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RESEARCH ARTICLE



Weed–crop competition under improved nutrient management reveals trade-off between yields and weed diversity in organic farming

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ABSTRACT

In the pursuit of more sustainable agriculture, weeds play a dual role by threatening crop production and simultaneously contributing to farmland biodiversity. Management actions such as the use of fertilisers (fertilisation) may change weed abundance and community composition with consequences for both weed–crop competition and biodiversity. Alleviating the balance between yield and biodiversity requires a mechanistic understanding of how fertilisation impacts weed diversity and functional community composition. To investigate this, an experiment was conducted in an organic spring wheat field in Sweden, using a split-plot randomised complete block design with crossed fertilisation and weeding treatments. The experimental design took advantage of existing variation in soil conditions, resulting in different concentrations of available nitrogen in the soil supply. With increased fertilisation and soil nitrogen supply, crop yield increased, whereas weed evenness decreased. Additionally, average weed seed mass, specific leaf area and nectar production of the weed community decreased with higher soil nitrogen supply, whilst the relevance of the weed communities for biodiversity increased. Importantly, the results showed that weed-induced yield loss depended on the fertilisation rate and soil nitrogen supply. This suggested that development of sustainable weed management should not only focus on minimising weed abundance but also on identifying nutrient management regimes that minimise the trade-offs between yield, competition, and biodiversity.

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Introduction

Agricultural intensification has been, and still is, one of the main threats to biodiversity (Emmerson et al. 2016; Carmona et al. 2020), jeopardising the functions and resilience of arable ecosystems (Cabell and Oelofse 2012). Farmland biodiversity has declined because of intensive management, including the use of pesticides and synthetic fertilisers (Robinson and Sutherland 2002; Geiger et al.

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2010), and landscape simplification, including reduced landscape diversity and loss of natural and semi-natural habitats (Robinson and Sutherland 2002; Donald et al. 2006; Carvalheiro et al. 2013). Consequently, farmland biodiversity loss can be mitigated by restoring diverse agricultural landscapes (Fahrig et al. 2011; Jeanneret et al. 2021) and by alternative farming practices such as using organic management (Tuck et al. 2014; Albrecht et al. 2016; Stein-Bachinger et al. 2021). Arable fields are an important habitat for several wild plant species (referred to as weeds), which can play an important ecological role as they support biodiversity at higher trophic levels, for example, insects and birds (e.g. Marshall et al. 2003; Blaix et al. 2018; Smith et al. 2020). At the same time, weeds can be viewed as a threat to agricultural production, since they compete with the crop for essential resources such as nutrients, light, and water. This competition can ultimately cause reduced quantity and quality of yields (Oerke 2006; Little et al. 2021). The apparent trade-off underscores the need to find management regimes that balance the positive and negative aspects of weeds.

Farming practices can alter the competitive dynamics between plants if they favour or disfavour certain species more than others. For example, fertilisation may promote weed growth because many weed species are efficient nitrogen users (i.e. have a high ability to translate increased N into biomass). The yield gain from fertilising can then be limited due to increased weed competitiveness, especially if weed control is insufficient (MacLaren et al. 2020). The competitive effect of the plant is related to certain functional traits, including the ability to grow fast and efficient capture of nutrients and water from the soil (Gaba et al. 2017). As an example, plants that grow taller or have larger leaves have a comparably higher light capturing ability and can shade other species (Gaba et al. 2017). However, management favouring weeds that are efficient nutrient users, or nitrophilic, will also increase weed–weed competition, which may lead to shifts in the community composition with losses of rare and oligotrophic weed species (Storkey et al. 2010; Rotches-Ribalta et al. 2015). Inadvertent selection for more competitive weeds would be particularly unfortunate in situations where efficient control measures are lacking, for example, in the face of herbicide resistance or under certification schemes that restrict herbicide use, such as organic farming.

Nutrient availability and efficient weed control are the main limitations to high yields of many organically grown crops (Alvarez 2022). Beyond addition of nutrients through regular fertilisation, effective nutrient management in organic farming also relies on maintaining high soil fertility. Soil nutrient supply is determined by the physical, chemical and biological properties of the soil and may vary greatly even within fields. This variation calls for adaptation of fertilisation regimes to the soil nutrient supply, for efficient and sustainable nutrient management (Diacono et al. 2013). Furthermore, the mineralisation of nutrients from the soil has both short- and long-term effects (Zhang et al. 2022). High amounts of nutrients, particularly nitrogen, can therefore be available before the establishment of the crop or when crop requirements are low. The long-term effects are especially notable after termination of perennial leys (Kayser et al. 2010). Fertilisation typically has a more short-term immediate effect and can be applied according to crop requirements. This is especially true when using biogas digestate and other amendments with high content of mineral nitrogen (Nkoa 2014). Therefore, fertilisers and soil nutrient supply may impact the weed–crop competitive dynamics differently and their interactive effects remain understudied. Furthermore, weed–crop competition studies in naturally occurring multi-species weed communities in real production contexts are uncommon (Little et al. 2021), but see Adeux et al. (2019). Many weed–crop competition experiments have also not considered consequences on weed diversity and provision of ecosystem services. To fill these knowledge gaps, a field experiment was designed in an organic spring wheat (*Triticum aestivum* L.) field. First, the study aimed to increase the understanding of the impact of nutrient availability and fertilisation on weed abundance and community composition and ensuing consequences on weed–crop competition. Second, the resulting weed communities were assessed in terms of potential for biodiversity conservation and ecosystem services along the same gradients in nutrient conditions. A novel experimental approach was used, where organic crop fertilisation and weed pressure were manipulated while accounting for

natural variations in soil nitrogen supply and weed community structure to understand the ecological mechanisms behind weed–crop competition.

Materials and methods

Experimental design

The study was conducted in 2022 in a 7 ha organic spring wheat field located in the agricultural plain of the Västergötland region, Sweden (58°21'56'N, 13°17'34'E). The area has mean annual precipitation and temperature of around 584 mm and 7.3°C, respectively (long-term average at the nearby Lanna research station; Swedish Meteorological and Hydrological Institute 2023), with Cambisol soils. The consequences of two different experimental factors on crop yield and weed communities were investigated. The first factor was different application rates of biogas digestate fertiliser and the second factor was hand weeding (either leaving or removing all weeds). A split-plot randomised complete block design was used (Altman and Krzywinski 2015) in a chessboard setup, with a grid pattern of 96 blocks (16 × 16 m) each containing the four different rates of fertilisation (Supplemental Figure S1). Within this chessboard design, 10 blocks were randomly selected for this specific study, such that adjacent blocks were not chosen, to ensure that distances between selected blocks were always larger than relevant treatment distances within blocks. Within these main fertilisation plots in the 10 blocks, two sub-plots (1 × 1 m) were placed 75 cm from the block edge and randomly subjected to weeding or to be left undisturbed. The experimental field had a natural variation in soil conditions, resulting in different amounts of nitrogen made available to plants through mineralisation before and during the growing season. This gradient of soil nitrogen supply between blocks was utilised, in addition to the fertilisation treatment, to evaluate the separate and interactive effects of background nitrogen levels in the soil and fertilisation on weed–crop competition. The plots where the weed community was left untouched were in addition used to determine the effect of fertilisation and soil nitrogen supply on weed diversity and weed functional trait composition.

Field and experimental management

The field had been certified organic since 2004, in accordance with the national KRAV regulations (KRAV 2022; Uppsala, Sweden), and by extension also the EU regulation (EU 2018/848; EU 2018) for organic farming. The crop sequence was dominated by grass-clover ley and cereals. The preceding crop was a 5-year-old grass-clover ley that was cut once during 2021, in mid-July, and the biomass was removed. In previous years, the ley was typically harvested twice per annum. In late August 2021, the ley was cultivated, terminated and incorporated by ploughing followed by harrowing in the spring for seedbed preparation. No fertiliser was added during the ley period, but approximately 25 kg K ha⁻¹, in the form of kalimagnesia, was evenly added before harrowing and sowing of the spring wheat. The spring wheat (*Triticum aestivum* L.), cultivar Quarna, was sown on 25 April 2022 with a density of 230 kg ha⁻¹, and the chessboard trial was established at the time of fertilisation (19 May). No mechanical weeding was performed after sowing, except for the hand weeding treatment included in the experimental design. After a very rainy autumn in 2021 that did not allow for the planned winter wheat crop, the weather during the growing season in 2022 was favourable for spring wheat growth, with timely rains and no extreme temperatures (Supplemental Figure S2).

The fertiliser treatment consisted of four rates of biogas digestate fertilisation: 1) a control treatment with no fertiliser added (0 kg N ha⁻¹), 2) a low fertilisation treatment (50 kg N ha⁻¹), 3) a medium fertilisation treatment (100 kg N ha⁻¹), and 4) a high fertilisation treatment (150 kg N ha⁻¹). The assumption was that nitrogen was the most limiting nutrient to plant growth, which is typical in well managed fields. The fertiliser treatment levels were selected to include the common

rates that Swedish organic farmers use for biogas digestates (the lower levels), to match a nitrogen demand according to general recommendations for spring wheat with an expected yield level of about 4 t ha⁻¹ (the medium level), and to exceed the demand with the highest fertilisation level to be able to calculate optimal fertilisation rates. This meant that only the 50 kg N ha⁻¹ and, in some cases, the 100 kg N ha⁻¹ rate, would be expected to be economically relevant in practice. The biogas digestate was delivered by a local producer (Gasum AB, Lidköping) where the raw feedstock material used for the biogas production originated mainly from plant-based by-products from local food industries and this was certified for use in organic farming. The biogas digestate had a large portion of the nitrogen in an available form (6 kg N t⁻¹ of which 3.4 kg t⁻¹ was NH₄⁺ based on analysis of the biogas digestate used in this study, see Supplemental Table S1). The nitrogen levels in the fertilisation treatments were calculated based on the ammonium ion (NH₄⁺-N). The product had a low dry matter content (7.3 %) and was applied using a manure spreader equipped with trailing hoses.

The weeding treatment of the design was based on a complete removal of all weeds in half of the sub-plots, performed manually every second week from fertilisation (a month after sowing) to harvest. To avoid edge effects of weeds around the weeding treatment sub-plots, a buffer zone of 25 cm (two rows of wheat) was established, and this buffer zone was weeded every fourth week. The initial weed ground coverage, before the first weeding and start of the surveys, was affected by the fertilisation treatment because it formed a crust in between the rows that slightly delayed weed emergence in the highly fertilised sub-plots ($\chi^2 = 9.8$, df = 3, $p = 0.02$). The weed coverage of the highly fertilised sub-plots did, however, recover quickly and was at the start of surveys 2 weeks later, not different between the fertilisation rates ($\chi^2 = 6.4$, df = 3, $p = 0.10$). The initial weed coverage also increased with the soil nitrogen supply ($\chi^2 = 23.9$, df = 1, $p < 0.001$).

Field surveys and harvest

Crop and weed surveys were made every 2 weeks, with the first visit 3 weeks after fertilisation followed by five more visits (for details on dates and sampling see Supplemental Table S2) until harvest (17–19 August). To assess the competition between the crop and the weeds, and the species and trait composition of the weed community, the ground coverage of each species was estimated visually. Visual estimations were used to be able to easily, non-destructively and repeatedly sample the plots, and weed cover has been shown to well represent competition and weed communities (Lutman et al. 1996; Nkurunziza and Milberg 2007). The ground coverage of the crop, the weed community as a whole, as well as of each weed species separately were estimated to the nearest 5%. Species with a too low cover to be considered 5% coverage was instead assigned the value of 1%. Vertical overlap between species was handled by dividing it between the two species. A weed was defined as any plant species that was not spring wheat.

In addition, crop and weed height was estimated during late flowering stage of the wheat. Crop height was measured by placing a ruler in the middle of the sub-plot and reading the average height to the top of the crop's leaves. The weed height for each species in each sub-plot was assessed on a categorical scale based on how high it was in relation to the crop height, as either 1) overgrowing the crop: the majority of the weed plants of the species reached above the height of the crop; 2) growing with the crop: the majority of the weed plants of the species reached above one-third of the crop's height but not above the crop; or 3) growing below the crop: the majority of the plants of the species did not reach above one-third of the height of the crop. In addition to nutrients and weeds, diseases and pests may also influence yields and competitive relationships. These were therefore quantified by randomly selecting nine tillers in each sub-plot and counting: 1) the number of aphids on them (mainly *Sitobion avenae* recorded) and 2) the disease prevalence on the two top-most leaves of each tiller (singular rare occurrences of *Drechslera tritici-repentis*).

At harvest (17–19 August), the wheat spikes in each sub-plot were harvested by hand and brought to the laboratory to dry (at 55°C for 24 h). After drying, the samples were threshed and

weighed. The grain protein content was determined using near infrared transmittance (NIT) spectroscopy (FOSS Infratec1241 NIT equipment, Hillerød, Denmark). The soil nitrogen supply of each block was estimated from the full-scale chessboard experiment. The plots in the full-scale experiment (yellow area in Supplemental Figure S1) were managed in the same way as the experimental plots in this study and were harvested using a plot combine in 2 m wide and 6 m long net areas in the centre of each full-scale plot on 23 August. The nitrogen yield (grain yield times grain nitrogen concentration) of the unfertilised harvest plot within a block was used as a proxy for soil nitrogen supply for all the experimental sub-plots of the same block. Therefore, soil nitrogen supply was estimated using separate measurement than the yield and grain protein content investigated in the experiment.

Diversity and trait data

Weed diversity was analysed using two metrics: species richness, to draw conclusions on the number of species found, and Pielou's evenness index (see Mouillot and Leprêtre 1999 for more information), to describe the relative abundances of the different species within the communities. Pielou's evenness index was calculated from the Shannon diversity index (see Mouillot and Leprêtre 1999 for more information) using the relative abundance of each species based on the ground coverage. For analysis of shifts in the functional trait composition of the weed community, which may have important implications for competition, species-specific trait values were retrieved from the TRY plant trait database (Kattge et al. 2020; for contributing datasets see Supplemental Table S3). Focus was on the traits in the LHS spectrum, deemed important for competition (Westoby 1998), which includes vegetative height, specific leaf area and seed dry mass. These traits were chosen since they indicate important characteristics for competition, height being important for light interception, specific leaf area indicating the resource use of both nutrients and light, and seed dry mass being important for seedling success while reducing dispersal (Gaba et al. 2014). To assess the importance of the weed community for the conservation of weed-associated biodiversity, two indicators from Tyler et al. (2021) were used. The first was a logarithmic indicator of biodiversity relevance, reflecting how many other species rely on, or utilise, the plant as a food source, substrate, shelter or mutualistic partner. The second indicator was a nectar production indicator, which reflects the average nectar production per species per year, on a coarse logarithmic scale. The diversity, trait and indicator data were assessed on the total weed community, where the relative weed cover of each species was averaged over the entire season for each sub-plot. This was done to be able to draw general conclusions of the effects on the entire weed community present in the field. The diversity indices were calculated on this aggregated dataset, and the trait and indicators were summarised using community weighted means, weighted by the average relative cover of each species (BAT-package in R: Cardoso et al. 2022). The trait and indicators chosen were only weakly correlated with each other (Kendall correlations) based on the species level values (absolute correlations between 0.05 and 0.22; Supplemental Figure S3), but more strongly when summarised into the community weighted means (absolute correlations between 0.23 and 0.55; Supplemental Figure S3).

Statistical analyses

All statistical analyses and graphs in this study were specified and made in R (version 4.4.2, R Core Team 2024). The statistical models were linear mixed effect models to account for the split-plot randomised complete block design in the random structure. The statistical models were primarily run with Gaussian error distribution (lme4: Bates et al. 2015; lmerTest::; Kuznetsova et al. 2017) and when not appropriate according to model diagnostics, other options were considered. Fertilisation was treated as a factor in all analyses to allow for nonlinear relationships. Due to signs of non-linear relationships between soil

nitrogen supplies and some response variables, the soil nitrogen supply was tested both as log-transformed and non-transformed (linear) versions in all analyses. Transformations did not markedly change the results, so only the non-transformed results have been presented here. Checks of model assumptions were run, through residual diagnostics (DHARMA: Hartig 2022) and signs of multicollinearity issues (car: Fox and Weisberg 2019). Model statistics were extracted from the full statistical models (Anova, results with stepwise backward model selection can be found in Supplementary Table S4), and factor-level comparisons extracted with Tukey-adjustment for multiple testing (emmeans: Lenth 2023). Graphs show effects (effects: Fox and Weisberg 2019) and displays wald confidence intervals (95%), also including letters for factor-level comparisons (multcomp: Hothorn et al. 2008) and raw data points. An overview table of all the models with response variables, fixed and random effects, error distributions and which dataset was used can be found in Supplementary Table S5.

To understand how the weed competition effect on the crop is mediated by nutrient levels, analyses were performed to investigate how the crop (yield and grain protein) responded to weed removal, fertilisation and to the soil nitrogen supply. This also involved all potential two-way interactions and the three-way interaction. Diseases were nearly absent in the field, consequently disease prevalence was not considered in the analyses. Aphids were present, and aphid abundance was partially explained by fertilisation treatments and soil nitrogen. However, aphid abundance had no effect on yield or grain protein content when included in the models, nor did it generate multicollinearity issues, and analyses performed without aphid abundance as covariate yielded nearly identical results. The randomised complete block design was considered by the random intercept of both block and fertilisation within block (main-plot treatment). These statistical models performed well under normal (Gaussian) error distributions and all assumptions of normality and residual distribution, multicollinearity (variance inflation) and dispersion were fulfilled, except slight quantile deviations for the yield-models. In the analysis of yield, the variance of the random block–fertilisation interaction was slightly negative and set to zero. The variance explained by the random block–fertilisation interaction was generally very small also in the other analyses.

Further investigation of weed–crop competition was performed on only the weedy subset of the data, to analyse if also weed cover and height affected the crop and not just weed removal since complete weed removal is not a realistic scenario in organic farming. In these cases, blocks were considered as a random intercept. Yield was tested against fertilisation, soil nitrogen supply and their interactions with total weed cover. The interaction between fertilisation and the soil nitrogen supply was omitted due to the reduced sample size and as it was not identified as important in the previous analyses of yield. Similarly, crop height was tested using fertilisation, soil nitrogen supply and their interaction with the cover of tall weeds growing with or above the crop but not to each other due to the same limitation in sample size. Due to very few weeds overgrowing the crop (Supplemental Figure S4), in the statistical analyses the overgrowing weeds were pooled with the weeds growing with the crop. All assumptions checks (same as above) for these analyses were satisfactory.

Finally, the investigations explored if the weed community was affected by fertilisation, the soil nitrogen supply and/or a possible interaction between the two. These analyses concerned effects on total weed cover, species richness and evenness, as well as the community weighted trait and indicator data to understand functional implications. In these statistical models, the design was accounted for by block number as a random intercept. Analyses revealed that the statistical models of these weed community measures followed normal error distributions and could be approximated with such, except total weed ground cover which was analysed with beta regression (glmmTMB: Brooks et al. 2017). All model assumptions of normality and residual distribution, multicollinearity (variance inflation) and dispersion were fulfilled.

Results

Crop yield and weed–crop competition

Yield was affected by an interaction between weeding, fertilisation and the soil nitrogen supply, such that without fertilisation, the effect of weeding on yield depended on the soil nitrogen supply, with higher rate of gain in weed-free compared to weedy plots (slope comparisons in [Figure 1a](#), Supplemental Table S7). Weeding increased yield at low fertilisation rate, but not at medium and high rates, or in unfertilised sub-plots (as seen by the vertical separation of the lines in [Figure 1a](#); [Table 1](#)). Soil nitrogen supply related positively to yield in general ([Table 1](#)), with similar effects regardless of fertiliser rate in weedy plots, but in weed-free plots soil nitrogen had less effect on yield the more fertilisation that was applied (slope comparison in [Figure 1b](#), Supplemental Table S7). The grain protein content was, in absolute terms, 0.5 percentage points higher in the weeded treatment than in the control, on average ([Table 1](#), [Figure 2a](#)). Notably, fertilisation had greatest effect on protein content in conditions with high soil nitrogen supply ([Table 1](#), [Figure 2b](#)).

The height of the crop (at the end of crop flowering), using only data from the weedy plots, showed that the crop height was impacted by weed height, measured as the cover of weeds growing taller than a third of the crops' height ([Table 1](#), [Figure 3](#)). The increase was about 8 cm across the range of coverage of tall weeds (6% to 47% ground coverage). The ground cover of all weeds was related to an interaction between fertilisation and soil nitrogen supply where it increased with fertilisation at low levels of soil nitrogen supply and decreased with fertilisation at high levels of soil nitrogen supply ([Figure 4](#), [Table 2](#)). However, the weed ground cover did not relate to yields of weedy plots ([Table 1](#)).

Weed community shifts

In total 39 weed species were found across the growing season in the experiment. The most common species based on the ground cover was *Fallopia convolvulus* (L.) Á. Löve, *Chenopodium album* L., *Lamium purpureum* L., *Stellaria media* (L.) Vill. and *Fumaria officinalis* L. (Supplemental Figure S5 and for full species list see Supplemental Table S6). The species richness of the weed community was not influenced by fertilisation, soil nitrogen supply nor their interaction ([Table 2](#)). However, the weed community evenness related to fertiliser rate in a complex manner, being significantly lower at medium fertiliser rate (0.8) than at lower rates (0.75), whereas a high fertiliser rate was characterised by intermediate evenness ([Figure 5a](#), [Table 2](#)). Weed community evenness also decreased with increasing soil nitrogen supply ([Figure 5b](#), [Table 2](#)). Within the weed community, a relative increase in coverage of *Fallopia convolvulus* could be seen with increased fertilisation (Supplemental Figure S5a), and a relative increased cover of *Chenopodium album* with higher soil nitrogen supply (Supplemental Figure S5b).

Specific leaf area and seed dry mass were negatively related to soil nitrogen supply (loss of about 3 mm² mg⁻¹ and 1 mg, respectively) but remained unaffected by all other variables ([Table 2](#), [Figure 6\(a-b\)](#)). Vegetative height of the weed community did not relate to soil nitrogen supply but appeared to increase with fertilisation ([Table 2](#), [Figure 6c](#)). However, the post-hoc comparison did not reveal any significant differences (Supplemental Table S7, [Figure 6c](#)). Contrastingly, the two indicators reflecting the importance of the weed community for associated biodiversity were influenced by soil nitrogen supply, but not fertilisation ([Table 2](#)). The number of associated species dependent on the weeds (biodiversity relevance) increased with increased soil nutrient supply whilst the nectar production of the weed community decreased with increased soil nutrient supply ([Figure 7](#), [Table 2](#)).

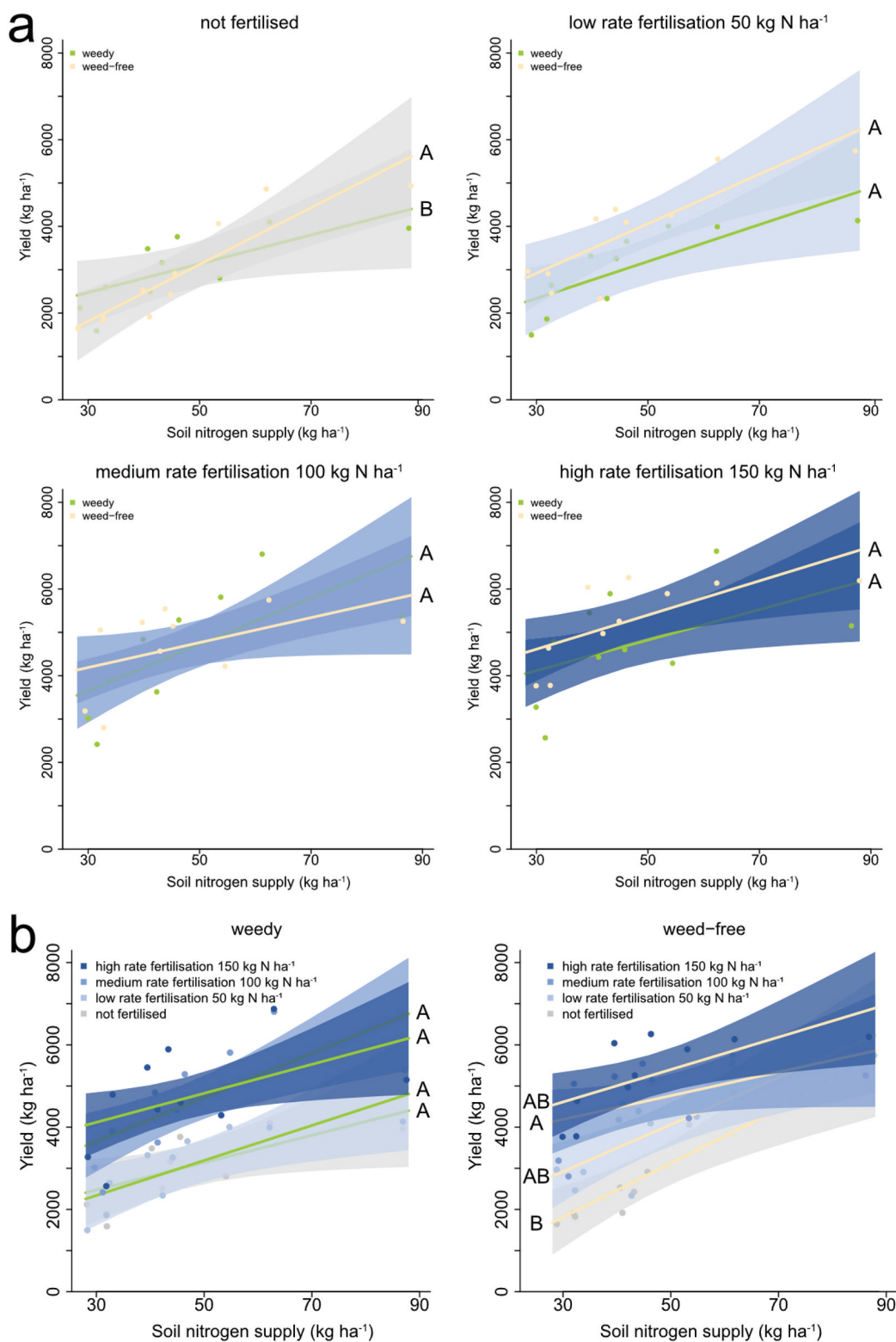


Figure 1. Effects of the three-way interaction between weeding, fertilisation and soil nitrogen supply on spring wheat yield, as divided by (a) fertilisation and (b) weeding. Mean and 95% confidence intervals from modelled effects and points showing raw data. Slopes with different letters within each individual plot indicate significant differences between means ($p < 0.05$).

Table 1. Results of the analysed linear mixed models of yields. χ^2 , df and p -values are extracted anova of the full model. Bold highlights significant explanatory variables ($p < 0.05$). All analyses used gaussian models.

Yield (all plots)			
	χ^2	df	p
Weeding x Fertilisation x Soil nitrogen	9.21	3	0.027
Weeding x Fertilisation	10.77	3	0.013
Weeding x Soil nitrogen	0.94	1	0.331
Fertilisation x Soil nitrogen	2.43	3	0.488
Weeding	9.69	1	0.002
Fertilisation	199.22	3	<0.001
Soil nitrogen	12.27	1	<0.001
Aphids	0.35	1	0.556
Grain protein content (all data)			
	χ^2	df	p
Weeding x Fertilisation x Soil nitrogen	5.56	3	0.135
Weeding x Fertilisation	1.21	3	0.749
Weeding x Soil nitrogen	1.88	1	0.170
Fertilisation x Soil nitrogen	19.58	3	<0.001
Weeding	23.58	1	<0.001
Fertilisation	82.17	3	<0.001
Soil nitrogen	68.90	1	<0.001
Aphids	1.11	1	0.291
Yield (weedy plots)			
	χ^2	df	p
Fertilisation x Weed cover	4.77	3	0.190
Soil nitrogen x Weed cover	0.88	1	0.352
Fertilisation	81.70	3	<0.001
Weed cover	1.66	1	0.198
Soil nitrogen	5.97	1	0.015
Crop height (weedy plots)			
	χ^2	df	p
Fertilisation x Cover tall weeds	4.81	3	0.186
Soil nitrogen x Cover tall weeds	2.26	1	0.133
Fertilisation	13.70	3	0.003
Cover tall weeds	4.60	1	0.032
Soil nitrogen	18.17	1	<0.001

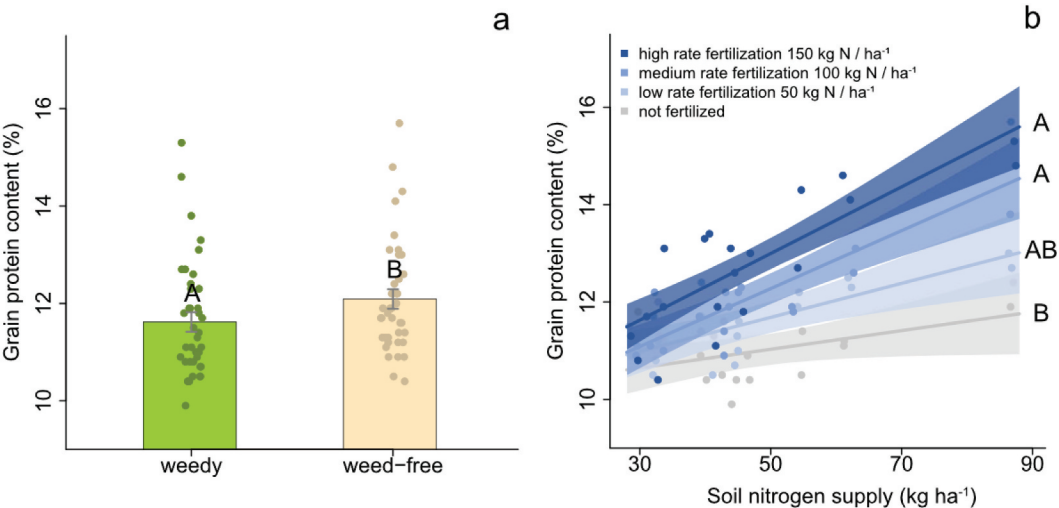


Figure 2. Effects of (a) weeding treatment, and (b) the interaction between fertilisation and soil nitrogen supply on grain protein content. Mean and 95% confidence intervals from modelled effects and points showing raw data. Bars and slopes with different letters indicate significant differences ($p < 0.05$).

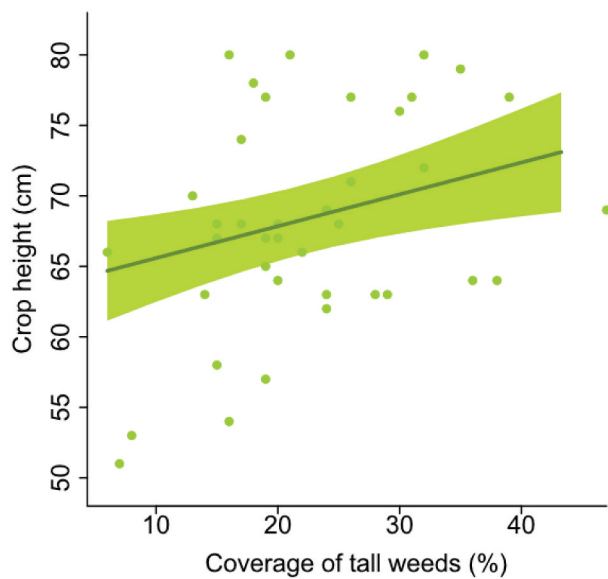


Figure 3. Crop height as related to the cover of tall weeds (weeds growing above a third of the crops height). Mean and 95% confidence intervals from modelled effect and points showing raw data.

Discussion

Weed–crop competition

The results showed that the spring wheat overall benefitted from increased fertilisation, although this depended on weeding and the soil nitrogen supply. By the vertical separation of the lines in [Figure 1a](#), it appeared that a yield loss due to weeds only occurred at the low rate of fertilisation. In the absence of fertiliser, the effect of weed removal on yield depended on the soil nitrogen supply

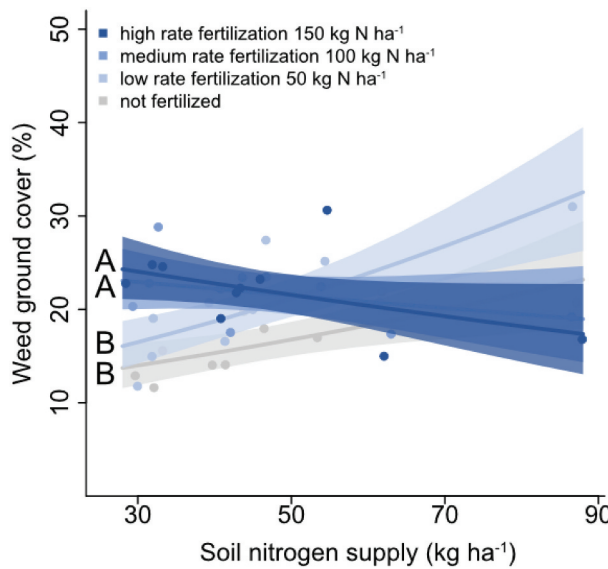


Figure 4. Weed ground cover in response to fertilisation and soil nitrogen supply. Mean and 95% confidence intervals from modelled effect and points showing raw data. Slopes with different letters indicate significant differences ($p < 0.05$).

Table 2. Results of the analysed linear mixed models of the weed community. χ^2 , df and p -value are extracted from anova of the full model. Bold highlights significant explanatory variables ($p < 0.05$). All analyses used Gaussian models except weed cover which was analysed with beta regression.

	Weed cover			Weed richness			Weed evenness		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
Fertilisation x Soil nitrogen	42.62	3	<0.001	1.43	3	0.699	6.36	3	0.095
Fertilisation	32.99	3	<0.001	0.32	3	0.955	19.47	3	<0.001
Soil nitrogen	2.97	1	0.085	1.55	1	0.214	4.28	1	0.038
	Specific leaf area			Seed dry mass			Vegetative height		
	χ^2	df	p	χ^2	df	p	χ^2	df	p
Fertilisation x Soil nitrogen	0.90	3	0.825	6.74	3	0.081	2.11	3	0.550
Fertilisation	2.11	3	0.551	3.55	3	0.314	8.71	3	0.033
Soil nitrogen	6.81	1	0.009	14.26	1	<0.001	1.24	1	0.266
	log(Biodiversity relevance)			log(Nectar production)					
	χ^2	df	p	χ^2	df	p			
Fertilisation x Soil nitrogen	2.54	3	0.468	1.58	3	0.663			
Fertilisation	1.28	3	0.734	3.36	3	0.339			
Soil nitrogen	6.84	1	0.009	13.97	1	<0.001			

with stronger effect in weed-free plots (Figure 1a), presumably explained by a high competition for the soil nitrogen supply when nitrogen from fertilisation was absent. At the low fertilisation rate, where weed removal increased crop yield, the results suggested that the weeds started competing for the fertilised nitrogen with the crop. At medium and high fertilisation there was little difference between weed-free and weedy plots, also in respect to the response to the soil nitrogen supply (Figure 1a) which implied that nutrient levels were sufficient and little competition occurred. At these higher fertilisation rates, weeds could thus rather be seen as opportunistic and co-existing with the crop, without inflicting detrimental competitive effects (Esposito et al. 2023). As nutrient levels increase, such as through fertilisation, it is expected that nutrients are no longer as limited and thus competition for nutrients decrease and competition for light becomes more important (Tilman

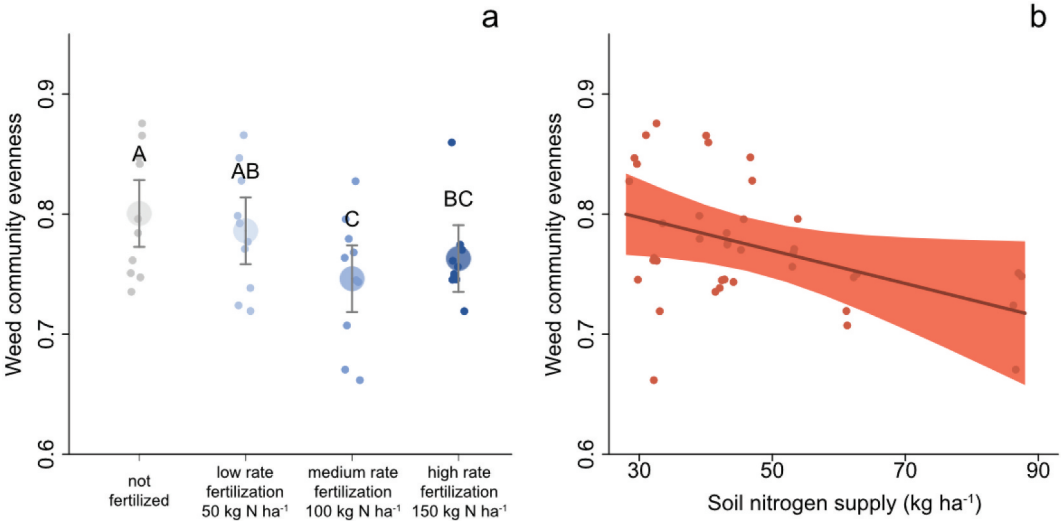


Figure 5. Effects of (a) fertilisation and (b) soil nitrogen supply on weed community evenness. Mean and 95% confidence intervals from modelled effects and points showing raw data. Means with different letters indicate significant differences ($p < 0.05$).

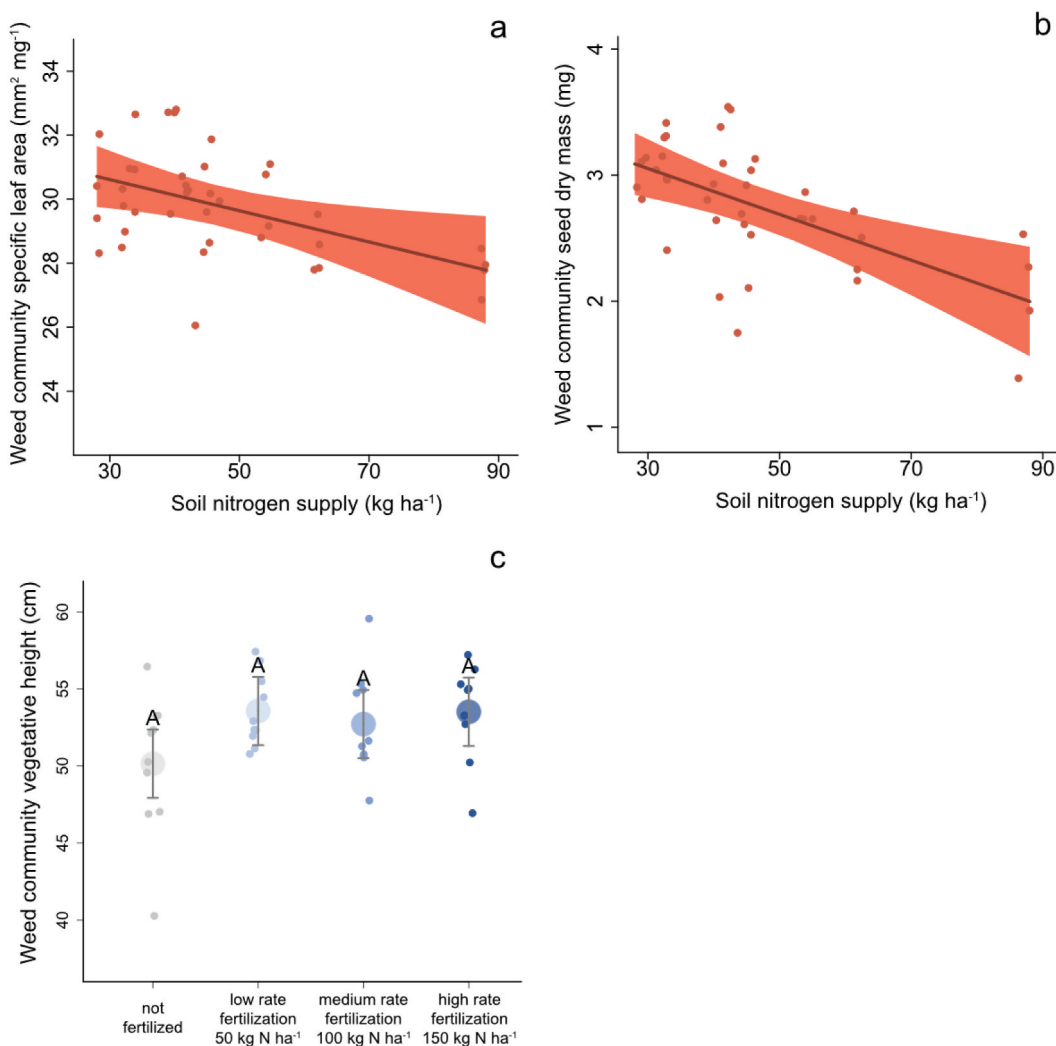


Figure 6. Effects of fertilisation or soil nitrogen supply on weed community functional trait composition calculated by community weighted means, (a) specific leaf area, (b) seed dry mass and (c) vegetative height. Mean and 95% confidence intervals from modelled effects and points showing raw data. Means with different letters indicate significant differences ($p < 0.05$).

1982). In this study, the crop had an advantage for light capture by emerging early and becoming taller than the weeds, although there was a weak apparent relationship of increased crop height with a higher cover of tall weeds. A taller crop could make the competition for nitrogen asymmetric as a larger size benefits nutrient uptake (Schwinning and Weiner 1998). Additionally, the nitrogen demand of the crop was rather high (as seen in the weed-free sub-plots, Figure 2), which further suggested that the competitiveness of the crop may increase with nitrogen fertilisation (compare Ampong-Nyarko and De Datta 1993; Wang et al. 2019). However, in this study, it could not be determined how the nitrogen demand of the crop compared to the nitrogen demand of the weeds, since a crop-free control was not included in the design. Furthermore, the competitive ability of the weeds may be better estimated through biomass or a direct measure of weed height, but such measures are more labour and time intensive to collect. Further investigations, using more detailed measures and involving the use of more elaborate statistical analyses such as Structural Equation

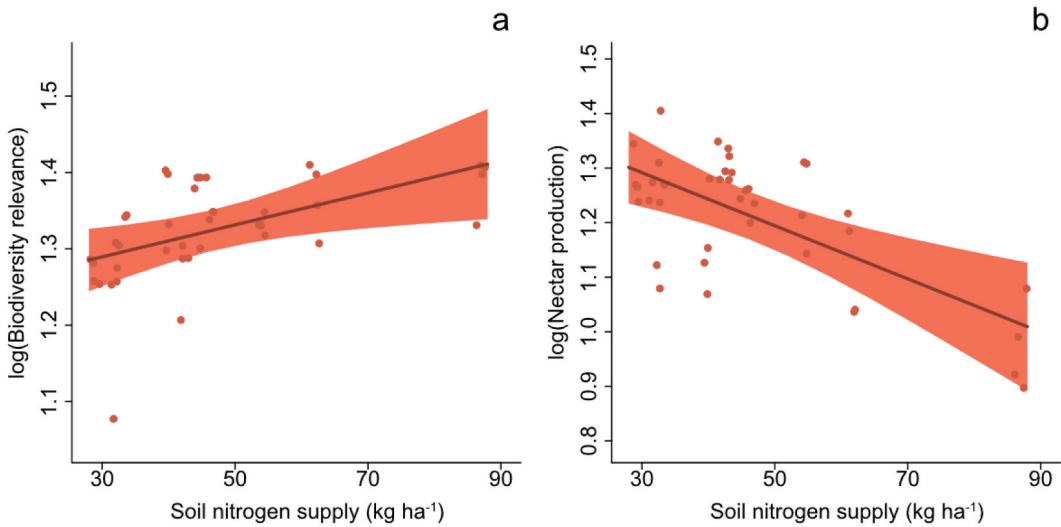


Figure 7. Relationship between soil nitrogen supply and the biodiversity importance of the weed community calculated by community weighted means of (a) biodiversity relevance, and (b) nectar production. Mean and 95% confidence intervals from modelled effects and points showing raw data.

Modelling or Partial Least Square path modelling (see, for example, Quinio et al. 2017), could reveal the apparent complexity of direct and indirect links between nutrients, weeds and yield.

For grain protein content, there was an interactive effect between fertilisation and soil nitrogen supply where both improved protein content and a general positive relationship between grain protein content and weeding (Figure 2). The general positive effect of weeding on grain protein content could be explained by the relatively high weed abundance also late in the season (Supplemental Figure S6) when grain protein was formed (compare Adeux et al. 2019). Higher soil nitrogen supply increased the positive effect of fertilisation on grain protein content (Figure 2b), probably through luxurious uptake of available N late during the crop cycle (De Oliveira Silva et al. 2021).

Soil nitrogen supply had a stronger effect on yield when fertilisation was lower in weed-free plots (Figure 1b), as expected since the two nutrient sources complement each other. But in weedy plots this interaction did not exist (Figure 1b), most likely due to the high competition from weeds when nutrient levels were low. Apart from the direct implications of nutrient availability, this study also showed the potential for indirect links with yield through altered weed community composition and competitiveness of the weed community. Specifically, soil nitrogen supply was associated with a loss of evenness and functional trait composition (Table 2, Supplemental Figure S5b), where there was a negative relationship to the community weighted mean specific leaf area and seed mass (Figure 6(a,b)). The decrease in seed mass with higher levels of nutrients was in accordance with earlier research (Gaba et al. 2014; Bergholz et al. 2015), whereas high specific leaf area indicated an efficient conversion of nutrients into leaf biomass and high ability to capture light (Gaba et al. 2014) and should therefore increase, and not decrease, along nutrient gradients (see, for example, Knops and Reinhart 2000; Freschet et al. 2015; Perthame et al. 2022). These results were likely driven by *Chenopodium album* in both cases, a species with low specific leaf area and small seeds, whose relative cover increased with increased soil nitrogen supply, contrary to larger-seeded species such as *Fallopia convolvulus* (Supplementary Figure S5). *Chenopodium album* is known for efficient nutrient uptake and rapid growth (Bajwa et al. 2019) but it is unclear why it responded more to the soil nitrogen supply than to the fertilisation (Supplemental Figure S5). Regarding the association between soil nitrogen supply and these functional traits, it could not be determined if this was an

effect of soil nitrogen supply per se or if the effects were linked to other processes, since the pattern in soil nitrogen supply matched patterns in productivity of the preceding ley and soil clay content. Some common weeds (such as *Chenopodium album*) can persist in field seedbanks for several years because they produce large amounts of seeds with long survival time (Dekker 1999).

Understanding the causal relationships between soil conditions, soil fertility, weed community composition, weed seed banks and ultimately competition and crop management are topics that require further research, where studying other traits or applying a strategy-based framework (e.g. CSR-strategies: Grime 1977) could be useful. It is also important to stress that the underlying trait data used in this study only reflected interspecific trait variation, whereas intraspecific trait variation may be important to understand mechanisms of competition (Gibson et al. 2017; Romillac et al. 2023). In addition, the species pool of weeds was restricted in this study because it was limited to one field and 1 year and thus shifts in community-weighted traits mainly reflected shifts in relative abundance rather than competitive exclusion or species turnover across larger spatial scales.

Weed diversity and conservation

Weed species richness was not influenced by either fertilisation or the soil nitrogen supply (Table 2), but species losses may be difficult to detect in short-term studies like this. Soil nitrogen supply was also not associated with weed species richness (Table 2), which could indicate that the underlying process causing the variation in soil nitrogen supply had little impact on the weed species pool or had not been going on for long enough. The exact process cannot be determined in this study, but the pattern in soil nitrogen supply matched patterns in productivity of the preceding ley and soil clay content (data not shown). Still, weed community composition changed as evenness generally decreased in response to both increased fertilisation and soil nitrogen supply (loss of around 6% and 10%, respectively), although the effect was not the largest and the highest rate of fertilisation deviated from the trend (Figure 5). A loss of evenness due to high nutrient conditions may be explained by the growth of competitive, fast-growing species being favoured at the expense of rarer and nutrient sensitive (usually oligotrophic) arable weeds (Storkey et al. 2010; Rotches-Ribalta et al. 2015). High fertilisation rates and soil nitrogen supply were in this study also associated with higher crop growth (Figures 1 and 2), which additionally favours competitive or stress-tolerant weed species that can survive in the dense crop vegetation (Pyšek and Lepš 1991). Over time, the loss of evenness and shifts in weed community composition could become even more pronounced as larger and more abundant species are likely to gain a reproductive advantage, especially if nutrient levels remain high. If the higher fertilisation is reoccurring and given enough time, such shifts in the weed community could come with the risk of competitive exclusion and thus a loss of species richness too (compare Gause 1934; Pyšek and Lepš 1991), although such effects could also be overwritten by other management practices. Shifts in the weed community and loss of weed diversity is a concern for crop production as diverse weed communities with high evenness are associated with reduced yield losses compared to more skewed weed communities, dominated by a few abundant species (Storkey et al. 2018; Adeux et al. 2019). It has been suggested that this is due to the lower biomass of more diverse communities and the lower share of competitive species (Adeux et al. 2019).

The shift in weed community evenness was reflected in the indices describing the overall nectar production and biodiversity relevance of the weed communities', but only in relation to the soil nitrogen supply and not fertilisation (Table 2). Increasing soil nitrogen supply was positively related to community weighted mean biodiversity relevance and negatively related to nectar production (Figure 7). In plots with high soil nitrogen supply, weed communities were dominated by *Chenopodium album* (Supplemental Figure S5b), a fast-growing annual plant commonly found on organic farms (Hyvönen et al. 2003), which does not produce nectar but instead supports a relatively diverse assemblage of associated species (Tyler et al. 2021). In contrast, in plots with low soil nitrogen supply, weed communities were characterised by a relatively high abundance of

Fallopia convolvulus (Supplemental Figure S5), which produces relatively large amounts of nectar (Tyler et al. 2021). Thus, the results most likely reflected the contrasting relative abundance of these two common species along the gradient of soil nitrogen supply, a contrast that was not very apparent for fertilisation (Supplemental Figure S5a).

It is possible that the stronger effect of soil nitrogen supply can be explained by a low share of species who benefit from short-term resource pulses or the long-term ley preceding the wheat particularly favouring species with long seed longevity, such as *Chenopodium album*. Complementary sampling such as density counts of the weed community or seed bank may help resolve this question. Nevertheless, both fertilisation and soil nitrogen supply related to shifts in the weed community composition, which in the case of soil nitrogen supply could also affect other taxa that depend on weeds in their life cycle. This underlines the importance of considering the whole agroecosystem when evaluating effects of management practices.

Generalisation

This experimental study contributed to a deeper understanding of the mechanisms driving weed–crop interactions, and how they are related to weed diversity and associated biodiversity, which has hitherto been understudied. For example, the study showed how the abundance of specific species plays into competition and strong evidence that the fertilisation both interacted and acted differently than soil nutrient supply on competition and weed community composition. This was potentially explained by the differences in timing and availability of the nutrients from the two sources that resulted in both short-term and long-term effects. The study showed particular relevance as it demonstrated that even in multi-species weed communities it was possible to distinguish effects of competition with the added benefit of assessing the consequences for biodiversity. Such understanding is important if sustainable weed management practices that maintain both yields and biodiversity are to be developed. This study therefore provided directions for future investigations on nutrient management and showed the need for even more detailed investigations.

It needs to be acknowledged that this study only showcased the outcomes of weed–crop interactions mediated by fertilisation and soil nitrogen supply under the specific conditions and weed community of the studied field, and this may vary between years and fields. For example, if the weeds are strong competitors (Menalled et al. 2004; Blackshaw and Molnar 2009), emerge early (Liebman et al. 2004) and/or have the advantage in competition for light (Santos et al. 2004), they may cause larger yield losses and the addition of nutrients may not lead to yield increases, especially without adequate weed control (Menalled et al. 2004; Mahajan and Timsina 2011). Dynamics of competition between crop and weeds are also highly dependent on fertiliser type and application strategy (Di Tomaso 1995; Blackshaw et al. 2005), crop type (Andersson and Milberg 1998; Rydberg and Milberg 2000; Smith and Gross 2007; Fried et al. 2008; Meiss et al. 2010) pedoclimatic conditions (Fried et al. 2008) and surrounding landscape (Gaba et al. 2010; Armengot et al. 2012; Petit et al. 2016; Alignier et al. 2020; Bourgeois et al. 2020). This study was based on a single-site experiment which is useful for a mechanistic understanding of weed–crop–nutrient interactions, but further research is needed to investigate whether the conclusions from this study hold under varied sets of environmental conditions and weed species pools. Moreover, experimental studies come at the cost of realism. Importantly, the weeding treatment used in this study does not mimic a realistic management scenario of an organic spring wheat field, because large-scale weed management is most likely much less efficient (see Armengot et al. 2013), such that this study may have overestimated the potential yield increase of weeding. Similarly, the highest fertilisation rate used in this experiment is currently not economically realistic for a commercial organic farm. Hence, these studies need to be complemented with field-scale studies using realistic weeding and fertilisation regimes.

Nevertheless, the experiment showcased that milling quality (>13% protein content; Figure 2b) and yield quantities comparable to those of conventional spring wheat in the region (4650 kg ha⁻¹;

Jordbruksverket 2023) could be achieved with high organic fertilisation in combination with high levels of soil nutrient supply, even with weeds present. This study therefore showed that weeds are not always detrimental to crop production, corroborating earlier research (Adeux et al. 2019; Esposito et al. 2023). Importantly, this study showed that a goal of eradication of weeds is not necessary for high crop production and that a holistic approach, considering both the benefits and costs associated with weeds, should be considered to support the design of sustainable farming systems. Thus, aims to improve yield, such as through fertilisation and soil fertility management should be evaluated against potential undesirable effects, for example, changes in the weed community and its benefits, as demonstrated in this study. Other studies have also shown this trade-off (see, for example, Berquer et al. 2023) which emphasise that for sustainable weed management the aim should be weed communities of low competitiveness and high diversity which provide many ecosystem benefits (MacLaren et al. 2020). If the crop is the stronger competitor, the need for weed control will be reduced (Weiner 2023) and weeds could instead contribute to biodiversity and supporting ecosystem services (Esposito et al. 2023). The competitiveness of the crop can be enhanced through, for example, choice of variety (Feledyn-Szewczyk and Jończyk 2015), sowing density (Kristensen et al. 2008; Kolb et al. 2010) and adapted tilling (Andersson and Milberg 1998; Swanton et al. 1999; Blackshaw et al. 2000). In addition, precision agriculture tools may be useful to tailor when, where and how fertilisers are applied, to ensure a net gain of nutrient management for the crop (Diacono et al. 2013) without affecting the weed community and enhancing negative effects of competition such as increased yield loss.

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