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Cover crops promote crop productivity but do not enhance weed management in tillage-based cropping systems

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Abstract

Cover crops (CC) have been proposed as a promising ecological tool to manage weeds and increase crop productivity. We hypothesized that the repeated use of CC could increase crop yield directly through nitrogen release or indirectly through a modification of weed communities. Data were collected on CC biomass, weed biomass, weed community composition, and crop yield during one complete rotation cycle (CC-sunflower-durum wheat-CC-maize-durum wheat) from 2011 to 2015, 18 years after the beginning of a long-term, single-site, split-split plot experiment focusing on tillage systems (conventional (CT) vs. reduced (RT)), nitrogen rates and CC species (*Brassica juncea* (L.) Czern. (Bj), *Vicia villosa* Roth (Vv), *Trifolium squarrosum* L. (Ts) and a winter baresoil control). Univariate response variables were analyzed with generalized mixed effect models and community data was analyzed with multivariate linear models. During the fallow period, Bj suppressed weed biomass by 79, 75, 34, and 28% in CT:2012, RT:2012, CT:2014 and RT: 2014, respectively, whereas Vv only suppressed weed biomass by 69 and 37% in CT and RT in 2012, respectively. Greater weed suppression for Bj than Vv or Ts at lower levels of CC productivity (200 g dry biomass/m^2) was attributed to the importance of CC traits such as nitrophily, allelopathy and/or quick soil coverage. The weed suppressive effect of CC during the fallow period was greater in CT (β_{slope}=-0.28) than in RT (β_{slope}=-0.16), possibly due to contrasted weed flora and/or CC growth dynamics. Tillage and herbicides overrode the potential effect of CC on weed communities in the subsequent crops. The integration of a highly productive legume CC, such as Vv, allowed to increase maize productivity by 65 and 23% at N0 and N1, respectively. CC effects on sunflower and durum wheat yield were limited due to dry weather conditions and quick nitrogen release in time, respectively. These results highlight the importance of legume CC for sustaining crop productivity while reducing nitrogen fertilisation. Further studies need to identify less intensive weed management practices that can complement potential CC effects rather than override them.

Keywords: weed:crop interference, weed composition, *Vicia villosa* Roth, *Brassica juncea* (L.) Czern., reduced tillage, ploughing

Highlights:

- The weed suppressive potential of cover crops is not limited to biomass production
- Cover crops had no clear effect on weed communities in the subsequent weeded crops
- Management intensity overrode potential cover crop effects on weed communities
- *Vicia villosa* allowed to reduce N fertilisation and reach maximum maize yield

1. Introduction

Heavy reliance on agricultural inputs (*e.g.* herbicides, nitrogen (N) fertilisers) and intensive tillage to increase crop productivity has generated a wide array of environmental impacts (*e.g.* water and air pollution, soil erosion, decline in weed diversity and soil fertility) (Stoate et al., 2009). Hence, reconciling crop productivity and environmental sustainability represents one of the main challenges of agriculture worldwide (Stoate et al., 2009). Cover crops (CC) appear as a promising tool to improve weed management and crop productivity (Blanco-Canqui et al., 2015). However, farmers currently lack information on how to maximize the long-term contribution of contrasted CC species to weed management and crop productivity (Blanco-Canqui et al., 2015).

CC effects on crop productivity have been related to the amount of inorganic N released by CC through residue mineralisation and its dynamics with respect to the subsequent crop N requirements in time (Magdoff, 1991; Salmerón et al., 2011). Beside soil resource availability, CC traits (*e.g.* relative growth rate, N acquisition rate) and management (*e.g.* termination date and strategy) dictate the total amount of N accumulated in CC biomass and its C:N ratio (Wayman et al., 2015), which determines the proportion of N released from CC residues through N mineralisation (*e.g. Fabaceae* with low C:N mineralize quicker than *Brassicaceae* or *Poaceae* with high C:N) (Justes et al., 2009). CC effects on the productivity of subsequent crops have been shown to decrease with increasing levels of N fertilisation of the subsequent crops (Marcillo and Miguez, 2017). However, little is known on the long-term cumulative effect of contrasted cover crop types on crop productivity and their potential to reduce N fertilisation (Constantin et al., 2011). Similarly, little is known on how tillage intensity may influence CC biomass production (Salmerón et al., 2011; Büchi et al., 2018) or mineralisation rate of CC residues over the long-term (Varco et al., 1989; Drinkwater et al., 2000). CC residues are expected to mineralize faster under conventional than reduced tillage because of greater soil temperatures, pore space, and contact between CC residues and soil bacteria (Lupwayi et al., 2004). Nevertheless, reduced tillage has been shown to improve soil aggregate stability (Sapkota et al., 2012), soil biological activity, and soil water content (Blevins et al., 1983), conditions which are also favourable to CC residue mineralization. Furthermore, increased N availability after CC termination could stimulate weed germination (Wayman et al., 2015), alleviate weed:crop competition for N, or increase weed:crop competition for a new limiting resource (Casper and Jackson, 1997).

CC can offset weed:crop competitive relationships through a modification of weed community abundance and/or structure in the subsequent crops (Buchanan et al., 2016; Baraibar et al., 2018). The weed suppressive effect of CC has been repeatedly affirmed based on the negative relationship between CC and weed biomass during the fallow period (Wittwer et al., 2017). However, authors have also highlighted the importance of CC traits (*e.g.* rapid emergence, early soil cover, N uptake, allelopathy) in suppressing weeds during the fallow period (Dorn et al., 2015). Hence, uncertainty remains as to whether or not the weed suppressive effect of CC during the fallow period can be simply attributed to biomass productivity (Baraibar et al., 2018; Smith et al., 2020). Moreover, little is known on how CC management practices can be adapted to maximize weed suppression during the fallow period. Excessive N fertilisation of previous cash crops could give N-demanding CC species, such as *Brassica juncea* (L.) Czern., a competitive advantage over weeds during the subsequent fallow period (Sturm et al., 2017). Certain CC species could be better suited to grow in specific tillage systems and compete with the target weed community (*e.g.* grasses under reduced tillage). Furthermore, little research has focused on how weed suppression during the fallow period transcribed into weed:crop interference in the subsequent crops (Brennan and Smith, 2005; Buchanan et al., 2016).

The weed suppressive effect of CC in the subsequent crops has mainly been affirmed in no-till systems (*i.e.* cropping systems in which CC residues are left on the soil surface and act as a mechanical barrier against weed germination) (Teasdale, 1996), based on the negative relationship between biomass of CC mulch and weed abundance measured early in the next crop growing season (Buchanan et al., 2016). Little is known about the long-term contribution of CC to weed management in tillage-based cropping systems (*i.e.* cropping systems in which termination of CC is ensured via ploughing (CT) or superficial disking (RT) and in which in-crop weed control is ensured by herbicides) (Brennan and Smith, 2005; Baraibar et al., 2018).

The objective of this study was to investigate the long-term contribution of contrasted CC species to weed management and crop productivity in tillage-based systems. We hypothesized that (i) contrasted CC species generate contrasted weed communities and levels of N availability and that (ii) these changes affect crop productivity and reliance on N fertilisers. In order to benefit from potential long-term effects, the present study focused on four years of data (CC biomass, crop yield, weed biomass and weed community composition in both CC and subsequent crops), *i.e.* one rotation cycle, collected 18 years after the beginning of a long-term factorial experiment on tillage systems, N rates and CC types.

2. Material and Methods

2.1. Site characteristics

The long-term experiment was located at the Center for Agri-environmental Research ‘E. Avanzi’ of the University of Pisa, Pisa, Central Italy (43°40’N, 10°19’E). The soil was a Typic Xerofluvent (further information concerning soil characteristics can be found in Supp. Tab. 1). The site was subject to a Mediterranean climate, with mild winters, very warm summers and rainy autumns. Temperatures (maximum, average, minimum) and monthly precipitations over the four-year period in which data were collected can be found in Supp. Fig. 1. Further information concerning cropping sequence and weed communities prior to the beginning of the long-term experiment can be found in Bàrberi & Mazzoncini (2001), Moonen & Bàrberi (2004), and Mazzoncini et al. (2011).

2.2. Experimental set-up

Over the 1993-2015 period of the long-term experiment, three crop sequences followed one another: a maize (*Zea mays* L.) monoculture (1993-1998), a two-year durum wheat (*Triticum turgidum* L. subsp. *durum* (Desf.) Husn.) – maize rotation (1999-2006) and a four-year durum wheat – sunflower (*Helianthus annuus* L.) – durum wheat – maize rotation (2007-2015). The experiment was set up as a split-split plot in a randomized complete block design (PennState, 2019). The three experimental factors were tillage system (main plots), N fertilisation (sub-plots), and CC type (sub-sub plots). 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). CT averaged 1.0 primary tillage operations per year (*i.e.* disk or mouldboard ploughing, 30 cm depth, performed in autumn every year), 3.4 secondary tillage operations per year (*i.e.* disk or rotary harrow and field cultivator, 10-20 cm in depth) and 0.8 superficial tillage operations per year before sowing (*i.e.* tine harrow, <10 cm in depth). RT averaged 2.0 secondary tillage operations per year and 0.5 superficial tillage operations per year carried out before sowing. Chiselling (30 cm depth) was introduced in RT prior to cover crop sowing in 2011, 2013 and 2015 and represented the main tillage tool for the subsequent summer crops. Mechanical weeding frequency was slightly higher in CT than in RT (0.6 vs. 0.3 operations per year). CT averaged 1.3 equivalent full dose herbicide applications per year (9% glyphosate, 24% pre-emergence, and 67% post-emergence) whereas RT averaged 2.0 applications (41% glyphosate, 7% pre-emergence, and 52% post-emergence). The four mineral N rates tested were N0 (0 kg N ha^{-1} for all crops), N1 (50 kg N ha^{-1} for sunflower, 60 kg N ha^{-1} for winter wheat, 100 kg N ha^{-1} for maize), N2 (two times N1), and N3 (three times N1). Only half of the theoretical dose for winter wheat was applied in 2013 because heavy rainfall and waterlogging limited crop establishment. The four CC types tested were a non-legume (*Secale cereale* L. from 1993 to 2001 and *Brassica juncea* (L.) Czern. (Bj) onwards), a low nitrogen supply legume (*Trifolium incarnatum* L. from 1993 to 2003 and *Trifolium squarrosum* L. (Ts) onwards), a high nitrogen supply legume (*Trifolium subterraneum* L. from 1993 to 2001, 50% *Vicia villosa* Roth (Vv) plus 50% *Secale cereale* L. in 2003 and *Vicia villosa* Roth onwards) and a control (baresoil, C). Cover crops were sown every autumn during the maize monoculture phase and between every winter (*i.e.* durum wheat) and summer crop in the subsequent phases (*i.e.* every two years). In both tillage systems, CC species were broadcast seeded manually in autumn (on September 22nd and 19th in 2011 and 2013, respectively, see Supp. Tab. 2 for CC sowing rates) and terminated at the early flowering stage (BBCH 60) in the following spring (April 10th and March 20th in 2012 and 2014, respectively). In both tillage systems, CC sowing was systematically preceded by tillage (disk harrow, rotary harrow or chisel). 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. Control plots (*i.e.* baresoil fallow) were managed identically to CC plots, with the exception of CC sowing. Each of the 32 treatments (2 tillage systems x 4 N rates x 4 CC types) was replicated four times in 21 m wide and 11 m long plots, resulting in a total of 128 elementary plots of 231 m² (*i.e.* statistical unit). More detailed information on agricultural practices over the four-year period on which data were collected can be found in Supp. Tab. 3.

2.3. Weed, cover crop and crop sampling

Weed and crop data were collected over one complete rotation cycle, *i.e.* CC 2011-2012, sunflower 2012, winter wheat 2012-2013, CC 2013-2014, maize 2014 and winter wheat 2014-2015. Cover crop and weed biomass (in CC) were collected prior to CC termination in two 0.5 m² quadrats per elementary plot. Crop biomass at maturity was collected in two 1 m² (durum wheat) or two 2 m² (sunflower and maize, i.e. row crops) quadrats per elementary plot. Weed biomass at crop maturity was collected in the same quadrats as crop biomass but was limited to half of the quadrat surface for sunflower (1 m²) and to a fourth for maize (0.5 m²). All 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% grain moisture content.

Weed community composition was assessed in all phases of the crop sequence (*i.e.* CC and cash crops) by visually estimating the percent cover of each weed species on a positively unbounded scale, in order to account for different strata of vegetation (each species cover was however bounded to a maximum of 100%) (Galland et al., 2019). This visual assessment took place at grain filling, *i.e.* after weeding operations, within two 1 m² (cover crop 2012, sunflower 2012 and durum wheat 2013), two 0.5 m² (cover crop 2014), four 0.5 m² (maize 2014) or four 1 m² (durum wheat 2015) quadrats per elementary plot.

2.4. Numerical and statistical analysis

2.4.1. Weed diversity assessment

Weed diversity was assessed as the effective number of species at the quadrat level, *i.e.* the exponential of the Shannon diversity index: $\exp(-\sum_{i=1}^{SR} p_i \log(p_i))$ where SR: species richness, *i*: one of the SR species of the community and p_i: relative cover of species *i*. This index has the advantage of being expressed on a linear scale, in terms of number of equally-common species, *i.e.* a true measure of diversity (Chao and Jost, 2015).

2.4.2. Univariate analysis

All univariate response variables were analyzed at the quadrat level with linear or generalized mixed effect models, using the lme4 package of the R software version 3.5.1 (R Development Core Team, 2019), in order to account for the nature of the different response variables and the hierarchical structure of the experiment.

Cover crop biomass, crop yield, weed biomass and weed diversity were regressed against block, tillage system, N, CC species and all possible interactions between the latter three factors. To identify if the experimental factors could offset the negative effect of weed biomass on crop yield while avoiding model overfitting, we compared, based on Akaike's Information Criterion with small-sample correction (AICc), a full model which integrated all possible interactions between weed biomass, tillage system, N, and CC to all possible nested models (while respecting marginality constraints) (Barton, 2019). The model with the lowest AICc was selected. The same strategy was used to identify if the experimental factors could modify the relationship between CC and weed biomass, except that the response variable was weed biomass and the covariate was CC biomass.

Block was always considered as a fixed factor. Crop density (as continuous variable) was added as a covariate for the analysis of sunflower and maize yield (in both approaches, *i.e.* considering weed biomass or not). Year (and its interaction with experimental factors) was added as a fixed factor when multiple years of data were available for the same response variables (*i.e.* response variables related to cover crops or durum wheat). Control variables (block, year, crop density) were never subject to model selection. Block:tillage, block:tillage:N and block:tillage:N:CC were always considered as random effects whereas block:year, block:year:tillage, block:year:tillage:N and block:year:tillage:N:CC were considered as additional random effects when multiple years of data were available for the same response variables.

2.4.3. Multivariate analysis

Weed community composition was averaged as to obtain one value per elementary plot:year and, hence, avoid an additional level of nesting (pseudoreplication level). Similarly, all phases of the crop sequence were analyzed independently to account for differences in sampling effort and quadrat size between years, resulting in six sub-datasets (one for each CC:year and crop:year) of 128 rows (*i.e.* elementary plots). For each sub-dataset, a Bray-Curtis dissimilarity matrix was computed between all possible pairs of rows. The effect of experimental factors was assessed by fitting a full multivariate linear model on each of the six Bray-Curtis dissimilarity matrices using the RRPP R package (Collyer and Adams, 2018). To respect the hierarchy of the design (PennState, 2019), random effects (block:tillage, block:N, block:tillage:N) were explicitly modelled and effects were tested against the appropriate error term (block and tillage were tested against the block:tillage error term, N and tillage:N against the pooled block:N and block:tillage:N error term, and the remaining effects against the residuals).

3. Results

3.1. Determinants of cover crop biomass

Cover crop biomass was mainly driven by year x CC species, tillage x CC species and N x CC interactions (Fig. 1, Supp. Tab. 4). Bj, Vv and Ts produced 176, 186 and 71% more biomass in 2012 than 2014, respectively (Fig. 1a). Bj outperformed Vv and Ts by 15 and 111% in 2012, respectively, and by 17 and 66% in 2014, respectively. Bj and Ts were 38 and 76% more productive in CT than in RT, respectively, whereas Vv showed similar productivity in both tillage systems (Fig. 1b). Bj outperformed Vv and Ts by 53 and 230% respectively in CT whereas Bj and Vv showed similar productivity in RT and outperformed Ts by 4-fold (Fig. 1b). Bj was the only CC species which responded positively to N levels, *i.e.* 103% increase from N0 to N2 (Fig. 1c). Vv outperformed Bj by 41% at N0 whereas Bj outperformed Vv by 27, 81, and 86% at N1, N2, and N3, respectively. Ts was the least productive CC at all N levels.

[Figure 1]

3.2. Determinants of crop yield

Sunflower yield was driven by N x CC (Fig. 2a, Supp. Tab. 4). Significance of the interaction was mainly justified by the fact that Vv outperformed Bj by 64% at N0 (Fig. 2a). The most parsimonious model of sunflower yield did not support the inclusion of weed biomass on top of N, CC and N x CC.

[Figure 2]

Maize yield was driven by tillage system x N and N x CC interactions (Fig. 2b and Fig. 2c, Supp. Tab. 4). Maize yield did not significantly differ between tillage types from N0 to N2 (Fig. 2b). However, CT outyielded RT by 17% at N3 (Fig. 2b). This was congruent with the fact that maize yield increased by 12% from N1 to N2/N3 in CT whereas it remained stable from N1 to N3 in RT (Fig. 2b). At N0, Vv and Ts outyielded C by 65 and 26%, respectively, whereas no significant differences were observed between Bj and C. At N1, Vv outyielded C by 23% while no differences were observed between C and Bj (Fig. 2c). No differences between CC species were observed at N2 or N3 (Fig. 2c). Across all combinations of CC species and N, only N1:Vv and N1:Ts were able to reach the level of productivity observed at N2 and N3 (*i.e.* maximum productivity). The most parsimonious model of maize yield did not support the inclusion of weed biomass (either as a main effect or in interaction with the experimental factors) on top of N, CC species, tillage system, N x CC species and N x tillage system.

Durum wheat yield was driven by tillage x N x CC interactions and year x tillage x N (Fig. 2d, Supp. Fig. 2, Supp. Tab. 4). In 2013, RT outyielded CT by 25% at N1 whereas CT outyielded RT by 40% at N3. In 2015, CT outyielded RT by 23 and 13 % at N1 and N3, respectively. Vv outyielded C by 33 and 35% at CT:N0 and RT:N1,, respectively (Fig. 2d). No CC species were able to maintain maximum durum wheat yield while reducing N fertilisation. In CT, durum wheat yield gradually increased from N0 to N3 in both 2013 and 2015 (Supp. Fig. 2). In RT, maximum durum wheat was observed at N1 and N2 in 2013 and 2015, respectively. The most parsimonious model of durum wheat included N x tillage x weed biomass (on top of CC, N, tillage, weed biomass, N x weed biomass, N x tillage, year x N, tillage x weed biomass, year x tillage, and year x tillage x N). However, the interaction was only justified by that fact that the slope between weed biomass and durum wheat yield was steeper at N3 than at N0 in CT (Supp. Fig. 3).

3.3. Factors shaping weed communities

3.3.1. Weed biomass

Weed biomass in CC was driven by year x tillage x CC species and year x tillage x N (Fig. 3a, Supp. Fig. 4, Supp. Tab. 4). In 2012, Bj, Vv, and Ts reduced weed biomass by 79, 69, and 24% in CT, respectively (Fig. 3a). Only Bj (-75%) and Vv (-37%) were capable of significantly reducing weed biomass in RT in 2012. In 2014, Bj was the only CC capable of significantly reducing weed biomass (-34% in CT and -28% in RT). Weed biomass was greater at N3 than at N0 across all combinations of tillage system and years, except in CT, in 2012 (Supp. Fig. 4). The most parsimonious model of weed biomass in cover crop included CC x CC biomass and tillage x CC biomass (on top of tillage, N, CC, CC biomass, CC x N, CC x tillage, CC x year, N x CC biomass, tillage x year, and CC x tillage x year). The slope (on square root scale) between CC biomass and weed biomass was steeper in CT than in RT and steeper for Vv and Ts than for Bj (Fig. 4 for 2012 and Supp. Fig. 5 for 2014). All slopes were significantly different from zero except Bj in CT.

[Figure 3]

[Figure 4]

Weed biomass in sunflower was not influenced by any of the experimental factors (Supp. Tab. 4).

Weed biomass in maize was driven by N and by tillage system x CC species (Fig. 3b, Supp. Tab. 4). Weed biomass at N3 was 68, 42 and 41% greater than at N0, N1 and N2 respectively. On average, weed biomass was 3 times greater in RT than in CT. The first order interaction was justified by the fact that C, Bj and Ts showed 2.6 – 4.4 times more weed biomass in RT than CT whereas VV only showed 1.7 times more weed biomass in RT than CT (Fig. 3b).

Weed biomass in durum wheat was driven by year x tillage x N, year x N x CC, and tillage x N x CC interactions (Fig. 3c, Supp. Tab. 4). Across all N rates and CC species, weed biomass was 2 and 39 times greater in RT than in CT in 2013 and 2015, respectively (Fig. 3c). Within all combinations of year and tillage system, no differences between combinations of N rates and CC species were found (except within CT, in 2015, but weed biomass was extremely low, *i.e.* 1 to 5 g of dry matter m^{-2}).

3.3.2. Weed diversity

Weed diversity in CC was driven by a CC species x year interaction (Supp. Tab 4). In 2012, weed diversity was greatest in C, intermediate in Ts (-16% compared to C), and lowest in Bj (-38%) and Vv (-46%). In 2014, all CC reduced weed diversity to a similar extent (-13 to -15%). Weed diversity in sunflower was driven by tillage system (Supp. Tab. 4) and was slightly higher in CT than in RT. Weed diversity in maize was driven by N rate (Supp. Tab. 4) and was slightly higher at N3 than at N0. Weed diversity in durum wheat was mainly driven by tillage system x N interactions (Supp. Tab. 4, Fig. 5): it gradually decreased from N0 to N3 in CT whereas it remained stable across all N levels in RT.

[Figure 5]

3.3.3. Weed community composition

In both cover crop seasons, *Poa annua* L., *Capsella bursa-pastoris* (L.) Medik. and *Veronica* spp. were associated to RT whereas *Lolium* spp. was associated to CT (Supp. Fig. 6a-b, Supp. Tab. 5a). Bj was the only CC capable of completely outcompeting *C. bursa-pastoris* (L.) Medik. in both tillage systems of the 2012 CC season (*C. bursa-pastoris* (L.) Medik. was not a dominant species in the 2014 CC season). However, tillage system significantly interacted with CC in both CC seasons (Supp. Tab. 5a). The interaction was justified by that fact that, unlike other CC species, Vv consistently reduced the percent cover of *Poa annua* L., thereby homogenizing weed communities between tillage systems (Supp. Fig. 6a-b).

In all subsequent crops, *Cynodon dactylon* (L.) Pers. and *Equisetum arvense* L. were consistently associated with RT whereas *Solanum nigrum* L., *Datura stramonium* L., *Xanthium orientale* subsp. *italicum* (Moretti) Greuter, and *Polygonum* spp. were associated with CT (Supp. Fig. 6c-f, Supp. Tab. 5b-c). Tillage system significantly interacted with N in sunflower (Supp. Tab. 5b). Increasing levels of

N generated a reduction of *Cynodon dactylon* (L.) Pers. and an increase of *Datura stramonium* L. in CT whereas weed communities remained homogeneous across the different levels of N in RT (Supp. Fig. 6c). In maize, N fertilisation significantly interacted with CC species (Supp. Tab. 5b). Vv was the only CC capable of reducing the percent cover of *Equisetum arvense* L. at N0 (Supp. Fig. 6d).

4. Discussion

4.1. Weed suppression by cover crops during the fallow period

In accordance with previous studies (Buchanan et al., 2016; Alonso-Ayuso et al., 2018), highly productive CC allowed to suppress weed growth during the fallow period, with respect to the baresoil fallow (*e.g.* -79 and -69% for Bj and Vv in CT in 2012, respectively)). In 2014, intense precipitations (*i.e.* 1010 mm from the beginning of September to the end of April, vs. 332 mm in 2012) most likely limited CC development and hence, weed suppression. Nevertheless, the weed suppressive potential of CC could not be simply attributed to biomass productivity (Campiglia et al., 2010; Radicetti et al., 2013). The relationship between CC and weed biomass (*i.e.* slope and intercept of the regressions in Fig. 4) also depended on CC species. In 2012, Bj suppressed weeds to a greater extent than Vv or Ts at low levels of CC productivity (200 g DM m^{-2}) whereas Bj and Vv suppressed weeds to a similar extent at higher levels of CC productivity (400 g DM m^{-2}). Within all combinations of tillage systems and years, the lowest weed biomass was observed for Bj in N0 even though Vv was 4 to 100% more productive at that N rate. Such results challenge the beliefs that higher CC biomass is necessarily required to reduce weed growth during the fallow period (MacLaren et al., 2019) or than N fertilisation enhances the weed suppressive potential of N-demanding CC species, such as Bj (Sturm et al., 2017). Bj's greater potential to reduce weed growth at lower levels of CC productivity (such as in 2014) could be related to quick N uptake (Tribouillois et al., 2015), early soil cover (Teasdale, 1996), and/or allelopathic effects (as suspected with *Capsella bursa-pastoris* (L.) Medik. (Couëdel et al., 2017)). In contrast, Vv's potential to reduce weed growth at high levels of CC productivity could be related to a smothering effect. Ts showed the same slope and intercept as Vv but was never able to reach high biomass productivity (maximum observed biomass for Ts was 386 and 185 g DM/m^2 in 2012 and 2014, respectively) and hence smother weeds.

At the same biomass level, CC were more suppressive in CT than in RT. Two hypotheses can be formulated to explain this undocumented phenomenon. First, coarser soil structure in RT than in CT (Schlüter et al., 2018) could have delayed CC emergence and CC:weed interference through reduced seed:soil contact (Teasdale, 1996; Munkholm et al., 2008; Büchi et al., 2018). This may also explain why small seeded CC species (*i.e.* Bj and Ts; 1000 seed weight for Bj, Vv and Ts was 2.9, 34.8 and 3.3 g respectively) were less productive in RT than CT (Uchino et al., 2011; Büchi et al., 2018). In addition, weed communities selected by RT could have shown trait values that allowed them to overcome CC competition (Adeux et al., 2019). For example, *Poa annua* L., one of the dominant weeds in RT, might have avoided CC competitive effects thanks to its rapid growth rate, shallow root system, and high tolerance to shading (Warwick, 1979).

Finally, the high level of weed biomass (*i.e.* 58 and 134 g DM/m² in 2012 and 2014, respectively) observed in the most suppressive treatment (*i.e.* CT:N0:Bj) could question the importance of CC for weed suppression in real farming conditions (Teasdale, 1996). Further studies aiming to characterize weed seed rain (Doisy et al., 2014) or weed phenology would allow to identify which species (if any) are capable of producing seeds during the fallow period (Brennan and Smith, 2005) and whether or not they may jeopardize long-term weed management.

4.2. Weed suppression by cover crops during the subsequent crops

Contrary to previous studies (Campiglia et al., 2010; Wayman et al., 2015; Buchanan et al., 2016), CC showed no clear long-term effect on weed communities (*i.e.* abundance and structure) in the subsequent crops. Such discrepancies may be explained by differences in CC termination method and timing of weed samplings. Studies reporting an effect of CC on weed communities in the subsequent crops (Campiglia et al., 2010; Wayman et al., 2015; Buchanan et al., 2016) have mainly resorted to non-chemical termination methods which maintained CC residues on the soil surface (*e.g.* flail mowing, roller-crimping) and to weed samplings carried out before direct weed control. By contrast, in the present study, CC residues were soil incorporated (*i.e.* CC were terminated by tillage in both tillage systems) and weed samplings were carried out after herbicide applications. The incorporation of CC residues did not allow the expression of a weed suppressive mulch (Teasdale, 1996) and the weed sampling strategy adopted did not allow to identify whether (i) CC had simply no effect on weed communities or whether (ii) CC effects on weed communities were overridden by tillage and/or herbicides. Tillage could have overridden differences in weed seed production during the fallow period (Brennan and Smith, 2005) and herbicides could have overridden differences in weed communities before weeding. Patch spraying could have allowed to adjust herbicide use based on emerged weed flora and therefore, reveal the potential of CC to reduce herbicide use in tillage-based systems. Finally, the fact that no CC species were able to alleviate weed:crop interference suggests that was not driven by N availability (Casper and Jackson, 1997) or that increasing N availability led to competition for other resources, such as light and/or water (Hautier et al., 2009).

4.3. Cover crop effects on crop yield

Cover crop effects on crop yield were determined by CC type and biomass, adequate combination between N fertilisation – CC N release – crop N requirements, weather conditions, and the position of the crop in the rotation with respect to CC termination. In both tillage systems, growing Vv during the fallow period resulted in the highest maize grain yield increase at N0 (+65%) and N1 (+23%) with respect to the control. The positive effect of Vv on maize grain yield decreased with increasing levels of N, highlighting the opportunity to reduce N fertilisation while maintaining maize grain yield (Liebman et al., 2012; Marcillo and Miguez, 2017; Wittwer et al., 2017). The integration of Ts also allowed a gain in maize grain productivity, but the gain was significant only at N0 (+26% with respect to C), most likely because of lower cover crop biomass (76 g DM/m^2 across tillage systems, N rates and years) and hence, lower potential N release (Mazzoncini et al., 2011). Such results are in line with the results obtained by Mazzoncini *et al.* (2011) on the same experiment in 2008, which highlight greater total soil nitrogen content for Vv (5.71 Mg/ha) than Bj (5.40 Mg/ha) and an intermediate level for Ts (5.50 Mg/ha). Nevertheless, measures of soil available N could have provided a finer understanding of CC effects on crop productivity as total soil nitrogen content does not reflect the quantity of N available for crop growth after CC termination. The lack of a legume CC or N effect in sunflower, even though CC biomass was 151% higher before sunflower (2012) than maize (2014), suggests that sunflower yield was restricted by other factors than N, such as the extremely dry weather conditions encountered in 2012 (176 mm of rainfall from sunflower sowing to harvest). The only negative CC effect was observed for Bj at N0 in sunflower. The high quantity of residues produced by Bj prior to sunflower planting in 2012 was possibly associated to a high C:N ratio, which could have resulted in soil inorganic N immobilization by microbial biomass (Trinsoutrot et al., 2000). Furthermore, Bj might also have depleted soil N resources during the fallow period. In contrast, Bj residues possibly showed a more balanced C:N ratio in 2014 due to lower CC productivity. Therefore, sufficient N could have been released by mineralization to meet microbial N requirements but in insufficient amounts to generate net N mineralization and promote crop growth (Trinsoutrot et al., 2000). A more systemic approach could have allowed to maximize CC benefits by adapting CC termination date depending on CC species level of maturity (Mirsky et al., 2009). To maximize CC benefits, we would encourage farmers to select CC species based on the subsequent crop N requirements but to possibly reconsider the choice of the subsequent crop based on actual CC performance. Finally, it is important to note that the intensity of legume CC effects on crop yield decreased considerably in time after CC termination. The effect of Vv was still visible in durum wheat at CT:N0 and RT:N1, which may justify the importance of CC in stockless cereal-based organic systems. However, our results also suggest that legume CC released N quickly in time and that little benefit can be expected from CC one year after CC termination in more productive systems. Finally, the fact that Vv had a positive effect on durum wheat yield at RT:N1 but not at RT:N0 may highlight that N fertilisation is required to stimulate long-term CC mineralization in RT systems (Drinkwater et al., 2000).

5. Conclusion

The complexity of long-term CC effects on crop productivity and weed management were revealed through an in-depth analysis of CC biomass, weed biomass, weed community composition, and crop yield during one complete rotation cycle, sampled 18 years after the beginning of a factorial experiment on tillage systems, N fertilisation and CC. Our findings should encourage the selection of weed suppressive CC based on traits other than biomass productivity. Increased mineral N availability did not appear as a sustainable solution to increase the weed suppressive potential of CC. Further experiments encompassing a wider diversity of CC types may identify CC species or mixtures best adapted to grow in reduced or conventional tillage systems and to suppress the associated weed flora. Further research should also address weed seed production during the fallow period to characterize potential long-term risks. In our study, potential CC effects on weed communities in the subsequent crops were possibly overriden by tillage and herbicides, highlighting the necessity to reduce management intensity to maximize potential cover crop benefits on weed management. Mechanical methods of CC termination which maintain residue on the soil surface (e.g. roller-crimping) appear as a promising solution to reduce herbicide reliance and increase CC benefits on weed management. Patch spraying could also allow growers to benefit from reduced weed pressure. Finally, we encourage to position highly productive legume CC prior to high N-demanding summer crops with the aim of reducing standard nitrogen fertilisation levels.

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Author's contribution

MM designed the study. MM, PB and DA funded the experiment and planned data collection. SCo and NMJ provided additional funding for GA's work. SCa and DA collected the data. GA analyzed the data. All authors were involved in the interpretation of the results and contributed to writing the original version of the manuscript and improving the subsequent ones.

Conflict of interest

The authors declare no conflict of interest.

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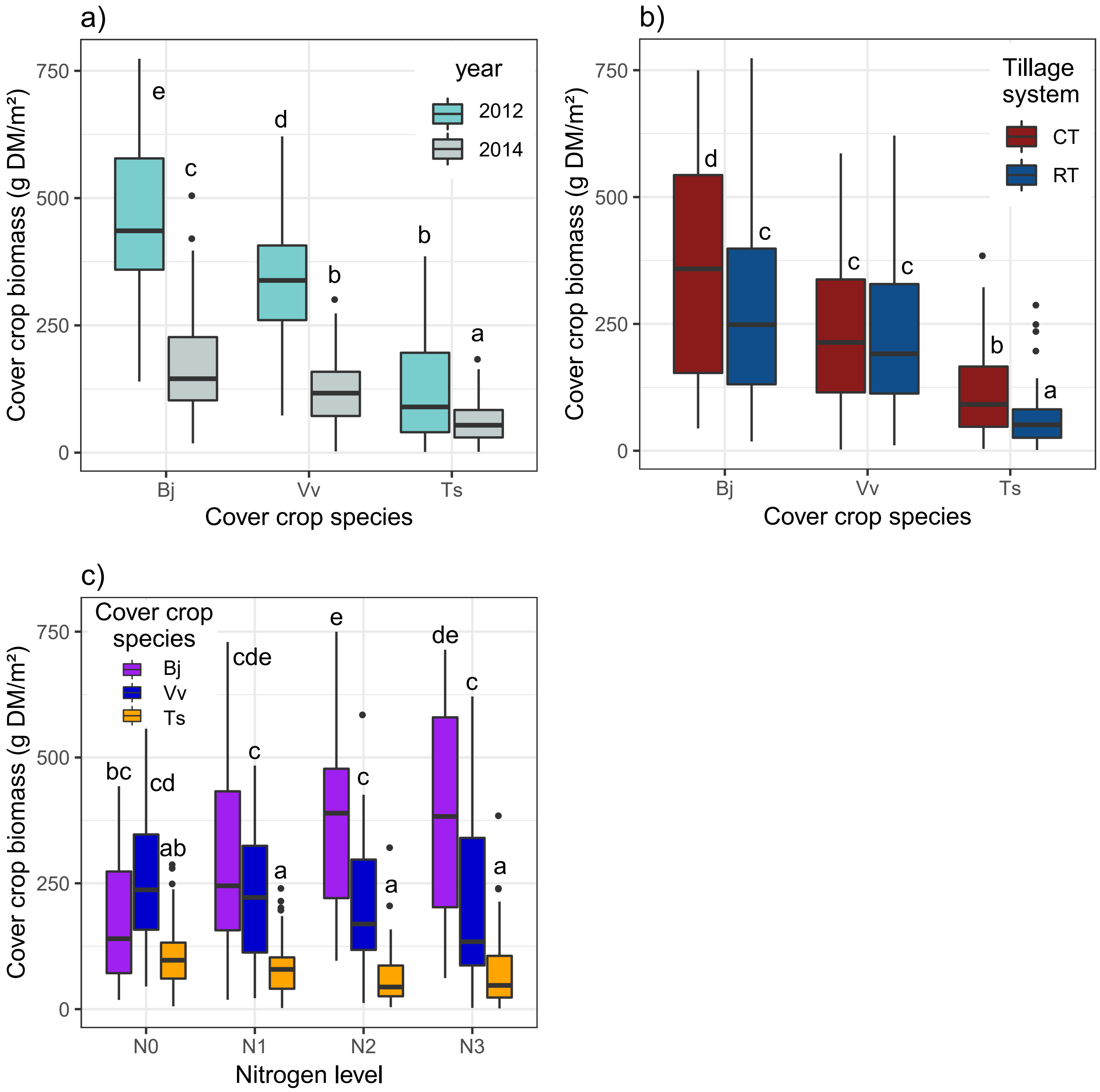
Figure 1: Boxplots highlighting the interaction effect between cover crop species and a) year, b) tillage system, and c) nitrogen level on cover crop biomass in 2012 and 2014 (years were pooled for graphs b) and c)). Boxplots sharing the same letter are not significantly different at $p<0.05$ (p value adjustement: multivariate t method). 384 observations (2 pseudoreplications x 96 elementary plots x 2 years) were available for all graphs. CT: Conventional tillage; RT: Reduced tillage; Bj: *Brassica juncea*; Vv: *Vicia villosa*; Ts: *Trifolium squarrosum*.

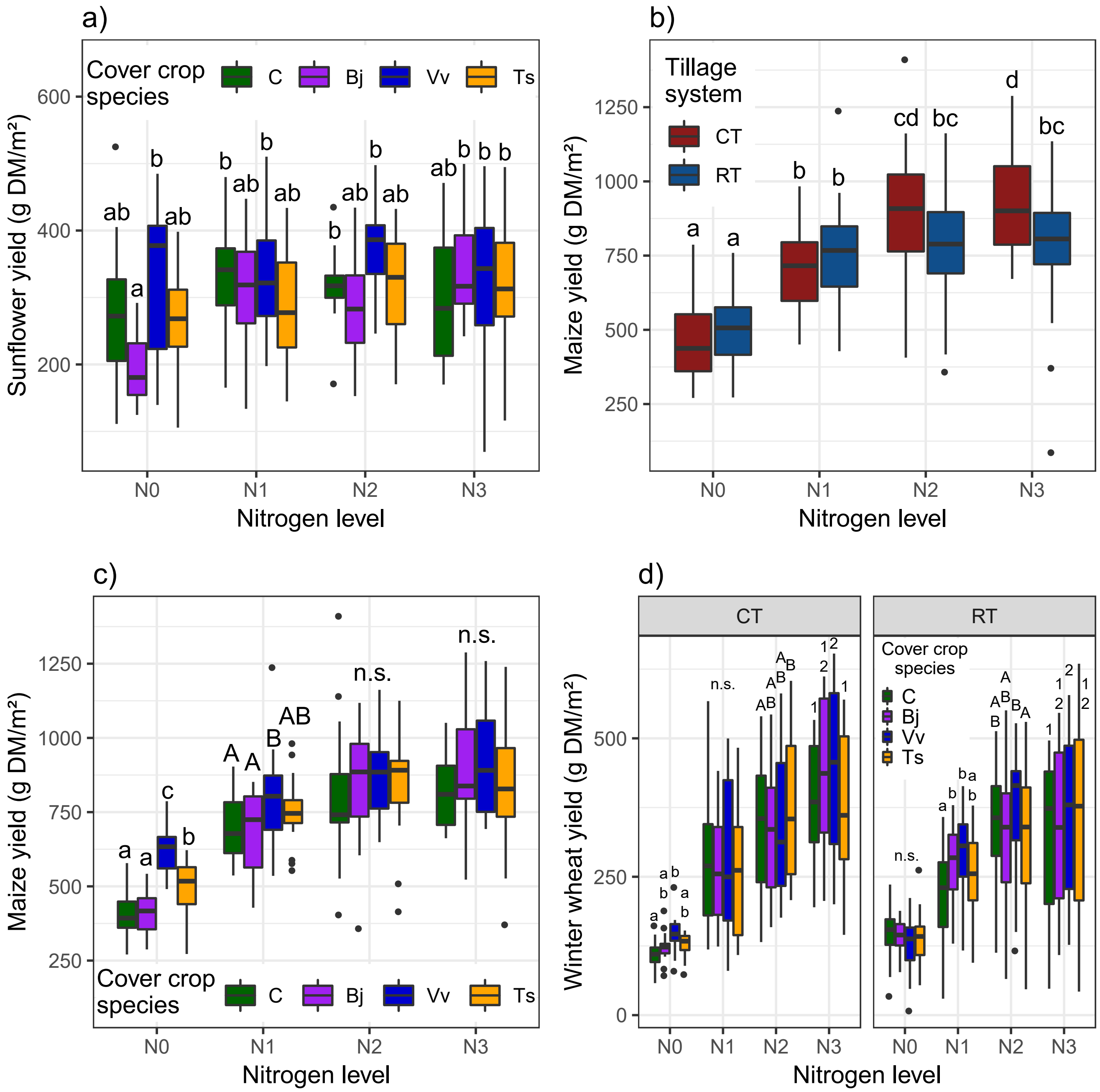
Figure 2: Boxplots highlighting the interaction effect between a) cover crop species and nitrogen level on sunflower yield in 2012, b) tillage system and nitrogen level on maize yield in 2014, c) nitrogen level and cover crop species on maize yield in 2014, and d) tillage system, nitrogen level and cover crop species on durum wheat yield in 2013 and 2015 (pooled data). Boxplots sharing the same symbol (lower or uppercase letter, arabic numbers) are not significantly different at $p<0.05$. Within a graph or panel, different symbols refer to different families of contrasts (p value adjustement: multivariate t method). 256 observations (2 pseudoreplications x 128 elementary plots) were available for both graph a), b), and c) whereas 512 observations (2 pseudoreplications x 128 elementary plots x 2 years) were available for graph d). CT: Conventional tillage; RT: Reduced tillage; C: Control (baresoil); Bj: *Brassica juncea*; Vv: *Vicia villosa*; Ts: *Trifolium squarrosum*.

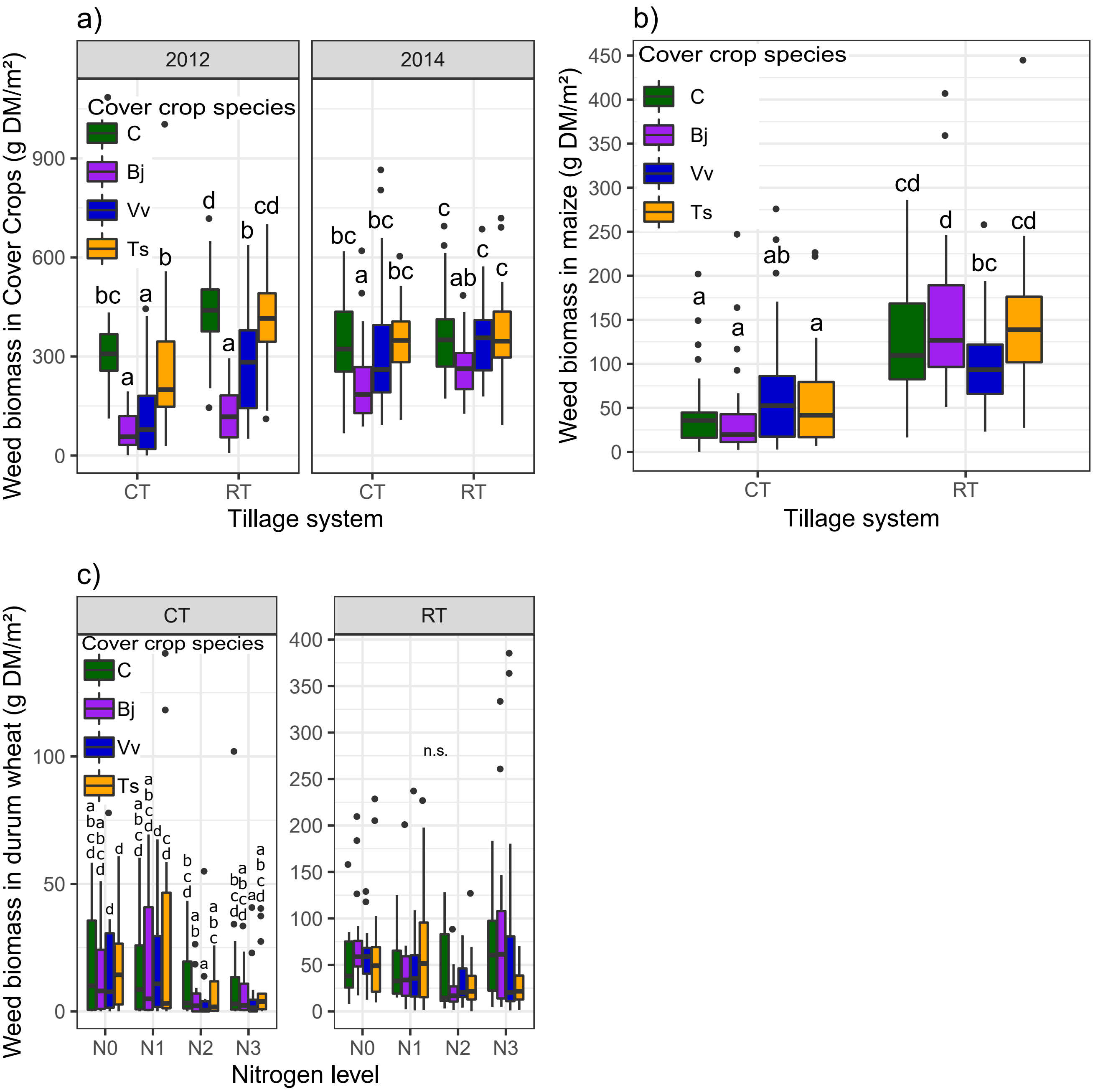
Figure 3: Boxplots highlighting the interaction effect between a) cover crop species and year on weed biomass in cover crops (2012 and 2014), b) cover crop species and tillage system on weed biomass in maize in 2014 and c) tillage system, nitrogen level and cover crop species on weed biomass in durum wheat in 2013 and 2015 (pooled data). Boxplots sharing the same letter are not significantly different at $p<0.05$ (p value adjustement: multivariate t method). 256 observations (2 pseudoreplications x 128 elementary plots) were available for both graph b) whereas 512 observations (2 pseudoreplications x 128 elementary plots x 2 years) were available for both graph a) and b). CT: Conventional tillage; RT: Reduced tillage; Bj: *Brassica juncea*; Vv: *Vicia villosa*; Ts: *Trifolium squarrosum*.

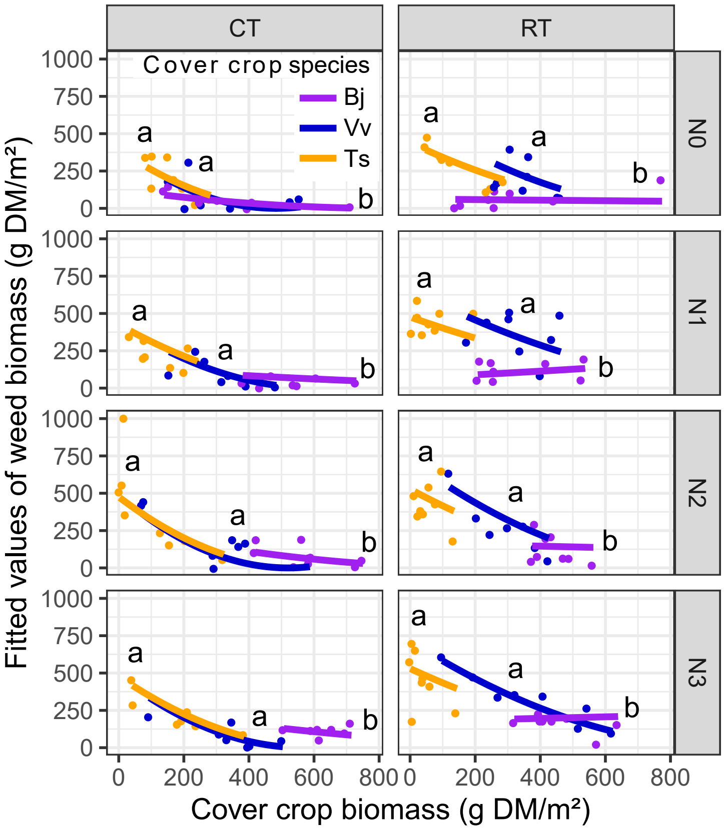
Figure 4: Fitted values of weed biomass in cover crops as a function of tillage system, nitrogen level, cover crop species and cover crop biomass in 2012. Predictions were based on generalized linear mixed model taking into account random effects. The regression line shows an average plot value (*i.e.* prediction at the population level). Slopes sharing the same letter are not significantly different at $p < 0.05$ (p value adjustement: multivariate t method). All slopes are significantly different from zero, except Bj in CT. 8 observations (2 pseudoreplications x 4 blocks) were available for each slope (384 observations total). CT: Conventional tillage; RT: Reduced tillage; Bj: *Brassica juncea*; Vv: *Vicia villosa*; Ts: *Trifolium squarrosum*.

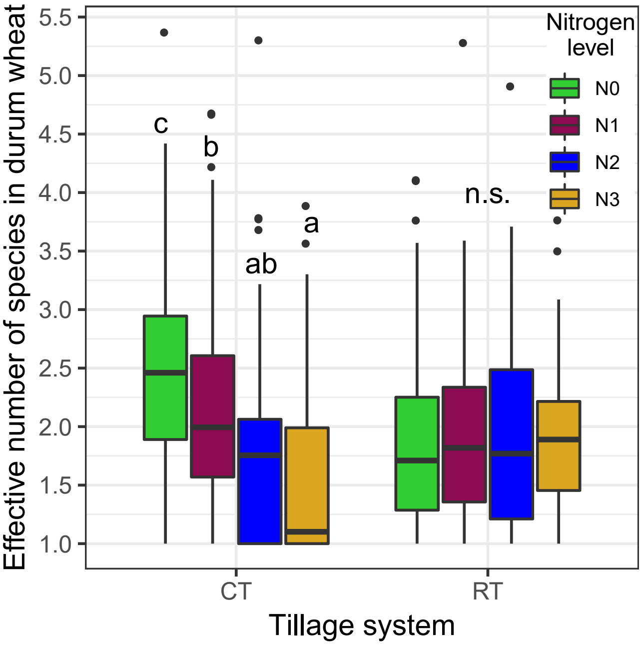
Figure 5: Boxplots highlighting the interaction effect between tillage system and nitrogen level on the effective number of weed species in durum wheat in 2013 and 2015 (pooled data). Boxplots sharing the same letter are not significantly different at $p<0.05$ (p value adjustement: multivariate t method). 256 observations (2 pseudoreplications x 128 elementary plots) were available. CT: Conventional tillage; RT: Reduced tillage.


a)
Cover crop biomass (g DM/m²)
750
500
250
0
year
2012
2014
e
c
d
b
b
a
Bj
Vv
Ts
Cover crop species
b)
Cover crop biomass (g DM/m²)
750
500
250
0
Tillage system
CT
RT
d
c
c
c
b
a
Bj
Vv
Ts
Cover crop species
c)
Cover crop biomass (g DM/m²)
750
500
250
0
Cover crop species
Bj
Vv
Ts
bc
cd
ab
cde
c
a
e
c
a
de
c
a
N0
N1
N2
N3
Nitrogen level


a)
Cover crop species
C
Bj
Vv
Ts
Sunflower yield (g DM/m²)
600
400
200
ab
a
b
ab
b
ab
b
ab
b
ab
b
ab
ab
b
b
b
N0
N1
N2
N3
Nitrogen level
b)
Tillage system
CT
RT
Maize yield (g DM/m²)
1250
1000
750
500
250
a
a
b
b
cd
bc
d
bc
N0
N1
N2
N3
Nitrogen level
c)
Maize yield (g DM/m²)
1250
1000
750
500
250
a
a
c
b
A
A
B
AB
n.s.
n.s.
Cover crop species
C
Bj
Vv
Ts
N0
N1
N2
N3
Nitrogen level
d)
CT
RT
Winter wheat yield (g DM/m²)
500
250
0
a
a b
b
a
b
n.s.
AB
AB
AB
AB
1 2
2
1
1
Cover crop species
C
Bj
Vv
Ts
n.s.
a
b
ba
b
A
AB
BA
B
2
1
1
2
2
1
N0
N1
N2
N3
N0
N1
N2
N3
Nitrogen level


a)
2012
2014
Cover crop species
C
Bj
Vv
Ts
Weed biomass in Cover Crops (g DM/m²)
0
300
600
900
bc
a
a
b
d
a
b
cd
bc
a
bc
bc
c
ab
c
c
CT
RT
CT
RT
Tillage system
b)
Cover crop species
C
Bj
Vv
Ts
Weed biomass in maize (g DM/m²)
0
50
100
150
200
250
300
350
400
450
a
a
ab
a
cd
d
bc
cd
CT
RT
Tillage system
c)
CT
RT
Cover crop species
C
Bj
Vv
Ts
Weed biomass in durum wheat (g DM/m²)
0
50
100
n.s.
0
50
100
150
200
250
300
350
400
N0
N1
N2
N3
N0
N1
N2
N3
Nitrogen level


CT
RT
N0
N1
N2
N3
Cover crop species
Bj
Vv
Ts
a
b
Fitted values of weed biomass (g DM/m²)
Cover crop biomass (g DM/m²)
0
250
500
750
1000
0
200
400
600
800


Effective number of species in durum wheat
5.5
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
c
b
ab
a
n.s.
Nitrogen level
N0
N1
N2
N3
CT
RT
Tillage system