# Direct seeding associated with a mixture of winter cover crops decreases weed abundance while increasing cash-crop yields

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# Winter cover crops decrease the abundance of weeds while increasing cash-crop yields

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**Abstract**

In this study, we aim to evaluate the respective and combined effect of soil tillage reduction and winter cover crops (CCs) on both weed species recruitment and sunflower (*Helianthus annuus*) yields. By controlling the species composition and propagule pressure of weeds, we tested four soil cover rotation treatments with winter CCs (either *Camelina sativa* or a winter CC-mix of Leguminosae-Brassicaceae) or nothing (control) followed by a sunflower culture or nothing (control) in combination with two soil preparation treatments (reduced tillage *vs*. direct seeding) in a randomized complete block design with three replicates per treatment. Our experiment thus comprised 24 experimental units (4 m × 1 m). In each experimental unit, seeds of 40 weed species were sown in May 2017 and seedling emergence was subsequently monitored in mid-July, August and September 2017. We used generalized linear models to analyze the effect of soil cover rotation, soil preparation and the two-way interaction term on species richness, abundance (i.e. number of individuals), and sunflower yield. We additionally used linear mixed-effects models to analyze species relative abundance changes throughout the monitoring period and relative to an exhaustive vegetation survey performed at the beginning of the experiment. Our results show that reduced tillage may increase weed species richness under some circumstances, as well as the abundance of two annual species (i.e. *Viola arvensis* and *Fumaria officinalis*). Winter CC-mix reduces the abundance of the most dominant weed species (i.e. the grass *Echinochloa crus-galli*) while increasing the average weight of sunflower seeds per stem. Irrespective of the tillage treatment, we found that *C. sativa* favors the presence of patrimonial weed species at the expense of noxious species. We conclude that direct seeding associated with winter CC-mix allows controlling weed abundance while increasing cash-crop yields, and thus meets criteria for a sustainable agriculture.

**Keywords:** *agricultural practices, weed community, reduced tillage, permanent plant cover, Camelina sativa.*

## 1. Introduction

A considerable increase in food production has been achieved since WWII by using monocultures of high-yielding crop varieties, high amount of fertilizers and pesticides, and increased consumption of fossil fuel, water and topsoil compared with the situation prevailing before WWII (Tilman, 1999). Agriculture intensification, however, led to unprecedented rates of environmental degradation, including soil, air and water pollution, soil erosion, and biodiversity loss (Galloway et al., 2008; Robinson and Sutherland, 2002; Stoate et al., 2001). In particular, arable plant species (weeds) dramatically declined in many rural landscapes over the last few decades (Firbank, 2008; Rich and Woodruff, 1996; Storkey et al., 2013; Sutcliffe and Kay, 2000). Weeds not only represent an important part of plant biodiversity in otherwise highly managed farmlands, but also have cultural and aesthetic values (Swift et al., 2004). They also deliver important ecosystem services, by serving as forage for pollinators, food for granivorous rodents, birds and insects, as well as shelter for auxiliary arthropods (Isaacs et al., 2009; Marshall et al., 2003).

Making agriculture more sustainable and reducing its negative impacts on ecosystem integrity and human health, while maintaining or increasing yields, is thus challenging for the 21st century (Fedoroff et al., 2010). This is the rationale behind conservation agriculture, a system of agronomic practices that include tillage reduction, permanent soil cover, and crop rotations (Hobbs, 2007; Nichols et al., 2015; Palm et al., 2014). However, reduced tillage is hardly adopted by farmers since it is believed to increase weed infestation, which in turn can be responsible for decreased crop yields (Belz, 2007; Einhellig, 1996). Empirical evidence for this statement is inconstant and crop-specific (Armengot et al., 2015; Légère et al., 2013) and it is likely that a threshold in weed abundance must be passed before effective yield declines (Armengot et al., 2015; Sans et al., 2011). Most weeds are annual species which are adapted to cyclic soil disturbances and cropping (Gaba et al., 2017), and hence are r-strategists (Grime,

2006) with a short life cycle, high fecundity and fertility, and dense soil seed banks (Bakker et al., 1996; Grime, 1998). The seed bank is the main source of weed occurrence in crops (Cavers and Benoit, 1989) and inversion tillage system is considered to reduce both seed bank density and recruitment from the seed bank (Nichols et al., 2015).

There is thus a balanced trade-off to be found between the preservation of weed diversity and maintenance of crop yields. The use of cover crops (CCs) has been suggested an efficient mean of suppressing weed emergence in reduced till systems (Baraibar et al., 2018; Kunz et al., 2016; Rueda-Ayala et al., 2015; Teasdale et al., 2007), through direct competition for space and resources or the release of allelochemicals (Björkman et al., 2015; Finney et al., 2015). The suppression of certain competitively dominant weed species might release other weed species from competitive exclusion, thereby increasing weed species diversity while increasing yields of the cash crop (Clements et al., 1994; Radicetti et al., 2013), but this hypothesis has not been tested so far.

The common practice is to use winter CC between two cash crops, with residues retained on the ground (Mirsky et al., 2011; Teasdale and Mirsky, 2015). It has been suggested that a mixture of CC species (e.g. grasses and Leguminosae) is more weed suppressive than a monoculture (Baraibar et al., 2018; Lawson et al., 2015) due to functional complementarity (Hooper et al., 2005; Loreau et al., 2001) and thus greater CC biomass (Baraibar et al., 2018; Lawson et al., 2015). However, empirical support is still limited and CC impacts on weed communities likely depend upon CC types, sowing and mulching dates, and cash crop type (Alonso-Ayuso et al., 2018; Buchanan et al., 2016; Campiglia et al., 2012). An overlooked alternative is the insertion of a spring or summer short-cycle cash crop between two main crops, allowing the harvest of three cash crops over two years. Several candidate species can be found in the *Brassicaceae* family, which can be cultivated as oil seed plants and are also well documented for their allelopathic effects on weed germination (Haramoto and Gallandt, 2005;

Petersen et al., 2001). However, the efficacy of this alternative in controlling weeds has been poorly documented so far. Here we aim at contributing to fill this gap of knowledge.

Assessing the impact of cropping systems on weed community diversity is not a trivial task. Available studies usually used an experimental design where cash crops and CCs were controlled in a randomized complete block design (Alonso-Ayuso et al., 2018; Baraibar et al., 2018) but without controlling for local and proximal weed species pools. Such study designs assume that the distribution of weed species is more or less homogeneous both aboveground (i.e. standing individuals and seed rain) and belowground (i.e. soil seed bank). This is obviously an unrealistic assumption, especially in reduced tillage systems. Seeds exhibit highly clustered spatial patterns, both as seed rain and belowground (Dessaint et al., 1991; Plue and Hermy, 2012), due to the already patchy distribution of mother plants, itself associated with the spatial heterogeneity of the environment (Plue and Hermy, 2012). Consequently, the fundamental assumption of the independence of observations underlying most statistical analyses is likely violated. Spatial autocorrelation at the plot scale must thus be compensated for (Fortin et al., 1990) or, alternatively, should be overcome by using an adequate study design. Here, we retained the latter option, by controlling for the seed input (i.e. species composition and number of seeds per species).

The objective of this study is to evaluate the respective and combined effect of soil preparation (reduced tillage *vs*. direct seeding) and CCs (two different CCs *vs*. no CC) on weed species recruitment and yields in following sunflower cultures. For this purpose, we implemented a controlled field experiment using a randomized block design, with barley-sunflower-wheat as principal cash crop rotation and either a functionally diverse mixture – including Leguminosae and Brassicaceae – or a *Camelina sativa* harvested cash crop as winter CC inserted between barley and sunflower. Here, we assume that direct seeding of winter CC, either throughout the diversity-complementarity hypothesis or via the allopathic effect of *C.*

*sativa*, is likely to suppress the most dominant and competitive weed species while increasing weed species richness and sunflower yields.

## 2. Materials and Methods

### *2.1. Study site and experimental design*

We conducted our experiment in an arable field located in North France (Sorrus; latitude: 50.463208°; longitude: 1.748206°; altitude 40 m) (Fig. 1A) (Appendix A). The climate is oceanic, characterized by a mean annual precipitation of 872 mm and a mean annual temperature of 10.8 °C. Monthly precipitation are regularly distributed throughout the year and mean temperature ranges from 4.7 °C (January) to 17.6 °C (August). The experiment was installed on a plateau, where the substrate consists of Quaternary loess with a high proportion of sand (ca. 50%), onto which luvisols have developed. Prior to the experiment, soil pH, C and N content were 6.5, 9.43 g $kg^{-1}$ and 0.91 g $kg^{-1}$ on average, respectively. The regional landscape is dominated by croplands, intensively cultivated for cereals, rapeseed and sugar beet. Prior to the experiment, the field was cultivated with direct seeding farming practices since 15 years.

We used a randomized complete block design (Figs. 1B and 1C) with three blocks (3 replicates), and two factor variables (see (i) and (ii) listed bellow) with two and four levels of treatments, respectively, hence making 8 different combinations of treatments repeated 3 times ($N$ = 24 plots of 12 m × 8 m, with a buffer zone of 1 m between two plots).

(i) Soil preparation treatments (2 levels corresponding to 2 tillage treatments). We compared “reduced tillage” with a non-inversion method (using a Chisel plough) *vs*. “no tillage”, also refereed as “direct seeding”.

(ii) Soil cover rotation treatments (4 levels corresponding to 4 scenarios). The first scenario was *Camelina* (*Camelina sativa*) as a short-cycle cash crop followed by sunflower (*Helianthus annuus*) to test the potential allelopathic effect of *Camelina* on weed recruitment. The second scenario was an intercropping with a functionally diverse and complementary mixture of CCs (*Raphanus sativus* var. *longipinnatus*: 2 kg $ha^{-1}$, *Fagopyrum esculentum*: 6 kg $ha^{-1}$, *Trifolium michelianum*: 3.5 kg $ha^{-1}$, *Trifolium pratense*: 2.5 kg $ha^{-1}$ and *Trifolium* *hybridum*: 2.5 kg ha$^{-1}$) followed by sunflower to test the diversity-complementarity hypothesis on weed recruitment. The third scenario was nothing during winter followed by sunflower, which is the conventional rotation. Finally, the fourth scenario was nothing all the time, i.e. the control treatment.

*2.2. Site preparation*

Chisel plowing was applied on 21st July 2016, just after the previous barley crop was harvested, across 12 out of the 24 experimental plots. On the same day, the winter CC was sown (i.e. CC-mix and *Camelina*) in half of the studied plots (see Fig. 1C for details on plot location across the experimental site). Nitrogen fertilizer (ammonium nitrate, $NH_4NO_3$) was applied at a rate of 80 kg.ha$^{-1}$ to all the plots through the fertilizer hopper on 8th August 2016. In the first two weeks of April 2017, *Camelina* seeds were harvested and the cover crop residue (i.e. the whole biomass for CC-mix, but only the vegetative part of the plant for *Camelina*) was grinded in all CC plots and left decaying on the ground, except in the reduced tillage treatment, where deep ripping and power harrowing were performed. The amount of C and N returned to the soil was measured at 1399.0 and 25.3 kg ha$^{-1}$ in *Camelina* plots and 3844.2 and 236.5 kg ha$^{-1}$ in CC-mix, respectively. On the same day, glyphosate (Round-up®) and anti-slug treatments were applied over the 24 plots. No weed species showed resistance against glyphosate in the study plots. On 28th April 2017, sunflower (cash crop) was sown in its corresponding plots and, on the next day, herbicide (Prowl400®: 400 g L$^{-1}$ pendimethaline) was applied over the 24 plots. On 14th June 2017, another round of nitrogen fertilizer ($NH_4NO_3$) was applied at a rate of 70-80 kg ha$^{-1}$ to all plots. All details concerning the planning of events to ensure site preparation are presented in the timeline in Appendix A.

*2.3. Seed preparation*

We had chosen 40 weed species (Appendix B) to cover a large spectrum of life forms (grass *vs*. forbs) and plant traits such as life span (annuals *vs*. perennials), canopy height and dispersal strategy (e.g. gravity-, wind-, bird-, ant-dispersed). Seeds were collected from wild plants growing in regional cultivated lands to ensure a local provenance, except for three species (*Cyanus segetum, Coriandrum sativum* and *Reseda lutea*) for which we used commercial seeds. The total number of seeds available for each of the 40 species was divided into 27 equal portions (24 portions for the experimental site and 3 portions for greenhouse germination tests) (see Appendix B for more details on propagule pressure). Then, we pooled each portion of the 40 species into a single mixture to get one mixture for each of the 27 experimental units. By doing so, we ensured a similar composition and propagule pressure across the experimental sites and for the germination test. On 18th May 2017, the seed mixture was sown in each of 24 subplots (1 m × 4 m) that were disposed inside each 12 m × 8 m experimental plots to avoid edge effects (Fig. 1B). When present, the resident weeds were removed prior to sowing. Each subplot was protected with a porous net during one month to avoid seed predation by birds and small rodents. The next day, we settled the greenhouse experiment in triplicate (3 mixtures of seeds) using the same seed mixture. Seeds were spread over steam-sterilized compost-filled containers and allowed to germinate under a natural light regime and a temperature regime ranging from 25 / 20 °C day / night. The containers were kept moist by regular watering. Three control containers containing only steam-sterilized compost were distributed among the other containers to detect eventual contamination. No contamination was detected. We monitored seedling emergence to determine seed viability. All seedlings were identified, counted and removed at weekly intervals from May 2017 until June 2018.

### *2.4. Vegetation survey and data collection*

On 4th July 2017, we performed an exhaustive vegetation survey across each of the 24 experimental plots to record the species-specific percentage cover of all vascular plant species co-occurring at the plot level. It allowed us to get the complete picture of the local species assemblages before we started to collect data on weed species. From the exhaustive vegetation survey, we ranked each of the studied weed species from the most to the least abundant within a given plot. This initial ranking of weed species was used as a common and independent reference point to subsequently analyze the changes in weed species' relative abundance over the monitoring period: from mid-July to September (see section 2.5.3). Indeed, we monitored each of the 40 studied weed species in each subplot at 3 dates throughout the vegetation season (17th July, 29th August, 26th September). More specifically, we counted the total number of individuals per weed species. For highly abundant species (i.e. *Echinochloa crus-galli*, *Poa annua*, *Senecio vulgaris* and *Viola arvensis*), we randomly put a 14.5 cm × 23 cm wooden frame on the ground and counted the total number of individuals occurring within that frame before multiplying it by the total number of frames we could arrange to estimate the area covered by the species across the subplot.

On 26th September 2017, following the last vegetation survey, we randomly collected 10 sunflower individuals from an area of 1 $m^2$ within each of the 24 studied subplots (240 individuals in total). Each of the 240 harvested individuals was measured for plant canopy height prior to harvest. Back from the field, sunflower seeds were separated from their corresponding stem before being weighted and counted separately for each of the 240 individuals.

*2.5. Data analysis*

Based on our full factorial experimental design, we aim at testing the respective pure effects of soil preparation (reduced tillage *vs*. direct seeding) and soil cover rotation (*Camelina* / sunflower, CC-mix / sunflower, nothing / sunflower, nothing / nothing) as well as the two-way interaction effect between both variables on: (1) weed species richness in July, August and September (i.e. the total number of weed species out of the 40 studied species that germinated per subplot); (2) weed total and species-specific abundance in July, August and September (i.e. the total number of individuals across all weed species co-occurring in a given subplot as well as the species-specific total number of individuals per subplot); (3) weed species' relative abundance changes between the exhaustive vegetation survey from early July and the three subsequent weed monitoring surveys performed in mid-July, August and September (i.e. the change in the rank value of a given weed species according to its total abundance in the subplot and relatively to the total abundance of the other co-occurring species); and (4) sunflower yield at the end of the experiment (i.e. sunflower height average weight of seeds per stem inside a given subplot).

*2.5.1. Species richness*

Here, the response variable is species richness per subplot (count data: one richness value per subplot). Hence, we used the "glm" function from the "stats" package to fit generalized linear models (GLMs) with a Poisson distribution. We built a list of candidate models including, as predictor variables, soil preparation or soil cover rotation or both simultaneously (see Appendix C for the full list). In addition to these two variables of main interest for the study, some of the candidate models included "block" (B1, B2, B3) and "date" (17th July, 29th August, 26th September) as covariates to account for potential confounding effects. All possible two-way interaction terms involving soil preparation or soil cover rotation were tested. For each candidate model, we computed the Akaike Information Criterion (AIC) and ranked all models according to their AIC values, with the best model being the one with the lowest AIC value (Burnham and Anderson, 2002). Once the best candidate model was selected, we extracted the coefficient estimates, standard errors and associated p-values for each of the predictor variables listed in the best model. Finally, we ran an Analysis of Variance (ANOVA) of the best model, using Type-II or Type-III ANOVA depending on whether there was a non-significant or a significant interaction term, respectively. We used the "ANOVA" function from the "car" package in R.

*2.5.2. Species' abundance*

Here, the response variable is multivariate with the individual species abundance by subplot matrix being the matrix of response variables (zero-inflated distribution: several species abundance values, including many zeros, per subplot). Hence, we used a modelling approach very similar to the GLM approach with a negative binomial distribution but adapted to high-dimensional data, such as multivariate abundance data in ecology (cf. the species × subplot matrix of abundance values) (Wang et al., 2012). Similar to our analyses on species richness, we tested the same list of candidate models (Appendix C) using the same model selection procedure as above but running the "manyglm" function from the "mvabund" package in R (Wang et al., 2012). Once the best candidate model was selected, we extracted the global statistics across all species as well as species-specific statistics such as the coefficient estimates of all the species individually to study their corresponding behavior according to the predictor variables listed in the best model. We used the "anova.manyglm" function from the "mvabund" package to generate an analysis of deviance table for the best candidate model.

### *2.5.3. Changes in species' relative abundance*

For each monitoring period (late July, August, September), we ranked weed species according to their abundance values in the subplot, from the most to the least abundant, similar to the ranking we performed for the initial exhaustive vegetation survey in the rest of the plot (early July). In case of absence of one or several of the species in any of the subplots and at any dates, we ranked these species after the least abundant species. Then, we computed for each species separately, the differences in their rank value between a given monitoring period and the initial exhaustive vegetation survey (i.e. reference point), leading to three rank difference values per species and per subplot. Using each of these values as the response variable, we ran linear mixed-effects models (LMMs) with a Poisson distribution (similar to count data). We used soil preparation, soil cover rotation and block as the three fixed effect variables in the model and set species as a random variable interacting with both soil preparation and soil cover rotation (random slope terms) in the model. Because the three rank differences per species and per subplot are not independent from each other (same reference point each time), we ran our single candidate model three times. Finally, we extracted, for each species, the estimated mean and 95% confidence interval of the rank difference.

*2.5.4. Crop growth and yield*

Crop yield was quantified by measuring both sunflower height (height of 10 random sunflower plants per 4 $m^2$ subplot) and the average weight of seeds per stem (g). Both sunflower height and weight of seeds per stem were treated as response variables in GLMs with a Gaussian distribution. We tested the same list of candidate models (Appendix C) and used the same approach for model selection as we did for analyzing species richness and species absolute abundance.

All statistical analysis were performed using the “car”, “ggplot2”, “gridExtra”, “lme4”, “Matrix”, “MuMIn”, “mvabund”, “nlme”, “reshape2” and “stats” packages in the R software environment version 3.4.1 (R Core Team 2017).

## 3. Results

A total of 40 weed species were monitored in both field and greenhouse over the study period. Twenty-eight species germinated in the greenhouse while 35 species germinated in the field (see Appendix D for details on species germination success) regardless of both the soil preparation and soil cover rotation. The majority of these species were characterized by autumn germination and early spring flowering. *Poa annua* and *Echinochloa crus-galli* were the most abundant species across all treatments studied (see Appendix E for detailed information about species richness and species total abundance). These species (*Poa annua* and *Echinochloa crus-galli*) were highly abundant in the field, likely due to their presence and persistence in the soil seed bank.

### *3.1. Species richness*

The best candidate model to explain weed species richness includes soil cover rotation, date, and the interaction between block and soil preparation (see M24 in Appendix C for the complete model formula). We found a significant interaction effect between block and soil preparation on weed species richness (Table 1 and Table 2), such that reduced tillage had a negative impact on weed species richness in block 3 but a positive impact in blocks 1 and 2 (Table 1). We found no effect of soil cover rotation on weed species richness.

### *3.2. Species abundance*

Similarly to the analyses on species richness, the best candidate model to explain the overall abundance (number of individuals) of weed within the subplots includes soil cover rotation, date, and the interaction between block and soil preparation (see candidate model M24 in Appendix C for the complete model formula). Yet, the interaction term between block and soil preparation was not significant this time. We found that the overall abundance of weed, irrespectively of the species considered, was higher (Table 3): during July than during August; when there was no soil cover rotation (nothing / nothing) than when *Camelina* was used in intercropping followed by sunflower; under reduced tillage than under direct seeding; and in block 3 than in block 1 (see Appendix F for the effect of block and date on the most abundant weed species). In addition, further analyses at the species level (Table 4) showed that the abundance of some weed species are clearly affected by both soil cover rotation and soil preparation (see Appendix G for more details about all the studied species). For instance, the abundance of both *Viola arvensis* and *Fumaria officinalis* increased under reduced tillage (Fig. 2A and Table 4, respectively) while the abundance of the most dominant weed species, i.e. *Echinochloa crus-galli*, decreased when using a CC-mix in intercropping followed by sunflower (Table 4).

*3.3. Changes in species' relative abundance (species rank difference)*

Irrespective of soil preparation (reduced tillage *vs*. direct seeding), using *Camelina* as a winter CC before sunflower had important effects on the ranking of weed species abundance over time relative to the control and conventional treatments which had no effect (Fig. 3). For instance, some perennial species in particular (*Artemisia vulgaris, Plantago lanceolata*) were clearly positively impacted by *Camelina* at all dates, as well as several annual species (e.g. *Coriandrum sativum*, *Centaurea cyanus, Poa annua, Matricaria chamomilla*) in July and August. At the same time, *Camelina* had a negative impact on the relative abundance of the geophyte *Cirsium arvense*, as well as of several annuals (e.g. *Persicaria maculosa*, *Chenopodium album, Senecio vulgaris, Capsella bursa-pastoris, Atriplex patula*). Noteworthy, *Cyanus segetum* and *Coriandrum sativum* are patrimonial species (i.e. rare species, usually on the red list of threatened species, with a scientific, symbolic or cultural value) while *Cirsium arvense* is a noxious weed. Using CC-mix as winter cover before sunflower only had a marginal effect on the ranking of weed species abundance during July favouring the relative abundance of some species like *Artemisia vulgaris*, *Coriandrum sativum,* and *Centaurea cyanus* under direct seeding treatment but decreasing the relative abundance of the same species under reduced tillage treatment (see Fig. 3). The opposite was true for *Perisicaria maculosa* (see Appendix H for relative abundance of the studied weed species).

*3.4. Crop yield*

The best candidate model to explain sunflower height and the average weight of seeds per stem (Appendix I) includes block, soil cover rotation and soil preparation as predictor variables (see candidate model M13 in Appendix C for the complete model formula). None of the variables were significant in explaining sunflower height but the average weight of seeds per stem was significantly higher in block 3 than in block 1 and when CC-mix were used in intercropping (Table 5).

## 4. Discussion

In this study, we test the relative importance of soil preparation and winter CCs in explaining weed community dynamics over a single season (i.e. richness, abundance, and change in relative abundance). We evidence that winter CC suppresses the most dominant weed species (e.g. *Echinochloa crus-galli*), especially when using a Leguminosae-Brassicaceae mixture as CC. Winter CC does not impact weed species richness, while soil preparation (i.e. reduced tillage *vs*. direct seeding) has complex effects. Interestingly, the use of winter CC-mix was associated with increased cash-crop yield, in contrast with *Camelina*. Below, we discuss these main results in details.

### *4.1.Impact of soil preparation*

Soil preparation, not CCs, impacts weed species richness with reduced tillage interacting with experimental block to increase species richness in two of the three blocks, as compared to direct seeding treatment, while the reverse was found in the third block. The effect of soil preparation on weed species richness is still debated. Reduced tillage has been shown to increase the number of weed species (Santín-Montanyá et al., 2016), but this effect likely depends upon crop rotation (Legere et al., 2005; Stevenson et al., 1998). Compared to conventional tillage (i.e. inversion tillage; Clements et al., 1994) and direct seeding (Kraska, 2012; Plaza et al., 2015), reduced tillage appeared less detrimental to weed species diversity, by providing safe sites for weed establishment. However, in contrast with our findings, other studies have found no increase in weed species richness in reduced tillage systems when compared to other soil preparation treatments (i.e. direct seeding and conventional tillage; Barroso et al., 2015; Bilalis et al., 2001). The 3-years study of Barroso et al. (2015) assessed the effect of two different cropping systems (*Medicago sativa* and *Triticum aestivum*) under three different soil preparations (herbicide, tillage and reduced tillage) and showed no significant impact of soil preparation on both weed species diversity and abundance. Mas and Verdú (2003) showed that during a 4-years study of three different crops (*Pisum sativum*, *Triticum aestivum* and *Hordeum vulgare*), direct seeding system recorded the highest weed diversity as compared with other tillage systems (i.e. conventional tillage). Noteworthy, the previously mentioned studies (Barroso et al., 2015; Mas and Verdú, 2003) are considered long-term studies unlike our study which was a short-term assessment (single season), underpinning the importance of the study duration in explaining the significant effect of soil preparation on weed community assembly. It has been argued however, that there is no clear increase or decrease of weed diversity with the change of tillage practices alone (Barroso et al., 2015). This suggests that the interaction between tillage treatment and crop rotation from one side (Legere et al., 2005; Swanton et al., 1993), and between tillage treatment with herbicide use from the other side (Locke and Bryson, 1997; Mohler, 1993), might be crucial to weed community structure. In our study, the block effect cannot be attributed to differences in interspecific competition among blocks (Grime, 1998; Huston, 1979) since the dominant grass species (*Echinochloa crus-galli*) as well as the overall abundance of all weed species were the lowest in the block where species richness was lower, irrespective of the soil treatment. Instead, the block effect may be attributed to small-scale differences in unmeasured local environmental conditions, such as soil fertility (Stevenson et al., 1997) or other abiotic factors, which can have an overriding effect on soil preparation in explaining weed species richness (Pal et al., 2013).

While reduced tillage increases the relative abundance of some annual species (e.g. *Fumaria officinalis* and *Viola arvensis*), direct seeding rather promotes perennial species (e.g. *Artemisia vulgaris*). This is highly consistent with former findings (Santín-Montanyá et al., 2018; Thomas and Frick, 1993; Travlos et al., 2018). For instance, Thomas et al. (2004) found that perennial species (e.g. *Cirsium arvense* and *Sonchus arvensis*) tend to dominate in direct seeding systems while annual species (e.g. *Setaria viridis*) are associated with a range of tillage systems: from intensive conventional tillage to direct seeding systems. Similarly, Bilalis et al.,

(2001) showed that the abundance of annual species (e.g. *Stellaria media*) is high in conventional and reduced tillage systems, while perennials (e.g. *Malva sp.*) increase their abundance under direct seeding system. It has been suggested that the proportion of perennial weeds increases as tillage is gradually reduced from conventional tillage to direct seeding, since most annuals are adapted to cyclic soil disturbances (Gaba et al., 2017), and mostly recruit from soil seed banks (Auskalniene et al., 2018; Shaukat and Siddiqui, 2004). Another explanation would be that herbicides are more effective against annuals than against perennials (Derr, 1994), and the use of reduced tillage systems (or even conventional tillage) may help in managing herbicide-resistant weeds that may characterize direct seeding systems (i.e. perennials); this is considered one of the emerging challenges especially in cereal cropping systems (Thomas et al., 2007). However, our results support the hypothesis of a species-specific response to soil preparation, as previously suggested by several studies (Blackshaw, 2004; Derksen et al., 1993; Tuesca et al., 2001). The weak difference between reduced tillage and direct seeding in our study can also be explained by the fact that even the direct seeding system experiences cyclic soil disturbances at the time of harvesting, so that the soil disturbance regime may not strongly differ between the two systems (Mohler et al., 2001).

### *4.2. Impact of cover crops*

It is noteworthy that the use of *Camelina* as winter CC increases the relative abundance of several patrimonial species (e.g. *Coriandrum sativum*) at the expense of certain noxious species (e.g. *Cirsium arvense*), irrespectively to the type of soil preparation. *Camelina* impacts the relative abundance of weed species in a way which is independent from the biological type. Some perennials (e.g. *Artemisia vulgaris*) as well as some annuals (e.g. *Matricaria recutita*) are favored by *Camelina*, while some other perennials (e.g. *Cirsium arvense*) and annuals (e.g. *Atriplex patula*) are suppressed (see Fig. 3).

In comparison, the winter CC-mix (Leguminosae-Brassicaceae) has a weak effect on the relative abundance of weed species, which further depends upon soil preparation. For example, *Coriandrum sativum* is favored in direct seeding plots only, while *Persicaria maculosa* is favored in reduced tillage plots only. This is consistent with several studies, where CCs were associated with lower weed abundances (i.e. higher soil fertility) (Drinkwater et al., 1998; Plaza et al., 2015; Teasdale, 1996), though this suppressive effect is likely species-specific (Creamer et al., 1996) and soil preparation-dependent (Shrestha et al., 2002). Winter CCs are thought to exert a physical barrier against upward seedling growth since they have a head start over weeds that allows them to pre-empt space and resources before weeds and thus to outcompete them and ultimately to prevent the soil seed bank from replenishment (Lawley et al., 2012; Weber et al., 2017). Even after grinding, the resulting CC mulch still forms a physical barrier against seed germination. *Camelina* is believed to further impact weed germination via allelopathic effects, especially towards annual species (Leather, 1983; Massantini et al., 1977).

In contrast with *Camelina* as a winter CC, the Leguminosae-Brassicaceae CC increases both weed diversity and yields of the cash crop (as measured via mean seed mass per stem of sunflower). These positive effects may be attributed to the Leguminosae species which are well-documented for supplying nitrogen via their $N_2$-fixing symbiotic bacteria (Mazzoncini et al., 2011; Rangel et al., 2017), increasing soil organic matter (Raphael et al., 2016), reducing soil compaction and erosion (Baumhardt et al., 2015), improving the C:N ratio associated with microbial community (Frasier et al., 2016) and breaking up pest and disease cycles (Flint, 2018). This is supported by the higher amount of C and N returning to the soil with CC-mix than with *Camelina* (3844.2 vs 1399.0 and 236.5 vs 25.3 kg $ha^{-1}$ for C and N, respectively; see *Site preparation* section) and consistent with earlier findings which show a CC-induced increase of crop yield when Leguminosae are included (Snapp et al., 2005; Tonitto et al., 2006), while *Camelina* is associated with lower crop yields (Gesch and Archer, 2013; Johnson et al., 2017).

### 4.3. Concluding remarks

Our study clearly shows that winter Leguminosous-Brassicaceae CC intercrop combined with direct seeding ensures higher weed diversity and sunflower yields than with reduced tillage or other soil cover types. On the other hand, *Camelina* as a monospecific winter CC ensures selective weed control towards less noxious weeds but more patrimonial, non-problematic weeds. As a CC, *Camelina* has the potential to allow reducing herbicide application (Crowley, 1999; Crowley and Fröhlich, 1998). Its weak detrimental effect on sunflower yield is likely compensated by the fact that, as an oil seed plant, *Camelina* represents a second cash crop whose seeds have a high economic added value (Keske et al., 2013).

Both types of rotation thus meet the criteria of a sustainable agriculture. However, further work is needed to make sure that these results hold true on the long-term and to assess whether they can be retrieved for other cash crops or in other soil and climate contexts.

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**Author contributions**

G.D., F.D, J.L., A.A., and D.C.K conceived the research idea as well as the analytical framework; A.A., F.S., B.B., F.D., O.C. and F.D. collected data in the field; A.A., F.S. and J.L. performed all statistical analyses; EGM provided maps and GIS support. A.A. led the paper writing. All co-authors discussed the results, provided feedback, and commented on the initial version of the manuscript.

## Author declaration

We wish to draw the attention of the Editor to the following facts that may be considered as potential conflicts of interest and to significant financial contributions to this work. We wish to confirm that there are no known conflicts of interest associated with this publication.

We confirm that the manuscript has been read and approved by all named authors and there are no other persons who satisfied the criteria for authorship but are not listed. We further confirm that all of us have approved the order of authors listed in the manuscript.

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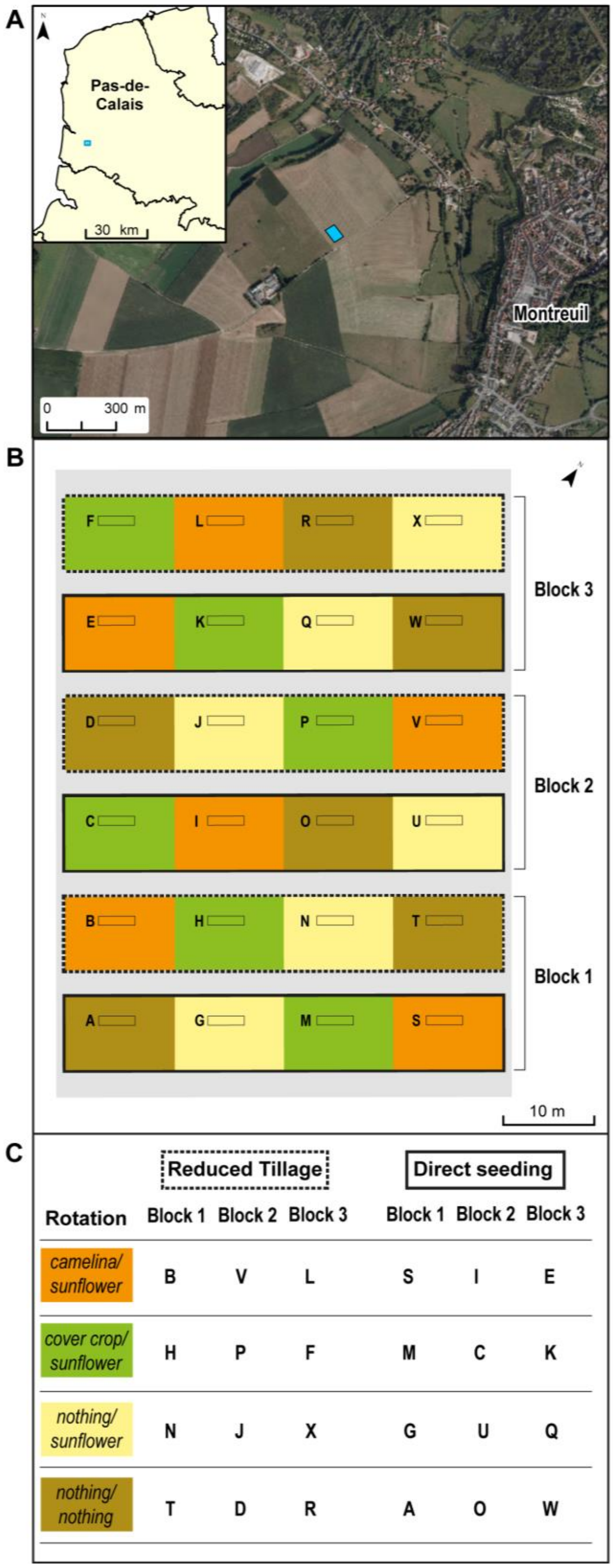


**Figure 1:** Experimental site (A), where the field was organized in a randomized block design (B) with 3 repetitions for every treatment (C) in studying the effect of two different soil preparations (reduced tillage vs direct seeding) and four different soil cover rotations on weed community.

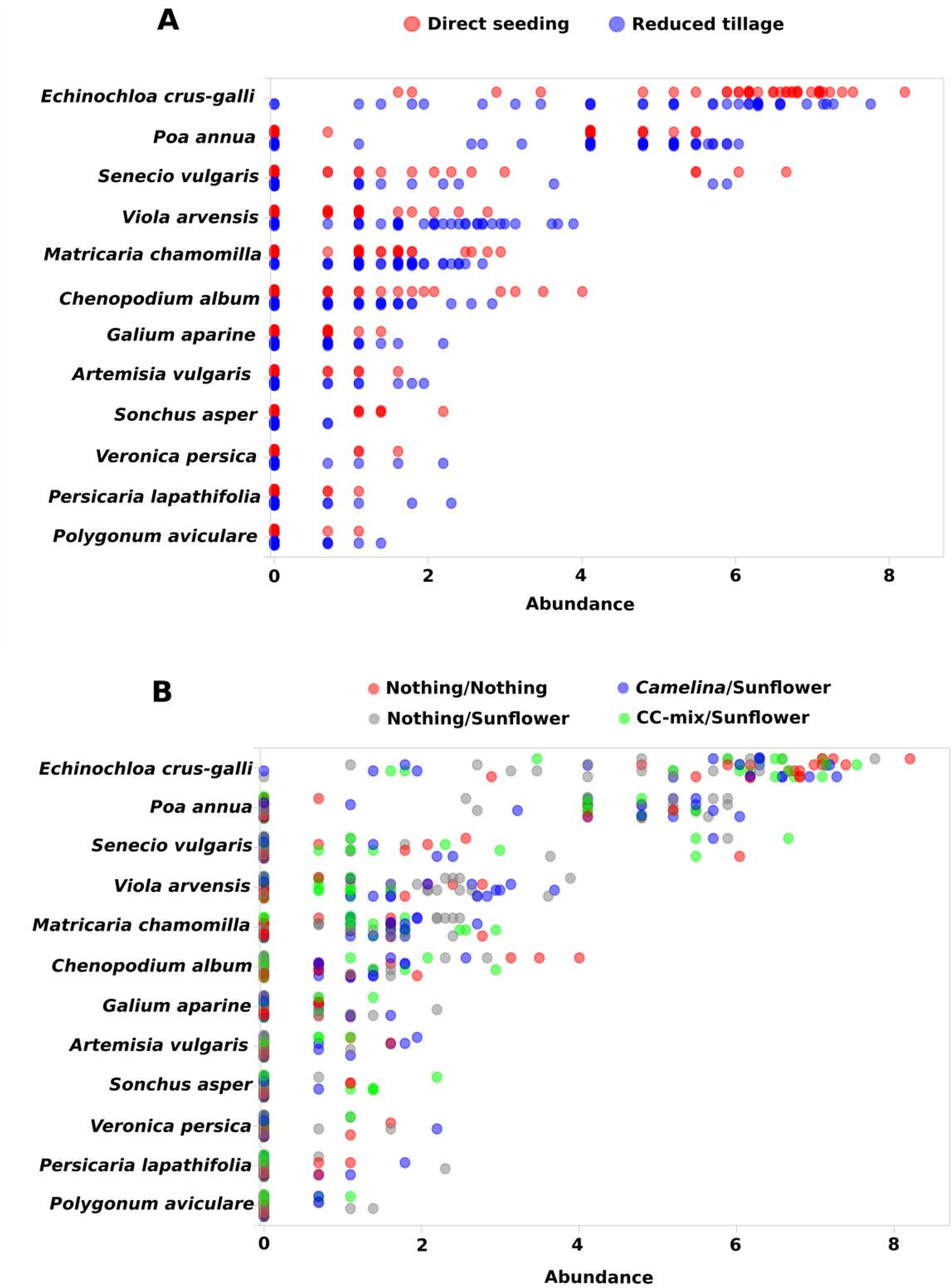


**Figure 2:** Abundance of weed species according to (A) the difference in soil preparation (reduced tillage vs. direct seeding treatments) and (B) the different soil cover rotation (4 levels). Only the most abundant species are presented.

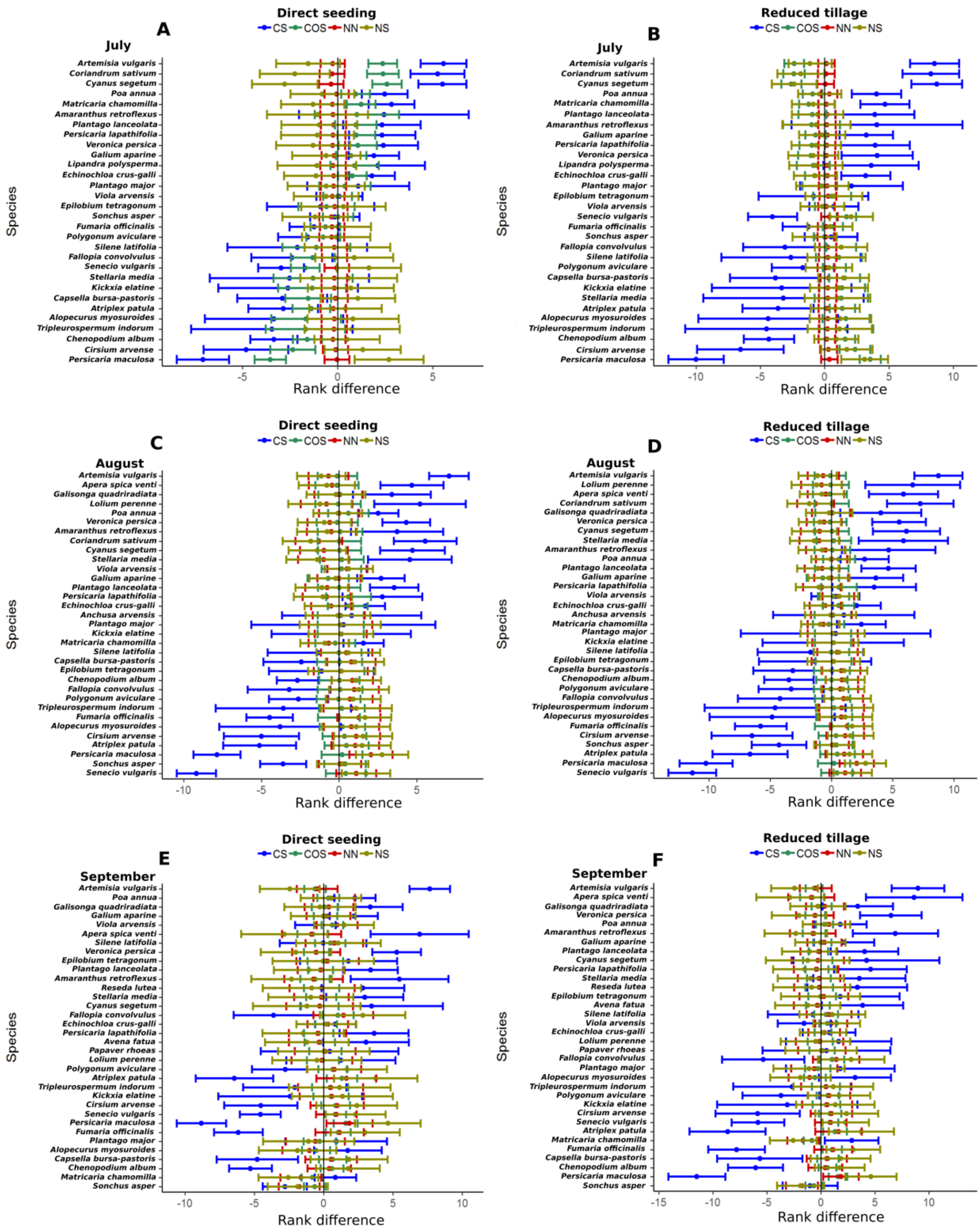


**Figure 3:** Estimated mean and 95% confidence interval of the rank difference values from the model used (see section 2.5.3 in materials and methods) at 3 different dates (July - August - September) studying the relative abundance change of weed species as function of soil cover rotations (4 levels) and soil preparation (reduced tillage vs direct seeding). CS corresponds to *Camelina* and sunflower rotation. COS corresponds to CC-mix with sunflower rotation. NN

corresponds to the soil left without both winter and summer covers. NS corresponds to soil left in winter and cultivated with sunflower as summer crop. Species are oriented along the vertical axis according to decreasing order of the mean rank difference between treatments. Note that only the species that succeeded to germinate in either the subplots or the plots are presented along the vertical axis.

**Table 1:** Coefficient estimates from the best candidate model (see M24 in Appendix C) linking species richness to soil preparation, soil cover rotation, date and block effect. Bold values represent significant ($p<0.05$) effects. The intercept represents the average weed species richness value for block1 in July under direct seeding treatment and under the *Camelina* / sunflower rotation treatment. Estimates need to be interpreted against the intercept value. Hence, the average weed species richness value for block1 in July under reduced tillage treatment and under the *Camelina* / sunflower rotation treatment is 1.403+0.631 = 2.034.

| Effect | Estimate | Std. Error | z value | Pr(>\|z\|) |
|---|---|---|---|---|
| **(Intercept)** | 1.403 | 0.194 | 6.003 | **<0.001** |
| **block2** | -0.048 | 0.220 | -0.22 | 0.825 |
| **block3** | 0.579 | 0.192 | 3.008 | **0.002** |
| **reduced tillage** | 0.631 | 0.190 | 3.308 | **<0.001** |
| **CC-mix / sunflower** | 0.020 | 0.142 | 0.142 | 0.886 |
| **nothing / nothing** | 0.060 | 0.141 | 0.424 | 0.671 |
| **nothing / sunflower** | -0.218 | 0.152 | -1.43 | 0.151 |
| **August** | -0.237 | 0.126 | -1.87 | 0.060 |
| **September** | 0.093 | 0.130 | 0.717 | 0.473 |
| **block2: reduced tillage** | -0.030 | 0.274 | -0.11 | 0.912 |
| **block3: reduced tillage** | -0.729 | 0.253 | -2.87 | **0.004** |

**Table 2:** Output of Type III ANOVA representing the best candidate model (M24 in Appendix C) studying species richness with the change of soil preparation, soil cover rotation, date and block. Bold values represent significant ($p<0.05$) effects. The intercept represents the average weed species richness value under direct seeding treatment and the interaction with rotation, block and date variables.

| | **Sum Sq[1]** | **[2]Df** | **F value** | **p value** |
|---|---|---|---|---|
| **(Intercept)** | 471 | 1 | 122,5 | **<0,001** |
| **rotation** | 21 | 3 | 1,79 | 0,1595 |
| **reduced tillage** | 55 | 1 | 14,33 | **<0,001** |
| **block** | 20 | 2 | 2,61 | 0,0814 |
| **date** | 19 | 2 | 2,50 | 0,0909 |
| **reduced tillage:block** | 49 | 2 | 6,41 | **0,0029[3]** |

[1] Sum of squares or the total variance of the dataset.
[2] Degree of freedom

**Table 3:** Overall statistics of the best candidate model selected (see M24 in Appendix C for the model formula) to study the impacts of soil preparation, soil cover rotation, date and block on weed species abundance (outcomes of the “manyglm” function from the “mvabund” package). Bold values represent significant ($p<0.05$) effects across all 40 studied weed species. Coefficient estimates are available at the species level (see Table 4 and Appendix G). Wald value in “mvabund” estimates the covariance matrix of parameter estimates using a sandwich-type estimator that assumes the mean-variance relationship in the data is correctly specified and that there is an unknown but constant correlation across all observations. The intercept represents the average weed species abundance value for block1 in August under direct seeding treatment and under the Camelina / sunflower rotation treatment.

| Effect | Wald value | Pr(>wald) |
|---|---|---|
| **(Intercept)** | 20.560 | **<0.001** |
| **block2** | 3.405 | 0.212 |
| **block3** | 5.745 | **0.005** |
| **reduced tillage** | 5.824 | **0.008** |
| **CC-mix / sunflower** | 5.976 | **0.02** |
| **nothing / nothing** | 7.052 | **<0.001** |
| **nothing / sunflower** | 4.522 | 0.103 |
| **July** | 8.934 | **<0.001** |
| **September** | 5.024 | **0.047** |
| **block2:reduced tillage** | 2.538 | 0.551 |
| **block3:tillage** | 2.792 | 0.501 |

**Table 4:** Detailed statistics of the best candidate model selected (see M24 in Appendix C for the model formula) at the species level to study the impacts of soil preparation, soil cover rotation, date and block on weed species abundance individually. Bold values represent significant ($p<0.05$) effects (A) and their corresponding coefficient (B) across the five affected weed species (see Appendix G for the complete species abundance analysis). The intercept in table B represents the weed species abundance value for block1 in August under direct seeding treatment and the *Camelina* / sunflower rotation treatment.

| **A) P-Table** | ***Echinochloa crus-galli*** | ***Fumaria officinalis*** | ***Senecio vulgaris*** | ***Veronica persica*** | ***Viola arvensis*** |
|---|---|---|---|---|---|
| **block** | 0,078 | 0,986 | 0,986 | 0,974 | 0,953 |
| **reduced tillage** | 0,251 | **0,04** | 0,988 | 0,966 | **0,001** |
| **rotation** | **0,038** | 1 | 0,084 | 1 | 1 |
| **date** | 0,484 | 0,16 | **0,001** | **0,012** | 0,911 |
| **block:reduced tillage** | 0,943 | 0,997 | 0,974 | 0,417 | 0,343 |

| **B) Coefficient Table** | ***Echinochloa crus-galli*** | ***Fumaria officinalis*** | ***Senecio vulgaris*** | ***Veronica persica*** | ***Viola arvensis*** |
|---|---|---|---|---|---|
| **(Intercept)** | 7,63 | -13,61 | -5,58 | -24,95 | -0,12 |
| **block2** | -0,43 | 0 | -0,33 | 0 | 0,13 |
| **block3** | -1,48 | 0 | 1,09 | 12,61 | 2,03 |
| **reduced tillage** | -1,02 | **12,1** | -0,94 | 9,34 | **2,19** |
| **CC-mix / sunflower** | **-1,05** | -0,41 | 1,09 | 2,2 | 0,44 |
| **nothing / nothing** | **0,62** | -0,41 | 3,71 | 0,38 | -0,46 |
| **nothing / sunflower** | **0,03** | -0,41 | 2,48 | -0,59 | -0,16 |
| **July** | -0,75 | 2,08 | **7,4** | 0 | -0,87 |
| **September** | -0,5 | -9,21 | **1,32** | **13** | -0,67 |
| **block2:reduced tillage** | 0,64 | -1,79 | -0,68 | 1,97 | 0,92 |
| **block3:reduced tillage** | -0,23 | -1,1 | -0,77 | -10,86 | -1,37 |

**Table 5:** Coefficient estimates from the best candidate model (see candidate model M13 in Appendix C) linking crop yield, either measured as sunflower height (A) or as the average weight of sunflower seeds per stem (B), to soil preparation, soil cover rotation (only 3 levels here as the nothing / nothing control treatment could not be considered for crop yield) and block effect. Bold values represent significant ($p<0.05$) effects. The intercept represents the average crop yield value (height in cm or weight in g) for block1 under direct seeding treatment and the *Camelina* / sunflower rotation treatment. Estimates need to be interpreted against the intercept value. Hence, the average sunflower seed mass per stem for block3 under the CC-mix / sunflower rotation treatment is 34.7+42.1+21.9 = 98.7 g.

| | **(A) Sunflower height (cm)** | | | |
|---|---|---|---|---|
| | **Estimate** | **Std. Error** | **t value** | **Pr(>\|t\|)** |
| **(Intercept)** | 146 | 8.92 | 16.3 | **<0.001** |
| **block2** | -3.83 | 8.92 | -0.42 | 0.675 |
| **block3** | 7.66 | 8.92 | 0.85 | 0.407 |
| **CC-mix /sunflower** | -0.66 | 8.92 | -0.07 | 0.941 |
| **nothing/sunflower** | 1.99 | 8.92 | 0.22 | 0.826 |
| **reduced tillage** | 12.6 | 7.28 | 1.73 | 0.107 |
| | **(B) Weight of seeds per stem (g)** | | | |
| | **Estimate** | **Std. Error** | **t value** | **Pr(>\|t\|)** |
| **(Intercept)** | 34.7 | 9.69 | 3.58 | **<0.001** |
| **block2** | 9.89 | 9.69 | 1.02 | 0.327 |
| **block3** | 42.1 | 9.69 | 4.34 | **<0.001** |
| **CC-mix /sunflower** | 21.9 | 9.69 | 2.26 | **0.042** |
| **nothing/sunflower** | 5.08 | 9.69 | 0.52 | 0.609 |
| **reduced tillage** | 9.46 | 7.91 | 1.19 | 0.254 |

**Appendix A:** Picture **(A.1)** of the field experimental site showing the dimensions of a sample of the studied 24 plots (4 m × 1 m) and its corresponding included subplot (12 m × 8 m), in addition to the spacing between plots (1 m). The table on the next page **(A.2)** shows the timeline of the different operations in the course of the experiment. The eight treatments were replicated three times (hence three blocks).

**Appendix B:** List of the 40 weed species sown in the 24 subplots of the experiment and in the greenhouse (three replicates). Species nomenclature follows J.-M. Tison, B. de Foucault et al. 2014 Flora Gallica. Ed. Biotope 1195p.

**Appendix C:** List of candidate models together with their corresponding AIC values for the three response variables studied. Y corresponds to weed abundance or weed richness or sunflower yield (weight of seeds/stem or height).

**Appendix D:** Species germination percentage in the greenhouse versus the field. Extreme values (>100%) in the field are due to the seedbank effect. Nomenclature follows Flora Gallica (2014).

**Appendix E:** Weed species richness and total weed abundance per plot for each of the two soil preparation treatments, each of the four soil cover rotation scenarios and for each of the three block repetitions.

**Appendix F:** Abundance of each individual weed species according to the block (A) and date (B) effect. Only the most abundant weed species are displayed.

**Appendix G:** Detailed outputs of the best candidate model selected (see M24 in Appendix C for the model formula) at the species level to study the impacts of soil preparation, soil cover rotation, date and block on weed species abundance individually (outcomes of the "manyglm" function from the "mvabund" package). Bold values represent significant ($p < 0.05$) effects (A) and their corresponding coefficient estimates (B) (**Attached as an excel file for the sake of clarity**).

**Appendix H:** Impact of soil preparation, soil cover rotation, block and date on weed species relative abundance (**Attached as an excel file for the sake of clarity**).

**Appendix I:** Difference in sunflower height (A) and weight of seeds per stem (B) for different soil preparations, soil cover rotations and blocks. Abbreviations in x-axis are for the three variables. CSN corresponds to *Camelina* and sunflower rotation without tillage (i.e. direct seeding). CST corresponds to *Camelina* and sunflower rotation with reduced tillage. COSN corresponds to CC-mix with sunflower rotation without tillage (i.e. direct seeding). COST corresponds to CC-mix with sunflower rotation with reduced tillage. NNN corresponds to the soil left without both winter and summer covers and without tillage (i.e. direct seeding). NNT corresponds to the soil left without both winter and summer covers and with reduced tillage. NSN corresponds to soil left in winter and cultivated with sunflower as summer crop without tillage (i.e. direct seeding). NST corresponds to soil left in winter and cultivated with sunflower as summer crop with reduced tillage.