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► To cite this version:

Alicia Rouge, Guillaume Adeux, Hugues Busset, Rodolphe Hugard, Juliette Martin, et al.. Carry-over effects of cover crops on weeds and crop productivity in no-till systems. *Field Crops Research*, 2023, 295, pp.art. 108899. 10.1016/j.fcr.2023.108899 . hal-04052344

HAL Id: hal-04052344

<https://hal.inrae.fr/hal-04052344>

Submitted on 13 Mar 2024

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Carry-over effects of cover crops on weeds and crop productivity in no-till systems

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ARTICLE INFO

Keywords:

Cover crop termination
Nitrogen
Weed-crop competition
Spring barley
Winter linseed
Yield

ABSTRACT

The carry-over effect of cover crops on weeds and crop productivity in the subsequent crops has been related to cover crop composition and cover crop termination methods but their interaction with soil resource availability remains poorly documented, as well as the relative importance of each of these factors. This study investigated the effect of cover crop management (*i.e.* cover crop mixture, fertilisation, irrigation, termination method and their combinations) on weed biomass and crop productivity in two subsequent crops (spring barley followed by winter linseed). We hypothesised that cover crop management could affect productivity of the subsequent crops through both weed suppression and nitrogen supply. Two experiments spanning a duration of two years were set-up, on two different fields in two different years, to investigate the effect of cover crop mixture (2 or 8 species including or not legume species, plus a bare soil control), water and nitrogen availability at cover crop sowing and cover crop termination methods (rolling, herbicide-use and winter-kill control) on weed biomass and crop productivity of the two subsequent unweeded, unfertilised and directly seeded crops. Weed biomass and crop productivity in both subsequent crops were affected by multiple interactions between cover crop mixture, soil resource availability, cover crop termination method and experiment. In experiment 1, combinations of cover crop management alternative to the reference (*i.e.* bare soil, without fertilisation and irrigation, winter-killed) mainly showed beneficial carry-over effects (*i.e.* lower weed biomass and higher crop productivity) in the subsequent spring barley while having no effect in winter linseed. In experiment 2, alternative combinations of cover crop management mainly showed no effects or detrimental carry-over effects (*i.e.* higher weed biomass and lower crop productivity) in spring barley while having some positive effects in winter linseed (*i.e.* only when cover crops were terminated with herbicide-use). Crop productivity was mainly affected by weed biomass which was significantly reduced almost only when cover crops were terminated with herbicide-use. Crop productivity was also affected but to a lesser extent by cover crop soil-mediated effects (*e.g.* nitrogen supply). These results highlight complex interactions between cover crop management and environmental conditions on the carry-over effects of cover crops in the subsequent crops. Cover crops may not play an essential role for weed management in no-till and herbicide-free systems, particularly at low levels of cover crop biomass production.

1. Introduction

Agriculture has heavily relied on pesticides and fertilisers to enhance crop production over the last decades. However, the oversimplification of crop rotations and the over-reliance on pesticides, is questioned due to their negative impacts on the environment and human health (Liu *et al.*, 2015). Cover crops can be established during the fallow period

separating two main cash crops and increase cropping sustainability through multiple ecosystem services (*e.g.* reducing soil erosion, improving soil properties). Cover crops can suppress weeds (Osipitan *et al.*, 2018), the pests susceptible of generating the highest potential yield losses (Oerke, 2006), and can further improve subsequent crop yield through nitrogen release (Blanco-Canqui *et al.*, 2015). The carry-over effect of cover crops on weeds and crop productivity in the

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<https://doi.org/10.1016/j.fcr.2023.108899>

Received 19 October 2022; Received in revised form 15 March 2023; Accepted 17 March 2023

Available online 21 March 2023

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subsequent crops has been related to cover crop composition and cover crop termination methods (Nichols et al., 2020b) but their interaction with soil resource availability remains poorly documented, as well as the relative importance of each of these factors.

In no-till systems, optimising cover crop management (*i.e.* cover crop composition, fertilisation, irrigation and termination) for weed suppression is essential to maintain crop yields because weeds can compete with the crop if they are not well terminated before the subsequent crop is sown (Vincent-Caboud et al., 2019), the outcome of weed-crop competition being largely driven by who is established first (Horvath et al., 2023). Cover crops can reduce weed establishment and growth during the fallow period (Teasdale et al., 2007), with varying efficacy depending on cover crop composition and soil resource availability (Rouge et al., 2022). However, in a recent meta-analysis of cover crop experiments, Nichols et al. (2020b) concluded that the effect of cover crop management on weeds in the subsequent crops remained variable and uncertain. Cover crop carry-over effects on weeds have been mostly related to cover crop biomass (*i.e.* through mulch effects) (Osipitan et al., 2018) and cover crop termination method (Creamer and Dabney, 2002; Alonso-Ayuso et al., 2020). Adeux et al. (2021) showed that cover crops had no effect on weeds in the subsequent crops when cover crops were terminated by tillage and/or when in-crop weed management relied on herbicides, and concluded that intensive weed management could override the potential effect of cover crops on weeds in the subsequent crops. Alternative cover crop termination methods such as mowing or rolling have been investigated (Carrera et al., 2004; Wayman et al., 2014; Büchi et al., 2020) and are reported to be as efficient in reducing weed biomass in the subsequent crop as herbicide-use or tillage (Osipitan et al., 2018). In no-till systems, mulch resulting from unburied cover crop biomass can limit germination of weed species and act as a physical barrier against early weed establishment (Teasdale and Mohler, 2000). Indeed, numerous studies have reported a positive relationship between cover crop biomass and weed suppression in the subsequent crops established under no-till systems, namely through increased mulch thickness and persistence (Bärberi and Mazzoncini, 2001; Osipitan et al., 2018; Grint et al., 2022b; Menalled et al., 2022). Ranaivoson et al. (2018) highlighted that weeds were effectively suppressed when cover crop mulch biomass exceeded 10 t ha^{-1} . Reaching such levels of cover crop biomass depends on many factors such as cover crop composition and seeding rate (Mirsky et al., 2012), cover crop sowing and termination dates (Mirsky et al., 2009, 2017), and soil resource availability (Rouge et al., 2022). Therefore, understanding the interactions between cover crop management practices and their relative importance in determining weed and crop productivity in less-disturbed and low-input systems remains at stake.

Poaceae (*e.g.* rye, oat) or *Brassicaceae* (*e.g.* mustard) cover crop monocultures are usually associated to higher biomass productivity than *Fabaceae* cover crops, especially when soil nitrogen availability is high (Bybee-Finley et al., 2017; Smith et al., 2020; Adeux et al., 2021). Such highly productive cover crop species are expected to generate high quantities of mulch once terminated and hence limit weed emergence and yield losses due to weeds in the subsequent crops. However, *Poaceae* and *Brassicaceae* usually show high C/N ratios, which may reduce the subsequent crop yields (Finney et al., 2016) due to mineral nitrogen immobilisation (Wells et al., 2013). Including productive legume species in a cover crop mixture can reduce the C/N ratio and may increase both soil nitrogen availability and subsequent crop yield (Snapp et al., 2005; Marcillo and Miguez, 2017; Hunter et al., 2019; Adeux et al., 2021). Cover crop mixtures comprising legumes and non-legumes have been reported to be as effective in releasing nitrogen and improving crop yield as legume monocultures (Finney et al., 2016). Therefore, cover crop mixtures of legume and non-legume species could represent a promising option to increase crop yield through both weed suppression and nitrogen release (Couédel et al., 2019). Nevertheless, the relative importance of these two underlying processes remains to be quantified.

Finally, numerous studies have focused on the carry-over effect of

autumn sown cover crops on weeds in the subsequent spring/summer crop (Campiglia et al., 2010; Almoussawi et al., 2020; Pittman et al., 2020) but the longer effects remain poorly documented. Nichols et al. (2020a) recently analysed five long-term (>10 years) no-till rye cover crop experiments and reported that no clear conclusion could be drawn concerning the effect of the rye cover crop on weed seedbank density: rye had a negative effect on seedbank density in 2 out of 5 cases, no effect in 2 out of 5 cases and slightly positive effect in 1 out of 5 cases. Cover crops could exhibit longer term effects on weeds through mulch persistence (Osipitan et al., 2018), allelopathy or simply by favouring the weed suppressive effect of the subsequent crop. Besides, most weeds are annuals and have different emergence periodicity (Grundy, 2003). Hence, the suppressive effect of autumn sown cover crops on weed seed shed during the winter fallow period is expected to be more visible in the subsequent autumn sown crop than in the subsequent spring sown crop (Adeux et al., 2023).

The present study aimed to investigate the effect of cover crop management (*i.e.* cover crop mixture, fertilisation, irrigation, termination method and their combinations) on weed biomass and crop productivity in a subsequent two-year crop sequence composed of one spring and one winter crop, and relate these carry-over effects to cover crop and weed biomass and nitrogen content quantified during the cover crop period (Rouge et al., 2022). Considering tillage, herbicides and fertilisers may override cover crop carry-over effects, our study was the first to assess these effects in direct-seeded (*i.e.* no-till), unweeded and unfertilised crops. We hypothesised that cover crop management could affect productivity of the subsequent crops through both weed suppression and nitrogen supply (Supp. Fig. 1).

2. Material and methods

2.1. Site characteristics

Two experiments spanning a duration of two years were set-up, on two different fields in two different years, one field experiment in 2016–2018 and another in 2017–2019 (further denoted experiment 1 and experiment 2, respectively), both at the INRAE experimental site in Bretenièrre (47°14'11.2" N, 5°05' 56.1" E), 15 km south-east of Dijon, France. Both fields were characterised by a clay (40 %) - silt (50 %) soil texture, a soil pH of 7, a percentage of organic matter of 2 %, and a calcareous bedrock. The site is flat and subject to a semi-continental climate, with a mean annual precipitation of 765 mm and an average daily temperature of 10.5 °C, with strong variations between winter and summer (see average monthly temperature and rainfall over the course of the two experiments in Supp. Fig. 2).

2.2. Experimental set-up

Following winter wheat, a cover crop / spring barley / summer bare soil fallow period / winter linseed succession was replicated over the course of experiment 1 (2016–2018) and 2 (2017–2019). Four cover crop mixtures (2leg-: 2 species without legumes, 2leg+: 2 species including a legume, 8leg-: 8 species without legumes and 8leg+: 8 species including legumes) including a wide range of species commonly used by French farmers (Supp. Table 1, black oat, winter rye, sorghum, foxtail millet, common vetch, berseem clover, faba bean, brown hemp, brown mustard, field mustard, lacy phacelia, niger seed, buckwheat, linseed), plus a bare soil control were tested. Cover crops were sown in summer (on the 10th of August 2016 and 28th of July 2017 in experiment 1 and 2, respectively) at their recommended pure stand seeding rate divided by the number of species in the mixture and majored by 15 % (Supp. Table 1). Cover crop mixtures were designed to generate a gradient of biomass productivity and nitrogen content, based on the ability of each cover crop species to respond to soil resource availability in pure stands. *Poaceae* and *Brassicaceae* species were expected to quickly pre-empt nitrogen and produce high biomass while *Fabaceae*

species could avoid nitrogen competition through symbiotic nitrogen fixation and exhibit high nitrogen concentration in their biomass. Cover crop mixtures were composed of 2 or 8 species, as two is the minimum richness for a mixture and eight the maximum species richness commonly used by French farmers when selecting cover crop species able to grow in a given season (here winter fallow). A further increase in cover crop species richness would have either induced functional redundancy or the inclusion of less relevant species in terms of biomass productivity or weed suppression (Smith et al., 2020). Two levels of irrigation (W-: 0 mm or W+: 40 mm) and nitrogen fertilisation (N-: 0 kg N ha⁻¹ or N + : 30 kg N ha⁻¹ through the application of 90 kg ha⁻¹ of ammonium nitrate 33.5 %) were applied once, at cover crop sowing, to mimic contrasted levels of soil resource availability. Three cover crop termination methods were implemented [winter-kill control, rolling (done on the 15th of December 2016 and 3rd of December 2017 in experiment 1 and 2, respectively) or herbicide-use (i.e. glyphosate 3 L ha⁻¹ + 2,4 dichlorophenoxyacetic acid 0.3 L ha⁻¹, applied on the 28th of February 2017 and 8th of March 2018 in experiment 1 and 2, respectively)]. Cover crop termination was timed to maximise its efficacy, i.e. cover crops were rolled early in the morning on the first day of frost of the season or sprayed with herbicides two weeks before the sowing of the subsequent spring barley.

The experiments were set-up following a split-split-split plot design with cover crop mixture as the only completely randomised factor for practical machinery reasons (Supp. Fig. 3). All three blocks were first divided in half with the upper part being fertilised and the lower part being unfertilised. Blocks were then divided perpendicularly to introduce the irrigation factor. The irrigation ramp covered the width of a whole block so was positioned in between two blocks, resulting in an alternating irrigation pattern across the experiments. The two nitrogen strips spanning the whole experiment were divided into three, one for each cover crop termination method. Finally, the four cover crop mixtures and bare soils were randomly allocated to five 10 m² plots within each combination of block, fertilisation, irrigation and cover crop termination method, resulting in 60 combinations repeated 3 times across a total of 180 plots. Since weeds are known to be patchily distributed within a field (Hughes, 1990), four weed species commonly found in Burgundy fields and able to germinate in summer (i.e. at cover crop sowing) (*Echinochloa crus-galli*, *Veronica persica*, *Geranium dissectum* and *Chenopodium album*) were sown at 60 seeds m⁻² each across all plots at cover crop sowing to homogenise weed pressure within each experiment.

Spring barley was sown (cv. Sebastian at 140 kg ha⁻¹ and cv. Planet at 171 kg ha⁻¹ for experiment 1 and 2, respectively) after cover crop termination (on the 13th of March 2017 and 21st of March 2018 in experiment 1 and 2, respectively) and harvested at maturity (on the 15th of July 2017 and 19th of July 2018 in experiment 1 and 2, respectively, Supp. Fig. 2). Before the sowing of winter linseed, weeds were terminated with herbicide-use (i.e. glyphosate 3 L ha⁻¹, on the 26th of July 2017 and 29th of September 2017) in experiment 1 and with waterproof silage tarp (placed during the whole fallow period) in experiment 2. Winter linseed was sown (cv. Angora at 25 kg ha⁻¹ and 23 kg ha⁻¹ in experiment 1 and 2, respectively) on the 22nd of September 2017 and 11th of September 2018 in experiment 1 and 2, respectively, and harvested on the 13th of July 2018 and 5th of August 2019 in experiment 1 and 2, respectively (Supp. Fig. 2). Both subsequent crops were direct seeded with a JD 750 A direct driller, and conducted without fertilisation, irrigation nor in-crop weeding until harvest.

2.3. Cover crop, crop and weed sampling

Weed (per species) and crop (spring barley, winter linseed) above-ground biomass were sampled at crop flowering in both experiments, in all 180 plots, with two randomly positioned 0.25 m² quadrats per plot. All biomass samples were oven dried at 80 °C for 72 h and weighed. Total dry weed biomass was computed as the sum of weed biomass per

species in each quadrat. As crop grain yields were assessed at the plot level, weed and crop dry biomass were averaged at the plot level for data analysis.

Spring barley and winter linseed grain yields were measured at maturity by harvesting the whole plot with an experimental combine harvester. As crop biomass at crop flowering and crop grain yield at crop maturity were highly and positively correlated in 3 out of 4 cases (Supp. Fig. 4), only crop grain yields are presented.

To explain to which extent cover crop carry-over effects were related to cover crop weed suppression or cover crop nitrogen supply, total autumn cover crop and weed biomass and total autumn cover crop and weed nitrogen content were computed at the plot level as the sum of cover crop and weed aboveground biomass and nitrogen content measured as described in Rouge et al. (2022), 90 days after cover crop sowing (i.e. at cover crop mixtures peak biomass and before early frost, as shown in Supp. Fig. 2). We considered that total autumn cover crop and weed biomass and nitrogen content were representative of the amount of biomass and nitrogen returned to the soil at cover crop termination because cold temperatures restrained cover crop and weed growth between biomass sampling and cover crop termination.

2.4. Data analysis

Statistical analyses were performed with the R software version 4.0.2 (R Core Team, 2020). Weed biomass and crop grain yield (in both subsequent spring barley and winter linseed) were analysed at the plot level. To identify whether cover crop management could have an effect on crop grain yield through mechanisms independent of weed-crop competition, (i) crop grain yield for each crop and experiment was first regressed against weed biomass with a generalised linear model with a gaussian distribution and a log link, available in the R 'stats' package, and (ii) the response residuals (i.e. predicted minus observed data) from these regressions were extracted. These response residuals are then called crop grain yield residuals throughout the manuscript. Weed biomass, crop grain yield and crop grain yield residuals were all modelled as a function of cover crop mixture, fertilisation, irrigation, cover crop termination method, experiment (confounded with field), and all possible interactions between these five factors with generalised linear mixed effect models, available in the R 'glmmTMB' package (Brooks et al., 2017), with tweedie distributions and log links for weed biomass and crop grain yield, and gaussian distributions without link for crop grain yield residuals.

To explain to which extent crop grain yields were affected by cover crop management through weed suppression (i.e. mulching) and/or nitrogen supply, (i) weed biomass in the subsequent crops was modelled as a function of experiment, cover crop termination method, total autumn cover crop and weed biomass and all possible interactions between the three latter, and (ii) spring and winter crop grain yields were modelled as a function of experiment, cover crop termination method, total autumn cover crop and weed nitrogen content and all possible interactions between the three latter with generalised linear mixed effect models with a tweedie distribution and a log link. Cover crop mixture, fertilisation and irrigation factors were not considered in these regressions due to collinearity with total autumn cover crop and weed biomass and total autumn cover crop and weed nitrogen content. Root mean square errors were calculated for each generalised linear mixed effect model using the function `rmse` of the R 'Metrics' package (Hamner et al., 2018).

For all generalised linear mixed effect models an *a priori* set of five plausible random effect structures were defined and compared using Akaike's Information Criterion (AIC), in order to better capture the structure of the experimental design (Supp. Tables 2 and 3). The model with the lowest AIC was retained for analysis. The absence of confounding factors with the non-randomised nitrogen, irrigation and cover crop termination method strips was confirmed through an investigation of within-field yield variability of the preceding winter wheat crop and

soil electrical resistivity (Supp. Fig. 5). Significance of effects was determined through Type III Wald Chi-Square tests using the function Anova of the R ‘car’ package (Fox et al., 2020).

For all response variables (i.e. weed biomass, crop grain yields and crop grain yield residuals), combinations of cover crop mixture, fertilisation, irrigation and cover crop termination method were compared to a reference (i.e. bare soil, without fertilisation and irrigation and winter-kill), in order to assess the benefit of implementing cover crops, manipulating soil resource availability and/or applying mechanical or chemical cover crop termination. Control-versus-alternative combination contrasts were adjusted using the R ‘emmeans’ package (Lenth, 2021).

3. Results

Crop grain yields decreased when weed biomass at crop flowering increased in both experiments 1 and 2 (Fig. 1). Weed biomass response to cover crop management was then investigated to determine to which extent the 59 combinations of cover crop mixture, soil resource availability and cover crop termination method alternative to the reference (i.e. bare soil, without fertilisation and irrigation, winter-killed) affected in-crop weed biomass. Then, crop grain yields and crop grain yield residuals (i.e. after the removal of weed biomass effects, see Section 2.4.) response to cover crop management were investigated by comparing the 59 alternative combinations of cover crop mixture, soil resource availability and cover crop termination method to the reference. Finally, beneficial cover crop management combinations, i.e. improving crop yield and reducing weed biomass, were identified. These combinations were considered as beneficial at the cropping system level since a lower weed biomass in crops will potentially decrease crop yield losses and weed seed shed, thereby reducing weed infestation and crop yield losses in the subsequent crops.

3.1. First subsequent crop: spring barley

3.1.1. Cover crop management effects on weeds

Weed biomass in spring barley was affected by a five-way interaction between cover crop mixture, fertilisation, irrigation, cover crop termination method and experiment (Table 1). In experiment 1, alternative combinations of cover crop management showed either similar (in 34 combinations) or lower (in 25 combinations) weed biomass than the reference (Fig. 2). Lower weed biomass was observed in all the

combinations terminated with herbicide-use (i.e. in 20 out of the 25 combinations), as well as in 2 combinations terminated with winter-kill and 3 terminated with rolling, regardless of cover crop mixture and soil resource availability. In experiment 2, alternative combinations of cover crop management showed either higher (in 20 combinations), similar (in 30 combinations) or lower (in 9 combinations) weed biomass than the reference (Fig. 2). Lower weed biomass was mostly observed in the combinations of fertilised cover crop mixtures and a bare soil terminated with herbicide-use (i.e. in 8 out of the 9 combinations). Higher weed biomass was mainly observed in the combinations of unfertilised cover crop mixtures terminated with winter-kill or rolling (i.e. in 14 out of the 20 combinations).

In both experiments, when cover crop mixtures and bare soils were terminated with rolling or winter-kill, weed biomass in spring barley was mainly composed of winter wheat volunteers and *Geranium dissectum*, the two main weed species present during the cover crop period (Fig. 3). In experiment 1, the biomass of these two weed species increased between cover crop and spring barley biomass sampling times whereas in experiment 2, weed biomass of *Geranium dissectum* decreased between the cover crop and spring barley biomass sampling times (Fig. 3). Herbicide-use termination changed the dominant weed species in the subsequent spring barley compared to the cover crop period. In these treatments, weed communities were mainly composed of spring/summer weed species such as *Convolvulus arvensis* or *Lysimachia arvensis* and *Polygonum aviculare*, in experiment 1 and 2, respectively.

Finally, weed biomass in spring barley was affected by total autumn cover crop and weed biomass, regardless of experiment and cover crop termination method (p-value = 0.01, Supp. Table 4; RMSE = 42 g DM m⁻²). However, the relationship between weed biomass in spring barley and total autumn cover crop and weed biomass was very weak (Supp. Fig. 6a).

3.1.2. Cover crop management effects on crop grain yields

Spring barley grain yield was driven by three four-way interactions involving cover crop mixture and termination as well as either experiment and fertilisation, experiment and irrigation or fertilisation and irrigation (Table 1). In experiment 1, alternative combinations of cover crop management showed either higher (in 48 combinations) or similar (in 11 combinations) spring barley grain yield than the reference (Fig. 4). Similar spring barley grain yields were observed in the combinations of bare soils (i.e. in 5 out of the 11 combinations) or 2-species legume-based cover crop mixtures (i.e. in 4 out of the 11 combinations),

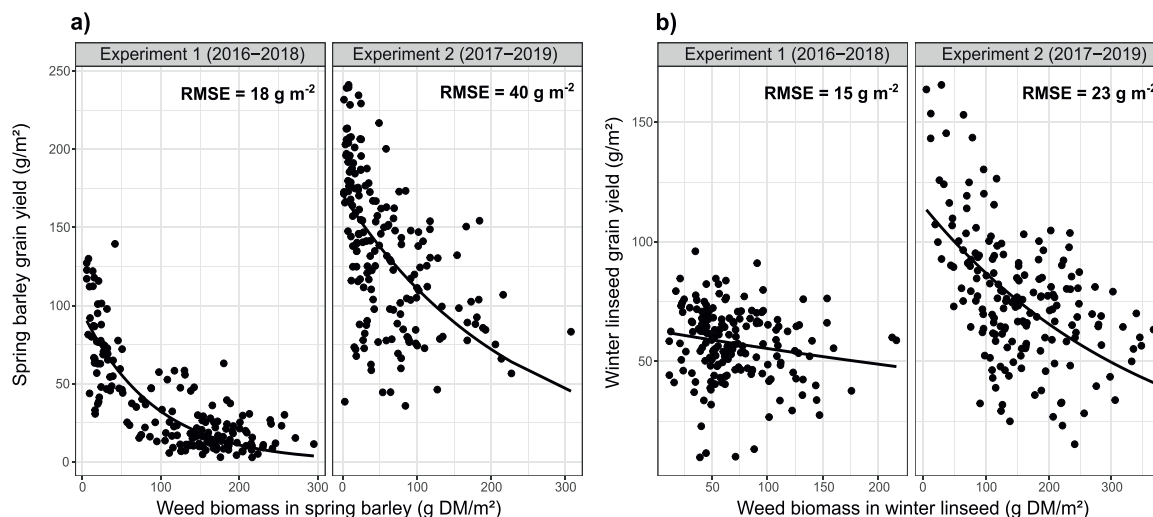


Fig. 1. Relationship between a) spring barley grain yield (at 0% grain moisture) and weed biomass in spring barley (g of dry matter (DM) m⁻², sampled at crop flowering) and b) winter linseed grain yield (at 0% grain moisture) and weed biomass in winter linseed (g DM m⁻², sampled at crop flowering), for both experiment 1 (2016–2018) and 2 (2017–2019). Predictions were based on generalised linear models. The regression lines show an average value (i.e. population level slope). Root mean square error (RMSE) are indicated in bold for each regression line.

Table 1

ANOVA table (type III Wald Chi-Square tests) highlighting the effect of experiment (exp, as factor), fertilisation (N), irrigation (W), cover crop mixture (CCm), cover crop termination method (term), and all possible interactions between these five factors on weed biomass in crops, crop grain yield and crop grain yield residuals (i.e. after the removal of weed biomass effects). Results were obtained with generalised linear mixed effect models. Significant p-values at $p < 0.05$ are highlighted in bold.

Factors	Spring Barley									Winter linseed								
	Weed biomass			Crop grain yield			Crop grain yield residuals			Weed biomass			Crop grain yield			Crop grain yield residuals		
	X ²	Df	p-value	X ²	Df	p-value	X ²	Df	p-value	X ²	Df	p-value	X ²	Df	p-value	X ²	Df	p-value
exp	11.9	1	0.0005	180	1	<0.0001	0.03	1	0.86	106	1	<0.0001	8.03	1	0.005	0.44	1	0.51
N	18.3	1	<0.0001	28.2	1	<0.0001	10.3	1	0.001	0.41	1	0.52	0.90	1	0.34	1.03	1	0.31
W	0.21	1	0.64	31.9	1	<0.0001	8.59	1	0.003	1.14	1	0.29	0.23	1	0.63	0.31	1	0.58
CCm	4.89	4	0.30	80.0	4	<0.0001	68.3	4	<0.0001	8.50	4	0.07	8.66	4	0.07	11.3	4	0.02
term	76.2	2	<0.0001	689	2	<0.0001	24.7	2	<0.0001	83.0	2	<0.0001	63.3	2	<0.0001	13.4	2	0.001
exp:N	3.89	1	0.05	11.6	1	0.0007	0.76	1	0.38	2.50	1	0.11	0.01	1	0.93	1.28	1	0.26
exp:W	0.05	1	0.82	16.9	1	<0.0001	5.47	1	0.02	1.13	1	0.29	1.70	1	0.19	2.04	1	0.15
N:W	0.55	1	0.46	0.04	1	0.84	0.13	1	0.72	1.01	1	0.32	6.10	1	0.01	2.67	1	0.10
exp:CCm	37.5	4	<0.0001	332	4	<0.0001	70.4	4	<0.0001	3.15	4	0.53	6.40	4	0.17	7.80	4	0.10
N:CCm	19.3	4	0.0007	117	4	<0.0001	41.6	4	<0.0001	4.83	4	0.30	14.1	4	0.01	18.4	4	0.001
W:CCm	8.88	4	0.06	5.89	4	0.21	36.8	4	<0.0001	3.59	4	0.46	4.21	4	0.35	5.10	4	0.28
exp:term	4.27	2	0.12	171	2	<0.0001	27.4	2	<0.0001	28.6	2	<0.0001	35.0	2	<0.0001	5.45	2	0.07
N:term	19.4	2	<0.0001	1.46	2	0.48	10.6	2	0.01	5.90	2	0.05	1.63	2	0.44	3.94	2	0.14
W:term	6.47	2	0.04	6.34	2	0.04	4.83	2	0.09	1.08	2	0.58	3.66	2	0.16	2.15	2	0.34
CCm:term	7.17	8	0.52	89.3	8	<0.0001	48.5	8	<0.0001	11.6	8	0.17	9.40	8	0.31	8.96	8	0.35
exp:N:W	1.16	1	0.28	11.2	1	0.0008	2.59	1	0.11	0.12	1	0.73	3.35	1	0.07	3.15	1	0.08
exp:N:CCm	28.7	4	<0.0001	22.0	4	0.0002	30.5	4	<0.0001	10.0	4	0.04	3.88	4	0.42	6.86	4	0.14
exp:W:CCm	2.31	4	0.68	8.60	4	0.07	26.4	4	<0.0001	14.0	4	0.01	6.95	4	0.14	8.87	4	0.06
N:W:CCm	5.97	4	0.20	3.04	4	0.55	1.64	4	0.80	2.62	4	0.62	5.42	4	0.25	2.92	4	0.57
exp:N:term	2.33	2	0.31	3.95	2	0.14	8.36	1	0.02	5.94	2	0.05	2.85	2	0.24	5.92	2	0.05
exp:W:term	3.86	2	0.15	6.47	2	0.04	2.13	2	0.34	4.65	2	0.10	6.93	2	0.03	3.58	2	0.17
N:W:term	0.89	2	0.64	1.02	2	0.60	2.41	2	0.30	3.00	2	0.22	5.57	2	0.06	2.08	2	0.35
exp:CCm:term	6.64	8	0.58	69.1	8	<0.0001	31.3	8	0.0001	36.4	8	<0.0001	11.2	8	0.19	15.5	8	0.05
term																		
N:CCm:term	7.14	8	0.52	46.8	8	<0.0001	12.6	8	0.13	17.2	8	0.03	8.33	8	0.40	12.4	8	0.13
W:CCm:term	17.1	8	0.03	14.8	8	0.06	23.7	8	0.003	20.6	8	0.01	15.0	8	0.06	36.0	8	<0.0001
exp:N:W:CCm	8.07	4	0.09	2.82	4	0.59	2.85	4	0.58	10.2	4	0.04	1.84	4	0.76	5.07	4	0.28
exp:N:W:term	2.84	2	0.24	4.43	2	0.11	1.79	2	0.41	4.07	2	0.13	2.82	2	0.24	1.32	2	0.52
exp:N:CCm:term	10.9	8	0.21	39.0	8	<0.0001	17.3	8	0.03	28.5	8	0.0003	12.6	8	0.13	18.9	8	0.02
exp:W:CCm:term	4.85	8	0.77	17.6	8	0.02	21.6	8	0.006	13.3	8	0.10	4.56	8	0.80	20.1	8	0.01
N:W:CCm:term	11.3	8	0.19	18.8	8	0.02	25.5	8	0.001	9.13	8	0.33	4.04	8	0.85	6.38	8	0.60
exp:N:W:CCm:term	16.8	8	0.03	9.32	8	0.32	21.5	8	0.006	3.73	8	0.88	8.56	8	0.38	5.97	8	0.65

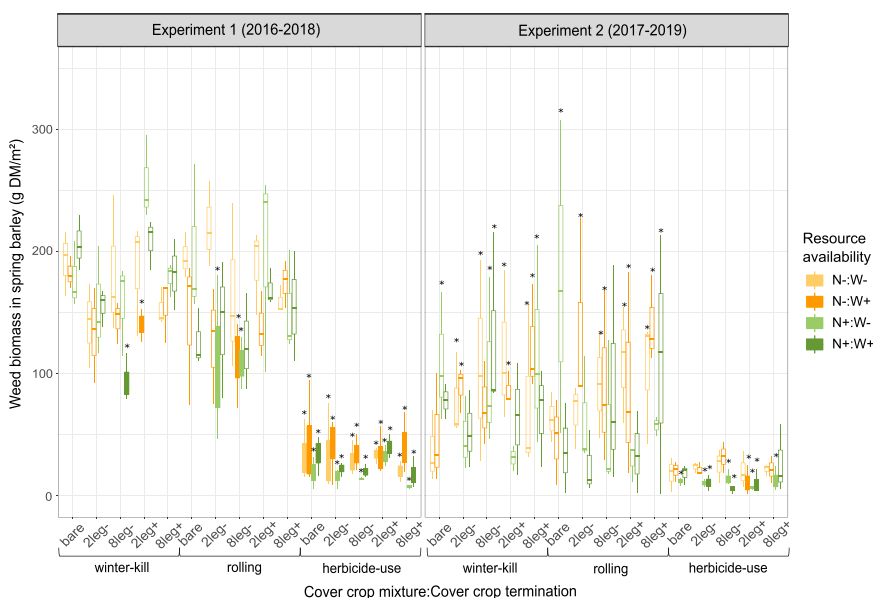


Fig. 2. Effect of cover crop mixtures, nitrogen and water resources at cover crop sowing and cover crop termination methods on weed biomass in spring barley (g of dry matter (DM) m⁻²). N-: no nitrogen fertilisation, N+: 30 kg N ha⁻¹ at cover crop sowing; W-: no irrigation, W+: 40 mm at cover crop sowing; bare: bare soil; 2leg-: 2 cover crop species without legumes; 2leg+: 2 cover crop species including a legume; 8leg-: 8 cover crop species without legumes; 8leg+: 8 cover crop species including legumes. Each combination of cover crop mixture, nitrogen, water and cover crop termination method was statistically compared to the reference (i.e. bare soil, N-W-, winter-kill). Boxplots highlighted with an asterisk differed from the reference (p-value < 0.05). Filled boxplots highlight lower values than the reference.

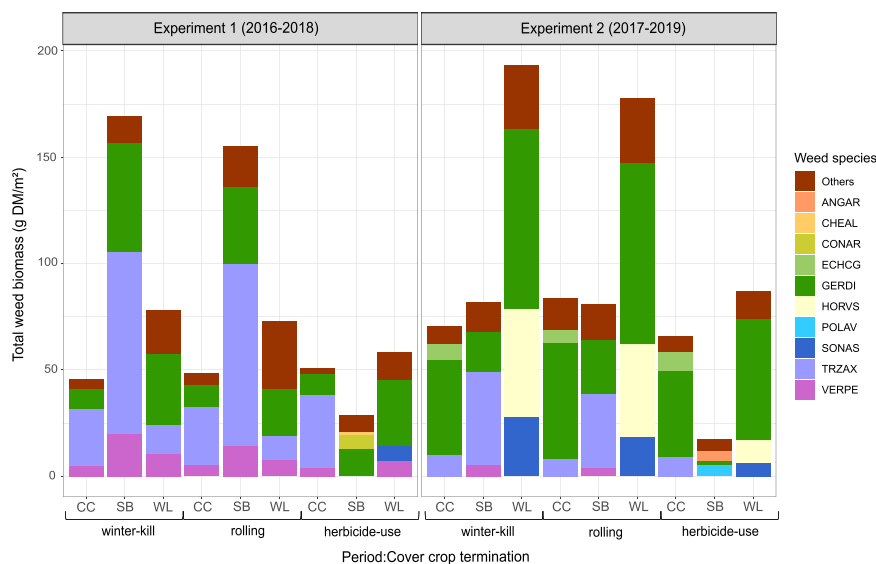


Fig. 3. Total weed biomass (g of dry matter (DM) m⁻², averaged by plot) and by weed species in the cover crop (CC), spring barley (SB) and winter linseed (WL) succession depending on the cover crop termination method (winter-kill, rolling, herbicide-use) for experiment 1 and 2. ANGAR: *Lysimachia arvensis*; CHEAL: *Chenopodium album*; CONAR: *Convolvulus arvensis*; ECHCG: *Echinochloa crus-galli*; GERDI: *Geranium dissectum*; HORVS: *Hordeum vulgare* (spring barley volunteers); POLAV: *Polygonum aviculare*; SONAS: *Sonchus asper*; TRZAX: *Triticum aestivum* (winter wheat volunteers); VERPE: *Veronica persica*.

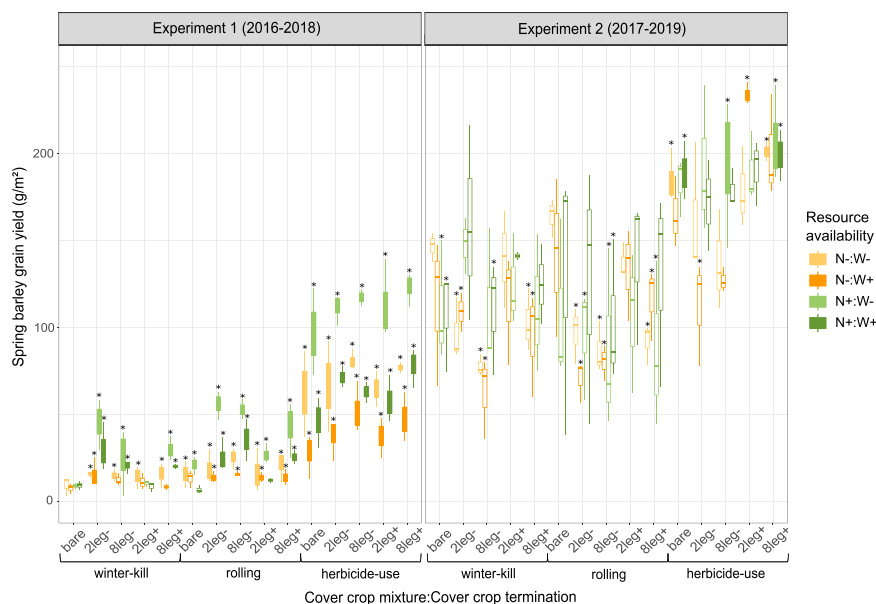


Fig. 4. Effect of cover crop mixtures, nitrogen and water resources at cover crop sowing and cover crop termination methods on spring barley grain yield (at 0 % grain moisture). N-: no nitrogen fertilisation, N+ : 30 kg N ha⁻¹ at cover crop sowing; W-: no irrigation, W+ : 40 mm at cover crop sowing; bare : bare soil; 2leg-: 2 cover crop species without legumes; 8leg-: 8 cover crop species without legumes; 2leg+ : 2 cover crop species including a legume; 8leg+ : 8 cover crop species including legumes. Each combination of cover crop mixture, nitrogen, water and cover crop termination method was statistically compared to the reference (i.e. bare soil, N-W-, winter-kill). Boxplots highlighted with an asterisk differed from the reference (p-value < 0.05). Filled boxplots highlight higher values than the reference.

terminated with winter-kill or rolling. In experiment 2, alternative combinations of cover crop management showed either higher (in 7 combinations), similar (in 32 combinations) or lower (in 20 combinations) spring barley grain yields than the reference (Fig. 4). Higher spring barley grain yields were observed in the combinations of cover crop mixtures and bare soils terminated with herbicide-use only, regardless of soil resource availability. Lower spring barley grain yields were mainly observed in the combinations of unfertilised cover crop mixtures terminated with winter-kill or rolling (i.e. in 12 out of the 20 combinations).

Analysis of spring barley grain yield residuals (i.e. after the removal of weed biomass effects) highlighted a significant five-way interaction between experiment, cover crop mixture, fertilisation, irrigation and cover crop termination method (Table 1). This highlights a possible soil-mediated effect of cover crops on subsequent spring barley grain yield (e.g. through nitrogen supply or immobilisation). In experiment 1, alternative combinations of cover crop management showed either higher (in 4 combinations), similar (in 54 combinations) or lower (in 1 combination) spring barley grain yield residuals than the reference

(Fig. 5). Higher spring barley grain yield residuals were observed only in the combinations of fertilised and non-irrigated cover crop mixtures, terminated with herbicide-use. In experiment 2, alternative combinations of cover crop management showed either higher (in 27 combinations), similar (in 29 combinations) or lower (in 3 combinations) spring barley grain yield residuals than the reference (Fig. 5). Higher spring barley grain yield residuals were observed in the combinations of fertilised and winter-killed 2-species cover crop mixtures (i.e. in 4 out of the 27 combinations), and in the combinations of herbicide-terminated legume-based cover crop mixtures or fertilised non-legume-based cover crop mixtures (i.e. in 12 out of the 27 combinations).

Finally, spring barley grain yield was affected by total autumn cover crop and weed nitrogen content, regardless of cover crop termination method in both experiments (p-value = 0.0004, Supp. Table 5; RMSE = 28 g m⁻²). The relationship between spring barley grain yield and total autumn cover crop and weed nitrogen content was positive in each experiment but to a greater extent in experiment 2 than experiment 1 (Supp. Fig. 7).

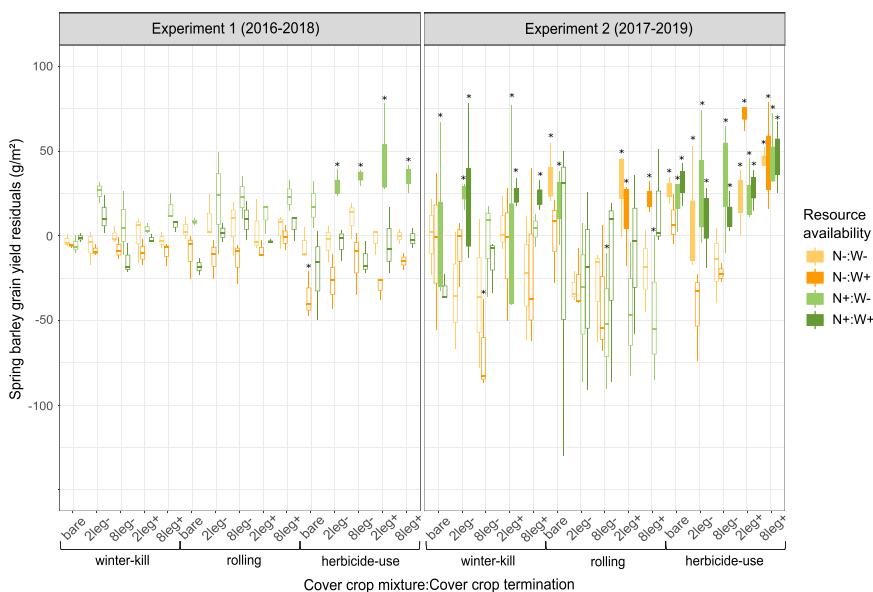


Fig. 5. Effect of cover crop mixtures, nitrogen and water resources at cover crop sowing and cover crop termination methods on spring barley grain yield residuals. Spring barley grain yield residuals were extracted from the regression of spring barley grain yield against weed biomass in spring barley. Spring barley grain yield residuals show the spring barley grain yield after the removal of weed biomass effects. N-: no nitrogen fertilisation, N + : 30 kg N ha⁻¹ at cover crop sowing; W-: no irrigation, W + : 40 mm at cover crop sowing; bare : bare soil; 2leg-: 2 cover crop species without legumes; 2leg+: 2 cover crop species including a legume; 8leg-: 8 cover crop species without legumes; 8leg+: 8 cover crop species including legumes. Each combination of cover crop mixture, nitrogen, water and cover crop termination method was statistically compared to the reference (i.e. bare soil, N-:W-, winter-kill). Boxplots highlighted with an asterisk differed from the reference (p-value < 0.05). Filled boxplots highlight higher values than the reference.

3.2. Second subsequent crop: winter linseed

3.2.1. Cover crop management effects on weeds

Weed biomass in winter linseed was driven by a four-way interaction between experiment, cover crop mixture, fertilisation and cover crop termination method (Table 1). In experiment 1, alternative combinations of cover crop management showed either higher (in 3 combinations), similar (in 55 combinations) or lower (in 1 combination) weed biomass than the reference (Supp. Fig. 8). Lower weed biomass was observed in the combination of unfertilised and non-irrigated 2-species legume-based cover crop mixture terminated with rolling. In experiment 2, alternative combinations of cover crop management showed either similar (in 43 combinations) or lower (in 16 combinations) weed biomass than the reference (Supp. Fig. 8). Lower weed biomass was observed in the combinations of cover crop mixtures and bare soils terminated with herbicide-use only, regardless of soil resource availability.

Weed biomass in winter linseed was mainly composed of *Geranium dissectum* in experiment 1, and *Geranium dissectum* and spring barley volunteers in experiment 2 (Fig. 3). In both experiments, dominant weed species in winter linseed did not differ between cover crop termination methods as they did in spring barley.

Finally, weed biomass in winter linseed was affected by total autumn cover crop and weed biomass, regardless of experiment and cover crop termination method (p-value = 0.04, Supp. Table 4; RMSE = 50 g DM m⁻²). However, the relationship between weed biomass in winter linseed and total autumn cover crop and weed biomass was weak and positive (Supp. Fig. 6b).

3.2.2. Cover crop management effects on crop grain yields

Winter linseed grain yield was influenced by a three-way interaction between experiment, cover crop termination method and irrigation (Table 1). In experiment 1, alternative combinations of cover crop management showed either similar (in 55 combinations) or lower (in 4 combinations) winter linseed grain yield than the reference (Supp. Fig. 9). In experiment 2, alternative combinations of cover crop management showed either higher (in 16 combinations), similar (in 41 combinations) or lower (in 2 combinations) winter linseed grain yield than the reference (Supp. Fig. 9). Higher winter linseed grain yields were mainly observed in the combinations of cover crop mixtures and bare soils terminated with herbicide-use (i.e. in 14 out of the 16 combinations).

Analysis of winter linseed grain yield residuals (i.e. after the removal of weed biomass effects) highlighted two significant four-way interactions between experiment, cover crop mixture, cover crop termination method and either fertilisation or irrigation (Table 1). In experiment 1, alternative combinations of cover crop management showed either similar (in 56 combinations) or lower (in 3 combinations) winter linseed grain yield residuals than the reference (Supp. Fig. 10). In experiment 2, alternative combinations of cover crop management showed either higher (in 9 combinations) or similar (in 50 combinations) winter linseed grain yield residuals than the reference (Supp. Fig. 10). Higher winter linseed grain yield residuals were observed in the combinations of herbicide-terminated fertilised and irrigated cover crop mixtures and bare soil (i.e. in 5 out of the 9 combinations).

Finally, winter linseed grain yield was slightly affected by total autumn cover crop and weed nitrogen content in interaction with cover crop termination method (p-value = 0.05, Supp. Table 5; RMSE = 19 g m⁻²). The relationship between winter linseed grain yield and total autumn cover crop and weed nitrogen content was significantly different between winter-kill and herbicide-use termination methods but any slope was significantly different from zero (Supp. Fig. 11).

3.3. Agronomic pathways for enhanced multiple carry-over effects of cover crops

Carry-over effects of cover crop management combinations were considered as beneficial when they both enhanced subsequent crop yield and reduced weed biomass in the subsequent crops (Fig. 6).

In experiment 1, cover crop management showed beneficial carry-over effect in spring barley in 24 out of the 59 combinations of cover crop mixture, soil resource availability and cover crop termination method alternative to the reference (Fig. 6. 1a). These combinations corresponded to all the cover crop mixtures and bare soils terminated with herbicide-use (i.e. 20 combinations), one cover crop mixture terminated with winter-kill and three cover crop mixtures terminated with rolling, regardless of soil resource availability. The 8-species non-legume-based cover crop mixture was the most frequent cover crop mixture in these beneficial agronomic pathways. Cover crop management mainly showed no carry-over effect, either positive or negative, in the subsequent winter linseed (i.e. same level of crop grain yield and weed biomass in 51 out of the 59 combinations) (Fig. 6. 1b).

In experiment 2, cover crop management mainly showed no (in 18 combinations) or a detrimental (i.e. lower level of crop grain yield and

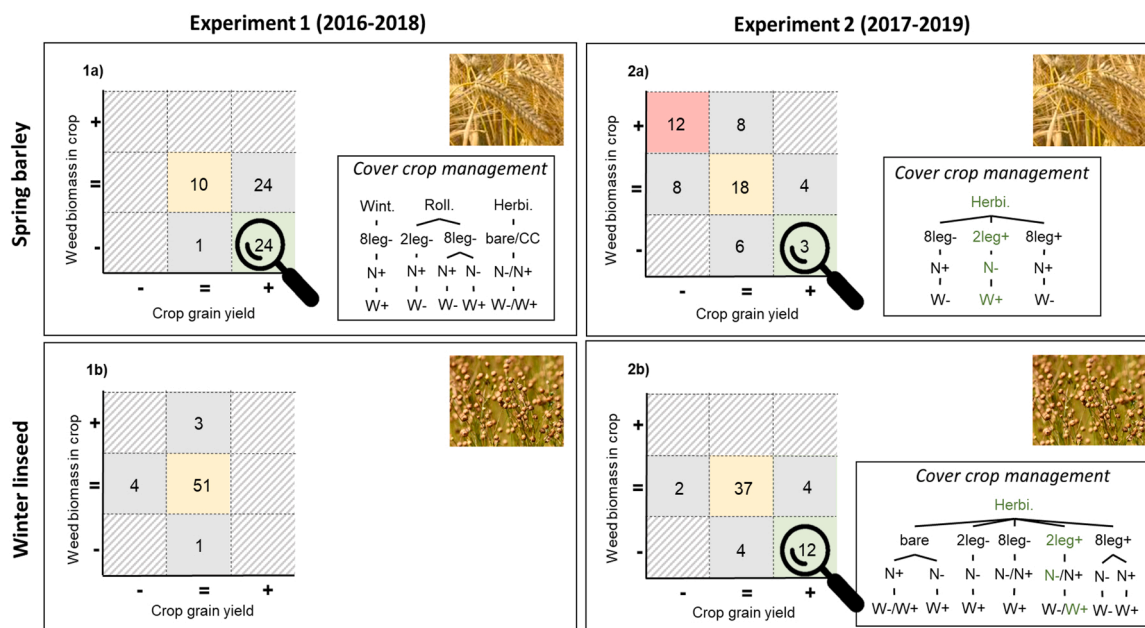


Fig. 6. Synthesis of the effect of cover crop (CC) mixture (bare : bare soil; 2leg-: 2 CC species without legumes; 8leg-: 8 CC species including legumes), soil resource availability (N-: no nitrogen fertilisation, N + : 30 kg N ha⁻¹ at cover crop sowing; W-: no irrigation, W+ : 40 mm at cover crop sowing) and cover crop termination method (Wint.: winter-kill; Roll.: rolling; Herbi.: herbicide-use) on weed biomass (at crop flowering) and crop grain yields (at maturity) in a) spring barley and b) winter linseed, for both experiments 1) in 2016–2018 and 2) in 2017–2019. Alternative treatments (N = 59) were compared to the reference (i.e. bare soil, N-:W-, winter-kill). Green cells highlight beneficial carry-over effect of cover crops, i.e. higher (+) crop grain yields and lower (-) weed biomass in crops compared to the reference; yellow cells correspond to no cover crop carry-over effects, i.e. similar (=) crop grain yields and similar weed biomass; red cells correspond to detrimental cover crop carry-over effects, i.e. lower crop grain yields and higher weed biomass. Figures in cells are the number of treatments out of 59. The cover crop management treatment written in green (2a and 2b) is the only one which provided beneficial cover crop carry-over effect in the two subsequent crops.

higher weed biomass, in 12 combinations) carry-over effect in the subsequent spring barley. Only 3 out of the 59 combinations of cover crop mixture, soil resource availability and cover crop termination method alternative to the reference showed beneficial carry-over effect in spring barley (Fig. 6. 2a). These combinations corresponded to cover crop mixtures terminated with herbicide-use, regardless of soil resource availability. Cover crop management mainly showed no carry-over effect in the subsequent winter linseed (in 37 combinations). Beneficial carry-over effects in winter linseed were observed in 12 out of the 59 combinations of cover crop mixture, soil resource availability and cover crop termination method alternative to the reference (Fig. 6. 2b), but again, only when cover crops or bare soils were terminated with herbicide-use.

Among the 59 alternative combinations tested in each experiment, only one (and in experiment 2 only), showed beneficial carry-over effect in both subsequent spring and winter crops, i.e. unfertilised and irrigated 2-species legume-based cover crop mixture, terminated with herbicide-use (written in green in Figs. 6, 2a and 2b).

4. Discussion

Overall, even though the experiment was set-up in absence of tillage, in-crop chemical weeding and fertilisers, i.e. factors known to override the carry-over effect of cover crops (Adeux et al., 2021), our study showed that sowing cover crops (in comparison to bare soil) even with optimised management (irrigation, fertilisation and termination tool) had a weak effect on weeds and crop productivity through mulch and nitrogen supply effects. Secondly, our results showed that spring and winter crop yields generally decreased with increased weed biomass in crops, a well-known relationship (Oerke, 2006). Finally, the carry-over effects of cover crop management on weeds and crop productivity decreased over the crop succession, with winter linseed grain yield being improved through both a lower weed biomass and cover crop nitrogen

supply effects only when cover crops were terminated with herbicide-use and only in experiment 2. These observations validate our hypothesis that cover crops could affect the productivity of both subsequent spring and winter crops through their ability to suppress weeds and supply nitrogen. However, these effects were weak and variable (i.e. positive or negative). Thus, we discuss the importance of cover crop management for weed suppression in the subsequent crops and its impact on crop productivity, and provide insights for cover crop-based weed management and crop productivity in no-till systems.

4.1. Are cover crops a suitable tool to suppress weeds in subsequent crops in no-till systems?

Weed biomass in the subsequent crops was mainly driven by cover crop termination method, with herbicide-use being generally the only way to reduce in-crop weed biomass compared to the reference. In spring barley (i.e. the first subsequent crop), cover crop termination with herbicide-use reduced weed biomass in all combinations of cover crop mixture and soil resource availability in experiment 1, but not in experiment 2. In experiment 2, cover crop termination with herbicide-use reduced weed biomass in spring barley in only half of the alternative combinations. Differences in herbicide efficacy to terminate weeds between experiments could be related to contrasted weed development stages at cover crop termination (Janska et al., 2010). We argue that the development stage of the dominant weed species *Geranium dissectum* at cover crop termination was more advanced in experiment 2 than in experiment 1 (the biomass of *Geranium dissectum* being higher in experiment 2 than experiment 1, Fig. 3). The advanced phenological stage of *Geranium dissectum* in experiment 2 could have favoured its susceptibility to frost and reduced its biomass in the subsequent spring barley, whereas in experiment 1, *Geranium dissectum* was not winter-killed and continued its growth in the subsequent spring crop. In winter linseed (i.e. the second subsequent crop), cover crop termination

with herbicide-use was the only method that reduced weed biomass compared to the reference for almost all cover crop mixtures and soil resource availability combinations, but only in experiment 2. In experiment 1, the application of herbicides between spring barley and winter linseed probably overrode the potential cover crop carry-over effects on weeds, whereas in experiment 2, the waterproof silage tarp did not seem to alter cover crop carry-over effects. We argue that the dominant weed species in winter linseed *Geranium dissectum* was less abundant in herbicide-terminated plots in experiment 2 because it shed less seeds at spring barley harvest (*Geranium dissectum* biomass being lower in spring barley after herbicide-terminated plots than winter-killed or rolled plots, Fig. 3). Moreover, the biomass of spring barley volunteers (*i.e.* the second dominant weed species in winter linseed) was also lower in herbicide-terminated plots than in winter-killed or rolled plots (Fig. 3), suggesting that the combine harvest machine was more efficient in harvesting more grains in herbicide-terminated plots as weeds are known to increase harvest difficulties and seed losses (Burnside et al., 1969; Yvoz et al., 2021). Unfortunately, no phenological weed survey was done in this study to confirm our hypotheses and studies focusing on cover crop termination efficacy at different development stages of weeds remain absent from the literature.

In both subsequent crops and experiments, rolling did not improve weed management compared to the winter-kill reference. Autumn-emerging grasses, either weeds or crop volunteers such as wheat in our experiment, are known to be less sensitive to rolling at early stages (probably tillering in our experiment) than at flowering (Mirsky et al., 2009). These non-terminated weeds continued their growth in the subsequent spring barley in plots where cover crops were not terminated with herbicide-use (Fig. 3). In the actual context of potential glyphosate ban in Europe, it is important to note that, even if cover crop mixture can be designed to improve weed suppression (Bybee-Finley et al., 2022) and be frost-terminated with or without being rolled, these methods do not terminate most weed species emerging in cover crops and especially not the most troublesome grasses.

Implementing cover crops and managing soil resource availability was generally of little use for improving weed suppression in the subsequent crops. The weed suppressive effect of cover crops highlighted by Rouge et al. (2022) during the cover crop period did not effectively carry-over to the subsequent crops. In spring barley, most of the combinations of cover crop mixture and soil resource availability had no effect on weed biomass when terminated with winter-kill or rolling in experiment 1 and half of these combinations showed higher weed biomass in experiment 2. Thus, instead of showing a weed suppressive effect in the subsequent spring crop through mulching, we hypothesise that cover crops may have favoured weeds in the subsequent spring barley in experiment 2 by protecting them from frost or promoting new germinations, as soil temperature under the cover crops is usually higher than in bare soils during the winter (Blanco-Canqui et al., 2015). The dominant weed species (*i.e.* *Geranium dissectum* and winter wheat volunteers), which showed lower levels of biomass in cover crop mixtures than in bare soil during the cover crop period (Rouge et al., 2022), were probably at earlier development stages under cover crop mixtures than they were in the bare soil reference and thus less sensitive to winter-kill (Janska et al., 2010) or rolling (Mirsky et al., 2009).

Irrigation and nitrogen fertilisation did not significantly enhance the weed suppressive effect of cover crops during the autumn-winter cover cropping period (Rouge et al., 2022) or during the subsequent two-year crop sequence, at least from a biological standpoint. However, fertilised cover crop mixtures appeared to limit weed pressure in the subsequent spring barley of experiment 2. Fertilisation enhanced cover crop biomass productivity during the autumn-winter cover cropping period (Rouge et al., 2022), and higher mulch quantity, thickness and cover possibly enhanced weed suppression in the subsequent spring barley crop. However, this effect was weak compared to the effect of cover crop termination method. Therefore, this study highlights that cover crops may not play an essential role for weed suppression in the subsequent

crop, unlike suggested by many studies (Osipitan et al., 2018; Almousawi et al., 2020; Pittman et al., 2020; Pinto et al., 2021; Tadiello et al., 2022), probably due to the moderate level of cover crop productivity achieved in this study (*i.e.* mostly under 4 t ha^{-1} , Supp. Fig. 6). A further increase of cover crop nitrogen fertilisation (30 kg N ha^{-1} in our study) may have increased cover crop biomass and weed suppression in the subsequent crop through and increased mulch thickness and persistence effect as high soil nitrogen availability favours non-legume species in a cover crop mixture (Baraibar et al., 2020; Rouge et al., 2022). See Section 4.3 for further discussion on the role of cover crops for weed management in no-till systems.

4.2. Did cover crops improve subsequent crop productivity? How so?

Crop productivity was largely driven by weed biomass in both subsequent crops, with crop productivity being higher and weed biomass being lower than the reference mostly when cover crops were terminated with herbicide-use. However, cover crops also affected subsequent crop productivity after statistically removing the effect of weed biomass (*i.e.* crop grain yield residuals), potentially revealing a soil-mediated cover crop carry-over effect. Spring barley productivity (*i.e.* the first subsequent crop) was improved in experiment 1 after almost all the combinations of cover crop management alternative to the reference whereas only 7 combinations, all terminated with herbicide-use, improved spring barley productivity in experiment 2. In both experiments, cover crop mixtures showing the highest nitrogen content during the autumn period (Rouge et al., 2022) generally resulted in higher spring barley productivity in absence of weeds (*i.e.* after removal of weed biomass effects). Thus, we argue that cover crops supplied nitrogen to the subsequent spring barley, as shown in previous studies (Snapp et al., 2005; Marcillo and Miguez, 2017; Hunter et al., 2019; Adeux et al., 2021). The effect of cover crop nitrogen supply was even more visible when cover crops were terminated with herbicides, which are known to enhance nitrogen mineralisation (Snapp and Borden, 2005; Gaupp-Berghausen et al., 2015). Nevertheless, spring barley productivity was affected differently by the combinations of cover crop mixtures, soil resource availability and cover crop termination methods when considering or not the effect of weeds. Thus, weeds may have competed with the crop for resources (*e.g.* the nitrogen released by cover crops) or cover crops may have favoured nitrogen immobilisation in some combinations as microbial communities enrolled in nitrogen cycling can be affected by cover crop mixtures (Romdhane et al., 2019). Moreover, cover crop nitrogen release generally did not enhance spring barley productivity when cover crops were winter-killed, even though winter-kill has been shown to result in net nitrogen mineralisation (White et al., 2016), increasing nitrogen quantity in the soil (Romdhane et al., 2019). This observation suggests a mismatch between cover crop nitrogen release and spring barley nitrogen uptake in time. Finally, no notable beneficial soil-mediated effect was observed on spring barley productivity when cover crops were terminated with rolling, either because rolling favoured nitrogen immobilisation, as previously shown by Wells et al. (2013) and Clark et al. (2017), or because rolling favoured microbial denitrifiers responsible for nitrogen losses to the atmosphere, as shown by Romdhane et al. (2019) in our experiment 1. Hence, we conclude that optimising cover crop management to optimise cover crop nitrogen release in the subsequent crops is of little use, especially when weeds are not well managed at cover crop termination.

Finally, while most of the studies focused on one subsequent spring crop only, our study revealed that cover crop management can have an effect in the longer-term. However, this longer-term effect (*i.e.* higher subsequent winter linseed grain yield) was observed only in experiment 2 when fertilised and irrigated cover crop mixtures terminated with herbicide-use were implemented. Again, weeds may have blurred the relationship between cover crop nitrogen supply and crop productivity. As previously mentioned, weeds generated harvesting difficulties during harvest of spring barley in experiment 2, resulting in more abundant

spring barley volunteers in the winter linseed crop in non-herbicide-terminated combinations, which reduced linseed productivity (Marshall et al., 1995). Considering the cost of sowing cover crop mixtures at high seeding rates, applying 30 kg of nitrogen ha⁻¹, irrigating with 40 mm of water, and spraying herbicides, in comparison to the reference (i.e. bare soil, without fertilisation and irrigation, winter-killed), we advocate that return on investment is low and carry-over effects of cover crops are not economically affordable (Bergtold et al., 2019). We discuss this issue in the next section.

4.3. Insights for cover crop-based weed management and crop productivity in no-till systems

First of all, our study showed that herbicide use generally remained the best cover crop termination method to maximise the beneficial carry-over effect of cover crops in the subsequent crops, albeit weak and variable. Herbicide-use remains the most common method to terminate cover crops in no-till systems, partly because cover crop mixtures are usually not designed to be terminated by other methods such as rolling. However, even when cover crop mixtures are composed of cover crop species that are easily terminated at flowering (e.g. niger, phacelia, faba bean), herbicides are still applied to terminate the weeds growing below the cover crop canopy. Indeed, our results confirmed that rolling is not a weeding technique susceptible of substituting herbicide application, since most weeds at their early stage of development are not sensible to rolling. However, the number of active herbicide substances is decreasing on the market and the European Union is discussing the ban of glyphosate (Antier et al., 2020). Therefore, if glyphosate is banned, no other herbicide-based options will be available on the market in France to effectively terminate weeds and cover crops.

Cover crop termination relying on non-chemical methods question the role of cover crops in no-till systems to suppress weeds. Indeed, our experiments showed that only 4 combinations of cover crop mixture and soil resource availability terminated with winter-kill or rolling provided beneficial effects, and these effects were observed in only spring barley of experiment 1. Among these 4 combinations, 3 corresponded to 8-species non-legume-based cover crop mixtures, i.e. the most weed suppressive cover crop mixtures observed by Rouge et al. (2022) during the fallow period. Considering climate change will most likely decrease the amount and/or evenness of precipitation during the summer period, decrease the number of frost days and their intensity during the winter, and increase uncertainties in weather forecasting, we argue that weed management in glyphosate-free no-till systems cannot only rely on cover crops as concluded by other authors (Mischler et al., 2010; Dorn et al., 2013; Grint et al., 2022a), even when cover crop management (cover crop composition, fertilisation, irrigation) aims to optimise cover crop development. As a matter of fact, over the two experiments, we observed only one combination of cover crop management providing a beneficial carry-over effect in both subsequent spring and winter crops, and this combination was terminated with herbicide-use. Besides, this combination was neither the most weed suppressive nor the most productive cover crop mixture in terms of cover crop biomass during the fallow period (Rouge et al., 2022).

Our results also question the importance of cover crops for weed management in the subsequent crops. According to some studies, cover crops have to reach at least 8 t ha⁻¹ (Ashford and Reeves, 2003; Mirsky et al., 2013; Wallace et al., 2017) to 10 t ha⁻¹ (Ranaivoson et al., 2018) of dry matter to provide a significant weed suppressive mulch effect. In most pedoclimatic conditions, such levels of cover crop biomass can only be reached by highly competitive and tall cover crop species which over-winter and continue their growth in early spring (Baraibar et al., 2018). Reaching such a high level of cover crop biomass is nearly impossible with existing species and cultivars, particularly considering the short time frame available for cover crop growth during the autumn period, as it was the case in our study. To enlarge the cover crop growing time period, enhance cover crop biomass and limit nitrate leaching

(Thomsen and Hansen, 2014), farmers could consider relay cropping by broadcasting cover crop seeds before harvest of the preceding crops (St Aime et al., 2021). However, attention should be paid to cover crop species to avoid cover crop-crop competition (Evans et al., 2016).

As previously mentioned, weed management in no-till systems cannot only rely on the weed suppressive effect of cover crops observed during the autumn period, and we argue that the return on investment of implementing cover crop and enhancing its growth with optimised management could be low in no-till and herbicide-free systems. Cover crops have to be combined with other weeding strategies to effectively reduce in-crop weed pressure in no-till and herbicide-free systems (Fogliatto et al., 2020; Colbach and Cordeau, 2022). Using waterproof silage tarp in experiment 2 between the subsequent spring and winter crops was not a suitable weeding strategy, contrary to the conclusions drawn by Lounsbury et al. (2022), since weed biomass in linseed significantly increased compared to weed biomass in the previous spring barley. In addition, this tool is restricted to small plots and high value cash crops, such as vegetables. Further studies on different crops, pedoclimates, and rotations are required to confirm the generalisability of our conclusions. For instance, the weed suppressive effect of cover crops could be more important in diversified crop rotations, showing effects on both spring and winter crops, and with long fallow periods which favour the ability of cover crops to produce large amounts of biomass (Anderson, 2015). In addition to field experiments, simulations with mechanistic models (Colbach et al., 2021) of various crop successions integrating or not cover crops over many years and across diverse environmental conditions (e.g. soil, climate, weed flora) could be explored. These simulations could provide additional clues on the relative importance of cover crops for weed management and their impacts on crop productivity, particularly in no-till and herbicide-free cropping systems (Colbach and Cordeau, 2022).

5. Conclusion

The carry-over effects of cover crop management were investigated on two different fields in two different years by manipulating cover crop mixtures, soil resource availability at cover crop sowing (irrigation and nitrogen fertilisation) and cover crop termination methods. Our study showed that weeds in the subsequent crops and crop productivity were affected by multiple interactions between cover crop mixture, soil resource availability, cover crop termination method and experiment. The weed suppressive effect of cover crops observed during the cover crop period did not effectively carry-over to the subsequent crops, or was weak and unstable across crop succession. Cover crop termination method was the main driver of weed biomass in the subsequent crops, and weed biomass the main driver of reduced crop productivity. Herbicide-terminated cover crops generally achieved lower weed biomass in crops and higher crop productivity. Nevertheless, implementing cover crop and enhancing its growth with nitrogen fertilisation at cover crop sowing did not generally decrease weed biomass and increase crop productivity to a greater extent than leaving an unfertilised, non-irrigated bare soil terminated with winter-kill. This study highlights that cover crops may not play an essential role for weed management in no-till and herbicide-free systems, particularly at low levels of cover crop biomass production. Further replications over a broader range of pedoclimatic conditions should allow us to confirm this conclusion. Finally, while some cover crop mixtures could supply nitrogen to the subsequent crops, inefficient termination of weeds at cover crop termination allowed them to compete with the crop for this resource, and potentially mitigate the positive effect of cover crops. For this reason, studies focusing on cover crop carry-over effects on the subsequent crop should focus on disentangling the mechanisms responsible for beneficial and/or detrimental cover crop carry-over effects, such as weed suppression, nitrogen supply or nitrogen immobilisation.

Author's contribution

SC and JM designed the experiment. SC, DM and JPG funded the research. RH and JM conducted the experiment and collected soil data and all crop yields. SC, GA, HB and AM sampled biomass. AR analysed the data. AR, DM, GA, JPG and SC were involved in the interpretation of the results and contributed to writing the original version of the manuscript and improving the subsequent ones. All authors agreed to the final version of the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

Acknowledgments are expressed to the French Ministry of Agriculture which funded the Ph.D. thesis of Alicia Rouge.

We thank Léa Grall, Alexandre Lachmann, Florence Strbik, Eric Vieren, Emeline Felten, Claude Sarrasin, Séverin Yvoz, Marion Schwartz, Auxence Baudron (UMR Agroécologie – INRAE Dijon) and Benjamin Pouilly, Pascal Farcy, Jeremy Gervais, Philippe Chamoy, Loïc Dumont, Valérie Dufayet, Laurent Falchetto (U2E Domaine d'Époisses – INRAE Bretenière) for their assistance in the field. The project was funded by INRAE, the French Burgundy region (FABER Couv'Herbi project), the Casdar VANCOUVER, RAID and ENGAGED projects funded by the French Ministry in charge of Agriculture and Food (Ministère de l'Agriculture et de l'Alimentation, avec la contribution financière du compte d'affectation spéciale 'Développement agricole et rural'), ANR COSAC project (ANR-14-CE18-0007) and ANR PPR SPECIFICS project (ANR-20-PCPA-0008), and the European Union's Horizon 2020 Research and Innovation Program under grant agreement (no. 727321-IWM PRAISE).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2023.108899.

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