WEED RESEARCH An International Journal of Weed Biology, Ecology and Vegetation Management

DOI: 10.1111/wre.12164

Weed flora shifts and specialisation in winter oilseed rape in France

G FRIED*, B CHAUVEL† & X REBOUD†

*Anses, Laboratoire de la Santé des Végétaux, Unité entomologie et plantes invasives, CBGP - Campus International de Baillarguet, Montferrier-sur-Lez Cedex, France, and †INRA, UMR1347 Agroécologie, Dijon, France

Received 4 December 2014
Revised version accepted 23 March 2015
Subject Editor: Peter Lutman, UK

Summary

Temporally repeated data sets can provide useful information about the management practices governing changes in the arable weed flora. This study aimed (i) to investigate changes in the most common weed species in winter oilseed rape crops in France between the 1970s and the 2000s and (ii) to pinpoint the main plant biological traits and associated management practices underlying the development of a specific weed flora in this crop. We compared two large-scale surveys covering France in the 1970s and the 2000s, the later survey including several floristic samplings, on two dates, and both herbicide-free control and treated plots. This last survey aimed to identify the species best able to maintain high densities over a growing season of oilseed rape. Since the 1970s, the frequency of two-thirds (69%) of the 26 most common species has changed, spectacularly in some cases, with several species once considered rare becoming very common (e.g. *Geranium dissectum*) and, conversely, some formerly common species becoming rarer (e.g. *Stellaria media*). Our results indicated a general strong increase in specialist weeds of oilseed rape. Weed species success was favoured by tolerance to oilseed rape herbicides and germination synchronous with the crop. The proportion of specialist oilseed rape weed species tended to increase with herbicide treatment intensity and to decrease with increases in the proportion of spring-sown crops in the rotation. Changes to the rotation may therefore constitute an additional or alternative means of controlling some weeds well adapted to oilseed rape crops.

Keywords: community changes, plant functional traits, specialist weeds, weed dynamics, crop rotation, *Brassica napus*.

FRIED G, CHAUVEL B & REBOUD X. (2015). Weed flora shifts and specialisation in winter oilseed rape in France. *Weed Research*.

Introduction

Large-scale weed surveys have shown that species frequencies in arable fields can change considerably within a few years (Andreasen & Stryhn, 2008; Salonen *et al*., 2013). Such surveys provide an opportunity to explore the contribution of cropping practices to the selection of particular weeds. Relationships between the flora and agricultural practices are generally investigated by comparing floristic data with the farming practices applied over the sampling season (Pinke *et al*., 2012). However, this approach may fail to capture the dynamics of the weed flora. Two species with the same frequency of occurrence at sampling time *t* may be considered equivalent in such analyses, despite actually tending to increase or decrease in the medium term, in response to ongoing changes to a given practice. It may therefore be more relevant to target

Correspondence: Dr G Fried, Anses, Laboratoire de la Santé des Végétaux, CBGP, F-34988 Montferrier-sur-Lez Cedex, France. Tel: (+33) 4 67 02 25 53; Fax: (+33) 4 67 02 00 70; E-mail: guillaume.fried@anses.fr

cropping practices associated with changes in frequency between two sampling dates, rather than current frequency, when determining the mechanisms governing the composition of weed communities.

Difficulties determining the comprehensive history of changes in management practices are a key limitation of long-term studies (but see Hallgren *et al.*, 1999). However, some approaches using functional traits can infer the effects of cropping practices indirectly from changes in the weed flora. Such trait-based approaches based on community assembly theory assume that cropping practices act as filters, imposing constraints on weed species and limiting the expression and adaptation value of certain traits (Booth & Swanton, 2002). Species increasing in frequency would be expected to share a restricted range of trait values, different from those of species becoming less common. If links between certain traits and filters are assumed (for a comprehensive list, see Gaba *et al.*, 2014), changes in the functional traits of weed communities can directly highlight the management practices acting as drivers of flora composition (Fried *et al.*, 2012).

The objectives of this study were to identify the species associated with oilseed rape (*Brassica napus* L.) crops and the weed characteristics and management practices underlying this association. Oilseed rape (OSR) has been cultivated for centuries, but has been of significance only since the 1950s in Europe. The area under OSR in France increased fivefold over the last 40 years, peaking at 1.6 million hectares in 2007. As the principal dicotyledonous autumn-sown crop, OSR plays an important role in agricultural systems based on rotations otherwise dominated by winter cereals. It is sown at the end of summer (about one month before winter cereals) and treated with a specific spectrum of herbicides, which may have promoted the selection of specialist weeds adapted to OSR crops and seldom encountered before the spread of this crop. 'Specialist', as opposed to 'generalist', is defined here according to the concept of 'ecological specialisation' (Devictor *et al.*, 2010), which is assessed as the variation in performance of a species across a range of environmental conditions (Grinnelian specialisation). In our case, specialisation refers more precisely to the variation in the frequency of occurrence and density in different crop types. We addressed the following questions:

(i) Which species display specialisation for current OSR crop conditions?
(ii) Which species can maintain their density over a single growing season and after herbicide treatments in current OSR crop conditions, and which species have increased and decreased in frequency in OSR crops in different regional contexts since the 1970s?
(iii) Which species traits are correlated with specialisation and success in OSR crops?
(iv) Which management practices most influenced OSR specialisation in the weed community in the 2000s?

We hypothesised that species displaying specialisation for OSR crops would be more likely to belong to the Brassicaceae family than to other families, as they would have the same phenology as OSR and would tolerate the main herbicides used on OSR. We also expected this group of species to have increased in frequency since the 1970s, with some management practices (high herbicide pressures, winter crop rotation) potentially increasing their proportion in the weed communities.

Materials and methods

Weed surveys

Vegetation data were extracted from two national weed surveys conducted in France. The initial survey, performed between 1973 and 1976, sampled 2170 fields (Barralis, 1977), 198 of which were OSR fields representative of the main production areas in northern France (Fig. 1). In this data set, only constancy (Co; the proportion of surveys containing a particular species) and mean density (D) were reported for the 26 most frequent weed species in the three main production areas (Fig. 1): West (W), North-Paris Basin (NPB) and East (E). Data for these three regions were extracted from the Biovigilance Flore 2002–2010 survey (see Fried *et al.*, 2008), for 419 OSR fields from the 5382 fields sampled during this period.

For the 2000s, each field was surveyed four times in one cropping season. Floristic surveys were carried out on two dates: an autumnal survey (N1) about one month after planting (early October) and a second survey (N2) in spring, after the last herbicide application (mid-March). In each survey, weeds were recorded in control plots (C) of ~100–150 m² (identical soil preparation and sowing practices, but no chemical or mechanical weeding, allowing the soil seedbank to express its potential) and adjacent treated plots (T) of 2000 m² (50 × 40 m), both located at least 20 m from field boundaries. The treatments applied were identical to those used for the rest of the field and were left to the farmers' discretion. The four surveys are thus indicated as C_{N1}, C_{N2}, T_{N1} and T_{N2}. For the 1970s, constancy was assessed on the control plots (i.e. with no herbicide treatments) only, but the weed sampling strategy was similar in the two surveys. For each plot, we recorded all the plant species present, using six semi-quantitative classes derived from the Braun-Blanquet cover-abundance scale and adapted to arable weed community records: + = 1

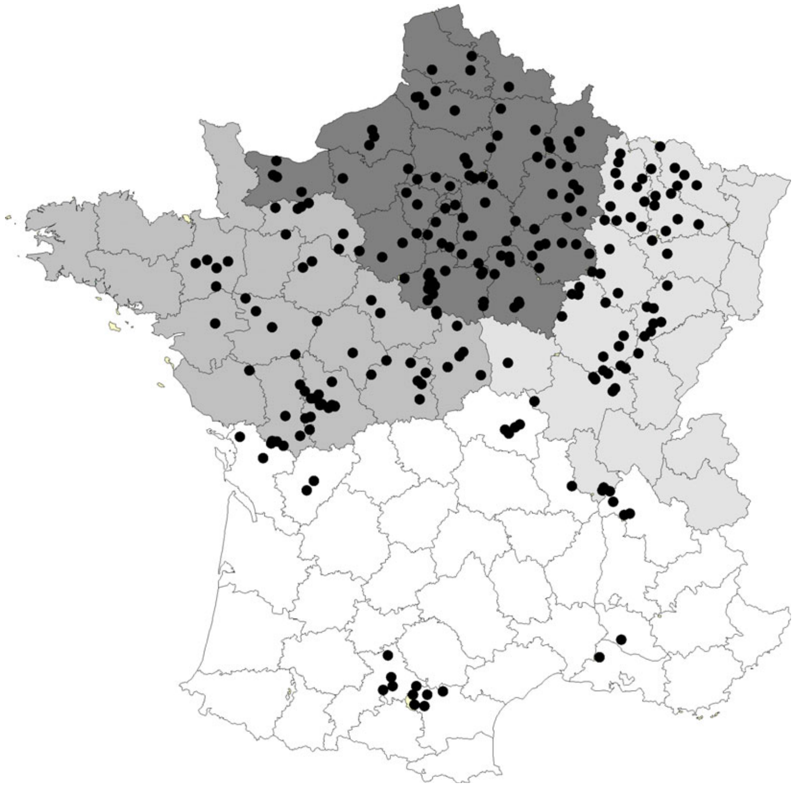

Fig. 1 Map of the three main regions sampled in the 1970s and sampling points in the 2000s. From left (West) to right (East), the mid-grey regions correspond to the 'West of France (W), the dark grey regions correspond to the 'North-Paris Basin' (NPB) and the light grey regions correspond to the 'East of France' (E). Black dots indicate fields sampled in the 2002–2010 period.

individual per 2000 m²; 1 ≤ 1; 2 = 1–2; 3 = 3–20; 4 = 21–50; 5 ≥ 50 individuals per m². In subsequent calculations, we used the median density (D) of each class: + = 0.001, 1 = 0.5, 2 = 1.5, 3 = 11.5, 4 = 35.5 and 5 = 75.5. The constancy of each species, for each period, was calculated as the number of fields in which a species was found with an abundance score ≥2 (i.e. ≥1 individual per m²) divided by the total number of fields sampled. Identification problems led to a few species being grouped at genus level, for example *Cerastium* spp., *Lolium* spp. and *Valerianella* spp.

Trait selection

We focused on 12 characteristics known to respond to selective pressure in cultivated fields, regardless of crop type (Table S1). As suggested by Gaba *et al.* (2014), we used the L-H-S (leaf–height–seed) framework, which summarises the major dimensions of variation in plant responses to environment (Westoby, 1998), using only three traits relating to resource use (specific leaf area), competitiveness (maximum plant height) and regeneration (seed mass). Germination (based on our internal compilation of traits in a weed-oriented database) and flowering (based on Julve, 1998) dates and durations were explored as target variables potentially related to the timing of disturbances for crop sowing and harvest. These variables were coded, using month as a unit. OSR is sown from mid-August to early September, so September was considered the first month for germination (species able to germinate in September were coded 1). In addition to these traits (*sensu* Violle *et al.*, 2007), Raunkiaer's life forms (therophytes, geophytes, hemicryptophytes) were considered, because they have been shown to illustrate the response of weeds to different levels of soil disturbance due to tillage (Zanin *et al.*, 1997). We also included the distinction between broad-leaved and grass weeds widely used in weed science, due to its importance for herbicide-based weeding strategies.

Two indicators of ecological performance (*sensu* Violle *et al.*, 2007) were also used: Ellenberg values for light (Ellenberg-L) and nitrogen (Ellenberg-N), adapted to France (Julve, 1998), reflecting the ability of weed species to compete in fertilised crops and to tolerate densely sown crops (Kleijn & van der Voort, 1997). Finally, herbicide sensitivity (Herb. sens.) in OSR crops in the 2000s was obtained from Mamarot and Rodriguez (2003) (see Table S2 for mean values of Herb. sens. and detailed calculations). This index represents the average response of sensitive weed populations in OSR and does not take resistant populations into account.

Management practices and environmental data

Three management variables were retained to cover the main types of disturbances (Gaba *et al.*, 2014). The influence of past management was summarised as the proportion of spring-sown crops in the last five years: maize (*Zea mays* L.), sunflower (*Helianthus annuus* L.), sugar beet (*Beta vulgaris* L.), potato (*Solanum tuberosum* L.), soya bean (*Glycine max* (L.) Merr.) and sorghum (*Sorghum bicolor* (L.) Moench). Herbicide use in the year of the survey was assessed with the treatment frequency index (TFI), calculated as the cumulative ratio of the dose applied to the recommended dose, for all treatments applied during the OSR growing season, from sowing to harvest (Halberg, 1999). This single index thus summarises the intensity of chemical use. Tillage practices were assessed by determining whether the fields were cultivated by mouldboard ploughing (including depth of ploughing), reduced cultivation or no-tillage systems. Table 1 summarises the mean values of these variables for the three regions studied. Environmental gradients of potential importance at this scale (Lososová *et al.*, 2004) are described by four variables: soil pH, longitude, latitude and altitude.

Statistical analysis

We applied the IndVal procedure (Dufrêne & Legendre, 1997) to the 5382 sampled fields from the Biovigilance data set, including all crop types, to identify specialist weeds of OSR. The IndVal procedure calculates the indicator value ($IndVal_{ij}$) of species *i* as the product of relative average abundance (A) and relative constancy (B) in *j* clusters, according to the following formula: $IndVal_{ij} = A_{ij} * B_{ij} * 100$. It identifies species significantly more associated with particular clusters than expected by chance. In this case, the *j* clusters were based on crop type, classified into 10 categories: 1 – maize; 2 – OSR; 3 – potato; 4 – protein crops (pea and field bean in this study); 5 – sorghum; 6 – soya bean; 7 – spring cereals; 8 – sugar beet; 9 – sunflower; and 10 – winter cereals. Relative abundance (A_{ij}) was calculated from the maximum density scores obtained for the four surveys carried out in a given field during one crop season (i.e. $D_{max} = \max\ [D(C_{N1}),\ D(C_{N2}),\ D(T_{N1}),\ D(T_{N2})]$. Maximum density was used to capture the highest potential of each species in OSR without reference to more specific conditions (season, before or after treatment). The IndVal score for the 'OSR' cluster ($IndVal_{OSR}$) measured the degree of specialisation for OSR crops.

For 318 fields for which all management practices were available, we calculated the mean degree of specialisation for OSR at the community level (IV_{com}), as follows:

$$IV_{com} = \sum_{i=1}^{n} \frac{IndVal_{OSRi}}{n} \quad (1)$$

with *n* the number of species in the community. A generalised linear model (GLM) with a Poisson error distribution was used to assess the significance of IV_{com} variation in relation to the management practices and environmental conditions described above. Collinearity problems were avoided by excluding other initially included variables with *r* values greater than 0.6 (e.g. soil organic matter, tillage depth achieved with soil preparation tools other than mouldboard ploughs) from the analysis (retaining the variables least correlated with all other variables). We then performed hierarchical partitioning (using the R package 'hier.part') to determine the independent contribution of each variable to the explained variation of IV_{com}.

For the 2000s data set, we used the four annual surveys conducted in the same fields (C_{N1}, C_{N2}, T_{N1} and T_{N2}), to measure changes in the density D (i.e. number of individuals per unit area) of the main species (CDS) during an OSR growing season in the control plots only (1), and the differences between control and treated plots at different times in the season (2).

For each species *i* in each field *k*:

(1)

$$CDS_{season\,i.} = mean(CDS_{season\,ik})\ with\ CDS_{season\,ik} = \frac{D_{ik}(C_{N1}) - D_{ik}(C_{N2})}{D_{ik}(C_{N1}) + D_{ik}(C_{N2})}$$

(2)

$$CDS_{treatment\,i.} = mean(CDS_{treatment\,ik})with\ CDS_{treatment\,ik} = \frac{D_{ik}(C_{N1}) - D_{ik}(T_{N1})}{D_{ik}(C_{N1}) + D_{ik}(T_{N1})} + \frac{D_{ik}(C_{N2}) - D_{ik}(T_{N2})}{D_{ik}(C_{N2}) + D_{ik}(T_{N2})}$$

CDS_{season} and $CDS_{treatment}$ range from −1 to 1 and from −2 to 2, respectively. Negative values indicate a higher density of the species in spring than that in autumn (CDS_{season}) or in treated plots than in control plots ($CDS_{treatment}$) and *vice versa*. This calculation was applied only to the 128 species recorded in at least five fields.

We used the control plots of the two large-scale surveys conducted 30 years apart to identify long-term temporal trends for the principal weed species of OSR. We used the methodology developed by Fried *et al.* (2012) for the same data sets. Changes in species status (at national or regional scale) were considered significant if mean constancy rank in the first survey lay outside the two-tailed 95% bootstrap confidence interval for mean constancy rank in the second survey, after adjusting for sampling effort.

Table 1 Percentage of spring crops, proportion of fields with no or reduced tillage, mouldboard plough tillage depths in conventional tillage systems, cumulative ratio of the herbicide dose applied to the recommended dose for all treatments applied during the crop growing season, from sowing to harvest (TFI), and mean specialisation of weed communities for OSR crops ($IndVal_{OSR}$) in the three main regions studied

	West	North-Paris Basin	East
% spring crops	15.92 ± 21.79	4.56 ± 9.82	9.88 ± 13.54
% reduced or no tillage	44.84	49.71	70.42
Mouldboard plough tillage depths (cm)	19.89 ± 3.60	21.45 ± 3.09	23.25 ± 3.81
Herbicide pressure (TFI)	1.54 ± 0.89	1.60 ± 0.67	1.68 ± 0.50
Mean $IndVal_{OSR}$	7.95 ± 5.04	9.34 ± 6.62	9.97 ± 7.07

Finally, we investigated whether weed characteristics could account for success in OSR crops. We constructed conditional inference trees (using the ctree function of the R package 'party') with (i) IndVal values for OSR ($IndVal_{OSR}$), (ii) species status (increasing, stable, decreasing) for long-term trends and (iii) CDS indices for short-term trends as the response variables, and all 12 species characteristics considered as potential explanatory variables. Conditional inference tree construction is described in more detail by Hothorn *et al.* (2006). We then analysed the correlations between $IndVal_{OSR}$, CDS indices and species status changes. The values of these indices were compared across botanical families (in Kruskal–Wallis tests), to determine whether species from Brassicaceae were disproportionately successful, as might be expected if crop mimicry makes a major contribution to weed community assembly. All statistical analyses were performed with R version 3.1.1. (R Core Team, 2014).

Results

Traits and management practices favouring specialisation for OSR

In the 2000s, the 419 OSR fields surveyed harboured 203 weed species in total (i.e. 58% of the species recorded in the Biovigilance survey). IndVal values were highest in OSR for 59 species (16.9%), and 15 species (4.3%) could be considered specialist weeds of OSR, with $IndVal_{OSR}$ values significantly higher in OSR than would be expected by chance alone (Table 2). The three highest significant scores were obtained for *Geranium dissectum* L. ($IndVal_{OSR}$ = 23.39), *Capsella bursa-pastoris* (L.) Medik (12.91) and *Viola arvensis* Murray (10.44).

Conditional inference trees indicated that OSR specialisation was associated principally with germination date, with higher $IndVal_{OSR}$ values for species germinating before December ($P < 0.041$, Fig. 2A). Autumn-germinating species with a mean seed mass greater than 4 mg displayed even stronger specialisation ($P < 0.001$, Fig. 2A). Taxonomic affiliation was also correlated with specialisation level ($P = 0.004$, Table 3), with higher $IndVal_{OSR}$ values recorded for weed species of the Geraniaceae and Asteraceae families than for those of Polygonaceae (Table S3).

The mean degree of specialisation at community level (IV_{com}) was positively correlated with TFI and latitude and negatively correlated with the proportion of spring crops and tillage depth (Table 4). Latitude explained the highest proportion of the variance (34%), whereas management practices together accounted for 39% of the variance, the largest contributions being those of tillage depth (20%) percentage of spring crops in the rotation (10%) and TFI (9%, Fig. 3).

Effects of season and herbicide treatments

Seventy-six of the 128 species recorded in at least five fields (59%) had positive CDS_{season} values, indicating an increase in density between autumn and spring in the control plots (median = −0.10; Q1 = −0.34; Q3 = 0.19, see Table 2 for the values for the main species). The conditional inference tree for CDS_{season} (Fig. 2B) split species firstly by germination date ($P < 0.001$) and then by Ellenberg-L indicator values. Species combining early germination and shade tolerance (e.g. *Anthriscus caucalis* M. Bieb., *Arabidopsis thaliana* (L.) Heynh.) displayed the greatest increases in density during the growing season (Fig. 2B), whereas spring-germinating, light-demanding species displayed the most significant decreases in density (e.g. *Amaranthus retroflexus* L., *Chenopodium album* L.). Taxonomic affiliation was correlated with CDS_{season} (Table 3), the values for Amaranthaceae weed species being lower than those for weeds from Apiaceae and Caryophyllaceae (Table S3).

$CDS_{treatment}$ ranged from −0.41, corresponding to higher densities in treated plots, for *Elymus repens* (L.) Gould, to 1.25, indicating higher densities in control plots, for *Myosotis arvensis* (L.) Hill (median = 0.78, Q1 = 0.31, Q3 = 1.00). Only 14 species (11%) achieved higher densities in treated plots. $CDS_{treatment}$ depended principally on herbicide tolerance (Fig. 2C), survival being better for species with a mean sensitivity to OSR

Table 2 Status, rank, constancy and density of the main weed species in oilseed rape in France. Constancy is the number of fields in which a species has been observed with a score >1 (≥1 individual per m²) divided by the total number of field surveyed. Density is the mean number of individuals per m² based on the following formula: $D = \frac{75.5*N5+35.5*N4+11.5*N3+1.5(N-N5-N4-N3)}{N}$ with N, the number of fields surveyed; N5, N4 and N3, the number of field in which the species has a score of 5, 4 and 3 (Barralis, 1977). $IndVal_{OSR}$ gives the degree of specialisation of a species for OSR crops (P-values associated with the permutation test: $*P < 0.05$, $**P < 0.01$). CDS indices indicate the difference in density of individual species between control and treated plots and between autumn and spring surveys. Species in bold typeface are increasing in constancy nationwide. Underlined species are significantly associated with OSR crops, according to the IndVal procedure

		Rank‡		Constancy (%)		Density (ind. per m²)			Changes in the density of species (CDS)	
Species	Status [W, N, E]†	2000s	1970s	2000s	1970s	2000s	1970s	$IndVal_{OSR}$	Treatment $CDS_{treatment}$	Season CDS_{season}
Viola arvensis	**+ [=, +, +]**	**1 [1–4]**	**11**	**25.8**	**20.4**	**9.8**	**5.5**	**10.44****	**0.41**	**−0.32**
Alopecurus myosuroides	= [−, =, =]	2 [1–5]	1	24.3	58.0	12.8	18.6	8.19	1.01	−0.15
Matricaria chamomilla (+*Tripleurospermum inodorum*)	= [−, =, =]	3 [1–6]	3	22.4	34.4	6.2	3.7	2.28	0.94	−0.19
Capsella bursa-pastoris	**+ [=, =, =]**	**4 [1–6]**	**7**	**22.2**	**26.8**	**6.7**	**5.6**	**12.91****	**0.80**	**−0.16**
Sinapis arvensis	= [=, =, =]	5 [3–10]	9	18.6	21.6	5.6	4.1	6.37	0.42	0.06
Mercurialis annua	**+ [+, +, N]**	**6 [3–12]**	**25**	**17.4**	**3.2**	**8.1**	**1.4**	**2.67**	**0.38**	**0.27**
Veronica persica + polita	= [−, =, =]	7 [3–12]	4	17.2	31.8	6.6	4.4	6.40	0.68	−0.61
***Lolium* spp.**	**+ [−, N, +]**	**8 [4–14]**	**20**	**16.5**	**5.1**	**9.5**	**1.6**	**5.26**	**1.09**	**−0.23**
Geranium dissectum	**N+ [N+, N+, N+]**	**9 [5–15]**	**>26**	**15.3**	**–**	**5.5**	**–**	**23.39****	**0.26**	**0.00**
Galium aparine	= [=, =, −]	10 [6–17]	10	13.6	21.6	3.5	3.8	3.63	0.83	−0.29
Senecio vulgaris	**+ [+, =, =]**	**11 [6–17]**	**18**	**13.6**	**6.4**	**3.2**	**3.1**	**5.40**	**1.01**	**0.02**
Sonchus asper	**N+ [N+, N+, N]**	**13 [6–18]**	**>26**	**13.4**	**–**	**3.9**	**–**	**8.04**	**1.15**	**0.09**
Chenopodium album	**N+ [N+, N+, ?]**	**12 [6–18]**	**>26**	**13.4**	**–**	**5.4**	**–**	**0.69**	**0.86**	**0.93**
Raphanus raphanistrum	= [=, =, −]	14 [7–19]	14	12.4	11.5	5.1	2.8	3.78	0.24	0.29
Poa annua	= [+, −, =]	15 [9–21]	12	11.0	15.9	8.0	6.0	2.68	1.19	−0.43
Stellaria media	− [−,−,−]	16 [9–21]	2	11.0	56.0	6.5	13.7	2.65	1.20	−0.24
Veronica hederifolia	− [−, =, =]	17 [9–21]	6	11.0	28.0	4.4	5.8	2.28	0.91	−0.49
Papaver rhoeas	− [−,−,−]	18 [12–23]	5	9.8	29.9	4.7	6.4	2.95	0.91	−0.20
Euphorbia helioscopia	N [N+, N, N]	20 [15–28]	>26	7.6	–	2.1	–	5.21	0.13	−0.10
Aphanes arvensis	− [−, −, =]	19 [15–28]	8	7.6	22.9	7.4	5.4	6.47	0.90	−0.37
Myosotis arvensis	= [−, −, =]	21 [16–30]	16	7.4	7.0	6.8	1.7	5.89*	1.25	−0.51
Cirsium arvense	N [N, N, N]	22 [16–31]	>26	6.9	–	2.7	–	1.44	0.21	0.30
Lapsana communis	N [?, ?, N]	23 [17–31]	>26	6.9	–	4.5	–	4.73*	0.94	0.19
Geranium rotundifolium	N[?, N, N]	24 [16–32]	>26	6.7	–	5.1	–	6.12**	0.53	0.01
Solanun nigrum	N [N, N, ?]	25 [17–33]	>26	6.4	–	3.5	–	0.30	0.96	0.90
Bromus sterilis	N [?, N, N+]	26 [19–38]	>26	5.3	–	10.6	–	5.97*	0.74	−0.17
Fumaria officinalis	− [=,−,−]	27 [20–39]	15	5.0	10.2	2.4	2.9	0.50	0.06	0.35
Lamium purpureum	− [−, −, −]	35 [24–54]	17	3.6	6.5	5.4	2.5	2.57	0.93	−0.01
Valerianella spp.	?[?, ?, ?]	38 [29–69]	>26	2.4	–	2.9	–	4.30*	0.63	−0.46
Helminthotheca echioides	?[?, ?, ?]	38 [30–68]	>26	2.4	–	2.2	–	6.08*	0.62	−0.15
Cerastium spp.	− [−, −, −]	41 [31–69]	22	2.1	4.5	9.0	1.9	1.05	0.52	−0.16
Arabidopsis thaliana	− [−, =, −]	44 [32–71]	26	1.9	3.0	3.6	2.5	1.68	0.66	−0.95
Avena fatua	− [−, −, −]	49 [34–72]	13	1.7	12.7	3.0	5.2	0.45	0.79	−0.16
Sisymbrium officinale	?[?, ?, ?]	49 [33–72]	>26	1.7	–	3.3	–	3.66**	0.31	0.29
Calepina irregularis	?[?, ?, ?]	49 [34–72]	>26	1.7	–	6.4	–	3.46**	0.13	−0.39
Picris hieracioides	?[?, ?, ?]	56 [36–73]	>26	1.4	–	1.7	–	4.28*	0.50	−0.15
Geranium columbinum	?[?, ?, ?]	62 [38–74]	>26	1.2	–	1.5	–	2.28*	0.21	0.02
Poa trivialis	− [−, −, −]	72 [41–74]	19	1.0	5.1	3.8	2.1	0.34	1.02	−0.82
Barbarea intermedia	?[?, ?, ?]	75 [45–91]	>26	0.7	–	2.0	–	2.66*	0.13	0.06
Elymus repens	− [−, −, −]	84 [52–93]	21	0.5	4.5	2.9	1.4	0.03	−0.41	0.17
Carduus pycnocephalus	?[?, ?, ?]	100 [64–138]	>26	0.2	–	–		2.13*	−0.21	−0.22
Avena sterilis subsp. *ludoviciana*	− [−,−,−]	>138	23	0.0	4.4	0.0	1.4	–	–	–
Spergula arvensis	− [−,−, −]	>138	24	0.0	3.8	0.0	2.4	–	–	–

†Species status at the national level: '+' increasing, '='stable, '−' decreasing in frequency, 'N+' species increasing in frequency and new to the list of the top 26 species; 'N' new species entering the top 26 species for which status cannot be estimated; '?' species for which status cannot be determined. Status changes are indicated in brackets for the three regions studied: W: West, NBP: North-Paris Basin, E: East.

‡Rank = average constancy rank of the species given by the bootstrap process, with the 95% confidence interval in bracket.

Table 3 Correlation between the three indices, taxonomic affiliation to botanic families and status changes since the 1970s (increasing, stable or decreasing). Correlations are based on *Spearman's* rank *correlation* coefficient (rho) for the comparison between quantitative indices, Kruskal–Wallis *H*-tests for the comparison of qualitative and quantitative indices and Fisher's exact test for the comparison of two qualitative variables. $IndVal_{OSR}$ reflects the degree of ecological specialisation for oilseed rape. The CDS indices correspond to the difference in density of individual species between control and treated plots ($CDS_{treatment}$) or between autumn and spring (CDS_{season}). Bold values indicate significant correlations

	$IndVal_{OSR}$	$CDS_{treatment}$	CDS_{season}	Family	Status change since 1970s
$IndVal_{OSR}$		*P* = 0.205	*P* = 0.145	***P* = 0.004**	***P* = 0.001**
$CDS_{treatment}$	*rho* = 0.148		*P* = 0.088	***P* = 0.005**	*P* = 0.482
CDS_{season}	*rho* = −0.170	*rho* = −0.210		***P* = 0.005**	*P* = 0.185
Family	***H* = 25.577**	***H* = 25.439**	***H* = 25.380**		*P* = 0.695
Status change since 1970s	***H* = 13.160**	*H* = 1.458	*H* = 3.374	/	

herbicides ≤2.9 (i.e. mean control efficiency of 70–85%). Among the most sensitive species, those with flowering seasons of more than four months had lower densities in treated plots. Significant differences were observed between botanic families (Table 3), with Brassicaceae species maintaining higher densities in treated plots than Poaceae species (Table S3). CDS_{season} and $CDS_{treatment}$ were not significantly correlated ($P = 0.09$, $r = -0.21$, Table 3).

Long-term changes in species status

Between the 1970s and the 2000s, 13 species showed a decrease in ranking status, eight showed no significant change, and eight showed an increase in ranking status (Table 2). Only two of the increasing species were already common in the 1970s (*V. arvensis*, *C. bursa-pastoris*), and only a few of the declining species retained any great importance (e.g. *Veronica hederifolia* L. and *Stellaria media* (L.) Vill with Co >10%). Conversely, most other species increased considerably in constancy, either from prior rare status, defined as Co<5% in agricultural fields (*Mercurialis annua* L., *Lolium* spp.), or from a complete absence from the list of the 26 most common weeds in OSR in the 1970s (*G. dissectum*, *Sonchus asper* (L.) Hill). Finally, some species declined strongly, becoming rare in the second survey (*Spergula arvensis* L., *E. repens*).

No weed characteristic was significantly associated with long-term changes in the status of weed species. The maintenance of high densities at the end of the season or after herbicide treatment was not correlated with long-term success either (Table 3). Instead, four of the five OSR specialist weeds for which a status could be determined were increasing at least in one region. $IndVal_{OSR}$ values were not randomly distributed across species status changes at the national level ($P = 0.001$, Table 3), with increasing ($IndVal_{OSR}$=8.60 ± 7.17) or stable (4.61 ± 2.18) species displaying significantly greater specialisation for OSR than declining species (1.65 ± 1.80) in Wilcoxon pairwise comparisons.

Discussion

One aim of this study was to highlight the filtering process (Weiher & Keddy, 1999) underlying the assembly of weed species in oilseed rape (OSR) crops. Against expectation, no particular trait was associated with increasing or decreasing frequencies of weed species over large regional and temporal scales. However, several traits were correlated with the density of weed species in OSR at the field scale.

Weed species traits favoured in OSR crops

We aimed to identify not only the species successful in OSR crops in France, but also the species traits accounting for this success. Autumn germination was identified twice (for OSR specialisation and for an increase in density between autumn and spring) as the most important trait for success, consistent with OSR being the only true autumn crop sown as early as mid-August in France. Weed germination date is known to respond strongly to crop sowing date, due to the stimuli for dormancy release provided by previous soil disturbance, such as soil tillage (Benech-Arnold *et al.*, 2000). However, species germinating in September were no more successful than those germinating later in autumn. Moreover, some spring-germinating species, such as *C. album* and *M. annua,* also increased in frequency in the long term. These species are not particularly frost tolerant and were therefore absent from the spring surveys, but they may interfere with the early stages of OSR development and produce seeds before winter.

Comparisons of the 'potential' weed flora in control plots with the filtered flora expressed in treated plots showed that the resulting assembly of weed species was largely determined by natural tolerance to herbicides.

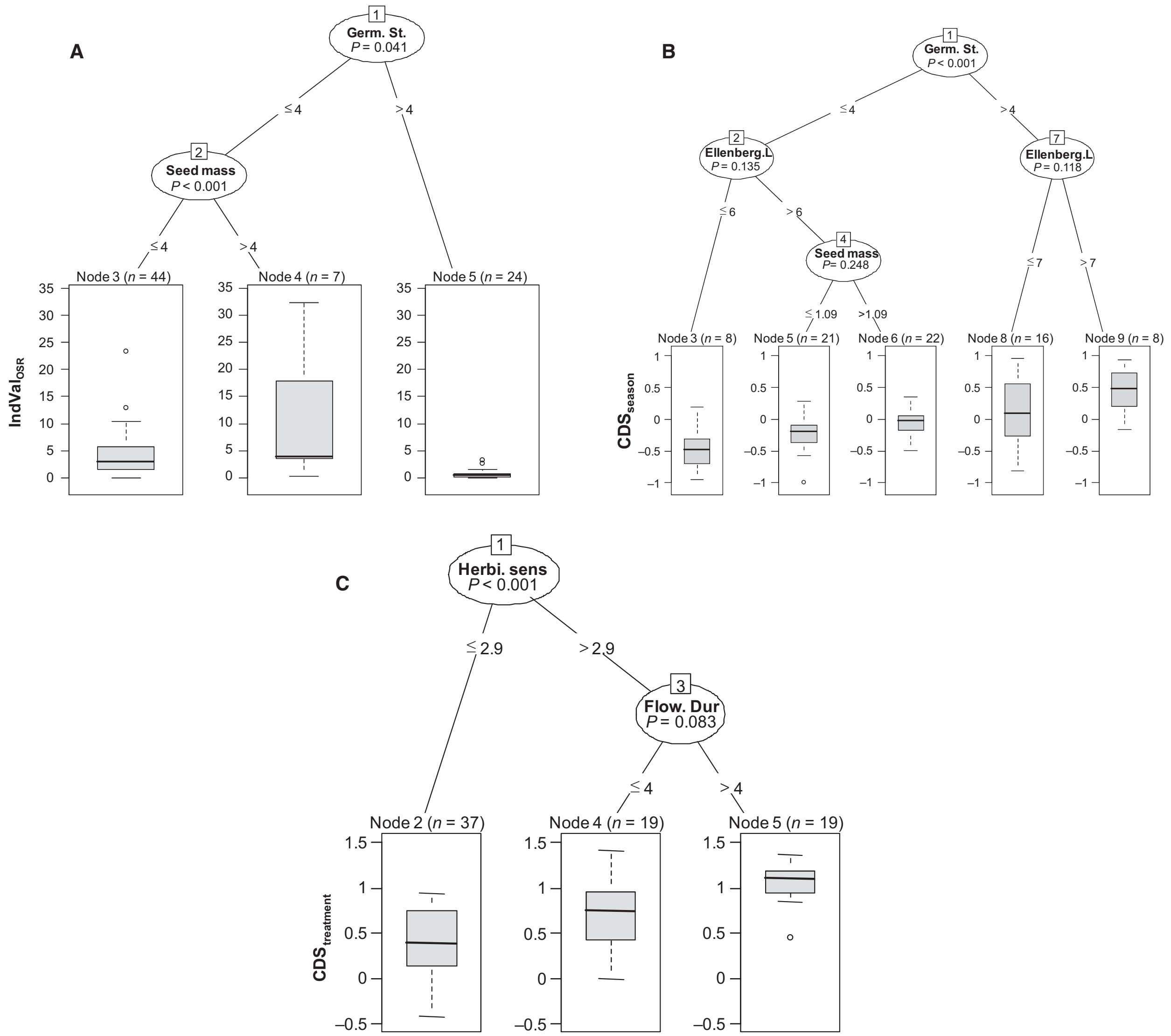

Fig. 2 Conditional inference trees describing the influence of weed characteristics on (A) the degree of specialisation for oilseed rape ($IndVal_{OSR}$), (B) the changes in density over a growing season of oilseed rape (CDS_{season}) and (C) the differences in species density between control and treated plots ($CDS_{treatment}$). Inner nodes (ovals) indicate the variables used for splitting, and threshold values are given on the line. *n* is the number of species for each terminal node; the boxplots show the distribution of $IndVal_{OSR}$, CDS_{season} and $CDS_{treatment}$. Germ. st.: start of germination; Flow. Dur: flowering duration Herb. sens.: sensitivity to OSR herbicides.

This may appear obvious, but the effects of herbicides have rarely been determined at community level, due to the lack of large-scale surveys including control plots.

Weed species from the same family as OSR (Brassicaceae) maintained higher densities in treated plots, indicating that herbicide pressure could lead to a phylogenetically convergent community structure (Cavender-Bares *et al.*, 2009). This may correspond to the result, at community level, of a phenomenon known as 'crop mimicry' or 'Vavilovian mimicry' (McElroy, 2014), in which the individuals of a population are selected on the basis of their morphological or biochemical resemblance to the crop, enabling them to escape some selection pressures (seed sorting, weeding).

Among early-germinating species, those with heavy seeds displayed greater specialisation. The threshold value of 4 mg is striking, in that this is the mean weight of OSR seeds. However, this trait is related to many ecological processes, making it difficult to interpret. It may also reflect greater competitiveness at the seedling stage (Susko & Cavers, 2008) or a capacity to germinate in the shade (Milberg *et al.*, 2000), consistent with the trend observed for Ellenberg-L. Increases in density between autumn and spring in control plots presumably reflect the ability of weeds to compete with the crop and to withstand winter frost. Although not significant, the tendency towards greater success for shade-tolerant species, whether early or late germinating (Fig. 2B), suggests that the lower light levels under

Table 4 Effects of management variables and environmental conditions on the mean degree of specialisation for OSR in the fields surveyed as estimated by the generalised linear model (n = 318 fields). Bold values indicate significant effects

Explanatory variables	*Z*-value	*P*(>|z|)
Management variables		
Tillage depth	**−5.054**	**<0.001**
% Spring crops	**−2.704**	**0.002**
TFI	**3.059**	**<0.001**
Environmental conditions		
Longitude (X)	1.944	0.052
Latitude (Y)	**6.559**	**<0.001**
Altitude (Z)	0.472	0.637
pH	−0.810	0.417

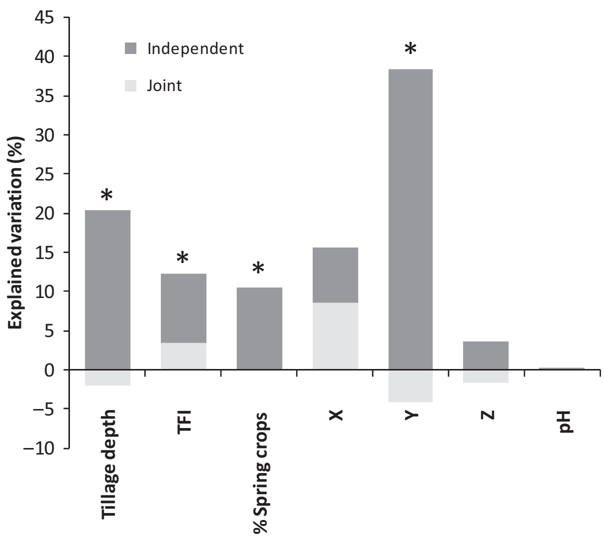

Fig. 3 The independent and joint contributions (given as the percentage of the total explained variance) of each predictor variable, as estimated from hierarchical partitioning. Variables marked with an asterisk independently explained a greater proportion of the variance than would be expected by chance (with $P < 0.05$ level).

the OSR canopy may influence the composition of the weed community. In a similar study, Hanzlik and Gerowitt (2011) found that OSR crop density affected the occurrence of rare weeds, which they assumed to be less shade tolerant.

Influence of management practices

Current constancy and long-term status in OSR may also reflect general trends in management practices (e.g. adoption of no-tillage practices) or success in the other crops of the rotation. *Geranium dissectum* and *V. arvensis* are clearly favoured by OSR, as reported by other studies in Europe (Froud-Williams & Chancellor, 1987; Hanzlik & Gerowitt, 2011), but *Bromus sterilis* L. is increasing in frequency only in OSR crops in eastern France (Table 2), where no-tillage systems prevail (Table 1). These examples show that weed species may increase in frequency in a given crop, grown under contrasting cropping systems, at the national scale, for various reasons, making it difficult to identify individual traits responsible for shifts in the weed flora.

Interestingly, the mean degree of specialisation for OSR at community level (IV_{com}) highlighted the conditions under which communities with different levels of specialisation may develop. The strong influence of latitude may express the influence of the OSR cropping history, which has been cultivated for much longer in northern France, with a more recent expansion of OSR cultivation in the south. As expected, intense selection pressures and stable conditions were found to favour specialist weeds of OSR: strong herbicide pressure within OSR crops and a low frequency of spring-sown crops in the rotation lead to high degrees of community specialisation. Including spring-sown crops in the rotation is known to have a major impact on the dynamics of winter annual weeds, including OSR specialists (Milberg *et al.*, 2001), and our results suggest that such a strategy would be particularly effective for limiting *G. dissectum* or *V. arvensis*. Conversely, if selection pressures remain unchanged, other OSR specialist species identified in this study (*Barbarea intermedia* Boreau, *Sisymbrium officinale* (L.) Scop.) may become increasingly common in OSR.

Conclusion

A comparison of the weed floras of OSR and other crops with identification of the species best maintaining their density during the growing season or after herbicide treatments demonstrated the importance of traits relating to phenology (start of germination, duration of flowering), seed mass and sensitivity to OSR herbicides. As expected, taxonomic patterns were identified, with species from Brassicaceae and from certain other families, such as Geraniaceae and Asteraceae, more successful in OSR than species from other families. High herbicide pressure, no-tillage and a low proportion of spring crops in the rotation were associated with a high degree of OSR specialisation at the community scale.

Acknowledgements

We thank all those involved in the ‘Biovigilance Flore’ weed survey for providing data and the French Ministry of Agriculture for funding this monitoring. This study was funded in part by the ANR-OGM VigiWeed and PSPE1 Vespa projects.

References

Andreasen C & Stryhn H (2008) Increasing weed flora in Danish arable fields and its importance for biodiversity. *Weed Research* **48**, 1–9.

Barralis G (1977) *Répartition et densité des principales mauvaises herbes en France*. INRA-AFPP, Paris, France.

Benech-Arnold RL, Sánchez RA, Forcella F, Kruk BC & Ghersa CM (2000) Environmental control of dormancy in weed seed banks in soil. *Field Crops Research* **67**, 105–112.

Booth BD & Swanton CJ (2002) Assembly theory applied to weed communities. *Weed Science* **50**, 2–13.

Cavender-Bares J, Kozak KH, Fine PVA & Kembel SW (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters* **12**, 693–715.

Devictor V, Clavel J, Julliard R *et al.* (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology* **47**, 15–25.

Dufrêne M & Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**, 345–366.

Fried G, Kazakou E & Gaba S (2012) Trajectories of weed communities explained by traits associated with species' response to management practices. *Agriculture, Ecosystems & Environment* **158**, 147–155.

Fried G, Norton LR & Reboud X (2008) Environmental and management factors determining weed species composition and diversity in France. *Agriculture Ecosystems & Environment* **128**, 68–76.

Froud-Williams RJ & Chancellor RJ (1987) A survey of weeds of oilseed rape in central southern England. *Weed Research* **27**, 187–194.

Gaba S, Fried G, Kazakou E, Chauvel B & Navas M-L (2014) Agroecological weed control using a functional approach: a review of cropping systems diversity. *Agronomy for Sustainable Development* **34**, 103–119.

Halberg N (1999) Indicators of resource use and environmental impact for use in a decision aid for Danish livestock farmers. *Agriculture, Ecosystems & Environment* **76**, 17–30.

Hallgren E, Palmer MW & Milberg P (1999) Data diving with cross-validation: an investigation of broad-scale gradients in Swedish weed communities. *Journal of Ecology* **87**, 1037–1051.

Hanzlik K & Gerowitt B (2011) The importance of climate, site and management on weed vegetation in oilseed rape in Germany. *Agriculture, Ecosystems and Environment* **141**, 323–331.

Hothorn T, Hornik K & Zeileis A (2006) Unbiased recursive partitioning: a conditional inference framework. *Journal of Computational and Graphical Statistics* **15**, 651–674.

Julve P (1998) Baseflor. Index botanique, écologique et chorologique de la flore de France. 4 mars 2012 edn., http://philippe.julve.pagesperso-orange.fr/catminat.html

Kleijn D & van der Voort LAC (1997) Conservation headlands for rare arable weeds: the effects of fertilizer application and light penetration on plant growth. *Biological Conservation* **81**, 57–67.

Lososová Z, Chytrý M, Cimalová S *et al.* (2004) Weed vegetation of arable land in Central Europe: Gradients of diversity and species composition. *Journal of Vegetation Science* **15**, 415–422.

Mamarot J & Rodriguez A (2003) *Sensibilité des mauvaises herbes aux herbicides en grandes cultures*. ACTA, Paris, France.

McElroy JS (2014) Vavilovian Mimicry: Nikolai Vavilov and His Little-Known Impact on Weed Science. *Weed Science* **62**, 207–216.

Milberg P, Andersson L & Thompson K (2000) Large-seeded species are less dependent on light for germination than small-seeded ones. *Seed Science Research* **10**, 99–104.

Milberg P, Hallgren E & Palmer MW (2001) Timing of disturbance and vegetation development: how sowing date affects the weed flora in spring-sown crops. *Journal of Vegetation Science* **12**, 93–98.

Pinke G, Karácsony P, Czúcz B, Botta-Dukát Z & Lengyel A (2012) The influence of environment, management and site context on species composition of summer arable weed vegetation in Hungary. *Applied Vegetation Science* **15**, 136–144.

R Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Salonen J, Hyvönen T, Kaseva J & Jalli H (2013) Impact of changed cropping practices on weed occurrence in spring cereals in Finland - a comparison of surveys in 1997–1999 and 2007–2009. *Weed Research* **53**, 110–120.

Susko DJ & Cavers PB (2008) Seed size effects and competitive ability in *Thlaspi arvense* L. *(Brassicaceae)*. *Botany* **86**, 259–267.

Violle C, Navas ML, Vile D *et al.* (2007) Let the concept of trait be functional!. *Oikos* **116**, 882–892.

Weiher E & Keddy P (1999) *Assembly Rules as General Constraints on Community Composition*. Cambridge University Press, Cambridge, UK.

Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**, 213–227.

Zanin G, Otto S, Riello L & Borin M (1997) Ecological interpretation of weed flora dynamics under different tillage systems. *Agriculture, Ecosystems and Environment* **66**, 177–188.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 List of selected traits, indicator values and functional groups, with their abbreviations, units, basic statistics and the management practices assumed to filter species by acting on these traits (Gaba *et al.*, 2014).

Table S2 The sensitivity to herbicides (Herb. sens.) registered for OSR in the 2000s, by Mamarot and Rodriguez (2003). A nine-level scale (1–9) summarises the percentage of weed control achieved with each herbicide for each weed species, based on numerous herbicide trials, with 1 indicating a low efficiency (less than 70% control) and 9 indicating a high efficiency (more than 95% control). Herb. sens. is the mean value of this nine-level scale of weed control for all 20 herbicides registered for OSR in France during the 2000s.

Table S3 Median values of specialisation for OSR ($IndVal_{OSR}$), differences in density between control and treated plots ($CDS_{treatment}$) and between autumn and spring surveys (CDS_{season}), by botanic family. Numbers in brackets indicate the first and third quartiles. Different letters indicate significant differences in post hoc multiple comparison tests. N indicates the number of weed species in the family occurring in oilseed rape. Bold values refer to families which have a significant higher or lower values compared to most other families.