteristics favoured under these conditions to establish as arable weeds (Kropa et al. 1971). Ever since, the continuous introductions of novel crops and associated agricultural practices have exerted novel selection pressures leading to genetic adaptive changes at the intraspecific weed species level such as herbicide resistance evolution (Roux & Reboud 2007), as well as to shifts in the composition of weed communities (Haas & Streibig 1982). The traits exhibited by a species determine its success or failure at each stage of the crop life cycle and associated cultivation practices (Booth & Swanton 2002). When looking at long-term data on plant communities, one might expect that successful or 'winning' species share common traits that differ from those carried by species that have decreased. For some traits, it is possible to establish a more or less direct link to a selection pressure. For example, the general increase in the value of the N- Ellenberg score in long-term vegetation data has been linked to the overall eutrophication of agricultural habitats due to atmospheric deposition and increased fertiliser use (Smart et al. 2003). As a result, the identification of individual traits that are strongly associated with specific species trends should facilitate the identification of pressures driving changes in species composition. Analysing individual traits independently can, however, potentially be limiting as a given species can exhibit many environment-favourable traits but still fail to increase because of a single trait maladapted to that environment while a species with sub-optimal characteristics but no severely maladapted trait could become more common. Some authors have therefore favoured a multi-trait approach through the use of functional groups, defined as a set of plants sharing common biological characteristics as well as ecological behaviour and/or effects on ecosystem processes (Noble & Gitay 1996; Lavorel & Garnier 2002).

This paper presents a functional analysis of trends in the frequency of occurrence of individual arable weed species between the 1970s and the 2000s in sunflower crops in France. Sunflower was introduced in France after WWII and the area of planting increased dramatically between the 1970s and 2000s so that by 2005 it held the rank of the 5th largest crop nationally (710 000 ha). Trifluralin has been used intensely since the crop was introduced so that the same constant herbicide selection pressure has been exerted over the last 30 years. In parallel, the general pressures occurring in French agricultural landscapes have also changed considerably with, for example, a doubling in the use of fertilizers (Anon. 2007). We hypothesise that these changes have led to important shifts in the composition of weed assemblages in crops of sunflower (*Helianthus annuus*) between the 1970s and the 2000s. We analysed the links between changes in the status of individual species (decreasing, stable increasing) during the 30-year period and the evolution of the representation of traits mostly indicative of pressures related to changes in agricultural practices. This functional analysis relied on two complementary methods. The first method assessed the degree of association between individual and changes in the status of species (winning versus losing species) between the 1970s and the 2000s; the second method refined the classification of arable weed into functional groups differing in their responses to changes in the agricultural environment over the past 30 years. Changes in the trait profile of weed communities over the last 30 years are discussed in terms of the factors likely to have engendered those shifts.

Material and Methods

Long-term trends in the arable flora of sunflower crops were derived from two distinct large scale surveys. The first survey was conducted between 1973 and 1976 and sampled a total of 2170 fields across France (Barralis 1977). Among those, 59 samples were recorded in sunflower crops and those were located in specific areas of France (App. 1). The second survey is an ongoing monitoring programme (Biovigilance Flore) designed to measure the impact of any introduced innovation in agriculture in France (Delos et al. 2006). Between 2002 and 2006, 212 out of 2773 samples were recorded in sunflower crops, mostly located in the geographical areas where the 1970s data was recorded although a few new locations were sampled (electronic archive). Overall, 168 species were recorded in the two surveys. To avoid noise arising from accidental species, only the 104 species observed at a frequency greater than 2% in either of the two surveys were considered in the analyses.

Species sampling in each field

The sampling strategy was similar in both surveys and consisted of a comprehensive recording of all species occurring within a 2000 m² area (40 m × 50 m). The frequency of individual species for each period was the ratio between the number of fields where a species was found and the total number of fields sampled in the survey. Species abundance was recorded using six cover abundance classes as developed in Barralis (1976).

Changes in species status between surveys

In order to homogenize the sampling effort between the two surveys (59 vs. 212 samples), a bootstrap procedure was conducted on the 2000s data set and adjusted to the smallest sampling size. From 2000 bootstrap re-sampling, we produced a 95% confidence interval around the mean frequency rank of any given major species. This procedure accounts for between year and between area variations. Each species observed at a given rank in the first survey and falling outside the boundaries of the 95% bootstrap confidence interval of the second survey is considered to have experienced a significant change in status between the two surveys.

Species traits

We selected a set of ten biological and two agronomic traits and five ecological indicator values (IV) that are listed in Table 1. The selection process attempted to optimise the representation of traits or IV that are known to have links with the pressures occurring in agricultural landscapes, i.e changes in the overall agricultural environment but also pressures that relate to the nature and timing of agricultural practices associated with the cultivation of sunflower crops.

Some biological traits were clearly indicative of specific environmental conditions. Plant size was relevant as taller plants have lower probabilities of extinction than shorter plants in open environments (Leach & Givnish 1996; Duncan & Young 2000). Raunkiaer biological types could be related to tillage regime: reduced tillage depth is predicted to favour perennial species (Zanin et al. 1997). Phenological traits (germination, flowering, life cycle duration) are important in regularly disturbed habitats (Noble & Gitay 1996; McIntyre et al. 1999) and could be related to crop life cycle and timing of management practices. Differences in seed longevity may differentiate species according to their ability to wait for favourable conditions. Finally, seed bank density was used as a proxy for seed production. As expected, agronomic traits such as the sensitivity to herbicides registered for sunflower crops (synthesized

Table 1. Traits used to partition the functional groups and their discriminating value. *P*-values are given for Fisher's Exact Tests between increasing and decreasing species (#) and between functional groups (##). The five last columns give, for each group, the attributes of traits that significantly differ from other functional group. The number in brackets refers to the attributes given in column 2. These columns give a description of trait attributes attached to each functional groups. Examples of species names for each group can be found in Table 2. The levels of significance are based on χ^2 scores (*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.d.: not discriminant)

Traits and sources	Attributes	Correlation ratio to MCA axes 1 & 2	P-value of Fisher's Exact Tests		Attributes best discriminating between the five functional groups				
			#	##	a1	a2	b	c1	c2
Size (cm) Fournier (1936)	(1) 2-15 and 5-30; (2) 20-60; (3) 30-100; (4) > 100	0.458 , 0.033	0.279	2.47 x 10 ⁻⁸	n.d.	n.d.	(3)-(4)*	(1)***	n.d.
General stem form Mamarot (2002)	(1) prostrate; (2) rising; (3) erect; (4) voluble or climbing	0.108 , 0.203	0.007	9.45 x 10 ⁻⁵	n.d.	n.d.	n.d.	(1)***	(2)**
Seed dispersal mode Molinier & Müller (1938); van der Pijl (1982)	(1) no mechanism; (2) wind-disseminated; (3) animal-disseminated	0.170 , 0.026	0.133	0.003	n.d.	n.d.	(1)	(3)**	n.d.
Seed bank density (seed.m ⁻²) Thompson et al. (1997)	(1) 1-57; (2) 58-227; (3) 228-517; (4) > 518	0.002 , 0.139	0.878	0.416	n.d.	n.d.	n.d.	n.d.	n.d.
Seed longevity (year) Thompson et al. (1997)	(1) 1-6; (2) 7-20; (3) 21-39; (4) > 39	0.131 , 0.084	0.834	2.39 x 10 ⁻⁵	(3)*	(2)**	(4)*	(1)***	(1)-(2)
Position of dormant bud (Raunkiaer biological types) Jauzein (1995)	(1) therophyte; (2) hemicryptophyte; (3) geophyte	0.149 , 0.016	0.730	0.101	n.d.	n.d.	n.d.	n.d.	n.d.
Season of germination Jauzein (1995); Mamarot (2002)	(1) winter; (2) spring; (3) summer; (4) all year round	0.237 , 0.203	0.101	6.81 x 10 ⁻⁵	n.d.	(1)*	(3)**	(1)	(4)**
Peak season of flowering time and fruit production Fournier (1936)	(1) all year round; (2) spring to autumn; (3) spring to summer; (4) summer to autumn	0.607 , 0.540	0.044	< 2.2 x 10 ⁻¹⁶	(2)**	(3)***	(4)***	n.d.	(1)***
Life cycle duration (from germination phase to fruit production phase) Mamarot (2002)	(1) < 3 months; (2) 3-6 months; (3) > 6 months	0.136 , 0.031	0.695	2.83 x 10 ⁻⁵	n.d.	(3)**	(1)	(3)	n.d.
Population theoretical flowering duration Fournier (1936)	(1) < 3 months; (2) 3-5 months; (3) 6-12 months; (4) >12 months	0.569 , 0.407	0.398	< 2.2 x 10 ⁻¹⁶	(2)**	n.d.	(1)***	(3)***	(4)***
Seed dispersal by cultural practices Häfliger & Brun-Hool (1968)	(1) not dispersed; (2) weakly dispersed; (3) highly dispersed	0.065 , 0.060	0.676	0.096	n.d.	n.d.	n.d.	n.d.	n.d.
Herbicide tolerance Calculated from Mamarot & Rodriguez (2003)	(1) not sensitive; (2) weakly sensitive; (3) sensitive; (4) very sensitive	0.103 , 0.111	0.042	0.005	(2)*	(3)	(1)	(4)*	n.d.
Ellenberg-L Light indicator value	(1) 4-5-6; (2) 7; (3) 8-9	0.213 , 0.207	0.035	0.001	(2)	(1)*	(3)*	n.d.	n.d.
Ellenberg-T Temperature indicator value	(1) 5; (2) 6; (3) 7-8; (4) x	0.075 , 0.320	0.464	2.67 x 10 ⁻⁵	n.d.	n.d.	(3)	n.d.	(4)***
Ellenberg-F Soil moisture indicator value	(1) 3-4; (2) 5; (3) 6-7-8-9; (4) x	0.165 , 0.235	0.200	1.46 x 10 ⁻⁵	(1)**	(4)**	(3)**	n.d.	(2)
Ellenberg-R Soil pH indicator value	(1) 2-4-5-6; (2) 7; (3) 8-9; (4) x	0.057 , 0.236	0.558	0.004	(3)	(4)*	n.d.	(1)*	(2)
Ellenberg-N Nitrogen availability indicator value	(1) 3-4; (2) 5-6; (3) 7; (4) 8-9; (5) x	0.139 , 0.227	0.003	< 2.2 x 10 ⁻¹⁶	(1) - (2)	n.d.	(4)**	n.d.	(5)***

For the five Ellenberg IV-values above, numbers refer to indicator values as explained in Ellenberg et al. (1992).

from Mamarot & Rodriguez 2003) and the capacity for seed dispersal by soil cultivation (Häfliger & Brun-Hool 1968) had direct relevance to agricultural practices. In the same way, several IV proposed by Ellenberg et al. (1992) could be directly related to agricultural management filters: the increasing level of NPK-supply is expected to favour nitrophilous competitive weeds (Haas & Streibig 1982). Light penetration into the crops could directly be related to weeds performance

(Kleijn & van der Voort 1997): densely-sown cereals are predicted to favour shade-tolerant species while larger crop row spacing would better maintain high light requiring species. Last, systematic liming, drainage or irrigation is expected to disadvantage the specialist species of extreme environments.

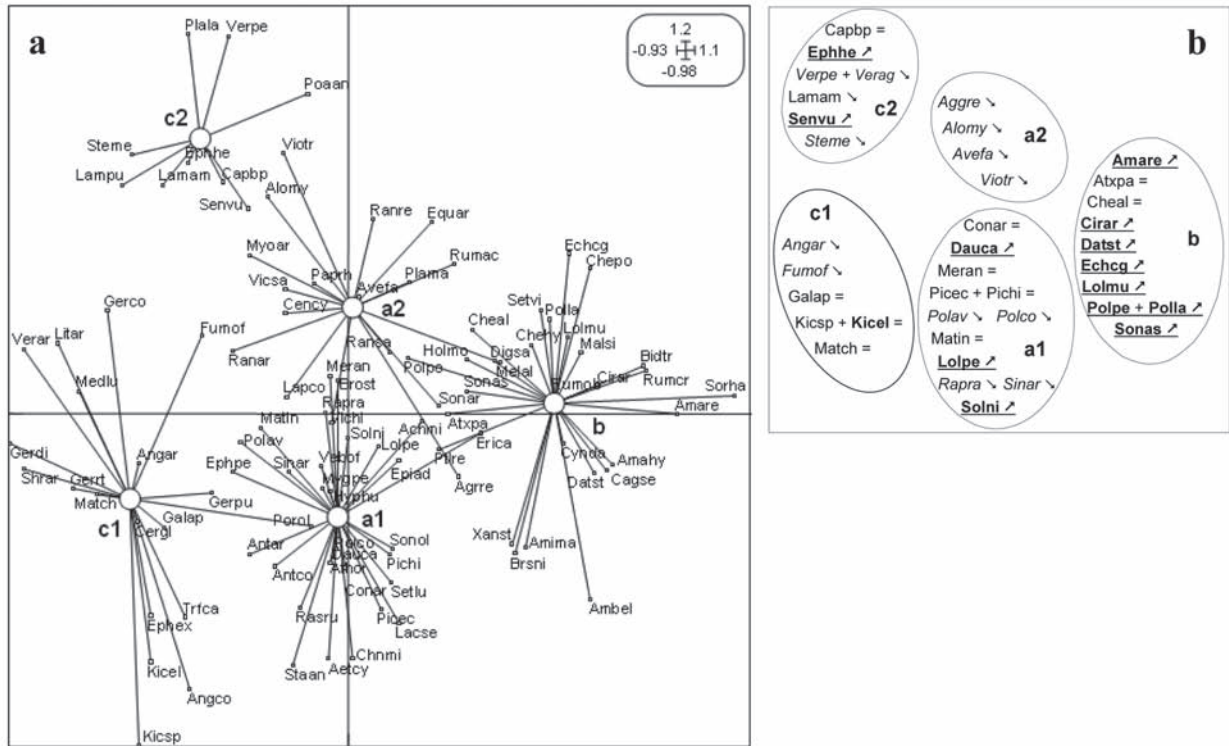


Fig. 1. (a) Weed species (WSSA computer code) partitioned into functional groups over the first and second axes of an MCA of species similarity based on functional trait analysis. (b) Simplified representations of the functional groups. Only the species whose status is significantly stable (=), decreasing (∩) or increasing (↗ and underlined) are represented.

Data analysis

Two approaches were used to analyse the data. The first approach examined how each trait taken independently matched species status changes. The frequency of the 64 trait attributes in the increasing and in the decreasing species was tested using two-way χ^2 tables. We assumed that the proportion of attributes would be unbalanced for traits linked to the environmental filters that were most likely involved in vegetation changes.

The second approach consisted of an *a priori* clustering of species into functional groups and an analysis of which functional groups significantly contained excess or deficit of species having changed status. The species/traits matrix was submitted to Multiple Correspondence Analysis (MCA), an extension of Principal Components Analysis to multi-state discrete characteristics (Tenenhaus & Young 1985), and performed using ADE4 software (Thioulouse et al. 1997). The Euclidian distances between species in the MCA trait-multidimensional space was then used to conduct a Ward ascendant hierarchy grouping (Ward 1963) which identified clear cut and non-redundant groups. To test the robustness of the Ward ascendant hierarchy, we used

K-means (Legendre & Legendre 1998) as an alternative method of non-hierarchical clustering, as suggested by Fukami et al. (2005). Fisher's Exact Test was performed to identify the traits significantly associated with each of the functional groups. The association between traits and species status was assessed by (1) testing whether increasing, stable and decreasing species were randomly distributed into the identified functional groups (Fisher's Exact Test) and (2) comparing the range of scores of species belonging to the increasing, stable and decreasing groups along axes 1, 2 and 3 of the MCA ordination using a one-way ANOVA. Finally, we compared the observed mean dissimilarity coefficient between functional groups and between increasing, stable and decreasing species based on shared genera and families to the distribution of the mean coefficient generated from 1000 random re-samplings of the dataset in order to test whether segregation at a higher taxonomic level covaried with trait segregation.

Table 2. Development of the status of sunflower crop weeds over a 30-year period. WSSA codes refer to abbreviations used to represent species in an MCA ordination as presented in Fig. 1. Group indicates membership to one of the five identified functional groups. ChS. is the significant Changing Status of the species, + = increasing, ± = stable, - = decreasing and new = new species entering among the 26 most frequent species. Rank = average frequency rank of the species given by the bootstrap process with the 95% confidence interval rank in brackets. For each period, species frequency (F₁₉₇₀ and F₂₀₀₀) and density (D) are also indicated. The frequency of individual species for each period was the ratio between the number of fields where a species was found and the total number of fields sampled in the survey. Species abundance was recorded using six cover abundance classes as developed in Barralis (1976) and was used to compile mean species density $D = [11.5*n_3 + 35.5*n_4 + 75.5*n_5 + 1.5*(N - n_3 - n_4 - n_5)] * (N-1)$, where n_3 , n_4 and n_5 are the number of fields where the species was noted at scores 3, 4 and 5, respectively and N is the total number of occurrences of the species. Species in bold indicate a significant change in status.

Weed species	WSSA computer codes	Group	ChS.	2002-2004			1973-1976		
				Rank	F ₂₀₀₀	D	Rank	F ₁₉₇₀	D
<i>Chenopodium album</i>	CHEAL	b	±	1 [1-2]	50.0	8.6	2	54.3	11.8
<i>Solanum nigrum</i>	SOLNI	a1	+	2 [1-3]	43.4	9.6	13	15.2	2.9
<i>Polygonum persicaria</i> + <i>P. lapathifolium</i>	POLPE / POLLA	b/b	+	3 [2-5]	37.3	7.3	6	25.4	4.0
<i>Mercurialis annua</i>	MERAN	a1	±	4 [2-8]	34.9	7.2	5	28.8	6.9
<i>Sonchus asper</i>	SONAS	b	+	5 [3-10]	30.6	2.4	16	13.6	2.2
<i>Senecio vulgaris</i>	SENVU	c2	new	6 [3-10]	29.7	2.8	>26	<6.8	<2.0
<i>Polygonum aviculare</i>	POLAV	a1	-	7 [4-10]	28.8	5.0	3	47.5	8.0
<i>Fallopia convolvulus</i>	POLCO	a1	-	8 [4-11]	27.8	2.6	1	59.3	7.8
<i>Amaranthus retroflexus</i>	AMARE	b	new	9 [4-13]	25.9	4.0	>26	<6.8	<2.0
<i>Convolvulus arvensis</i>	CONAR	a1	±	10 [4-13]	25.5	5.1	11	18.6	2.3
<i>Echinochloa crus-galli</i>	ECHCG	b	+	11 [8-17]	20.2	7.4	24	8.5	3.4
<i>Kickxia spuria</i> + <i>K. elatine</i>	KICSP / KICEL	c1/c1	±	12 [8-16]	19.8	2.7	10	20.3	4
<i>Cirsium arvense</i>	CIRAR	b	new	13 [9-19]	17.9	5.9	>26	<6.8	<2.0
<i>Anagallis arvensis</i>	ANGAR	c1	-	14 [10-19]	17.4	3.9	4	33.9	5.3
<i>Sinapis arvensis</i>	SINAR	a1	-	15 [11-24]	14.1	4.6	7	23.7	7.3
<i>Galium aparine</i>	GALAP	c1	±	16 [12-26]	13.7	2.3	20	10.2	2.6
<i>Atriplex patula</i>	ATXPA	b	±	17 [12-28]	12.7	2.3	20	10.2	3.2
<i>Matricaria recutita</i> + <i>M. maritima</i>	MATCH / MATIN	c1/a1	±	18 [13-25]	12.7	6.0	24	8.5	2
<i>Alopecurus myosuroides</i>	ALOMY	a2	±	19 [13-30]	11.8	3.7	12	16.9	4
<i>Euphorbia helioscopia</i>	EPHHE	c2	new	20 [14-29]	11.3	1.8	>26	<6.8	<2.0
<i>Avena sativa ssp. fatua</i>	AVEFA	a2	±	21 [14-31]	10.8	4.8	13	15.2	4.6
<i>Lolium multiflorum</i> + <i>L. perenne</i>	LOLMU / LOLPE	b/a1	new	22 [13-33]	10.8	5.9	>26	<6.8	<2.0
<i>Capsella bursa-pastoris</i>	CAPBP	c2	±	23 [15-37]	9.4	5.9	20	10.2	2
<i>Datura stramonium</i>	DATST	b	new	24 [14-44]	8.0	7.8	>26	<6.8	<2.0
<i>Daucus carota</i>	DAUCA	a1	new	25 [17-45]	8.0	2.3	>26	<6.8	<2.0
<i>Picris echioides</i> + <i>P. hieracioides</i>	PICEC / PICHI	a1/a1	±	26 [17-47]	2.7	1.8	20	10.2	2
<i>Fumaria officinalis</i>	FUMOF	c1	-	30 [21-63]	5.2	3.5	16	13.6	2.2
<i>Veronica persica</i> + <i>V. agrestis</i>	VERPE / VERAG	c2	-	35 [22-64]	5.1	2.8	7	23.7	2.8
<i>Raphanus raphanistrum</i>	RAPRA	a1	-	46 [25-70]	3.8	2.3	13	15.2	2.9
<i>Stellaria media</i>	STEME	c2	-	53 [28-69]	3.3	1.9	7	23.7	5.3
<i>Viola tricolor ssp. arvensis</i>	VIOAR	a2	-	54 [27-72]	3.3	2.3	16	13.6	3.3
<i>Elytrigia repens</i>	AGRRE	a2	-	56 [30-70]	2.8	1.5	19	11.8	2.7
<i>Lamium amplexicaule</i>	LAMAM	c2	-	> 104	±	±	26	6.8	2

Results

Changes in the weed flora from 1970 to 2000

Comparison between the two surveys showed that within the species groups with the highest frequencies, 14 species had decreased in frequency, 12 species had shown no significant change and 13 species had increased in frequency (Table 2). Among these most frequent species, 69% significantly changed status. Some increasing species were already common in the 1970s: *Solanum nigrum*, *Polygonum persicaria*, *Sonchus asper*, while some decreasing species remained major weeds until today: *Fallopia convolvulus*, *Polygonum aviculare*, *Anagallis arvensis*, *Sinapis arvensis*. Other species increased substantially from a status of rare to

major weeds in sunflower crops: *Amaranthus retroflexus*, *Senecio vulgaris*, *Cirsium arvense*, or strongly decreased between the two surveys and acquired a status of minor species in the second survey (*Stellaria media*, *Raphanus raphanistrum*, *Viola tricolor ssp. arvensis*, *Fumaria officinalis*, *Elytrigia repens*). A more comprehensive description of species status changes is provided in Fried et al. (2006).

Relations between single traits and species status

When grouped according to their change in ranking status (increasing vs. decreasing species) five out of the 17 functional traits studied showed significant differences among increasing and decreasing species (see Fisher's Exact Test in Table 1). Increasing species were species

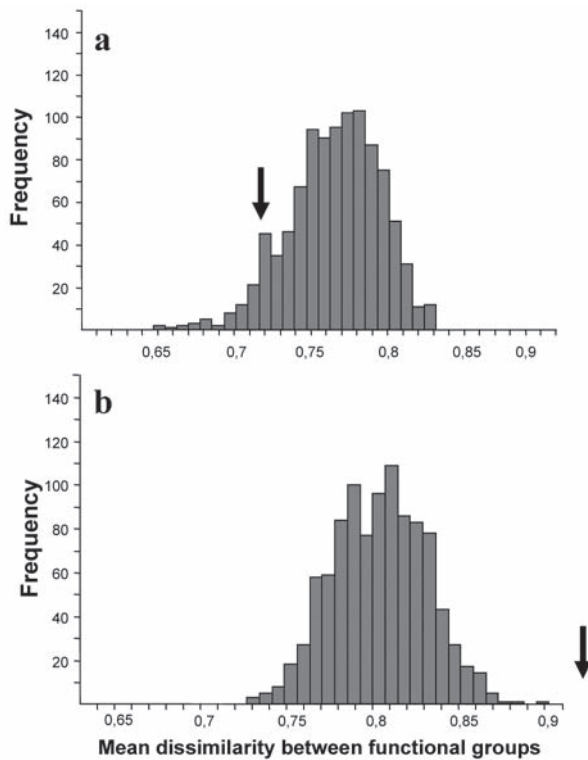


Fig. 2. Measures of dissimilarity between functional groups based on (a) the family and (b) the genus shared. Histograms represent the values of mean dissimilarity between functional groups simulated for 1000 random permutations of the rows (family or genus) and of the columns (functional groups). The arrows represent the mean dissimilarity values observed between functional groups for the real matrix.

with an erect stem ($p = 0.007$), had a peak of flowering and fruit production from summer to autumn ($p = 0.044$), were significantly more nitrophilous ($p = 0.003$), more heliophilous ($p = 0.035$) and less sensitive to the main sunflower herbicides ($p = 0.042$).

Composition and evolution of the functional groups

Species classification

Fig. 1 and Table 1 summarise the results of species and functional traits reciprocal ordination according to MCA. The first three MCA axes accounted for 21.2 % of the variance in species data. Axis 1 (eigenvalue, $\lambda = 0.20$) was positively correlated with the phenology of the weed species (germination and flowering peaks, maximum flowering duration, timing for seed production), the species plant height (size) and light requirements. It opposes small winter germinating species or ‘all-year-round’ germinating and flowering species against tall summer germinating species (Fig. 1a). The second axis

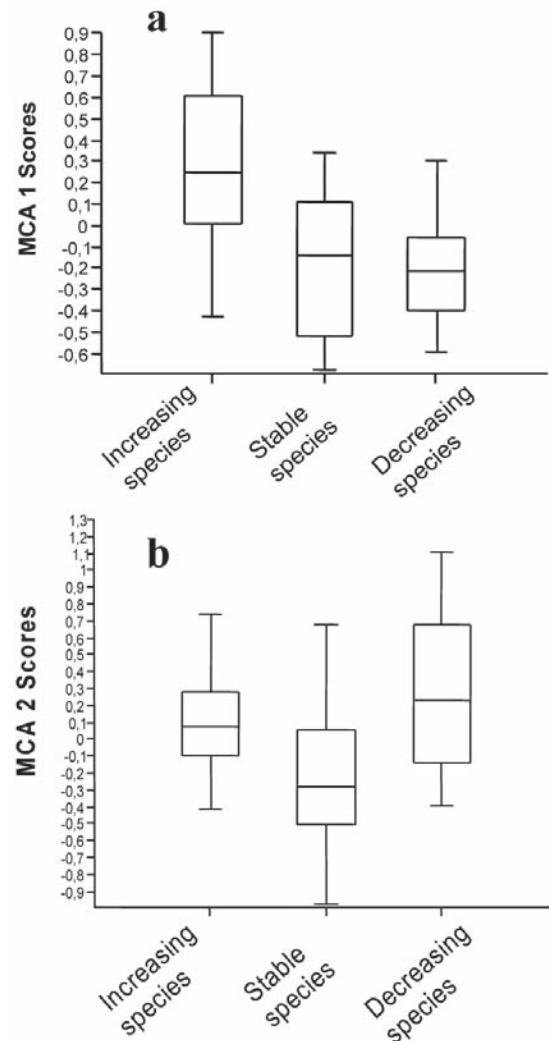


Fig. 3. Distribution of species scores along MCA axis 1 (a) and axis 2 (b) when belonging to increasing, stable and decreasing groups, respectively. Box = interquartile range, containing 50% of the values; line across box = median; whiskers = highest and lowest values.

($\lambda = 0.18$) represented an ecological gradient according to species responses to light, temperature, soil moisture, soil pH and nitrogen availability. Specialist species (xero-thermophilous species specialized on acid or basic poor soils) were negatively correlated to this axis and contrasted with the more generalist species (indifferent to soil reaction, nitrogen availability and moisture and supporting reduced temperature and light condition). The third axis ($\lambda = 0.17$) was less straightforward as it mixed phenological features (especially preferential season of germination and flowering peak period) with morphological traits (size and general plant shape) but

Table 3. Number of species of each functional group according to species status.

Functional Groups	Species status			Total
	Increasing	Stable	Decreasing	
a1	3	5	4	12
a2	0	0	4	4
b	8	2	0	10
c1	0	4	2	6
c2	2	1	4	7
Total	13	12	14	39

Fisher's Exact Test, $p = 0.0013$.

also some IV related to soil-nitrogen availability and temperature requirements (data not presented).

The Ward ascendant hierarchy classification identified three main functional groups along axis 1 (a, b and c). Groups a and c were further partitioned along axis 2 into the a1-a2 and c1-c2 subgroups (see Fig. 1a). The main characteristics of the five functional groups and the traits that contributed most to their discrimination are summarized in Table 1. There was a high level of agreement between the classifications resulting from the Ward ascendant hierarchy and the *K*-means clustering. The outcome only differed for 13 species and for six of those the mismatch was between the subgroups identified along axis 2.

In terms of phylogeny, the 104 species used in the analysis belonged to 73 genera and 27 families, following APGII classification (Anon. 2003). The observed mean dissimilarity coefficient between functional groups or between increasing, stable and decreasing species based on shared families did not significantly differ from the simulated coefficients obtained by randomly sampling the total species pool (Fig. 2a). The same analysis conducted on the 73 genera, however gave a significant clustering of the different genera into the five functional groups (Fig. 2b).

Weed community changes at the functional group level

Species scores on MCA ordination axes significantly differed between increasing, stable and decreasing species on axis 1 ($p < 0.001$) and axis 2 ($p = 0.019$) but not on axis 3 ($p = 0.905$). Increasing species showed higher scores on axis 1 (Fig. 3a) mainly associated with phenology, plant size and light requirements while decreasing species showed higher scores on axis 2 (Fig. 3b). Contingency tables showed that changes in species status were not randomly distributed between the functional groups (Fisher's Exact Test, $p = 0.0013$), with an excess of increasing species in the b-group and an excess of decreasing species in the a2 group (see Table 3 and Fig. 1b). The b-group contained more than 60% of the

increasing species.

Discussion

The functional trait-based approach applied to long-term vegetation change

With a change in status for nearly 70% of the species considered in the study, our results confirm other large-scale weed surveys that showed that species frequencies can change rapidly in arable field environments (Andreasen et al. 1996; Hyvönen et al. 2003). We also show that the changes observed in the status of species were not random but could be associated with the traits they carry: increasing species mostly belonged to a single functional group while decreasing species were mostly clustered into a second single subgroup. The phylogenetic independence test showed that our classification of arable weeds into functional groups or between increasing, stable and decreasing species was not influenced by the membership of a species to a botanical family. There was, however, a significant excess of species of the same genus in the same functional groups or species changes directions. This simply means that other unmeasured traits that align with taxonomic lineage (at the genus level) could have covaried with the ones we have highlighted but this does not invalidate the ecological importance of the traits we have measured.

Our study provides additional evidence that trait-based approaches are an appropriate way to find general assembly rules in long-term survey data. For example, Leach & Givnish (1996) showed that fire suppression in grassland remnants over a 30-50 year period drove species that were short, small-seeded and nitrogen fixers to extinction. Similarly, Duncan & Young (2000) established from historical records that species that were already initially rare, short in stature, gymnosperms and dicotyledons rather than pteridophytes and monocotyledons were more likely to have disappeared after European settlement in New Zealand. The present study is the first to illustrate similar trends in agricultural land.

The factors driving changes of species status in sunflower crops

We identified five traits significantly discriminating between decreasing and increasing species in sunflower crops. These traits may be indicators of the changes in the environment of sunflower weed species that had the most impact on their dynamics and were mostly related to the evolution of agricultural practices. The

selection of some nitrophilous species would pinpoint the effect of increased fertiliser applications. The level of N-supply would be a good example of continuous long-term selective pressure in arable fields as the amount of fertilization has increased in all crop types during the last 50 years (Agreste 2006). Other traits or IV tend to indicate that some sunflower-associated agronomic practices may have induced a widespread shift in weed species composition, namely specific sunflower timing of cultivation (peak season of flowering), herbicide use (herbicide tolerance) and crop row spacing (Ellenberg-L). Repeated trifluralin spraying has most likely favoured some tolerant species, either poorly affected by the herbicide or which avoided the selection pressure through late germinations. The large row spacing in sunflower crops has created a more open environment favourable to erect heliophilous species and less favourable to the prostrate shade-tolerant species that have a more obvious competitive advantage in narrowly spaced, densely sown cereals. Finally, the sunflower life cycle would be favourable for species flowering and producing seed between July and October (75 % of the species in the b-group) as crop and weed maturity synchronization ensures that these species will finish their cycle at sunflower harvest and contribute to the soil seed bank with new viable seeds. In contrast to the response to soil-nitrogen availability, these traits are more specifically adapted to sunflower crop conditions and may be couterselected in the other crops of the rotation. The persistence of winter annuals (groups c1 or a2) in sunflower crops may also be an effect of the preceding crop which could account for the presence of non-adapted species.

Single trait versus functional group approach

Our functional group approach indicates that species with many favourable traits could be disadvantaged by possession of a single negative trait such as herbicide sensitivity or an unsuitable life cycle phenology. Our results show that not all species with highly favourable characters for one of the traits outlined above have increased. For example, only two (*Cirsium arvense* and *Daucus carota*) of the 11 species least sensitive to sunflower herbicides have been observed to increase while none of the most heliophilous (*Lactuca serriola*, *Verbena officinalis*) or the most nitrophilous (*Calystegia sepium* and *Rumex obtusifolius*) have increased so far. The case of *Centaurea cyanus* is another illustration, the species is tolerant of sunflower herbicides but this is not sufficient as its winter germination does not allow the species to perform well in this particular crop. These examples illustrate why a ‘functional group approach’ based on multivariate analysis might be superior to a

‘species contrast approach’ as it will incorporate all the traits on a statistical basis and allow account to be taken of possible cumulative/antagonistic effect of traits on ‘invasiveness’. In other words, our analysis highlights the fact that a species cannot progress by possessing ideal characteristics for any single trait, but rather has to combine benefits based on many traits as proposed by Booth & Larson (1999).

Using the traits that best discriminate the b increasing group from the a2 regressing group on MCA axis 1 has proved effective. It identified not only four out of five traits already identified in the single trait approach, but it also indicated that increasing species of group b mainly differed from decreasing species of group a2 by a greater size, a greater seed longevity, a summer against a winter germination and a much more rapid life cycle. The functional group approach highlighted a combination of eight traits that would define some ‘optimal’ profile for weeds to spread in sunflower crops and could therefore assist in targeting species of intermediate occurrence today but which could expand further in sunflower crops. According to the ‘Biovigilance Flore’ weed survey, some of these species are already presenting locally high densities, e.g. *Ammi majus*, *Chenopodium polyspermum*, *Ambrosia artemisiifolia*, *Sorghum halepense* or *Cynodon dactylon*. Their local success could be viewed as a premise for a more general tendency to invade. In addition, several species of group b are already among the dominant weeds in sunflower crops of other regions of Europe, such as *S. halepense* in Romania (Poienaru et al. 2005), *A. artemisiifolia* in Hungary (Tóth et al. 1997) or *Rumex crispus* which formed part of the 10 most frequent weeds in Portugal (Monteiro et al. 1995). These two facts argue strongly for the functional groups approach to build up further predictions.

Overall, the two approaches we have tested showed that the success of group b in sunflower cropping can be viewed as a result of the general compatibility of the weed attributes and crop life cycles and associated cultural practices. The specialization of farming systems with repetition of the same predictable disturbances at more regular intervals (sowing date around April 15, trifluralin as main herbicide...) has created particular selection pressures leading to a specialization of the arable flora with one functional group predominantly favoured. Our study therefore shows that the reduction of the functional diversity may also occur through increased specialisation rather than by further enhanced spread of the most generalist species.

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