Long-term cover cropping in tillage-based systems filters weed community phenology: A seedbank analysis

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ABSTRACT

Context: Little is known about the long-term contribution of cover crops to weed management in tillage- and herbicide-based systems.
Research questions: Do cover crops mainly filter weed species capable of setting seeds during the fallow period? Can cover crop biomass productivity explain differences in weed suppression among cover crop species? Does reduced weed seedbank density translate into lower weed biomass and higher crop productivity?
Methods: Soil samples (0–15 cm) were collected in 2018 after cover crop termination and used in a greenhouse seedling emergence assay to assess the topsoil weed seedbank capable of germinating 25 years after the beginning of a split-plot experiment on tillage systems (conventional *vs.* reduced) and cover crops (bare soil control, *Brassica juncea* (brown mustard), *and Vicia villosa* (hairy vetch)). Total density and density of the 10 most abundant weed species in the topsoil seedbank were related to observations of weed species visual soil cover, total weed biomass, cover crop biomass, and cash crop grain yield made during the six years which preceded the weed seedbank assessment. Weed seedling density was also used to compute community weighted mean of germination and flowering period.
Results: In comparison with the bare soil control, hairy vetch suppressed total weed seedling density by 40%, whereas brown mustard showed no effect. In comparison with the bare soil control, hairy vetch suppressed weed seedling density of *Cerastium glomeratum* (−87%), *Veronica persica* (−86%), *Capsella bursa-pastoris* (−57%) and *Poa annua* (−42%), whereas brown mustard only suppressed *C. bursa-pastoris* (−65%) and *V. persica* (−49%). The suppressive effect of hairy vetch on these four species translated into a significant reduction of community weighted mean of autumn/winter germination period and March to July flowering period. The contrasted suppressive effect of brown mustard and hairy vetch on weed seedling density of these four species was related to contrasted competitive interactions during the four previous cover crop seasons. However, differences in weed suppression between hairy vetch and brown mustard could not be fully explained by differences in biomass productivity. Management intensity (*e.g.* herbicides and tillage) potentially smoothed out differences in weed suppression between cover crop treatments because no effect of cover crops were observed on total weed biomass or gain yield of the subsequent crops over the 2012–2017 period.
Conclusion: Cover crops contribute little to weed management in herbicide and tillage-based cropping systems.
Implication: The weed suppressive effect of cover crops should be further explored in cropping systems which minimise herbicide use and tillage intensity.

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1. Introduction

Agro-ecological weed management approaches are required to reduce cropping system reliance on herbicides (Petit et al., 2018). Cropping system diversification is currently identified as one of the five pillars of integrated weed management (IWM) (Riemens et al., 2022). In temporal terms, one option to diversify cropping systems is through the introduction of cover crops (CC), which represent a promising tool to suppress weeds and provide a wide set of other ecosystem services (*e.g.* increase in soil organic matter and nitrogen availability or reduction of soil erosion) (Blanco-Canqui et al., 2015). Numerous studies have focused on the weed suppressive effect of CC in no-till systems (Osipitan et al., 2019) because CC residues are maintained on the soil surface after CC termination and act as a barrier against weed germination and establishment in the subsequent crops (Teasdale, 1996). However, in no-till systems, subsequent crop establishment (*i.e.* termination of CC, weeds and/or crop volunteers) is often ensured by herbicide applications (*e.g.* glyphosate), usually resulting in higher total herbicide use in such systems (Adeux et al., 2019). Hence, tillage remains one of the most cost-effective CC termination methods in a context of pesticide reduction (Möhring et al., 2020) or prohibition (*e.g.* organic farming, herbicide ban). Research is required to identify if CC also contribute to long-term weed management in tillage-based cropping systems (Schipanski et al., 2014), or whether their weed suppressive effect is mainly effective in the short term (*i.e.* during the fallow period) and/or associated to surface mulch in no-till systems.

Reducing weed seedbank density represents a central task in IWM. It can be achieved by reducing weed seed viability or by reducing seed set of growing weeds. In tillage-based systems, CC could reduce weed seed production during the fallow period through competition for light, water and soil resources (Teasdale et al., 2007; Lawley et al., 2012), or through the release of different allelopathic compounds, as reported for *Brassica* spp. (Rehman et al., 2019) and *Vicia* spp. (Geddes et al., 2015).

Weed seed capture studies could provide valuable information on which weed species can germinate and set seeds during the fallow period which separates cash crop harvest and sowing but remain scarce (Brennan and Smith, 2005). Indeed, the weed suppressive effect of CC has been repeatedly affirmed based on reduced weed biomass in the presence of a CC during the fallow period (Bàrberi and Mazzoncini, 2001; Wittwer et al., 2017; Florence et al., 2019; Rouge et al., 2022). Hence, the long-term weed suppressive effect of CC, reflected through shifts in the weed seedbank, remains poorly documented, especially in tillage-based systems (Restuccia et al., 2020; see Nichols et al., 2020 in the case of no-till systems). Autumn sown CC species could reduce biomass of long-cycle autumn/winter germinating weed species (*e.g. Lolium multiflorum* Lam., *Alopecurus myosuroides* Huds., *Papaver rhoeas* L.) which are terminated by tillage operations and/or herbicide applications before being able to flower, and hence lack to contribute to a significant reduction of the weed seedbank, compared to a bare soil control managed identically (except CC sowing). In temperate environments, very few weed species are capable of completing their life cycle and producing a substantial number of seeds during the short fallow period which separates harvest of a preceding winter crop (June-July) and sowing of a subsequent one (October). However, cropping systems which include crop sequences of two summer crops (*e.g.* maize-maize) or a winter and summer crop (*e.g.* durum wheat-maize) leave a 5–6 month time frame available for weeds to complete their life cycle and for autumn-sown/spring-terminated CC to suppress them. Hence, over the long-term, autumn-sown/spring-terminated CC could reduce relative abundance of weed species showing a non-seasonal or autumn/winter germination period and an early spring flowering period (Moonen and Barberi, 2004).

The weed suppressive effect of CC during the fallow period has essentially been related to CC biomass productivity (MacLaren et al., 2019; Osipitan et al., 2019), which varies according to multiple factors (CC type, growing degree days, resource availability…) (Baraibar et al.,

2018; Rouge et al., 2022). However, recent studies have shown that certain CC species could be more suppressive than others at lower levels of biomass productivity (Adeux et al., 2021; Rouge et al., 2022). Such results could suggest the importance of trait hierarchies (*i.e.* whom possesses the most advantageous value of given trait) between CC and weed species, such as differences in nitrogen acquisition rate (Tribouillois et al., 2015) or early soil cover (Brennan and Smith, 2005), or release of allelopathic compounds, which are not necessarily reflected by biomass productivity. Contrasted competitive or non-competitive interactions between combinations of CC and weed species could result in weed:CC species-specific responses (Moonen and Barberi, 2004). For example, hairy vetch (*Vicia villosa* Roth.) could suppress rosette forming weed species more efficiently than brown mustard (*Brassica juncea* L. Czern.), due to a dense surface mat, whereas brown mustard could suppress more efficiently N demanding species than hairy vetch, due to quick N pre-emption (Tribouillois et al., 2015).

The suppressive effect of CC on weed seed set during the fallow period (Brennan and Smith, 2005), combined with the potential release of allelopathic compounds after soil incorporation of CC residues (Moonen and Barberi, 2006), could result in reduced weed seed recruitment from the seedbank in subsequent cash crops and hence, reduced weed:crop competition and crop yield loss (Cousens et al., 1987). However, the long-term cumulative effect of such effects and their importance for long-term weed management in subsequent cash crops remains poorly documented, especially when considering potential interactions with other management factors, such as tillage and herbicides (Schipanski et al., 2014). The meta-analysis carried out by Osipitan et al. (2018) reported that CC could suppress weeds at the beginning of cash crop growth to a similar extent than mechanical and chemical weed control methods. However, no long-term effects on weed seedbanks or potential interactions with tillage system were explored. In a later meta-analysis, Osipitan et al. (2019) reported that CC provided greater in-crop weed suppression in reduced tillage systems (where CC are mechanically terminated) than in no-till systems (where CC are chemically terminated). Such results could arise from efficient mechanical termination of CC and weeds (Mirsky et al., 2010) but also the diluting effect of tillage on weed seed distribution in the soil profile. Indeed, strong weed community filters (*e.g.* tillage and/or herbicides, choice of crop) may override the significance of weaker weed community filters (*e.g.* CC) when combined at the cropping system level (Smith and Mortensen, 2017), and explain the lack of a positive effect of CC on subsequent crop yield through weed suppression (Bàrberi and Mazzoncini, 2001; Hodgdon et al., 2016; Osipitan et al., 2019).

The general objective of this study was to investigate the long-term effect of two functionally contrasted CC species, brown mustard (non-legume, rosette species, high N uptake) and hairy vetch (legume, climbing, N fixer), on weed species abundance, weed community phenology, and crop productivity, across two tillage-based systems (CT: conventional tillage; RT: reduced (non-inversion) tillage). More specifically, we focused on whether weed seedbank status in 2018 could be related to contrasted CC:weed interactions during the fallow period and the importance of CC for weed management and subsequent cash crop productivity. To do so, multiple data types were combined: CC biomass and weed species cover in CC (2012, 2014, 2016 and 2018), subsequent cash crop grain yield and weed biomass in cash crops (2012–2017), a greenhouse weed seedbank germination assay in 2018, and information on weed species germination and flowering periods. We asked (i) Do winter CC mainly filter weed species capable of germinating and setting seed during the winter fallow period? (ii) Are differences in weed seedbank replenishment between CC species related to CC biomass at termination? (iii) Do CC contribute to weed management in subsequent cash crops and/or to subsequent cash crop yield? We hypothesized that, in tillage- and herbicide-based systems, (i) CC would reduce overall weed seedbank density mainly by filtering weed species capable of germinating and setting seed during the cover cropping period, due to termination methods (*i.e.* soil tillage) which effectively terminate CC

and weeds but prevent the barrier effect of surface CC mulch on weed germination and development in the subsequent crops, (ii) that weed species would show contrasted responses between CC, irrespective of CC biomass productivity, and (iii) that long-term contribution of CC to weed management in cash crops of tillage-based systems would be of little agronomic relevance due to the overriding effect of management intensity (*e.g.* tillage and herbicides).

2. Material and methods

2.1. Site characteristics

The long-term "Cover crop" experiment was located at the Centre for Agri-environmental Research 'E. Avanzi' of the University of Pisa, San Piero a Grado, Pisa, Central Italy (43∘40′N, 10∘19′E). The soil was a Typic Xerofluvent with loam texture (see Supplementary tables in Adeux et al., 2021 for precise information concerning soil characteristics). The site is subject to a Mediterranean climate, with mild winters, very warm summers and rainy autumns (see Supp. Fig. 1 for rainfall, minimum and maximum temperatures over the 2011–2018 period, *i.e.* the period of focus in this article). Further information concerning climate, cropping sequences and weed communities can be found in Bàrberi and Mazzoncini (2001), Moonen and Barberi (2004), Mazzoncini et al. (2011) and Adeux et al. (2021).

2.2. Experimental set-up

Over the 1993–2018 period of the long-term experiment, three crop sequences followed one another: (i) a grain maize (*Zea mays* L.) monoculture (1993–1998 (Bàrberi and Mazzoncini, 2001)), (ii) a two-year durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf.) Husn.) – grain maize rotation (1999–2006 (Moonen and Barberi, 2004)) and (iii) a four-year durum wheat – sunflower (*Helianthus annuus* L.) – durum wheat – grain maize rotation (2007–2018 (Adeux et al., 2021), the present study covering only the 2011–2018 period, Fig. 1). Due to

massive seed predation and crop failure, sunflower in 2016 was replaced by grain millet (*Panicum miliaceum* L.). The experiment was set up as a split-split plot in a randomized complete block design. The three experimental factors were tillage system (main plots), N fertilization (sub-plots), and CC type (sub-sub plots). However, only the farmers' standard nitrogen rate level (N2) (*i.e.* 200 kg N ha^{-1} as urea for maize, 120 kg N ha^{-1} as ammonium nitrate for wheat and 100 kg N ha^{-1} as urea for sunflower) was sampled in the present study, yielding a split-plot in a randomized complete block design (main plot: tillage, subplot: CC). The two tillage systems tested, *i.e.* conventional tillage (CT) and reduced tillage (RT), differed in terms of tillage disturbance (intensity and frequency) and herbicide use (type and quantity, see Fig. 1 for an overview of management practices over the 2011–2018 period considered in this study). Primary tillage was ensured by moldboard ploughing in CT (*i.e.* inversion tillage, 30 cm depth) and by chiseling in RT (*i.e.* no inversion, 30 cm depth, only before CC). Both CT and RT relied on disk or rotary harrow and field cultivator (10–20 cm depth) for secondary tillage. Three of the four CC treatments present on the long-term experiment were included in the present study: (i) a non-legume (rye (*Secale cereale* L.) from 1993 to 2001 and brown mustard onwards, except in 2018 when it was replaced by white mustard (*Sinapis alba* L.), an even faster growing mustard species (Tribouillois et al., 2015) which aimed to increase soil water availability in the spring), (ii) a high nitrogen supply legume (subterranean clover (*Trifolium subterraneum* L.) from 1993 to 2001, 50% hairy vetch plus 50% rye in 2003, and hairy vetch as pure stands onwards, except in 2016 when it was replaced by common vetch (*Vicia sativa* L.), due to unavailability of seeds on the market) and (iii) a winter bare soil, weedy control. Due to limited available space in the greenhouse for the seedbank assessment (see following section), the low nitrogen supply legume treatment (crimson clover (*Trifolium incarnatum* L.) from 1993 to 2003 and squarrose clover (*Trifolium squarrosum* L.) onwards) was not included in this study. This was also justified by the fact that previous studies on the same experiment showed no suppressive effect of squarrose clover on total weed biomass during the winter fallow period
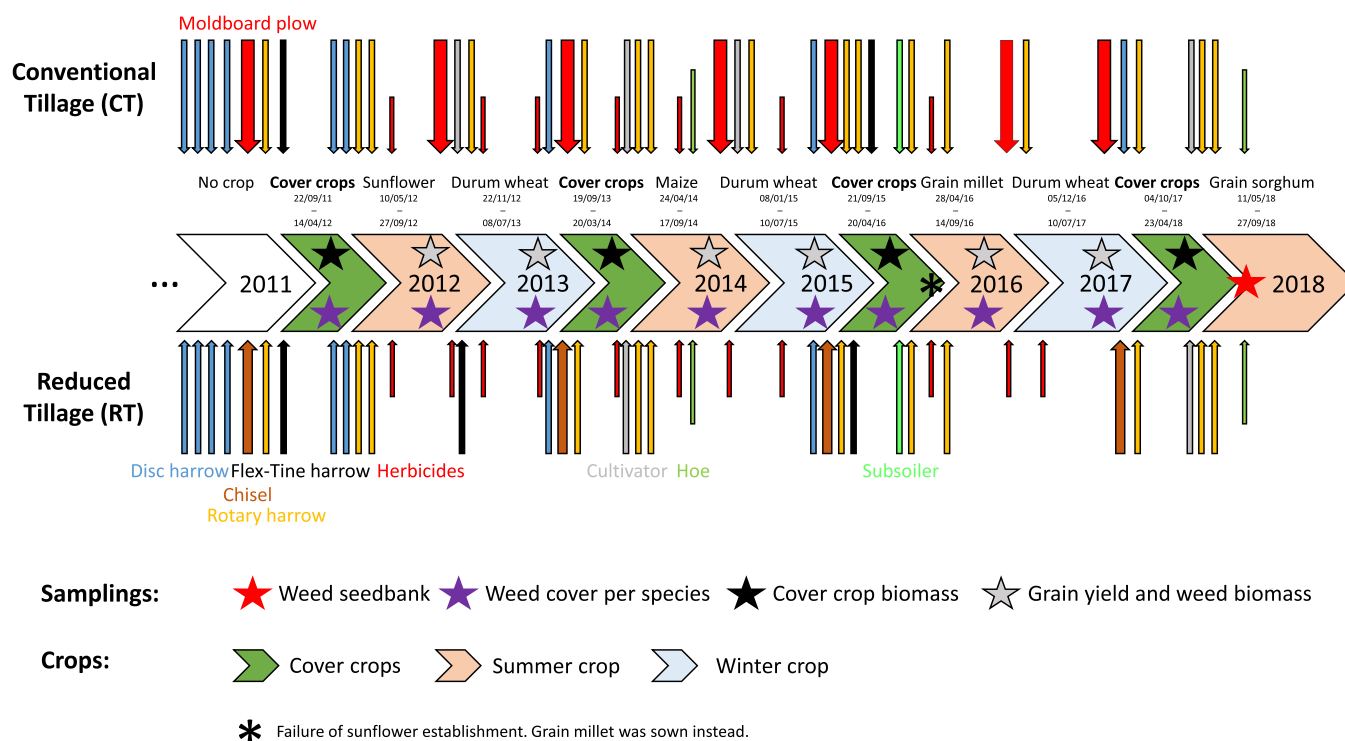

Fig. 1. Chronological overview of the crop sequence, management practices in conventional (CT) or reduced tillage (RT) systems, and samplings (in both cover crops and cash crops) during the six years which preceded seedbank sampling (harvest 2012 to harvest 2017) and for which weed data was available. Colour codes for management practices are indicated at first occurrence. Dates below crops refer to sowing and harvest dates (or destruction in the case of cover crops).

(Adeux et al., 2021). During the first crop sequence (*i.e.* maize mono-culture, 1993–1998), CC were broadcast seeded manually after maize harvest in autumn and terminated the following spring before the subsequent maize was sown. During the two following crop sequences (1999–2006 and 2007–2018), CC were broadcast seeded manually after durum wheat harvest in autumn (on 22/09 in 2011, 19/09 in 2013, 21/09 in 2015, and 04/10 in 2017) and terminated at the early flowering stage (BBCH 60) the following spring (on 10/04 in 2012, 20/03 in 2014, 20/04 in 2016, and 23/04 in 2018) before the subsequent summer crop was sown. Hence, CC were grown every year during the first crop sequence and every two years during the two following crop sequences, covering a growth period of roughly 6 months every time (Fig. 1). In both tillage systems, CC sowing was systematically preceded by tillage. Main tillage operations (*i.e.* moldboard ploughing for CT or chiseling for RT) were always carried out before CC seedbed preparation, which was ensured by disk or rotary harrow in both tillage systems. In CT, CC were terminated mechanically (*i.e.* CC residues were incorporated in the soil with a disk harrow). In RT, CC were terminated chemically (*i.e.* CC residues were left on the soil surface after an application of glyphosate at 0.9 kg a.i. ha^{-1}) from 1994 to 2002 and mechanically with a disk harrow afterwards. Disk harrowing was preceded by chopping when CC biomass was high. Control plots (*i.e.* bare soil fallow) were managed identically to CC plots, with the exception of CC sowing. Each of the 6 treatments (2 tillage systems x 3 CC treatments) was replicated in four blocks, yielding a total of 24 plots (*i.e.* statistical unit, 21 m wide and 11 m long) for the present study.

2.3. Weed seedbank sampling and greenhouse weed seedbank germination assay

The superficial weed seedbank (0–15 cm) of all 24 plots was sampled one week after CC chopping, on the 27/04/2018 (Fig. 1). Samples were limited to 15 cm depth to reflect the active seedbank (*i.e.* weeds capable of germinating after CC termination) rather than to provide a precise estimation of total seedbank density. Indeed, very few weed species (absent in this experiment) are capable of germinating below 15 cm (Benvenuti et al., 2001; Grundy et al., 2003) and shallow tillage operations at or after CC termination limit the recruitment of seeds from deeper soil horizons. Four composite samples of four soil cores each (auger diameter= 4 cm) were taken from each of the 24 plots, resulting in a total of 96 seedbank samples. Samples were maintained in cold storage (5 °C) for two months and submitted to a greenhouse germination assay on the 02/07/2018. Each composite sample of four soil cores was spread on top of a geotextile membrane which was placed in a plastic tray (length: 44 cm, width: 29 cm, depth: 7 cm) filled only 1 cm deep with vermiculite substrate. Soil samples did not exceed a depth of more than 2 cm once spread, thereby ensuring that all germinated individuals could emerge (Mahé et al., 2021). Micro-aspersion irrigation frequency was adjusted weekly to prevent soil samples from drying out. Vermiculite substrate and holes at the bottom of plastic trays ensured adequate drainage. Weed seedlings in each sample were counted per species and immediately removed every two to three weeks from 20/07/2018–25/10/2018. When germination of spring/summer species declined near the end of summer, samples were let to dry out and were then crumbled by hand before applying irrigation again. This aimed to mimic stubble cultivation and to further stimulate germination of autumn/winter species.

2.4. Weed phenology and community weighted means (CWM) based on weed seedbank density

Data on germination and flowering period of all the weed species identified during the weed seedbank assessment were retrieved from a weed field guide (Mamarot and Rodriguez, 2014) and the Italian Acta Plantarum website (Acta Plantarum, 2007), respectively, to test whether CC could influence weed community functional structure in terms of phenology. Five germination periods were identified, ranging from non-seasonal to spring, summer (or staggered over spring and summer), or autumn/winter preferential. Flowering period was chosen as a proxy to seed set, considering the lack of references on seed maturity timing for a wide range of weed species. Five flowering periods were also identified, ranging from non-seasonal to different overlapping periods between March and October. Community weighted means (CWMs) of germination and flowering period reflect the relative proportion of weed community total abundance (here seedling density) represented by species possessing a given trait value (in this case, a specific germination or flowering period). CWMs were computed at the plot level (the four composite samples of four soil cores were pooled) to overcome the patchy distribution of weed species and the low area covered by one composite seedbank sample.

2.5. Vegetation sampling in cover crops and cash crops

All possible available data concerning CC biomass production and weed cover over the 2012–2018 period were used to relate weed seedbank status in 2018 to contrasted competitive interactions during the previous cover cropping periods and investigate the importance of CC for weed management in cash crops.

Weed cover in CC was visually assessed per species prior to CC termination in two 1 m^2 quadrats per plot in 2012 or two 0.5 m^2 quadrats per plot in 2014, 2016, and 2018 (Fig. 1). Weed species cover was also visually assessed per species at grain filling/crop maturity (Fig. 1), *i.e.* after all weeding operations, in sunflower in 2012 (two 1 m^2 quadrats per plot), in durum wheat in 2013 (two 1 m^2 quadrats per plot), in maize in 2014 (four 0.5 m^2 quadrats per plot), in durum wheat in 2015 (four 1 m^2 quadrats per plot), in grain millet in 2016 (two 0.54 m^2 quadrats per plot) and in durum wheat in 2017 (two 1 m^2 quadrats per plot).

CC biomass was collected prior to CC termination in 2012, 2014, 2016, and 2018 in two 0.5 m^2 quadrats per plot, in the same areas as those sampled for weed cover in CC (Fig. 1). Crop biomass was collected at crop maturity in durum wheat in 2013, 2015, and 2017 (two 1 m^2 quadrats per plot), in sunflower in 2012 and maize in 2014 (two 2 m^2 quadrats per plot), and in grain millet in 2016 (two 0.54 m^2 quadrats per plot, Fig. 1), in the same areas as those sampled for in-crop weed species cover. Weed biomass was collected concurrently in the same quadrats but was limited to half of the quadrat surface for sunflower (1 m^2) and to a fourth for maize (0.5 m^2, Fig. 1). All biomass samples were oven dried for 48 h at 60 °C. Crop samples were then passed through a threshing machine to assess grain yield at 0% moisture content.

2.6. Statistical analysis

All response variables were analyzed with the R software version 4.1.1 (R Development Core Team, 2021) and the development (for zero-inflation) version 1.1.2.3 of the glmmTMB package (Brooks et al., 2017) in order to account for the hierarchical structure of the experiment (split-plot), sampling designs (pseudo-replication at the sub-plot level) and the different type of response variables (biomass: always positive and continuous, counts: greater than zero and whole, cover: bounded between 0% and 100%).

Separate models were fitted for each year (when multiple years of data were available for a given response variable) to keep model complexity low. All response variables were modelled as a function of block, CC, tillage system, and the interaction between the two latter. Tillage strip (unique ID per combination of block and tillage system accounting for the split plot design) and plot (unique ID per combination of block, tillage system, and CC accounting for pseudoreplication at the plot level) were always included as random intercepts (except for plot in CWM analysis because data was pooled at the plot level). For analysis of weed seedling density (total and for the top ten most abundant weed species), three models with different distributions and/or

parametrization appropriate for count data (negative binomial with linear or quadratic parametrization or Poisson, all log linked) were fitted and the model with the lowest Akaike's Information Criterion (AIC) was retained for analysis. A beta family with logit link was used for analysis of CWM of germination and flowering period and weed species cover data (transformed into proportion, *i.e.* between 0 and 1). Rather than adding a small constant when a weed species was absent from certain quadrats, all 36 possible combinations of zero-inflated fixed and random effects were compared for weed species cover and the model with the lowest AIC was retained for analysis. For biomass data (CC biomass, weed biomass in cash crops, cash crop grain yield), three log-linked distributions appropriate for continuous and positive data (Tweedie, gamma, and Gaussian) were fitted and the model with the lowest AIC was retained for analysis. A list of all the models retained for analysis can be found in Supp. Table 1. Significance of fixed effects was determined by type III likelihood ratio tests as implemented in the monet package (Singmann, 2022). Contrasts between treatment levels were adjusted with the emmeans package (Lenth et al., 2022). Model diagnostics were inspected with the DHARMa package (Hartig, 2022).

3. Results

3.1. Greenhouse weed seedbank germination assay

Overall, 1842 seedlings corresponding to 44 weed species were identified during the greenhouse weed seedbank germination assay (Table 1). *Poa annua* L. represented 74.1% of total seedling density whereas the other top 10 species represented between 4.5% and 0.4% of the total. Community level analyses were hence highly influenced by the variability of *Poa annua*. Among the top ten species, five (*i.e. Poa annua* L., *Cerastium glomeratum* Thuill., *Stellaria media* (L.) Vill., *Veronica persica* Poir., *Capsella bursa-pastoris* (L.) Medik.) showed the combined theoretical ability to germinate and flower during the cover cropping period (September – April). Four other top species (*i.e. Digitaria sanguinalis* (L.) Scop., *Chenopodium album* L., *Solanum nigrum* L., *Polygonum aviculare* L.) were typical of spring-summer sown crops (sunflower, maize, grain millet). Tables summarizing all significance of effects (block, CC, tillage, and CC:tillage interaction) for all the response variables analyzed, least square means, and multiple comparisons can be found in Supp. Table 2–8.

3.2. Effect of cover crop and tillage system on weed seedling density

Hairy vetch significantly reduced total weed seedling density by 40% (across both tillage systems, Fig. 2, Supp. Table 2) compared to the winter bare soil control. No significant differences were observed between the winter bare soil control and brown mustard across both tillage systems. Although the interaction between tillage system and CC was not significant, it is worth noting that, compared to the winter bare soil control, brown mustard reduced total weed seedling density by 22% in CT whereas it increased it by 25% in RT.

Of the ten most abundant weed species (Supp. Table 2), hairy vetch significantly reduced seedling density of *Poa annua* (−42%, Fig. 3A), *Cerastium glomeratum* (−87%, Fig. 3C), *Veronica persica* (−86%, Fig. 3E), and *Capsella bursa-pastoris* (−57%, Fig. 3G), compared to the winter bare soil control. The effect was consistent across both tillage systems. Compared to the winter bare soil control, brown mustard showed a significantly suppressive effect only on *Veronica persica* (−49%, Fig. 3E) and *Capsella bursa pastoris* (−65%, Fig. 3G), which was also consistent across both tillage systems. Compared to the winter bare soil, both CC species showed a suppressive effect on *Stellaria media* (−36% for brown mustard and −13% for hairy vetch) but the differences were not significant so no further investigation was carried out (Supp. Table 2). No significant interaction between CC and tillage system was detected for seedling density of any of the ten most abundant weed species (Supp. Table 2). Nevertheless, it is worth noting that brown mustard reduced

Table 1

Summary of the weed species identified in the seedbank germination assay and present in the analyses, the number of individuals counted per species (and percentage out of total density considering *Poa annua* or not), and their germination and flowering periods. Species are named according to The World Flora Online (http://www.worldfloraonline.org/).

Species Latin names (ranked by decreasing order of abundance)	n° of individuals counted	% total	Germination period	Flowering period
Poa annua L.	13591	74.1	non-seasonal	non-seasonal
Cerastium glomeratum Thuill.	821	4.5	autumn/winter	March - July
Digitaria sanguinalis (L.) Scop.	720	3.9	summer	June - October
Stellaria media (L.) Vill.	617	3.4	non-seasonal	non-seasonal
Polygonum aviculare L.	499	2.7	spring	May - November
Veronica persica Poir.	433	2.4	non-seasonal	non-seasonal
Sonchus asper (L.) Hill	377	2.1	non-seasonal	June - October
Chenopodium album L.	340	1.9	spring/summer	June - October
Solanum nigrum L.	189	1.0	summer	May - November
Capsella bursa-pastoris (L.) Medik.	81	0.4	autumn/winter	non-seasonal
Taraxacum sp.	78	0.4	non-seasonal	non-seasonal
Erigeron sumatrensis Retz.	75	0.4	non-seasonal	June - October
Portulaca oleracea L.	73	0.4	summer	May - November
Cardamine hirsuta L.	56	0.3	autumn/winter	March - July
Datura stramonium L.	51	0.3	summer	June - October
Setaria pumila (Poir.) Roem. & Schult.	42	0.2	summer	June - September
Amaranthus retroflexus L.	38	0.2	summer	June - October
Plantago major L.	38	0.2	spring/summer	May - November
Lolium multiflorum Lam.	27	0.1	non-seasonal	June - September
Verbena officinalis L.	25	0.1	spring	June - October
Thlaspi arvense L.	18	0.1	non-seasonal	June - September
Echinochloa crus-galli (L.) P.Beauv.	15	0.1	summer	June - October
Veronica arvensis L.	15	0.1	autumn/winter	indifferent
Epilobium tetragonum L.	14	0.1	non-seasonal	June - September
Heliotropium europaeum L.	11	0.1	summer	June - October
Convolvulus arvensis L.	10	0.1	spring/summer	May - November
Lepidium coronopus (L.) Al-Shehbaz	10	0.1	autumn/winter	March - July
Helminthotheca echioides (L.) Holub	10	0.1	autumn/winter	June - September
Cuscuta sp.	8	< 0.1	summer	June - October
Euphorbia helioscopia L.	8	< 0.1	non-seasonal	non-seasonal
Kickxia spuria (L.) Dumort.	8	< 0.1	spring/summer	June - October
Poa trivialis L.	8	< 0.1	autumn/winter	March - July
Anagallis arvensis L.	6	< 0.1	spring	May - November
Centaurium erythraea Rafn	6	< 0.1	spring	June - September

(*continued on next page*)

Table 1 (*continued*)

Species Latin names (ranked by decreasing order of abundance)	n° of individuals counted	% total	Germination period	Flowering period
Setaria viridis (L.) P. Beauv.	5	< 0.1	summer	June - October
Arenaria serpyllifolia L.	4	< 0.1	non-seasonal	March - July
Plantago lanceolata L.	4	< 0.1	non-seasonal	non-seasonal
Erigeron canadensis L.	3	< 0.1	non-seasonal	June - October
Viola arvensis Murray	2	< 0.1	autumn/winter	June - September
Vulpia myuros (L.) C.C. Gmel.	2	< 0.1	autumn/winter	March - July
Arabidopsis thaliana (L.) Heynh.	1	< 0.1	autumn/winter	March - July
Hypericum humifusum L.	1	< 0.1	spring/summer	June - September
Lamium amplexicaule L.	1	< 0.1	non-seasonal	non-seasonal
Fallopia convolvulus (L.) Á. Löve	1	< 0.1	spring	June - October
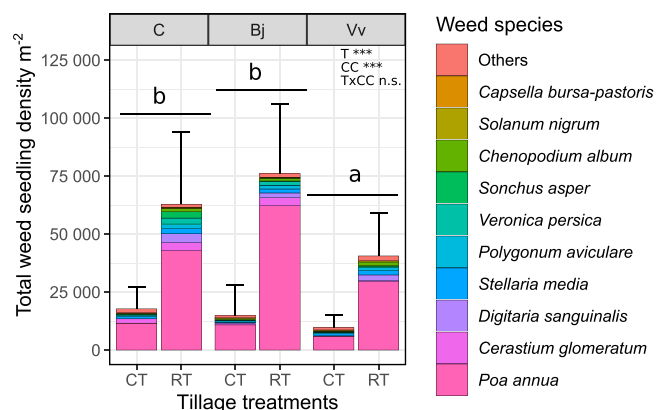
Fig. 2. : Effect of cover crop (C: bare soil; Vv: *Vicia villosa*; Bj: *Brassica juncea*) and tillage treatments (CT: conventional tillage; RT: reduced tillage) on observed mean weed seedling density (sampled after cover crop termination in 2018 and computed over all composite seedbank samples). Error bars represent standard deviation computed over all composite seedbank samples. Cover crop treatments sharing the same letter are not significantly different at $P < 0.05$ when pooled across tillage treatments. See Supp. Table 2 for statistical details. Note: *Vicia villosa* was replaced by *Vicia sativa* and *Brassica juncea* was replaced by *Sinapis alba* in the 2015–2016 and 2017–2018 growing seasons, respectively.

seedling of *Poa annua* by 16% in CT whereas it increased it by 52% in RT, compared to the winter bare soil control.

3.3. Effect of cover crop on weed community phenology

Compared to the winter bare soil control, both brown mustard and hairy vetch reduced the proportion of autumn-winter germinating species (brown mustard: −33%; hairy vetch: −66%, Fig. 4A) and March-July flowering species (brown mustard: −37%; hairy vetch: −62%, Fig. 4B) across both tillage systems, *i.e.* CWM autumn-winter germination period and CWM March-July flowering period, respectively (Supp. Table 3). Nevertheless, the difference with the winter bare soil control was significant only for hairy vetch for both CWMs. CC had no significant effect on the proportion of non-seasonal germinating and flowering species, probably due to the high variability of the dominant (Table 1) weed species *Poa annua* (particularly in RT for the winter bare soil control and brown mustard).

3.4. Investigation of competitive interactions during the past cover cropping periods

3.4.1. Cover of Poa annua

In 2012, *Poa annua* was not recorded in 15 out of 16 quadrats in hairy vetch (across both tillage systems, Fig. 3B). Hence, no statistical tests including hairy vetch were performed. When the CC level hairy vetch was removed from the analysis (Supp. Table 4), no significant effect of CC was observed, even though percentage cover of *Poa annua* was 41% lower in brown mustard than in the winter bare soil control (across both tillage systems). In 2014, hairy vetch significantly reduced percentage cover of *Poa annua* by 58% (across both tillage systems and in comparison with the winter bare soil control), whereas no significant differences could be observed between brown mustard and the winter bare soil control. In 2016, CC showed a marginal effect ($P = 0.10$), even though both common vetch and brown mustard reduced percentage cover of *Poa annua* by 50% and 37% (across both tillage systems and in comparison with the winter bare soil control), respectively. In 2018, hairy vetch significantly reduced percentage cover of *Poa annua* by 70% (across both tillage systems and in comparison with winter bare soil control). Although the interaction between tillage system and CC was not significant, it is worth noting that percentage cover of *Poa annua* was 3 times greater in white mustard (which replaced brown mustard in 2018) plots than in the winter bare soil control plots in RT and similar between white mustard and winter bare soil control plots in CT.

3.4.2. Cover of Cerastium glomeratum

In 2012, *Cerastium glomeratum* was recorded in only two quadrats out of 48 (Fig. 3D). In 2014, both hairy vetch and brown mustard reduced percentage cover of *Cerastium glomeratum* (across both tillage systems), by 72% and 43%, respectively, but the difference with the winter bare soil control was significant for hairy vetch only (Supp. Table 4). In 2016, *Cerastium glomeratum* was recorded in only 16 out of 48 quadrats (across all six treatments), *i.e.* not enough for a reasonable further investigation. The deviation of brown mustard in RT was mainly driven by two quadrats with 10% cover (all others were ≤1%). In 2018, no differences in percentage cover of *Cerastium glomeratum* were observed between CC treatments in CT. In RT however, hairy vetch reduced percentage cover of *Cerastium glomeratum* by 91% compared to the winter bare soil control whereas white mustard increased its cover by nearly a 4-fold.

3.4.3. Cover of Veronica persica

Hairy vetch and brown mustard significantly reduced percentage cover of *Veronica persica* in both 2012 (hairy vetch: −78%, brown mustard: −51%) and 2014 (hairy vetch: −49%, brown mustard: −43%) across both tillage systems, compared to the winter bare soil control (Fig. 3F, Supp. Table 4). In 2016, no significant differences were observed between CC treatments. In 2018, hairy vetch significantly reduced percentage cover of *Veronica persica* by 60% (across both tillage systems and compared to the winter bare soil control) whereas no difference was observed between white mustard and the winter bare soil control.

3.4.4. Cover of Capsella bursa-pastoris

In 2012, *Capsella bursa-pastoris* was not recorded in 14 out of 16 quadrats for brown mustard (across both tillage systems). Hence, no statistical tests including brown mustard were performed. When the CC level brown mustard was removed, the model highlighted a significantly higher suppressive effect of hairy vetch on *Capsella bursa-pastoris* in RT (−82%) than CT (−63%, Fig. 3H, Supp. Table 4). In 2014, hairy vetch and brown mustard significantly reduced percentage cover of *Capsella bursa-pastoris* (by 63% and 49%, respectively, compared to the winter bare soil control) but in RT only. In 2016, *Capsella bursa-pastoris* was not recorded in any quadrats for brown mustard (across both tillage types). After the removal of brown mustard from the model, it highlighted a significantly 68% lower cover of *Capsella bursa-pastoris* (across both
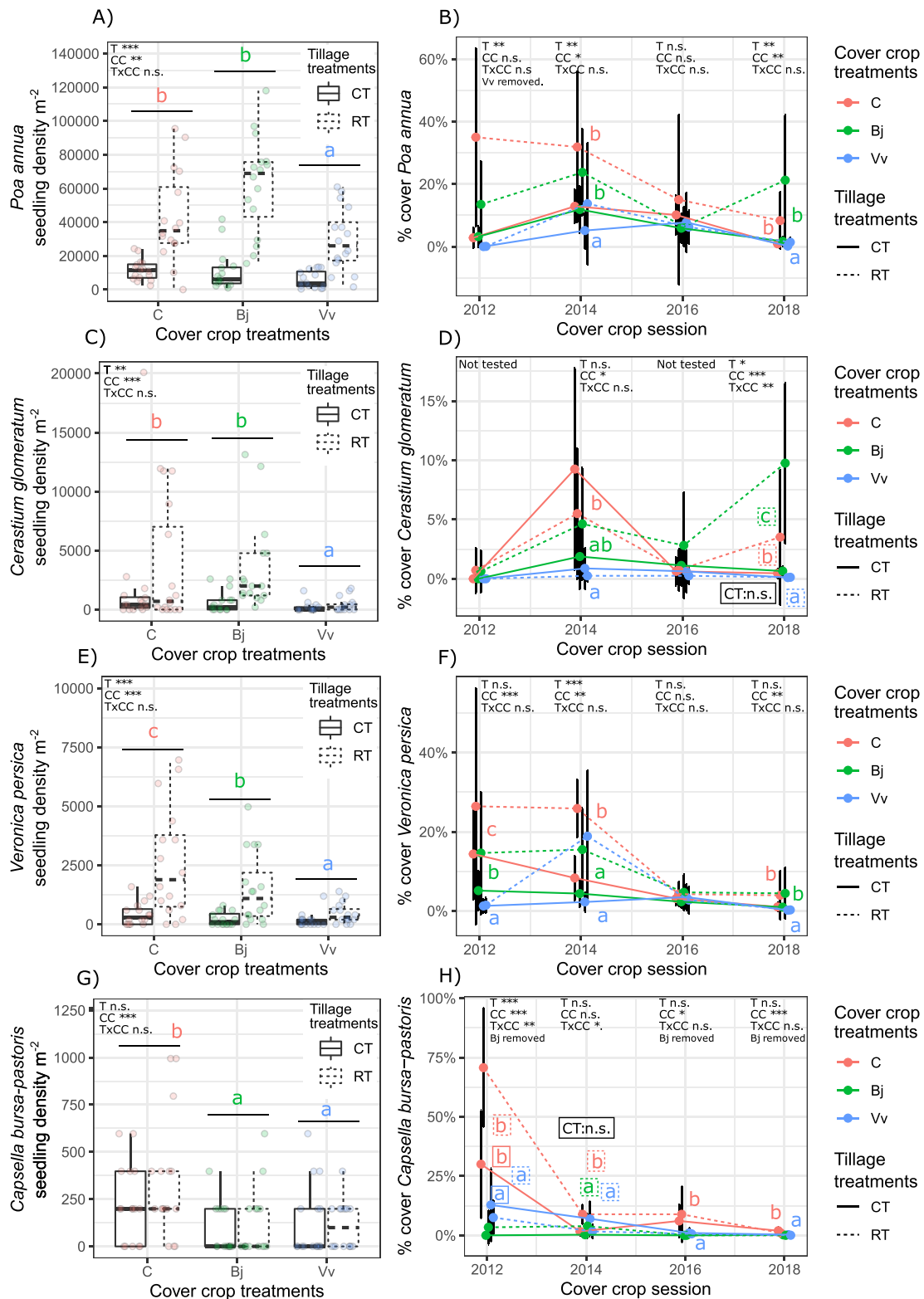
Fig. 3. : Left - Effect of cover crop (C: bare soil; Vv: *Vicia villosa*; Bj: *Brassica juncea*) and tillage treatments (CT: conventional tillage; RT: reduced tillage) on seedling density (sampled after cover crop termination in 2018) of *Poa annua* (A), *Cerastium glomeratum* (C), *Veronica persica* (E), and *Capsella bursa-pastoris* (G). Data points represent composite seedbank samples (4 composite samples of 4 soil cores per plot). Cover crop treatments sharing the same letter are not significantly different at P < 0.05 when pooled across tillage treatments. See Supp. Table 2 for statistical details. Right - Effect of cover crop (C: baresoil; Vv: *Vicia villosa*; Bj: *Brassica juncea*) and tillage treatments (CT: conventional tillage; RT: reduced tillage) on percentage cover (dot and whiskers: observed mean and standard deviation over all quadrats, respectively) of *Poa annua* (B), *Cerastium glomeratum* (D), *Veronica persica* (F), and *Capsella bursa-pastoris* (H) in the 2011–2012, 2013–2014, 2015–2016, and 2017–2018 cover crop seasons. Treatments sharing the same letter (boxed in continuous or dashed lines: contrasts within CT or RT, respectively) are not significantly different at P < 0.05. See Supp. Table 4 for statistical details. Note: *Vicia villosa* was replaced by *Vicia sativa* and *Brassica juncea* was replaced by *Sinapis alba* in the 2015–2016 and 2017–2018 growing seasons respectively.
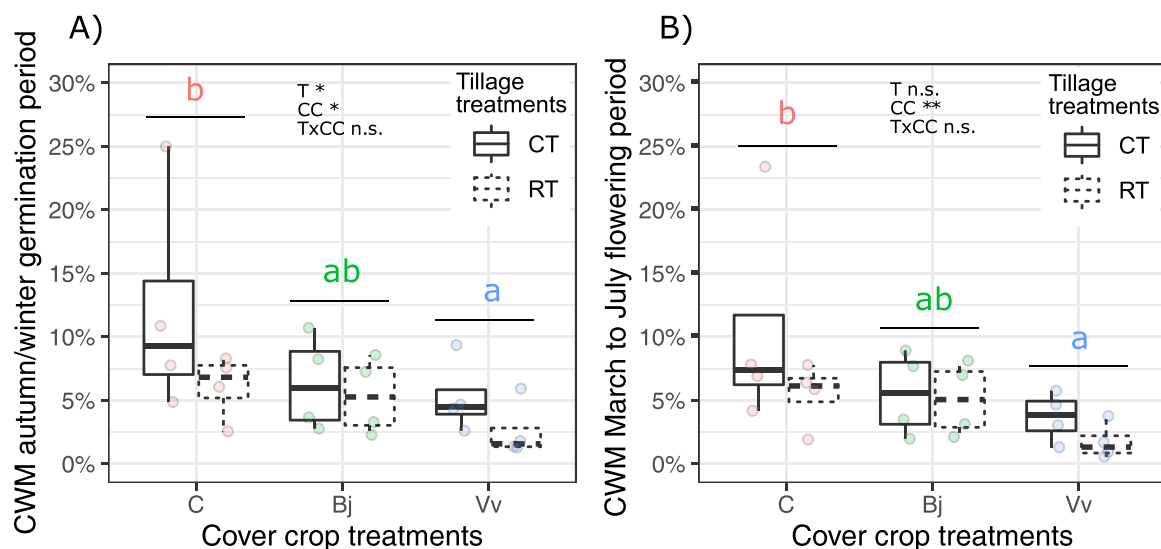
Fig. 4. : Effect of cover crop (C: bare soil; Vv: *Vicia villosa*; Bj: *Brassica juncea*) and tillage treatments (CT: conventional tillage; RT: reduced tillage) on community weighted means (CWM) of autumn/winter germinating species (A) and March to July flowering species (B). Community weighted means were weighted by seedling density and computed at the plot level (the 4 composite samples of 4 soil cores were pooled). CWMs can be interpreted as the relative proportion of weed community total abundance (here seedling density) represented by species possessing a given trait value (in this case, a specific germination or flowering period). Treatments sharing the same letter (boxed in continuous or dashed lines: contrasts within CT or RT, respectively) are not significantly different at $P < 0.05$. See Supp. Table 3 for statistical details. Note: *Vicia villosa* was replaced by *Vicia sativa* and *Brassica juncea* was replaced by *Sinapis alba* in the 2015–2016 and 2017–2018 growing seasons respectively.

tillage systems) in common vetch than in the winter bare soil control. In 2018, *Capsella bursa-pastoris* was not recorded in any quadrats of white mustard in RT. After the removal of white mustard from the model, it highlighted a significantly 81% lower cover of *Capsella bursa-pastoris* in hairy vetch than in the winter bare soil control (across both tillage systems).

3.4.5. Cover crop biomass

In both 2012 and 2014, brown mustard was significantly more productive than hairy vetch across both tillage systems, by 69% and 99%, respectively (Fig. 5, Supp. Table 5). In 2016, brown mustard showed 8 times more standing biomass than common vetch across both tillage systems, partially because winterkilling of common vetch had already initiated its decomposition. The interaction between tillage and CC in 2016 was justified by the fact that common vetch showed 2 times

Fig. 5. : Effect of cover crop (C: bare soil; Vv: *Vicia villosa*; Bj: *Brassica juncea*) and tillage treatments (CT: conventional tillage; RT: reduced tillage) on cover crop biomass productivity (dot and whiskers: observed mean and standard deviation computed over all quadrats) during the 2011–2012, 2013–2014, 2015–2016 and 2017–2018 cover crop seasons. Treatments sharing the same letter (boxed in continuous or dashed lines: contrasts within CT or RT, respectively) are not significantly different at $P < 0.05$. See Supp. Table 5 for statistical details DM: dry matter. Note: *Vicia villosa* was replaced by *Vicia sativa* and *Brassica juncea* was replaced by *Sinapis alba* in the 2015–2016 and 2017–2018 growing seasons respectively.

more standing biomass in CT than RT (albeit low biomass in both cases: CT= 75 g DM m^{-2}; RT= 29 g DM m^{-2}). In 2018, hairy vetch was 7 times more productive than white mustard across both tillage systems. Once again, the interaction between tillage and CC was justified by the fact that white mustard was 4 times more productive in CT than RT (albeit low biomass in both cases: CT= 146 g DM m^{-2}; RT= 33 g DM m^{-2}).

3.5. Contribution of cover crops to long term weed management in cash crops

All four weed species (*i.e. Poa annua, Cerastium glomeratum, Veronica persica, Capsella bursa-pastoris*) were observed at very low cover, if not absent, in all winter and summer sown cash crops (2012–2017). Only *Veronica persica* reached an average cover greater than 1% in a given crop (maize in 2014) but no significant effect of CC was observed (Supp. Table 6).

CC showed a significant effect on weed biomass in cash crops in only two out of 6 years (durum wheat 2015 and 2017) and differences between CC levels during these two years were of little biological relevance (Supp. Fig. 2, Supp. Table 7). Indeed, the significant effect of CC in durum wheat 2015 was driven by a 3 g DM m^{-2} weed biomass difference between hairy vetch and the winter bare soil control in CT. Similarly, the significant effect of CC treatments on weed biomass in durum wheat in 2017 was driven by a difference of 26 g DM m^{-2} of weed biomass between the winter bare soil control (40 g DM m^{-2}) and hairy vetch/common vetch (14 g DM m^{-2}) across both tillage systems.

Cash crop grain yield was influenced by CC treatments in sunflower in 2012 and grain millet in 2016 only. In 2012, sunflower grain yield was reduced by 23% in the presence of brown mustard in RT, whereas no differences were observed between hairy vetch and the winter bare soil control in RT, or between all CC treatments in CT (Supp. Fig. 3, Supp. Table 8). In 2016, grain millet grain yield was overall low but increased by 30% in the presence of hairy vetch/common vetch (across both tillage systems and compared to the winter bare soil control), whereas no differences were observed between brown mustard and the winter bare soil control.
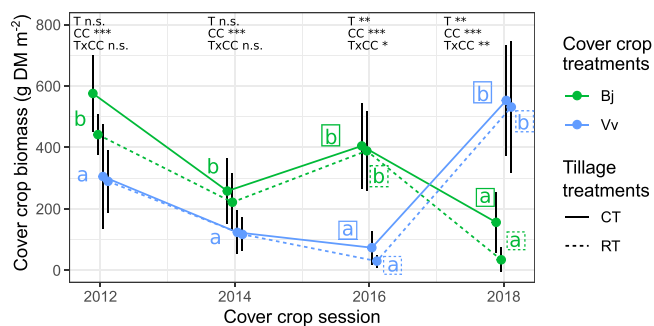
4. Discussion

4.1. Long-term cover cropping reduces weed seedbank replenishment in tillage-based systems

Previous studies investigating the effect of CC on weed seedbanks have reported contrasting results (Moonen and Barberi, 2004; Mirsky et al., 2010; Alonso-Ayuso et al., 2018). Moreover, the majority of relevant studies were conducted in plots where CC treatments were implemented less than 3 years and hence, provided little information on the long-term effect of CC on weed seedbanks. Nichols et al. (2020) recently synthesized seedbank data from 5 long-term rye CC experiments but no clear conclusion could be drawn: rye had a negative effect on seedbank density in 2/5 cases, no effect in 2/5 cases, and a non-biologically meaningful increase in 1/5 cases. Moreover, most experiments were conducted in no-till systems, where CC carry-over effects are expected to be more pronounced, due to the concentration of weed seeds on the soil surface (Swanton et al., 2000) and the presence of a surface mulch (Teasdale, 1996). Our results showed that long-term cover cropping with hairy vetch reduced total seedling density by 40% across both the CT and RT systems compared to the winter bare soil control. To our knowledge, this is the first time such sizeable effects of CC on weed seedbanks are detected in the absence of a surface mulch, thereby validating our hypothesis of a weed suppressive effect of CC on weed seedbank replenishment in tillage-based systems.

Greater total seedling density was observed after white mustard (which replaced brown mustard during the 2017–2018 cover cropping period with the aim to increase water availability in the spring due to its quicker growth) than after the winter baresoil control plots in RT (+25%) whereas an opposite trend was observed in CT (−22%). Differences were even more pronounced (−16% in CT and +52% in RT) when considering seedling density of the dominant weed species *Poa annua* (which represented 74% of total abundance). Indeed, the suppressive effect of white mustard/brown mustard on *Veronica persica* and *Cerastium glomeratum* partially compensated the increase in *Poa annua* in RT plots. The lack of a significant interaction between tillage system and CC on total seedling density and seedling density of *Poa annua* could be related to high variability in white mustard/brown mustard and baresoil control plots in RT and a weak suppressive of white mustard/brown mustard in CT plots, along with low statistical power. Greater seedbank density of *Poa annua* after white mustard/brown mustard than after the winter bare soil control in RT plots could be related to the poor development of white mustard (which was even more pronounced in RT plots than CT plots) due to excessive rainfall (839 mm from sowing to termination) and the positive effect of twenty-five years of cover cropping on soil fertility. Indeed, Mazzoncini et al. (2011) reported a positive effect of both CC species on soil organic carbon and nitrogen content on the same experiment. Greater nutrient or water availability were possibly not recovered by the poorly established and developed white mustard CC and could have rather enhanced growth and seed set of the nitrophilic and mesohydric weed species *Poa annua* (Warwick, 1979). This hypothesis is supported by greater cover of *Cerastium glomeratum* in white mustard plots than in winter bare soil control plots in RT but is not completely satisfactory as opposite trends were observed for the nitrophilic weed species *Lolium multiflorum* (data not shown). Future studies manipulating plant communities could shed light on the complexity of interactions (competitive and non-competitive) between CC and weed species, as well as the cascading effect between weed species, under contrasted levels of resource availability (Rouge et al., 2022).

Dominance of weed species with transient seedbanks, such as *Poa annua* (Lush, 1988), could point out to a disproportionate effect of recent farming practices and dominant species in weed community seedbank analyses (Cordeau et al., 2022) and the need for repeated seedbank measurements (Cardina et al., 2002) to disentangle the short and long-term effects of farming practices on weed seedbanks. Nevertheless, *Poa annua* can also be maintained over the long-term by reduced or no

tillage practices (Törresen et al., 2006).

4.2. Long-term cover cropping filters community weed phenology

Species with non-seasonal germination periods represented the greatest part of total seedling density. The dominance of species with non-seasonal germination could result from the selection of generalist species in cropping systems integrating a diverse suite of weed management tactics (e.g. crop rotation, tillage, herbicides, CC) (Fried et al., 2010) and may explain the difficulty to reveal long-term CC effects on weed seedbanks. Indeed, species with non-seasonal germination have more opportunities to overcome periodic disturbances and replenish their seedbank than species with strict germinations periods.

Compared to the winter bare soil control, hairy vetch and brown mustard both significantly suppressed *Veronica persica* (although hairy vetch to a greater extent) and *Capsella bursa-pastoris*, whereas only hairy vetch suppressed *Poa annua* and *Cerastium glomeratum*. All four of these species presented the ability to germinate and flower during the winter cover cropping period. Only a trend was observed for the fifth species sharing these characteristics, i.e. *Stellaria media*, possibly because of high plasticity in growth habit (Turkington et al., 1980), which could allow it to partially overcome competition. The suppressive effect of CC on weed species sharing these characteristics was highlighted at the community level by a negative effect of hairy vetch on CWM autumn/winter germination period and CWM March-July flowering period, thereby validating our first hypothesis. This is the first time to our knowledge that shifts in weed community phenology in response to CC are reported, whether in tillage-based or no-till systems. None of the ten most abundant weed species showing spring or summer germination periods and flowering later in the season (summer or late summer) were affected by CC species. Moreover, the effect of CC on weed biomass in subsequent cash crops was only detectable in winter crops. These results stress that – in tillage-based systems – fall sown / spring terminated CC reduce weed seed set of species capable of completing their life cycle during this time frame and hence, do not result in lower weed abundance in subsequent summer crops. In line with these observations, Swanton et al. (1999) reported no effect of a rye CC in a 9-year maize monoculture. Similarly, Lawley et al. (2011) showed that forage radish (*Raphanus sativus* L. var. *longipinnatus*) could provide complete suppression of winter annual weeds from fall to spring but that these effects did not carry-over to the subsequent summer crop.

4.3. Long-term cover cropping acts as a repetitive little hammer

The contrasted suppressive effect of CC on seedling density of *Poa annua*, *Cerastium glomeratum*, *Veronica persica*, and *Capsella bursa-pastoris* was likely related to contrasted competitive interactions during the cover cropping period. The suppressive effect of hairy vetch on seedling density of these four species was related to reduced cover of all four species during the cover cropping periods. Similarly, the suppressive effect of brown mustard on seedling density of *Veronica persica* and *Capsella bursa-pastoris* was related to reduced cover of these two species during the cover cropping periods. Absence of a weed suppressive effect of brown mustard on cover of *Veronica persica* in 2016 and 2018 (when brown mustard was replaced by white mustard) but a significantly weed suppressive effect on seedling density could point to a long-term carry-over effect of CC on weed seedbanks, as brown mustard significantly reduced cover of *Veronica persica* in 2012 and 2014. The suppressive effect of hairy vetch on seedling density of *Cerastium glomeratum*, although it was absent in 2012 and nearly so in 2016, also highlights that weed:CC competitive outcomes may result from CC:weed competitive interactions in specific years, which promoted weed species germination and development. The fact that reduced cover (i.e. a proxy for biomass - seed production) during the cover cropping period translated into lower seedbank density only for these four species stresses the importance of accounting for weed species phenology when studying the

suppressive effect of CC during the fallow period only (MacLaren et al., 2019). In their framework for long-term management of weed seed-banks, Swanton and Booth (2004) classified management tactics according to whether they increased seed mortality, reduced weed seed germination and emergence, removed above-ground biomass, or reduced seed production. Our results suggest that CC terminated by soil incorporation in conventional or reduced tillage systems limit seed production during the cover cropping phase (with respect to a winter bare soil control). Moreover, the additive and negative effect of cover cropping and conventional tillage on weed seedbank replenishment underlines a complementary effect of these two management practices, as previously suggested by Mirsky et al. (2010).

4.4. Cover crop biomass productivity is not the unique driver of weed suppression

Higher weed suppressive effect on weed species cover (and hence seedling density) could not easily be related to greater CC biomass productivity. Hairy vetch suppressed *Poa annua*, *Cerastium glomeratum*, and *Veronica persica* to a greater extent than brown mustard (and *Capsella bursa-pastoris* to a similar extent) although it produced significantly less biomass prior to CC termination in 2012 and 2014 (and 2016 but hairy vetch was replaced by common vetch, whose biomass was sampled after winterkilling). The low productivity of white mustard (which replaced brown mustard in 2018, before weed seedbank sampling) precludes once again clear-cut conclusions between brown mustard and hairy vetch. For example, the weed suppressive effect of brown mustard on cover of *Poa annua* or *Cerastium glomeratum* could have been compensated by high seed production in 2018 in white mustard, which would explain the lack of effect of brown mustard on germinable seed-bank density of *Cerastium glomeratum* or *Poa annua*. Only elements in support of our second hypothesis can be provided. For example, the difference between CC was striking during the 2012 cover cropping period, when the highly productive brown mustard showed no effect on percentage cover of *Poa annua*, whereas hairy vetch nearly filtered out the species. CC:weed specific responses have been reported in many studies, yet the mechanisms at play remain to be identified (Moonen and Barberi, 2004; Alonso-Ayuso et al., 2018; Rouge et al., 2022). Similarly, Nichols et al. (2020) found no relation between CC productivity or stability and weed seedbank abundance. The greater weed suppressive effect of hairy vetch could rather result from key competitive traits (Funk and Wolf, 2016) allowing it to smother short cycle weed species of small stature. It could be hypothesized that, contrary to brown mustard, hairy vetch can overcome early weed establishment due to its ability to climb on top of its competitors and to create a dense mat at the soil surface which inhibits light penetration and the further development of weeds, especially after mild and rainy autumns suitable for its quick development. Moreover, early weed nitrogen uptake can be compensated by nitrogen fixation in the case of hairy vetch but not brown mustard. An additional explanation for the contrasted effect of CC species on weed seed germination could include the allelopathic characteristics of each CC species (Geddes et al., 2015; Rehman et al., 2019). Unfortunately, allelopathic effects could not be disentangled from the other effects previously depicted (Mahé et al., 2022). Weed density samplings during CC growth and at early growth stages of subsequent crops could have allowed further exploration.

4.5. Management intensity overrides the weed suppressive effect of cover crops

The suppressive effect of CC on weed seedling density had little repercussions on weed:cash crop competitive interactions (here assessed through weed biomass) and crop grain yield, as we hypothesized and as previously reported by Dorn et al. (2015), Lawley et al. (2011), or Osipitan et al. (2018). Out of the four species for a which a CC effect was observed on weed seedling density, only *Veronica persica* was observed

in one of the previous cash crops with an average percent cover > 1% (*i. e.* maize in 2014). Moreover, CC showed no effect on cover of *Veronica persica* in this summer crop in 2014. It appears unlikely that these species were strictly associated to the winter cover cropping period considering their generalist character (Fried et al., 2010), or their ability to also germinate in winter sown durum wheat. Alternatively, we hypothesize that differences in weed seedbank density and hence emerged weed density between CC and control plots did not translate into differences in weed cover (or biomass) in cash crops because efficient weed control (*e.g.* herbicides and/or mechanical weeding) homogenized these differences (or completely filtered out the species) early in the season, as observed by Bàrberi and Mazzocini (2001), Dorn et al. (2015), or Lawley et al. (2011). Indeed, all four species are susceptible to a wide range of herbicides and are not usually considered problematic. Weed density measures per species prior to weeding operations (Osipitan et al., 2018) would have allowed to test such hypothesis and are warranted in future experiments. It also cannot be rejected that these short-cycle species were present in cash crops but not captured by weed samplings (species cover, total weed biomass) at crop maturity (Hanzlik and Gerowitt, 2016). In this case, the weed suppressive effect of CC treatments should have translated into a positive effect of CC on crop productivity but this was not observed in any of the cash crops over the 2012–2017 period. We rather attribute the positive effect of hairy vetch on grain millet grain yield to improved soil fertility (nitrogen content, organic matter…), that sufficiently met the low nutrient demand of this short-cycle crop. Similarly, Hodgdon et al. (2016) attributed greater sorghum-sudangrass hybrid (*Sorghum bicolor* (L.) Moench x *S. bicolor* var. *sudanense*) yield (and weed biomass) after different legume-based CC to nitrogen fixation and release. Furthermore, it also appears probable that potential differences in initial weed density across CC treatments did not result into considerable variations of weed biomass and crop productivity due to the low competitive effect of all four species. As a matter of fact, Storkey et al. (2006) identified *Cerastium fontanum* (a weed species closely related to *Cerastium glomeratum*), *Capsella bursa-pastoris*, and *Poa annua* as species which should be maintained in the agro-ecosystem due to their low competitive effects and high importance value for biodiversity (approximated by associated number of invertebrate species). In any case, it can be concluded that the contribution of CC to long-term weed management in tillage-based systems was overall low.

5. Conclusion

Little is known about the contribution of cover crops to long-term weed management in tillage and herbicide-based systems. Here, we show that, in such systems, cover crops have the potential to filter generalist short-cycle weed species capable of germinating and flowering during the cover cropping period (*e.g. Poa annua*, *Cerastium glomeratum*, *Veronica persica*, *Capsella bursa-pastoris*). The greater suppressive effect of hairy vetch on weed seedbank replenishment could not be related to biomass productivity but could rather reflect the importance of traits such as climbing ability, allowing it to overcome early competition and create a dense smothering mat, the ability to overcome nitrogen limitation through nitrogen fixation, and/or allelopathy. The suppressive effect of cover crops on seedbank replenishment of certain weed species did not translate into greater crop productivity because management intensity (*e.g.* tillage and herbicides) probably homogenized initial differences in emerged weed density and/or because the targeted species were poor competitors. This study stresses the importance of accounting for tillage system and overall management intensity when studying weed community response to cover cropping and when evaluating the real (*i.e.* effective) contribution of CC to weed management.

CRediT authorship contribution statement

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.

Acknowledgments

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2022.108769.

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