Carabids as weed seed control agents

Impact of soil cultivation on carabid weed seed regulation

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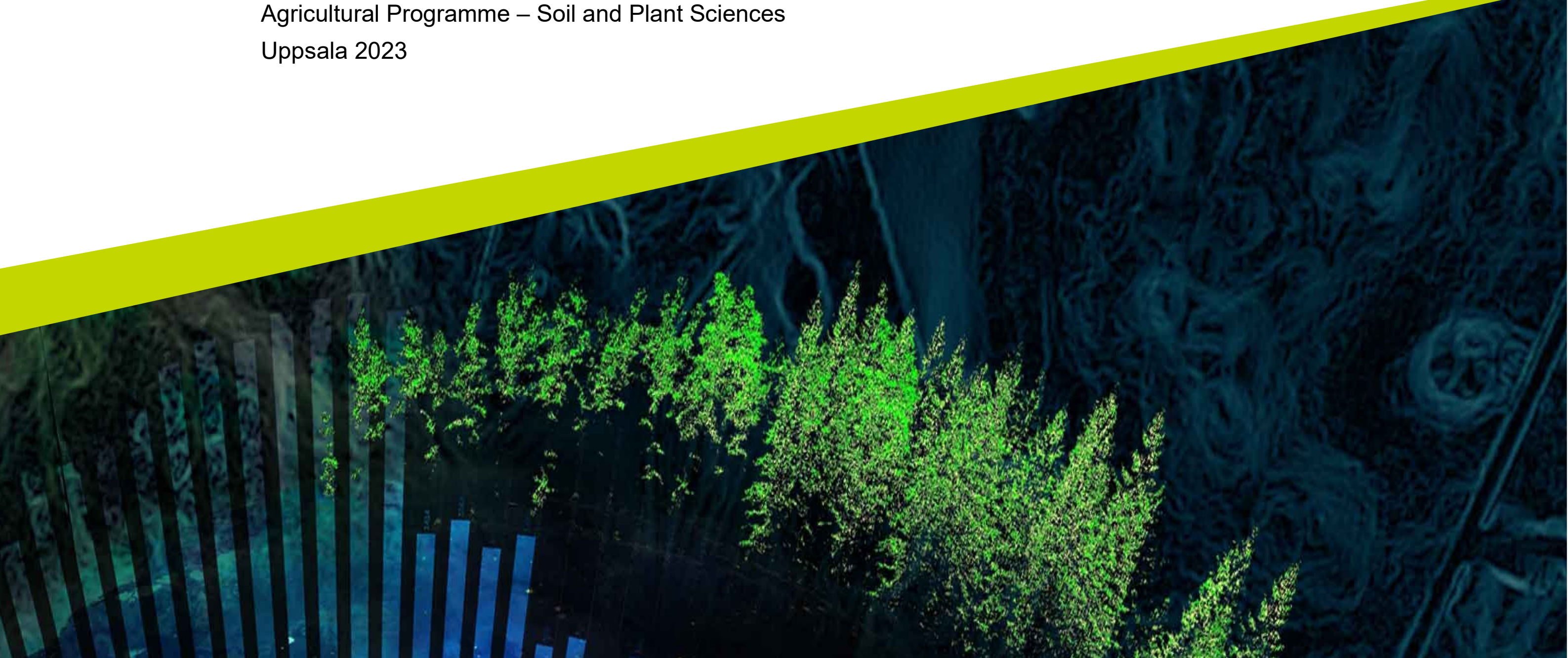

Carabids as weed seed control agent. Impact of soil cultivation on carabid weed seed regulation

Jordlöpare som bekämpare av ogräsfrö. Påverkan av jordbearbetning på jordlöpares förmåga till reglering av ogräsfrö.

Ellen Dahlgren

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Abstract

As weed seed predators, carabid beetles can regulate the weed seed bank within agricultural fields. Little is anyhow known about how weed seed bank regulation by carabids is affected by different tillage treatments with decreasing intensity, why this was here examined. Data on weed seed bank size, weed seed availability and carabid activity density were collected from field trials in Västergötland, Sweden. A weed seed bank regulation was estimated using the weed seed bank sizes from March and August. Weed seed predation strength was estimated using activity density and data on preferred prey choice. To study any differences over treatments were ANOVA and Tukey's test used and a piecewise structural equation model (pSEM) was formed and tested for all three tillage treatments separately to see whether any differences within the different treatments were present.

Weed seed bank size and weed seed availability increased significantly in the ploughed treatment, but not in fields with reduced tillage or direct seeding. The pSEM for direct seeding showed that more weed seed resources increase the carabid activity density in July which in turn increases the weed seed bank regulation. For reduced tillage treatment, a correlation between higher carabid activity density in June and lower weed seed availability in July, as well as lower weed seed availability in July compared to ploughing was found. Despite the indications of a greater seed build-up in ploughed and fewer weed seeds in reduced tillage was no difference in weed seed regulation from March to August, nor in weed seed predation strength was found.

The lack of differences in weed seed bank regulation could be caused by a lack of input data to the fields, where the interaction between chemical applications, chiefly herbicide use, would assist in disentangling the effect of the interaction between tillage and chemical herbicide control. Here, weed seed bank regulation was only assessed during the cropping season, while other outcomes would be possible if assessing annual weed seed bank regulation. To be able to use results about weed seed bank regulation by carabids to give clear advice to farmers should long-term effects be examined.

Keywords: weed seed predation, weed seed bank regulation, weed seed predation strength, seed predation strength, carabid beetles, tillage, piecewise structural equation model

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Abbreviations

pSEM	Piecewise Structural Equation Model
GLM	Generalised linear model
LM	Linear model

1. Introduction

Weeds can be a major constraint to agricultural production and potentially decrease yields by up to 34%, higher than by both pests and pathogens (Oerke 2006). In modern conventional agriculture, weed management relies on a combination of chemical and mechanical methods such as herbicide applications and soil inversion (Lundkvist 2014). Although both chemical and mechanical weed control have been proven to be effective, their high usage has led to undesirable effects. Herbicide use has given rise to herbicide resistance, (Heap 2014), can cause damage to carabid DNA (Cavaliere et al. 2019) and has been found in groundwater (Boström et al. 2016). Mechanical management of weeds, such as the usage of inverse soil tillage, has led to high operation costs (Arvidsson et al. 2010), soil erosion (Bogunovic et al. 2018) and can reduce the abundance of beneficial organisms such as carabid weed seed predators by directly killing them (Thorbek & Bilde 2004). Alternative weed management is to enhance weed seed predation by seed predators. Even though it has been shown that the seed predators can regulate weed populations (Daouti 2021) and reduce the weed seed bank size (Bohan et al. 2011; Carbonne et al. 2019, 2020; Daouti 2021) it is unknown, to what extent soil cultivation has an impact on weed seed predators' potential to regulate weeds.

In agricultural fields, weed seed predation by both invertebrates and vertebrates can contribute to weed regulation (Cromar et al. 1999; Westerman et al. 2003; Holmes & Froud-Williams 2005; Daouti et al. 2022). Ground-dwelling invertebrates, such as carabid beetles (Coleopter: Carabidae) are of high importance for weed seed regulation (Cromar et al. 1999) and can reduce the size of the weed seed bank (Bohan et al. 2011; Carbonne et al. 2019, 2020; Daouti 2021).

The carabid beetles' regulatory effects on the weed seed abundance can be measured in different ways, such as with direct measures of the size of the seed bank (Bohan et al. 2011; Carbonne et al. 2020; Daouti 2021) or indirectly such as seed predation rates, seed mortality or seed removal rates (Menalled et al. 2007; Carbonne et al. 2019, 2020).

Weed seed bank regulation and weed seed removal have been shown to increase with higher carabid activity density (Menalled et al. 2007; Carbonne et al. 2020) and seed mortality per carabid decreases with increasing seed availability

(Carbonne et al. 2019). The weed seed bank is the major source for sprouting weeds in the field (Skuodienė et al. 2013; Auškalnienė et al. 2018) and therefore has been the target of research to explore the effects of tillage on weed communities. Some studies have found greater weed seed bank sizes in fields with no-till treatments compared to ploughed fields (Conn 2006; Auškalnienė et al. 2018) while others have found more seeds in the ploughed fields (Clements et al. 1996) or no difference (Bàrberi & Lo Cascio 2001). Findings agree anyhow on that most of the seeds in the weed seed bank, in fields with direct seeding are occurring in the top-most layer of the soil (Clements et al. 1996; Skuodienė et al. 2013).

Effects of different tillage treatments on carabid activity density, even though broadly examined, are not straightforward. Carabid abundance has in some cases been reported to be higher in ploughed systems than systems with direct seeding (Baguette & Hance 1997; Hatten et al. 2007; Menalled et al. 2007) but also the opposite has been found (Kosewska et al. 2014). Thorbek & Bilde (2004) also found fewer carabids in the ploughed system and attributed it to that the ploughing directly kills the carabids. Carabid activity density has also been shown to increase with seed availability (Bohan et al. 2011; Carbonne et al. 2022).

A wide variety of carabid species contributes to weed seed predation and to understand the impact of carabids on the regulation, they have been divided into three predatory groups based on their prey type preference: carnivores, herbivores, and omnivores. This grouping has recently been questioned as a study showed that three omnivorous species predated more on weed seed than other animal prey, highlighting that weed seeds could be a greater prey resource for omnivores than expected (Frei et al. 2019). Carabids' diet consists of, apart from weed seeds, alternative prey such as aphids, spiders, collembola and earthworms (Lövei & Sunderland 1996; Carbonne et al. 2020; De Heij & Willenborg 2020). Weed seed bank predation has been reported to be higher in fields with direct seeding during the cropping season compared to fields with ploughing. After the harvest was the predation anyhow lower in the fields with direct seeding compared to ploughing (Trichard et al. 2014).

To understand the impact of carabids on weed seed regulation, detailed information about their diet is needed. Apart from carabid activity density, a metric of weed seed predation strength has been used. The metric is estimated from activity density, metabolic rate and preference to plant prey based on molecular gut content based on the methodology described by Daouti (2021) and Daouti et al. (2022).

1.1 Aim and hypothesis

This thesis aims to examine how three different tillage treatments (ploughing, reduced tillage, and direct seeding) affect weed seed bank regulation by carabids over one cropping season. Specifically, the research questions to be answered are:

1. How is the weed seed bank regulation by carabids affected by three tillage treatments?
2. What differences in weed seed bank size and regulation, weed seed availability, carabid activity density and weed seed predation strength exist between the different tillage treatments?

Based on existing knowledge in the subject area, a priori piecewise structural equation model (pSEM) was formed (Figure 1). In the model, it was expected that the seeds in the weed seed bank have a positive effect on the weed seed availability in June (Skuodienė et al. 2013; Auškalnienė et al. 2018). The weed seed availability is in turn expected to both have a negative effect on the weed seed bank regulation (Carbonne et al. 2019) and a positive on the carabid activity density in the following month of July (Bohan et al. 2011). The carabid activity density is also expected to positively affect the weed seed bank regulation (Menalled et al. 2007; Carbonne et al. 2020). More weed seeds, both in the weed seed bank size and weed seed availability are expected in the fields with direct seeding than ploughing (Conn 2006; Auškalnienė et al. 2018). The carabid activity density is expected to be higher in the fields with direct seeding than in ploughing (Thorbek & Bilde 2004). Weed seed bank predation is expected to be higher in the fields with direct seeding than ploughing (Trichard et al. 2014).

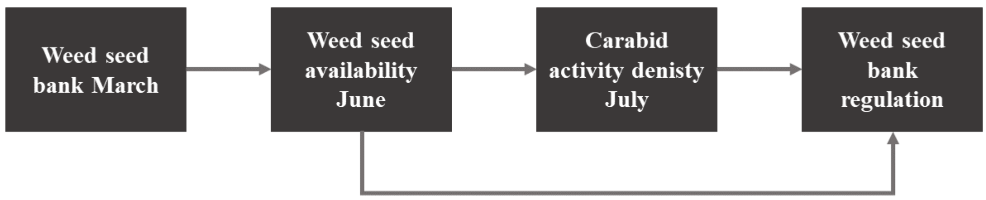

Figure 1. Priori piecewise structural equation model displaying the hypothesis, the weed seed bank in March is expected to have an effect on the weed seed availability in June, which is expected to affect both carabid activity density in July and the weed seed bank regulation. The carabid activity density in July is also expected to have an effect on the weed seed bank regulation.

2. Methods and materials

2.1 Experimental design

The field experiment was carried out in 30 winter oilseed rape fields in Västergötland, Sweden 2021. Before sowing were three different tillage treatments implemented to create a decreasing level of disturbance between the groups. 10 fields were ploughed with soil inversion of 30-40 cm, 10 fields with reduced tillage, 5-10 cm of inversion and 10 fields were sown using no-till. A 12 x 12 m sampling space with a 12 m buffer from the edge was created in each field. Fieldwork was conducted from March until August 2021 to estimate carabid activity density, weed seed bank and weed seed availability. The experiment had been designed to avoid the influence of the surrounding landscape.

2.2 Weed seed bank size and regulation

The weed seed bank was sampled from the field with soil samples, in two sessions, one in March (S_1) during the start of the cropping season and one in August (S_2) after crop harvest. Using a soil corer (10 cm deep and 5 cm in diameter) were five soil samples in each sampling space extracted and merged into one sample. Seed bank size was determined in the lab using the seedling emergence method. After sieving the soil and removing stones with a diameter >10 mm, 1.2 L of the soil was placed in germination trays in the greenhouse (12-h photoperiod, 18°C day and 15°C-night temperature). The trays were allowed for drainage after daily watering. Emerging seedlings were counted for 18 weeks until no more seeds were germinating. The number of seed sprouting from the soil core samples taken from each field was summarised for both time stamps and the regulation was then calculated:

$$regulation = -\frac{S_2 - S_1}{S_1}.$$

A negative value indicates an increase in the seed bank, and a positive decrease (Daouti 2021).

2.3 Weed seed availability

Suction samples of the soil surface material were performed in each field, both in June and July. Each suction sample consists of two suctions performed 0,5 meters apart. For each sample, the number of weed seeds was counted in the lab.

2.4 Carabid activity density

Carabid activity density (individuals/plot/day) was sampled during two sessions, in June and July in each field. The traps consisted of a plastic cup (11.5 cm diameter × 11 cm depth; Noax Lab, Farsta, Sweden) filled with 100 mL of soapy water and were dug into the soil. The traps were emptied after 4 days (96 hours). Carabids from the traps were sieved and preserved in 70% ethanol until further identification. In the lab, carabid beetles were counted and identified at the species level following Lindroth (1985).

2.5 Weed seed predation strength

Based on carabid beetles' activity density and previous knowledge of species-specific plant prey specialization determined by molecular gut content analysis, the potential strength of weed seed predation by carabid species at each field (PS) was calculated following the methodology described by Daouti (2021) and Daouti et al. (2022). Using the potential strength of predation (R) for each carabid species (i) was this done as follows:

$$PS = \sum_{i=1}^{n} R_i$$

Specifically, seed predation strength was estimated using data on carabid beetles' activity density (A_i), their metabolic rate (I_i), and their plant prey specialisation (d_i). Based on the formula:

$$R_i = d_i \times A_i \times I_i,$$

For each species, the amount of feeding events are related to their energy requirements (Brose et al. 2008), why feeding events were estimated to be related to the body mass of the species (Feit et al. 2019). A metabolic rate (I_i) relating feeding events to the carabid species' (i) body mass was estimated as described by Brown et al. (2004):

$$I_i = I_O \times M_i^{3/4}$$

where I_O is the metabolic constant for carabids (0,544) by Ehnes et al. (2011) and M_i is the mean body size for each carabid species. (M_i) was calculated using the formula by Jarošik (1989):

$$M_i = 0{,}03969 \times BL_i^{2{,}64}$$

where (BL_i) denotes the body length for each species. The estimation of body length was based on Lindroth (1985).

Plant prey specialisation d_i was calculated using molecular gut content from the project BioAWARE (Bohan 2022) following the methodology described by Daouti (2021). The BioAWARE data contained detections for six prey groups: earthworms, collembola, plant material and aphids *Metopolophium dirhodum*, *Rhopalosiphum padi* and *Sitobion avenae*. The data was collected from four European countries, but data on species and individuals from Sweden (Scania) was used for analysis. Using that data, the plant prey specialisation index d_i was calculated based on Blüthgen's et al. (2006) prey specialisation index, d'_i. Since Blüthgen's d'_i does not show the direction of the specialisation at the species level, total number of interactions for animal and plant prey were used. Specifically, when plant prey had been detected at a higher frequency than the total animal prey, d_i per carabid species i was calculated as: $d_i = 1 + d'_i$. When the total animal prey was detected at a higher frequency than plant prey, d_i was calculated as follows: $d_i = 1 - d'_i$. When the plant and animal prey species were recorded at the same frequency then $d'_i = d_i$. A higher value of d_i indicates a stronger plant prey specialisation. Calculation of the index d'_i were performed using the Bipartite package (Dormann et al. 2009) in R. Total number and distribution of prey interactions are found in Figure A1 and Table A1a in Appendix 1.

Not all species found in Västergötland were represented in the data for molecular gut content from BioAWARE or in the data used for body length estimations by Lindroth (1985) and were merged to higher taxonomic levels. The activity density of species in the same genus or tribe was added together, as closely related carabids are assumed to have similar diets (Petit et al. 2014). Data for molecular gut content was added for species available in the BioAWARE dataset and a mean body length was calculated for that genus or tribe. To be as specific as possible, species were first merged into genus level, but if not possible was tribe level used. All taxonomic data for merging were found at Artdatabanken (n.d.). For a species to have to be merged was only data from one dataset required to be missing (molecular gut content or mean body length), but in some cases were both data missing. When data for all species in a merged genus or tribe was available for one of the datasets was that data used. After re-grouping to match available data, the carabids found in the wet pitfall traps were used in the analysis as 31 species, 7 genera and 3 tribes. All species included in the genus and tribe merges and what species have been used to calculate these genera or tribe means is found in Table A1b in Appendix 1.

2.6 Statistical analysis

Analysis of variance (ANOVA) and Tukey's test were used to determine whether there was a difference in weed seed bank size and regulation, weed seed availability, carabid activity density and weed seed predation strength means over treatments. For weed seed bank size, weed seed availability, carabid activity density and weed seed predation strength were also different means over time tested. The ANOVA reveals whether a significant difference in mean between groups (i.e. tillage treatment) in the data exists. The Tukey's test then reveals what means are different from the others.

A pSEM was formed to examine the direct and indirect effects of weed seed and carabid abundance on weed seed predation (Figure 1). pSEM was used since it is suitable for small data samples, reveals missing pathways from the d-separation test and doesn't assume the data to be normal (Lefcheck 2014).

The pSEM was then tested separately for each tillage treatment. To perform the pSEM, a linear model (LM; for weed seed bank regulation) and a generalised linear model with negative binomial distribution were used (GLM.NB; for weed seed availability in June and carabid activity density in July). The negative binomial distribution for the GLM was used since the variables were neither normally distributed as raw data nor log-transformed and since overdispersion was found for Poisson distribution. For the LM, the weed seed bank regulation was log-transformed: $\log(weed\ seed\ bank\ regulation + 0.01)$, to assure the data was normally distributed and avoid infinity values. Normality was then tested by visual examination histograms and diagnostic plots as well as performing a Shapiro-Wilk normality test. To estimate the overall fit of the pSEMs were Fischer's statistics (Shipley 2016) and AIC values used. When possible, the model was improved by removing non-significant effects and adding significant pathways revealed by the d-separation test.

All measured and calculated variables (weed seed bank size and regulation, weed seed availability, carabid activity density and weed seed predation strength), even if not included in the pSEM, were correlations tested to examine further relationships.

All analyses were done in R version 4.2.2 (R Core Team 2022). The R packages AER (Kleiber & Zeileis 2008), MASS (Venables & Ripley 2002), lmtest (Zeileis & Hothorn 2002), dplyr (Wickham et al. 2023) and piecewiseSEM (Lefcheck 2016) were used to develop and analyse the pSEMs. For visualisation of results R packages ggplot2 (Wickham 2016), ggsci (Xiao 2023), ggpubr (Kassambara 2023), extrafont (Chang 2023) and multcompView (Graves et al. 2023) were used. pSEMs have been visualised using Microsoft PowerPoint. Literature was searched for and found on Primo and Google Scholar.

3. Results

3.1 Summary of the used variables

In the weed seed banks in March and August, in total 3553 weed seeds were found (mean ± standard deviation: 118.43 ± 64.9 per field). Specifically, 1009 (33.63 ± 22.94) weed seeds were found in March (before the season) and 2544 (84.8 ± 57.72) weed seeds in the weed seed bank in August, after the harvest (Figure 2). A mean weed seed bank regulation of -2.76 (± 4.40) per field was calculated (Figure 3).

From the suction sampling was a total weed seed availability of 9434 (314.47 ± 467.86 per field) weed seeds. In June was the weed seed availability 941 (31.37 ± 88.53 per field) weed seeds, while in July 8493 (283.1 ± 414.90 per field, Figure 4) weed seeds.

A total of 8713 (290.43 ± 111.52 per field) adult carabids were found in June and July from in total of 50 species. In the two sampling sessions in June and July were in total 4307 (143.57 ± 76.64 per field) and 4406 (146.87 ± 65.80 per field) adult carabids found respectively (Figure 5).

Seed predation specialisation (d_i) summarised per field ranged from 148.93 – 719.98 (335.28 ± 124.5). Weed seed predation strength in June ranged from 426.29 – 605.55 (542.94 ± 45.41) and in July from 875.54 – 1255.59 (1180.3 ± 82.38) (Figure 6).

3.2 Effects of tillage treatment on weed seed bank regulation

No significant difference between treatments was found for weed seed bank size during the early cropping season (March) nor after harvest (August). Between the two sampling sessions was there in the ploughed fields significantly more weed seeds in August than in March, ($F_{(5, 54)}$=5.20, P<0.01, Figure 2).

For weed seed bank regulation was no difference between the different treatments found, (F (2, 27)=0.73, *P*=0.49, Figure 3).

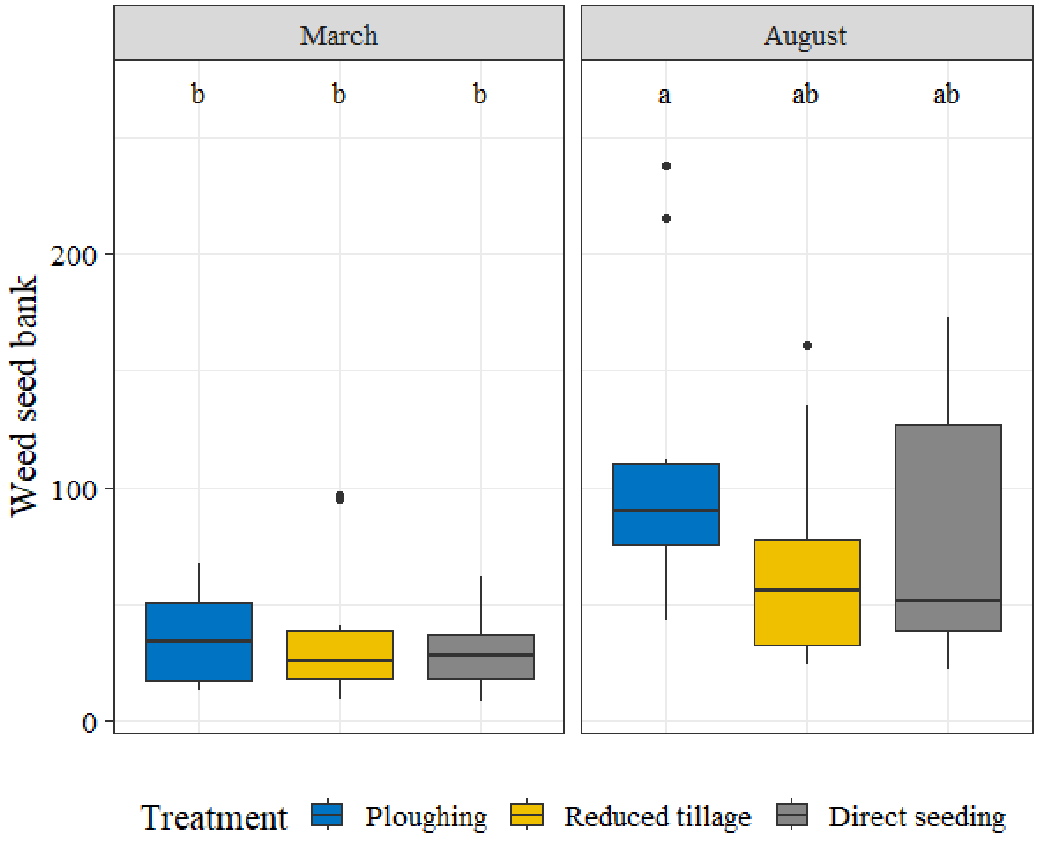

Figure 2. The weed seed bank in March and in August per field over the three different tillage treatments ploughing, reduced tillage and direct seeding. No significant difference was found between treatments in each sampling session but there is a difference over time with greater weed seed bank size in August for ploughing.

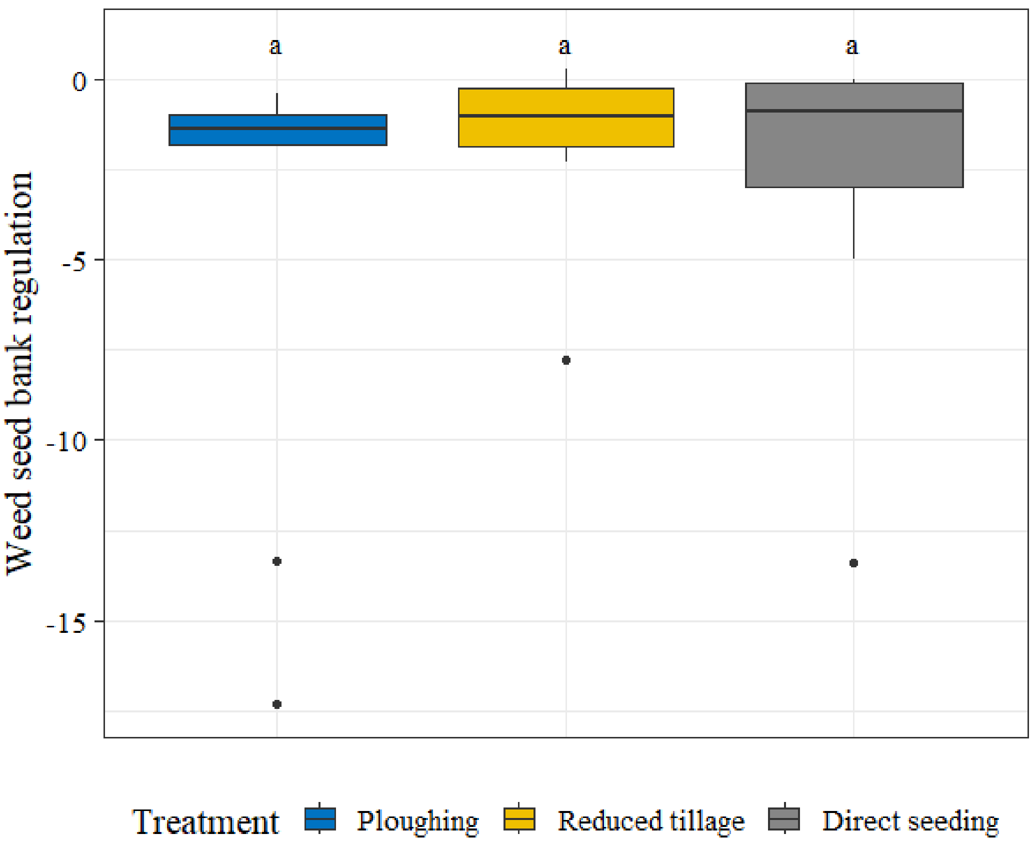

Figure 3. Weed seed bank regulation was calculated from weed seed bank sampling in March and August, in the three different tillage treatments ploughing, reduced tillage and direct seeding. No difference in weed seed bank regulation was found between treatments.

3.3 Effects of tillage on weed seed availability

From the suction samples of weed seed availability was it seen in the ANOVA and Tukey's test that in July, significantly fewer seeds were found in the fields with reduced tillage treatments compared to ploughing (F (5, 54)=4.65, $P<0.01$, Figure 4). In the ploughed treatment, the weed seed availability increased significantly from June to July, but not in the other treatments.

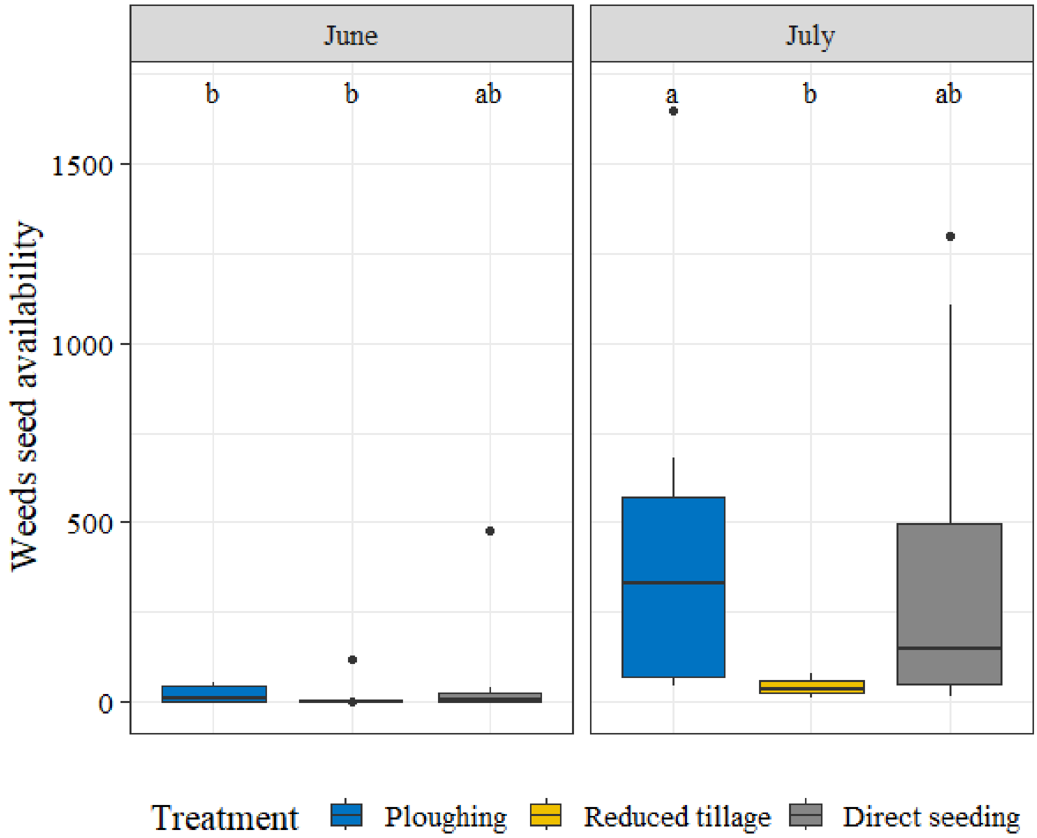

Figure 4. Weed seed availability per field in June and July over the three different tillage treatments ploughing, reduced tillage and direct seeding. In fields with reduced tillage was there a significantly lower weed seed availability compared to ploughing in July.

3.4 Effects of tillage on carabid abundance and weed seed predation strength

Carabid activity density did not differ within treatments nor over time between the treatments, ($F_{(5, 54)}$ =1.40, P=0.24, Figure 5).

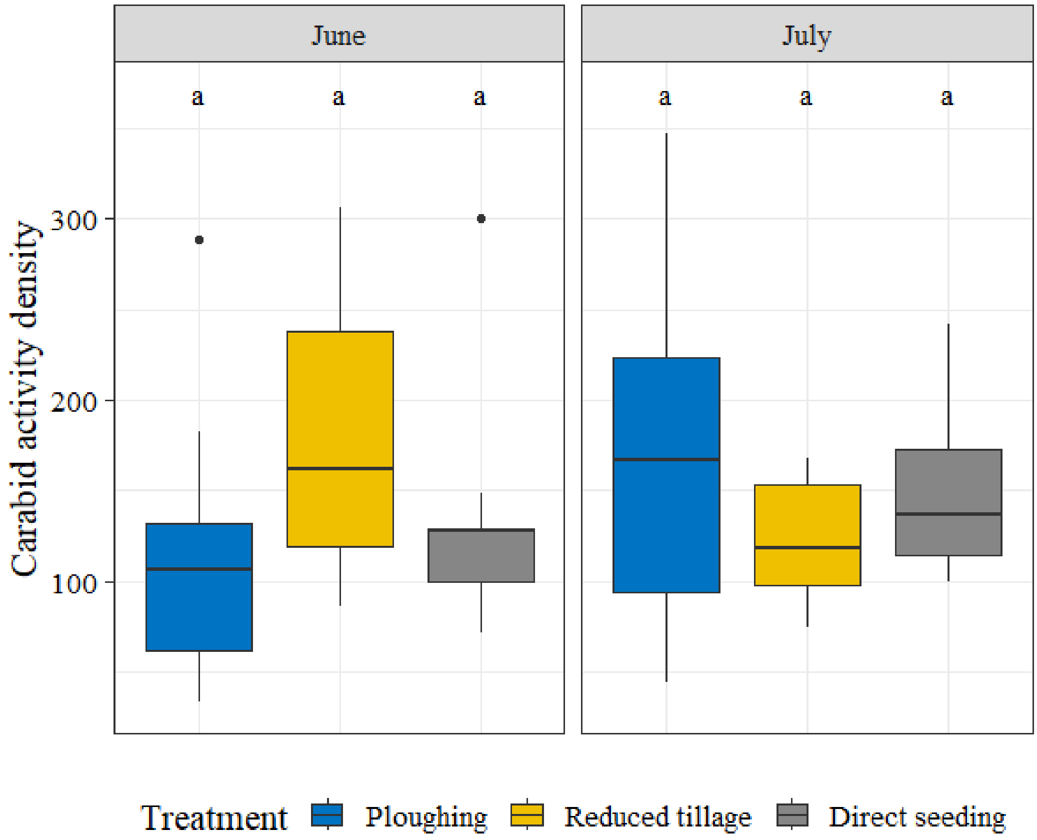

Figure 5. Carabid activity density per field in June and July over the three different tillage treatments ploughing, reduced tillage and direct seeding. No significant difference was found between treatments or over time.

For the weed seed predation strength, no difference between the three tillage systems was found, but a difference over the season ($F_{(5, 54)} = 268.3$, $P<0.01$, Figure 6) where the weed seed predation strength for all treatments was higher in July.

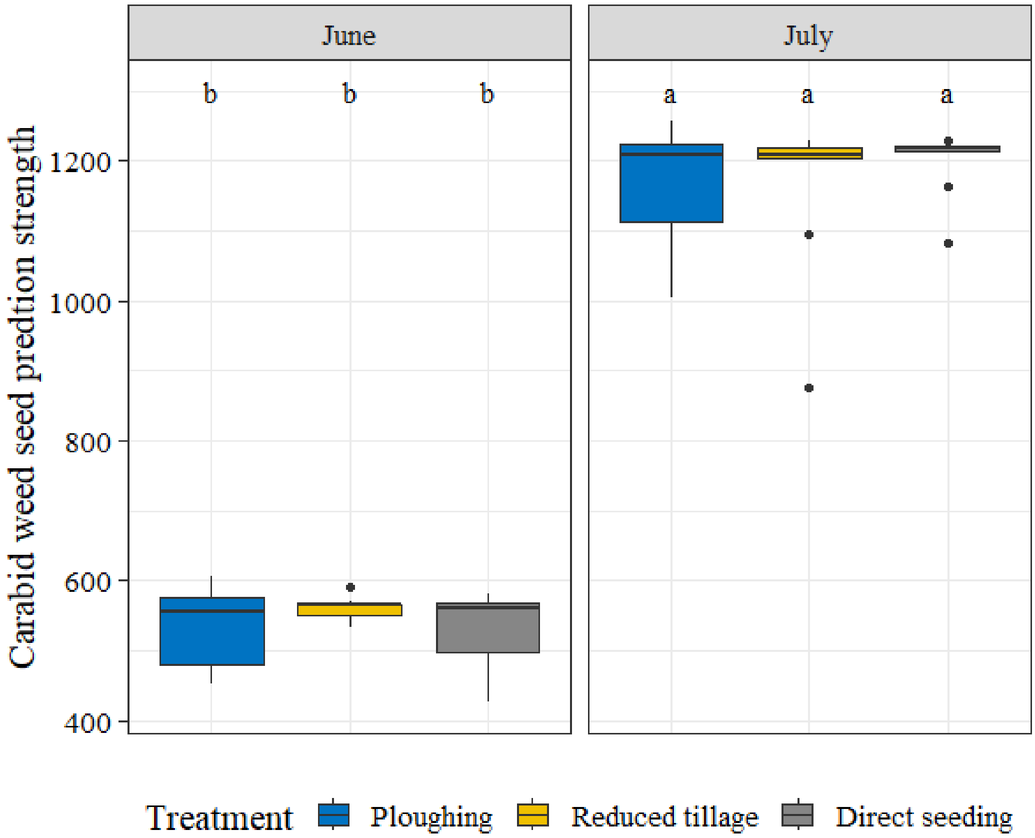

Figure 6. Carabid weed seed predation strength for June and July over the three different tillage treatments ploughing, reduced tillage and direct seeding. No significant difference was found between treatments in each sampling session but there is a difference over time.

3.5 pSEM

3.5.1 Ploughing treatment

The pSEM for the ploughed treatment showed a high fit (AIC = 21.03 and Fischer's C = 1.03, *P*=0.60; Figure 7, Appendix 2, Table A2a), but none of the tested pathways was shown to be significant and no missing pathways were found.

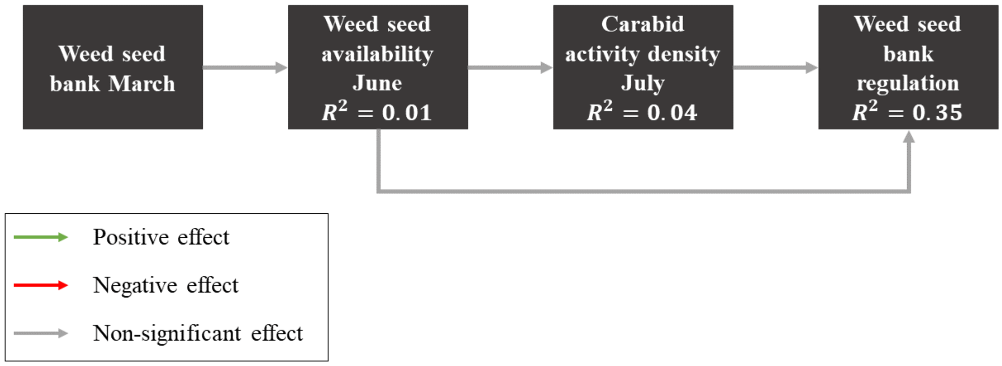

Figure 7. pSEM for ploughing treatment showed no significant pathways, but a good fit: AIC = 21.03 and Fischer's C = 1.03, P=0.60.

3.5.2 Reduced tillage treatment

The pSEM for the fields with reduced tillage had a good fit (AIC = 21.28 and Fischer's C = 1.28, P = 0.87, Figure 8, Appendix 2, Table A2b) but no significant effects were found, as well as no missing pathways. However, a negative correlation between weed seed availability in July and carabid activity density in June was observed (Figure 9).

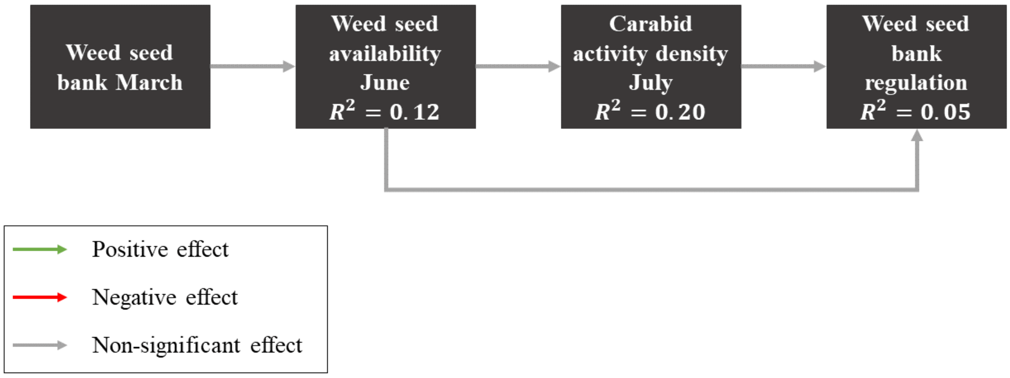

Figure 8. pSEM for reduced tillage showed no significant pathways, but a good fit: AIC = 21.28 and Fischer's C = 1.28, P = 0.87.

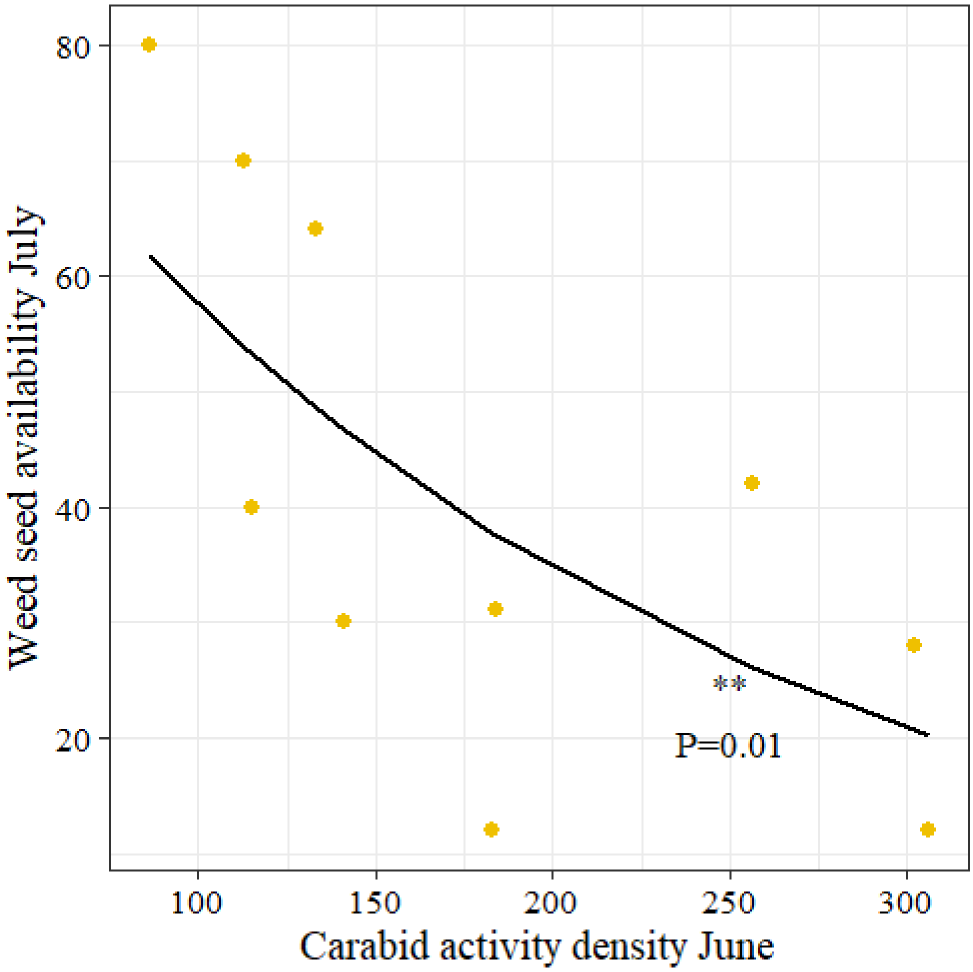

Figure 9. Generalised linear model for top-down effect on weed seed availability in July by carabid activity density in June (P=0.01).

3.5.3 Direct seeding treatment

The pSEM for direct seeding showed a good fit (AIC= 16.11, Fisher's C = 2.11, *P*=0.72, Figure 10, Table 1). A significant pathway was revealed by the d-separation test and was added to the pSEM. The weed seed bank in March was found to have a positive effect on the carabid activity density in July (Figure 11a), along with weed seed availability in June (Figure 11b). The carabid activity density had in turn a positive effect on the weed seed bank regulation (Figure 11c). The weed seed bank in March had no significant effect on the weed seed availability in June which in turn had no direct effect on weed seed bank regulation.

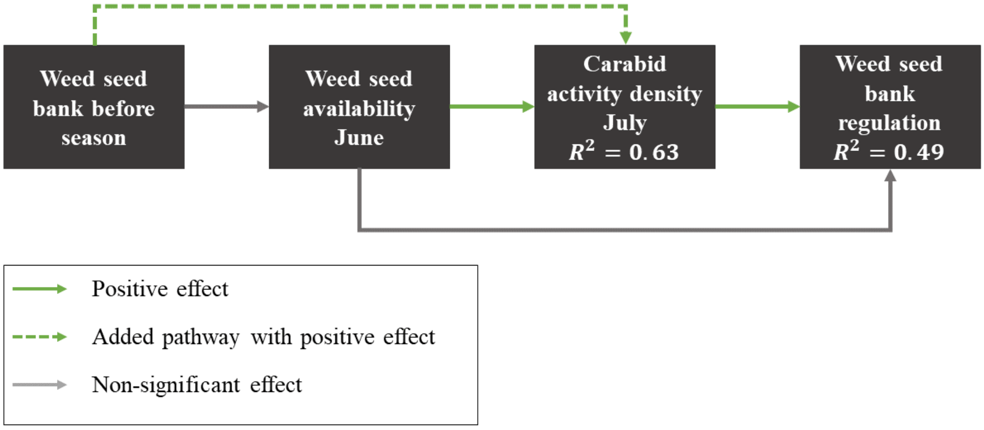

Figure 10. pSEM for direct seeding, showing that the weed seed bank in March and weed seed availability in June both have a positive effect on the carabid activity density in July, which in turn have a positive effect on the weed seed bank regulation.

Table 1. Coefficients to pSEM for direct seeding.

Response (y)	Activity density July	Activity density July	Weed seed bank regulation (log)
Predictor (x)	Weed seed bank in March	Weed seed availability June	Activity density July
Estimate	0.01	<0.01	0.03
Standard error	<0.01	<0.01	0.01
Degrees of freedom	7	7	8
Critical value	2.85	3.07	2.79
P-value	<0.01	<0.01	0.02
Standardised estimate	-	-	0.70

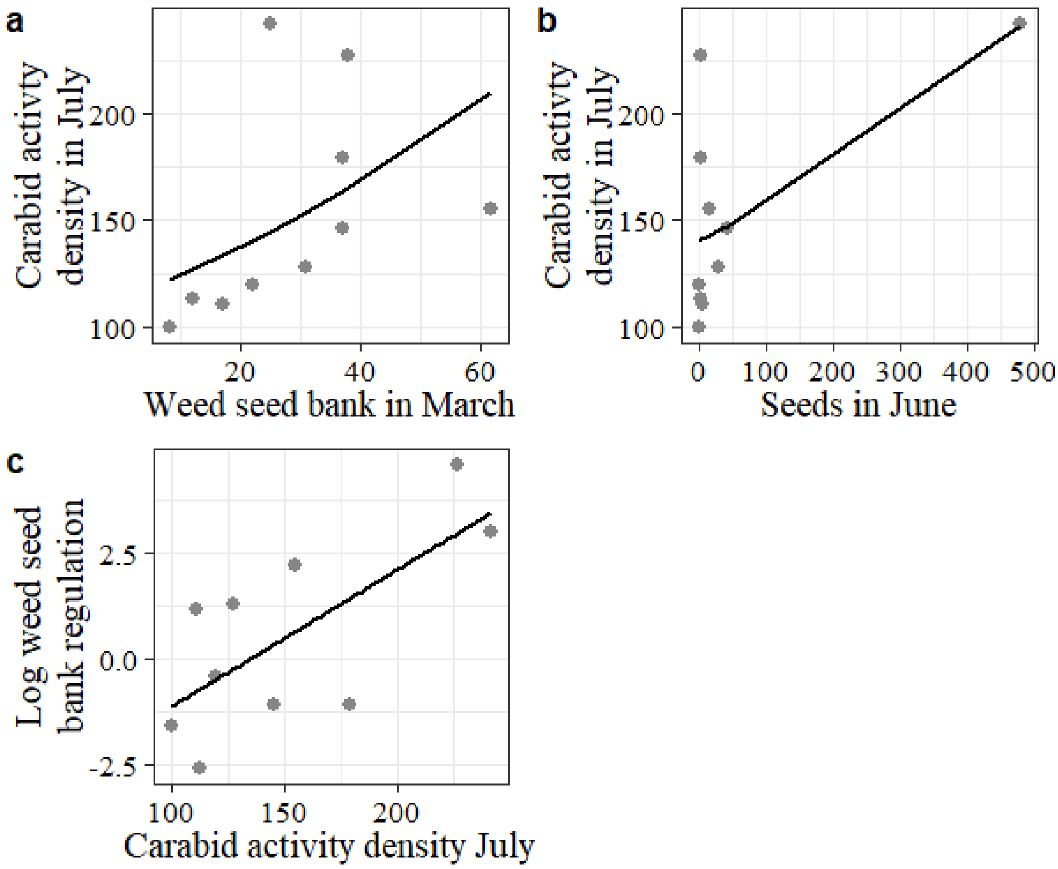

Figure 11. GLMs and LM from pSEM for direct seeding. GLMs for weed seed bank in March season (a) and weed seed availability in June (b) affecting carabid activity density in July and LM for carabid activity density affecting weed seed bank regulation (log-transformed) (c).

4. Discussion

Data was collected in field trials in Västergötland, Sweden. From a pSEM for direct seeding, the following was found, a positive effect of weed seed availability in June and weed seed bank in March on carabid activity density in July, that in turn had a positive effect on weed seed bank regulation. A negative correlation was found between weed seed availability in July and carabid activity density in June in fields with reduced tillage. No difference in weed seed bank regulation was found between the treatments.

4.1 Effect of tillage treatments on weed seed bank size, weed seed bank regulation, and weed seed availability

For both weed seed bank sizes in March and August, no difference between treatments was found. In the ploughed fields, however, the weed seed bank increased significantly from March to August and the weed seed availability increased from June to July. This indicates a slower build-up of weed seed bank size in fields with reduced tillage and direct seeding, compared to ploughed fields, either by limiting weed seed production or promoting weed seed predation. These findings agree with Clements et al. (1996) who found a greater weed seed bank in fields with ploughed treatment compared to tillage treatments with less disturbance to the soil. Since no difference was found in weed seed bank regulation between treatments, it can be assumed that there are missing parameters affecting the weed seed regulation which are not included here. To completely disentangle why there was a slower build-up of the weed seed bank in reduced tillage and direct seeding, herbicide data would be required to add and see if there is an effect of that on the weed seed bank. Since ploughing acts as a weed control could there potentially be higher herbicide use in reduced tillage and direct seeding, affecting weed seed production (Etana 2020). For all three treatments is there anyhow a trend for an increase in weed seed bank size, potentially caused by the crop itself, since winter oilseed rape in general is a weaker weed competitor than the preceding crop winter wheat (Lundkvist 2014). The weed shedding is likely to have occurred recently to weed seed bank measurement in August, why the weed seed bank could be greater in August than in March. If the weed seed bank had been examined over a whole year would that reveal if there indeed has been an increase in weed seed bank size this year or if the increase only is a seasonal variation.

The lack of differences in weed seed bank regulation between treatments could also be explained by that the regulation is here measured only during the cropping season (March-August) and does therefore not cover the whole period for when weed seed predation occurs (Holmes & Froud-Williams 2005; Carbonne et al. 2020). Carabid beetles have in this study been assumed to be the only predator to weed seeds, an assumption that doesn't reflect on reality, especially as no attempts to exclude large predators such as birds or rodents have been implemented. Regarding other weed seed predators are some affected by tillage, like earthworms (Chan 2001; Li et al. 2020), while mobile vertebrates most likely are not. Earthworm abundance is not added in the analysis here, and since they also are affected by tillage could the interaction between earthworm and carabid weed seed bank regulation be examined in further studies.

It has been found that seed predation by vertebrates (probably mostly mice) culminated in June, compared to invertebrates (the only species they give an example of that they found is *Harpalus rufipes*) which consumed most seeds in mid-June, July and August, and the importance of invertebrates during late cropping season was highlighted (Westerman et al. 2003). Weed seed predation by birds has been found to be greatest in spring and tended to be greater during autumn and winter by other animals than birds (rodents, carabids etc but no species or trophic group is given as an example) (Holmes & Froud-Williams 2005). It can, anyhow, be assumed that not much weed seed predation took place during the cropping season by birds in this study, given that winter oil seed rape early creates a dense crop canopy, making it hard for birds to reach the soil surface (ibid.). Another study has found that vertebrates predate on weed seeds during the cropping season and invertebrates (mainly carabids) after (Daouti et al. 2022). The literature here presented shows that carabid weed seed regulation could be of great effect late in the cropping season, or after it. Since the weed seed bank only was assessed before and after the cropping season (March and August), and not including a whole year, can some predation have been missed out from the data. Others have also concluded that basing the weed seed predation on two samples from the same cropping season is not sufficient to cover all regulation (Carbonne et al. 2020).

A lower weed seed availability was found in fields with reduced tillage in July, compared to ploughing. A potential explanation for this can be the strong negative effect of carabid activity density in June to weed seed availability in July. The higher number of predators in June, potentially via weed seed predation reduced the weed seed availability for reduced tillage treatment, compared to ploughing in particular. But this was not reflected in the weed seed bank regulation, as no difference was found between treatments. For weed seed predation to have a regulatory effect is timing crucial, and the peak in predation must take place at the same time as the peak in weed seed shedding (Daouti et al. 2022). As no weed seed bank regulation was found can it here be assumed that the weed seed shedding and predation did not overlap in time.

4.2 Effect of tillage treatment on carabid activity density and weed seed predation strength

Between treatments and within each sampling session was there no difference in carabid activity density, in contrast to what was expected (Thorbek & Bilde 2004; Kosewska et al. 2014). Causes for this could be that the tillage treatments for the trial only had been applied once, and the carabids had not adapted to the new treatments yet. Similarly, there was no difference in seed predation strength between the treatments.

From the field trials, some carabid larvae were collected in the pitfall traps, but not included in the analysis. In contrast to the carabid adults, the larvae are alternating habitats from above- and belowground, and prey on both recently dispersed seeds as well as the weed seed bank (Saska & Jarošík 2001; Blubaugh & Kaplan 2015; Thiele H-U 1977 see Frei et al. 2019). Pitfall traps are insufficient for capturing larvae as they are designed for ground-dwelling organisms (Frei et al. 2019; Jowett et al. 2021). To be able to use the carabid larvae in the analysis, new ways to sample them in fields are required (Blubaugh & Kaplan 2015). Since larvae are great weed seed predators could they have an impact on the weed seed bank regulation, that here is completely left out.

4.3 pSEM showed differences in weed dynamics and weed regulation within the three tillage methods

The pSEM for direct seeding showed a positive effect on weed seed bank regulation by carabids in July, which in turn was affected by weed seed availability in June (as was hypothesised) but also by the weed seed bank in March as revealed by the d-separation test. The high R^2 (how much of the variance for carabid activity density is explained by weed seed bank in March and weed seed availability in June) for carabid activity density in July shows that the carabids in these fields are strongly affected by the weed seed availability. More seeds lead to greater carabid activity density, leading to stronger regulation. This agrees with previous findings that have found a positive impact of seeds on carabid activity density (Daouti 2021).

The pSEM for both ploughing and reduced tillage had a high fit, but no significant effects were found. For both of these models was it clear that the included variables were not enough to explain the weed seed bank regulation.

Weed seed bank regulation is more complex than the model here designed. To develop a model that better reflects, more parameters should be added. Such parameters could be carabid larvae and earthworm activity density, chemical applications, and crop rotation (Saska & Jarošík 2001; Navntoft et al. 2006; De Heij & Willenborg 2020; Li et al. 2020).

In reduced tillage outside of the pSEM, was it found that weed seed availability in July decreased with carabid activity density in June. This differs from the structure of the priori pSEM in that it is a top-down interaction instead of a bottom-up one. The top-down effect means that a high activity density of carabids in June can reduce seed abundance in July, in contrast to that seed abundance was expected to increase the carabid activity density (Bohan et al. 2011).

Even though the weed seed predation strength was calculated with data on carabid activity density from the field trails in Västergötland, the prey specialisation index was calculated based on another experiment. A major improvement to a study like this would be to have used molecular gut content from the same field, as would better reflect the prey's availability. Carbonne et al. (2020) found that the amount of alternative prey available can decrease weed seed predation. The actual predation specialisation of the carabids in the fields in Västergötland could therefore differ from the ones here used for calculations, caused by differences in prey availability. The weed flora could also affect weed seed predation, as different weed species have been preferred differently by carabids (Hartke et al. 1998; Holmes & Froud-Williams 2005).

4.4 Conclusion

The goal of weed regulation is not to eliminate weeds from the fields, such an operation would be impossible, and keeping weeds in the fields is important to maintain a suitable habitat for the carabids (Brust 1990). When there is an established weed seed regulation in a field can that enhance regulation and suppression of the more problematic weeds (Daouti 2021). This thesis showed a pSEM for fields with direct seeding treatment that weed seed bank regulation did increase with higher carabid activity density. It also showed that the activity density is increasing when more weed seed resources are available, an effect found in direct seeding only, even though there was no difference in seed abundance or carabid activity density. Ploughed treatment was the only one to show an increase in weed seed bank size and weed seed availability, even though no difference in weed seed bank regulation was found. Findings do indicate that differences in seed abundances between the three tillage treatments exist and that weed seed regulation in fields with little disturbance is enhanced by great carabid activity densities. However, data on herbicide use was missing from the analysis, creating a knowledge gap on how the interaction between tillage management and herbicide use is affecting the weed seed bank predation. This study has focused on weed seed predation but since carabids also prey on aphids can they perform multiple ecosystem services, why carabid habitats should be promoted within agriculture.

For further research within the subject of weed seed bank regulation by carabids, long-term effects are desirable, how are the carabids' regulation different over treatments when it has been applied for much more than two years? If a good method for carabid larvae sampling is found could the addition of carabid larvae give additional knowledge of weed seed bank regulation below ground.

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Popular science summary

Common methods for weed control in modern conventional agriculture are herbicide application and soil inversion by tillage. Both methods have negative side effects such as herbicide resistant weeds and risk for soil erosion and damaging beneficial organisms when tilling the field. Carabid beetles is one such family and have in several studies been shown to have regulatory effects on the weed seed bank. Much remains unknown about how the carabids' prey choice is affected by the disturbance of tillage treatments, and this thesis aims to examine that, and whether there are any differences between tillage treatments.

In 30 fields located in Västergötland, Sweden, with three different tillage treatments, ploughing, reduced tillage and direct seeding, field work has been conducted. Data on weed seed bank size in March and August, weed seed availability in June, as well as July and carabid activity density (abundance) in June and July, were collected from the fields during 2021. The data on weed seed bank sizes was used to calculate a relative weed seed bank regulation over one cropping season. To estimate how specialised the carabids were in preying on weed seeds was a weed seed predation strength calculated using activity density, a metabolic rate derived from species mean body length and a prey specialisation index based on data from molecular gut content. To examine differences in the measured and estimated values were ANOVA and Tukey's test used. To investigate any differences within each tillage treatment was a causal model (piecewise structural equation model, pSEM) designed to explain the impact of the weed seed bank in March, weed seed availability in June and carabid activity density in July on the weed seed bank regulation.

The pSEM showed for direct seeding that both weed seed bank in March and weed seed availability in June had positive effects on the carabid activity density in July. The activity density in July had in turn a positive effect on the weed seed bank regulation. ANOVA and Tukey's test showed an increase in weed seed bank over the cropping season (from March to August) and in weed seed availability from June to July in the ploughed treatment only. Any difference between weed seed bank regulation between treatments was anyhow not found.

The findings of this thesis indicate that differences between the systems exist, but to get a clearer picture of the impact of tillage on weed seed bank regulation by carabids should interaction with herbicide use be added to the analysis.

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Appendix 1

Table A1a. Total interactions, mean and standard deviation per carabid species for prey types from molecular gut content.

Prey	Total interactions	Mean	Standard deviation
Plant prey	1183	28.85	65.46
Total animal prey	1205	29.39	57.28
Sitobion avenae	576	14.05	29.18
Rhopalosiphum padi	288	7.02	13.25
Collembola	214	5.22	9.88
Earthworms	86	2.10	4.55
Metopolophium dirhodum	41	1	2.14

Table A1b. Table displaying what species have been used for calculating a genus or tribe molecular gut content or mean body length as well as what species found in Västergötland are included in the genus or tribe

Genus	**Includes species (activity density)**	**Molecular gut content**	**Mean body length**
Agonum sp	*A. assimile*	*A. muelleri*	*A. duftschmidi*
	A. dorsale		*A. muelleri*
	A. obscurum		*A. sexpunctatum*
	A. thoreyi		*A. thoreyi*
Amara sp	*A. apricaria*	*A. aenea*	*A. aenea*
	A. lunicollis	*A. apricaria*	*A. anthobia*
		A. aulica	*A. aulica*
		A. bifrons	*A. bifrons*
		A. brunnea	*A. communis*
		A. communis	*A. consularis*
		A. familiaris	*A. familiaris*
		A. fulva	*A. fulva*
		A. municipalis	*A. littorea*
		A. plebeja	*A. lunicollis*
		A. similata	*A. ovata*
		A. tibialis	*A. plebeja*

			A. similata
Bembidion sp	*B. aeneum*	*B. guttula*	*B. aeneum*
		B. lampros	
		B. obtusum	
		B. aeneum	
		B. quadrimaculatum	
		B. tetracolum	
Carabus sp	*C. hortensis*	*C. granulatus*	*C. cancellatus*
	C. violaceus	*C. nemoralis*	*C. convexus*
			C. granulatus
			C. hortensis
			C. nemoralis
Harpalus sp	*H. rufibarbis*	*H. affinis*	*H. affinis*
		H. rufipes	*H. distinguendus*
		H. tardus	*H. griseus*
			H. latus
			H. luteicornis
			H. rubripes
			H. rufipes
			H. signaticornis
			H. smaragdinus
			H. tardus
Notiophilus sp	*N. aquaticus*	*N. aestuans*	*N. aquaticus*
	N. palustris	*N. palustris*	*N. palustris*
Pterostichus sp	*P. oblongopunctatus*	*P. melanarius*	*P. oblongopunctatus*
		P. niger	

Tribe	**Includes species (activity density)**	**Molecular gut content**	**Mean body length**
Harpalini	*Acupalpus meridianus*	*Harpalus affinis*	*Acupalpus meridianus*
	Anisodactylus binotatus	*Harpalus rufipes*	*Anisodactylus binotatus*
		Harpalus tardus	
		Ophonus rufibarbis	
Nebriini	*Leistus ferrugineus*	*Nebria brevicollis*	*Leistus ferrugineus*

Pterostichini	*Stomis pumicatus*	*Poecilus cupreus*	*Stomis pumicatus*
		Poecilus versicolor	
		Pterostichus melanarius	
		Pterostichus niger	

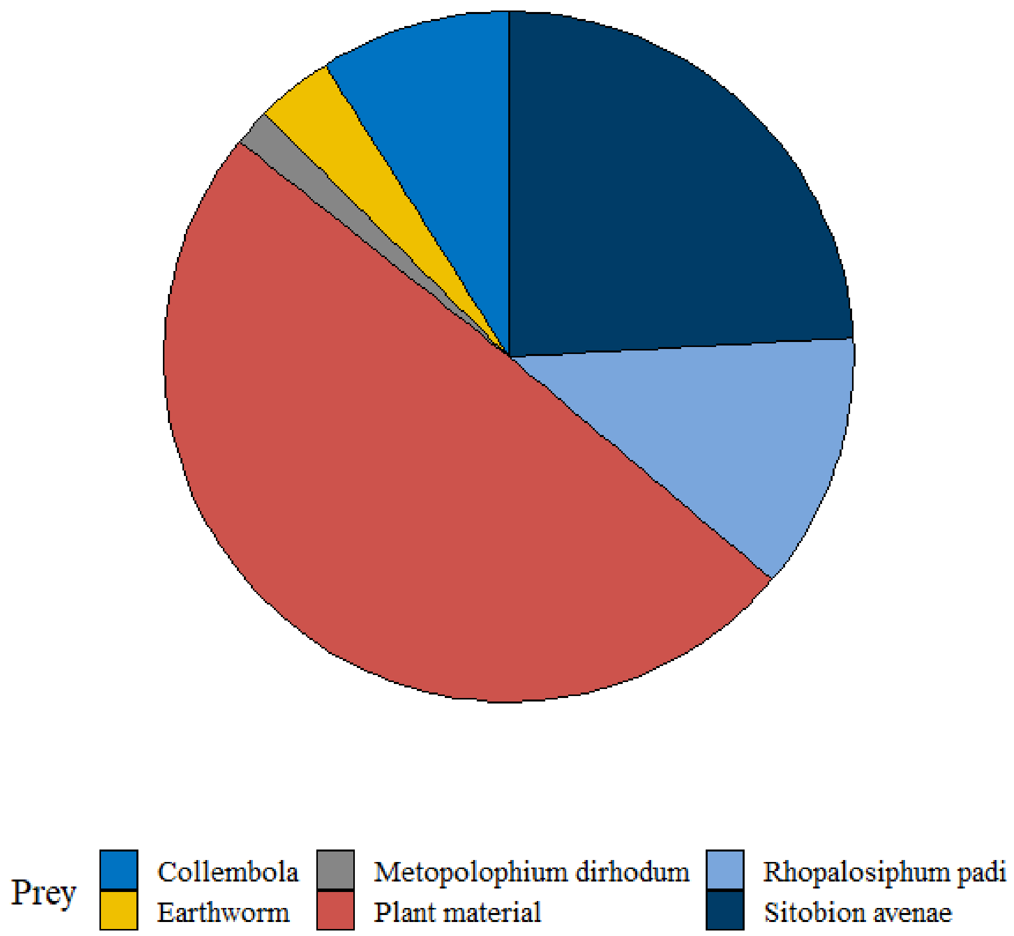

Figure A1. Pie chart displaying prey type found in molecular gut content data from BioAWARE. Out of 2388 prey interactions found were 1183 plant material, 576 Sitobion avenae, 288 Rhopalosiphum padi found, 214 collembola, 86 earthworm and 41 Metopolophium dirhodum interactions.

Appendix 2

Table A2a. Coefficients to pSEM for ploughing

Response (y)	Weed seed availability June	Activity density July	Weed seed bank regulation (log)	Weed seed bank regulation (log)
Predictor (x)	Weed seed bank in March	Weed seed availability June	Weed seed availability June	Activity density June
Estimate	-0.01	<0.01	-0.03	<0.01
Standard error	0.02	0.01	0.02	<0.01
Degrees of freedom	8	8	7	7
Critical value	-0.37	0.57	-1.84	1.01
P-value	0.71	0.57	0.11	0.35
Standardised estimate	-	-	-0.58	0.31

Table A2b. Coefficients to priori for reduced tillage

Response (y)	Weed seed availability June	Activity density July	Weed seed bank regulation (log)	Weed seed bank regulation (log)
Predictor (x)	Weed seed bank in March	Weed seed availability June	Weed seed availability June	Activity density July
Estimate	-0.10	<0.01	-0.01	<0.01
Standard error	0.08	<0.01	0.01	0.02
Degrees of freedom	8	8	6	6
Critical value	-1.32	1.53	-0.52	0.7
P-value	0.19	0.13	0.62	0.95

Standardised estimate	-	-	-0.23	0.03

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