



HAL
open science

Soil-mediated effects of cover crops on weed-crop competition

Alicia Rouge, John Wallace, Stéphane Cordeau, Delphine Moreau,
Jean-philippe Guillemin, Carolyn Lowry

► **To cite this version:**

Alicia Rouge, John Wallace, Stéphane Cordeau, Delphine Moreau, Jean-philippe Guillemin, et al..
Soil-mediated effects of cover crops on weed-crop competition. *Weed Research*, 2025, 65 (1), pp.e12680.
10.1111/wre.12680 . hal-04925910

HAL Id: hal-04925910

<https://institut-agro-dijon.hal.science/hal-04925910v1>

Submitted on 3 Feb 2025





HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

Soil-mediated effects of cover crops on weed-crop competition

Alicia Rouge^{1,2} | John M. Wallace³ | Stéphane Cordeau²  |
 Delphine Moreau²  | Jean-Philippe Guillemain²  | Carolyn J. Lowry³ 

¹AgroParisTech, Paris, France

²Agroécologie, INRAE, Institut Agro, Univ. Bourgogne, Univ. Bourgogne Franche-Comté, Dijon, France

³Plant Science Department, The Pennsylvania State University, University Park, Pennsylvania, USA

Correspondence

Carolyn J. Lowry, Plant Science Department, The Pennsylvania State University, University Park, PA, USA.

Email: cvl5836@psu.edu

Funding information

National Institute of Food and Agriculture; U.S. Department of Agriculture

Subject Editor: Matt Liebman, Iowa State University, Ames, USA

Abstract

According to the Resource Pool Diversity Hypothesis (RPDH), increasing cropping system diversity (e.g., crop rotation, fertility sources, and weed management) should increase soil resource pool diversity, and mitigate weed-crop competition intensity. Despite the growing interest in cover crop mixtures to provide weed control, our study is the first to test the effect of cover crop species and functional diversity on weed-crop competition intensity. We hypothesised that according to the RPDH, increasing cover crop species and functional diversity will mitigate weed-crop competition intensity. Using soils collected from a long-term field experiment comparing diverse cover crop mixtures to their mono-species counterparts, we investigated in a greenhouse whether the legacy of cover crops in the soil would alter the intensity of competition that two competitive weeds can exert on maize. No relationship between the relative weed-maize competition intensity and cover crop diversity was found, which failed to support our hypothesis. Nevertheless, the cover crop treatments varied in their effects on weed-crop competition intensity, with the cover crop mixture consisting of triticale, Austrian winter pea and crimson clover resulting in the lowest weed-crop competition intensity and highest maize biomass, regardless of the weed species competitor. Therefore, while cover crop legacies in the soil may affect weed-crop competition, increasing diversity alone is not sufficient to reduce competition intensity. Future research should investigate potential mechanisms driving cover crop legacy effects on weed-crop competition, especially in a field, where diversity in soil resources is likely to be greater compared to pots in a greenhouse.

KEYWORDS

competition intensity, diversity, greenhouse, long-term experiment, nitrogen

1 | INTRODUCTION

Weeds are a significant agricultural pest because they compete with the crop for vital resources (i.e., light, water, and nutrients), thereby decreasing crop yields (Oerke, 2006). Herbicides are the primary

method used to control or reduce weed abundance. However, the over-reliance on herbicides has led to negative environmental impacts, including biodiversity loss (Wilson et al., 1999), as well as increases in weed biotypes evolving resistance to herbicides (Heap, 2023). A better understanding of how farm management practices affect

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). *Weed Research* published by John Wiley & Sons Ltd on behalf of European Weed Research Society.

weed-crop competition is needed to reduce crop yield losses to weeds and the negative impacts of herbicides.

Weed-crop competition is driven by the availability of resources (forms and quantity), and the ability of plants to uptake and use these resources (e.g., resource acquisition strategy, growth rate) (Zimdahl, 2004). Competition intensity between crops and weeds is greater when they are competing for limited soil resources at the same time and in the same space (Violle et al., 2009), however, the outcome of competition is also greatly influenced by both the crop and weed relative emergence timing and their relative competitive ability for light (Little et al., 2021). Competition intensity between crops and weeds may be reduced when they can utilise different forms of nutrients when timing of resource uptake varies between species, or when species spatially differ in the volume of soil their roots occupy (Smith et al., 2010; Violle et al., 2009). The quantity and various forms of resources in the soil (e.g., pools of nitrogen include organic nitrogen, nitrate, nitrite, ammonium, etc.), hereafter referred to as 'soil resource pools', are dynamic in both space and time, and diversity within soil resource pools are driven by farm management practices such as crop rotation, fertilisation type and quantity, and weed management tactics, which mediate nutrient cycling in the soil.

According to the Resource Pool Diversity Hypothesis (RPDH), increasing cropping system diversity (e.g., crop rotation, source of fertility, weed management) will decrease weed-crop competition for soil resources due to an increase in soil resource pool diversity (Smith et al., 2010). Despite no direct test of the RPDH, Smith et al. (2010) found some support for the hypothesis in the agricultural literature by comparing weed-crop competition intensity along a gradient of cropping system diversity with the higher diversified cropping systems being organic cropping systems, characterised by high cash and cover crop diversity and use of green and animal manures, and lower diversified cropping systems being conventional cropping systems, characterised by low crop diversity and synthetic inputs. The authors suggested that increasing cropping system diversity decreased weed-crop competition intensity presumably through an increased soil resource pool diversity. Similarly, Ryan et al. (2010) reported similar maize (*Zea mays* L.) yields in organic and conventional cropping systems despite four- to seven-fold greater weed biomass in organic cropping systems. The authors attributed this finding to a higher soil resource availability and crop growth rate in the organic cropping systems. More recently, two greenhouse experiments attempted to find support for the RPDH. First, Poffenbarger et al. (2015) suggested that according to the RPDH, crops, and weeds would exhibit greater resource partitioning within soils collected from organically managed fields compared to conventionally managed fields. Second, Menalled et al. (2020) tested whether soils collected from plots with a history of both intra- and interspecific diversity influenced crop and weed competition. Both studies failed to support the RPDH. However, Poffenbarger et al. (2015) found some evidence of resource partitioning between maize and pigweed, and Menalled et al. (2020) found some evidence that soil nutrient availability and soil microbial diversity drove weed-crop competition. Looking forward, studies are needed to test the relative effects of biodiversity-based weed management practices in mitigating weed-crop competition intensity (Petit et al., 2018).

Cover crops, when cultivated during the fallow period between two main cash crops, can provide multiple ecosystem services in agricultural systems, such as increasing soil fertility, reducing nitrate leaching, and suppressing weeds (Blanco-Canqui et al., 2015; Daryanto et al., 2018; Shackelford et al., 2019). However, while many studies showed that cover crops suppress weeds during the cover cropping period (Baraibar et al., 2018; Rouge et al., 2022; Teasdale et al., 2007), their effects on weeds in the subsequent crop are more variable (Rouge et al., 2023). Previous studies have demonstrated that cover crops limit weed emergence in the subsequent crop in no-till systems when cover crops are terminated and left on the soil surface as mulch (Fisk et al., 2001; Mirsky et al., 2013; Moore et al., 1994). Less is known about cover crop soil-mediated effects on weed-crop competition in tillage-based cropping systems.

Cover crop species contain variable quantities of nutrients and release these nutrients at varying rates (Amsili & Kaye, 2021; Kuo & Sainju, 1998). For example, Poaceae (e.g., rye, oat) cover crop species usually show high C:N ratios and low nitrogen concentration in their tissues, resulting in a slower rate of net nitrogen mineralisation (Wells et al., 2013). In contrast, Fabaceae cover crop species (e.g., pea, clover), which can symbiotically fix atmospheric nitrogen, usually show low C:N ratios and high nitrogen concentration in their tissues, increasing nitrogen mineralisation into the soil (Marcillo & Miguez, 2017). Recently, Zhang et al. (2022) found that mixing non-legume and legume cover crop species increased soil organic carbon pool diversity compared to their mono-species counterparts. Thus, mixing functionally diverse cover crop species could mitigate weed competitiveness in the subsequent crop through an increase in soil resource pool diversity according to the RPDH (Smith et al., 2010). However, it often takes years for cover cropping to result in any measurable changes in the soil, such as increased soil organic carbon (Poepflau & Don, 2015), soil total nitrogen (Sainju et al., 2003), or the improvement of soil water dynamics (Basche et al., 2016). Therefore, it may require several years of implementing cover crop mixtures to measurably affect soil resource pools.

Despite the growing interest in cover crop mixtures, few studies have examined whether the soil legacy from cultivating diverse cover crop mixtures over the long term can reduce the intensity of subsequent weed-crop competition, presumably through greater resource pool diversity in the soil. Using soils collected from a long-term annual cropping system experiment comparing diverse cover crop mixtures to their mono-species cover crop counterparts, we investigated whether the soil legacy of cover crops would mediate the intensity of competition that two competitive weeds, can exert on maize in a greenhouse experiment. We hypothesised that increasing cover crop species and functional diversity will mitigate competition exerted by weeds on the subsequent crop according to the RPDH (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Long-term cover crop field experiment

To examine cover crop soil-mediated effects on weed-crop competition, we utilised a long-term (10 years) organic field experiment

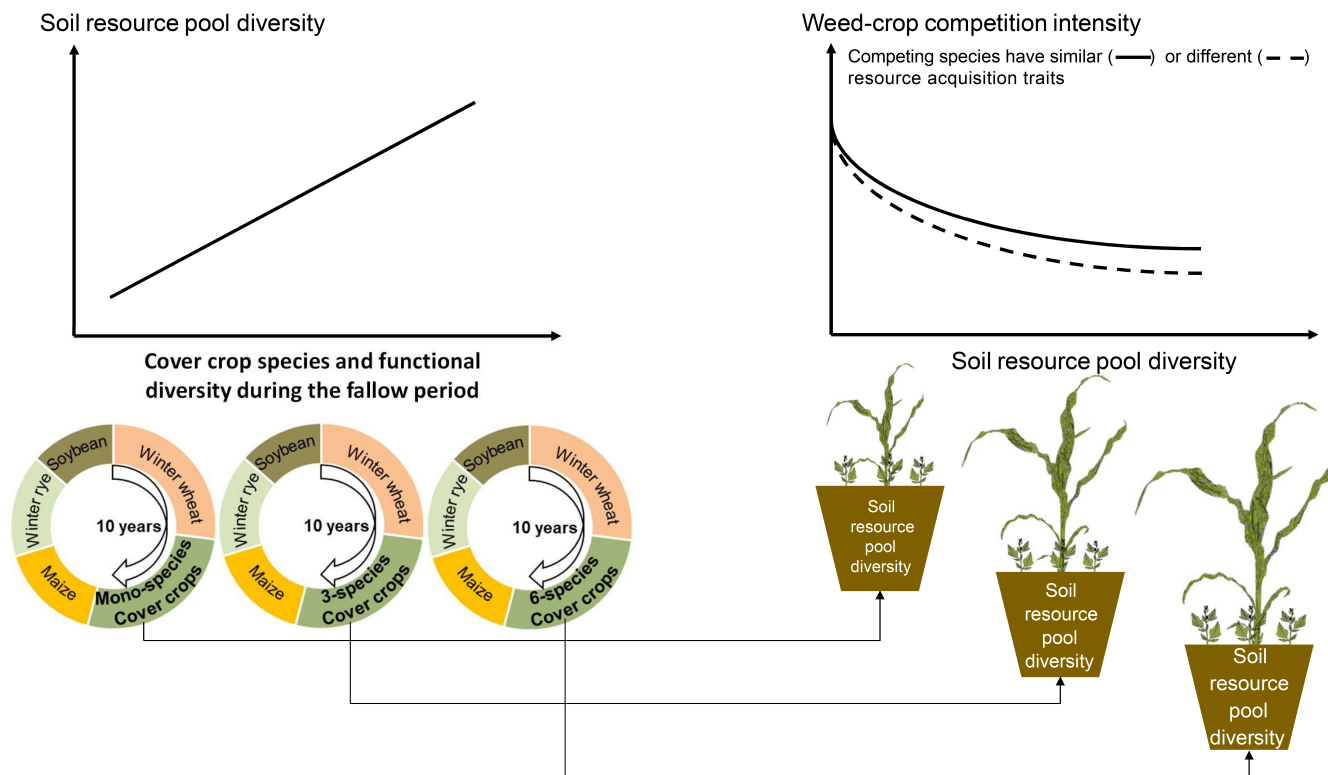


FIGURE 1 Resource pool diversity hypothesis developed by Smith et al. (2010) adapted to cover crop diversity: A higher cover crop diversity during the fallow period is expected to decrease weed-crop competition intensity in the subsequent crop through soil-mediated effects (i.e. an increase of soil resource pool diversity).

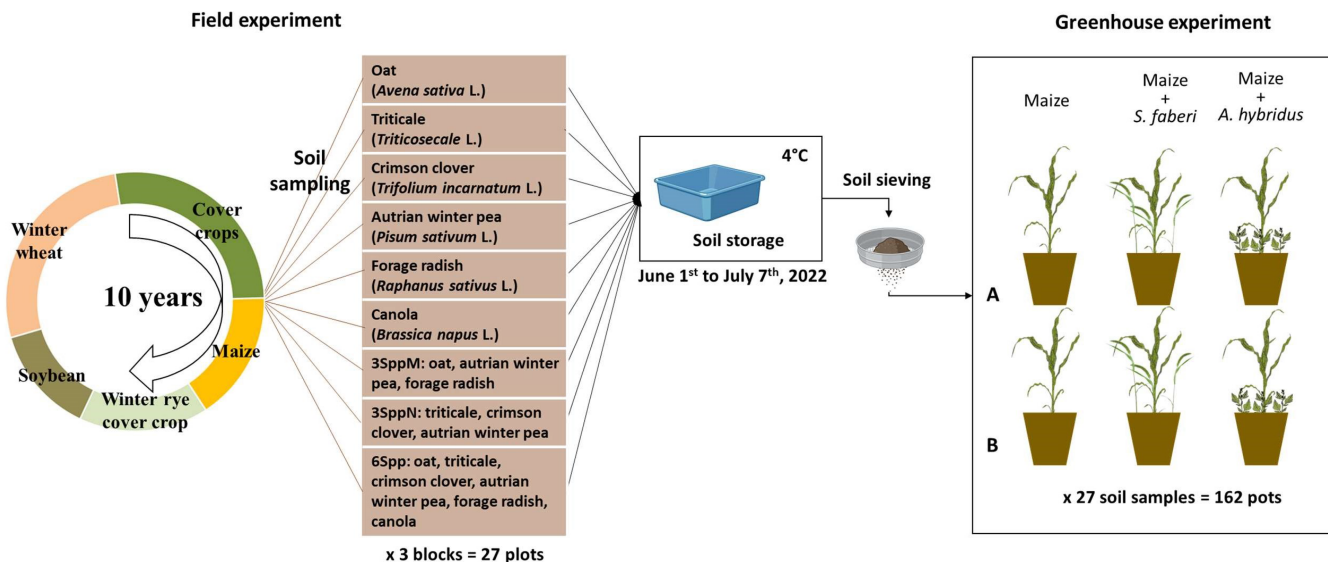



FIGURE 2 Greenhouse experimental set-up. Soil samples ($n = 27$) were randomly collected in each cover crop treatment ($n = 9$) and block ($n = 3$) of the long-term field experiment. Each soil sample was kept at 4°C and then used to fill six pots after soil sieving. Each pot was either planted with an individual maize alone, maize + *Setaria faberi*, or maize + *Amaranthus hybridus*. These latter treatments were repeated two times (A and B) per soil sample for a total of 162 pots in the greenhouse.

testing different cover crop treatments, varying in cover crop species richness and functional diversity (six mono-species cover crops and five cover crop mixtures described in Supp. Table 1). Cover crops are sown after winter wheat (*Triticum aestivum* L.) and incorporated into

soil before maize in a 3-year wheat–maize–soybean (*Glycine max* (L.) Merr.) rotation (Figure 2). This rotation experiment was established in 2012 at the Pennsylvania State University Russell E. Larson Agricultural Research Center, Rock Springs, Pennsylvania ($40^{\circ}43'N$,

TABLE 1 Main characteristics of the cover crop species chosen for the experiment.

	Cover crop treatment (scientific name)	Botanical family	Species richness	Number of functional group	Biological and functional characteristics
Cover crop diversity gradient LOW  HIGH	Oat (<i>Avena sativa</i> L.)	Poaceae	1	1	Fibrous, dense and deep root system/allelopathic plant/high C:N ratio/slow residue decomposition/highly productive/erect stem/50–150 cm high/fine leaves/winter kill
	Triticale (<i>Triticosecale</i> L.)	Poaceae	1	1	Fibrous, dense and deep root system/high C:N ratio/slow residue decomposition/highly productive/erect stem/tillering capacity/winter-hardy
	Canola (<i>Brassica napus</i> L.)	Brassicaceae	1	1	Taproot/erect stem/1 m high/high C:N ratio/slow residue decomposition/winter-hardy
	Forage radish (<i>Raphanus sativus</i> L.)	Brassicaceae	1	1	Taproot/erect stem/50–80 cm high/large leaves/high C:N ratio/slow residue decomposition/winter kill
	Crimson clover (<i>Trifolium incarnatum</i> L.)	Fabaceae	1	1	Taproot/erect stem/20–50 cm high/large leaves/symbiotic N fixation/low C:N ratio/fast residue decomposition/winter-hardy
	Austrian winter pea (<i>Pisum sativum</i> L.)	Fabaceae	1	1	Shallow taproot/climbing/symbiotic N fixation/low C:N ratio/fast residue decomposition/winter kill
	3SppN	Poaceae and Fabaceae	3	2	Mix of crimson clover, Austrian winter pea and Triticale characteristics
	3SppM	Poaceae, Brassicaceae, and Fabaceae	3	3	Mix of oat, Austrian winter pea and forage radish characteristics
	6Spp	Poaceae, Brassicaceae and Fabaceae	6	3	Mix of all species characteristics

Note: Cover crop treatments were ranked according to diversity gradients. Biological and functional characteristics of cover crops were found in papers characterising cover crop species (Amsili & Kaye, 2021; Hudek et al., 2022; Tribouillois et al., 2015).

77°55'W). Soils at the experimental location are a Murrill channery silt loam (fine-loamy, mixed, semiactive, mesic Typic Hapludult) with a 0%–3% slope. The average annual precipitation is 975 mm and mean monthly temperatures range from -3°C in January to 22°C in July.

Cover crop treatments were established in a randomised, full-entry complete block design (four blocks) (Supp. Figure 1). Cover crops were implemented four times in the rotation from 2012 (start of the experiment) and our experiment (2021–2022). Cover crop diversity is the only manipulated factor affecting soil resource pool diversity because the crops and cover crops are managed the same in every other factor throughout the crop rotation (Supp. Table 2). To manage for soil macronutrients, 9 and 4.5 tonnes ha^{-1} of poultry litter are added in the maize and wheat rotation phase, respectively. Soil pH is tested every 3 years, and thus far, was always found to be around 6.5 so no lime has been added. Other details about management of the experiment can be found in (Amsili & Kaye, 2021; Kaye et al., 2019). Daily precipitation and average daily temperature during the 2021–2022 cover cropping period, that is, before the beginning of the greenhouse experiment, can be found in Supp. Figure 2.

2.2 | Greenhouse experiment

Six days after cover crop ploughing in 2022, soil samples (0–15 cm depth) were randomly collected within each of the nine cover crop treatments chosen for our greenhouse experiment, in three of the four blocks of the field experiment (Figure 2). The fourth block of the field experiment was excluded because of substantial cover crop winter injury. Thenine cover crop treatments were selected to explore species richness and functional diversity gradients (Table 1). Both species richness and functional diversity increased in mono-species cover crops, three-species cover crop mixtures, and six-species cover crop mixtures (Table 1). Soil samples were kept at 4°C in the dark approximately 1 month until the greenhouse experiment was initiated.

Soils collected from individual plots were passed through a 4 mm sieve, combined with perlite (3:1 v/v ratio of soil: perlite), and then used to fill six pots (3.785 L) per field plot (Figure 2). Pots were distanced between 25 and 28 cm apart on greenhouse benches. We used maize (cv. Master Choice 3890) and two common and problematic annual weed species in maize to evaluate cover crop legacy effects on weed-crop competition: a monocot, *Setaria faberi* Herrm. (giant foxtail)

and a dicot, *Amaranthus hybridus* L. (smooth pigweed). Seeds for both weed species were collected in the fall of 2021 in fields adjacent to the long-term cover crop field experiment described in Section 2.1. Seeds were then separated from chaff, and stratified at 4°C in moist and dark conditions to break dormancy. Each pot in the greenhouse experiment was composed of either one maize plant, one maize plant + three *S. faberi* plants, or one maize plant + three *A. hybridus* plants (Figure 2). Each combination of cover crop soil legacy and maize-weed community was replicated six times (we sampled from cover crop field plots from three blocks in the field X 2 greenhouse pot subsamples per maize-weed combination grown in soil collected from each field plot) for a total of 162 pots. To ensure we had at least one maize plant per pot, we planted two maize seeds per pot in the centre and thinned to one plant immediately upon maize emergence. Weed seeds were planted in three locations in a triangle pattern around the central maize plant, with 10 seeds per location and weed seedlings were thinned so that pots had three weed plants each. We selected one maize plant and three weed plants because our goal was to maximise interspecific competition and minimise intraspecific competition within each pot. While we could not definitively know whether each plant came from our sown weed seeds compared to the background seed bank in the soil, because of the high density sown in very specific spots in the pot there was a high probability that each weed individual came from the seeds we planted. Seedlings were thinned approximately 10 days after sowing, and all individuals were selected to be at a similar size, with the first true leaf just emerging.

Pots were irrigated daily throughout the experiment with automatic irrigation, which was programmed to minimise hydric stress and leaching from the pots, which contained drainage holes. The greenhouse was lightened with LED lights, providing 6 mols of photosynthetically active radiation per day during 16 h, to minimise competition for light.

2.3 | Plants and soil assessments

Maize and weed aboveground dry biomass were used as indicators of relative competition intensity (RCI) (Trinder et al., 2021). We terminated the greenhouse experiment and measured maize and weed aboveground biomass 55 days after its initiation to avoid the maize and weeds from becoming overly root-bound within the pots. Maize plants ranged from the V6 to V8 growth stage at termination (Hanway, 1999). Plant samples were oven-dried at 60°C for 7 days and we recorded dry biomass weight.

Crop and weed competition intensity was assessed by calculating a competition index (Weigelt & Jolliffe, 2003) based on the measured aboveground dry biomass of maize grown alone and with each weed species. RCI (Grace, 1995) was calculated at the pot level as follows:

$$RCI = \frac{(P_{\text{mono}} - P_{\text{mix}})}{P_{\text{mono}}},$$

where P_{mono} is the aboveground biomass (g) of maize P_{mono} alone and P_{mix} the biomass (g) of maize grown with *S. faberi* or *A. hybridus*.

$RCI = 0$ means that maize biomass was the same whether grown alone or with weeds. $RCI > 0$ and < 0 indicate higher and lower maize biomass when maize was grown alone rather than with weeds, respectively. The higher RCI, the higher the competitive effect of weeds on maize.

To identify whether weeds competed with maize for soil nitrogen in each cover crop treatment, total carbon and nitrogen concentrations in the soil used to fill the pots, and nitrogen quantity in plants were assessed. Soil, maize, and weed total carbon and nitrogen concentrations were measured using the elemental organic combustion UNICUBE Analyser (Elementar, Germany), after grinding the samples to 1 mm particle size. Plant nitrogen quantity was then calculated by multiplying plant aboveground biomass by plant nitrogen concentration.

Finally, to explain potential soil-mediated effects of cover crops on weed-crop competition intensity, cover crop (per species) and weed (all species) fall (11 November 2021) and spring (11 May 2022) aboveground biomass were measured in the field, with three 0.25 m² quadrats per plot. Cover crop (per species) and weed (all species) biomass were oven-dried at 60°C for 7 days, and the dry matter biomass was weighed and averaged at the cover crop treatment level in both the fall and spring periods.

2.4 | Statistical analysis

Statistical analyses were performed with the R software version 4.2.1 (R Core Team, 2020), and in each of the analyses below we used generalised linear mixed effect models, available in the R 'glmmTMB' package (Brooks et al., 2017) with the interaction of cover crop treatment and block as a random effect to account for greenhouse pot subsamples.

To test our hypothesis that increasing cover crop species and functional diversity will mitigate competition exerted by weeds on the subsequent crop according to the RPDH, we tested the fixed effects of cover crop diversity (1, 3, or 6 cover crop species), weed species competitor (*S. faberi* and *A. hybridus*), and their interaction on the RCI between maize and each weed species competitor. In addition, we evaluated the effects of cover crop treatment, weed species competitor, and their interaction on RCI, weed biomass, or weed nitrogen quantity. Maize biomass and nitrogen quantity were independently modelled with cover crop treatment, weed species competitor, and their interaction as fixed effects to determine whether the effect of weed species competitor on maize growth varied.

Finally, to identify whether weed-crop competition was affected by cover crop treatments through varying soil resource availability, we included RCI as a response variable with weed species competitor, soil nitrogen concentration, or C:N ratio, and their interaction as fixed effects. To determine whether cover crop treatment affected soil resource availability, we included cover crop treatment as a fixed effect. Total nitrogen concentration and C:N ratio of soils samples used for the greenhouse experiment were included as response variables in separate models.

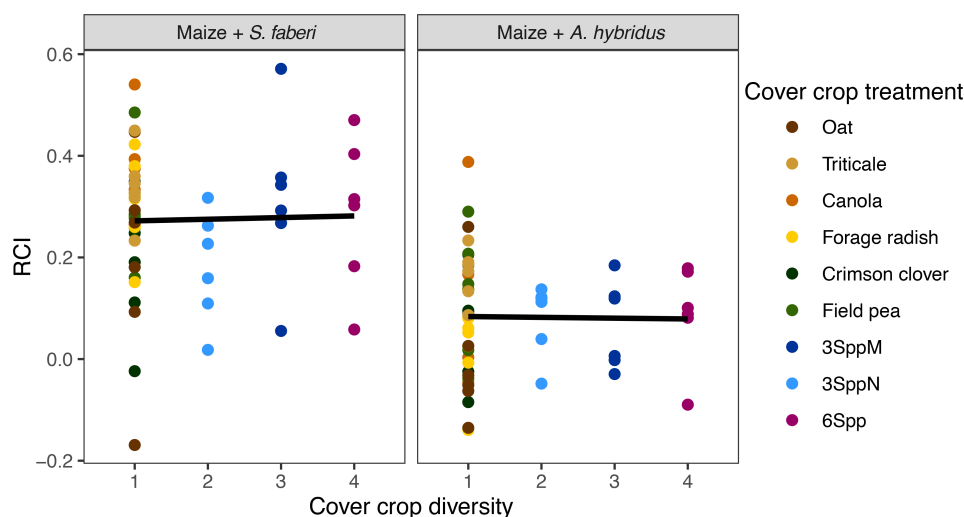


FIGURE 3 Effect of cover crop diversity on the relative competition intensity (RCI, unitless) between maize and each weed species competitor (i.e., *Setaria faberi* and *Amaranthus hybridus*). RCI was calculated at the pot level as follows: $RCI = \frac{(P_{mono} - P_{mix})}{P_{mono}}$, where P_{mono} is the aboveground biomass (g) of maize grown alone and P_{mix} the biomass (g) of maize grown with *S. faberi* or *A. hybridus*. Botanical families and cover crop treatments are graphically distinguished with different shapes and colours, respectively. P -value <0.05 indicates a slope different from zero. 3SppM: Cover crop mixture of oat, Austrian winter pea and Forage radish; 3SppN: Cover crop mixture of Crimson clover, Austrian winter pea and Triticale; 6Spp: Cover crop mixture of all species tested.

Maize biomass, weed biomass, and nitrogen quantity were modelled with a tweedie family and a log link function, which is currently used to meet model assumptions with skewed or bimodal data distributions (Dunn, 2022), and maize nitrogen quantity and RCI were modelled with a Gaussian family without identity link according to the data distributions. Significance of fixed effects was determined through Type III Wald Chi-Square tests using the function Anova of the R ‘car’ package (Fox et al., 2020). Contrasts were adjusted using the R ‘emmeans’ package (Lenth, 2021).

3 | RESULTS

3.1 | Cover crop legacy effects on weed-maize competition intensity

The RCI between maize and weeds was not affected by cover crop diversity ($\chi^2 = 0.01$; p -value = 0.93), nor the interaction between cover crop diversity and weed species competitor ($\chi^2 = 0.01$; p -value = 0.94). Thus, no relationship between cover crop diversity and RCI was found, neither when maize was grown with *S. faberi* nor with *A. hybridus* (Figure 3). RCI between maize and *S. faberi* was driven more by variation in maize biomass ($R^2 = 0.3$) versus *S. faberi* biomass ($R^2 = 0.07$). In contrast, neither variation in maize nor *A. hybridus* biomass were strong predictors of their RCI, likely because the *A. hybridus* did so poorly in the greenhouse experiment that competition was minimal.

RCI between maize and weeds were affected by cover crop treatment ($\chi^2 = 21$; p -value = 0.008) and weed species competitor ($\chi^2 = 82$; p -value <0.0001), but not their interaction (Figure 4; Supp.

Table 3). On average across cover crop treatments, RCI was higher (indicating greater competition) when maize was grown with *S. faberi* (27%) than with *A. hybridus* (8%). Trends indicate that when maize was grown with *S. faberi*, RCI was the highest in triticale and canola cover crop treatments (36% and 34%, respectively), and the lowest in 3SppN, oat, and crimson clover cover crop treatments (18%, 19%, and 20%, respectively) (Figure 4). Despite very low RCI when maize was grown with *A. hybridus*, RCI was the highest in triticale (17%) and the lowest in forage radish and oat (1% and 0.1%, respectively) (Figure 4).

3.2 | Cover crop legacy and weed species effects on maize growth

The effect of cover crop treatment on maize biomass depended on weed species competitors (Table 2, Supp. Table 3), while maize nitrogen quantity varied by cover crop treatment and weed species competitor as main effects (Table 3, Supp. Table 3). *S. faberi* reduced maize biomass and nitrogen quantity in all the cover crop treatments, on average from -28% to -31% (Tables 2 and 3). *A. hybridus* significantly reduced maize biomass only in triticale (-17%), canola (-13%) and Austrian winter pea (-15%) cover crop treatments (Table 2), and did not affect maize nitrogen quantity (Table 3). Grown alone, maize biomass was significantly lower in grass cover crop treatments (oat and triticale) than in 3SppN (Table 2). Grown with *S. faberi*, maize biomass was significantly lower in all the cover crop treatments, except legume mono-species cover crops (crimson clover and Austrian winter pea), than in 3SppN (Table 2). Grown with *A. hybridus*, maize biomass was significantly lower in grass and canola cover crop treatments than in 3SppN (Table 2). Similar to maize biomass, maize nitrogen quantity

FIGURE 4 Variation of the relative competition intensity (RCI, %) between maize and each weed species competitor (i.e., *Setaria faberi* and *Amaranthus hybridus*) for every cover crop treatment. Means RCI are indicated with bold dots, confidence intervals with bars, and row data with clear little dots. 3SppM: Cover crop mixture of oat, Austrian winter pea and Forage radish; 3SppN: Cover crop mixture of Crimson clover, Austrian winter pea and Triticale; 6Spp: Cover crop mixture of all species tested.

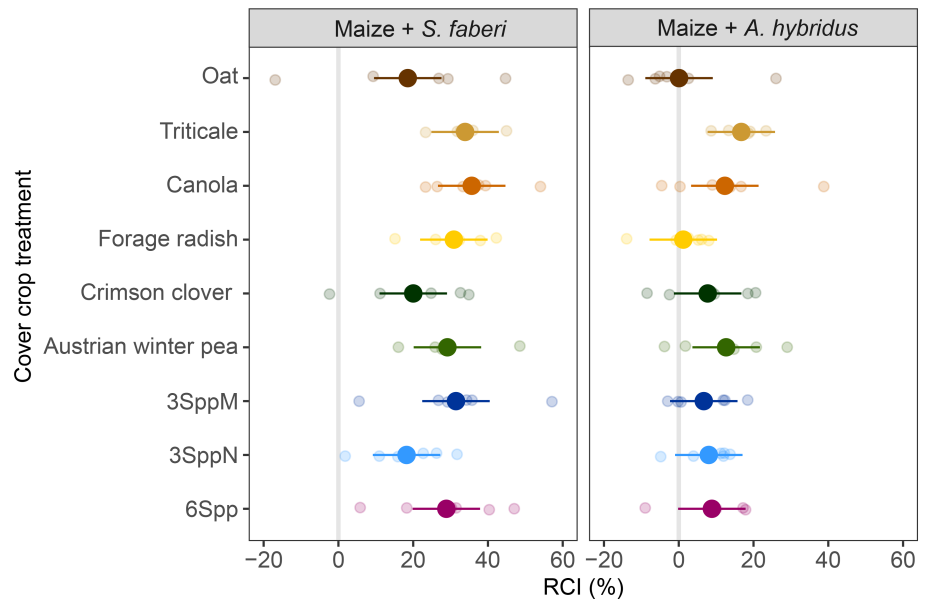


TABLE 2 Average (and standard error) of maize biomass (g) measured at biomass sampling within the competition greenhouse experiment.

Cover crop treatment	Maize biomass		
	Maize	Maize + <i>Setaria faberi</i>	Maize + <i>Amaranthus hybridus</i>
Oat	3.28 (0.48) A b	2.54 (0.28) B cd	3.16 (0.31) A bc
Triticale	3.35 (0.19) A b	2.19 (0.07) C d	2.78 (0.14) B c
Canola	3.57 (0.22) A ab	2.26 (0.11) C d	3.09 (0.21) B bc
Forage radish	3.81 (0.52) A ab	2.57 (0.30) B bcd	3.75 (0.51) A abc
Crimson clover	4.29 (0.21) A ab	3.42 (0.26) B ab	3.96 (0.30) A ab
Autrian winter pea	4.40 (0.50) A ab	3.19 (0.50) C abc	3.74 (0.25) B abc
3SppM	3.90 (0.41) A ab	2.56 (0.18) B bcd	3.62 (0.38) A abc
3SppN	4.77 (0.35) A a	3.9 (0.36) B a	4.34 (0.23) A a
6Spp	4.01 (0.34) A ab	2.87 (0.39) B bcd	3.64 (0.31) A abc

Note: Uppercase letters compare maize biomass by weed crop combination (i.e., maize alone, maize + *Setaria faberi* and maize + *Amaranthus hybridus*) within each cover crop treatment. Lowercase letters compare maize biomass and nitrogen quantity by cover crop treatment in each weed crop combination. Treatments sharing the same letter are not significantly different at p -value < 0.05. 3SppM: Cover crop mixture of oat, Austrian winter pea and Forage radish; 3SppN: Cover crop mixture of Crimson clover, Austrian winter pea and Triticale; 6Spp: Cover crop mixture of all species tested.

showed the highest values in the 3SppN cover crop treatment, and maize nitrogen quantity was significantly lower in the grass (triticale and oat), brassica (forage radish and canola) and the 3SppM cover crop treatments compared to 3SppN (Table 3). Using preplanned contrasts, we found that cover crop treatments that included a legume increased both maize biomass (p -value < 0.009) and nitrogen quantity (p -value < 0.002) compared to those that did not include a legume, regardless of whether maize was grown alone or with a weed species competitor.

Biomass and nitrogen quantity of *S. faberi* and *A. hybridus*, grown with maize, differed between the two species, but it did not differ by cover crop treatments (Table 4, Supp. Table 3). On average across cover crop treatments, *S. faberi* biomass and nitrogen quantity (0.84 g and 7.2 mg N, respectively) were higher compared to *A. hybridus* (0.12 g and 1.1 mg N, respectively).

3.3 | Soil resource availability effects on weed-crop competition

RCI between maize and weeds was not affected by soil nitrogen concentration ($\chi^2 = 2$; p -value = 0.16), soil C:N ratio ($\chi^2 = 0.002$; p -value = 0.96), nor cover crop C:N ratio in fall ($\chi^2 = 0.1$; p -value = 0.76) or spring ($\chi^2 = 3.1$; p -value = 0.08), nor was there any interaction with weed species competitor.

Cover crop (plus weeds) biomass and C:N ratio in the field varied among cover crop treatments and between fall and spring in each cover crop treatment (Supp. Figure 3 and Supp. Table 4). Crimson clover and Austrian winter pea were the most productive cover crop species in the fall (2.9 and 2.4 t ha⁻¹, respectively, when grown alone) and as expected, had the lowest C:N ratios. Oat, triticale, and canola had the highest C:N ratios in fall. Oat, forage radish, Austrian winter

TABLE 3 Average (and standard error) of maize nitrogen quantity (mg N) measured at biomass sampling within the competition greenhouse experiment.

Cover crop treatment	Maize nitrogen quantity			Cover crop main effect
	Maize	Maize + <i>Setaria faberi</i>	Maize + <i>Amaranthus hybridus</i>	
Oat	22.5 (1.54)	14.6 (3.13)	22.7 (1.64)	19.9 (1.51) cde
Triticale	21.5 (0.73)	13.8 (0.86)	19.6 (0.55)	18.3 (0.89) e
Canola	21.5 (1.15)	14.2 (0.64)	23.0 (1.60)	19.6 (1.13) de
Forage radish	25.4 (2.79)	14.8 (1.19)	24.5 (2.55)	21.5 (1.70) bcde
Crimson clover	26.8 (2.15)	20.2 (1.51)	24.4 (0.86)	23.8 (1.09) abc
Austrian winter pea	27.0 (1.19)	20 (2.03)	25.9 (0.73)	24.3 (1.08) ab
3SppM	25.4 (1.42)	17.3 (0.43)	26.0 (1.37)	22.9 (1.15) bcd
3SppN	30.7 (1.68)	23.5 (0.96)	29.0 (1.12)	27.7 (1.02) a
6Spp	26.9 (1.30)	18.4 (1.5)	24.9 (0.56)	23.4 (1.09) bcd
Weed species competitor main effect	25.3 (0.64) A	17.4 (0.65) B	24.4 (0.54) A	

Note: Uppercases compare the main effect of weed crop combination (i.e., maize alone, maize + *Setaria faberi* and maize + *Amaranthus hybridus*) on maize nitrogen quantity. Lowercases (in green) the main effect of cover crop treatment on maize nitrogen quantity. Treatments sharing the same letter are not significantly different at p -value < 0.05. 3SppM: Cover crop mixture of oat, Austrian winter pea and Forage radish; 3SppN: Cover crop mixture of Crimson clover, Austrian winter pea and Triticale; 6Spp: Cover crop mixture of all species tested.

TABLE 4 Average (and standard error) of weed biomass (g) and nitrogen quantity (mg N) measured at biomass sampling when grown in competition with maize within the greenhouse experiment.

	Weed biomass		Weed nitrogen quantity	
	<i>Setaria faberi</i>	<i>Amaranthus hybridus</i>	<i>Setaria faberi</i>	<i>Amaranthus hybridus</i>
Oat	0.83 (0.20)	0.11 (0.02)	7.5 (1.00)	0.99 (0.15)
Triticale	0.70 (0.03)	0.09 (0.03)	6.09 (0.27)	0.88 (0.26)
Canola	0.80 (0.05)	0.14 (0.05)	7.25 (0.31)	1.23 (0.4)
Forage radish	1.02 (0.18)	0.13 (0.06)	7.69 (0.80)	1.05 (0.5)
Crimson clover	0.80 (0.07)	0.16 (0.05)	6.43 (0.44)	1.32 (0.39)
Austrian winter pea	1.03 (0.19)	0.08 (0.02)	8.49 (1.10)	0.8 (0.21)
3SppM	0.91 (0.26)	0.10 (0.02)	7.96 (1.64)	0.81 (0.12)
3SppN	0.93 (0.19)	0.12 (0.03)	7.42 (0.97)	1.2 (0.23)
6Spp	0.85 (0.16)	0.16 (0.03)	6.28 (1.44)	1.45 (0.33)

Note: Weed species included *Setaria faberi* and *Amaranthus hybridus*. Weed biomass and N quantity differed between the two species but did not differ by cover crop treatments (Supp. Table 3). 3SppM: Cover crop mixture of oat, Austrian winter pea and Forage radish; 3SppN: Cover crop mixture of Crimson clover, Austrian winter pea and Triticale; 6Spp: Cover crop mixture of all species tested.

pea, and crimson clover biomass were reduced between fall and spring (-1.7 , -1.6 , -2.4 , and -1.6 t ha⁻¹, respectively, when grown alone). However, triticale and canola biomass increased between fall and spring ($+0.8$ and $+0.7$ t ha⁻¹, respectively, when grown alone). The 3SppN cover crop treatment resulted in the highest total biomass in the spring (>4 t ha⁻¹), with a high proportion of triticale (~ 2.5 t ha⁻¹) and crimson clover (~ 1.2 t ha⁻¹). In spring, crimson clover had the lowest C:N, while canola and triticale had the highest C:N ratio.

Total nitrogen concentration measured in soils before starting the greenhouse experiment varied by cover crop treatment ($\chi^2 = 24$; p -value = 0.002), but soil C:N ratio did not ($\chi^2 = 8$; p -value = 0.41; Supp. Table 5). Soil total nitrogen concentration was the highest in

3SppN and Austrian winter pea cover crop treatments, and was significantly lower than these cover crop treatments only in triticale.

4 | DISCUSSION

No relationship between RCI and cover crop diversity was found in our experiment, neither when maize was grown with *S. faberi* nor with *A. hybridus*, which fails to support our hypothesis that increasing cover crop species and functional diversity will mitigate competition exerted by weeds on the subsequent crop according to the RPDH. Potential explanations of the lack of support for our hypothesis could be that: (1) increasing cover crop diversity did not increase soil resource pool

diversity, or the magnitude of variation in soil resource pool diversity was not sufficient to affect weed-crop competition, (2) greenhouse experiments may be insufficient to test the RPDH, (3) the magnitude of weed-crop competition within our study was not sufficient to detect an effect of resource pool diversity, and (4) resource pool diversity may not be an important factor affecting weed-crop competition.

4.1 | Does cover crop diversity increase soil resource pool diversity?

While we measured soil total nitrogen and carbon concentrations in our experiment, we did not test the diversity of these resources. Testing cover crop effects on soil resource pool diversity could have included examining soil microbial diversity, the chemical compounds in soil (e.g. forms of nitrogen, such as variation in amino acid or other compounds in the soil), or variation in soil physical structure such as stable aggregate size. Conducting these analyses on the field soil we used within our greenhouse pots was outside the scope of our experiment. However, previous research from our long-term cover crop field experiment showed that soils within our cover crop treatments can differ in microbial communities as well as soil composition of physiochemical pools of soil organic carbon, which suggests that the soil from the long-term cover crop diversity experiment do vary in soil resource pools. In fact, Cloutier et al. (2020) showed in 2014, 4 years after the beginning of the experiment, that the 3SppN cover crop treatment and to a lesser extent the 6Spp cover crop treatment, contained greater microbial diversity than their mono-species counterparts. Recently, Zhang et al. (2022) showed that functionally distinct cover crop species contributed to different pools of organic carbon. While the proportion of plant-derived carbon in particulate organic matter was higher in triticale and canola cover crops, the proportion of microbial-derived carbon in mineral-associated organic matter was higher with crimson clover. Interestingly, the mixture of these species resulted in a higher concentration of plant-derived compounds in particulate organic matter compared to the crimson clover, and a greater accumulation of microbial-derived carbon in mineral-associated organic matter compared to the canola and triticale; suggesting that mixtures can increase both short- and long-term soil organic carbon pools compared to mono-species cover crops. Therefore, while we did not directly measure the diversity of soil resources in our experiment, there is some evidence from previous studies that suggests increasing cover crop diversity increases soil resource diversity.

Previous studies reported that weed-crop competition can be driven by soil resource availability and microbial communities (Menalled et al., 2020; Ryan et al., 2010). While there is some evidence suggesting that soil carbon pools (Zhang et al., 2022) and soil microbial composition (Cloutier et al., 2020) were more diverse in cover crop mixtures than in mono-species cover crops, mixtures did not result in lower weed-crop competition intensity than mono-species cover crops in our experiment. One explanation is that the magnitude of difference in soil resource pool diversity

between mixtures and mono-species cover crops was not sufficient to measurably affect weed-crop competition intensity. Within the long-term cover crop experiment, the cover crop treatments only occur once in every 3 years of the crop rotation, and therefore the cover crop treatments were in place only four times over the course of the study thus far, which could be lower than the time needed to mediate processes that affect soil resource pools (Basche et al., 2016; Poeplau & Don, 2015). Additionally, inversion tillage is included every year within the experimental cropping system, which may homogenise soil resource pools compared to reduced- or no-tillage systems.

4.2 | Can the effects of soil resource pool diversity on crop-weed competition be tested in the greenhouse?

Greenhouse experiments are valuable in that they enable one to control for more external factors compared to field experiments. However, to our knowledge, ours is the third experiment that used field soil collected from a crop diversity gradient in annual cropping systems to test the effect of soil resource pool diversity on weed-crop competition in a greenhouse. Previous greenhouse studies also failed to find support for the RPDH (Menalled et al., 2020; Poffenbarger et al., 2015). Perhaps the nature of experimental conditions in the greenhouse may inhibit the detection of effects from soil resource pool diversity. For example, prior to setting up our greenhouse experiment, the soil was sieved and combined with perlite, both of which were necessary to improve infiltration, drainage, and overall quality of the growing media within the greenhouse pots. However, soil processing may have lowered the cover crop legacy effects on diversity of resource pools within the soil, for example, by altering soil structure and/or microbial communities. This is consistent with Poffenbarger et al. (2015), who noted that soil conditions in the greenhouse will not be as heterogenous or complex as in the field. They also noted that competition between crops and weeds occurs on a longer time scale in the field compared to pots in the greenhouse, which greatly restricts both the duration of growth and overall plant size compared to the field, potentially reducing the potential for resource partitioning. Additionally, greenhouse pots restricted both horizontal and vertical root growth. And according to the RPDH, for diverse resource pools to alleviate competition, soil not only must contain a diversity of soil resources, but the competing plant species must differ in resource acquisition or foraging strategies (Smith et al., 2010). Therefore, potential differences among plant species that enable them to occupy diverse niches in how they forage for soil resources may have been limited within pots.

4.3 | Was the magnitude of weed-crop competition intensity sufficient to test the RPDH?

To find support for the RPDH, it is possible that one needs a higher level of weed-crop competition intensity than occurred within our

experiment. Maize competed with two weed species: a grass, *S. faberi* which is likely to have similar resource acquisition strategies to maize, and a dicot, *A. hybridus*, which most likely differs from maize in its resource acquisition strategy. Thus, according to Smith et al. (2010), the slope of the relationship between weed-crop competition intensity and cover crop diversity was expected to be steeper when maize was with *S. faberi* compared to *A. hybridus*. However, *A. hybridus* did not grow well in the greenhouse experiment (i.e., lower biomass compared to the *S. faberi* plants), resulting in lower competition intensity with maize than expected. Potentially, *A. hybridus* may have been more negatively affected by the reduced light conditions characteristic of greenhouses, and the low fertility conditions within our experiment. Most *Amaranthus* species are nitrophilic and their competitive ability can be negatively affected by low nitrogen availability (Blackshaw & Brandt, 2008). Additionally, we may have needed higher densities of the small-seeded *A. hybridus* to overcome the large initial size difference when competing with maize, which has a much larger seed and therefore, a larger starting mass.

S. faberi did suppress maize regardless of the cover crop treatment. But as *S. faberi* and maize are both grasses, they likely did not differ as much in resource acquisition strategies, which could have decreased the slope of the relationship between weed-crop competition intensity and cover crop diversity (Smith et al., 2010). Testing the RPDH with more competitive grass and broad-leaved weed species that had more similar seed size to maize and at higher seedling density should be explored to further test the hypothesis.

4.4 | Potential alternative drivers of weed-crop competition

Despite finding no relationship between cover crop diversity and weed-crop competition in our study, weed-crop competition did vary across the cover crop treatments. While we only measured soil total nitrogen and carbon in our soil samples, and we did not find a relationship between weed-crop competition intensity and soil total nitrogen quantity nor C:N ratio, it is possible that weed-crop competition was driven by cover crop nitrogen release, if cover crop treatments varied in nitrogen mineralisation rates. For example, maize biomass and N quantity were both greater when grown in cover crop treatments containing legumes compared to those that did not. However, we did not find similar increases in either *S. faberi* or *A. hybridus* biomass when grown in cover crop treatments with legumes. This suggests that either: (1) the competitive ability of both weeds was either less responsive to increased N availability; or (2) greater N availability increased maize competitive ability and suppression of neighbouring weeds so that we failed to detect any difference in weed biomass in treatments containing legumes compared to those that did not.

In our study, the 3SppN cover crop treatment (composed of triticale, Austrian winter pea, and crimson clover) resulted in the lowest competition intensity between each weed and maize, and the highest maize biomass whether maize grown alone or with *S. faberi* and

A. hybridus. This could be attributed to the greater cover crop biomass in the spring or the higher total nitrogen concentration measured in soils where 3SppN was incorporated. Previous work found that grass and legume cover crop mixtures have slower rates of N mineralisation (Kuo & Sainju, 1998), which may or may not more closely mirror N uptake rates of the crop and increase crop competitive ability (Little et al., 2021). However, other cover crop mixtures within our experiment (3SppM and 6Spp) did not result in lower weed-crop competition and higher maize biomass than legume mono-species cover crops. In addition, oats reduced weed-maize competition as well as maize biomass. This suggests that cover crop soil-mediated effects on weed-crop competition may be complex and need further investigation.

While we did not find support for our hypothesis, that increasing cover crop functional diversity can mitigate crop and weed competition, we suggest further experiments to test the RPDH in the field, with diverse weed communities and under various farm management practices such as tillage or no-till, or source of fertilisation. This could provide insights into the drivers of weed-crop competition in agricultural fields and help farmers design the best cover crop mixtures to minimise the negative effect of weeds on crops.

ACKNOWLEDGEMENTS

Acknowledgments are expressed to the French Ministry of Agriculture which funded the PhD thesis of Alicia Rouge, and the Fulbright Commission which funded her research project in the US. The authors thank the entire team at Pennsylvania State University responsible for maintaining the long-term cover crop diversity experiment, including Brosi Bradley Jason Kaye, Hannah Wells, Charlie White, Corey Dillon, and others. We also thank Olivia Trase, who assisted in coordinating soil sampling at the site. Finally, we thank Christopher Stampis, Megan Galvin, Christopher Orndorff, Nathaniel Briendel, Emma Rice, Nasib Koirala, and Katherine Blocklove for their assistance in the greenhouse. The project was supported by the USDA Hatch Appropriations under Project No. PEN04759 and PEN04764, and USDA NIFA Grant Award No. 1009362.

CONFLICT OF INTEREST STATEMENT

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.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/wre.12680>.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author, C.L., upon request.

ORCID

Stéphane Cordeau  <https://orcid.org/0000-0003-1069-8388>

Delphine Moreau  <https://orcid.org/0000-0003-2640-9931>

Jean-Philippe Guillemain  <https://orcid.org/0000-0001-5981-3901>

Carolyn J. Lowry  <https://orcid.org/0000-0002-7695-1596>

REFERENCES

- Amsili, J.P. & Kaye, J.P. (2021) Root traits of cover crops and carbon inputs in an organic grain rotation. *Renewable Agriculture and Food Systems*, 36, 182–191.
- Baraibar, B., Hunter, M.C., Schipanski, M.E., Hamilton, A. & Mortensen, D.A. (2018) Weed suppression in cover crop monocultures and mixtures. *Weed Science*, 66, 121–133.
- Basche, A.D., Kaspar, T.C., Archontoulis, S.V., Jaynes, D.B., Sauer, T.J., Parkin, T.B. et al. (2016) Soil water improvements with the long-term use of a winter rye cover crop. *Agricultural Water Management*, 172, 40–50.
- Blackshaw, R.E. & Brandt, R.N. (2008) Nitrogen fertilizer rate effects on weed competitiveness is species dependent. *Weed Science*, 56, 743–747.
- Blanco-Canqui, H., Shaver, T., Lindquist, J. et al. (2015) Cover crops and ecosystem services: insights from studies in temperate soils. *Agronomy Journal*, 107, 2449–2474.
- Brooks, M.E., Kristensen, K., Van Benthem, K.J. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.
- Cloutier, M.L., Murrell, E., Barbercheck, M., Kaye, J., Finney, D., García-González, I. et al. (2020) Fungal community shifts in soils with varied cover crop treatments and edaphic properties. *Scientific Reports*, 10, 6198.
- Daryanto, S., Fu, B., Wang, L., Jacinthe, P.-A. & Zhao, W. (2018) Quantitative synthesis on the ecosystem services of cover crops. *Earth-Science Reviews*, 185, 357–373.
- Dunn PK (2022). Tweedie: evaluation of Tweedie exponential family models. R package version 2.3.5. Accessed November 3, 2024 at: <https://cran.r-project.org/web/packages/tweedie/tweedie.pdf>
- Fisk, J.W., Hesterman, O.B., Shrestha, A., Kells, J.J., Harwood, R.R., Squire, J.M. et al. (2001) Weed suppression by annual legume cover crops in No-tillage corn. *Agronomy Journal*, 93, 319–325.
- Fox, J., Weisberg, S. & Price, B. (2020) Companion to applied regression. Version 3.0–8.
- Grace, J.B. (1995) On the measurement of plant competition intensity. *Ecology*, 76, 305–308.
- Hanway, J.J. (1999) How a corn plant develops. Iowa State University of Science and Technology Cooperative Extension Service. Special Report No. 48 <https://publications.iowa.gov/18027/1/How%20a%20corn%20plant%20develops001.pdf>. Accessed November 26, 2024 at:
- Heap, I. (2023) The International Herbicide-Resistant Weed Database.
- Hudek, C., Putinica, C., Otten, W. & De Baets, S. (2022) Functional root trait-based classification of cover crops to improve soil physical properties. *European Journal of Soil Science*, 73, e13147.
- Kaye, J., Finney, D., White, C., Bradley, B., Schipanski, M., Alonso-Ayuso, M. et al. (2019) Managing nitrogen through cover crop species selection in the U.S. mid-Atlantic. *PLoS One*, 14, e0215448.
- Kuo, S. & Sainju, U.M. (1998) Nitrogen mineralization and availability of mixed leguminous and non-leguminous cover crop residues in soil. *Biology and Fertility of Soils*, 26, 346–353.
- Lenth RV (2021) Estimated marginal means, aka least-squares means. CRAN R Package Version 1.6.0, 85.
- Little, N.G., Ditommaso, A., Westbrook, A.S., Ketterings, Q.M. & Mohler, C.L. (2021) Effects of fertility amendments on weed growth and weed-crop competition: a review. *Weed Science*, 69, 132–146.
- Marcillo, G.S. & Miguez, F.E. (2017) Corn yield response to winter cover crops: an updated meta-analysis. *Journal of Soil and Water Conservation*, 72, 226–239.
- Menalled, U.D., Bybee-Finley, K.A., Smith, R.G., Ditommaso, A., Pethybridge, S.J. & Ryan, M.R. (2020) Soil-mediated effects on weed-crop competition: elucidating the role of annual and perennial inter-crop diversity legacies. *Agronomy*, 10, 1373.
- Mirsky, S.B., Ryan, M.R., Teasdale, J.R., Curran, W.S., Reberg-Horton, C.S., Spargo, J.T. et al. (2013) Overcoming weed Management challenges in cover crop-based organic rotational no-till soybean production in the eastern United States. *Weed Technology*, 27, 193–203.
- Moore, M.J., Gillespie, T.J. & Swanton, C.J. (1994) Effect of cover crop mulches on weed emergence, weed biomass, and soybean (*Glycine max*) development. *Weed Technology*, 8, 512–518.
- Oerke, E.-C. (2006) Crop losses to pests. *The Journal of Agricultural Science*, 144, 31–43.
- Petit, S., Cordeau, S., Chauvel, B., Bohan, D., Guillemain, J.-P. & Steinberg, C. (2018) Biodiversity-based options for arable weed management: A Review. *Agronomy for Sustainable Development*, 38, 48.
- Poeplau, C. & Don, A. (2015) Carbon sequestration in agricultural soils via cultivation of cover crops—a meta-analysis. *Agriculture, Ecosystems & Environment*, 200, 33–41.
- Poffenbarger, H., Mirsky, S.B., Teasdale, J.R., Spargo, J.T., Cavigelli, M.A. & Kramer, M. (2015) Nitrogen competition between corn and weeds in soils under organic and conventional management. *Weed Science*, 63(2), 461–476.
- R Core Team. (2020) *R: a language and environment for statistical computing*. Vienna, Austria: RFFS Computing.
- Rouge, A., Adeux, G., Busset, H., Hugard, R., Martin, J., Matejcek, A. et al. (2022) Weed suppression in cover crop mixtures under contrasted levels of resource availability. *European Journal of Agronomy*, 136, 126499.
- Rouge, A., Adeux, G., Busset, H., Hugard, R., Martin, J., Matejcek, A. et al. (2023) Carry-over effects of cover crops on weeds and crop productivity in no-till systems. *Field Crops Research*, 295, 108899.
- Ryan, M.R., Mortensen, D.A., Bastiaans, L. et al. (2010) Elucidating the apparent maize tolerance to weed competition in long-term organically managed systems. *Weed Research*, 50, 25–36.
- Sainju, U.M., Whitehead, W.F. & Singh, B.P. (2003) Cover crops and nitrogen fertilization effects on soil aggregation and carbon and nitrogen pools. *Canadian Journal of Soil Science*, 83, 155–165.
- Shackelford, G.E., Kelsey, R. & Dicks, L.V. (2019) Effects of cover crops on multiple ecosystem services: ten meta-analyses of data from arable farmland in California and the Mediterranean. *Land Use Policy*, 88, 104204.
- Smith, R.G., Mortensen, D.A. & Ryan, M.R. (2010) A new hypothesis for the functional role of diversity in mediating resource pools and weed-crop competition in agroecosystems. *Weed Research*, 50, 37–48.
- Teasdale, J.R., Brandsaeter, L.O., Calegari, A. & Skora Neto, F. (2007) Cover crops and weed management. In: Upadhyaya, M.K. & Blackshaw, R.E. (Eds.) *Non-chemical weed management: principles, concepts and technology*. Wallingford, UK; Cambridge, MA: CABI, pp. 49–64.
- Tribouillois, H., Fort, F., Cruz, P., Charles, R., Flores, O., Garnier, E. et al. (2015) A functional characterisation of a wide range of cover crop species: growth and nitrogen acquisition rates, leaf traits and ecological strategies. *PLoS One*, 10, e0122156.
- Trinder, C.J., Brooker, R.W., Davidson, H. & Robinson, D. (2021) Directly quantifying multiple interacting influences on plant competition. *Plant, Cell & Environment*, 44, 1268–1277.
- Violle, C., Garnier, E., Lecoer, J., Roumet, C., Pothier, C., Blanchard, A. et al. (2009) Competition, traits and resource depletion in plant communities. *Oecologia*, 160, 747–755.
- Weigelt, A. & Jolliffe, P. (2003) Indices of plant competition. *Journal of Ecology*, 91, 707–720.
- Wells, M.S., Reberg-Horton, S.C., Smith, A.N. & Grossman, J.M. (2013) The reduction of plant-available nitrogen by cover crop mulches and subsequent effects on soybean performance and weed interference. *Agronomy Journal*, 105, 539–545.
- Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C. & Bradbury, R.B. (1999) A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture, Ecosystems & Environment*, 75, 13–30.
- Zhang, Z., Kaye, J.P., Bradley, B.A., Amsili, J.P. & Suseela, V. (2022) Cover crop functional types differentially alter the content and composition

of soil organic carbon in particulate and mineral-associated fractions.

Global Change Biology, 28, 5831–5848.

Zimdahl, R.L. (2004) In: Blackwell, W. (Ed.) *Weed-crop competition: a review*, 2nd edition. Ames, IA, USA: Blackwell Publishing.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Rouge, A., Wallace, J.M., Cordeau, S., Moreau, D., Guillemin, J.-P. & Lowry, C.J. (2025) Soil-mediated effects of cover crops on weed-crop competition. *Weed Research*, 65(1), e12680. Available from: <https://doi.org/10.1111/wre.12680>