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Crop competition in winter wheat has a higher potential than farming practices to regulate weeds

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Abstract. Management of biotic interactions has been recognized as a potential substitute for costly agrochemical inputs. Competition is one of the most important biotic interactions known to regulate populations and govern species assemblages. However, although theoretical and empirical work has been produced on competition, in situ experimental evidence is much scantier, mainly because of the difficulty of manipulating competition in the field. Arable weeds offer an outstanding opportunity to meet this challenge, because of the relative ease of in situ experimental manipulation and because of the urgent need to find sustainable weed management strategies. Here, we assess the importance of crop competition and two main conventional farming practices (N fertilizer and weed control) on weed species richness, abundance, and biomass. We set up an experiment with a design with two factors, presence/absence of crops and presence/absence of N fertilizer and weed control, in working farm fields with winter cereals as the target crop. We found that the crop competition reduced weed biomass production by almost 65%, as a result of the crop's competitive advantage from its greater ability to take up N, while the effect on weed species richness was less important. Our results also show that the effect of crop competition on the weed assemblage was much stronger than the effect of N fertilizer and weed control. The decrease in weed abundance and biomass mainly resulted from a strong effect of the crop on the dominant species, while the abundance of intermediate species tended to be much less affected, a result consistent with studies in grasslands where the removal of the dominant species provides a competitive release for subordinate ones. Our results further give experimental support for crop competition as a way to reduce costly agricultural inputs for weed control. Conducting experiments with farmers in their field is a valuable approach to generate knowledge for the future delivery of sustainable management.

Key words: agroecology; biological regulation; dominance; nitrogen; plant population and community dynamics; plant–plant interactions; species diversity; weed control.

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Introduction

Clarifying the underlying processes that influence the composition, the diversity, and the relative abundance of co-existing species in local communities has elicited keen interest from ecologists. Biotic and abiotic factors are now increasingly acknowledged as working together to shape community assemblies, but the balance between them in promoting species coexistence remains a central question (McGill et al. 2006, Agrawal et al. 2007, Weiher et al. 2011). This appears particularly relevant in the current transition toward agroecology, since biodiversity is recognized as a partial or even potentially complete substitute for costly agricultural inputs, such as fertilizers, pesticides, imported pollinators, and irrigation (Isbell et al. 2017). Competition is a key process influencing both the distribution and abundance of species (MacArthur 1972, Tilman 1982, Bengtsson et al. 1994). However, although much theoretical and empirical work under controlled conditions has been undertaken on competition while taking account of abiotic factors (Goldberg et al. 1999, Chesson 2000, Amarasekare 2002, Rees 2013, Huston 2014), in situ experimental evidence is much scantier, mainly because of the difficulty of manipulating competition in the field.

Arable weeds offer an outstanding opportunity to meet this challenge: first, for practical reasons, because of the relative ease of in situ experimental manipulation of the crop–weed competition and major abiotic factors affecting weed assemblages; and second, because the existence of crop–weed competition suggests that weed regulation by crop competition may be a sustainable option for weed management while reducing herbicides (Sardana et al. 2017). Crop plants are strongly dominant in arable fields and garner a disproportionate share of the pool of available resources due to a N supply level high enough to enhance their competitive ability (Iqbal and Wright 1997), as well as early establishment and high sowing density, and, therefore, drastically reduce the abundance and biomass of weed plants. However, there is little literature on the influence of crop competition on weed assemblages as most research has been into means of reducing the impact of weeds on crop production, focusing on the effects of crop–weed competition on the crop (Zimdahl 2007). Moreover, the effects of competition have mostly been investigated through pairwise crop–weed species interactions involving only a few weed species over a small range of abiotic conditions (Iqbal and Wright 1997, Blackshaw et al. 2004, Olsen et al. 2005, Kristensen et al. 2008, see Gibson et al. [2008] for an exception). In arable fields, crop plants, however, interact with multiple weed species. There are typically 25–45 weed species in wheat fields (Henckel et al. 2015), although on average four species are found in 1-m^2 quadrats (Bourgeois et al. *in preparation*). The competitive interactions between the crop plants and weeds are, therefore, diffuse (MacArthur 1972), and the effect of crop–weed competition varies with the different competitive abilities of the weed species constituting the assemblage (Blackshaw et al. 2004, Blackshaw and Brandt 2008). In addition, the weed assemblage is influenced by the legacy of past disturbances, depending on the crop history (Mahaut et al. 2018), as well as by spatial dispersal between fields (Henckel et al. 2015). Finally, crop–weed competition is directly affected by farming practices, including weed control measures, such as herbicide application and mechanical weeding, that may increase the dominance of the crop by decreasing weed abundance and biomass production, and N fertilizer, increasing the competitive ability of the crops against the weeds. Crop–weed interactions are, therefore, complex, being affected by both biotic and abiotic factors whose relative importance remains poorly understood.

In our study, we aimed at investigating the effect of the dominant species, that is, the crop, on weed assemblages, and comparing the effect of biotic (i.e., competition) and abiotic factors (i.e., N fertilizer and weed control) on weed assemblages and their ability to regulate weeds. We explored the effect of competition from crops and of these two major farming practices in working farm fields, in real farming conditions. We chose to work in real farming conditions to evaluate these effects over a wide range of weed assemblages and management strategies. Fields and farms were therefore selected to provide a good spread along a management intensity gradient, depending on the farming practices which were characterized mostly by the quantities of N fertilizer applied and the intensity of the weed control. All fields were sown with winter cereals (mainly winter wheat, *Triticum aestivum* L.) in the same restricted geographical area, thus avoiding potential confounding effects of pedoclimatic gradient (Fried et al. 2008) or crop sowing date (Gunton et al. 2011) on weed assemblages. Further, we address the effects of crop competition vs. N fertilizer and weed control within field comparisons. For each field, farmers were asked to use a split-plot design with two factors: presence/absence of crops and presence/absence of N fertilizer and weed control (herbicides and mechanical weeding). For each combination, we measured weed species richness, abundance, and aboveground biomass and N in aboveground biomass, as well as crop aboveground biomass and N in aboveground biomass.

The purpose of our study was to compare the combined effect of N fertilizer and weed control and the effect of the crops alone on the weed community assemblies in order to assess their potential to regulate weeds. Using the plots without crop plants, N fertilizer, nor weed control, we estimated the legacy effect from past weed management on the weed diversity and biomass. In these plots, we assumed that the weed community assembly was that for natural conditions, providing us with an estimate of the weed seed bank potential. We predicted that weed assemblages in less intensively managed fields would show a higher species richness. We then analyzed the consequences of the presence of the crop on weed assemblages. We predicted a significant decrease in weed abundance and biomass in the presence of this strongly dominant competitor, while the effect on weed species richness was less easy to predict. Although the mass ratio theory would predict a decrease in species richness (Grime 1998), the magnitude of this effect cannot be estimated as the weed assemblage may be modified by the presence of the crop. Finally, we explored the effect of N fertilizer and weed control on the competition between the crop and the weeds. The intensity of weed control should be reflected in weed abundance, but high N inputs, while hopefully increasing the crop biomass, may also increase weed abundance and biomass as well as the crop–weed competition.

Materials and Methods

Study area

The study site, the LTSER Zone Atelier Plaine & Val de Sèvre (450 km^2; Bretagnolle et al. 2018), is in central western France, in the south of the Deux-Sèvres department, Nouvelle *Aquitaine* region, France (46.23° N, 0.41° W). It is an agricultural landscape dominated by intensive cereal production, although winter oilseed rape, maize, and sunflower are also important crops. The soils are Rendzic Leptosols (IUSS Working Group 2014). Since 1994, land use has been recorded twice per year (April and June) for each of the ~16,000 fields (average field size of 5 ha) to record both early-harvested and late-sown crops. In total, 47 land-use categories, comprising 42 agricultural, three urban, and two forest use categories, have been recorded on vector maps, updating field boundaries when necessary, using ArcGIS 10.5 (ESRI, Redlands, California, USA).

In 2013 and 2014, we selected winter cereal fields according to their farming systems and location in the LTSER to include all the major soil types and agricultural systems, especially in terms of N fertilizer and weed control. Fields were not randomly selected since their inclusion was dependent on farmers being willing to set up the experimental design described below. A total of 56 fields were selected: 16 in 2013 and 40 in 2014, among which 23 fields were farmed organically. Most farmers in the 2013 experiment (14 fields) also took part in 2014 (20 fields). In 2014, one farmer had only one field in the experiment, one had three fields, and the rest had two fields.

Experimental design

Within each selected field, experimental plots of 150–200 m^2 were marked with permanent pennants (Fig. 1A, B), with one experimental plot in the center of the field in 2014 and two experimental plots, one in the center and one within the first five meters of the field (field edge), in 2013. The experimental plots were divided into four subplots of about 50 m^2 each with one of the four different combinations of absence/presence of crops and absence/presence of N fertilizer and weed control (Fig. 1A, B). The farmers themselves performed the experiment following their standard practices as for the rest of the field. No crop plots were created by lifting the seed drill. The absence of seed drilling could potentially affect weed assemblage. However, we believe it may be much weaker than the effect of tillage (Buhler 1997, Colbach et al. 2014), which was the same for the all four sub-plots. As a result, the cultivation parameters (sowing date, sowing density, tillage operations, and crop variety), N fertilizer (frequency, dates, and rates of application), and weed control programs varied from field to field (Appendix S2: Table S1). The farmers were interviewed at the end of the experiment to characterize their farming practices and gather general information about their farms.

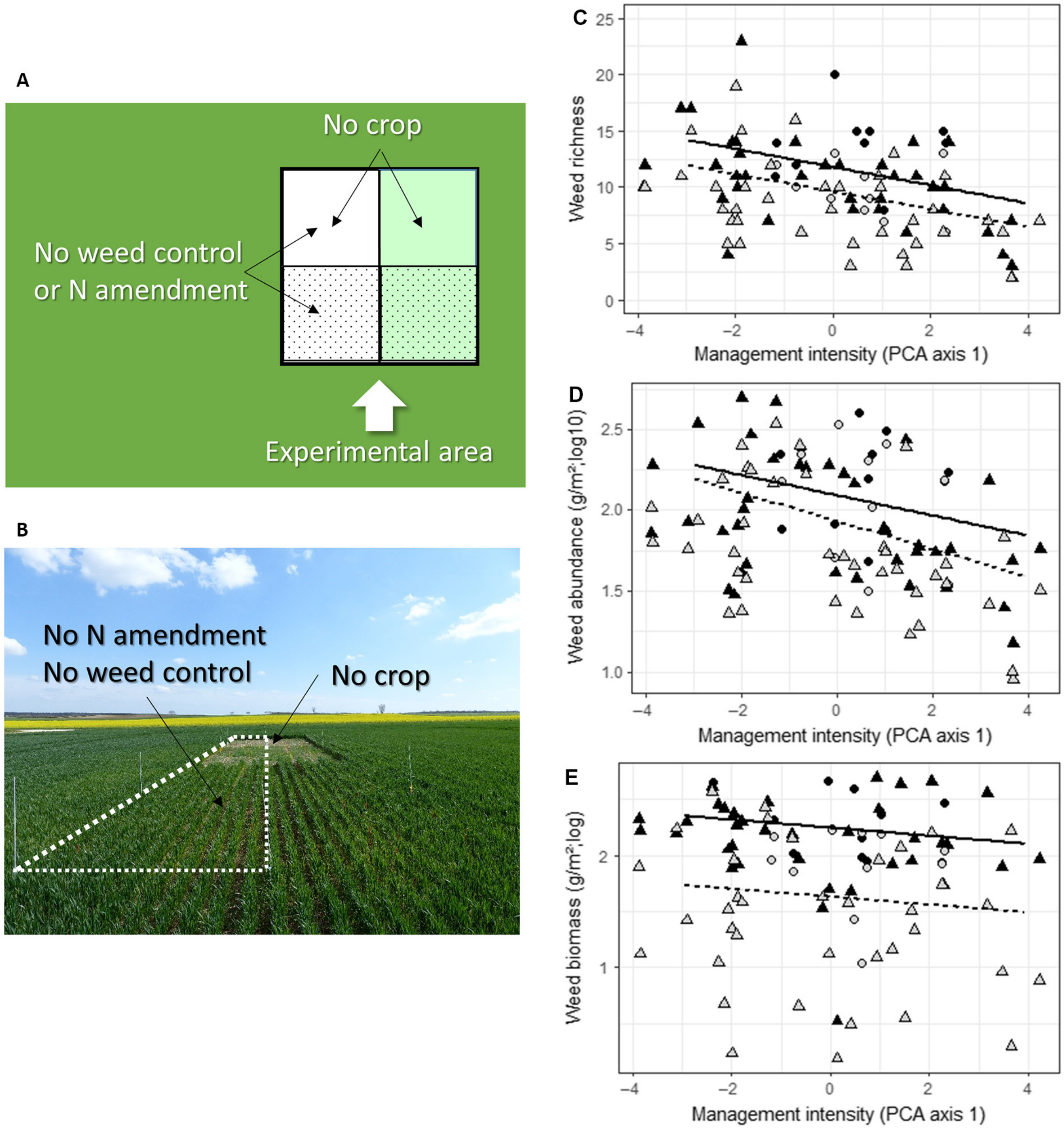

Fig. 1. (A) Schematic representation of the experimental design with the experimental plot and the four sub-plots, with the four different treatments, which enclosed the sampling quadrats. The light green areas indicate sub-plots with weed control and N fertilizer, and the dotted areas indicate sub-plots with crop plants. (B) Picture of the experimental design within a field (photograph: CEBC-CNRS). (C–E) Relationship between management intensity (principal component analysis [PCA] axis 1) and weed species richness (C), abundance (D), and biomass (E) in period 2. Open circles are for quadrats at the field edge, and triangles are for the field core. The solid line represents the predicted values of the linear models in the absence of the crops, and the dashed line is for the linear mixed models in the presence of the crops.

Each year, the experiment started when the crops were sown and ended at crop harvest. In each of the four sub-plots, two 1-m^2 sampling quadrats were delimited, located at least at 2 m from the sub-plot border and from each other to avoid border effects. We performed a preliminary analysis to determine whether the weed species richness and abundance were affected by the year (e.g., weather conditions) or the field position (field edge vs. field core). The results (Appendix S1) indicated that the weed species richness and abundance depended on the position of the quadrat within the field while the year did not have a significant effect. We, therefore, used the field position in all models.

Weed sampling

We recorded weed species identities and abundances in the quadrats in each sub-plot three times per year: before spring herbicide application (March, period 1), at the flowering of the crop (end of May–beginning of June, period 2), and at harvest (early July, period 3). In 2013, weed species and abundances were recorded in two 1-m^2 quadrats in period 1 and only one quadrat in periods 2 and 3. In 2014, one 1-m^2 quadrat was divided in four 0.25-m^2 sub-units in which weed abundances were estimated using scores on a $\log_{10}$ scale (scores 0 for absence, 1 for 1–9 individuals, 2 for 10–99 individuals, and 3 for 100–999 individuals per 0.25 m^2), and we used the geometric mean of the abundance scores for the sub-units for estimating weed abundance in each quadrat. The geometric mean was set to 0 in the sub-unit without weed individual observed. The two methods yielded very similar values for the weed abundances (Appendix S1). In both years, weed aboveground biomass and crop biomass were estimated by harvesting 0.36 m^2 in one of the two quadrats in period 2 and the whole 1 m^2 in the other quadrat in period 3. We harvested both dead and living weeds to get an accurate estimate of the weed biomass and N content. Samples were then oven-dried at 80°C for 48 h before weighing. C and N contents of the plant samples were determined by dry combustion using an automatic C/N-Analyser (reference method ISO 10694 & 13878, Forest Research, UK). N content values were then used to quantify the N amount in the aboveground weed biomass.

Quantitative analyses of the agricultural practices

To quantify the management intensity gradient, we first applied multivariate analyses (correspondence analysis and principal component analysis, PCA; see Appendix S2) to the raw data describing soil characteristics and crop sequences of the focal fields, and then, we used a PCA to characterize the management intensity gradient using farming practices as endogenous factors together with the first two and three axes previously identified for the soil characteristics and crop sequences, respectively. This final analysis gathered all the parameters related to the agricultural practices, crop sequences, and soil characteristics into synthetic variables representing the management intensity gradients, to rank the 56 fields (Appendix S2: Fig. S3). Five axes had eigenvalues higher than 1, but since more than 40% of the variance of the data was explained by the first two axes, only these two axes were considered in subsequent analyses (PCA axis 1 = 28.4% PCA axis 2 = 13.3%). The first axis opposed conventional (CF; positive values) and organic (OF; negative values) farming systems and was positively correlated with increasing quantities of N fertilizers and frequency of pesticide applications, and negatively correlated with decreasing tillage and mechanical weeding (details are presented in Appendix S2: Table S2). The first axis was therefore representative of a relevant management intensity gradient. The second axis mainly differentiated the fields based on their soil properties and crop sequences, from N-rich soils with a high proportion of legumes (other than alfalfa) and oilseed rape within the crop sequence over the previous decade, to fields with a high proportion of gravels, stones, and organic matter with a high proportion of maize and alfalfa within the crop sequence over the previous decade (Appendix S2).

Statistical analyses

Firstly, we used linear models (LM) with the management intensity gradient (PCA axis 1), soil characteristics (PCA axis 2), and quadrat position in the field (field position: edge or core) as explanatory variables to assess the legacy effects from previous years (including farming practices, past crop sequences, and soil characteristics) on weed species richness, abundance, and biomass. Weed abundance and biomass were $\log_{10}$-transformed to meet normality assumptions.

Secondly, we investigated the effect of the presence of crops with and without the two main farming practices (N fertilizer and weed control). We used linear mixed models with treatment (four combinations), management intensity gradient (PCA axis 1), soil characteristics (PCA axis 2), and position in the field (field edge or core) with the field identity as a random effect to assess the effects on weed species richness, abundance, biomass, and N in the aboveground biomass. We also included an interaction term between management intensity gradient (PCA axis 1) and position in the field, and between soil characteristics (PCA axis 2) and position in the field. We used post hoc tests to investigate the pairwise differences between treatments using least-squares means (the function lsmeans of the R package lsmeans; Lenth 2016).

Thirdly, we tested the role of deterministic drivers (e.g., competition) vs. stochastic drivers (e.g., random species loss) of changes in local weed assemblages in the presence and absence of crops in plots without N fertilizer and weed control. We first characterized the β-diversity between each pair of plots within each field using both incidence-based (Jaccard) and abundance-based (Bray-Curtis) compositional dissimilarity metrics (observed β-diversity). We used a null model procedure to simulate the compositional dissimilarity that would be expected due to underlying differences in species abundance (expected β-diversity; Gotelli and Entsminger 2003). Under this null model procedure, species assemblages in each plot were simulated by randomly sampling individuals from the reference species pool (the complete list of species in the two plots compared), while keeping the relative species abundance in the reference species pool and the total species abundance per plot constant. We calculated the standardized effect size (β-deviation) as the difference between the observed and the mean expected β-diversity based on 1000 iterations of the null model, divided by the standard deviation of the expected β-diversity (Kraft et al. 2011, Myers et al. 2013). A β-deviation of zero indicates that the observed β-diversity does not differ from the expected β-diversity with a random sampling of weed species, a positive β-deviation indicates higher β-diversity than expected by chance, a negative β-deviation indicates lower β-diversity than expected by chance, and a non-zero β-deviation could suggest that competition from the crop has a deterministic effect.

Finally, we compared the species frequency distribution diagrams (Fisher et al. 1943) between treatment plots to understand how the presence of crops and the two main farming practices alone or together affected weed assemblages. Log-transformed weed species abundances and biomass were used to rank species, respectively. We arbitrarily defined them as dominant, intermediate, and less frequent species based on the >90%, 90–25%, and <25% quantiles of the abundance distribution of weed species in plots without crop plants, N fertilizer, or weed control.

The analyses were repeated for the data from the three different sampling periods (Appendix S3). As the results were similar, only those at the flowering of the crop (period 2) are presented in the Results section. All analyses were performed using R software version 3.4.0 (R Core Team 2017).

Results

The legacy effect from past crop management

We first explored the legacy effect from past crop management on the weed assemblage by considering only quadrats without crop plants, N fertilizer, nor weed control. Weed species richness and abundance were significantly higher at the field edges with 13.2 ± 3.2 species and 200.7 ± 109.8 plants/m^2 than in the field core which had 10.3 ± 4.0 species and 119.1 ± 116.7 plants/m^2, while the difference was not significant for weed biomass with 225.1 ± 140.1 g/m^2 at the field edge and 183.6 ± 125.5 g/m^2 in field core (Table 1A). In the field core, weed species richness and abundance (Fig. 1C, D and Table 1A) decreased significantly along the management intensity gradient (PCA axis 1), while at the field edge, only abundance decreased significantly along this gradient. Weed assemblages with low species richness did not have significantly lower biomass than species-rich assemblages (Appendix S4). In addition, no significant relationships were found between weed species richness, abundance, or biomass and soil characteristics and crop sequences (PCA axis 2; Table 1A). We had predicted that weed diversity would be higher in less intensively managed fields, thus reflecting past weed

Table 1. Type II results of analyses on parameters describing the weed community: (A) linear mixed models (LMM) to test the effect of crop presence (CP) and (B) LMM to test the effect of experimental treatments (Treat) at four levels.

Models	Weed richness			Weed abundance			Weed biomass			Weed N amount		
	χ^2	df	Pr(>χ^2)	χ^2	df	Pr(>χ^2)	χ^2	df	Pr(>χ^2)	χ^2	df	Pr(>χ^2)
(A)												
CP	23.577	1	**>0.0001**	19.4511	1	**>0.0001**	61.061	1	**>0.0001**	52.433	1	**>0.0001**
PCA axis 1	15.450	1	**>0.0001**	12.0423	1	**0.0005**	1.345	1	0.2461	0.086	1	0.7695
PCA axis 2	2.477	1	0.11550	0.4435	1	0.5054	0.545	1	0.4604	0.986	1	0.3207
Field position	6.414	1	**0.01132**	12.8652	1	**0.0003**	5.471	1	**0.0193**	2.191	1	0.1388
CP × PCA axis 1	0.016	1	0.89920	1.7906	1	0.1809	0.0005	1	0.9827	1.745	1	0.1865
CP × PCA axis 2	0.824	1	0.36410	1.8885	1	0.1694	0.576	1	0.4477	1.016	1	0.3135
(B)												
Treat	71.788	3	**>0.0001**	68.918	**3**	**>0.0001**	129.441	**3**	**>0.0001**	146.562	**3**	**>0.0001**
PCA axis 1	24.125	1	**>0.0001**	17.450	**1**	**>0.0001**	5.816	1	**0.0159**	2.818	1	0.0932
PCA axis 2	3.377	1	0.0661	0.0002	1	0.9889	0.961	1	0.3271	0.314	1	0.5755
Field position	1.579	1	0.2089	14.422	1	**0.0002**	4.983	1	**0.0256**	6.736	1	**0.0095**
Treat × PCA axis 1	3.777	3	0.2866	8.930	3	**0.0302**	5.696	3	0.1274	2.406	3	0.4925
Treat × PCA axis 2	0.922	3	0.8201	4.819	3	0.1856	2.186	3	0.5348	0.992	3	0.8031

Notes: PCA, principal component analysis.

(A) Parameters tested were weed species richness, abundance, and biomass at crop flowering (period 2) in quadrats without crop plants, weed control, or N fertilizer in order to investigate the legacy effects from previous years (including farming practices, past crop sequences, and soil characteristics) taking field position into account. (B) Parameters tested were weed richness, abundance (log 10), biomass (log 10), and quantity of N in the aboveground biomass at crop flowering (log 10; period 2) in all sub-plots to investigate the effect of experimental treatments, management intensity (PCA axis 1), soil characteristics (PCA axis 2), and field position (field edge vs. field core), and the interactions between treatments and management intensity and between treatments and soil characteristics. Significant effects are shown in bold. Details of the effect of the treatments are presented in Table 2.

management as a "legacy effect" on the weed seed bank, and we found such a legacy effect for weed species richness and abundance mainly in the field core. This persisted over the cultivation season from period 1 to period 3 (Appendix S3: Fig. S1). However, weed biomass was not affected by the management intensity gradient.

The presence of crops affects weed biomass more than weed diversity

In the absence of N fertilizer and weed control, the presence of crops affected weed species richness, abundance, and biomass (Fig. 1C–E, Table 2), with an especially strong influence on weed abundance and biomass (30.0% and 63.4% lower than in the absence of crop plants). To a lesser extent, the management intensity and field position also influenced weed species richness, abundance, and biomass, with the interaction of management intensity and presence of crops having a significant effect (Fig. 1C–E, Table 1B). Weed species richness and abundance were lower in the presence of crops and in the field core, and decreased along the management intensity gradient (PCA axis 1; Table 1B).

The presence of crops had an effect on the weed assemblage structure. The rank–abundance plots showed that crop competition had a stronger effect on weed biomass (Fig. 2A) than on abundance (Fig. 3A). The effect was greatest for the most abundant and most productive species, while it was greater for moderately productive species than for moderately abundant species and was almost undetectable for the least productive and abundant species (Figs. 2A, 3A). Overall, the 10 most abundant species suffered a 65% biomass reduction, intermediate ranked species (from ranks 11 to 70, producing more than 1 g/m^2 in the absence of the crop) suffered a 38% biomass reduction, and the least productive and abundant species suffered only a 6% biomass reduction (Fig. 2A).

The presence of crops significantly reduced weed species richness (Table 2), whatever the management intensity (Fig. 1C), suggesting that adding a single dominant species, the crop, led to the loss of 2.3 ± 0.5 weed species (Table 2). The slopes of the model predictions were statistically similar for the presence or absence of the crops (Fig. 1C), revealing a constant decrease in weed

Table 2. Pairwise comparison of the effects of the treatments on weed species richness, abundance, biomass, and N amount in the aboveground biomass weed, based on linear mixed models (see Table 1B).

Treatments	Estimate	SE	df	*T* ratio	*P*
Weed species richness					
H0N0C0 vs. H0N0C1	−2.31	0.46	139.24	5.032	**<0.0001**
H0N0C0 vs. H1N1C0	−1.42	0.46	140.11	3.078	**0.0132**
H0N0C1 vs. H1N1C1	−1.45	0.47	140.82	3.116	**0.0118**
H1N1C0 vs. H1N1C1	−2.34	0.46	138.89	5.073	**<0.0001**
Weed abundance					
H0N0C0 vs. H0N0C1	−39.56	9.79	138.66	4.042	**0.0005**
H0N0C0 vs. H1N1C0	−9.02	9.85	139.1	0.916	0.7964
H0N0C1 vs. H1N1C1	−16.33	9.98	139.43	1.637	0.3614
H1N1C0 vs. H1N1C1	−46.88	9.85	138.5	4.758	**<0.0001**
Weed aboveground biomass					
H0N0C0 vs. H0N0C1	−111.93	23.95	132.3	4.673	**<0.0001**
H0N0C0 vs. H1N1C0	−3.59	25.54	141.13	0.14	0.9990
H0N0C1 vs. H1N1C1	−17.70	24.80	131.14	0.714	0.8915
H1N1C0 vs. H1N1C1	−126.04	25.50	125.7	4.942	**<0.0001**
Weed aboveground biomass N					
H0N0C0 vs. H0N0C1	−186.70	28.43	116.83	6.566	**<0.0001**
H0N0C0 vs. H1N1C0	1.29	28.67	119	−0.045	1.0000
H0N0C1 vs. H1N1C1	−4.13	28.49	115.47	0.145	0.9989
H1N1C0 vs. H1N1C1	−192.11	28.46	114.01	6.75	**<0.0001**

Note: H, N, and C represent weed control, N fertilizer, and crop. 0 and 1 indicate absence or presence. Bold values show significant *P*-values.

species richness along the management intensity gradient, and, therefore, a comparatively higher proportion of species lost in intensively managed fields with conventional herbicide-based systems. In poorer species pools, the presence of crops resulted in more depauperate weed assemblages than in less intensively managed fields. We found that most of the dominant species in terms of abundance were dicotyledonous and were generally not characterized by erect growth habit, regardless of the presence of crops or the N fertilizer and weed control (Appendix S5: Table S1). When considering species ranked by biomass, we found that several species of the Poaceae family with similar growth habits and functional characteristics (*Avena fatua*, *Alopecurus myosuroides*, *Lolium* sp., *Vulpia myuros*) were among the most productive ones, although again, the presence of the crop and the N fertilizer and weed control seemed not strongly influence the species ranking. However, some species with highly distinct growth strategies, such as creeping species (*Veronica persica*, *Veronica hederifolia*), could also produce a high biomass in all these conditions (Appendix S5: Table S2). Crops had similar effects on weed species richness, abundance, and biomass at harvest (period 3; Appendix S4).

The β-diversity between plots with and without crops, using both incidence-based and abundance-based metrics, was significantly higher than expected under the null hypothesis (Fig. 4A, B). The average β-deviation was strongly positive, suggesting that crop competition had a strong deterministic effect on the weed assemblage leading to greater compositional differences than expected under the null hypothesis (Fig. 4B). Moreover, for both metrics, the observed β-diversity was unrelated to the management intensity gradient ($LM_{Jaccard}$: $F_{1,46} = 0.19$, $P = 0.67$; and $LM_{Bray\text{-}Curtis}$: $F_{1,46} = 0.06$, $P = 0.81$), suggesting that the effect of crop competition did not depend on management intensity.

The reduction in weed biomass results from the N uptake by crop plants

The results presented above indicated that crop–weed competition was potentially a key process influencing the structure of the weed assemblages. We, therefore, tested the hypothesis that N was a limiting resource for which there was competition, and we analyzed whether the quantity of N in the aboveground weed biomass was affected by the presence of crops. Without N fertilizer and weed control, the quantity of N in the

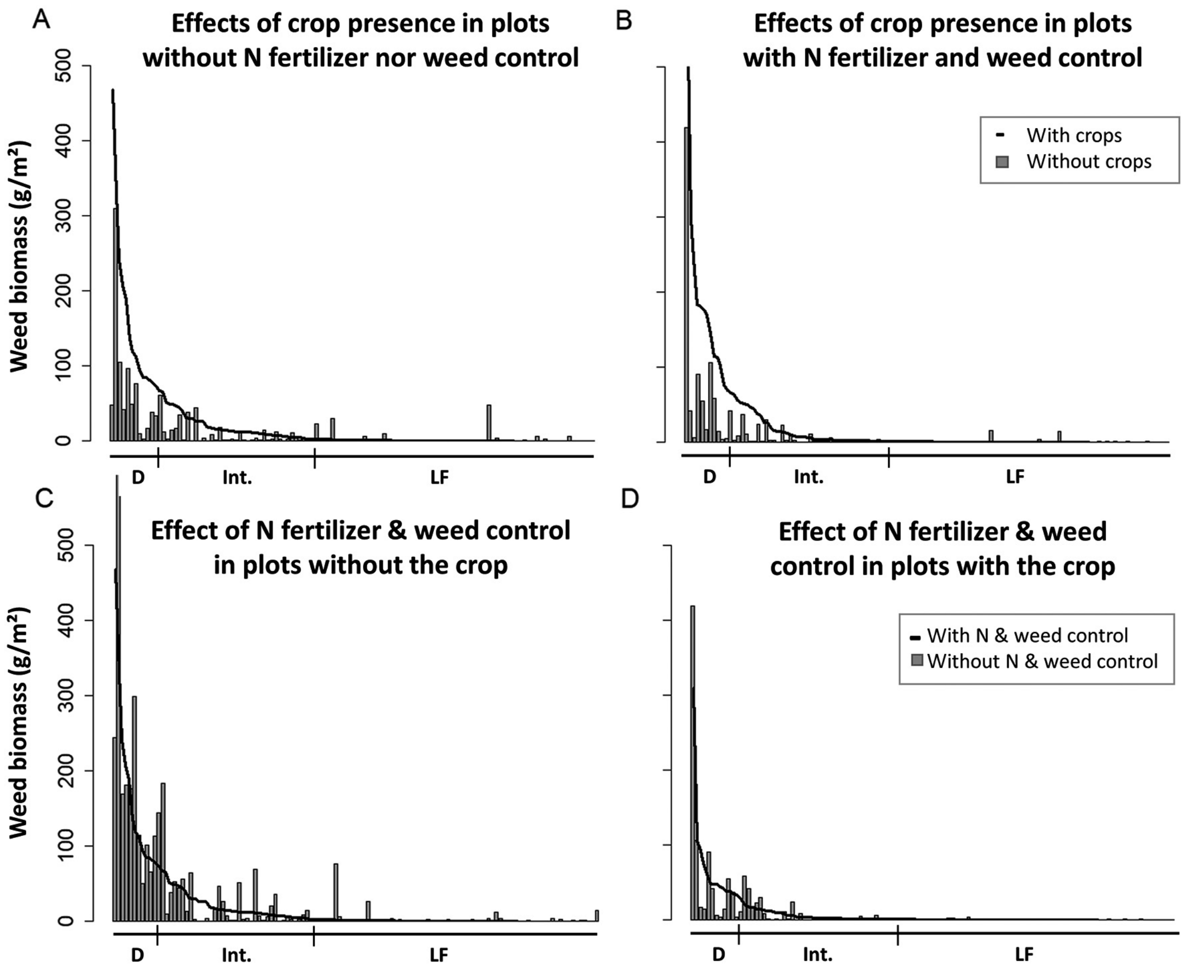

Fig. 2. Rank–abundance curves for all weed plant species in experimental plots. (A, B) Effect of crop presence in the absence (A) and presence (B) of N fertilizer and weed control; the black lines represent weed community structure in the absence of crop plants and the barplots are for the presence of crop plants. (C, D) Effect of farming practices in the absence (C) and presence (D) of crop plants; the black lines represent the weed community structure without N fertilizer and weed control, and the barplots are with N fertilizer and weed control. Weed species are ranked according to their abundance in the plots without crops, N fertilizer, and weed control (A, C), in the plots without crops but with N fertilizer and weed control (B), and in the plots with crops, but without N fertilizer and weed control (D). D, Int., and LF indicate the dominant, intermediate, and less frequent species (see *Materials and Methods* for details).

aboveground weed biomass decreased significantly by 72.9% in the presence of the crops (Table 1B, Fig. 4E), a value only slightly higher than the corresponding decrease by 63.4% in the weed biomass itself (Fig. 4D). This decrease was explained by a higher N uptake by crop plants which accumulated 81.2% of the total N in the aboveground biomass, while weeds accounted for only 18.8%. The higher N uptake by crop plants affected all weed species but mostly the dominant species, suggesting that these dominant species cannot produce high quantities of aboveground biomass when the available N is limited (Figs. 2A, 3A). The crop not only accumulated more N, but also seemed to be able to extract more N from the soil. In the absence of N fertilizer and weed control, the total quantity of N in the aboveground biomass was 50% higher in the presence of crops (398.8 g/m^2 ± 152.6) than in their absence (270.1 g/m^2 ± 194.9; Fig. 4E). As the total

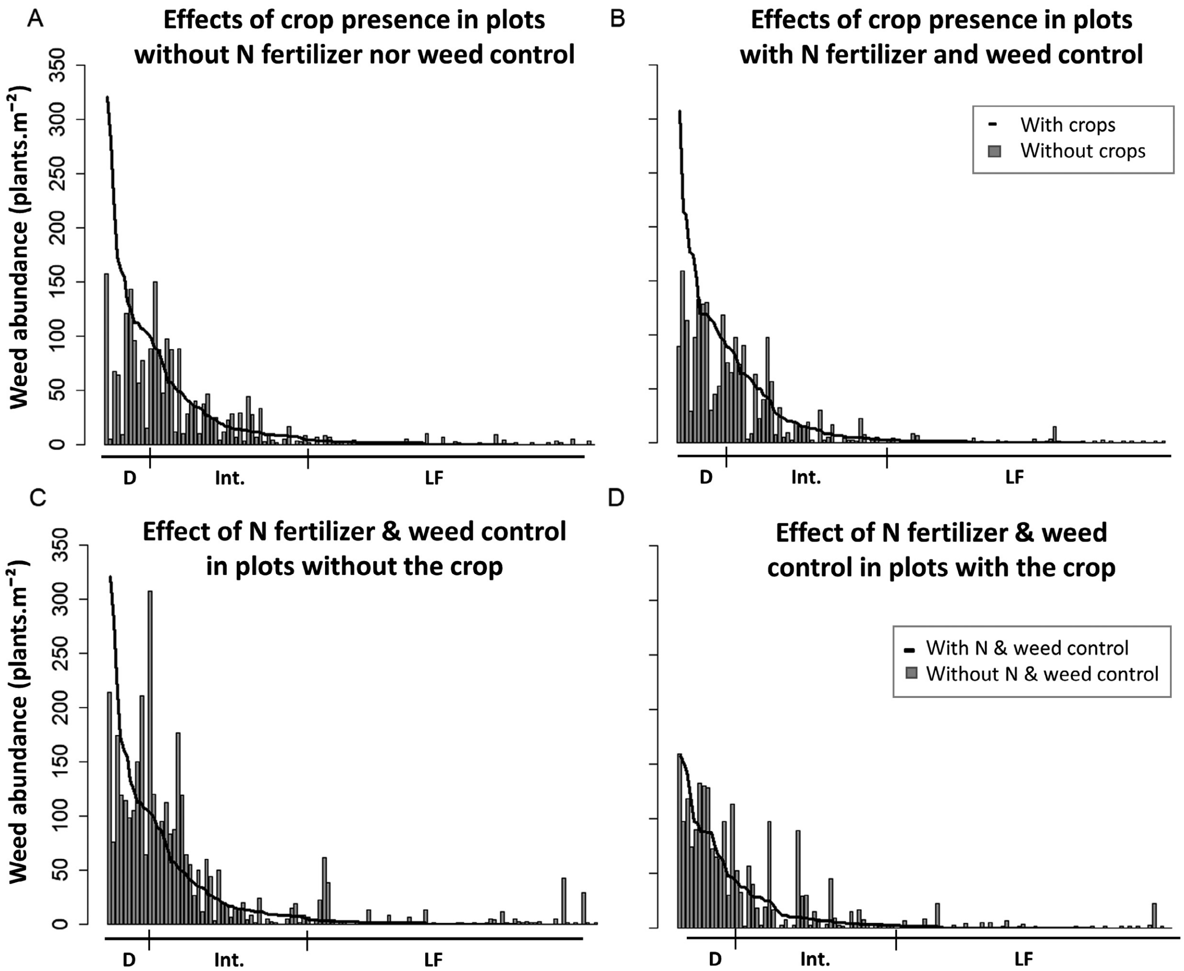

Fig. 3. Rank–abundance curves for all weed plant species in experimental plots. (A, B) Effect of crop presence in the absence (A) and presence (B) of N fertilizer and weed control; the black lines represent weed community structure in the absence of crop plants, and the barplots are for the presence of crop plants. (C, D) Effect of farming practices in the absence (C) and presence (D) of crop plants; the black lines represent the weed community structure without N fertilizer and weed control, and the barplots are with N fertilizer and weed control. Weed species are ranked according to their biomass in the plots without crops, N fertilizer, and weed control (A, C), in the plots without crops but with N fertilizer and weed control (B), and in the plots with crops, but without N fertilizer and weed control (D). D, Int., and LF indicate the dominant, intermediate, and less frequent species (see *Materials and Methods* for details).

aboveground biomass was higher in plots with crop plants (Fig. 4D), we suggest that N was not a limiting resource in the plots without crops.

Effect of farming practices on the weed assemblage

We further investigated the possible interactions between N fertilizer and weed control, and the presence of crops in the effects on weed species richness, abundance, biomass, and quantity of N in the aboveground weed biomass. Accounting for management intensity (PCA axis 1), soil characteristics (PCA axis 2), and quadrat position in the field, we found that N fertilizer and weed control significantly decreased weed species richness by 1.42 (± 0.46) species in the absence of the crop and by 1.46 (± 0.46) species in the presence of the crop (Tables 1B, 2). These decreases were however slightly lower than the difference in weed species richness of 2.30 ($\pm$ 0.46) between the presence and the absence of the crop (Table 2). Moreover, N fertilizer and weed control also reduced weed abundance, biomass, and quantity of N in the aboveground biomass, although this was not significant (Fig. 4D) unlike the presence of the crop which always resulted in a significant decrease for all these properties (Table 2).

N fertilizer and weed control in the presence of crops did not result in a strong reduction of the biomass of the dominant weed species (ranks 1–11), and although the biomass of intermediate species (ranks 12–74; Figs. 2D, 3D) decreased, several of them increased in abundance (Fig. 3D), suggesting that the size of individual plants of these species was reduced in the presence of crops. Similar patterns were observed in the absence of crops, where N fertilizer and weed control mainly affected the weed assemblage structure by changing the dominance in terms of both abundance and biomass (Figs. 2C, 3C). Unexpectedly, with N fertilizer and weed control, the quantity of N in the aboveground weed biomass was lower than without, suggesting that weeds did not benefit from the N fertilizer (Fig. 4E). In addition, while the quantity of N in the aboveground weed biomass did not vary along the management intensity gradient (PCA axis 1; Table 1B), it increased with the higher N fertilizer rates in the more intensively cultivated fields with conventional herbicide-based systems (Fig. 4F). Overall therefore, we found that the effect of the presence of the crops on the weed assemblages was far more pronounced than the effects of the farming practices alone and that the combined effect of the presence of the crops and the N fertilizer and weed control was of the same magnitude as the effect of the crops on their own.

Discussion

Our study provides the first experimental evidence, in real farming conditions, for the effects of the presence of the crop on weed assemblages, in interaction with manipulated farming practices, management intensity, past crop sequences, and soil characteristics. The presence of the crop alone reduced weed biomass by almost 65%, resulting from the competitive advantages of the crop plants which acquired a disproportionate share of the available resources to the detriment of the weeds. Moreover, the presence of crops on their own appeared to have more effect on weed assemblage than the combination of N fertilizer and weed control, with a substantial decrease in weed abundance and biomass. A schematic overview of our experimental results, which may serve as a general framework for future investigations of crop–weed interactions, is given in Fig. 5.

First, as expected and in accordance with previous studies, in the absence of the crop, N fertilizer, and weed control, the weed assemblages in less intensively managed fields had almost twice as many species as most intensively managed fields, which was probably the result of a more species-rich seed bank (Bàrberi et al. 1998, Menalled et al. 2001). Several empirical studies have revealed a decrease in weed species richness in intensively managed fields (Geiger et al. 2010, Batáry et al. 2012, Gaba et al. 2016). Our experimental field manipulation, however, further suggests the importance of a legacy effect in which the weed species richness reflects the past management intensity. These results are consistent with previous studies that showed that past agricultural management systems impact the size of the weed seed bank, but also its composition and relative abundance of species (Bàrberi and Lo Cascio 2001, Menalled et al. 2001, Murphy et al. 2006, Anderson et al. 2009, Bohan et al. 2011, Borgy et al. 2015). The magnitude of this legacy effect (an almost 50% of decrease in weed species richness) can be compared to the decrease of about 10% (1.5 species) induced by N fertilizer and weed control in the absence of the crop. The legacy effect of the overall management appears therefore about five times stronger than the current effect of N fertilizer and weed control, at least under the conditions encountered during the years studied. In addition, since we did not detect an interaction between past management and current (manipulated) farming practices, the weed species richness seemed to result mainly from the influence of the seed bank richness and composition—known to act as a buffer memory of past weed assemblages (Ryan et al. 2010)—rather than from farming practices acting on seedling survival processes and affecting the emergent weed flora, confirming recent empirical evidence (Mahaut et al. 2018). Finally, the major decline of weed species richness in the seed bank of intensively

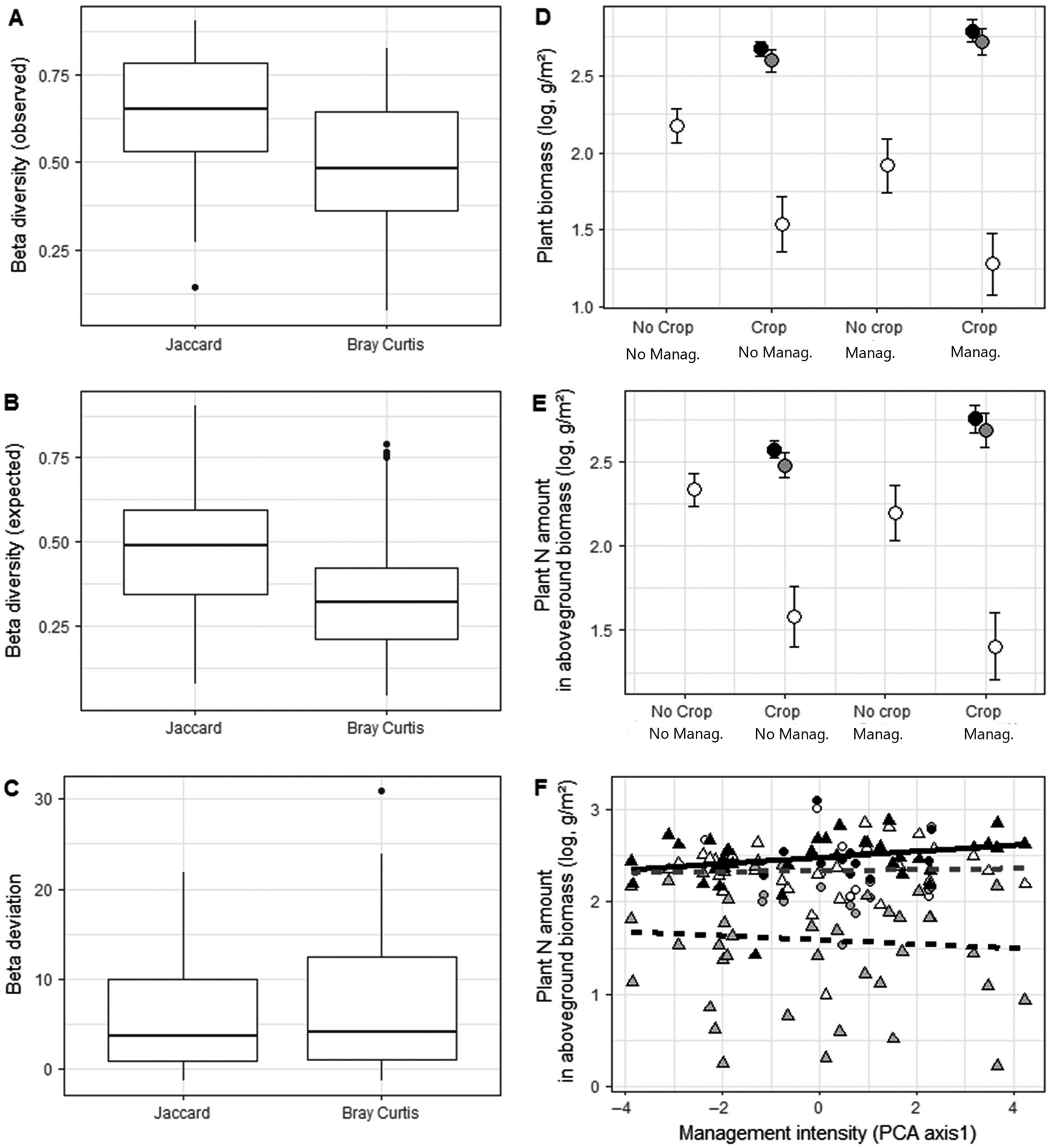

Fig. 4. (A) Observed β-diversity (Jaccard and Bray-Curtis dissimilarity) between weed communities with and without the crops in plots without N fertilizer and weed control. (B) Expected β-diversity from a null model based on random sampling from the "with and without crops, without N fertilizer nor weed control species" pool. (C) β-deviation, a standardized effect of β-diversity that controls for sampling from the "with and without crops, without N fertilizer nor weed control" species pool. Note that the β-deviations (both Jaccard and Bray-Curtis) are strongly positive, indicating higher β-diversity than expected for the null case. (D, E) Means (± confidence intervals) for weed (white dots), crop (gray dots), and total (black dots) biomass production (D) and N in the aboveground biomass (E) for the four treatments. Stars indicate significant differences in weed biomass (D) and N in the aboveground biomass (E) between the four treatments. (F) Relationship between the principal component analysis

(Fig. 4. *Continued*)
(PCA) axis 1 and the N in the aboveground biomass of crop (black dots) and weed plants (gray and white dots). The gray dotted line represents the N in the aboveground biomass in weeds in plots without crops and without N fertilizer and weed control. The dark dotted line and the solid line represent the N in the aboveground biomass in weed and crop plants, respectively, and in plots with crops but without N fertilizer nor weed control.

managed fields appears consistent with the decline of weed species richness documented for agroecosystems in recent decades in most West-European countries (Robinson and Sutherland 2002, Richner et al. 2015).

The presence of the crop, even in the absence of N fertilizer and weed control, had an overwhelming effect on several properties of the weed assemblages, especially weed biomass and abundance (average decrease of 63.4% and 30.0%, respectively), and to a lesser extent, weed species richness. However, considering that biomass is correlated with seed production at the species level (Lutman 2002, Lutman et al. 2011),

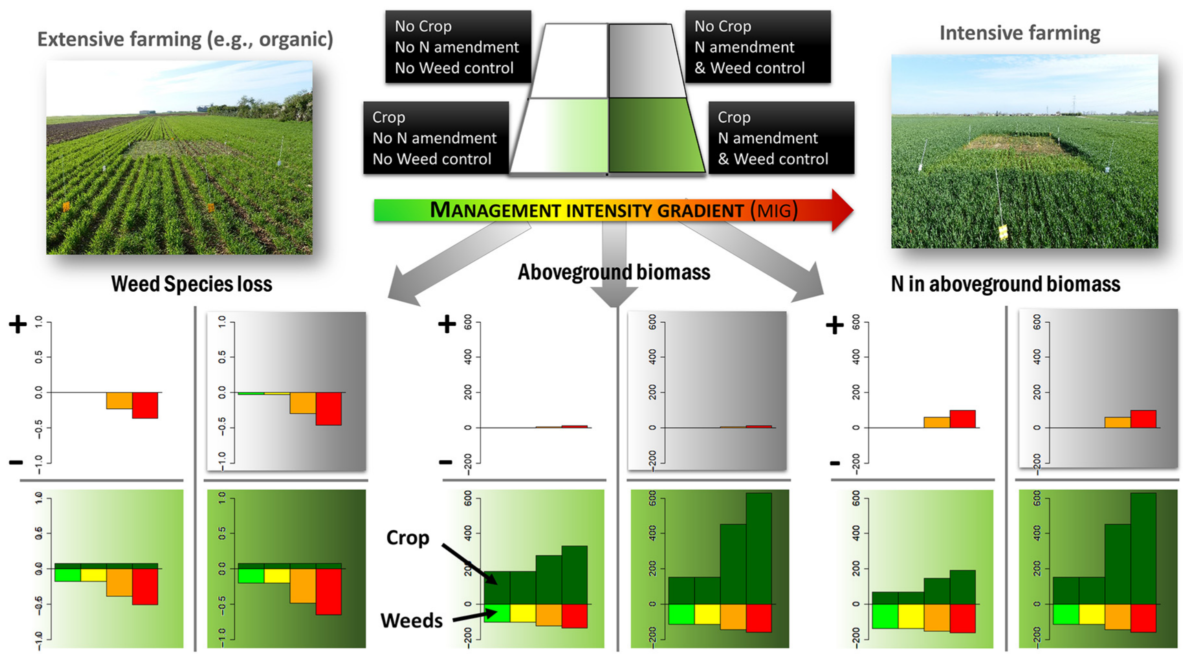

Fig. 5. Overview of the results of the experiment. From right to left, the three panels present the plant species richness (weed species richness and crop presence/absence), plant aboveground biomass, and N in the aboveground biomass for the four treatments as presented in the middle of the top part of the figure. The weed species richness values represent the species loss relative to the weed species richness in plots without crops, N fertilizer, nor weed control in the least intensively managed fields (light green bar in the top left figure). The baseline species richness from which losses are shown corresponds to species richness in fields with the lowest management intensity (right part of principal component analysis axis 1). Green bars show that in the presence of the crop, there is one more species, that is, the crop. The plant aboveground biomass values represent the aboveground biomass of weeds and the crop in the least intensively managed fields (light green bar in the top left figure). The N in the aboveground biomass values represent N in the aboveground biomass in weeds and the crop in plots without crops, N fertilizer, nor weed control in the least intensively managed fields (light green bar in the top left figure). Dark green bars indicate the values for the crop. Light green bars indicate the values for the least intensively managed fields, and red bars indicate the values for the most intensively managed fields. Yellow and orange bars indicate the values for the fields with intermediate intensity management.

a reduction in seed production, and hence a decrease in the number of seeds in the soil seed bank, is expected in the midterm. In this context, a species loss is likely especially for weed species with few individuals which are more prone to be strongly influenced by stochastic demographic processes. However, the importance of crop competition on species richness may still remain lower than the species loss induced by intensive weed management. Our results confirm the high competitive ability of cereals over weeds when the resources are limiting (Blackshaw and Brandt 2008), although they were obtained for 1-m^2 quadrats. At the weed assemblage level, the decrease in weed abundance and biomass mainly resulted from a strong effect of the crop on the dominant species, while the abundance of intermediate species tended to be much less affected. These results are consistent with studies in grasslands where the removal of the dominant grasses provides a competitive release for some subordinate species, induced by an increase in light availability at the local scale (Gurevitch and Unnasch 1989, McCain et al. 2010). In our experiment, the observed changes in weed assemblage structure in response to the presence of the crops were mostly driven by changes in quantity of N in the aboveground biomass. This would suggest that the crops' competitive advantage was associated with a superior ability to acquire N resources. However, competition for N might not be the only processes by which the crop reduces weed biomass: A high crop biomass may cause strong competition for light due to the early establishment of a high-density cover and fast growth ensuring preferential access to light during most of the crop cycle (Holt 1995). Given the unidirectional nature of the light resource, the taller, highly dominant, crop plants reduce the growth of their smaller neighbors by intercepting proportionally more of the light resource than their share of the biomass, in accordance with the "size-asymmetric competition" principle (Weiner 1990, Schwinning and Weiner 1998). The importance of light competition for the weed assemblage may, however, depend on the crop variety or species (Lemerle et al. 1995, Andrew et al. 2015).

The effects of N fertilizer and weed control based on herbicides and/or mechanical weeding were much lower than the direct effect of crop competition on weed biomass. We expected that crop–weed competition would be directly affected by the intensity of weed control which may exacerbate the effect of crop competition by decreasing weed abundance and biomass at a key period of the crop cycle, and by high doses of N fertilizers which generally increase the competitive ability of the crops against weeds (Iqbal and Wright 1997, Tang et al. 2014). In our experiment, the differences in amount of N fertilizer and intensity of weed control in plots with and without N fertilizer and weed control were, on average, of 161.02 ($\pm$ 34.63) kg N/ha and 26.1 ($\pm$ 27.89) kg N/ha in conventional and organic fields and of 1.50 ($\pm$ 0.76) treatment frequency index (TFI) in conventional and 1.87 ($\pm$1.82) numbers of mechanical weeding; thus, differences in resource amount and disturbances were high. These two main farming practices affected weed assemblages, but only slightly modified the effect of the presence of crops on weed abundance and biomass. In other words, we did not observe a stronger decrease in weed abundance or biomass when using N fertilizer and weed control in the presence of crop plants. Consequently, the crop competition alone was a stronger driver in reducing weed abundance and biomass than the environmental filtering associated with N fertilizer and weed control. Although our results were obtained on experimental plots in arable fields, the relatively low impact of N fertilizer and weed control on the weed assemblage opens new horizons for designing cropping systems less dependent on nitrogen inputs and intensive weed control in winter cereal crops. This inconsistency may result from the much smaller weed seed bank in the arable fields nowadays, especially for conventional herbicide-based systems (Marshall et al. 2003), compared to the larger weed seed banks present in the nineteen eighties, when the recommendations for these practices were originally formulated. Our results bring important insights both for agroecology and for ecology, by revealing the preponderant effect of biotic interactions over abiotic factors in crop–weed competition. Further experiments need to be performed in other regions with the same and other crops, and by considering the separate effects of fertilizers and weed control on crop–weed competition using a factorial design in addition to our approach.

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Data Accessibility

The data supporting the results will be archived in an appropriate public repository such as Dryad, and the data are available upon request from the corresponding author.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2413/full