Comparing weed density, species richness and weed trait values across strip edges, strip middles and pure stands in the Netherlands

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MSc thesis, formatted in the style of Weed Research

Comparing weed density, species richness and weed trait values across strip edges, strip middles and pure stands in the Netherlands

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Summary

Agricultural intensification, together with simplification and expansion of agricultural fields, contributed to a decline of weed diversity. While diverse weed communities can provide ecosystem services, their benefits depend not only on species richness, but require investigation into weed densities and traits. Trait-based approaches offer valuable insights into growth strategies of individual species. Spatial and temporal diversification practices, such as strip cropping, influence weed communities through altered resource availability and microclimates, compared to pure stands. Here, we explored how weed density, species richness and weed trait values varied between strip cropping systems and pure stands across 16 farm locations throughout the Netherlands. Quadrants were placed on strip edges, strip middles and in pure stands. The observed number of species and number of individuals were recorded and problematic weeds were sampled from the field to obtain data for 8 weed traits in total. This data was analysed using Generalised Linear Mixed Models (GLMM). The results show that strip cropping did not significantly impact weed density and species richness, but did affect weed traits. In particular, weeds were slightly taller and significantly heavier in strip middles, had significantly higher values of specific leaf area in pure stands and a significantly thinner average root diameter on strip edges. Limited differences in belowground trait values across the positions suggest greater expression of competitive ability in aboveground traits, although this may depend on other factors such as widths of the strips and temporal management on edges. Further research is therefore needed to explore the link between weed traits and their (dis)services in strip cropping systems.

Keywords: agroecology, crop diversification, intercropping, arable flora, functional traits, biodiversity

Introduction

Weeds are a major constraint to crop production and weed pressure is considered the main production-limiting factor in agricultural systems (Bajwa et al., 2015; Turner et al., 2007). The presence of weeds in agricultural systems significantly reduces cultivated crop yields, primarily through competition for light, water and nutrients (Bajwa et al., 2015). Herbicides are often used in conventional agricultural systems because they offer a cost-effective method to guarantee high yields and global food security (Aparecida et al., 2013; Gianessi, 2013; Ofosu et al., 2023). However, the reliance on chemical weed control combined with simplification and expansion of agricultural fields led to herbicide resistant, problematic weed species, and a severe decline in floral species richness, amounts of insects and increased soil degradation (Hofmeijer et al., 2021b; Ofosu et al., 2023; Raven & Wagner, 2021).

In response to the adverse effects of herbicides, there is a call for more sustainable methods to control weeds. According to Turner (2007) weed management involves the maintenance of weed species levels, without entirely eradicating weeds from a field. From this perspective, sustainable weed management practices should aim at minimizing the negative effects of weeds (Radicetti & Mancinelli, 2021). Achieving this requires an understanding of weed-crop interactions, and how weed communities respond to management practices (Gaba et al., 2017).

Weeds can play important roles in ecosystems, serving as valuable indicators for biodiversity or providing habitat for microbiota, insects and birds (Colbach et al., 2014). For instance, wildflowers can create a habitat for pollinators that pollinate the cultivated crops (Benvenuti & Bretzel, 2017). Weeds can also function as a food resource for organisms that play a role in pest suppression, and they protect bare soil from erosion by rainfall (Radicetti & Mancinelli, 2021). Additionally, some weeds can host arbuscular mycorrhizal fungi (AMF), which can enhance nutrient availability and soil fertility (Bàrberi et al., 2018). Yet, the ability of weeds to support biodiversity, relative to their ability to compete with crops, is influenced by the composition of the community (MacLaren et al., 2020).

The balance of negative and positive impacts of weeds on crop production can be determined by investigating weed density and weed species richness (MacLaren et al., 2020). Weed density and species richness is impacted by soil type, due to differences in soil pH, water availability and nutrient content (Booth & Swanton, 2002; Ługowska et al., 2016). Besides, studies showed that organic farming systems have higher weed densities and species richness compared to conventional systems, which can be mainly explained by the intensive use of chemicals under conventional management (Mwangi et al., 2024). Growing evidence suggests that a more diverse weed community is less competitive with any cultivated crop (Adeux et al., 2019; MacLaren et al., 2020). Conversely, at the same density level, a weed community can be composed of highly competitive species that harm crop yield (Bàrberi et al., 2018). For this reason, a more diverse weed community does not inherently lead to decreased weed pressure.

Understanding the impact of weed communities on ecosystem functioning requires further investigation into their expression through traits (Booth & Swanton, 2002; MacLaren et al., 2020), and how the values of these traits are distributed in the community (Schöb et al., 2012). A *trait,* in this context, refers to 'any morphological, physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level' (Violle et al., 2007). Traits offer insights into the ecological performance and growth strategies of individual species (Violle et al., 2007). Additionally, traits can be used to understand the response of species to environmental conditions and changing management (Pakeman et al., 2009, 2015). Exploring values of weed traits within a community can therefore offer insights into its competitiveness or ecological benefits. For instance, weeds in competitive communities express higher trait values for competitive traits such as increased plant height (PLH) (MacLaren et al., 2020), aboveground biomass (Schwartz et al., 2016) and a high specific leaf area (SLA) (Adeux et al., 2019). These weeds are considered problematic (Hofmeijer et al., 2018) and their competitive effect increases at higher densities (Adeux et al., 2019). Trait-based approaches have been used to provide insights into responses of weed communities to different agricultural practices (Gaba et al., 2017) and to understand weed community diversity (Hofmeijer et al., 2021b).

Weed diversity has been associated with spatial, temporal and genetic diversification practices and more complex systems (MacLaren et al., 2020; Storkey & Neve, 2018). One example is strip cropping, a form of intercropping, that can provide multiple ecosystem services without decreasing productivity of the system (Juventia & van Apeldoorn, 2024). In strip cropping systems, at least two crops are grown adjacent to each other in alternating strips, creating spatial heterogeneity (Juventia & van Apeldoorn, 2024). Temporal diversity is increased by managing these strips according to a crop rotation design, while genetic diversity is achieved by including different crops or cultivars (Juventia et al., 2022). The combination of temporal diversification and the higher number of edges in strip cropping systems results in more ecological niches, which can increase resource availability (Gu et al., 2021). More niches can alter microclimates (Campanelli et al., 2023), soil conditions and soil fungi (Riggi et al., 2025). For instance, in potato-ley strips, colonisation of arbuscular mycorrhizal fungi (AMF) in strip edges is higher than in the middle of the strips and pure stands (Riggi et al., 2025). Furthermore, Zhang et al. (2008) showed an increased accumulation of sunlight on strip edges, hence a higher weed biomass can be expected there. A recent study indeed reported a higher weed biomass and species richness on the strip edges compared to strip middles (Buitenhuis, 2022). However, a higher species richness does not always indicate less competition, and competitive effect of species expressed by trait values can be altered by weed density.

Głowacka (2013, 2014) reported a lower number of weeds in strip cropping systems and that strip cropping reduced the number of problematic weed species (*Echinochloa crus-galli, Chenopodium album and Galinsoga parviflora)* compared to pure stands. However, it remains unclear whether the difference in available resources on strip edges compared to strip middles lead to differences in weed trait values. Besides, if these trait values differ compared to pure stands. This led to the following research questions: 1) How does *weed density* and *species richness* vary between strip cropping systems and pure stands and how are these patterns influenced by soil type and farm management type?; 2) How do the *aboveground* and *belowground trait values* of the selected weed species differ between strip cropping systems and pure stands?

Based on the increased spatial and temporal diversification of strip cropping systems, I hypothesize that weed density and species richness differ between the edge and middle of a strip, with higher density and species richness on strip edges because of increased resource availability (Gu et al., 2021), and that pure stands have lower density and species richness than strip cropping systems. Besides, I expect differences in the weed trait values on strip edges, strip middles and pure stands. Specifically, I expect taller weeds in strip edges compared to middle of the strip and biomass (fresh weight and dry weight) is expected to follow similar patterns, reflecting the increased sunlight availability on strip edges (Zhang et al., 2008). As specific leaf area increases when light availability is limited (Yvoz et al., 2021), a higher specific leaf area is expected in pure stands. Due to the spatial interaction between the crop pairs (Riggi et al., 2025) and increased crop diversity (Brooker et al., 2015; Lee et al., 2023), AMF colonisation is expected to be higher on strip edges, followed by strip middles and pure stands. Subsequently, due to the higher resource availability on strip edges, I expect a lower specific root length, lower root tissue density and higher average root diameter at strip edges.

Methodology

Experimental design

This study was part of the project AGROSOIL, a collaboration between five European countries (*AGROSOIL — Agroecology Partnership*, z.d.). The main aim of AGROSOIL is to promote and increase the co-implementation of agroecological weed management through active stakeholder engagement. This study specifically focused on weed density and species richness, and weed functional traits, comparing strip cropping systems to pure stands.

This study was conducted on 16 farms in the Netherlands that had implemented strip cropping as part of their agricultural system. Data was collected in one round, between late June and mid-July 2025. The selected farms for this study were all part of the Cropmix network (*Akkerbouwers – CropMix*, z.d.). All farm locations in this study included a pure stand cultivated with the same crop as the crop grown in the strip cropping system – serving as the reference field. Thus, comparisons between strip cropping systems and pure stands were made using the same crop within each location, although the crops differed between locations. For each location, the crops in the strips received the same fertility and weed management as the crops in the pure stands.

This study primarily focused on weeds in cereal fields, as other studies have investigated weeds in cereal strip cropping system before (Campanelli et al., 2023; Gu et al., 2021). In the few cases where cereals were absent in the pure stand or strip cropping system of a farm location, a crop with a closed canopy was selected as an alternative. When no cereals or crops with a closed canopy were present, a crop with an open canopy was selected. Potatoes were used as the final option to be included in this study (dr. MAJ. Hofmeijer, personal communication, 2025). The farms that were included in this study consisted of both organic and conventional farming systems and the soil types varied between the farm locations (Table 1).

Table 1. Overview of the 16 farm locations. The different columns represent from left to right; cultivated crop, management type and soil type.

Farm location	**Cultivated crop**	**Management type**	**Soil type**
1	Spring barley	Conventional	Clay
2	Oats	Organic	Clay
3	Spring barley	Conventional	Sand
4	Spring barley	Conventional	Clay
5	Oats	Organic	Clay
6	Winter barley	Conventional	Clay
7	Onion	Organic	Clay
8	Winter barley	Conventional	Clay
9	Potato	Conventional	Loess
10	Potato	Conventional	Clay
11	Oats	Organic	Sand
12	Potato	Conventional	Peat
13	Potato	Conventional	Sand
14	Oats	Organic	Sand
15	Rapeseed	Organic	Sand
16	Lupin/oats	Organic	Clay

Sampling design

To evaluate weed density and species richness, 50 x 50 cm quadrants were randomly placed within each field. In both the strip cropping systems and the pure stand, six quadrants were used. Within the strip cropping system, three quadrants were placed on the strip edges and three in the middle of the strips (Figure 1). The first 20 meters from the boundary of a strip and pure stand were ignored to avoid edge effects (Sutcliffe et al., 2024).

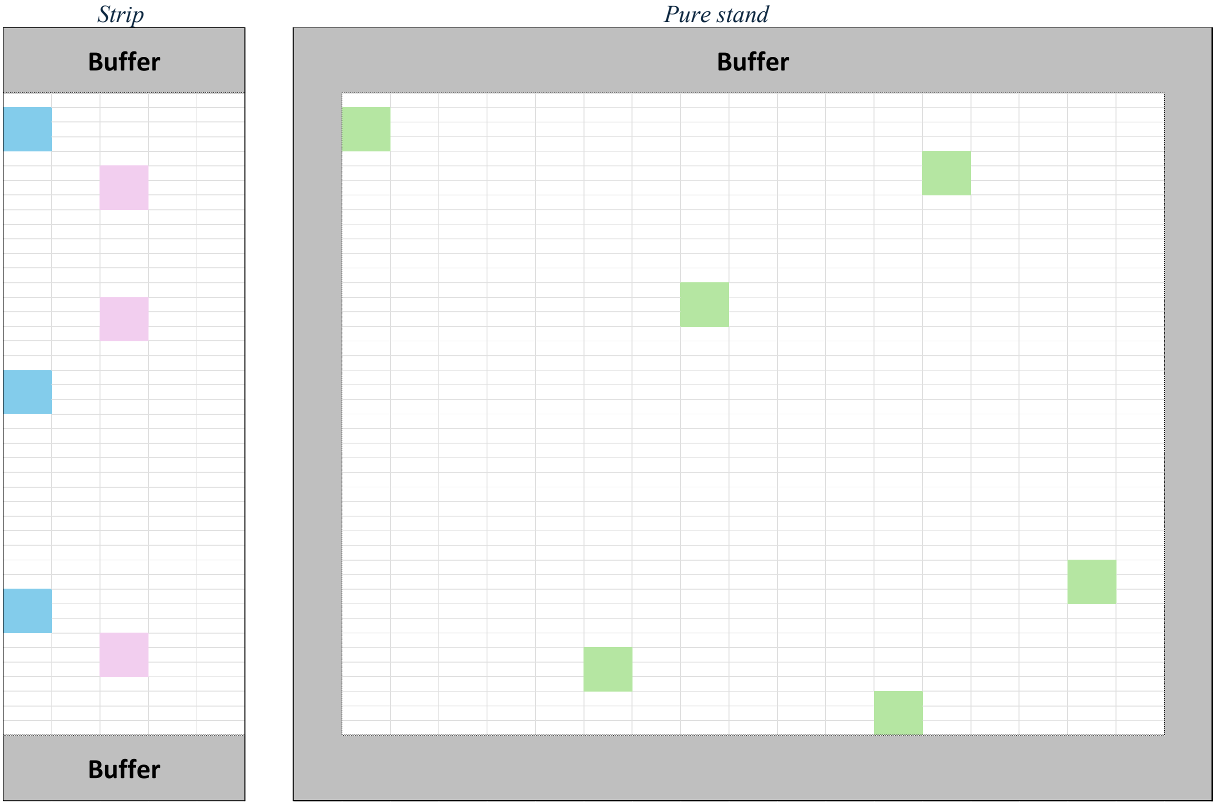

Figure 1. Schematic overview of weed counting and sampling. The grey area indicates the boundary area or buffer zone of 20 metres, which was ignored during this experiment to avoid edge effects. Blue boxes represent an example of randomly positioned quadrants on the strip edges, pink shows strip middles and green shows an example of the quadrants in pure stands. This figure is not on scale.

The observed weed species within the randomly positioned quadrants were identified using PlantNet (Pl@ntNet, 2019). All the individual plants of every weed species were counted and recorded on a data collection sheet and entered in Excel.

To assess aboveground and belowground weed traits in strip cropping systems and pure stands, a list of problematic weed species was used (Table 2) (dr. MAJ. Hofmeijer, personal communication, 2025). Weed trait data were obtained by sampling of weed species from the field. For each problematic weed species that occurred in the field, five individuals were collected from strip edges, strip middles and pure stands. The weeds were carefully excavated from the soil using either bare hands or a spade, collecting at least 20 centimetres of the root parts and stored in a plastic pouch before processing in the 'Unifarm' laboratory in Wageningen, the Netherlands.

The sampling of the problematic weeds was slightly adjusted due to an observation in the field on the first 11 locations. It occurred that, although a list of problematic species was established beforehand, other species appeared to be problematic as well. Therefore, all *Chenopodium sp.* and *Sonchus arvensis* were collected from farm locations 12 to 16.

Table 2. Overview of the weed species that were considered problematic in this study. These problematic weed species were sampled to assess aboveground and belowground weed traits.

Latin name	Botanical family	Common name	Dutch name
Galinsoga parviflora	Asteraceae	Gallant Soldier	Kaal knopkruid
Lolium sp.	Poaceae	Ryegrass	Engels raaigras
Chenopodium album	Amaranthaceae	Lamb's quarters	Melganzenvoet
Persicaria maculosa	Polygonaceae	Lady's thumb	Perzikkruid
Echinochloa crus-galli	Poaceae	Barnyard grass	Europese hanenpoot
Viola arvensis	Violaceae	European field pansy	Akkerviooltje
Convolvulus arvensis	Convolvulaceae	Field bindweed	Akkerwinde
Stellaria media	Caryophyllaceae	Chickweed	Vogelmuur
Poa annua	Poaceae	Annual meadow grass	Straatgras
Capsella bursa-pastoris	Brassicaceae	Shepherd's purse	Herderstasje
Cirsium arvense	Asteraceae	Creeping thistle	Akkerdistel
Polygonum aviculare	Polygonaceae	Birdweed	Gewoon varkensgras
Elytrigia repens	Poaceae	Couch grass	Kweek
Veronica arvensis	Plantaginaceae	Corn speedwell	Veldereprijs
Alopecurus myosuroides	Poaceae	Black grass	Duist
Apera spica venti	Poaceae	Common wind grass	Grote windhalm

Assessment of weed traits

The selected traits were based on weed (dis)services, the project AGROSOIL (*AGROSOIL — Agroecology Partnership*, z.d.), and personal communication (dr. MAJ. Hofmeijer, 2025). Aboveground traits included: plant height (PLH), specific leaf area (SLA), plant fresh weight (FW) and plant dry weight (DW). Belowground traits included: specific root length (SRL), root diameter (RD), root tissue density (RTD) and presence of mycorrhizae arbuscules (AMF) (Table 3).

Table 3. Overview of weed traits that were investigated in this study. The table includes the ecological interpretation of the weed traits.

Trait	Abbreviation	Unit	Ecological interpretation	References
Plant height	PLH	cm	For plants, investment in height can improve light capture PLH is used as a proxy for the ability of a plant to compete for light with adjacent plants and mainly crops.	(Falster & Westoby, 2003; Hofmeijer et al., 2021b)
Specific leaf area	SLA	$cm^2 \cdot g^{-1}$	A proxy for the ability of a plant to use light efficiently in resource-rich or resource-poor environments, within the trade-off between resource capture and retention.	(Hofmeijer et al., 2021b; Wilson et al., 1999)
Plant fresh weight	FW	g	Indicator for weed competitiveness.	(Zingsheim & Döring, 2024)
Plant dry weight	DW	g	Provides insights into biomass.	(Zingsheim & Döring, 2024)
Specific root length	SRL	$m \cdot g^{-1}$	SRL reflects a strategy of root foraging, where plants search for nutrients themselves, instead of relying on AMF. A high SRL indicates rapid nutrient acquisition.	(Bergmann et al., 2020; Gaba et al., 2017)

Root diameter	RD	mm	A proxy for soil nutrient acquisition and expected to indicate species symbiosis with AMF.	(Bergmann et al., 2020; Kramer-Walter et al., 2016; Tardy et al., 2017)
Root tissue density	RTD	$g \cdot cm^{-3}$	Root mass per unit of volume. RTD is associated with nutrient availability and acquisition; RTD has been shown to increase with decreasing nutrient availability. Roots with a high RTD were associated with a long lifespan, whereas species with a low RTD are short-lived.	(Bergmann et al., 2020; Kramer-Walter et al., 2016; Tardy et al., 2017)
Presence of mycorrhizae arbuscules	AMF	% (of counts per sample)	AMF can capture soil resources through symbiosis, to facilitate a cultivated crop. Species that symbiose with AMF, often have thick roots.	(Bàrberi et al., 2018; Bergmann et al., 2020)

Aboveground traits

The collected plants were directly processed or stored at a temperature of 4°C for at most 24 hours. The trait measurements were conducted in different steps. First, the plant roots and aboveground parts were separated. The roots were stored at 4°C in jars containing a 50% ethanol solution. After separation, plant height (PLH) was determined using a measuring tape placed next to the plant, from the base (cutting point) until the highest part of the plant.

To measure the specific leaf area (SLA) a destructive method was applied, where the plant leaves were separated from the stem. First, the leaf area was measured using a leaf area meter Model 3100c Area Meter by LI-COR (LI-COR Environmental, USA). To determine fresh weight (FW) the plants were weighed using the Mettler AJ100 analytical balance (Mettler Toledo, Switzerland). To measure the dry weight (DW), the plants were first dried in an oven at 70°C until completely dry for 48 hours at most (dr. MJ Zwetsloot, personal communication, 2025). After this, the dried plants were weighed again, using the Mettler AJ100 analytical balance (Mettler Toledo, Switzerland). SLA was calculated using the following formula (Wilson et al., 1999):

$$\text{SLA } (cm^2 \cdot g^{-1}) = \text{leaf area } (cm^2) / \text{total dry weight biomass } (g)$$

Belowground traits

The root samples stored in 50% ethanol solution were scanned for morphological traits using the WinRhizo root scanner (Regent Instruments Inc., QC Canada) and analysed using the RhizoVision Explorer software (Seethepalli et al., 2021). Prior to scanning, the roots were weighed to determine the total FW. Subsamples were collected from each sample by cutting 3-4 root branches, consisting of 1st to 3rd order roots from the main taproot. The roots from each subsample were spread out in a separate tray filled with water. Settings of the software were such that small soil particles and non-roots were ignored in the scanned image. Within RhizoVision, the analysis mode was set to 'broken roots'; DPI was set to 600; the image thresholding level was set to 150 and non-root objects of a maximum pixel size of 1 were filtered. No further adjustments were made within the settings of RhizoVision and a batch analysis was carried out.

The data that was derived from the scans was used to determine the specific root length (SRL), average root diameter (RD) and root tissue density (RTD). RD was derived from the output of the scans, and for SRL and RTD the following formulas were used (Bergmann et al., 2020):

$$\text{SRL } (\text{m}\cdot\text{g}^{-1}) = \text{total root length (m) / total dry weight roots (g)}$$

$$\text{RTD } (\text{g}\cdot\text{cm}^{-3}) = \text{total dry weight roots (g) / volume } (\text{cm}^{-3})$$

The scanned subsamples of the roots were weighed (FW) using a Mettler AJ100 analytical balance (Mettler Toledo, Switzerland) and dried in an oven at 70°C for 48 hours at most, or until completely dry (dr. MJ Zwetsloot, personal communication, 2025). The dried roots were weighed again, using the Mettler AJ100 analytical balance (Mettler Toledo, Switzerland) to determine the DW. The total DW of the roots was calculated from the total FW, using the ratio of water lost during the drying of root subsamples.

The last step involved the measurement the root colonisation of arbuscular mycorrhizal fungi (AMF). Vierheilig et al., (1998) developed an ink and vinegar method which was applied in this study. In this phase, a new set of subsamples were collected for AMF analysis. This again involved cutting 3-4 root branches, consisting of 1st to 3rd order roots from the main taproot. As described by (Vierheilig et al., 1998), the roots were first washed to remove any remaining soil particles. Then, the roots were boiled for 10 minutes in a 10% KOH solution and thereafter thoroughly rinsed with DI water to remove any remains of the KOH solution. Clean roots were stained with a 5% black ink (Parker Quink ink black) and 5% acetic acid (household vinegar). Roots were destained using tap water. To count mycorrhizal colonisation, the roots were transferred to Petri dishes and spread apart. Roots were placed on an object glass in 5 horizontal rows of root pieces. Presence of vesicles, hyphae and arbuscules were recorded for 100 counts per sample (20 counts for each horizontal row), using a 100x magnification on a micro wild M3 microscope (Wild Heerbrugg, Switzerland). For some counts, 250x magnification was used. When the root subsamples were too small to analyse AMF colonisation, roots from the same species and field position were combined on an object glass (dr. MJ Zwetsloot, personal communication, 2025).

Data analysis

Generalised Linear Mixed Models (GLMMs) were used for both research questions using the 'glmmTMB' (Magnusson et al., 2020) and 'lme4' (Bates, 2015) packages. GLMMs account for random variability across the different farm locations, which were included as random effects in all models. Explanatory variables within this research included position (strip edge, strip middle or pure stand), cultivated crop, soil type and farm management type (organic or conventional).

RQ1 aimed to explore how weed density and species richness patterns differ across strip edges, strip middles and pure stands. To investigate this, both the number of individuals per quadrant (weed density) and the number of species per quadrant (species richness) were counted. This count data did not meet the assumption of normality, as confirmed by QQ-plots using the 'DHARMa' package (Hartig, 2022), since some weed species were more abundant compared to relatively rare species. Therefore, a negative binomial distribution was used for these analyses. Weed density and species richness were used as response variables and the independent variable was position. Additionally, soil type and management type were included as fixed effects. Explanatory variable cultivated crop was not used in these models, as the experimental design was not set up to explain the effect of cultivated crop, because replicates were lacking. Some crops were only grown within a specific management system, for instance, potatoes were only grown under conventional management. Subsequently, an Analysis of Variance (ANOVA) and Tukey's Honest Significant Difference (HSD) post-hoc tests were carried out to test for significance between the three positions, using the 'car' package (Fox & Weisberg, 2025).

RQ2 aimed to explore aboveground and belowground traits of problematic weed species (Table 3), and whether these trait values differ between strip cropping systems and pure stands. Using GLMMs, each trait was analysed with cultivated crop as a fixed effect and weed species as a random effect. In these models, explanatory variables soil type and management type were excluded, as some weed species only occurred within a specific soil type or management type. As some trait data was positive and skewed to the right, a Gamma (link='log') distribution was used for the analyses. Again, an Analysis of Variance (ANOVA) and Tukey's Honest Significant Difference (HSD) post-hoc tests were carried out to test for significance between the three positions. Boxplots were generated using the 'ggplot2' package (Wickham, 2011), to visualise patterns per species and per trait to avoid interspecific variations.

All statistical analyses were performed using R-Studio (Version 4.5.1) (RStudio Team, 2019).

Results

Weed density and species richness

A total of 1592 individuals were found in this study and 69 different species were identified (Appendix A). The GLMMs revealed that weed density and species richness did not differ significantly between strip cropping systems and pure stands (Figure 2).

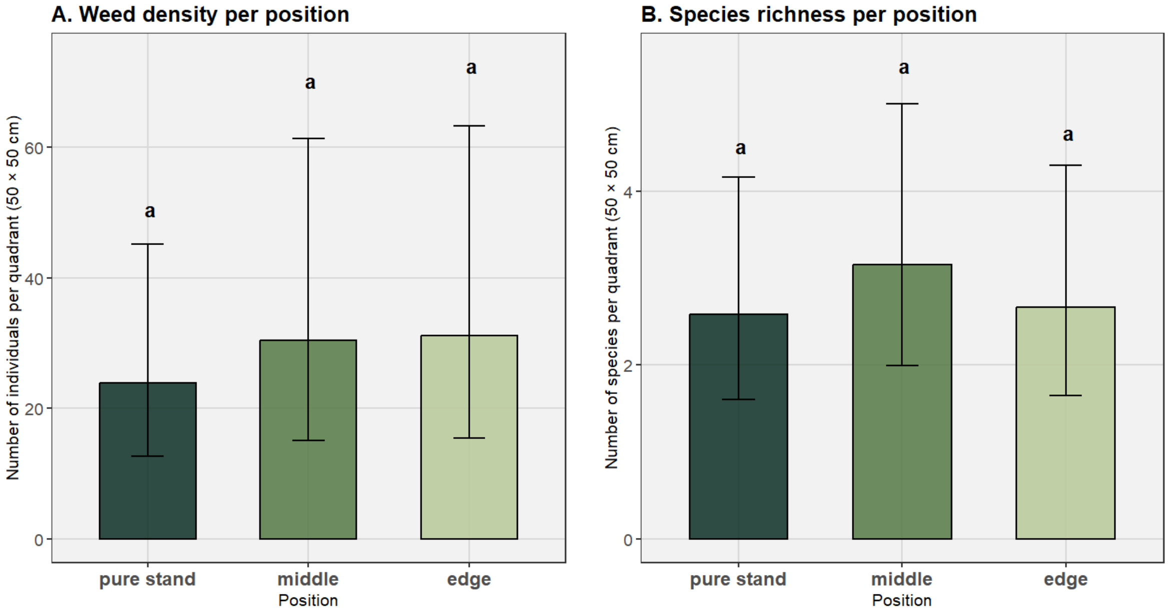

Figure 2 (A, B). Boxplots showing the model estimates of the recorded (A) weed density per position and (B) species richness per position. Significance letters indicate the level of significance and the error bars show the lower and upper limits (95% CI) around the estimate.

Soil type and management type were used as explanatory variables in the GLMMs. Interaction models between position and soil type, as well as position and management type did not show significant effects, therefore, the results are based on the main effects. Soil type had a significant effect on both weed density (p<0.001) and species richness (p=0.003). Particularly clay and loess soils had significantly lower weed densities (p<0.001; p=0.025) and weed species richness (p<0.001; p=0.019) compared to sandy soils (Figure 3). Indicating that, within this research, soil type can be a stronger predictor of weed density and species richness, compared to field positioning. Management type had only a marginally significant effect on both weed density (p=0.061) and species richness (p=0.064), indicating a slightly higher weed density and species richness on organically managed farm locations (Figure 3).

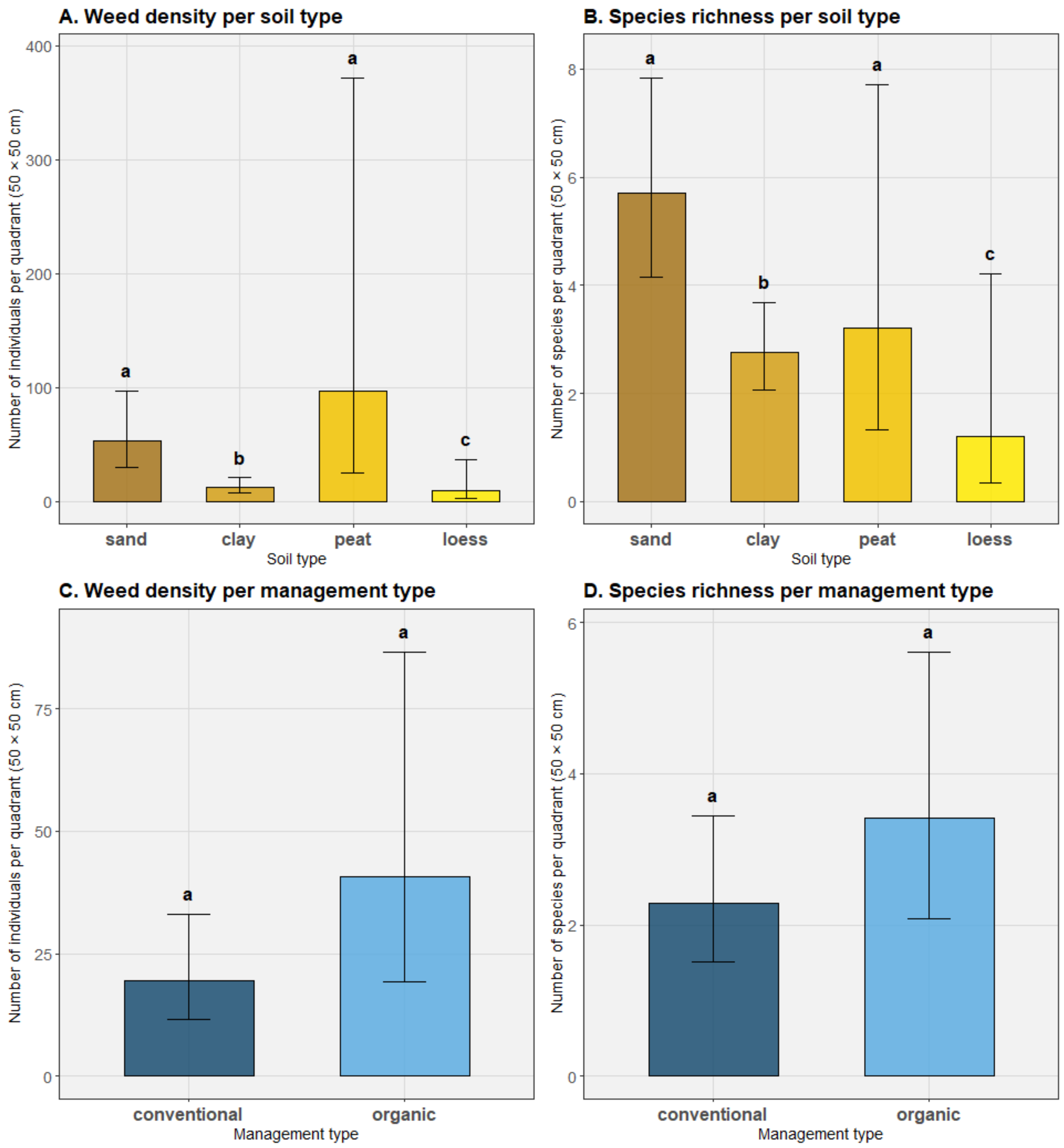

Figure 3. Boxplots showing the model estimates of the recorded (A) weed density per soil type, (B) species richness per soil type, (C) weed density per management type, (D) species richness per management type. Significance letters indicate the level of significance and the error bars show the lower and upper limits (95% CI) around the estimate.

Aboveground weed traits

For PLH, the GLMM showed a marginally significant position effect (p=0.056), meaning average plant height varied slightly between the positions, with the tallest weeds in strip middles (Figure 4). The effect of position on SLA was significant, as revealed by the GLMM (p=0.021). The Tukey post-hoc test indicated that weeds in pure stands had a significantly higher SLA compared to strip middles (p=0.015), but no other differences were found (Figure 4).

Similarly, the GLMMs testing for FW and DW showed a significant position effect (p=0.003 and p=0.002, respectively). FW was significantly higher in strip middles, relative to pure stands (p=0.005) and strip edges (p=0.022). DW showed similar patterns, with a significantly higher dry weight in strip middles, compared to pure stands (p=0.003) and strip edges (p=0.042). No differences were observed between pure stands and strip edges (Figure 4). An overview of the four aboveground traits of each problematic weed species can be found in Appendix B.

Cultivated crop was used as an explanatory variable in these models. All the aboveground traits appeared to be significantly affected by the cultivated crop present in the sampling field (PLH: p=0.004, SLA: p=0.011, FW and DW: p<0.001), suggesting that different cultivated crops select for different weed trait values (Appendix C).

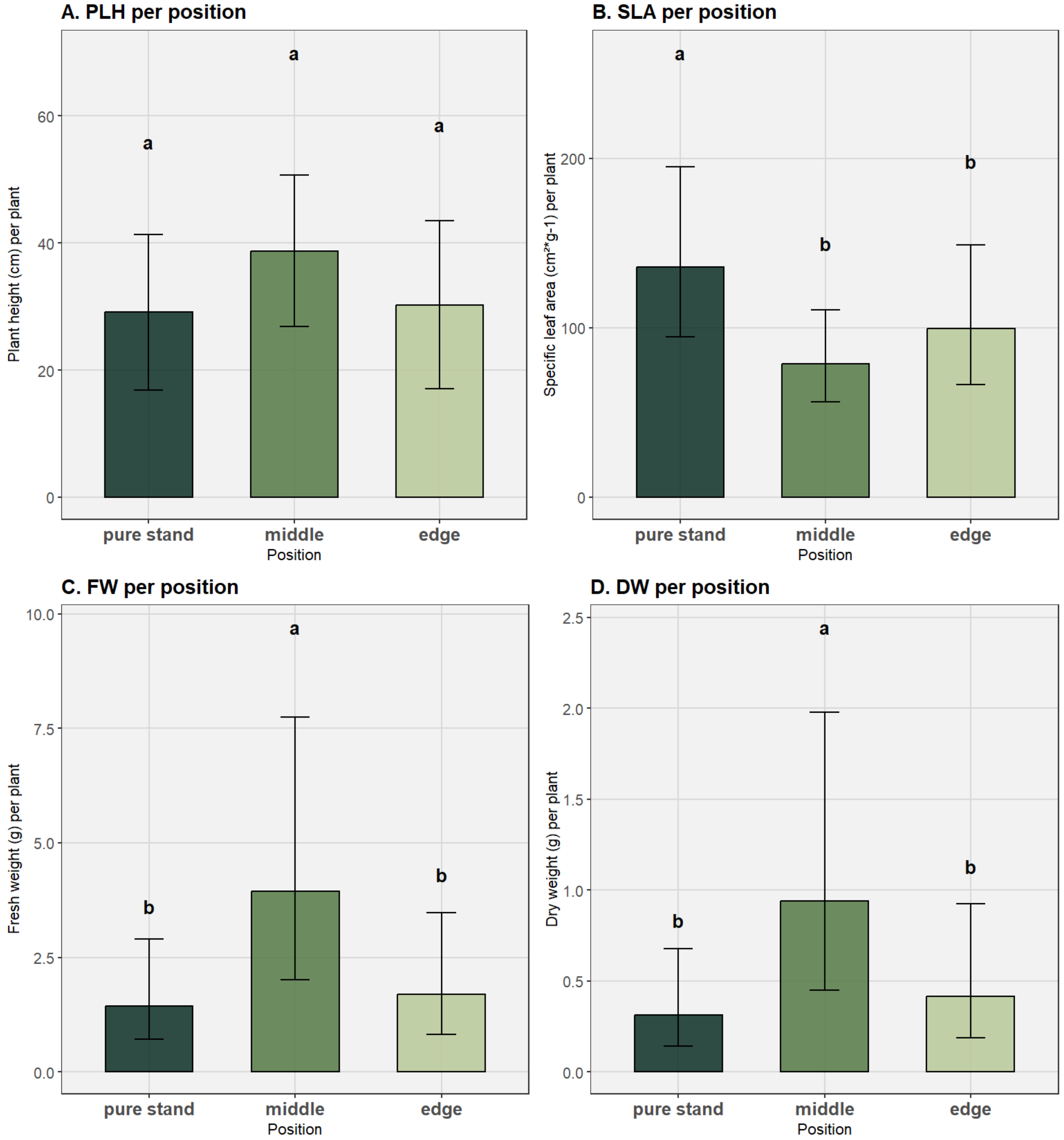

Figure 4. Boxplots showing the model estimates of the recorded (A) plant height (PLH) per position, (B) specific leaf area (SLA) per position, (C) fresh weight (FW) per position and (D) dry weight (DW) per position. Significance letters indicate the level of significance and the error bars show the lower and upper limits (95% CI) around the estimate.

Belowground weed traits

The patterns of belowground trait values showed limited variation across strip edges, strip middles and pure stands (Figure 5). For SRL and AMF colonisation, no significant position effect was found when tested with a GLMM. The GLMM testing RD, indicated a marginally significant position effect (p=0.052). Pairwise comparisons showed that the difference between strip middles and strip edges is significant (p=0.047). This indicates thinner roots on the strip edges, compared to strip middles. For RTD, the GLMM showed a marginally significant position effect (p=0.091). An overview of the four aboveground traits of each problematic weed species can be found in Appendix B.

SRL, RTD or AMF colonisation was not significantly influenced by the cultivated crop. However, cultivated crop had a significant effect on RD (p<0.001), indicated that the value of average root diameter was affected by the crop type (Appendix C).

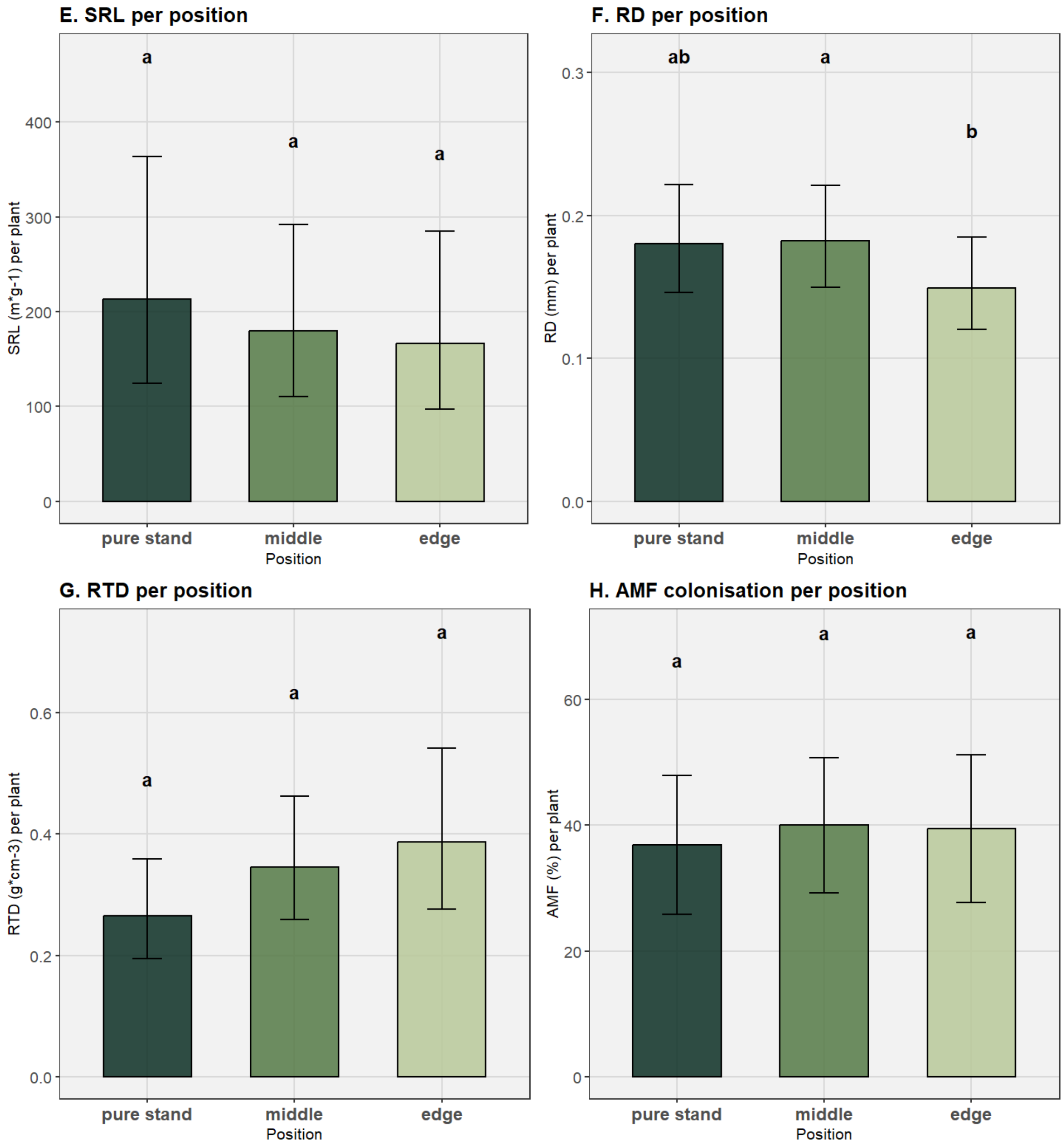

Figure 5. Boxplots showing the model estimates of the recorded (E) specific root length (SRL) per position, (F) root diameter (RD) per position, (G) root tissue density (RTD) per position and (H) AMF colonisation per position. Significance letters indicate the level of significance and the error bars show the lower and upper limits (95% CI) around the estimate.

Discussion

Previous studies showed that crop diversification practices such as strip cropping can influence weed density and species richness (Buitenhuis, 2022; Głowacka, 2013, 2014; Moinat, 2024) though differences in resource availability and microclimates (Buitenhuis, 2022; Campanelli et al., 2023; Smijers, 2025; Zhang et al., 2008). Our study expanded on this by investigating how trait values of problematic weed species differ across strip edges, strip middles and pure stands. The main findings are (I) weed density and species richness patterns did not differ between strip edges, strip middles and pure stands, (II) weed density and species richness patterns differed across soil types, with the highest values in sandy soils, (III) organically managed farms showed slightly higher values for both weed density and species richness, (IV) weeds in strip middles were taller and heavier, while specific leaf area was higher in pure stands, (V) average root diameter was lower on strip edges, whereas other belowground root trait values did not differ across field positions.

Weed density and species richness

The results of this study show no significant differences in weed density or species richness between strip edges, strip middles, and pure stands. Therefore, the hypothesis predicting higher weed density and species richness on strip edges is rejected. These findings are not in line with Buitenhuis (2022), who found a higher weed species richness on strip edges measured in barley (- pumpkin) strips. Our results are neither in agreement with part of the findings of Moinat (2024), who found lower weed densities on strip edges compared to strip middles in potato-grass, cabbage-oat and pumpkin-barley strips. At the same time, Moinat (2024) reported no significant difference in species richness between the strip edges and strip middles, which is in line with our results. Although the research site of both studies was one of our 16 farm locations, our study was conducted in different fields on the location. Perhaps, different cropping and (weed) management history could explain the difference in results. Moinat (2024) examined 3 pairs of crop types and Buitenhuis (2022) investigated only barley-pumpkin strips, whereas neighbouring crops differed across the farm locations in our study, even when the cultivated crop was the same. Competition with, or facilitation by a neighbouring crop can impact weed communities (Gaba et al., 2017), which may partially explain our different outcomes. For example, specific crop pairs can enhance resource uptake through complementary characteristics, limiting the available nutrients for weeds (Brooker et al., 2015; Juventia & van Apeldoorn, 2024), depending on the seeding time of the two crops (Gaba et al., 2017). Another explanation for the different outcomes can be the fact that weed communities can vary from year to year or even season to season, and depend strongly on weather circumstances (Holzner, 1978). Buitenhuis (2022) and Moinat (2024) conducted weed assessment in different years and earlier times in the growing seasons (March-July 2022; March and May 2023, respectively), while our fieldwork took place in June and July 2025. Future research could therefore aim to standardize crop pairs, sampling periods and site histories, to disentangle how strip edges and strip middles influence weed density and species richness.

The second hypothesis, stating that lower weed density and species richness will be found in pure stands compared to strip cropping systems is rejected as well. This is in line with findings of Głowacka (2013, 2014), who reported no effect of strip cropping on species richness, but contrasts with Głowacka (2014), who found reduced weed densities in strips compared to pure stands. However, Głowacka (2014) recorded weed species in maize, lupin and oats strips, which were grown side by side. Our study included more crop types and different crop neighbours, which may explain the difference in results. It could be that the architecture of the neighbouring crop impacts the light availability in the strips. For instance, a short neighbour crop such as sugar beet increases light availability on strip edges, potentially impacting the number of weeds that establish, due to the more favourable conditions (Radicetti & Mancinelli, 2021). In contrast with our results, Grote et al. (2023) found a higher species richness in wheat cultivated in strip cropping systems compared to pure stands, but stated that the increase of biodiversity depends on other factors such as strip width, crop type and crop pairing, which can be due to the influence on microclimates (Buitenhuis, 2022; Smijers, 2025). Garibaldi et al. (2023) observed a reduction in densities of problematic weeds in smaller fields with therefore more edges. However, their study only focused on pure stands. Nevertheless, as their results showed that a decrease of problematic weed was particularly related to increased edge densities, it may be that the same experiment in strip cropping systems shows similar results. Another explanation for our results can be the fact that temporal management causes damage in neighbouring strips when crops are temporally diverse, meaning that planting date of a neighbouring crop may impact weed density and species richness. Due to management on the strip edges, light transmission increased, which possibly stimulated weeds to grow (Smijers, 2025). Additionally, a neighbouring crop such as cabbage receives more fertilizer compared to for instance oats, which increases nitrate availability on strip edges (Smijers, 2025), and may increase weed growth. It remains unclear how strip width, crop type and pairing, as well as temporal management on strip edges can impact weed density and species richness in strip cropping systems. Hence, further research is required to explore these interactions.

Another factor that could explain the lack of significant differences in weed density and species richness between strip edges strip middles and pure stands is weed seed predation by insects, birds and small mammals, which can affect weed emergence (Bajwa et al., 2015), through reduction of the weed seedbank (Sarabi, 2019). Because predation increases by greater landscape complexity (Sarabi, 2019), it is expected that seed predation is increased in strip cropping systems. A recent study found a 15% increase in ground beetle richness in strip cropping system and a 30% average increase in activity density compared to pure stands (Croijmans et al., 2024). However, weed seed predation can be disrupted, depending on the availability of other food sources (Carbonne et al., 2020), meaning that increased activity density does not inherently lead to increased weed seed predation. Thus, further research is required to explore specifically whether weed seed predation is increased on strip edges, how this relates to crop type and management on the edges and how predation impacts weed densities and species richness.

Interestingly, soil type had a strong effect on weed density and species richness, which is in line with the study from Ługowska et al. (2016). Particularly in clay and loess soils, weed densities were reduced compared to sandy soils, which can be explained by the lower water-holding capacity or increased nutrient leaching in sandy soils (Ługowska et al., 2016). Therefore, competitive weeds that are well-adapted to resource poor environments may outcompete early seedlings of crops (Gaba et al., 2017) in sandy soils, increasing weed densities. Besides soil type, organically managed farms had slightly higher weed densities and species richness compared to conventional farm locations. This is in line with previous studies and can be due to decreased use of herbicides (Gaba et al., 2017; Mwangi et al., 2024). However, the effect of farm management type was statistically not significant, suggesting weed density and species richness was mostly impacted by soil type in this study. Further research could consider an experimental design that includes more replications of the soil-management combinations, to better disentangle the effect of strip cropping on weed density and species richness.

Aboveground traits

In contrast with our hypothesis, we observed slightly taller weeds in strip middles compared to strip edges and pure stands. Studies have highlighted that plant height (PLH) can be perceived as an indicator for the competitive ability of a weed species for light (Bàrberi et al., 2018; Gaba et al., 2017; Violle et al., 2009). Competition between weeds and crops mainly occurs when resources are limited (MacLaren et al., 2020). The fact that taller weeds were found in strip middles, knowing that PLH reflects competitive ability, could indicate a higher abundance of problematic, competitive weed species in strip middles, or perhaps a lower resource availability in strip middles. Another implication could be that strip edges have a suppressive effect on competitive traits such as plant height. For instance, Gu et al. (2021) showed that, due to complementarity effects of crop pairs, less resources are left for weeds which hampers their growth. Although this was examined in intercropping system and strip cropping systems include a temporal diversification practice, the seeding times may allow for a complementarity effect. This could for instance lead to higher weed densities on the strip edges, with smaller, less competitive weed species.

Our results show that SLA was significantly higher in pure stands compared to strip cropping systems, which supports our hypothesis. Specific leaf area (SLA) increases with decreasing light availability, which allows leaves to capture more sunlight under lower light conditions (Violle et al., 2009; Yvoz et al., 2021). This can be explained by more competition for light in pure stands, due to lower light availability (Zhang et al., 2008). Contrary to our expectations, SLA did not differ between the strip edges and strip middles, which is not in line with the study from Perronne et al. (2014), who observed higher trait values for SLA in strip middles compared to strip edges when measured in winter wheat. Additionally higher FW and DW values were observed on strip edges compared to strip middles (Buitenhuis, 2022; Perronne et al., 2014), which is not in line with our results. However, Borgy et al. (2016) stressed that trait values, especially SLA, are shaped by factors such as the growing season conditions and the canopy height of the cultivated crop. Thus, our results likely differ from Perronne et al. (2014), because our study was conducted on multiple locations with different cultivated crops and the trait values from our selected problematic weed species were not specifically measured in winter wheat.

Belowground traits

The average root diameter (RD) of weeds was lower in strip edges compared to strip middles, which is in contrast with our hypothesis. Plants with a lower RD make rapid use of nutrients (Tardy et al., 2017), which could therefore indicate a more exploratory rooting strategy, perhaps in response to greater belowground competition. However, in contrast with our hypothesis, SRL and RTD (associated with nutrient acquisition and root lifespan, respectively), showed no differences in values across strip edges, strip middles and pure stands, which may indicate less belowground competition overall. Interestingly, Kramer-Walter et al. (2016) stated that plants are less constrained in constructing their roots compared to their leaves, meaning that it could be that competition is mainly reflected in aboveground, competitive traits. To explore this, future research could consider linking aboveground and belowground traits to better understand trade-offs in resource acquisition.

Our results on AMF colonisation are in contrast with our hypothesis, but are consistent with those of Caruso (2023), who found no differences between strip edges and strip middles. However, Caruso (2023) did observe a higher AMF colonisation in strip cropping systems, compared to pure stands in both pot and field experiments, which has been shown before in oat-pea intercropping systems (Lee et al., 2023). Increased AMF colonisation is due to increased crop diversity in intercrops (Brooker et al., 2015; Lee et al., 2023), which can explain the higher AMF colonisation found in strips by Caruso (2023). An explanation for our results may be that the selected problematic species included AMF non-hosts, such as *Chenopodium album* and *Stellaria media,* which may rely on host-plant to promote AMF colonisation (Wang et al., 2022). Consequently, it may have been more challenging to identify whether the increased plant diversity in strip cropping systems positively affected AMF colonisation.

Limitations

This study has some limitations that should be considered. Firstly, aboveground and belowground traits were not linked to the same individual weed after sampling from the field. Therefore, no trade-off analyses could be performed between aboveground and belowground trait values. To address this, future research should aim at obtaining matched above- and belowground trait data. Secondly, on four farm locations (6 ,7, 8 and 10) in Zeeland, dry and compacted soil restricted the sampling of weeds from the field. Therefore, no samples were collected on these farms, which can potentially bias generalizing the trait results and drawing firm conclusions (Appendix D). In addition, on farm location 14, the cultivated crop was damaged by a combination of downbursts and a high abundance of *Fallopia convolvulus*¸ which restricted us from sampling from the field (Appendix D). To overcome these limitations, future studies could consider repeated sampling rounds to ensure data collection even when extreme weather or soil conditions occur. Thirdly, this study was conducted in the year 2025 and data was collected between late June and mid-July. As community composition and trait values can shift over the season, repeated sampling rounds would strengthen the results. To make the results even more robust, sampling across multiple years is suggested. Fourthly, a list of problematic species was established beforehand, which may not fully represent the trait distribution within the weed communities. Finally, other variables such as field history, crop pairs and strip width could have contributed to variation in our data. Future research could therefore consider these factors, to better disentangle the effects of strip cropping on weed communities and traits.

Conclusion

This study examined how weed density, species richness and weed trait values varied across strip edges, strip middles and pure stands. The results indicate that strip cropping did not significantly affect weed density or species richness and no differences were observed between strip edges and strip middles. These findings suggest that, under the studied conditions, strip cropping does not have an effect on the number individuals or the number of species compared to pure stands. Instead, variation in weed density and species richness was influenced by soil type, with the highest values observed in sandy soils. Furthermore, weed traits were more affected by position in the field. The problematic weeds that were investigated in this study were slightly taller and significantly heavier in strip middles compared to strip edges and pure stands, suggesting increased competition with the cultivated crop in strip middles. Besides, the higher values of specific leaf area in pure stands may reflect increased competition for light. Our results also indicated a lack of significant differences in belowground weed traits between strip edges, strip middles and pure stands, which can suggest limited belowground competition, or that weeds mainly express their competitive ability in the construction of their aboveground traits.

All together, our findings suggest that strip cropping does not affect weed densities and species richness, but can alter the functional growth strategies of problematic weed species expressed through their traits. Future research is needed to explore how trait-based weed responses vary across crop pairs, strip widths and temporal management practices on strip edges, as this remains . Besides, further research could build on this research by combining variation in trait values with effects on crop yield across strip edges, strip middles and pure stands.

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Appendix A

Overview of the recorded weed species.

Table A1. Recorded weed frequency, corresponding EPPO codes and botanical names of the 69 weed species.

Frequency	EPPO code	Botanical name	Frequency	EPPO code	Botanical name
299	CHEFI	*Chenopodium ficifolium*	5	TRFHY	*Trifolium hybridum*
225	POLCO	*Fallopia convolvulus*	4	GASPA	*Galinsoga parviflora*
120	AGRRE	*Elytrigia repens*	4	LACVI	*Lactuca virosa*
116	VIOAR	*Viola arvensis*	4	RAPRA	*Raphanus raphanistrum*
85	LOLPE	*Lolium perenne*	4	SETVE	*Setaria verticillata*
62	GASCI	*Galinsoga quadriradiata*	4	SOLLU	*Solanum villosum*
59	POAAN	*Ochlopoa annua*	4	TRFPR	*Trifolium pratense*
54	CHEAL	*Chenopodium album*	4	TUSFA	*Tussilago farfara*
41	TRFRE	*Trifolium repens*	3	ARBTH	*Arabidopsis thaliana*
38	POLAV	*Polygonum aviculare*	3	CHEPO	*Chenopodium acutifolium*
36	ACHMI	*Achillea millefolium*	3	STEPD	*Stellaria pallida*
34	ATXPA	*Atriplex patula*	2	ARISE	*Arenaria serpyllifolia*
30	POLLA	*Persicaria lapathifolia*	2	PAPRH	*Papaver rhoeas*
29	MATCH	*Matricaria chamomilla*	2	RANRE	*Ranunculus repens*
21	AETCE	*Aethusa cynapium subsp. elata*	2	RUMCO	*Rumex conglomeratus*
21	CHEVU	*Chenopodium vulvaria*	2	SONAS	*Sonchus asper*
21	RUMOB	*Rumex obtusifolius*	2	TAROF	*Taraxacum officinale*
21	STEME	*Stellaria media*	2	TARPA	*Taraxacum palustre*
20	CLTST	*Callitriche stagnalis*	2	VERFI	*Veronica filiformis*
19	GERRO	*Geranium robertianum*	1	ALOMY	*Alopecurus myosuroides*
19	VEROP	*Veronica opaca*	1	ANTTI	*Anthemis tinctoria*
18	ERICA	*Erigeron canadensis*	1	BRSNI	*Brassica nigra*
15	CIRAR	*Cirsium arvense*	1	CARHI	*Cardamine hirsuta*
15	TTTDD	*dicotyledonous weed plants*	1	CENJA	*Centaurea jacea*
13	MYOAR	*Myosotis arvensis*	1	CVPCA	*Crepis capillaris*
13	RANNE	*Ranunculus nemorosus*	1	ERYRE	*Erysimum repandum*
12	PLAMA	*Plantago major*	1	GNAUL	*Gnaphalium uliginosum*
12	RANLN	*Ranunculus lanuginosus*	1	LOTUL	*Lotus pedunculatus*
9	CENCY	*Centaurea cyanus*	1	MEDFA	*Medicago falcata*
9	ECHCG	*Echinochloa crus-galli*	1	ROPRA	*Rorippa palustris*
9	VERMO	*Veronica montana*	1	SADVA	*Samolus valerandi*
8	VICVI	*Vicia villosa*	1	SENSI	*Senecio sylvaticus*
6	SONAR	*Sonchus arvensis*	1	SOLTU	*Solanum villosum*
5	CAPBP	*Capsella bursa-pastoris*	1	VERPO	*Veronica polita*
5	POLPE	*Persicaria maculosa*			

Appendix B

A visualisation of the traits per species sampled from the field. The different traits are shown as separated panels. Separated graphs per species per traits were made to overcome interspecific variations within the boxplots.

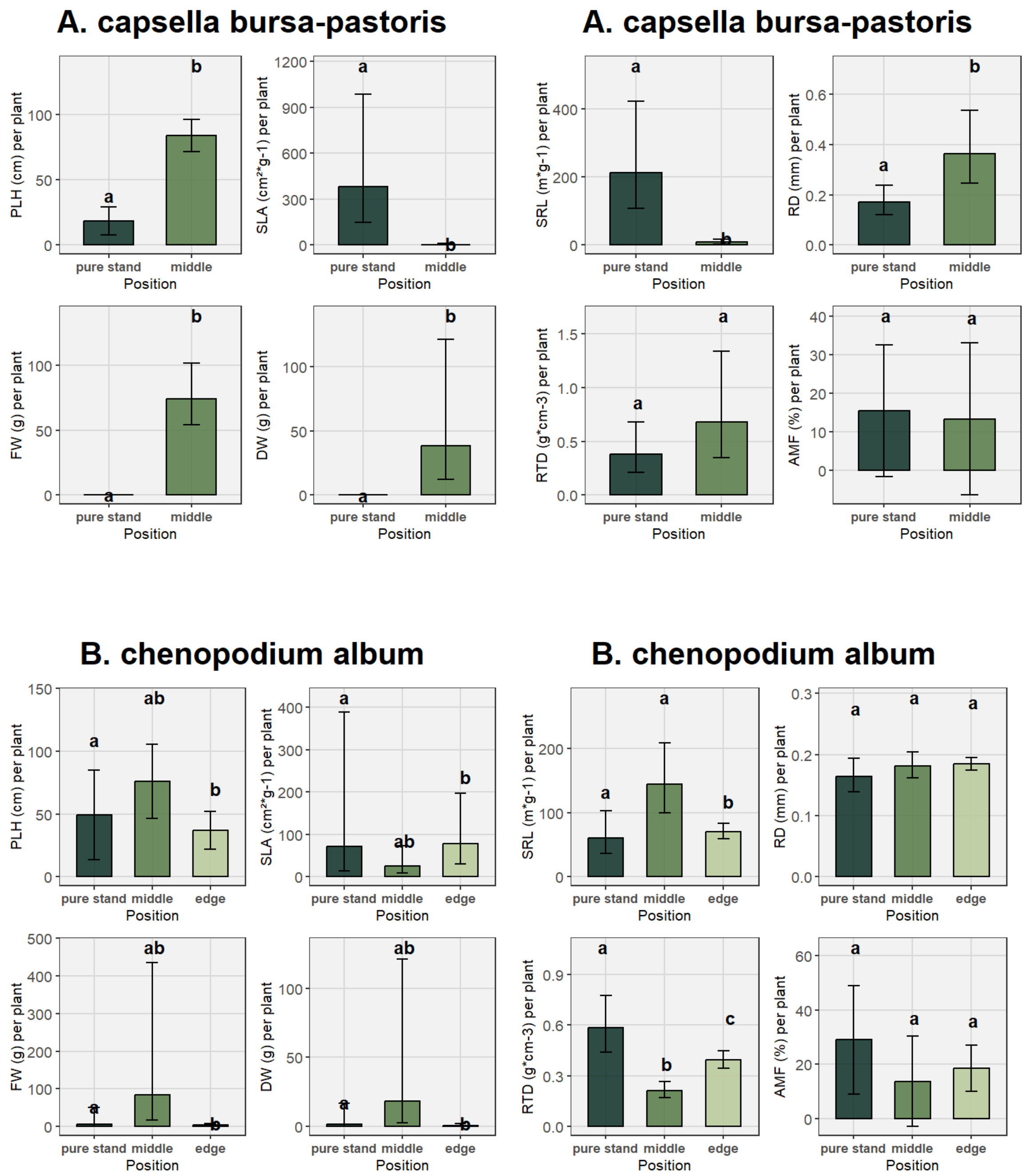

Figure B1. Continued

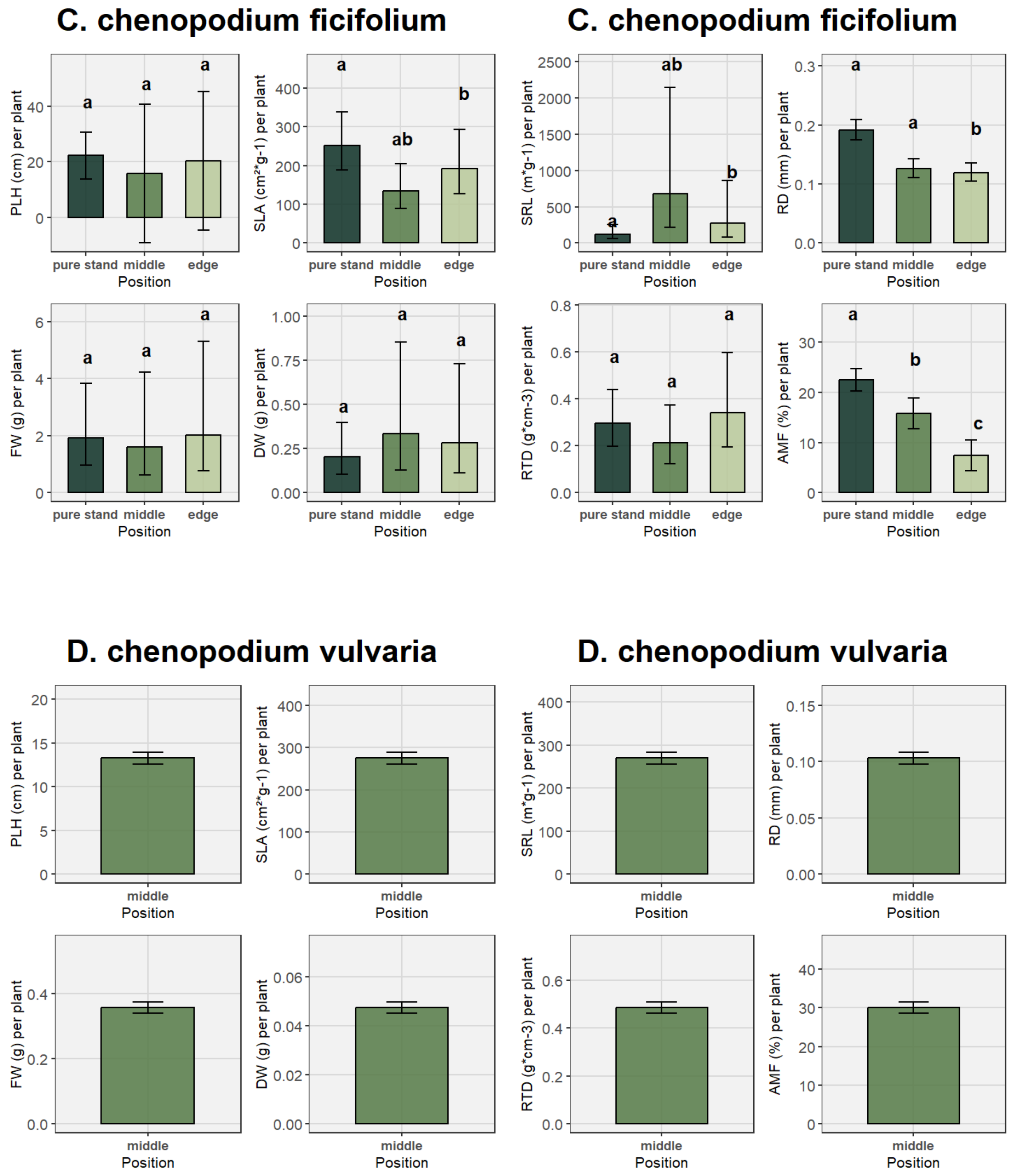

Figure B1. Continued

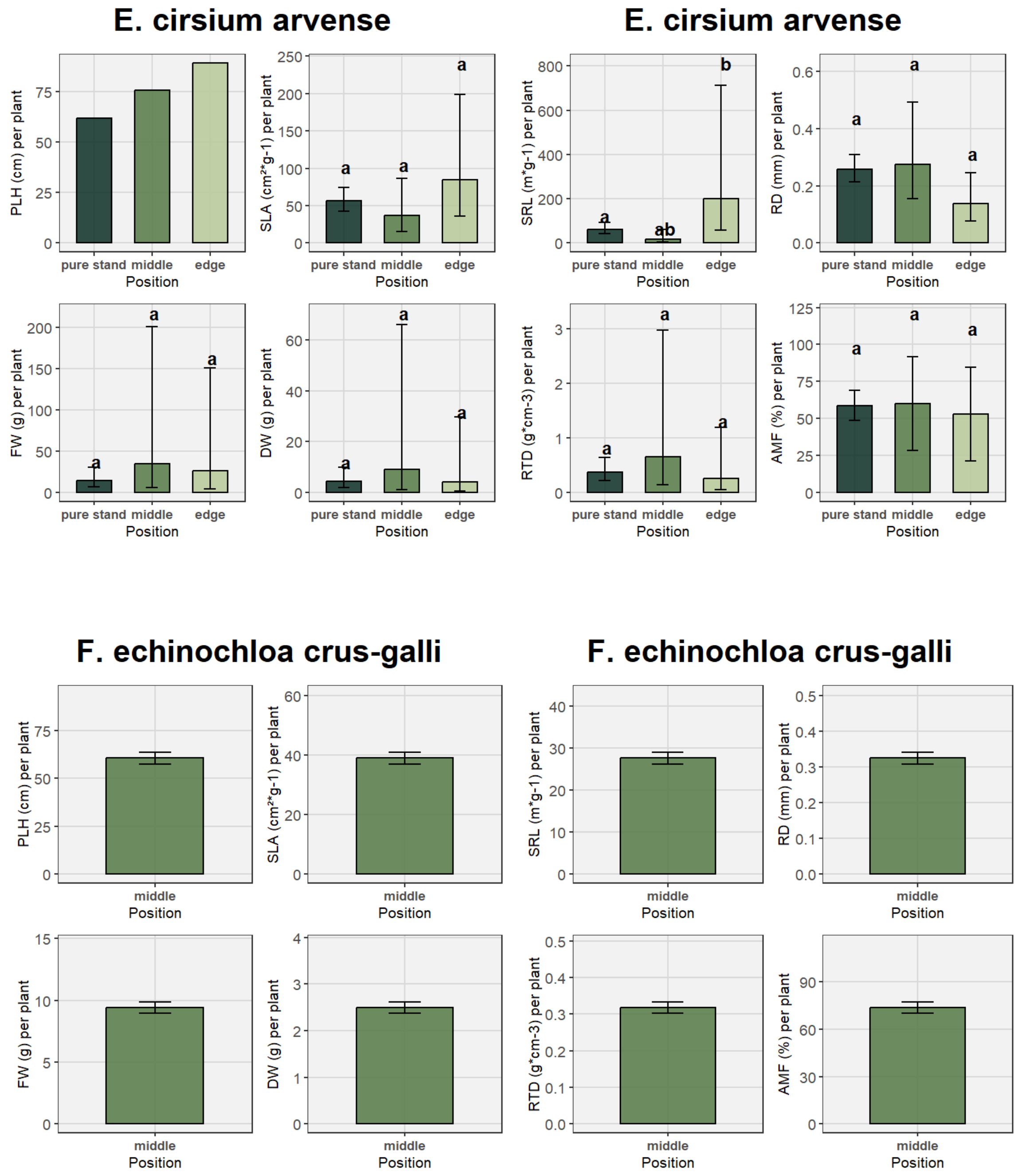

Figure B1. Continued

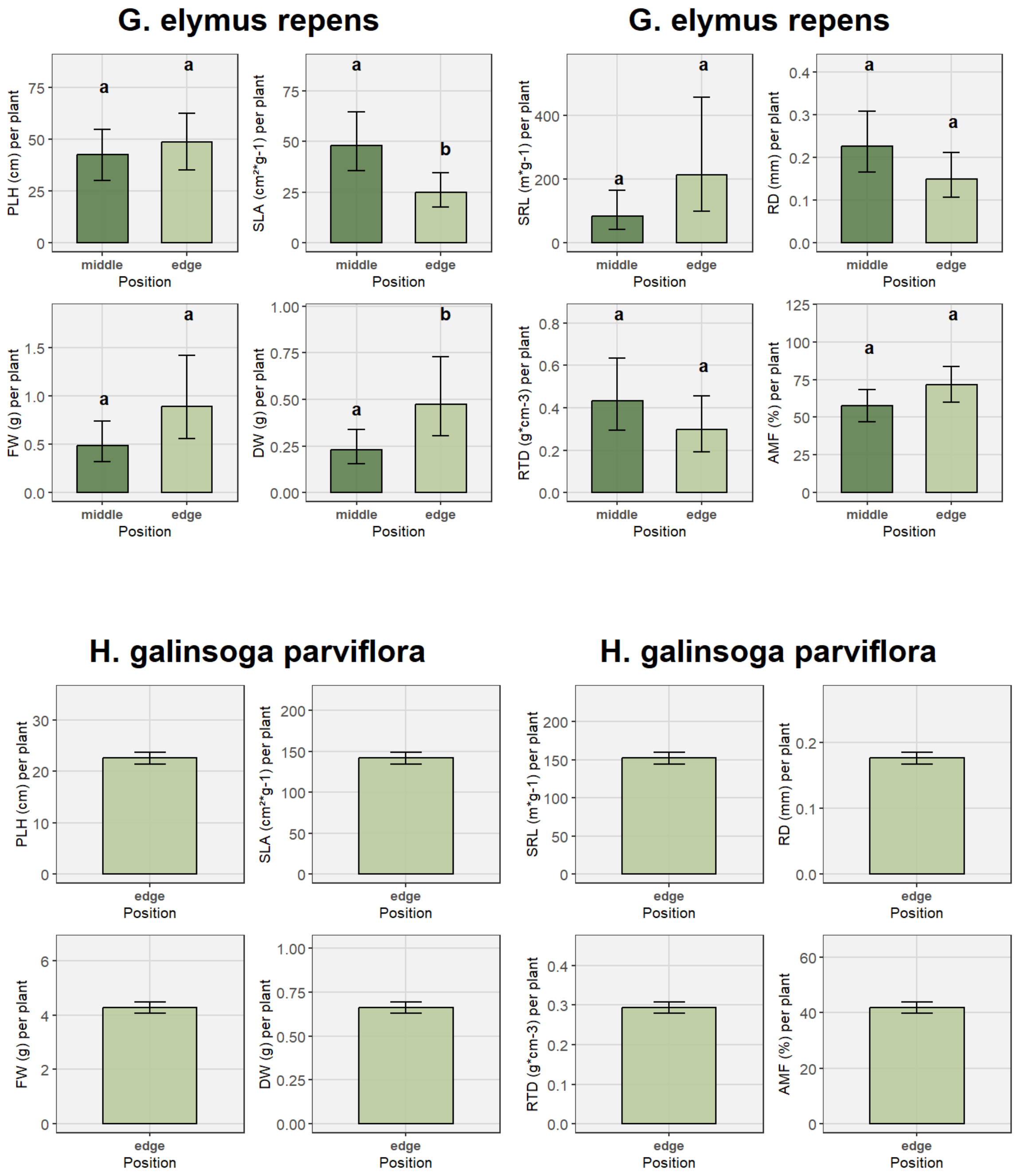

Figure B1. Continued

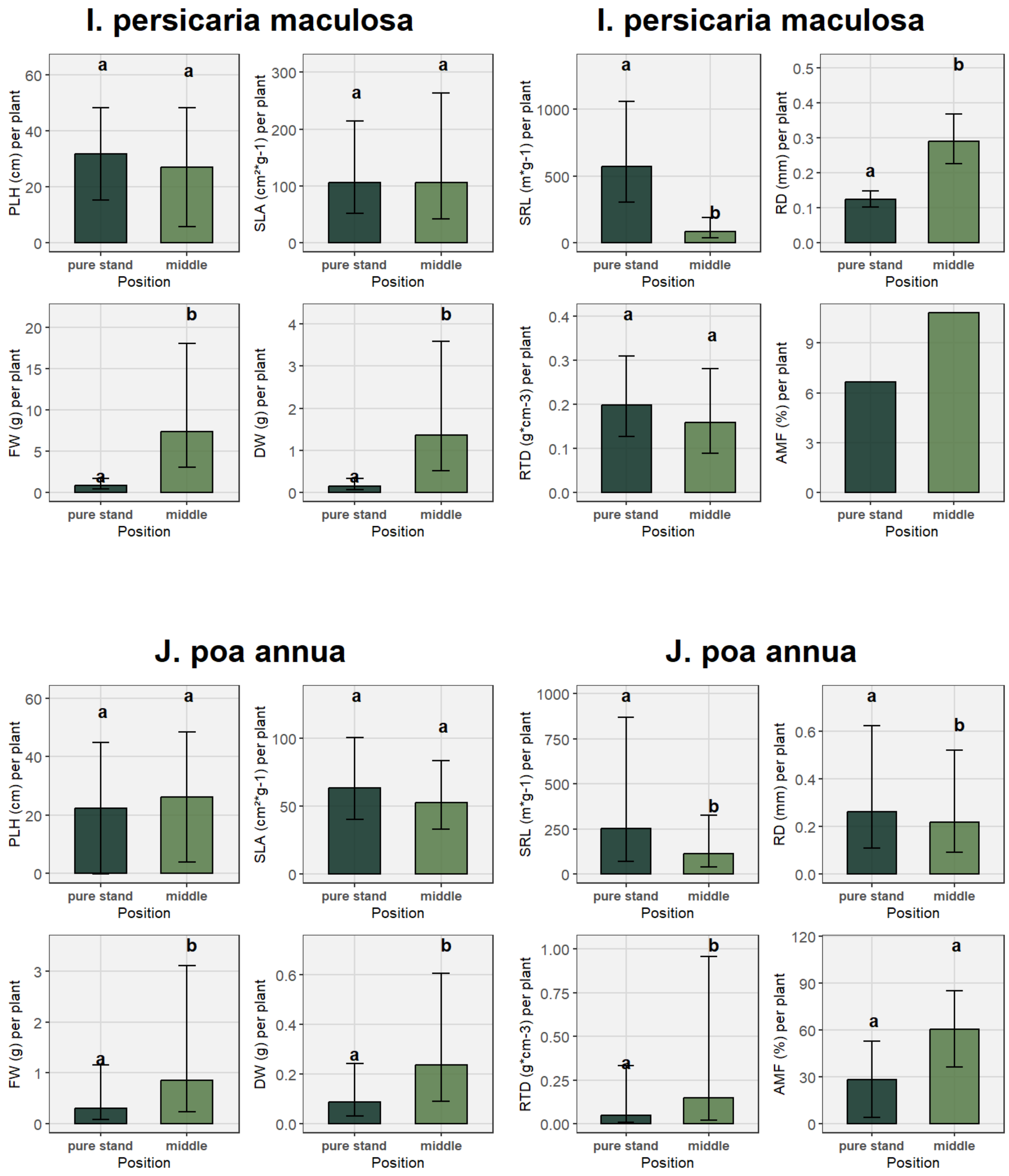

Figure B1. Continued

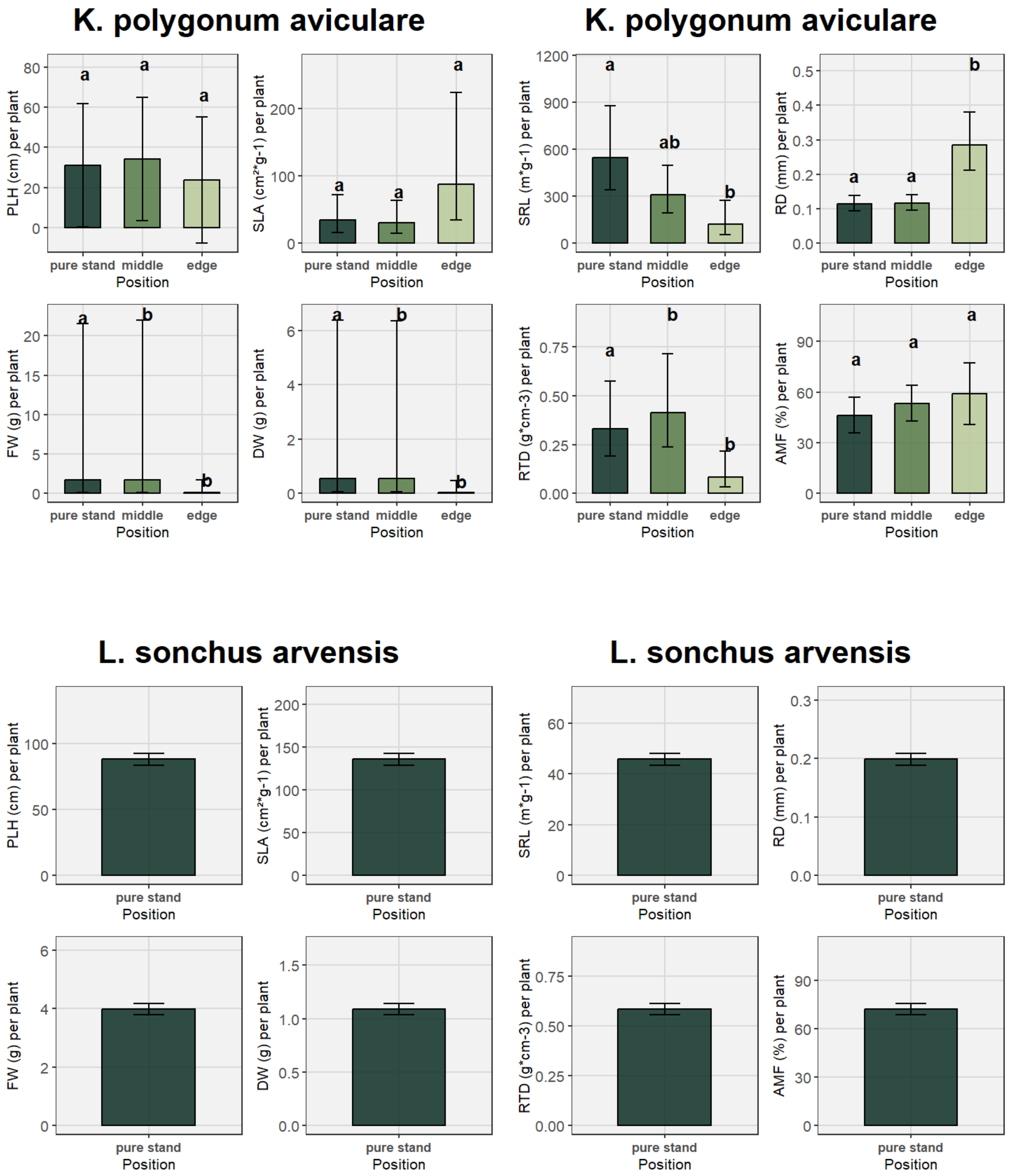

Figure B1. Continued

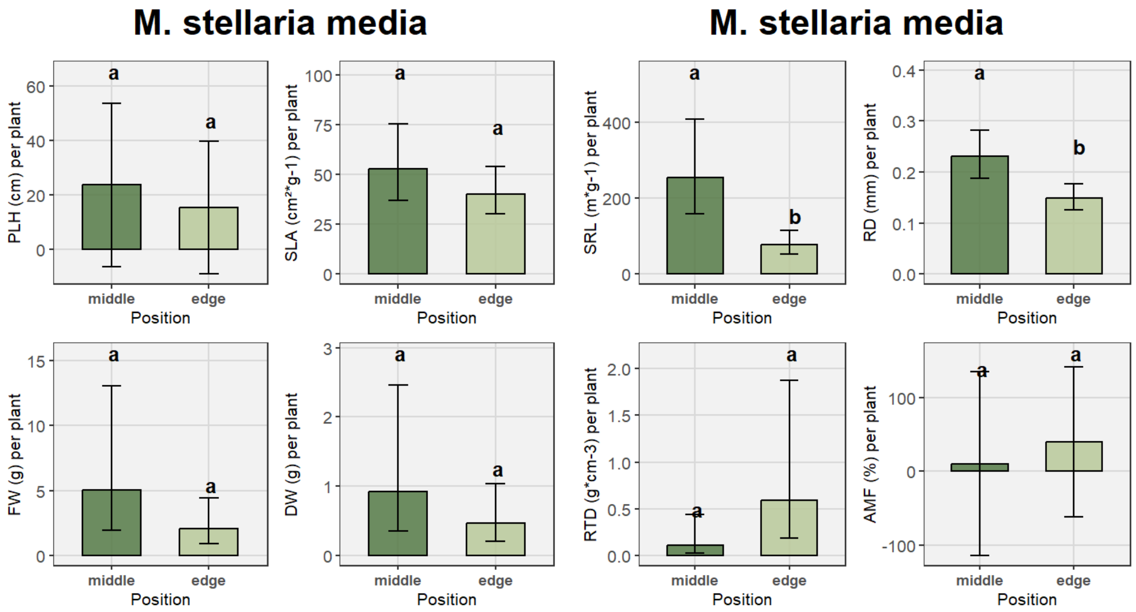

Figure B1 (A - M). An overview of the recorded weed species and the 8 traits that were assessed - plant height (PLH), specific leaf area (SLA), fresh weight (FW), dry weight (DW), specific root length (SRL), average root diameter (RD), root tissue density (RTD) and AMF colonisation (AMF) - per position. Species include (A) C. bursa-pastoris, (B) C. album, (C) C. ficifolium, (D) C. vulvaria, (E) C. arvense, (F) E. crus-galli, (G) E. repens, (H) G. parviflora, (I) P. maculosa, (J) P. annua, (K) P. aviculare, (L) S. arvensis and (M) S. media. Some species were sampled from all the positions in the field and include B, C, E, K. The other species only occurred on 2 positions (A, G, I, J, M) or 1 position (D, F, H, L). Traits are shown in panels; the four panels on the left show the aboveground traits and the four panels on the right show the belowground traits. Significance letters indicate the level of significance and the error bars show the lower and upper limits (95% CI) around the estimate.

Appendix C

Overview of the effect of cultivated crop type on aboveground and belowground weed traits.

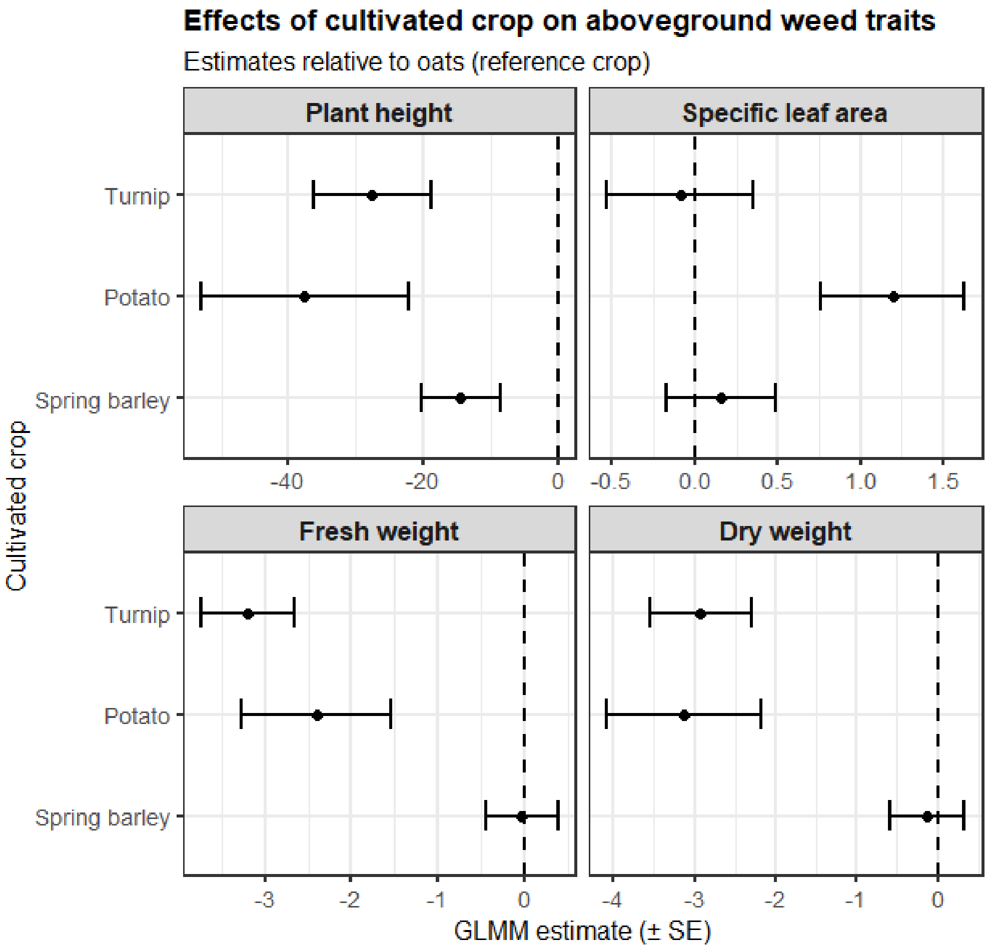

Figure C1. Continued

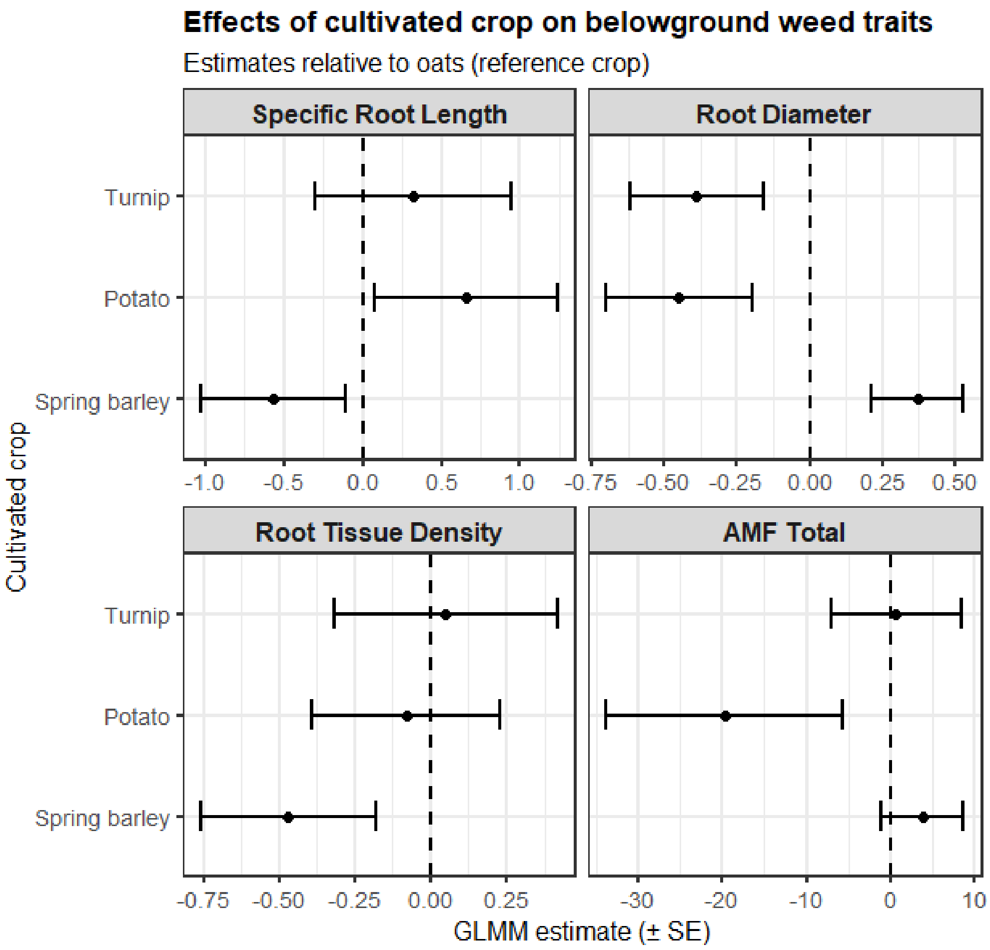

Figure C1. An overview of the model estimates of the main effect of cultivated crop type on the aboveground and belowground weed traits - plant height (PLH), specific leaf area (SLA), fresh weight (FW), dry weight (DW), specific root length (SRL), average root diameter (RD), root tissue density (RTD) and AMF colonisation (AMF). The black dotted line indicates the reference crop (oats) and the error bars show the lower and upper limits (95% CI) around the estimate.

Appendix D

Observation and sampling limitations in the field.

Figure D1. Farm locations 6 ,7 ,8 and 10. Example of dry soil conditions in Zeeland.

Figure D2. Farm location 14, oat field damaged by downbursts and high abundance of *Fallopia convolvulus*.