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Abstract

Biotic resistance theory suggests that diverse cover crop mixes may be more effective at weed suppression than a cover crop monoculture. However, evidence for this has so far been inconsistent. To investigate, we designed a trial to explicitly test the role of cover crop diversity in weed suppression, through comparing eight cover crop mixes that varied in species diversity, functional diversity, and composition. Mixes contained either one, four or eight species, in equal proportions. Three mixes contained only cereal species, three contained only legumes, and two contained a mix of cereals, legumes and brassicas. Research was conducted on two farms in South Africa's winter rainfall region, replicated over two years. Indicators of resource uptake by each mix in terms of light, soil nitrogen and water were measured at three time points throughout the season, approx. 50, 85 and 110 days after establishment (DAE). Aboveground biomass (dry weight) of cover crops and weeds within each mix was measured twice, at approximately 70 and 120 DAE. Regression analyses indicated that cover crop biomass was key to resource uptake and weed suppression, and that early-season nitrogen and later-season light availability had the

strongest influence on weed biomass. Neither species diversity nor functional diversity affected resource uptake or weed suppression by cover crops. These results indicate that it is important to consider the competitiveness of individual species when designing cover crop mixes. Diverse mixes remain valuable to perform multiple functions, but may contribute to weed problems if composed of poorly competitive species.

Introduction

Cover crops, defined as crops planted for a purpose other than harvest, are integrated into cropping systems to achieve a variety of goals. Cover crops can be used to conserve and enhance soil quality, provide resources to biodiversity, break pest and disease cycles, and suppress weeds (Snapp et al 2005, Blanco-Canqui et al 2015). Recently, cover crops comprising mixes of different species have become popular, as combining species with different properties creates a single crop that can perform multiple functions (Storkey et al 2015, Finney et al 2017). Combining multiple species may also increase the capacity of a cover crop to perform individual functions. This concept has not yet been extensively tested in cover crops, and there is mixed evidence so far (e.g. Döring et al 2012a, Finney et al 2016). However, in general, increased plant diversity is known to be associated with increased provision of several specific ecosystem functions (Isbell et al 2017), including productivity (Tilman et al 2012), soil carbon storage (Lange et al 2015), nutrient cycling (Oelmann et al 2011) and the support of further biodiversity (Scherber et al 2010). Diversity is thought to increase the magnitude and resilience of an ecosystem function because each species performs the function in a different way, or at different rates under different conditions, leading to a higher overall capacity to consistently perform the function (Díaz and Cabido 2001, Isbell et al 2011). Functional diversity (the diversity of species' traits that influence ecosystem functioning; Tilman 2001) is considered to have a stronger effect on ecosystem functioning compared with species diversity. Functionally different species are more likely to have distinct strategies (distinct niches) to perform the function, so their strategies are more likely to be complementary rather than overlapping, and lead to greater functioning (Díaz and Cabido 2001).

One function of cover crops that has potential to be improved by increased diversity is weed suppression. Cover crops primarily suppress weeds by competing with them for resources (although allelopathy can also play a role; Blanco-Canqui et al 2015). Thus, combining different species that acquire resources from their surrounding environment in different ways could result in increased overall resource capture, so that fewer resources remain available to weeds. This

concept has been explored in invasion ecology, where it was first put forward by Elton (1958) and forms a central pillar of the 'biotic resistance' or 'diversity-invasibility' hypothesis (Richardson and Pyšek 2006, Jeschke 2014). Biotic resistance can be defined as a resident community's capacity to resist invasion by alien species, and in the context of plant communities, diversity may contribute in two ways (Shea and Chesson 2002, Funk et al 2008). First, according to the niche differentiation hypothesis, the additive effect of each species acquiring resources in different ways could result in more efficient overall resource capture. Second, the sampling effect hypothesis states that a diverse community would be more likely to contain a few species that are particularly effective at resource capture, thereby lowering overall resource availability and reducing opportunities for invasion. The sampling effect may also manifest as an increased likelihood of limiting similarity, where the community contains species that use resources in similar a fashion to the invader, and these species are thus more likely to suppress the invader through competitive exclusion (limiting similarity) (Funk et al 2008).

Empirical support for a positive relationship between species diversity and biotic resistance via either niche differentiation, limiting similarity and/or the sampling effect has been inconsistent (Levine and D'Antonio 1999, Jeschke 2014). The current consensus in the literature is that diversity can play a role, but its effect is often obscured by other variables such as abiotic disturbance and fluctuating resource availability (Richardson and Pyšek 2006). Several authors have noted a scale-dependent pattern, where resident diversity increases biotic resistance at small spatial and temporal scales, but at landscape scales and over decades resident diversity is often the result of high resource availability and frequent resource fluctuations, conditions that also promote invasion by alien species (Levine 2000, Nunez-Mir et al 2017). However, the findings that diversity can increase resistance at small scales suggests that the principle could be applied to increase cover crop suppression of weeds at the scale of a farm field.

Few studies so far have investigated the relationship between the diversity of cover crop mixes and their capacity for weed suppression, and their findings have been inconsistent. Some previous studies suggest functional diversity may increase weed suppression (Linares et al 2008,

Döring et al 2012a), while others suggest that the biomass produced by a cover crop is the main predictor of weed suppression, and that diversity does not play a role (Brennen and Smith 2005, Smith et al 2014, Smith et al 2015, Finney et al 2016). These latter studies suggest that whilst the sampling effect may play a role in natural systems by increasing the chances that a particularly competitive species will be present, in agricultural systems we could simply choose to sow the most competitive species, or pick the species most likely to suppress locally abundant weeds through limiting similarity.

Another potential role of cover crop diversity in weed management is that diverse cover crops may help to promote a more beneficial weed community. Although weeds are considered primarily detrimental to crop production, weeds can benefit agroecosystem functioning by supporting other beneficial organisms (Petit et al 2011), and the provision of this service is expected to be higher when the weed community is more diverse (in this context, a low abundance of diverse weeds could perhaps be considered an unplanned but nonetheless beneficial component of a cover crop). A study by Palmer and Maurer (1997) indicated that diverse cover crop mixtures may promote weed diversity, possibly through the creation of diverse microhabitats and/or by combining different crops that promote or facilitate different groups of weeds. However, a more recent trial by Smith et al (2015) found no evidence for such a relationship.

Overall, there is a promising theoretical basis that increasing cover crop diversity could improve weed management, but inconsistent results from previous studies indicate a need for further experimental evidence. To investigate how cover crop diversity influences weed abundance and community composition, this paper presents a field trial designed to systematically test the effects of different levels of both species diversity and functional diversity on weeds, and to investigate whether any effect can be explained by increased resource capture. Specifically, we test the following hypotheses:

(A) increased cover crop species diversity and/or increased cover crop functional

diversity increases weed suppression;

(B) the capacity of a cover crop mix to suppress weeds can be explained by its ability to

capture resources;

(C) specific cover crop functional types are more effective at suppressing weeds of

comparable functional types;

(D) a more diverse cover crop mixture promotes a more diverse weed community;

(E) cover crops that are more effective in weed suppression result in higher cash crop

yields in the following year.

2. Methods

2.1 Trial overview, location and layout

To test our five hypotheses, we designed a field experiment consisting of cover crop mixes that

differed in species diversity, functional diversity, and the functional types of species included in

the mix. We assessed the effect of each mix on overall weed biomass, and identified whether the

species diversity, functional diversity, composition or biomass of each cover crop mix best

explained the effect on weed biomass (hypothesis A). To understand whether these cover crop

mix characteristics influenced weed biomass through reducing resource availability to weeds, we

explored how cover crop characteristics related to the availability of light, moisture and nitrogen

throughout the season, and also investigated whether or not weed biomass responded to the

availability of these resources (hypothesis B). To assess whether limiting similarity played a role

(hypothesis C) we explored whether different cover crop functional types reduced the biomass of

weeds of similar functional types to a greater degree. We also investigated whether weed

species diversity increases as cover crop diversity increases (hypothesis D). Lastly, to assess

the agronomic significance of the cover crop mixes, we explored how the different cover crop

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mixes and their ability to suppress weeds was linked to cash crop yields in the following year (hypothesis E).

The trial took place on two farms in South Africa's Western Cape winter rainfall region, Langgewens (33°17'0.78"S, 18°42'28.09"E) and Tygerhoek (34° 9'31.76"S, 19°54'36.77"E) Research Farms (Figure 1) of the Western Cape Government Department of Agriculture. Langgewens receives an average annual rainfall of 408 mm (SD = 109 mm) of which approximately 80% falls between April and September, while Tygerhoek receives an average annual rainfall of 511 mm (SD = 101 mm) with approximately 60% falling between April and September (based on rainfall records between 1996-2016). The dominant weed species at both sites are *Lolium* species, with the local population thought to be a hybrid complex of *L. rigidum, L. multiflorum* and *L. perenne* (Ferreira et al 2013). These research farms are representative of field cropping systems in the region, where most farms follow conservation agriculture practices, including no-tillage or minimum-tillage, crop rotation, and crop residue retention. The main crops are winter cereals, canola (*Brassica napus*), and legume forages. Due to the annual rainfall distribution, only one crop per year can be grown in the winter months, so a cover crop replaces a cash crop. Vineyards and orchards are also major cropping systems in the Western Cape winter rainfall region, and annual cover crops are used to protect soil and suppress weeds in winter. Findings from this trial are applicable to both annual field crop and perennial fruit and wine crop systems in the region.

The trial was laid out in randomised blocked design, with three blocks on each farm. Each treatment plot was 4.2 m wide by 20 m long. At Langgewens, the blocks were located on three separate fields that had been continuously cropped with wheat (*Triticum aestivum*) since 1996, and the trials were surrounded by wheat. At Tygerhoek, all blocks were located in a single field with a mixed cropping history and the field around the trial was left fallow. Cover crops were sown directly into the residue of the previous year's crop using a Kuhn Neo 13 no-tillage doubledisc planter (manufactured in Brazil), following typical practice in conservation agriculture systems. At Tygerhoek, there was minimal crop residue but a substantial amount of residue from

summer weeds, particularly from the knotweed *Polyganum aviculare.* In 2016, the trial at Tygerhoek was planted on 11 May and at Langgewens on 18 May; in 2017 Tygerhoek was planted on 3 May and Langgewens on 12 May. The first substantial rainfall of the season was unusually late at both farms in both years (late May in 2016 and early June in 2017), so the trials were planted into dry soil. In 2016, seedling emergence occurred approximately 15 days after planting, and in 2017 approximately 25 days after planting. At the end of the season (late September/early October), the cover crops were rolled using a roller-crimper to terminate their growth and prevent them from setting seed (the effectiveness of this termination was not formally assessed but will be considered in the discussion section). The roller-crimper used was constructed by staff in the Western Cape Government Department of Agriculture.

In 2017, cash crops were also planted into the cover crop plots of 2016, to investigate the effects of the mixes on subsequent yield, and whether any effects were linked to weed suppression during the cover crop year. At Langgewens the cash crop was wheat, and forage oats (*Avena sativa*) were used at Tygerhoek. The wheat was sown with a Piket Implements 20-row fine seed planter (manufactured in South Africa) and the forage oats with the Kuhn Neo 13 (manufactured in Brazil). Neither fertiliser nor herbicides were used throughout the season, to avoid obscuring the impact of the previous cover crop treatments. The wheat grain at Langgewens was harvested on 6th November 2017 (using a HEGE 140 combine plot harvester manufactured in Germany) and oat biomass samples collected by hand at Tygerhoek on 25th October 2017. The oat grain was not harvested at Tygerhoek as a forage cultivar was used, and thus the grain yield may not be reflective of growth conditions.

2.2 Species selection and mix composition

The trial consisted of nine treatments: a weed fallow or 'bare ground' (BG) control where no cover crops were planted, two monoculture controls (a single cereal, 1C; and a single legume, 1L), three four-species mixes (four cereals, 4C; four legumes, 4L; and a diverse mix, 4D), and three high richness mixes (cereals, HC; legumes, HL; and a diverse mix, HD) (Table 1).

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Treatments differed slightly between the two years of the trial. In the first year (2016), a total of 21 different species was used, and the HL and HD mixes contained 12 species each (Tables 1 and 2). In 2017, the number of species in the H mixes was reduced to eight: species that did not establish well in 2016 were excluded from the trial in 2017. In 2016 not enough cereal species could be obtained to create an HC mix (seed suppliers did not have these in stock), so this treatment was only implemented in 2017. The HC mix included two rye *(Secale cereale)* varieties, a spring variety and a stooling variety, in addition to six other cereal species. These two varieties were suggested by local agronomists to vary in phenology and growth habit as much as two different cereal species.

The selection of species to include in the trial was informed by common practices in the Western Cape (the species used for the 1C and 1L mixes are typical cover crops) and on advice from local experts, including government agronomists and commercial seed suppliers. Sowing rates were also based on advice from local experts. To create the mixes, the recommended sowing rate was divided by the proportion of the mix made up by each species; for example, in a four species mix, each species was sown at 25% of its recommended sowing rate (Table 1).

The functional diversity investigated in this study was diversity in spatial resource capture strategy: the species included differed in their growth forms and root architectures. Although plants do not compete for space *per se,* plants compete for the resources within a space (Booth et al 2003), and thus a group of plants capable of more completely occupying the threedimensional space around them would be expected to deplete resources more uniformly from that space and thus more effectively reduce resource availability to weeds. Specifically, diversity in growth form was expected to allow the cover crops to create a more complete canopy cover to restrict light availability to weeds, and diversity in root architecture to allow the cover crop to more effectively deplete the soil of moisture, nitrogen and other key nutrients (Figure 2).

Species were divided into the functional types of 'cereal', 'legume', 'brassica' and 'other'. These four groups have different strategies to utilise the space around them, and thus different

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strategies to acquire resources from that space (Figure 2). All cereal species included in the trial had a tufted, upright growth form and fibrous roots. Most legumes had prostrate or spreading growth forms, with a taproot and spreading lateral roots (with the exception of lupins, included in 2016 only, which had a more upright growth form). The two brassica species (white mustard and forage radish) had upright growth forms and deep taproots, while the 'other' consisted of chicory) in 2016 and flax in 2017 (this substitution was made given the very poor establishment of chicory in 2016). Chicory forms a rosette with a deep taproot, while flax has a shallow root system and slender upright growth form. In accordance with limiting similarity, cover crops with specific growth forms and root architectures were expected to suppress weeds with similar growth forms and root architectures, given that they are more likely to compete for resources within the same space. Weeds were divided into functional types that corresponded with those of the cover crops: 'grasses' (similar root architecture and growth form to cereals), 'short or prostrate herbs' (similar to legumes), and 'tall upright herbs' (similar to brassicas).

2.3 Data collection

2.3.1 Cover crop and weed biomass, diversity and composition

Aboveground dry-weight biomass of both cover crops and weeds was sampled twice in each year of the trial, once at 'mid-season' approximately 65 days after emergence (DAE) and once at 'end-season' approximately 140 DAE (just prior to termination). Biomass was not sampled prior to 65 DAE as competition between crops and weeds was not expected to be strong while plants were small and resources therefore not limiting (in the region, crop growth is typically slow in the cold winter months of June and July and begins to increase in August). A 0.5-m^2 biomass sample was cut from each plot, from two 0.25-m^2 sub-samples located a random number of paces from each end of the plot (placed either to the left or right to avoid cutting the same area in both sample events). To determine botanical composition, biomass was sorted into each species of cover crop and weed, then dried at 60°C for at least 72 hours, then weighed.

For both cover crop and weed species diversity and functional diversity we used the Shannon index (Magurran 2004) based on the biomass of each species:

$$-\sum_i p_i \ln p_i$$

where p is the proportion of biomass in species i. For functional diversity, the Shannon index was calculated using the biomass of each of the four functional types of cereal, legume, brassica and chicory/flax, and the matching weed functional types of grasses (cf. cereals), short/prostrate herbs (cf. legumes), and tall upright herbs (cf. brassicas). The Shannon index was used because it is relatively sensitive to the presence of rare species, and the weed community in the trial locations was largely dominated by *Lolium* spp. (Magurran 2004). Mix composition was determined by the biomass of the different functional types in each sample, for both weeds and cover crops.

2.3.2 Resource availability and capture

To investigate resource use by different cover crop mixes, we measured soil gravimetric water content, total mineral nitrogen, and percent of the ground covered by cover crops and by weeds (canopy cover), in each plot at three points throughout the season: approximately 50, 85 and 110 DAE. At each time point, four soil cores of a 4-cm diameter and 10-cm depth were taken from each plot and combined to form a representative soil sample. These soil samples were weighed wet, then dried at 60˚C for at least 72 hours, then weighed again to obtain the gravimetric water content. These samples were then tested for ammonium and nitrate content following indophenol-blue test (Keeney and Nelson 1982) and the salicylic acid method (Cataldo et al 1975), respectively. These two values were added together to obtain a value for total mineral nitrogen.

Canopy cover was visually estimated according to the Domin scale (Kent 2011) in three 1-m^2 quadrats in each plot, that were in fixed positions throughout the season to ensure biomass was not cut from these areas. Quadrats were located at 5-m intervals along each plot, 0.5-m in from

the edge (to avoid edge effects) on alternating sides of the plot; this meant quadrats were not disturbed during soil sampling down the centreline of the plots. Domin cover estimates were converted to the midpoint of each cover score (Lepš and Hadincová 1992), then these midpoints from the three quadrats were averaged to one representative value for each plot. Estimates were made by the same person to avoid observer bias.

In 2016, soil samples taken on the date of sowing in late April and again just prior to harvest in late September (one representative sample per plot per time point) were also tested for extractable phosphorus and sulphur, exchangeable calcium, magnesium and potassium, copper, zinc, manganese and boron content, according to methods set out by the Non-Affiliated Soil Analysis Work Committee (1990). These measurements were used to calculate differences in the soil nutrient content between the beginning and end of the season, to explore whether any treatments used more or less of each mineral, and thus to infer whether they may have played a role in competition between weeds and cover crops.

2.3.4 Subsequent cash crop year

Just prior to cash crop planting (in late April 2017) and at approximately 80 DAE for each cash crop, ground cover by cover crop and weed residue from the previous year was visually estimated in each plot (using the average of Domin estimates of two 1 m^2 randomly located quadrats). Also during the April pre-planting assessment, four soil cores (4-cm in diameter, 10cm deep) were collected and combined to form a representative sample, then tested for total mineral nitrogen (as in Section 2.3.2).

In November, wheat grain from each plot at Langgewens was harvested using a plot combine harvester, with only a central 1m strip in each plot harvested to avoid edge effects. The grain was weighed to obtain a yield value in kg ha^{-1} (wet grain weight was standardized to 14% moisture). Final oat biomass samples were cut at Tygerhoek from three 0.25-m^2 quadrats located randomly

along the centre line of each plot; these were combined to form a single representative sample for each plot. Oat biomass was separated from weed biomass, dried at

60˚C for 72 hours, and weighed.

2.4 Data analysis

All analyses were undertaken in the software R, version 3.4.3 (R Core Team, 2017). To detect differences between mid and end-season weed and cover crop biomass, composition, species diversity and functional diversity, type III analysis of variance (ANOVA) F tests on linear mixed effects regression models fitted with restricted maximum likelihood (REML) using Satterthwaite approximations for degrees of freedom (R package *lmerTest)* (Bolker et al 2008). For all models, block nested within farm and block nested within year were included as random intercept effects, and the relevant predictors for each hypothesis were included as fixed effects. Post-hoc pairwise comparisons were conducted from estimated marginal means using the Tukey adjustment (R package *emmeans)*. Marginal and conditional R^2 values for all models are provided in the results as an indication of how well variation in the data is described by both fixed and random effects in each model (R package *MuMIn*) (Nagasaka and Schielzeth 2014). The marginal R^2 indicates the proportion of variance explained by the fixed effects, while the conditional R^2 indicates variance explained by the entire model including both fixed effects and random effects.

Prior to analyses, all explanatory and response variables were standardised by subtracting the dataset mean and dividing by the standard deviation, so increase ease of interpretability of the relative effects of different variables (Schielzeth 2010). All models were checked to ensure they fulfilled assumptions of normality and equal variance by assessing trends in the residuals, and where necessary log transformations were used to correct for these. Models were also checked for influential outliers; any issues are reported in the results.

Differences between treatments are visualised using boxplots calculated in R's *graphics* package. The centre band shows the group median, the box represents the interquartile range, and the whiskers show either the minimum and maximum values, or 1.5 times the interquartile range on each side of the mean, where minimum and maximum values exceed this. Points indicate outliers that are more than 1.5 times the interquartile range away from the mean. Letters shown on the boxplots indicate pairwise differences according to the post-hoc comparisons (see above): treatments that are different to one another do not share a letter.

For those cover crop characteristics found to differ (P<0.05) between mixes, mixed effects linear regression models following the above procedure were then used to explore whether these were linked to differences in weed biomass (hypothesis A), and to resource levels: soil nitrogen content, moisture content, and cover crop canopy cover at different points throughout the season, and with differences in soil mineral levels between the start and end of the season. We also investigated whether weed biomass was related to these resource levels (hypothesis B). To explore limiting similarity (hypothesis C) we modelled whether the amount of each functional type of weed varied proportionally in response to the amount of different cover crop functional types in each mix, and we also tested whether weed diversity was linked to cover crop diversity (hypothesis D). To investigate cash crop yields in the subsequent years (hypothesis E), ANOVA and Tukey's HSD were employed to test for differences between mixes, and regression models used to explore relationships between cover crop biomass and weed biomass in the cover crop year, residue cover at the start of the cash crop year, mid-season weed cover during the cash crop year, and cash crop yield. Relationships between these continuous variables are graphically presented using the functions of R's *effects* package.

3. Results

3.1 Weed suppression by different mixes

Lower final weed biomass was observed in the cereal and diverse mixes compared with most legume mixes (ANOVA F = 13.42, P < 0.001) (Figure 3). Weed suppression was similar amongst all cereal and diverse mixes, whilst none of the legume mixes had fewer weeds than the bareground control.

3.2. Diversity, composition and productivity of different mixes

The species diversity (Shannon index) of the cover crop mixes was as intended: the controls had low relative diversity, the four-species mixes had an intermediate diversity, and the high species mixes had a higher diversity (Figure 4a; ANOVA F = 95.11, P < 0.001). However, the HL mix did not have a higher diversity than the 4-species mixes, as many of the legume species did not establish well, whilst the 4C mix had higher diversity than both other four-species mixes, and the HL mix. The Shannon index of functional diversity confirms that the 4D mix and HD mix were the only two mixes containing functional diversity, and furthermore that the HD mix had a higher functional diversity than the 4D mix (Figure 4b; ANOVA F = 116.95, P < 0.001). Biomass production differed substantially among mixes, with the cereal and diverse mixes producing more cover crop biomass than the legume mixes (Figure 4c; ANOVA F = 142.24, P < 0.001). The composition of the mixes varied as intended, with legume (L) mixes containing only legumes and cereal (C) mixes containing only cereals. The diverse mixes contained a mixture of cereals, legumes and brassicas, but their cereal components tended to be over-represented (Figure 4d).

3.3 Mix characteristics and weed suppression

Of the cover crop characteristics of species diversity, functional diversity, composition and biomass production, both total biomass production and the proportion of cereal biomass were associated with a reduction in weed biomass (P<0.05, Table 3, Figures 5a and 5b). Weed biomass was log-transformed to reduce unequal variance in model residuals. The cover crop composition variables of cereal, legume and brassica proportional biomass were collinear with one another (variance inflation factor > 2.5), and were not included in the same model. Including

cereal biomass resulted in the best model fit (lowest AIC), and so results from the model containing cover crop total biomass, cereal proportion, species diversity and functional diversity as fixed effects are reported (Table 3). Increasing the proportion of brassica biomass had a similar effect to increasing the proportional of cereal biomass, resulting in reduced weed biomass, while increasing the proportion of legume biomass had the opposite effect and was linked to increased weed biomass (results not shown).

3.4 Mix characteristics and resource capture

Overall, the two cover crop characteristics associated with weed suppression, total cover crop biomass and the proportion of cereals, explained only a small amount of variance in nitrogen and moisture availability within the experiment (Table 4). The majority of variance was explained by differences between experiment blocks, farms and years. However, mixes containing a higher proportion of cereals did reduce nitrogen and moisture availability slightly at 50 DAE (Table 4, Figure 6). Further nitrogen and moisture capture later in the season may have been obscured as rainfall increased, which raises soil moisture and thus also stimulates the release of nitrogen through mineralisation of crop residue and soil organic matter. However, by 110 DAE cereal biomass proportion had a small but significant positive relationship with moisture availability (Table 4), suggesting that mixes containing more cereals were using less moisture toward the end of season.

Higher total cover crop biomass was associated with increased canopy cover throughout the season, although with stronger effects at 85 and 110 DAE (Table 4, Figure 6c). Mixes with more cereals also had a slightly higher canopy cover at 85 DAE (Table 4). None of the soil minerals measured apart from nitrogen were observed to decrease in response to cover crop biomass or composition (results not shown), indicating that the capacity of cover crops to suppress weeds was not related to the capture of any of these minerals. Overall, these results suggest that more productive cover crop mixes were more able to capture light throughout the season, and mixes

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with a higher cereal content were additionally able to capture more nitrogen and moisture early in the season.

3.5 Weed biomass and resource availability

Resource availability at 50 DAE was used to predict the increase in weed biomass from midseason to end-season, to assess whether more weed biomass was produced where more resources were available. Weed biomass increased most where nitrogen was highest and where cover crop canopy was lowest at 50 DAE (Table 5), indicating that nitrogen and light availability allowed weeds to be more productive. The resource availability model predicted 20% of the observed variation in weed biomass between plots, with random location effects explaining another 50% of the variation (Table 5).

3.6 Limiting similarity and weed diversity

Thirty-six weed species were recorded in this study (Table 6). The weed community was overwhelmingly dominated by *Lolium* spp., which contributed 67% of total weed biomass in this study, across both farms and years. Proportions of different weed functional types did not vary ($P > 0.05$) in response to variation in the proportion of their corresponding cover crop functional types (results not shown), indicating that limiting similarity in terms of spatial resource capture traits did not occur. Cover crop diversity also did not increase weed diversity, either in terms of species or functional diversity ($P > 0.05$, results not shown).

3.7 Cover crop effects on cash crop yield in the following year

There were no effects of cover crop biomass or composition on conditions at the start of the subsequent cash crop season, in terms of soil mineral nitrogen, cover crop residue or weed cover (results not shown). However, weed cover in the middle of the cash crop season was higher where weed biomass at the end of the cover crop year was higher ($P < 0.05$), and where

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cover crop biomass and cereal proportion were lower ($P<0.05$) (Table 7). Cash crop yield was not affected by start-of-season nitrogen, residue or weeds ($P>0.05$, results not shown), but was reduced by mid-season weed cover. This effect was stronger on forage oat biomass yield at Tygerhoek than on wheat grain yield at Langgewens (Table 8, Figure 7). The two were modelled separately due to the different types of crops grown at each site.

4. Discussion

4.1 Cover crop diversity, resource capture, weed suppression and weed diversity

This study confirms that cover crops can be effective in suppressing weed biomass through reducing the availability of resources to weeds. However, neither species diversity nor functional diversity (in terms of the spatial resource capture traits explored in this study) increased the efficacy of cover crops in this regard (hypotheses A and B). There was also no evidence to suggest that cover crops with a particular growth form and root architecture suppressed weeds with comparable traits, and thus no evidence for limiting similarity (hypothesis C), nor any evidence that diverse cover crop mixes promoted weed diversity (hypothesis D). Our results indicate that the cover crop mixes composed mostly or entirely of cereals produced more biomass, captured more resources, and suppressed more weed biomass.

These findings agree with previous trials of cover crops that found that species able to produce a large quantity of biomass quickly are most capable of suppressing weeds (Palmer and Maurer 1997, Brennan and Smith 2005, Storkey et al 2011, Brust et al 2014, Smith et al 2014, Smith et al 2015), and that diversity does not necessarily result in increased function in this regard (Finney et al 2016). Additionally, recent studies on biotic resistance to alien plant invasions suggest that fitness differences between resident species and invaders determine resistance to a greater extent than resident diversity, or the functional similarity of dominant resident species to the invader (Byun et al 2013, Funk and Wolf 2016). In the context and conditions of this study, cereal

and brassica species were most capable of capturing resources and producing biomass rapidly, and thus had the greatest fitness advantage against weeds.

However, some studies of cover crop mixes have found an increased ability of diverse mixes to suppress weeds (Linares et al 2008, Döring et al 2012a), and several studies on plant invasions have found some evidence that functional group diversity increases resistance to invasion at scales comparable with this study, albeit less so than the fitness of dominant resident species (Richardson and Pyšek 2006, Byun et al 2013). It is possible that this effect of diversity would be seen in cover crops if all species included in a diverse mix are adequately competitive. This idea is supported by the findings of Wortmann et al (2012) and Smith et al (2014) that cover crop mixes typically have a Land Equivalent Ratio > 1, producing more biomass than can be accounted for by the productivity of each species grown in monoculture. Therefore, creating mixes containing only highly productive species may result in more effective weed suppression than a monoculture, whilst also increasing opportunities for cover crops to perform multiple functions through diversity. In this study both functionally diverse mixes contained at least two legume species, which produced substantially less biomass than the cereal and brassica species, and may therefore have negated any effect of diversity.

Previous trials on diverse cover crops and forage crops suggest that functional diversity in terms of phenology, rather than the spatial resource capture traits tested in this study, may be more important to weed suppression (Porqueddu et al 2008, Döring et al 2012b, Finn et al 2013). In this regard, it is the capacity of different species to capture resources and produce biomass at different points in the season (or in subsequent years in long-term leys) that results in greater overall weed suppression. This suggests that if limiting similarity does occur between crops and weeds, it may also be a largely phenological phenomenon, and that crops and weeds with high simultaneous resource demands may be most likely to compete with one another.

4.2 Differences between cover crop types

The cereal species included in this study were found to suppress weeds more effectively than the legume species (the brassicas and 'other' species were included in too few treatments to draw conclusions on their overall competitiveness). A key mechanism that appeared to give cereal cover crops a fitness advantage over weeds was rapid nitrogen, moisture and light capture early in the season, followed by restricting light availability to weeds later in the season. However, the availability of these resources could only explain approximately 20% of the variation in weed biomass between mixes (with a further 50% in variation linked to site and year effects), suggesting that competition for other resources, or allelopathy, may also have played a role in causing the remaining variation. There is evidence from other studies that several of the cover crop species included in this trial, particularly the cereals, are allelopathic (Jabran et al 2015, Rueda-Ayala et al 2015). Thus, it is plausible that cover crops suppressed weeds through both allelopathy and competition for resources. It is also possible that legumes confounded the suppressive effects of cereals through a facilitative effect on weeds: although most nitrogen fixed by legumes becomes available in the following season as their residues decompose, some nitrogen can be transferred from legumes to other plants within the first growing season (Pirhofer-Walzl et al 2012). However, given the overall low biomass produced by legumes, it is expected that any facilitative effect would be small.

The faster resource uptake and greater weed suppression of cereals compared with legumes was linked to differences in biomass production. This may be explained by life-strategy differences between these two crop types, with cereals appearing to have a 'faster' life strategy (Reich 2014) than legumes, which may have been enhanced by breeding for yield and competitiveness. Typically, plant species with a faster growth rate invest fewer resources in resilience to stress and disturbance, and thus would be capable of using those resources to produce more biomass to further enhance resource uptake (Garnier and Navas 2012, Reich 2014). Legumes may be constrained in their growth relative to cereals due to the need to direct sugars to feed their rhizobial mutualists and by investment in mechanisms that allow them to recover from grazing, as many of the legume species included in this trial were forage species.

However, a study by Tribouillois et al (2015) on cover crop traits found no evidence to suggest that cereals inherently grow faster or capture more nitrogen than legume crops in conditions of non-limiting resources. This suggests that the conditions in this study may have disadvantaged legumes compared with cereals, brassicas and weeds. Sowing depth may have been a constraint: in this trial the disc planter placed the seeds at approximately 15 mm below the soil surface, which is considered shallow for cereals but deep for legumes, apart from the largerseeded legumes (vetch and pea), which typically performed better. The weather conditions during the trial may also have played a role, with the first rainfall arriving later into winter in both years than is usual for the region. Legume varieties used in the region may not have been bred to tolerate such low soil temperatures when sufficient moisture becomes available for germination and establishment. Thus, we would not conclude from this study that cereal cover crops would always outperform legumes in competition against weeds.

4.3 Weeds and resource availability

That we were able to predict a substantial proportion of variation in weed biomass based on resource availability confirms the need to consider resource uptake capacity when choosing which species to include in a mix. In this regard, a cover crop's capacity to produce biomass is an important trait of interest, as shown in this study and confirmed by other trials of weed suppression by cover crops (Palmer and Maurer 1997, Brennan and Smith 2005, Storkey et al 2011, Brust et al 2014, Smith et al 2014, Finney et al 2016). The timing of that productivity may also be important (Döring et al 2012b, Finn et al 2013), but was not investigated in this trial. Our results also indicate that the functional type of the cover crop may play an additional role to biomass production, given that both cover biomass and cereal proportion were associated with reduced weed biomass. This suggests that different types of crops capture more resources per unit biomass, which is supported by our finding that a higher proportion of cereal cover crops was linked to a decrease in nitrogen, but total cover crop biomass was not (Table 4). It is also possible that certain crop types increase their competitiveness through other tactics such as allelopathy.

The weed response to resource availability observed in this study also has implications for other farm management practices beyond cover cropping, suggesting that resource availability to weeds should be considered and reduced wherever possible. The finding is also relevant to breeding of both cover crops and cash crops: rapid early growth and resource capture may be the best defence against weed competition throughout the season.

4.4 Cover crops, weeds, and cash crop yield in the following year

This study suggested a weak link between cover crop performance in weed suppression and subsequent cash crop yield, mediated by reduced weed cover following productive cover crops (hypothesis E). That a stronger effect on yield was not observed may have been partially related to several of the most weed-suppressive cover crop species (the cereals) returning as volunteer weeds in the subsequent cash crop, thus countering their contribution to weed suppression. Cover crop mixes present a challenge for non-chemical termination, as the roller-crimper technique is only effective in a short time window when cover crop plants are mature enough to be vulnerable, but have not yet set seed, and this time window may not overlap between all species in a mix. This effect may have allowed the cereals in this trial to either produce viable seed before termination, or recover to set seed afterwards.

There are also other characteristics of cover crops that contribute to subsequent cash crop yields aside from weed suppression (Snapp et al 2005, Blanco-Canqui et al 2015, Wittwer et al 2017). The addition of nitrogen to the soil by legumes is an important factor (Bedoussac et al 2015), and thus what the legume mixes lacked in weed suppressive capacity they may have made up for by providing nitrogen, or by reducing pathogen survival. Although soil nitrogen content at the start of the cash crop season was not associated with cash crop yield, further nitrogen may have been released to the cash crop from legume residues throughout the season.

4.5 Implications for design of cover crop mixes

The results of this study indicate that the recent enthusiasm for diverse cover crop mixes should be tempered with a focus on including sufficient quantities of species that are known to perform key functions effectively. In this regard, our results agree with those of Storkey et al (2015) who found that cover crop mixes best achieve their desired functions when species are included that each perform a specific function well. Finney et al (2016) suggest that biomass-driven functions of cover crops, such as weed suppression, are best achieved by selecting the most productive species rather than basing mixes on functional complementarity.

A diverse cover crop mix can offer advantages to farmers in terms of their capacity to perform multiple functions, such as building soil organic matter, fixing nitrogen, and supporting beneficial insects (Malézieux et al 2009, Isbell et al 2017, Finney et al 2017). Therefore, rather than avoiding diversity for the sake of weed suppression, we recommend that multi-species mixes are composed with a strong emphasis on the competitive ability of each species included in the mix. This will ensure that diverse cover crop mixes planted for the purpose of providing multiple functions can also adequately suppress weeds. It is important that cover crop mixes recommended to farmers do not promote weeds, and thus risk discouraging farmers from using cover crops, given the advances in agricultural sustainability offered by cover crops (Anderson 2015, Wittwer et al 17). Future research on improving cover crop mixes for weed suppression could therefore focus on the identification of highly productive (and therefore weed-suppressive) cover crop species and cultivars from a variety of plant families that could be combined in multispecies mixes that are appropriate to the farming systems in question. For example, our finding that cereals and perhaps brassicas are the most effective weed-suppressing cover crops in the Swartland and southern Cape of South Africa is not the most practical recommendation for the region's farmers, whose main cash crops are wheat, barley and canola. Closely related cover crop species run the risk of bridging pests and pathogens between cash crop years (Krupinksy et al 2002), and avoiding legumes leaves farmers burdened with the environmental and economic costs of synthetic nitrogen fertiliser (Bedoussac et al 2015). Research on identifying and

developing new cover crops is ongoing in central Europe (eg. Brust et al 2014, ThorupKristensen and Rasmussen 2015), but similar efforts will be needed in other regions to develop cover crops that suit the different climates, soils and farming systems around the world.

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Author contributions

CM designed the study with contributions all authors. CM undertook the data collection and analysis with advice and assistance from PS, and CM drafted the article. All authors contributed to critically revising and improving the article.

Conflicts of interest: none.

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FIGURES AND TABLES

Figure 1: The location of Langgewens and Tygerhoek Research Farms in South Africa.
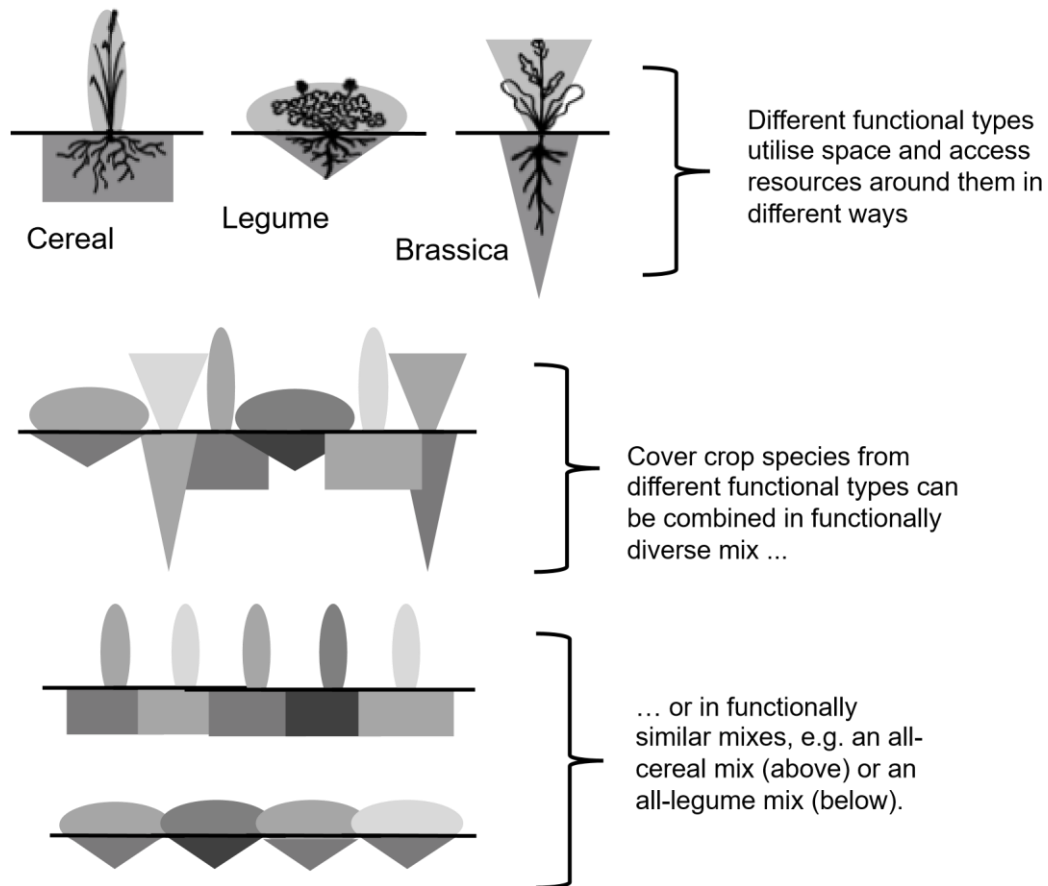
Figure 2: An illustration of the functional types used in this study, and the expected effects of functionally diverse or similar multi-species mixes on spatial resource capture. The shapes in the diagram represent the space occupied by the foliage and root systems of each functional type: cereals tend to be upright (represented by a tall oval) with a spreading fibrous root system (rectangle), while legumes tend to be prostrate (short oval) with many adventitious roots (shallow triangle), while brassicas are tall and spreading (triangle) with a deep taproot (deep triangle). The different shades represent that mixes can be composed of different species within the same functional type (e.g. a cereal mix could contain rye, barley, oats and triticale; Table 1).
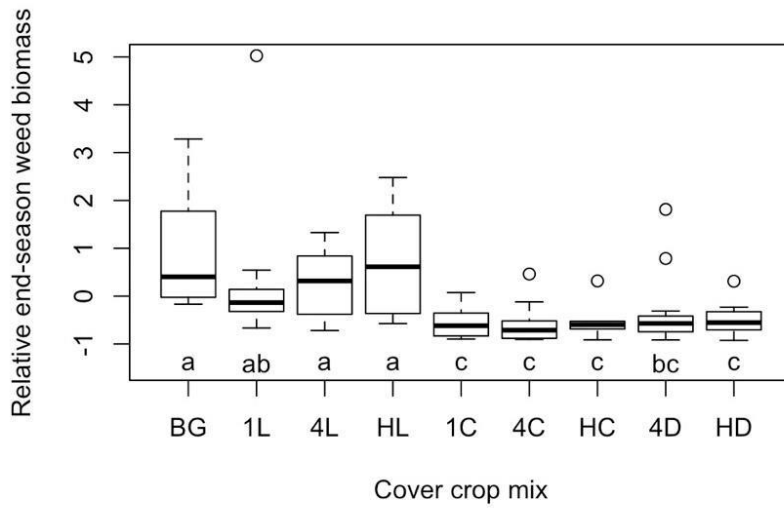
Figure 3: Boxplot of the relative final weed biomass in each of the cover crop mixes. Letters at the base of the plot indicate pairwise differences: mixes that are different from one another do not share a letter. Cover crop mix acronyms refer to the treatments described in Table 1.
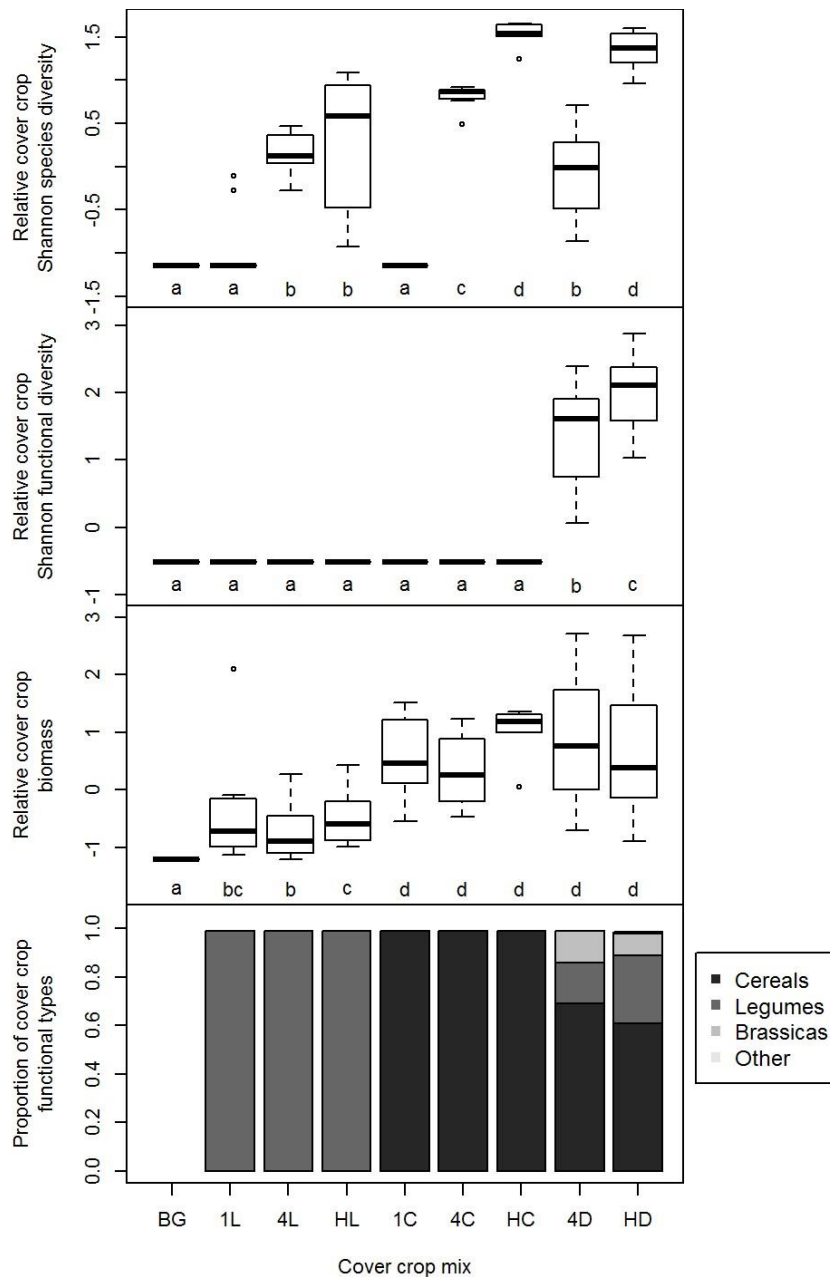
Figure 4: Relative Shannon species diversity, Shannon functional diversity, biomass and proportional functional composition of biomass in different cover crop mixes at the end of the season. Cover crop mix acronyms refer to the treatments described in Table 1. In the top three panels, letters at the base of the plots indicate pairwise differences: mixes that are different from one another do not share a letter. The bottom panel shows the mean proportion of each cover crop functional type in the different mixes. All cereal mixes contained only cereals and all legume mixes contained only legumes. Plots sown with the 4D mix contained a mean cereal proportion of 0.69 (standard error, S.E. = 0.05), a mean legume proportion of 0.17 (S.E. = 0.06), and a mean brassica proportion of 0.13 (S.E. = 0.04). Plots sown with the HD mix contained a mean of 0.61 cereals (S.E. = 0.04), 0.28 legumes (S.E. = 0.04), 0.1 brassicas (S.E. = 0.02), and 0.008

'others' (S.E. = 0.004; chicory or flax). This small proportion of 'others' is barely visible at the top of the HD bar.
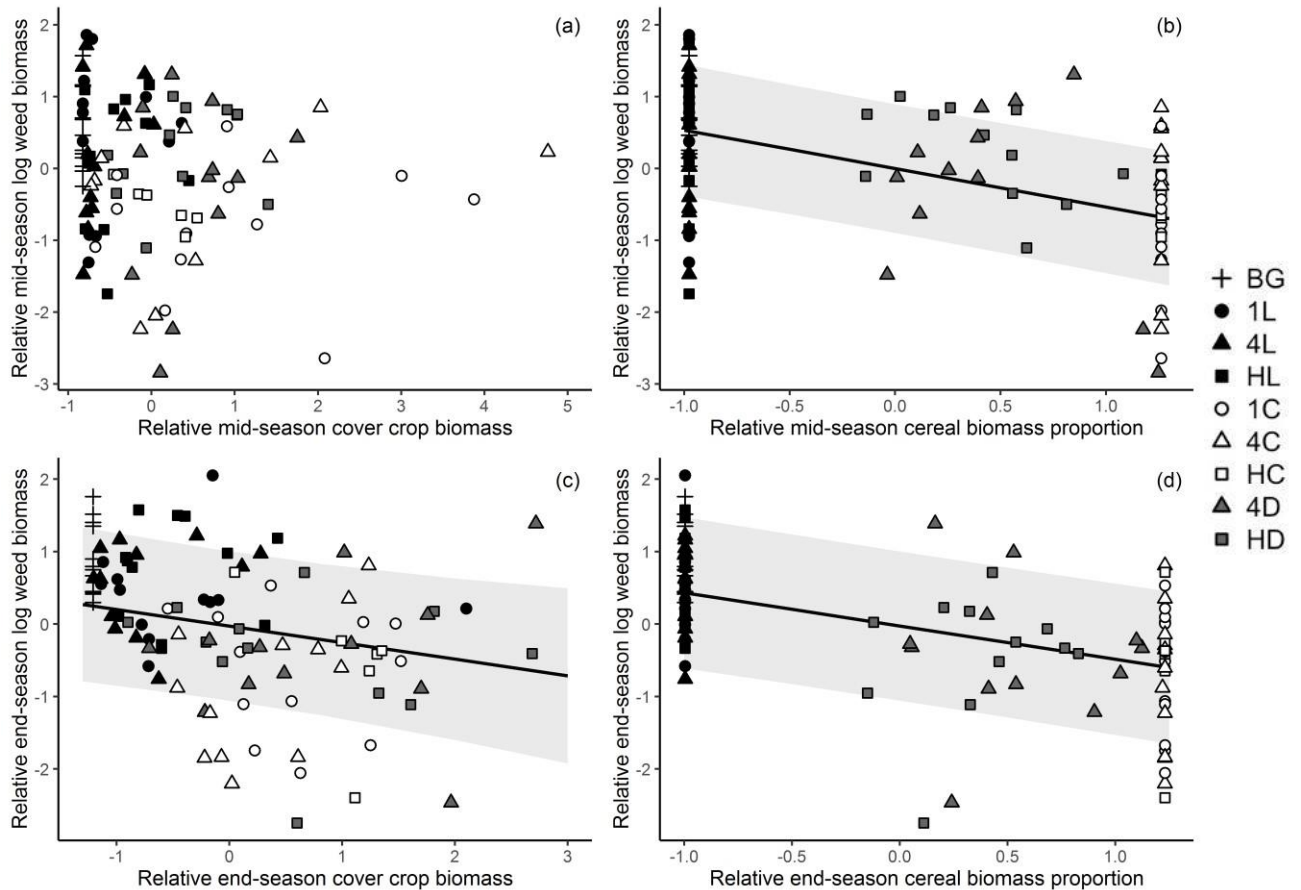
Figure 5: Relationships between cover crop biomass, cereal biomass proportion and weed biomass (Table 3) at mid-season (a and b) and the end of the season (c and d). Cover crop acronyms in the legend refer to mixes described in Table 1. The points indicate each plot in the experiment. The black lines show the predicted weed biomass across the range of the cover crop predictor variable from the models presented in Table 3 (with all other variables in the model held constant) and the grey ribbons indicate the 95% confidence interval of these values. No line or ribbon is shown in panel (a) as the model did not identify any significant relationship (Table 3).
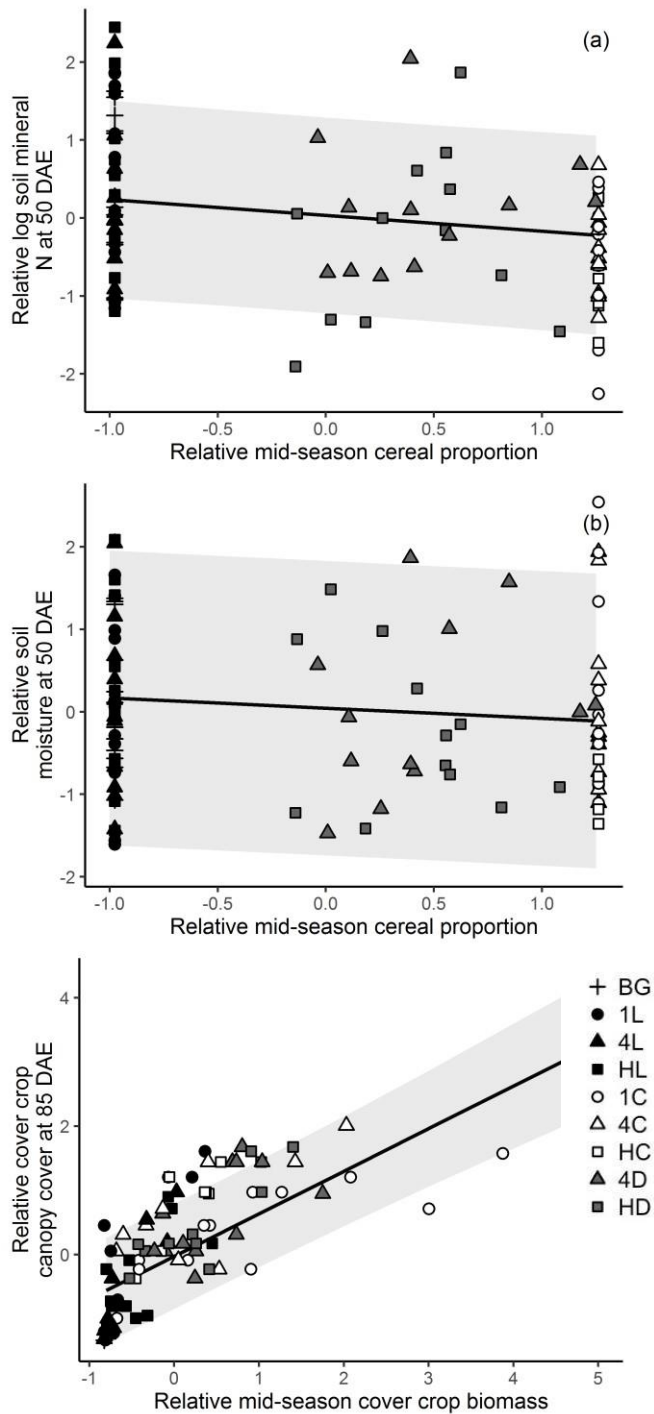
Figure 6: Relationships between cover crop biomass and resource capture: (a) mid-season cereal proportion and log soil nitrogen at 50 DAE, (b) mid-season biomass and moisture at 50 DAE, and (c) mid-season biomass and canopy cover at 85 DAE. Cover crop acronyms in the legend refer to mixes described in Table 1. The points indicate each plot in the experiment, while the black lines show the predicted resource level across the range of the cover crop predictor variable from the models presented in Table 4 (with all other variables in the model held constant). The grey ribbons indicate the 95% confidence interval of these values.
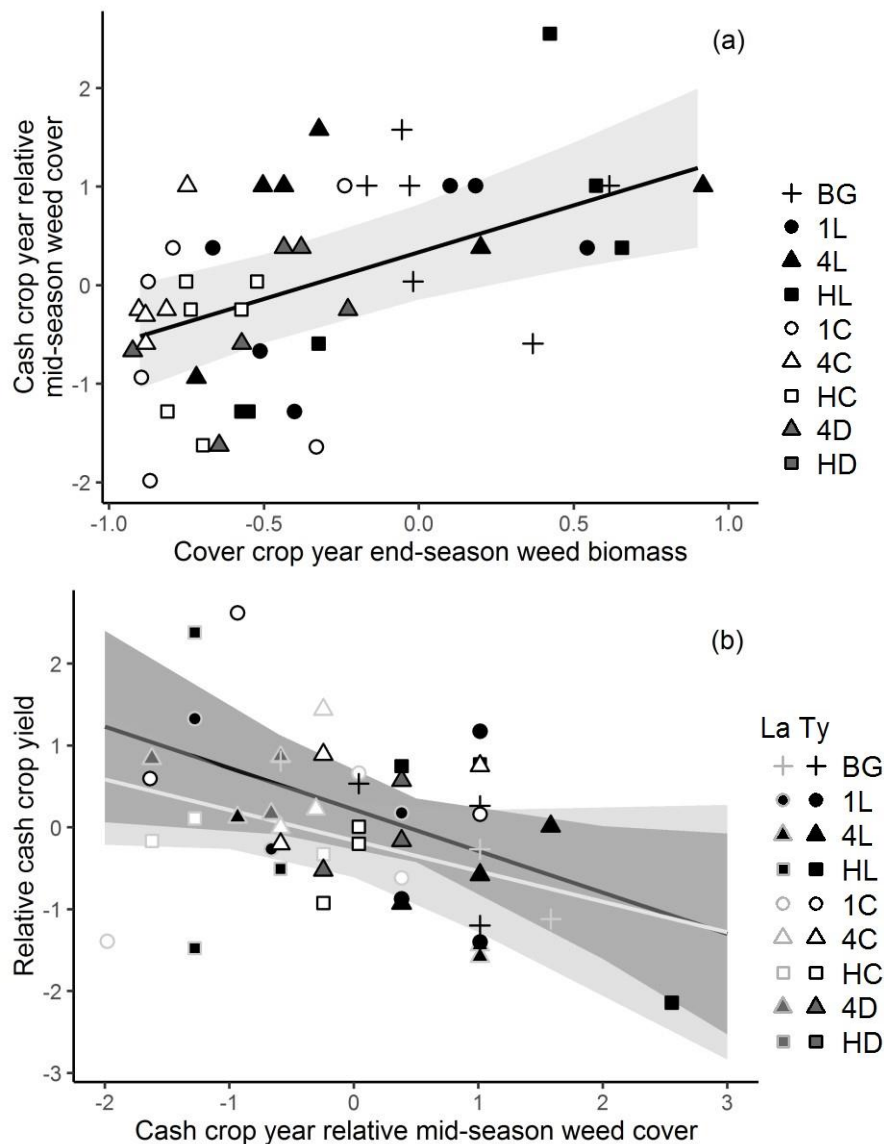
Figure 7: Weed biomass in the cover crop year affects mid-season weed cover in the cash crop year (a) and mid-season weed cover in the cash crop year affects wheat yield (b). The points indicate each plot in the experiment, and the lines and ribbons indicate the predicted response from the models presented in Tables 7 and 8 and their 95% confidence intervals respectively. In panel (b), observations and model results from different farms are plotted in different shades due to the cash crop being wheat (grain yield) at Langgewens (pale grey ribbon) and forage oats (biomass yield) at Tygerhoek (dark grey ribbon), which may have affected the relationship between weeds and yield. Cover crop acronyms in the legend refer to mixes described in Table 1, and the two farms are indicated by abbreviations: Ty = Tygerhoek and La = Langgewens.

Table 1: cover crop species included in each of the mixes containing either one or four species, and their sowing rates in kg ha^{-1} (indicated in italics). Refer to Table 2 for species names,

cultivars and functional types (NB. Sub. clover = Subterranean clover). Mixes were the same on both farms in each year, but differed between years (see main text). Mix names refer to the number of species (1 or 4), and to their functional composition, C = cereal, L = legume, and D = diverse (cereals, legumes and brassicas).

Single species and four species mixes

	1C	1L	4C	4L	4D
Year 1 (2016)	Triticale *(140)*	Barrel medic *(10)*	Triticale *(35)* Rye *(12.5)* Barley *(15)* Oats *(25)*	Barrel medic *(2.5)* Burr medic *(3.75)* Persian clover *(1.5)* Sub. clover *(3)*	Barrel medic *(2.5)* White mustard *(2.5)* Sub. clover *(3)* Triticale *(35)*
Year 2 (2017)	Triticale *(140)*	Burr medic *(15)*	Triticale *(35)* Oats *(25)* Barley *(15)* Rye *(12.5)*	Burr medic *(3.75)* Barrel medic *(2.5)* Field peas *(30)* Woolly vetch *(7.5)*	Burr medic *(3.75)* White mustard *(2.5)* Sub. clover *(3)* Triticale *(35)*

High species diversity mixes

	HC	HL	HD
Year 1 (2016)	*Treatment not included in 2016: insufficient cereal species available*	Burr medic *(1.25)* Barrel medic *(0.8)* Serradella *(3.6)* Berseem clover *(0.8)* Crimson clover *(1)* Balansa clover *(0.6)* Red clover *(0.8)* White clover *(0.8)* Persian clover *(0.5)* Sub. clover *(1)* Arrowleaf clover *(1.6)* Woolly vetch *(2.1)*	Oats *(8.25)* Chicory *(0.6)* Barley *(5)* Lupin *(5.8)* Barrel medic *(0.8)* Field peas *(10)* Forage radish *(0.8)* White mustard *(0.8)* Crimson clover *(1)* Sub. clover *(1)* Triticale *(11.7)* Woolly vetch *(2.1)*
Year 2 (2017)	Red oats *(10)* Oats *(12.5)* Saia oats *(12.5)* Barley *(7.5)* Rye, spring *(6.25)* Rye, stooling *(7.5)* Triticale *(17.5)*	Burr medic *(1.85)* Barrel medic *(1.25)* Field peas *(15)* Berseem clover *(1.25)* Crimson clover *(1.25)* Sub. clover *(2.25)* Common vetch *(3.75)*	Oats *(12.5)* Flax *(6.5)* Burr medic *(1.85)* Field peas *(15)* Forage radish *(1.25)* White mustard *(1.25)* Triticale *(7.5)*

Table 2: The species names, cultivars and functional type of all cover crops used in this study.

Cover crop	Species name	Variety	Functional type
Arrowleaf clover	*Trifolium vesiculsum*	Zulu	Legume
Balansa clover	*Trifolium michelianum*	Taipan	Legume
Barley	*Hordeum vulgare*	Moby	Cereal
Barrel medic	*Medicago truncatula*	Paraggio	Legume
Berseem clover	*Trifolium alexandrinum*	Elite	Legume
Burr medic	*Medicago polymorpha*	Santiago	Legume
Chicory	*Cichorium intybus*	Commander	Other
Common vetch	*Vicia sativa*	Timok	Legume
Crimson clover	*Trifolium incarnatum*	Blaza	Legume
Field peas	*Pisum sativa*	Arvika	Legume
Flax	*Linum ussitatissimum*	(unknown)	Other
Forage oats	*Avena sativa*	Outback	Cereal
Forage radish	*Raphanus sativa*	Maximus	Brassica
Lupins	*Lupinus angustifolius*	Bitter lupin	Legume
Persian clover	*Trifolium resupinatum*	Lightning	Legume
Red clover	*Trifolium pratense*	Barduro	Legume
Red oats	*Avena byzantina*	Red dawn	Cereal
Saia oats	*Avena strigosa*	Barsaia	Cereal
Serradella	*Ornithopus sativa*	Emena	Legume
Spring rye	*Cereale secale*	Arrow	Cereal
Stooling rye	*Cereale secale*	Barpower	Cereal
Subterranean clover	*Trifolium subterraneum*	Woogenellup	Legume
Triticale	*x Triticosecale*	Usgen 19	Cereal
Wheat	*Triticum aestivum*	SST 056	Cereal
White clover	*Trifolium repens*	Kotare	Legume
White mustard	*Sinapis alba*	Sito	Brassica
Woolly vetch	*Vicia villosa*	Haymaker	Legume

Table 3: Model estimates and statistical significance of the effects of different cover crop characteristics on log weed biomass. The relationships of weed biomass with cover crop biomass and with cereal biomass proportion are illustrated in Figure 5.

	Weed biomass dry weight kg ha^{-1} (log)					
	Mid-season		**Mid to end-season increase**		**End-season**	
Cover crop characteristics†	*Estimate*	*P-value*	*Estimate*	*P-value*	*Estimate*	*P-value*
Biomass	0.17	0.089	-0.15	0.105	-0.23	0.033*
Species diversity	0.05	0.583	-0.15	0.096	-0.09	0.251
Functional diversity	0.09	0.357	-0.08	0.370	0.02	0.832
Cereal biomass proportion	-0.54	<0.001*	0.38	<0.001*	-0.46	<0.001*
Marginal (conditional) R^2	*0.16 (0.51)*		*0.27 (0.54)*		*0.33 (0.68)*	

*Significant at the 0.05 probability level.

†Mid-season weed biomass and weed biomass increase are modelled on mid-season cover crop characteristics, while end-season weed biomass is modelled on end-season cover crop characteristics.

Table 4: Model estimates and statistical significance of the effects of cover crop biomass and cereal biomass proportion on soil nitrogen and moisture, and cover crop canopy cover (an indicator of light availability).

	Resource at 50 DAE†		Resource at 85 DAE†		Resource at 110 DAE†	
	Estimate	*P-value*	*Estimate*	*P-value*	*Estimate*	*P-value*
Nitrogen						
Cover crop biomass	-0.09	0.279	-0.10	0.083	0.03	0.605
Cereal biomass proportion	-0.26	0.003*	0.127	0.033*	-0.04	0.342
Marginal (conditional) R²	*0.07 (0.66)*		*<0.01 (0.87)*		*<0.01 (0.94)*	
Moisture						
Cover crop biomass	0.18	<0.001*	0.05	0.166	-0.07	0.070
Cereal biomass proportion	-0.12	0.005*	0.01	0.717	0.08	0.011*
Marginal (conditional) R²	*0.01 (0.93)*		*<0.01 (0.95)*		*<0.01 (0.97)*	
Cover crop canopy cover						
Cover crop biomass	0.55	<0.001*	0.66	<0.001*	0.64	<0.001*
Cereal biomass proportion	-0.03	0.620	0.14	0.036*	0.11	0.231
Marginal (conditional) R²	*0.18 (0.79)*		*0.47 (0.75)*		*0.44 (0.59)*	

*Significant at the 0.05 probability level.
†For the models at 50 DAE and 85 DAE use mid-season cover crop characteristics, and the model at 100 DAE uses end-season cover crop characteristics.

Table 5: Model estimates and statistical significance of the effect of resource availability at 50 DAE on the increase in weed biomass between the middle and end of the season.

	Effect on mid-season weed biomass	
Resources at 50 DAE	*Estimate*	*P-value*
Soil mineral nitrogen	0.28	0.006*
Soil moisture	-0.22	0.088
Cover crop canopy cover	-0.55	<0.001*
Marginal (conditional) R²	*0.21 (0.70)*	

*Significant at the 0.05 probability level.

Table 6: The weed species found, their functional type (see end of Section 2.2), and their average proportional biomass across all plots in the trial. Functional types are G = grass, SH = short, prostrate or rosette-forming herb, TH = tall upright herb. Some species are volunteers from the main crops grown on the research farms (wheat, canola, forage legumes). Both *Lolium* and *Conyza* species hybridise within their genus and were not identified to species level.

Species	Functional type	Average proportional biomass
Anagallis arvensis	SH	<0.01
Avena fatua	G	0.03
Bromus catharticus	G	<0.01
Bromus diandrus	G	0.04
Brassica napus	TH	0.03
Chenopodium album	TH	<0.01
Conyza spp.	TH	<0.01
Erodium moschatum	SH	<0.01
Euphorbia inaequilatera	SH	<0.01
Fumaria officinalis	SH	<0.01
Helminotheca echioides	SH	<0.01
Hypochaeris radicata	SH	<0.01
Lactuca serriola	SH	<0.01
Lepidium africanum	TH	<0.01
Lolium spp.	G	0.67
Malva parviflora	TH	<0.01
Medicago lupulina	SH	0.01
Medicago polymorpha	SH	0.01
Medicago truncatula	SH	<0.01
Plantago lanceolata	SH	<0.01
Polygonum aviculare	SH	<0.01
Pseudognaphalium luteoalbum	TH	<0.01
Raphanus raphanistrum	TH	<0.01
Rumex acetosella	SH	<0.01
Sonchus oleraceus	SH	0.02
Taraxacum officinalis	SH	<0.01
Triticum aestivum	G	0.12
Trifolium repens	SH	<0.01
Vicia sativa	SH	<0.01

Unknown species (8 morphotypes)	<0.01		

Table 7: Model estimates and statistical significance of the effects of end-season weed biomass, cover crop biomass and cover crop cereal proportion on mid-season weed cover in the cash crop year. Each of these variables were analysed in separate models due to collinearity among them, with each variable comprising a single fixed effect alongside the random effects of farm and year.

Model:	Estimate	P-value	Marginal (conditional) R^2
End-season weed biomass in cover crop year	0.94	0.001*	0.22 (0.29)
End season cover crop biomass	-0.67	<0.001*	0.21 (0.40)
End-season cover crop cereal proportion	-0.39	0.002*	0.13 (0.42)

*Significant at the 0.05 probability level.

Table 8: Model estimates and statistical significance of mid-season weed cover on cash crop yield, from separate regression models for each farm (as this data comprised a single year, simple regression rather than mixed effects models were used).

Model:	Estimate	P-value	Marginal (conditional) R^2
Effect on forage oat biomass yield of weed cover at Tygerhoek	0.94	0.001*	0.22 (0.29)
Effect on wheat grain yield of weed cover at Langgewens	-0.67	<0.001*	0.21 (0.40)

*Significant at the 0.05 probability level.