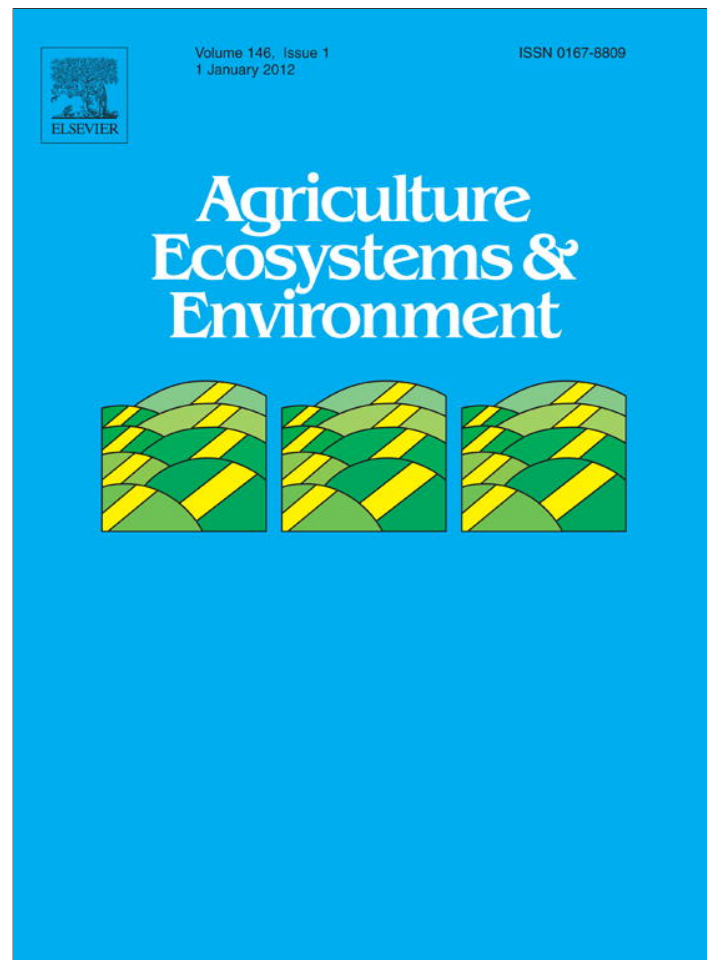


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## Trajectories of weed communities explained by traits associated with species' response to management practices

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### ABSTRACT

Two large-scale weed surveys conducted on winter wheat crops in France in the 1970s and the 2000s were used to determine the influence of management on weed communities. A trait-based approach was used to identify the mechanisms associated with the changing status of arable weeds over a 30 year period.

A three-table ordination method (RLQ analysis) of the data set was performed to relate the environmental table to the species trait table using a species composition table to extract the joint structure (synchronic analysis). We then conducted a diachronic analysis to investigate the relationship between traits, alone or in combination, and the changing status of weeds.

The synchronic analysis showed that tillage intensity filtered weeds according to height, seed weight, life forms and dispersal. Conversely, herbicides selected for species with delayed germination, which allows them to escape herbicide treatments. The diachronic analysis showed that successful weeds that have expanded were small plants, with rather light seeds, that can germinate over a long time frame during the vegetative period. This trait syndrome was probably favoured by profound changes in crop rotation and by increasing herbicide pressure. Our approach provides an excellent example of how future shifts in weed communities can be predicted and hence how weed management can be adapted so as to avoid promoting selection of problematic weeds.

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### 1. Introduction

The dramatic changes in composition and richness of arable weed communities following changes in crop husbandry since the 1950s are now well documented in Europe (Baessler and Klotz, 2006; Fried et al., 2009a). Following the review by Booth and Swanton (2002), who proposed to use community assembly rules as a tool in weed science, recent efforts have aimed to characterise specific management practices that act as filters, selecting for weeds according to their functional traits that respond negatively or positively to selection pressure. For instance, in winter wheat fields, a trait syndrome of short stature, large seed and late flowering has been identified as typical of species in decline since the 19th century (Storkey et al., 2010). In the flora of sunflower fields in France, changes since the 1970s are marked by the increase of tall, nitrophilous, late germinating and late flowering species

(Fried et al., 2009b). In glyphosate-resistant cropping systems, perennial species and annuals with late germination and short intervals between recruitment and anthesis are more frequent (Gulden et al., 2010). Although studies using trait-based approaches in arable agroecosystems have increased in recent years (Lososová et al., 2006; Storkey, 2006; Gunton et al., 2011), to date, only a small number of traits have been tested on large spatial and temporal scales. Traits are measurable properties of individuals that relate to their functioning and modulate their fitness (Violle et al., 2009); they therefore help to capture the interactions between organisms and their environment (both abiotic and biotic) and bring a functional perspective to the study of biodiversity and how functional biodiversity affects processes at higher levels of organisation (Garnier and Navas, 2012).

In this study, the response of weeds to agricultural practices was investigated by quantifying the relationships between weed traits and environment in winter wheat fields. In this synchronic analysis, we focused particularly on the relative impact of tillage systems, herbicide management and crop rotation. In a second step, we asked to which extent species with the same status (increasing

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vs. decreasing) share the same traits using a 30-year diachronic analysis. The hypothesis here is that the frequency of weeds with response traits (*sensu* Lavorel and Garnier, 2002) adapted to management factors will increase, while the frequency of weeds with one or more response traits not adapted to these management factors will decrease. To summarise, the following questions were addressed: (1) What are the links between management practices and weed traits? (2) Are there any trait syndromes associated with the increase or decrease of certain weed species in response to management practices? (3) Can this (these) trait syndrome(s) explain the changes that have been observed in the weed flora of winter wheat fields in France since the 1970s?

## 2. Materials and methods

Vegetation data were extracted from two national large-scale weed surveys conducted in France during the 1970s and the 2000s. The first survey was done between 1973 and 1976 and sampled a total of 2170 fields (Barralis, 1977), of which 768 were winter wheat fields representative of the main production areas under oceanic climate in north-western France (cf. Appendix A in Supplementary Materials). In this dataset, only the frequency and mean abundance of the 32 most frequent weed species were available. Data from the *Biovigilance Flore* survey (Fried et al., 2008) were used for the 2003–2006 period which involved 816 winter wheat fields out of the 2773 fields available and 206 weed species.

The weed sampling strategy was similar in both surveys (for more details, see Barralis, 1977 and Fried et al., 2008). In each surveyed field, a comprehensive vegetation record was carried out on a 2000 m<sup>2</sup> plot (50 × 40 m), positioned at least 20 m from field boundaries to avoid field edge effects. For each record, two or more trained persons walked across the surveyed area for a minimum of 20 min recording all species observed until no new species were found. Species abundance was recorded using six cover abundance classes, adapted from Barralis (1976), i.e. + = 1 individual/2000 m<sup>2</sup>; 1 = <1; 2 = 1–2; 3 = 3–20; 4 = 21–50; 5 = >50 individuals/m<sup>2</sup>. 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.

### 2.1. Management practices and environmental data

Seven management variables were included in the analysis. The 'Preceding Crop' included winter cereals (mainly *Triticum aestivum*, *T. durum* and *Hordeum vulgare*), winter oilseed rape (*Brassica napus*), sugar beet (*Beta vulgaris*), spring pea (*Pisum sativum*), maize (*Zea mays*) and sunflower (*Helianthus annuus*). Herbicide use was described by three variables: the treatment frequency index (TFI) that corresponds to the sum of the ratio of the applied dose to the recommended dose of all the treatments applied in a year, the number of active ingredients and the number of HRAC groups (herbicide classification according to primary site of action). Three kinds of tillage systems were distinguished: 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-crop passage(s). Tillage depth and sowing date were the two final management variables.

Environmental conditions were described by four variables representing two categories: (1) the soil condition group incorporated soil pH and soil texture (clay, clay loam, sandy clay, silt loam, silty clay, sandy loam and sand) and (2) the climatic conditions which included the mean annual temperature and rainfall over the 30 years separating the two surveys.

### 2.2. Trait data

Eight traits and two functional types were chosen to differentiate the response of weeds pertaining to various aspects of plant functioning in agricultural fields (Table 1). The traits include the three traits of the Leaf–Height–Seed (L–H–S) strategy scheme (Westoby, 1998): (a) Specific Leaf Area (SLA, the ratio of leaf surface to leaf dry mass) is particularly important because it is directly related to plant resource economy (Wright et al., 2004); (b) plant height (Ph) depicts species' carbon gain with respect to the plants' ability to compete for light (Westoby et al., 2002), explaining most of the variation in growth reduction observed in competing individuals (Violle et al., 2009) and (c) seed weight (Sw) is the result of a trade-off between producing a few large seeds, each with a high probability of a successful establishment, and producing many small seeds, each with a low probability of establishing (Moles and Westoby, 2006). Traits associated with persistence in disturbed habitats, such as the mode of species dispersal and phenological traits (Noble and Gitay, 1996; Gunton et al., 2011), were also included: germination start (Germ. st.), germination duration (Germ. rg.), flowering onset (Flow. on.) and flowering duration (Flow. dr.). Together with these eight traits, Raunkiaer's life forms (therophytes: Th., geophytes: Geo., hemicryptophytes: Hcr.) were considered because this plant classification has been successfully used to illustrate the response of weeds to the level of soil disturbance by tilling systems (Zanin et al., 1997). Finally, the classical distinction made in weed science between broadleaf (Bl.) and grass (Gr.) weeds was included.

Phenological traits were coded using month as a unit. Since the germination date of weeds is related to the sowing date of winter wheat (Gunton et al., 2011), it was coded from 1 corresponding to October, when winter wheat is sown, to 12 corresponding to September, just before the next crop is seeded. The same month-scale unit was used for germination duration. Flowering phenology was coded from 1 (January) to 12 (December). Three broad classes of seed dispersal were distinguished: by animals, by gravity or by wind. To avoid unbalanced classes, all the different types of animal dispersal modes were merged into one animal dispersal class. This grouping did not significantly change the results (data not shown). The units of the traits are given in Table 1. Missing values were replaced by average value of the traits (for nine species for Sw and for two species for SLA).

### 2.3. Data analyses

First, the direct relationship between management practices and weed species traits was investigated using a modern ordination method: the RLQ approach. The RLQ analysis was developed to study environmental filtering in ecological communities (Doledec et al., 1996) by elucidating combinations of traits that have the highest covariances with combinations of environmental characteristics. Recent applications of the RLQ approach include the analysis of community response to grazing (Saatkamp et al., 2010), land-use intensity (Lienin and Kleyer, 2011), or the effect of changes in agro-pastoral management on calcareous grassland communities (Drobnik et al., 2011).

The RLQ analysis is an extension of co-inertia analysis that performs a double inertia analysis of two arrays: the R-table (the sites described by the environmental descriptors table) and the Q-table (the species described by the 'traits' table) with a link expressed by a contingency table: the L-table (the sites described by species table). For this analysis, we used a subsample of 218 fields of the *Biovigilance Flore* survey, for which all environmental and management practices were available. The representativeness of these 218 subsamples was assessed based on their geographical distribution (cf. Appendix A in Supplementary Materials) and on the relative

**Table 1**

List of selected traits with their abbreviations, units, basic statistics and the management practices supposed to affect these traits.

Category of trait or classification	Trait	Abbreviation	Unit	Min	Max	Mean	Management practices
Phenology	Germination start	Germ. st.	month	0	10	2.42	Crop sowing date (Smith, 2006; Gunton et al., 2011) Crop rotation with varying sowing dates (Fried et al., 2010) Intensification (Storkey et al., 2010)
	Germination range	Germ. rg.	month	3	12	6.75	
	Flowering onset	Flow. on.	month	1	7	4.53	
	Flowering duration	Flow. dr.	month	2	12	5.12	
L-H-S Strategy	Specific Leaf Area	SLA	mm <sup>2</sup> /mg	10.89	65.67	28.47	Crop density (Dingkuhn et al., 1999). Disturbance frequency Fertilizer applications, seedling competition (Storkey et al., 2010)
	Plant height	Ph	cm	20	300	77.75	
	Seed weight	Sw	mg	0.02	31.30	2.79	
Mode of dispersal (Disp.)		Wind Gravity Animal	–	–	–	–	
Raunkier's life forms (RLF)		Therophytes: Th Hemicryptophytes: Hcr Geophytes: Geo	–	–	–	–	Tillage intensity (Zanin et al., 1997)
Plant classes		Gr: Grasses Bl: Broadleaf plants	–	–	–	–	Selective herbicides

proportion of the different management practices (data not shown). We also checked that species rank based on their frequencies was conserved in the subsample (Spearman's correlation,  $\rho = 0.91$ ,  $P < 0.001$ ).

First, a correspondence analysis (CA) was performed on the L-table after removing rare species recorded in less than 5% of the fields, as they may unduly influence the results (Kenkel et al., 2002). Next, a Hill and Smith analysis was performed on the R- and Q-tables (Hill and Smith, 1976). Here, it was carried out on the R-table using the row scores of the CA on the L-table as canonical factor and on the Q-table using the column scores of the CA on the L-table as canonical factor. Finally, the RLQ calculates two separate co-inertia analyses on the R-L and L-Q tables. RLQ selects the axes that maximise the co-variance between the site scores constrained by the environmental variables (the R-table) and the species scores constrained by the species traits (the Q-table). A Monte-Carlo permutation ( $n = 999$ ) test was used to test the significance of the link between the environmental table (R) and the trait table (Q).

Thereafter, the fourth-corner statistic (Dray and Legendre, 2008) was used to test the significance of the direct trait–environment relationships on these 218 fields. A permutation model (with 999 permutations) was applied to test the null hypothesis ( $H_0$ ) that species are distributed independently of their preferences for site conditions and of their traits (using a combination of permutation models 2 and 4 as proposed in Dray and Legendre, 2008).

To identify the functional groups of species with similar response to management practices and environmental conditions, the coordinates of the species in the RLQ multidimensional space were used. A Ward ascendant hierarchy grouping was performed to group species according to the Euclidian distances separating species coordinates. The Harabasz index was used to determine the optimal number of clusters (Gordon, 1999), i.e. the number of functional groups. We compared the values of the eight

quantitative traits between the groups with a Kruskal–Wallis  $H$ -test and the distribution of the two qualitative traits with a Fisher's exact test. All statistical analyses were performed with R software version 2.12.1 (R Development Core Team, 2004) using the library ade4 (Chessel et al., 2004).

To identify the temporal trends of the main weed species of winter wheat in France, the two above-mentioned large-scale weed surveys conducted at a 30-year interval were compared. For this purpose, the methodology developed on the same datasets by Fried et al. (2009b) was followed. To identify increasing and decreasing weed species, the sampling effort was homogenised between the two surveys (816 vs. 768 samples) using a bootstrap procedure conducted on the 2003–2006 period dataset and adjusted to the smallest sample size. From the 2000 bootstrap resampling, a 95% confidence interval was produced around the mean frequency rank of any given major species. This procedure accounts for temporal (between years) and spatial (between areas) variations. Significant changes in a species status were observed when its mean frequency rank in the first survey was out of the 95% bootstrap confidence interval of the mean frequency ranks of the second survey.

The second aim of our study was to determine the traits of weed species whose frequency has increased or decreased in winter wheat fields in France since the 1970s. To test this hypothesis, two complementary approaches were used. First, the relationship between each trait and species status changes (increasing/decreasing species) was examined with a Wilcoxon test for quantitative traits and a Fisher's exact test for qualitative variables. In addition, to take into account potential combination of traits associated with increasing or decreasing species, the functional groups highlighted in the synchronic RLQ analysis were also used. The association between traits and species status was assessed (1) by testing whether increasing, stable and decreasing species were randomly distributed among the functional groups

(Fisher's exact test) and (2) by comparing the range of the coordinates of the species belonging to the increasing and decreasing groups along axes 1 and 2 of the RLQ ordination. Finally, in analogy with the comparison of traits between increasing/decreasing species, the traits of the functional group with the highest proportion of increasing species were compared to those of the functional group with the highest proportion of decreasing species using a Wilcoxon test for quantitative traits and a Fisher's exact test for qualitative variables.

### 3. Results

The first two axes of RLQ accounted for 75% of the total inertia (44 and 31%, respectively). The Monte-Carlo test indicated that the co-structure between R and Q was significant ( $P < 0.001$ , based on 999 permutations). The first two RLQ axes accounted for most of the variance of the corresponding axes in the separate analyses of environmental descriptors (90% for Hill and Smith analysis of the R-table) and species traits (71% for Hill and Smith analysis of the Q-table), which demonstrates the strength of the link between environmental filters (including management practices) and species traits. Correlations between environmental descriptors and the RLQ axes are presented in Table 2. The first RLQ axis corresponded to a soil trophic gradient from the most acidic and light sandy soils to alkaline soils with clay textures (Table 2 and Fig. 1), along with a distinction according to the preceding crop (maize vs. sugar beet, sunflower and pea). The second axis discriminated untilled fields from those with regular tillage, and fields with maize from those with oilseed rape as the preceding crop. Regarding traits, the first axis was best correlated with Raunkiaer's life forms (separating Geo. and Hcr.), Ph and phenological traits: Germ. st., Germ. rg. and Flow. on. (Table 2 and Fig. 1). On the second axis, Raunkiaer's life forms were again well separated, opposing perennial and annual species. Modes of dispersal, discriminating wind-dispersed species from species dispersed by other means, were also associated with axis 2.

The results of the permutation tests of the fourth-corner analysis are detailed in Table 3. The main pattern revealed that tillage depth was negatively correlated with Ph, Sw and Flow. on. but was positively correlated with Germ. rg. Ph was also positively correlated with minimum tillage and negatively with conventional tillage. Wind-dispersed species were positively associated with no tillage and negatively associated with minimum tillage. The sowing date of wheat was positively correlated with weed Germ. st. and Flow. on. as well as with Ph, but was negatively associated with Germ. rg. Soil pH was positively associated with Ph and Germ. st. but was negatively associated with Germ. rg. The opposite pattern was found between these same traits and mean annual rainfall. Germ. rg. was positively correlated with maize as the preceding crop. Intensity of chemical weed control was positively linked to Germ. st. (number of herbicide groups), and negatively correlated with Flow. dr. (TFI). Raunkiaer's life forms, plant classification into broadleaf/grass weeds and SLA showed no significant relationships with management practices or environmental variables.

#### 3.1. Clustering of species in functional groups

The Ward ascendant hierarchy grouping performed on species coordinates in the RLQ multivariate space highlighted seven functional groups (FGs) clustering species with similar trait combinations and similar responses to management practices and environmental conditions (Fig. 1). Figs. 2 and 3 highlight the main differences in trait attributes between these functional groups. Ph, Sw, Dispersal modes, Raunkiaer's life form and all phenological

**Table 2**

Weighted correlation ratios between the management practices (A), the environmental descriptors (B), the species traits (C), and the two first axes of the RLQ analysis. Abbreviations are given between brackets.

Variables	Total dataset	
	Axis 1	Axis 2
<b>(A) Management practices</b>		
<i>Preceding crop</i>		
Winter cereals (W. cer.)	-0.082	0.066
Oilseed rape (O. rape)	0.072	0.305
Sugarbeet (Sbeet)	0.380	0.027
Pea	0.234	-0.088
Maize	-0.218	-0.137
Sunflower (Sflo)	0.287	-0.084
Sowing date (SD)	0.191	-0.112
<i>Tillage system</i>		
No-tillage (NT)	-0.088	-0.163
Minimum tillage (MT)	0.273	0.051
Conventional tillage (CT)	-0.121	0.008
Tillage depth (TD)	-0.118	-0.000
Treatment Frequency Index (TFI)	0.040	0.058
Number of herbicide ingredients (Herb. ingr.)	0.037	0.010
Number of HRAC families (HRAC)	-0.012	0.072
<b>(B) Environmental variables</b>		
Soil pH (pH)	0.231	0.064
<i>Soil texture</i>		
Clay	0.224	0.096
Clay loam	0.264	-0.204
Sandy clay	-0.134	-0.177
Silt loam	-0.055	-0.021
Silt clay	0.095	0.202
Sandy loam	-0.401	0.020
Sand	-0.353	0.016
Annual mean temperature (Temp.)	0.063	-0.109
Annual mean rainfall (Rain)	-0.166	-0.006
<b>(C) Species traits</b>		
<i>Raunkiaer's life forms</i>		
Therophytes	-0.000	0.055
Geophytes	0.459	-0.605
Hemicryptophytes	-0.356	-0.632
<i>Plant classes</i>		
Broadleaf plants	0.030	-0.030
Grasses	-0.163	0.163
<i>Mode of dispersal</i>		
Wind-dispersed	0.058	-0.195
Gravity	-0.070	0.105
Animal-dispersed	0.051	0.008
<i>L-H-S Strategy</i>		
Plant height	0.318	-0.011
Seed weight	0.055	-0.034
SLA	0.001	0.002
<i>Phenological traits</i>		
Germination date	0.194	-0.095
Germination range	-0.218	-0.100
Flowering date	0.200	0.012
Flowering duration	-0.106	-0.082

traits were significantly different among functional groups (see Figs. 2 and 3 for details).

FG#1 grouped small-sized annual species, with low Sw, relatively high SLA, able to germinate all year round, with early onset of flowering and flowering for most of the year. This FG was associated with conventional tillage, deep ploughing and maize as the preceding crop. In contrast, FG#4 was composed of typical annual weeds of winter cereals, only germinating in autumn, onset of flowering in April–May for two months, with poor natural dispersal ability (mainly by gravity), and medium SLA, Ph and Sw values. FG#4 was associated with winter cereals (and oilseed rape to a lesser degree) as preceding crops and early sowing dates. FG#3

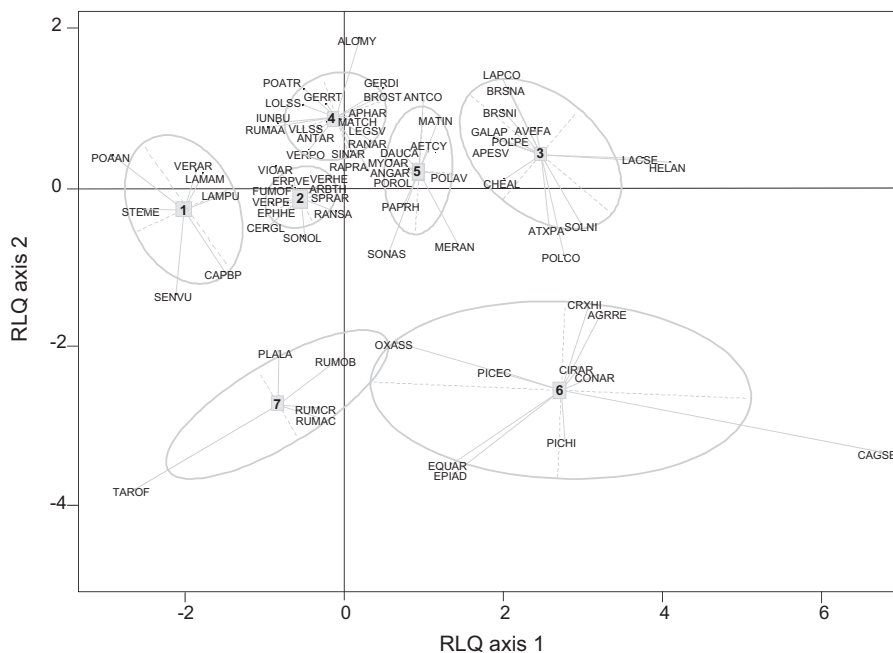


Fig. 1. Display of species with cluster groups along the two first RLQ axes (abbreviation explained in Table 4).

Table 3

Relationships between weed traits and agro-environmental parameters provided by the fourth-corner analysis.

	Raunkiers' life form	Mode of dispersal	Plant classes	Ph	Sw	SLA	Germ. st.	Germ. rg.	Flow. on.	Flow. dr.
Preceding crop	n.s.	n.s.	n.s.	W. cer.: $-0.05^+$ Sflo: $0.11^+$	n.s.	n.s.	n.s.	Maize: $0.11^+$	n.s.	n.s.
Tillage systems	n.s.	$\chi^2 = 9.58^+$	n.s.	MT: $0.12^{**}$ CT: $-0.10^{**}$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Soil texture	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Temp.	n.s.	n.s.	n.s.	$0.08^+$	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Rain	n.s.	n.s.	n.s.	$-0.09^+$	n.s.	n.s.	$-0.07^+$	$0.09^{**}$	n.s.	n.s.
pH	n.s.	n.s.	n.s.	$0.15^{**}$	n.s.	n.s.	$0.08^+$	$-0.12^{**}$	n.s.	n.s.
SD	n.s.	n.s.	n.s.	$0.09^{**}$	n.s.	n.s.	$0.17^{**}$	$-0.06^{**}$	$0.08^{**}$	n.s.
TD	n.s.	n.s.	n.s.	$-0.08^{**}$	$-0.08^+$	n.s.	n.s.	$0.04^+$	$-0.05^+$	n.s.
TFI	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$-0.05^+$
Herb. Ingr.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
HRAC	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$0.04^+$	n.s.	n.s.	n.s.

n.s.: non-significant. Tests of significance were obtained using a Pearson correlation coefficient for two quantitative variables, a Pearson Chi-square ( $\chi^2$ ) and G-statistic for two qualitative variables and pseudo-F and Pearson correlation coefficients  $r$  for one quantitative and one qualitative variable (abbreviations as in Table 1 for traits and Table 2 for environmental variables).

<sup>+</sup>  $P < 0.01$ .

<sup>\*\*</sup>  $P < 0.05$ .

was opposite to FG#1 on RLQ axis 1 and therefore clustered tall annual species, with a short germination period, starting to flower very late (June or July), with relatively low SLA values and rather high Sw (but with high variability). This group is associated with alkaline clay soils, with low soil disturbance (minimum tillage) and spring-sown crops (sunflower, sugar beet) as preceding crops. FG#2 and FG#5 had trait values intermediate to those of FG#1 and FG#4, and FG#4 and FG#3, respectively (Figs. 1–3). FG#6 concentrated tall Geo. and Hcr. species, with late onset of flowering (May–June), with relatively low values of SLA and mainly dispersed by wind. This group was generally associated with reduced-tillage systems (minimum or no tillage), on fertile soils with alkaline pH. Finally, FG#7 was composed of Hcr. species, mainly dispersed by wind, with intermediate values for Ph, Sw and SLA, germinating early, but potentially for more than 6 months, flowering in spring (mainly between April and June). This FG was clearly related to no-tillage systems.

### 3.2. Trends since the 1970s

Comparison of species frequencies between the two surveys revealed that 19 species decreased in frequency, four species showed no significant change and 16 species increased in frequency (Table 4). Among the increasing species, some were already relatively common in the 1970s (*Galium aparine*, *Viola arvensis*, or *Poa annua*) and among the decreasing species, some remained major weeds, i.e. *Veronica persica*, *Papaver rhoeas*, or were even problematic species with resistant populations (*Alopecurus myosuroides*) in the 2003–2006 period. Conversely, other species either increased substantially, graduating from a relatively rare status (not recorded in the list of the 32 main weeds in the 1970s) to being major weeds in winter wheat crops: *Senecio vulgaris*, *Sonchus* spp., or decreased markedly between the two surveys, acquiring a rare species status in the second survey (*Ranunculus arvensis*, *Ranunculus sardous*, *Legousia speculum-veneris*, *Anthemis arvensis*, *Valerianella* spp.).

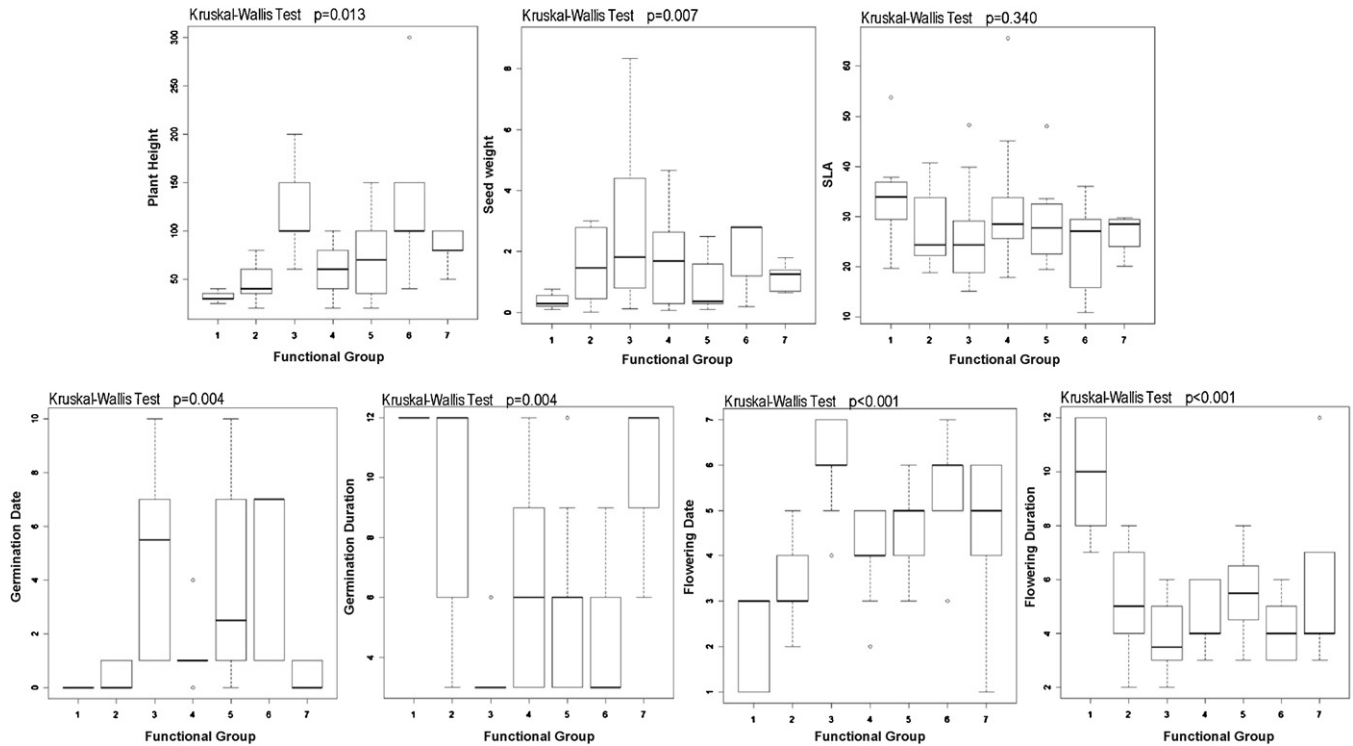


Fig. 2. Box plots of the distribution of quantitative traits between the seven functional groups. Number refers to the functional groups in Fig. 1.

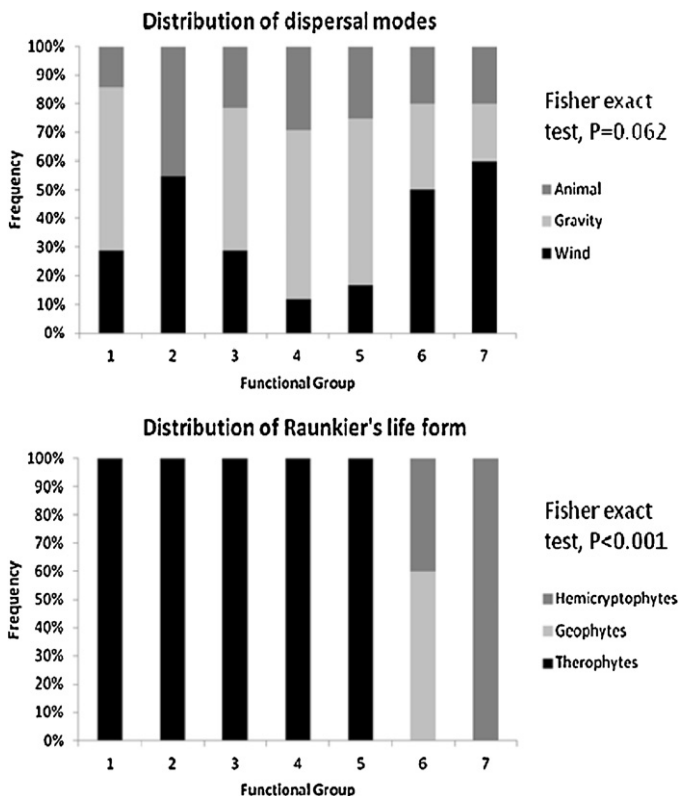


Fig. 3. Vertical bar graphs showing the distribution of the qualitative traits between the seven functional groups. Number refers to the functional groups in Fig. 1.

The average values of 3 out of the 10 traits significantly differed between the increasing and decreasing species (Table 5). Increasing species germinated earlier (Wilcoxon Test,  $U=113.5$ ,  $P=0.01$ ) and had longer germination (Wilcoxon test,  $U=124$ ,  $P=0.03$ ) and

flowering (Wilcoxon test,  $U=92.5$ ,  $P=0.01$ ) periods than decreasing species. Species in both groups had very similar values for Ph, SLA, Raunkiaer's life forms, dispersal modes and broadleaf/grasses classification. A trend for earlier flowering was detected in the increasing species group, although not significant (Wilcoxon test,  $U=141.5$ ,  $P=0.15$ ).

The coordinates of the increasing and decreasing species were significantly segregated along RLQ axis 2 (Table 5). Increasing and decreasing species status were not randomly distributed among the identified functional groups (FG) (Fisher's exact test,  $P=0.0091$ ): an excess of increasing species was observed in FG#1, while decreasing species were in excess in FG#4 and species with intermediate status in FG#2. The comparison of trait attributes between FG#1 (excess of increasing species) and FG#4 (excess of decreasing species) revealed that plants in FG#1 had significantly longer germination and flowering periods, and were significantly smaller (Table 5). No significant differences were found for SLA, although there was a non-significant trend for FG#1 to have smaller seeds.

#### 4. Discussion

The combination of synchronic analysis (identifying management practices that select for a suite of weed traits) and diachronic analysis (highlighting the changing status of weed species) demonstrated the potential of a trait-based approach for understanding the community assembly rules in weed communities. The synchronic analysis showed significant correlations between phenological traits, Ph, Sw and management practices (Table 3). Axis 1 of the RLQ analysis reflected both a disturbance gradient according to tillage depth, opposing conventional tillage to minimum tillage and a trophic gradient, opposing acidic sandy soils and alkaline clay soils. Axis 2 opposed fields with no tillage to the other tillage systems (conventional or minimum) and segregated most of the preceding crops sown in spring on one end of axis 2, whereas crop sequences with only winter crops were generally on the other end. To a lesser extent, axis 2 discriminated fields with

**Table 4**  
Trends in the status of the main weeds occurring in winter wheat since the 1970s.

Species	Abbrev	Status	Funct. group	2003–2006			1973–1976		
				Rank	Freq.	D	Rank	Freq.	D
<i>Galium aparine</i>	Galap	+	3	1[1]	46.81	5.55	8	24.88	6.46
<i>Veronica hederifolia</i>	Verhe	=	2	2[2]	40.32	8.86	2	43.66	8.35
<i>Stellaria media</i>	Steme	=	2	3[3–5]	37.38	13.29	3	32.62	6.27
<i>Viola arvensis</i>	Vioar	+	2	4[3–4]	37.25	13.2	11	15.35	3.97
<i>Senecio vulgaris</i>	Senvu	+(new)	1	5[3–6]	37.01	6.72	>32	–	–
<i>Alopecurus myosuroides</i>	Alomy	–	4	6[5–7]	36.03	16.36	1	51.03	23.43
<i>Veronica persica/polita</i>	Verpe/Verpo	–	2/4	7[6–8]	35.29	7.86	5	29.33	3.65
<i>Poa annua</i>	Poaan	+	1	8[6–8]	34.93	17.82	13	10.57	3.91
<i>Matricaria recutita/inodora</i>	Match/Matin	–	4/5	9[8–9]	33.95	6.31	6	27.7	3.96
<i>Papaver rhoeas</i>	Paprh	–	5	10[10]	31.25	3.76	4	30.65	7.40
<i>Lolium spp.</i>	Lolss	+	4	11[11]	24.88	9.15	15	8.52	3.73
<i>Polygonum aviculare</i>	Polav	–	5	12[12]	20.83	15.33	7	27.41	6.04
<i>Sinapis arvensis</i>	Sinar	=	4	13[13]	19.00	3.5	14	9.59	2.48
<i>Fumaria officinalis</i>	Fumof	=	2	14[13–15]	18.26	5.50	17	8.33	2.18
<i>Capsella bursa-pastoris</i>	Capbp	+	1	15[14–16]	17.89	5.89	21	6.24	1.91
<i>Aphanes arvensis</i>	Aphar	–	4	16[14–16]	17.65	9.16	9	22.38	5.98
<i>Fallopia convolvulus</i>	Polco	–	3	17[17–19]	16.30	5.98	12	15.22	3.26
<i>Cirsium arvense</i>	Cirar	+	6	18[17–19]	15.81	5.42	24	5.18	1.77
<i>Sonchus asper/oleraceus</i>	Sonas/Sonol	+(new)	2/5	19[17–19]	15.69	1.88	>32	–	–
<i>Raphanus raphanistrum</i>	Rapra	–	4	20[20]	12.87	6.79	18	8.19	2.93
<i>Myosotis arvensis</i>	Myoar	+	5	21[20–22]	12.13	4.67	25	4.95	1.70
<i>Lamium purpureum</i>	Lampu	+(new)	1	22[21–22]	11.76	2.27	>32	–	–
<i>Cerastium glomeratum</i>	Ceragl	–	2	23[23–26]	10.66	8.58	20	6.99	1.72
<i>Geranium dissectum</i>	Gerdi	+(new)	4	24[23–27]	10.42	3.07	>32	–	–
<i>Mercurialis annua</i>	Meran	+(new)	5	25[23–27]	10.42	2.93	>32	–	–
<i>Chenopodium album</i>	Cheal	+(new)	3	26[23–28]	10.17	4.16	>32	–	–
<i>Veronica arvensis</i>	Verar	+(new)	1	27[23–28]	10.17	8.76	>32	–	–
<i>Anagallis arvensis</i>	Angar	–	5	28[26–30]	9.68	3.77	22	6.23	2.60
<i>Lapsana communis</i>	Lapco	+(new)	3	29[27–30]	9.44	4.34	>32	–	–
<i>Taraxacum sect. ruderale</i>	Tarof	+(new)	7	30[28–30]	9.31	4.12	>32	–	–
<i>Avena fatua</i>	Avefa	–	3	31[31]	8.21	6.39	10	16.26	7.64
<i>Anthemis arvensis</i>	Antar	–	4	32[32–34]	7.23	3.64	29	3.62	1.40
<i>Ranunculus sardous</i>	Ransa	–	4	34[32–34]	6.86	2.35	30	2.74	2.11
<i>Ranunculus arvensis</i>	Ranar	–	4	36[35–38]	6.13	2.15	19	8.18	2.28
<i>Apera spica-venti</i>	Apesv	–	3	38[36–39]	5.76	10.75	23	5.21	2.85
<i>Arabidopsis thaliana</i>	Arbth	–	2	39[36–40]	5.64	5.76	26	4.74	2.54
<i>Legousia speculum-venris</i>	Legsv	–	4	66[62–68]	1.84	2.61	28	4.29	1.71
<i>Valerianella spp.</i>	Vlss	–	4	70[65–70]	1.72	1.5	27	4.42	1.67
<i>Avena ludoviciana</i>	Avelu	–	3	125[121–132]	0.37	1.5	16	8.43	4.49

Status: “+”: increasing, “=”: stable, “–”: decreasing, new=new species entering among the 32 most frequent species. Funct. group: Membership to the seven functional groups identified in the RLQ analysis. Rank: Average frequency rank with the 95% confidence interval rank in brackets. Species frequency (Freq.) and density (D) are also indicated where  $D = [11.5 \times n_3 + 35.5 \times n_4 + 75.5 \times n_5 + 1.5 \times (N - n_3 - n_4 - n_5)]/N$ , 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.

more intensive weed control by herbicides. The diachronic analysis revealed that the changes observed in the status of species over a 30 year period were not random and that increasing and decreasing weed species had specific response trait attributes.

#### 4.1. The ‘winning’ trait combination

A separate analysis of traits revealed that three phenological traits effectively discriminated among decreasing and increasing species in winter wheat crops; these traits were Germ. st., Germ. rg. and Flow. dr. RLQ analysis of the combination of traits showed that one functional group was almost exclusively composed of increasing species, and was clearly separated from another functional group clustering nearly half of the decreasing arable weeds. In addition to the high variability in phenological traits (i.e. long germination and flowering periods), the trait combination associated with functional group harbouring an excess of increasing species had attributes adapted to regular disturbance: short stature and, to a lesser degree, lower Sw. It is particularly striking to note that, apart from *V. persica* and *Lamium amplexicaule*, all other species able to germinate year-round and that start flowering in the winter (i.e. *Stellaria media*, *P. annua*, *S. vulgaris*, *Lamium purpureum*, *Veronica arvensis*, *Sonchus asper*, *Sonchus oleraceus*, *Taraxacum sect. Ruderale*, which represent half of the increasing species) increased in

frequency (mainly members of FG#1). Two hypotheses can be formulated to explain this pattern. First, a longer germination and flowering periods increase the probability of escaping herbicide applications. Thus, the increase of most species in FG#1 may reflect the long-term result of increasing herbicide pressure over the last 30 years. Second, species that germinate all year round can produce seeds in most crops of the rotation (regardless of sowing date). The correlation of increasing species with the negative coordinates of the RLQ axis 2, which was associated with summer-sown preceding crops, also appears to highlight the important effect of new crop sequences on the changing status of arable weeds (Bohan et al., 2011). This was particularly illustrated by the positive correlations between Germ. rg. and maize as the preceding crop. Species with long germination periods are probably less sensitive to the dramatic modifications in crop sequences, such as the increasing rate of maize as the preceding crop of winter wheat (areas cultivated with maize increased from  $1.8 \times 10^6$  ha in 1970 to  $3.2 \times 10^6$  ha in 2002). In this context, the best strategy for a weed to persist in winter wheat (with high frequencies) would be to cope with fluctuating inter-annual conditions and to replenish the seed bank by producing seeds in all the crops of the rotation. Species with this strategy correspond to those of FG#1, which shows high variability in phenological trait attributes compared to the specialist weed species of winter wheat, such as those in FG#4 with life cycles in synchrony



**Table 5**  
Differences in mean traits values according to species status (diachronic analysis) and membership to FG#1 (excess of increasing species) and FG#4 (excess of decreasing species). Standard deviations are given between brackets. For categorical variables, the distribution across categories is given.

	Increasing species	Decreasing species	Statistical tests	FG#1	FG#4	Statistical tests
<i>Traits (and units)</i>						
Plant height (cm)	67.65 (±39.26)	65.16 (±33.35)	<i>Wilcoxon-Test</i> $P=0.90$	32.14 (±5.67)	52.53 (±25.76)	<i>Wilcoxon-Test</i> $P=0.01$
Seed weight (mg)	1.32 (±1.99)	3.48 (±6.85)	$P=0.70$	0.38 (±0.25)	2.47 (±4.09)	$P=0.07$
SLA (mm <sup>2</sup> /mg)	31.48 (±9.47)	31.50 (±10.65)	$P=0.58$	34.32 (±10.49)	31.52 (±10.92)	$P=0.34$
Germination date (month)	1.47 (±2.87)	2.11 (±2.42)	$P=0.01$	0 (±0)	0.94 (±0.90)	$P<0.01$
Germination range (month)	8.65 (±4.23)	6.16 (±3.08)	$P=0.03$	12 (±0)	6.88 (±3.48)	$P<0.01$
Flowering onset (month)	3.82 (±1.85)	4.53 (±0.90)	$P=0.15$	2.14 (±1.06)	4.24 (±0.83)	$P<0.01$
Flowering duration (month)	6.82 (±3.07)	4.42 (±1.68)	$P=0.01$	9.86 (±2.19)	4.47 (±1.18)	$P<0.01$
<i>Raunkier's Life form</i>						
Therophytes	17	21	<i>Fisher's Exact Test</i> $P=0.21$	7	17	<i>Fisher's Exact Test</i> $P=1$
Geophytes	1	0		0	0	
Hemicryptophytes	1	0		0	0	
<i>Plant classes</i>						
Broadleaf plants	15	18	$P=1$	6	12	$P=0.62$
Grasses	2	3		1	5	
<i>Dispersal mode</i>						
Wind	6	7	$P=0.91$	2	1	$P=0.29$
Gravity	6	9		4	11	
Animal	5	5		1	5	
<i>Species score in RLQ Table</i>						
Axis 1	-0.26 (±1.69)	0.49 (±0.99)	<i>Wilcoxon-Test</i> $P=0.10$	-	-	-
Axis 2	-0.23 (±1.19)	0.43 (±0.63)	$P=0.05$			

with the winter wheat cycle, but poorly adapted to other crops of the rotation. This result is very consistent with the increasing proportion of generalist weed species found in weed communities of north-eastern France over the same period and within fields under crop rotation alternating maize and wheat (Fried et al., 2010).

However, the presence of increasing species in the other functional groups showed that different regional contexts (a particular crop sequence, tillage systems) may favour other types of strategies. The typical 'oilseed rape – winter wheat – winter barley' crop sequence employed on calcareous plateaus, may explain the increase of *Geranium dissectum* and *Lapsana communis* (close to 'oilseed rape' as the preceding crop in Fig. 1), which is consistent with the strong increase in these species in oilseed rape fields (Hanzlik and Gerowitt, 2011). In contrast, in alluvial plains, the generalised increase of summer-sown crops (maize and sunflower), probably influenced the increase of some spring-germinating annuals in FG#3 and FG#5, i.e., *Chenopodium album* or *Mercurialis annua*.

#### 4.2. Weed traits in response to tillage

The impact of tillage systems on increasing and decreasing species over the last 30 years seems limited, probably because no-tillage and minimum-tillage systems have only been adopted recently on a large scale in France (Debaeke and Orlando, 1994). However, the increase in some perennial species, such as *Cirsium arvense* (FG#6) or *T. sect. Ruderalia* (FG#7), may be directly associated with the development of no-tillage or minimum-tillage cropping systems. Interestingly, the gradient of soil disturbance, measured as tillage depth and number of tillage passages (contrasting minimum tillage with conventional tillage on RLQ axis 1, Fig. 1) showed some trends consistent with ecological theories. Ph, Sw and Flow. on. in arable weeds decreased with the intensity of soil disturbance measured by the tillage depth (TD) and the number of passages. A trait-syndrome of short stature, small seeds and early flowering (FG#1) seemed to be more adapted to deep ploughing preceded by several tillage passages (which plays the role of a false seedbed). Here, low Sw appears to be related to high seed production and a large seed bank (i.e., high number of seed in the soil),

which are typical features of weed species that face recurrent disturbance (Moles and Westoby, 2006). On the other hand, in fields with only one passage of superficial tillage, weed species showing other strategies were found, such as those found in FG#3 and FG#6, which include tall plants with larger seeds. These trait attributes are usually associated with competitive strategies adapted to habitats in later succession phases. Species of these groups, e.g. *Carex hirta*, *Lactuca serriola*, *L. communis*, are indeed more frequently encountered in ruderal habitats (roadsides, field margins, etc.) or in early secondary successions, after cultivation has been abandoned.

#### 4.3. Traits involved in species response to herbicides and sowing date

In our synchronic study, the RLQ analysis was not able to clearly highlight the effect of herbicides on the selection for particular traits in the weed community. Surprisingly, there were no negative relationships between Sw and herbicide pressure, either measured by TFI or the number of active ingredients. Regarding the intensive use of herbicides, the number of herbicides used from different HRAC groups seems to favour late germinating species. This reflects the fact that late emergence allows species to avoid herbicide pressure. The observed weed communities in arable fields are not only the result of agricultural practices, but are also influencing farm management decision rules. For example, the persistence of *C. arvense* after the first application of herbicide(s) may induce the application of another, more specific treatment.

Finally, this study also confirmed the importance of weed germination date. The sowing date of the crop has previously been shown to be one of the major filters on weed species composition in analyses of the flora of all crop types (Smith, 2006; Gunton et al., 2011). Our results extend these findings within a given crop type, because a high correlation between the sowing date of wheat, Germ. st. and Flow. on. of weeds (Fig. 1, Table 3) was observed. In late-sown wheat fields (usually after a late-harvested crop sowed in spring such as sugar beet), species that have an early germination peak are less abundant. The positive correlation between Germ. rg. and maize as preceding crop illustrates the key role of being adapted to contrasting crop sequences.

#### 4.4. Contribution of the trait-based approach to the management of agroecosystems

Our results revealed a close relationship between weed traits and management practices; this should help to predict a weed flora trajectory in response to specific practices. For example, species of FG#6 and FG#7 (Fig. 1) should be particularly monitored in the coming years because they may be favoured by reduced-tillage systems that are becoming more and more popular. Diversification in tillage practices could thus be an alternative solution to curb the increase in weed species with traits adapted to reduced tillage.

Similarly, diversification of rotations with the introduction of crops with different sowing dates would be an efficient strategy for controlling weeds with early germination peaks. This strategy has been shown to be effective on *A. myosuroides* (Chauvel et al., 2009), which was here more frequently encountered in early-sown wheat crop preceded by a winter crop (Fig. 1). However, the results of the present study suggests that this type of strategy with a crop sequence including varying sowing dates favours species with highly variable phenology. In particular, current short crop rotations that include only one winter- and one spring-sown crop (wheat and maize; both treated with herbicides) strongly select for species with highly variable germination dates. These species also have very short life cycles and generally have low seed weight (see FG#1). However, apart from *S. media*, these small-sized species of FG#1 are much less competitive (Storkey, 2006) than wheat-specialist weeds, such as *A. myosuroides*, *Avena fatua*, *G. aparine*, which are typically associated with wheat after winter crops.

Plant height is often related to response to disturbance (Díaz et al., 1992), with small plants being more adapted to disturbances. The relationship of species phenology to timing of disturbance is also important when disturbance is episodic, with a strong relationship between colonisation, timing of disturbance, “seasonality of germination” and “duration of reproductive period” (Chiarello, 1989). However, not all traits included in the L-H-S strategy are relevant to arable fields, while they are considered as major axes of specialisation of plant species on large ecological gradients (Westoby, 1998). In particular, our results demonstrate that SLA may not be a good predictor of changes in agricultural management.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2012.06.005>.

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