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Intercropping and pollination mediate faba bean (*Vicia faba*) yield and nodulation

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ABSTRACT

Legume productivity depends on biotic interactions above and below ground, such as pollination and *Rhizobia* symbiosis. Yet, these interactions remain unexplored, particularly in the context of different cropping systems. This study investigated the interactive effects of intercropping and pollination on faba bean nodulation and yield in an organic system, where faba bean and pumpkin were alternated in 3 m-wide strips and compared to faba bean plants grown as a monocrop. Faba bean nodulation and yield were evaluated in open (insect-pollinated) and bagged (self-pollinated) plants. Results showed that faba bean yield and nodulation were enhanced at strip edges. Nodule mass increased by 45 %, the number of active nodules increased by 33 %, and seed weight per plant was 61 % higher compared to monocrops. Insect pollination treatment also increased nodule mass by 19 % and seed weight by 37 %. We found that pollination treatment influenced the relationship between active nodules and yield parameters with insect-pollinated plants being less dependent on active nodules for productivity. In addition, we found complex interactions between cropping system, pollination treatments and nodulation, whereby, in intercropping systems, both yield and nodulation benefit from pollination but not in monocropping systems. Our findings confirm that intercropping positively affects faba bean yield and nodulation, likely driven by nutrient competition and resource use complementarity between crops. Importantly, we provide the first evidence of pollination affecting faba bean-*Rhizobia* symbiosis, likely through shifts in plant resource allocation. These findings underscore the need to better understand interactions between above- and belowground symbioses for the transition towards sustainable agriculture.

1. Introduction

Industrial agriculture, characterized by large fields cultivated with a single crop species, is considered a major driver of soil degradation and biodiversity loss (Campbell et al., 2017). Such homogenous arable landscapes dominated by few crop species are prone to pest outbreaks and heavily rely on agrochemical inputs to maintain high crop yields (Emmerson et al., 2016). Crop diversification, by which diversity is added to cropping systems on a temporal (e.g. crop rotation), genetic (e.g. adding multiple crop species/cultivars) and/or spatial scale (e.g. using different crop configurations), is a promising strategy to promote soil fertility, nutrient cycling and biodiversity while maintaining crop yield (Beillouin et al., 2021; Tamburini et al., 2020). One mean of increasing crop diversity is intercropping, where two or more crop species are cultivated on the same field. Intercropping promotes more efficient use of above- and belowground resources, such as light, water or nutrients, through resource use complementarity and facilitation (Justes et al., 2021). Complementarity occurs when crop species differ in plant traits, e.g. root distribution (Liu, 2020), canopy structure (Li, 2021) or temporal growing period (Wang, 2023), resulting in reduced competition and more complete uptake of resources (Duchene, 2017; Justes et al., 2021). Facilitation occurs when a crop species positively

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impacts a neighbouring crop species (Duchene, 2017). Complementarity and facilitation are most pronounced when direct interactions between crop species occur, i.e. when plants from two or more crop species are growing side-by-side (Wang, 2020).

Legumes play a key role in intercropping systems due to their ability to provide various ecological benefits (Ditzler et al., 2021). One such ecological benefit is the ability to biologically fix nitrogen (N), thereby enriching the amount of available N in the soil (Duchene et al., 2017) and reducing the need for N fertilizers in companion or following crops (Peoples et al., 2009). Legumes fix N from the atmosphere through a symbiosis with *Rhizobia*, soil bacteria that trigger the formation of nodules in the roots of leguminous plants (Roy et al., 2020). Although the efficiency of biological N fixation (BNF) differs among legume species and symbionts, BNF allows legumes to produce high yields at low N fertilisation rates (Mathesius, 2022). BNF is energy costly for the host plant and is mainly driven by N limitation and demand (Duchene et al., 2017). Faba bean (*Vicia faba* L.), a highly efficient N-fixing legume (Liu et al., 2019), is the third most widely cultivated legume in Europe (FAOSTAT, 2024). Enhanced nodulation has been shown to significantly increase its biomass and yield (Allito et al., 2021; Denton et al., 2017). Higher nodule mass has been found in faba bean-cereal intercropping systems compared to respective monocropping systems (Li et al., 2016, 2009; Liu et al., 2019). However, benefits of intercropping on faba bean yield appear highly variable, depending on cereal species, cultivars and sampling years (De Long et al., 2023; Streit et al., 2019). Therefore, the impact of intercropping on faba bean nodulation and yield parameters, particularly when faba bean is combined with non-cereal crops, remain to be investigated.

In addition to symbioses with *Rhizobia*, faba bean yield benefits from insect pollination due to greater ovule fertilization and thereby enhanced seed set (Marzinzig et al., 2018). A recent meta-analysis reports a yield reduction of 21–43 % without insect pollination (Bishop and Nakagawa, 2021). Pollination and belowground root-symbioses affect plant resource allocation and plant traits independently, but less is known about their interactive effects (Barber and Soper Gorden, 2015). Interactions between plant root-symbionts and pollination have been found for arbuscular mycorrhizal fungi (AMF), with increased AMF associations leading to greater bee visitation mediated by enhanced flower size (Guzman et al., 2025). Despite the importance of the N-fixing symbiosis in legumes, surprisingly little research has been dedicated to better understand the interactions among N-fixing bacteria, plant traits and plant–pollinator interactions (but see: Barber and Soper Gorden, 2015). While both, intercropping and pollination modify plant resource allocation between growth and reproduction (Gaudio et al., 2021; Riggi et al., 2022; Fairhurst et al., 2022), their interaction via faba bean-*Rhizobia* symbiosis is unknown.

To assess the effects of intercropping and pollination on faba bean nodulation and yield, we carried out a field experiment, where faba bean was either strip-intercropped with pumpkin (*Cucurbita maxima*), or grown as a monocrop control. In strip-intercropping, two or more crops are grown in multi-row parallel strips wide enough to be managed with existing machinery but close enough to enable ecological interactions such as resource use complementarity, facilitation or competition (Ditzler et al., 2023). Faba bean and pumpkin crop traits differ in terms of canopy structure, temporal growing pattern and N demand, allowing for complementarity in resource uptake. We focused on the edges of the strip, where complementarity in resource use is expected to be most pronounced (Wang et al., 2023). We anticipate that faba bean nodulation and yield will be enhanced at the edges of the strip compared to the monocrop due to resource use complementarity, and that yield will be reduced in the absence of insect pollination. We also hypothesise that insect pollination might lead to increased nodulation to supply the higher number of developing seeds with nitrogen. Finally, we expect cropping system, pollination treatment as well as nodulation to synergistically affect faba bean yield.

2. Material & methods

2.1. Experimental set-up

To assess the effect of cropping system (intercrop *versus* monocrop) and pollination (insect-pollination *versus* self-pollination) on faba bean nodulation and yield, a field experiment was conducted in 2023 at Droevendaal Organic Experimental Farm, Wageningen, the Netherlands (51°59’27.4”N; 5°39’36.0”E) (Supplementary material A). This experiment took place within a system trial strip-intercropping experiment on a loamy-sand soil, which started in 2018 and investigates multiple crop combinations (Figure SA.1). Faba bean - pumpkin strips (3 m width) were grown in four replicated blocks with a faba bean monocrop control in each block (Fig. 1, Figure SA.1). Individual strips contained six rows of faba beans and three rows of pumpkin plants. Three paired strip-intercropping and monocropping systems of 55 m x 55 m and 9 m x 9 m respectively (Block 1–3), as well as and one larger paired strip-intercropping and monocropping system both of 72 m x 72 m (Block 4) were used (Figure SA.1). The four Blocks were located in four different fields, located 100–200 m apart (Figure SA.1). We used the commonly cropped faba bean cultivar “Tiffany”, which was sown on May 2nd 2023 (Fig. 1a). No fertilizer was applied in the faba bean strip and monocrop. Pumpkin (var. Flexi kuri) was sown on May 19th, and pumpkin strips were fertilized with 15 ton/ha cattle slurry before sowing on May 16th (Table SA.1). No pesticides were applied. Soil characteristics did not significantly differ between cropping systems (Table SA.2, Table SA.3).

All data was collected from faba bean plants at the strip edge, (i.e. the faba bean row directly bordering the pumpkin strip), and in the monocrop at least 1 m from the plot edge (Fig. 1b). Data from the centre of the strip (1.5 m from the edge of the strip) were also collected, however, these results did not significantly differ compared to the monocrop treatment. As we were interested in plant-plant interactions rather than broader cropping system comparisons, results collected from the centre of the strip are presented in Supplementary material B. Sampling occurred using plant quartets, consisting of four nearby plants spaced approximately 20 cm apart to minimize disturbance during sampling. Plants were selected at the onset of faba bean blooming, with quartets including plants of similar height and bud numbers (Fig. 1c). In each block, five plant quartets were located in each cropping system treatment (edge of strip-intercropping ($N = 79$ plants) and monocropping ($N = 78$ plants Table SD.1)) (Figure SA.1). Within each of the four blocks, plant quartets were placed in the same strip to reduce spatial variation. Each plant quartet consisted of two plant pairs, one plant pair was used to assess nodulation parameters at the end of faba bean flowering (BBCH 65–75, Lancashire et al., 1991), while the other plant pair was used to assess yield parameters at full plant maturity (BBCH 90) (Fig. 1b,c). Plant quartets were 10 m apart in the strip edge. In the monocrop, plant quartets were located approximately 4–5 m apart. To minimize plot edge effects, we did not sample within the 10 % distance of strip heads, and monocrop plot perimeters, which were regarded as buffer zones.

To explore the effect of pollination on faba bean yield and nodulation, we compared yield and nodulation parameters between open, insect pollinated plants (P +), and bagged, only self-pollinated plants (P-), in each plant pair (Fig. 1c). We assumed that the level of self-pollination was the same in the open and bagged plant treatment, as we expected no effect of bagging (Lundin and Raderschall, 2021). Tull-net bags (15 cm×20 cm, mesh size < 1 mm) were adjusted twice per week such that they only covered open flowers to avoid potential effects on pod development. Due to early flowering caused by early season drought, plants were bagged during the onset of crop bloom (June 21st, growth stage BBCH 60). To estimate the proportion of pods that were insect pollinated in the bagged treatment because of this, we marked the highest node at which open flowers were present at the time of bagging. On average 9.7 % of the pods per plant set from flowers that were open

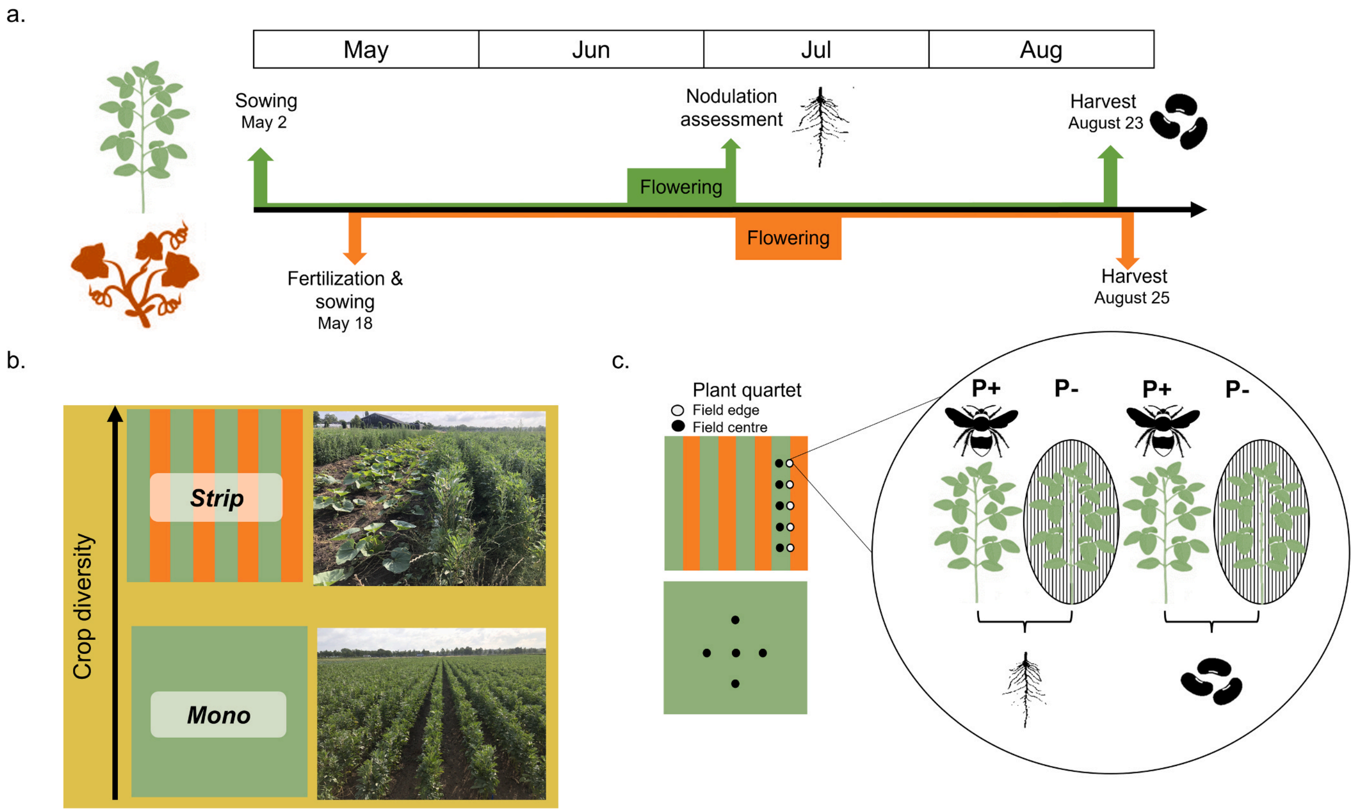

Fig. 1. a. Overview of faba bean (green) and pumpkin (orange) growing period and faba bean nodulation and yield assessment. b. Schematic setup of the faba bean (green) and pumpkin (orange) strip-intercropping and monocropping design with pictures taken in the field on 4th of July 2023 (© CropMix). c. Set-up of faba bean plant quartets within the fields. Plant quartets were located at the strip centre, strip edge of the intercropping treatment and in the centre of the monocropping treatment. One pair in each quartet was used to assess nodulation parameters mid-season; the other plant pair was used to assess yield parameters at full plant maturity. One plant in each pair was bagged (P-) to exclude insect pollinators and one left open for insect pollination (P +).

before bagging and thus were potentially insect pollinated, yet we did not exclude these pods from our analyses. Bags were removed after crop bloom to minimise their effect on plant growth and pod development. We expected no effect of bagging on yield, as a recent study found similar faba bean yield in bagged hand pollinated plants compared to open plants (Lundin and Raderschall, 2021). Faba bean flowers were predominately visited by bumblebees and honeybees (Supplementary material C). There were no differences in pollinator visitation rates in strip-intercropping and monocrop systems (Supplementary material C), therefore we assumed that insect-pollinated plants received similar numbers of pollinator visits irrespective of cropping system.

2.2. Nodulation and mid-season faba bean parameters

Nodulation parameters and mid-season faba bean response parameters (Table 1) were assessed during the onset of pod filling stage (growth stage BBCH 65–75, between the 3rd and 7th of July). The pod fill stage is suitable for assessing nodulation because of high nodule activity (Seeger et al., 2022). Nodulation and mid-season plant parameters (Table 1) were assessed in 69 plants instead of 80 due to management-related constraints which made it impossible to sample 11 plants in the strip-crop edge of Block 1 and 3 (Table SD.1). Plants were carefully excavated circa 30 cm deep using a spade, leaving the root system as intact as possible, this method, as opposed to a more standardized method (Streit et al., 2019) was possible as the texture of the soil was very sandy. Roots were cut off at the stem and washed using a sieve. Nodules were detached from the roots and counted. To determine the proportion of active nodules, 20 random nodules per plant were dissected to assess the pigmentation status. Active nodules are red pigmented by the presence of leghaemoglobin; changes of nodule colour indicate inactivity (Puppo et al., 2005). Pigmentation was categorized as pink/red (active nodule) or white/green/brown (inactive nodule) (Seeger et al., 2022). The proportion of active nodules was estimated by dividing the number of red/pink nodules by 20 (total subsample size). Nodules, roots and aboveground biomass were oven-dried for 72 h at 70°C and dry matter (DM) was recorded. Leaf nitrogen (N) (g/kg DM) and phosphorus (P) (g/kg DM) content were spectrophotometrically determined in dried, grinded leaves following H_2SO_4-Se digestion, according to the protocol of Houba (1988).

Table 1
Measured parameters related to nodulation, yield and plant response.

Assessment period	Category	Parameters
Mid-season (BBCH 65–75, July 3–7)	Nodulation parameters	Nodule mass (g) Nodule numbers Percentage active nodules (%)
	Faba bean plant	Leaf N content (g/kg DM) Leaf P content (g/kg DM) Root biomass (g) Shoot biomass (BBCH 65–75) (g)
Full maturity (BBCH 90, August 21)	Yield parameters	Seed weight per plant (g) Individual seed weight (g) Total number of seeds per plant Total number of pods per plant Average number of seeds per pod N content in seeds (g/100 g) Total N in seeds per plant (g)
	Faba bean plant	Shoot biomass (BBCH 90) (g)

2.3. Yield and full maturity faba bean parameters

Yield and plant response parameters (Table 1) were assessed on 78 plants at full plant maturity (2 plants died before the end of the experiment Table SD.1) (BBCH 90, August 21st). Plants were carefully excavated. For each plant, the number of pods per plant, seeds per pod and total number of seeds per plant were recorded. Seeds, and aboveground biomass were oven-dried for 72 h at 70°C and then weighed. Mean individual seed weight was obtained by dividing seed weight per plant by seed number per plant. N content in seeds (g/100 g) was spectrophotometrically determined in a representative subsample of 55 plants across treatments. Seeds were dried and grinded following H_2SO_4-Se digestion according to the protocol of Houba (1988). The total amount of N in seeds per plant (g) was calculated by multiplying the N content in seeds (g/100 g) by the bean DM per plant.

2.4. Statistical analyses

In total, 20 plant quartets were sampled per cropping system treatment (i.e. strip-intercrop edge and monocrop), however due to some plant losses during the season, this resulted in a total of 147 individual faba bean plants instead of 160 (see Table SD.1 for an explanation). The data was analysed in two steps, firstly, we evaluated the effects of cropping system and pollination treatments on nodulation and on yield parameters separately, as the data was collected at different crop stages (Table 1). Secondly, we investigated the effect of nodulation, pollination treatment and intercropping on yield by combining data from the plant pairs used to assess nodulation and yield in the quartet (Fig. 1c). All statistical analyses were performed using (generalized) linear mixed-effect models (‘*glmmTMB*’, Magnusson et al., 2021) in R version 4.3.1 (R Core Team, 2024). For all models, assumptions were validated using residual diagnostics, and count data models were checked for over- or underdispersion (‘*DHARMa*’, Hartig and Lohse, 2020). The amount of variance attributable to different factors was analysed using Anova type III (‘*car*’, Fox et al., 2019). Estimated marginal means were obtained using the ‘*emmeans*’ package (Lenth et al., 2023). Model outcomes were visualised using ‘*ggplot2*’ and ‘*sjPlot*’ (Lüdecke et al., 2024; Wickham et al., 2020). R-squared values were calculated (‘*MuMin*’, Barton, 2018).

The effects of cropping system, pollination treatments and their interaction on (a) nodulation parameters (nodule mass, nodule number, proportion of active nodules), (b) yield parameters (bean DM per plant, seeds per pod, pods per plant, seeds per plant and N content in seeds per plant) and (c) faba bean plant parameters (root DM, shoot DM, leaf N and P content) were analysed. All response variables followed a Gaussian distribution except for nodule number, total pods, total seeds per plant for which a Poisson distribution was used. For the proportion of active nodules, a binomial distribution was used. Explanatory variables included cropping system (strip-intercrop edge and monocrop) and pollination treatment (P + and P-) and their interaction. The interaction between cropping system and pollination treatment was never significant and did not improve model fit (AICc) and was therefore excluded from all models. For models assessing nodulation parameters, root biomass was also included as a covariate to account for variability in root size. Random effects included quartet nested within block (1| block/quartet). Spatial autocorrelation was assessed by calculating the Moran’s I statistic and its associated *p*-value using coordinates of the plant quartets. We found no spatial autocorrelation.

Finally, to investigate the impact of nodulation, cropping system and pollination treatments on yield, data from each faba bean quartet was combined, following similar approaches by De Notaris et al. (2023) and Gedamu et al., (2021). This was necessary as destructive sampling for nodulation was done on one plant pair in the quartet while yield parameters were obtained on the other plant pair in the quartet (Fig. 1c). Therefore, data between plant pairs were pooled per treatment combination (pollination and cropping system). As some faba bean plants could not be assessed, this resulted in a sample size of $n = 40$ for the insect-pollinated, and $n = 27$ for the self-pollinated treatments (Table SD.1). Fixed effects included one three-way and all two-way interactions between cropping system, pollination treatment, and the nodulation parameter (i.e. nodule mass and proportion of active nodules). Block was included as a random effect.

3. Results

3.1. Nodulation and plant parameters at crop bloom

We found significant main effects of cropping system and pollination treatments on three nodulation parameters (Table 2). Post-hoc tests indicate that nodule mass (g) was 45 % higher in the strip-intercropping compared to the monocropping treatment (0.08 ± 0.02, $p = 0.002$, Fig. 2e) and 19 % higher in the insect- than in the self-pollination treatment (est±se=0.04 ± 0.01, $p = 0.018$, Fig. 2a). Total nodule number per plant was only affected by the pollination treatment, with 2 % more nodules in the insect- than in the self-pollinated treatment (0.07 ± 0.03, $p = 0.013$, Fig. 2b). The proportion of active nodules was 33 % greater in the strip-intercropping compared to the monocropping (0.80 ± 0.23, $p < 0.001$, Fig. 2f). Regarding faba bean plant parameters, only shoot biomass (g) was affected by the cropping system, with 19 % greater shoot biomass in the strip-intercrop compared to the monocrop (1.63 ± 0.77, $p = 0.040$, Fig. 2g). Self-pollination treatment resulted in 5 % higher leaf N (g/kg DM) (2.01 ± 0.72, $p = 0.007$), and 12 % higher leaf P (g/kg) content (0.43 ± 0.11, $p < 0.001$) (Figure SD.2). Self-pollinated plants had 23 % lower shoot biomass (-1.91 ± 0.48, $p < 0.001$, Fig. 2d) and 11 % lower root biomass (-0.15 ± 0.07, $p = 0.052$, Figure SD.2).

3.2. Yield parameters

We found significant main effects of cropping system and pollination treatment on all yield parameters assessed except individual seed weight (Table 3). Post-hoc tests show that seed weight per plant (g) was 61 % higher (3.98 g ± 1.16, $p = 0.001$) and total number of seeds per plant were 16 % higher (0.40 ± 0.13, $p = 0.003$) in the strip-intercrop compared to the monocrop, and 37 % (est±se=2.71 g ± 0.70, $p < 0.001$) and 13 % (0.33 ± 0.05, $p < 0.001$) higher in insect-pollinated plants compared to self-pollinated plants (Fig. 3). Seeds per pod and pods per plant were 19 % (0.45 ± 0.20, $p = 0.018$) and 13 % (0.23 ± 0.10, $p = 0.021$) greater in the strip-intercropping compared to the monocropping treatment (Figure SD.2). While we found no differences in N content in seeds (g/100 g) between pollination and cropping system treatments (Table 3), total plant N content in seeds (g) was 55 % (1.96 ± 0.61, $p = 0.002$) greater in the strip-intercropping treatment (Figure SD.2).

3.3. Interactive effects between pollination treatment and nodulation on yield

The number of seeds per pod was explained by an interaction between the pollination treatment and the proportion of active nodules (Table 4). In insect pollinated plants, there was no effect of active nodules on the number of seeds per pod. In self-pollinated plants, the number of seeds per pod increased with increasing proportion of active nodules (est±se=2.40 ± 0.78, CI: 0.83/3.91) (Fig. 4a). A significant three-way interaction among cropping system, pollination treatment and the proportion of active nodules on total seeds per plant was found (Table 4, Fig. 4b). Insect-pollinated plants in the monocropping treatment showed a negative relationship between the proportion of active nodules and total seeds per plant (-1.26 ± 0.40, CI:-2.06/-0.46) (Fig. 4b). In contrast, in self-pollinated plants, the relationship between total seeds per plant and active nodules was positive for both cropping systems (monocropping: 1.03 ± 0.46, CI:0.17/1.89, strip-intercropping: 1.31 ± 0.60, CI:0.12/2.50) (Fig. 4b).

Table 2

Anova results for the nodules and plant response variables collected in June ($n = 69$, Table SD.1). Chi-square values (X^2) and associated p-values are shown. R-squared values (%) represent the percentage of variance explained by the fixed effects (R^2m) and both the fixed and random effects (R^2c). Significant results are shown in **bold** ($p < 0.050$). NI – variables Not Included in the model.

Response variables	Cropping system		Pollination treatment		Root biomass (g)			
	X^2	p-value	X^2	p-value	X^2	p-value	R^2m	R^2c
Nodule mass (g)	10.67	**0.001**	5.89	**0.015**	23.82	**< 0.001**	52	76
Nodule number	0.34	0.558	6.16	**0.013**	108.57	**< 0.001**	46	95
Active nodules (%)	11.99	**< 0.001**	0.00	0.946	NI		18	74
Leaf N (g/kg DM)	0.26	0.607	7.72	**0.005**	NI		8	46
Leaf P (g/kg DM)	0.11	0.731	13.30	**< 0.001**	NI		11	47
Root biomass (g)	1.23	0.266	3.90	**0.048**	NI		5	68
Shoot biomass (g)	4.38	**0.036**	15.37	**< 0.001**	NI		20	60

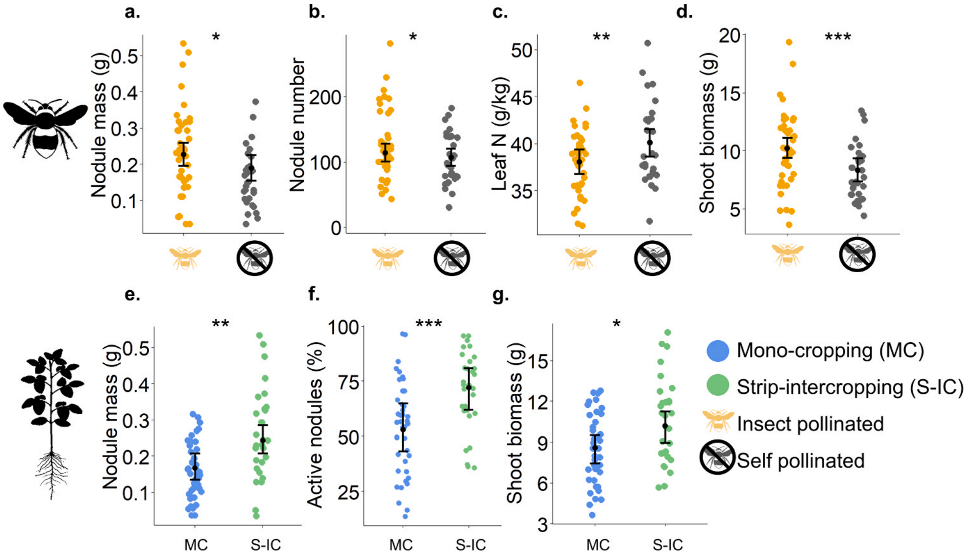

Fig. 2. Model estimates for faba bean nodulation and plant response parameters in relation to the pollination treatment (a-d) and cropping system (e-g). Whiskers represent 95 % confidence intervals and a point mean estimate. Note that in some of the plots, the y-axis does not start at zero. Significance is shown as p-value *< 0.05, ** < 0.01, ***< 0.001.

Table 3

Anova results for the yield and plant parameters collected in August ($n = 78$ except for N content analyses $n = 55$, Table SD.1). Chi-square values (χ^2) and associated p-values are shown. Significant results are shown in **bold** ($p < 0.05$). R-squared values (%) represent the variance explained by the fixed effects (R^2m) and the fixed and random effects (R^2c). Plots for significant results and raw data are shown in Fig. 3 and Figure SC.2.

Response variables	Cropping system		Pollination treatment			
	X^2	p-value	X^2	p-value	R^2m	R^2c
Seed weight (g)	11.85	**< 0.001**	14.95	**< 0.001**	20	65
Individual seed weight (g)	0.75	0.384	0.03	0.857	0	4
Seeds per plant	8.72	**0.003**	35.47	**< 0.001**	21	82
Seeds per pod	4.86	**0.027**	0.26	0.608	7	14
Pods per plant	5.27	**0.02**	12.86	**< 0.001**	17	32
N content in seeds (g/ 100 g)	0.12	0.725	0.09	0.754	0	0
Plant N content (g)	10.08	**0.001**	0.15	0.690	16	72
Shoot biomass (g)	0.24	0.618	1.11	0.291	1	26

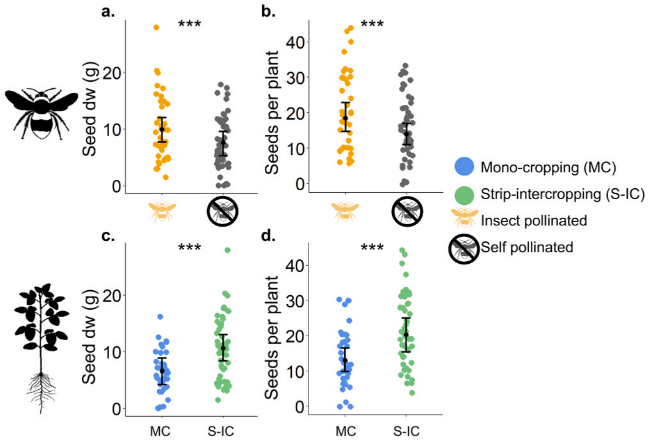

Fig. 3. Model predictions for faba bean yield parameters in relation to the pollination treatment (a, d) and cropping system (b, c, e, f). Whiskers represent 95 % confidence intervals and the mean point estimate. Significance is shown as p-value *< 0.05, ** < 0.01, ***< 0.001.

4. Discussion

4.1. Cropping system and pollination treatment increased faba bean nodulation

In line with previous faba bean-cereal intercropping experiments, we found that nodule mass and the proportion of active nodules were higher in faba bean plants at the strip edge compared to when grown in the monocrop (Bargaz et al., 2021; Li et al., 2016, 2009; Liu et al., 2017) (Fig. 5a). It is possible that higher nodule mass at the edge of the strip in our strip-intercropping experiment is driven by competition for N between faba bean and pumpkin due to a high N demand of pumpkin (Naderi et al., 2017, Duchene et al., 2017), and the short temporal niche

Table 4
Anova results for the seeds per pod and seeds per plant in relation to the cropping system, pollination treatment, proportion of active nodules (Nodulation) and their two- and three-way interactions. Chi-square values and associated p-values are shown. R-squared values represent (%) the variance explained by solely the fixed effects (R^2_m) and the fixed and random effects (R^2_c). Plots are shown in Fig. 4.

Explanatory variable		Seeds per pod	Seeds per plant
	R^2_m	18	35
	R^2_c	32	85
Cropping system	X^2	1.64	8.43
	p-value	0.199	**0.003**
Pollination treatment	X^2	8.51	29.53
	p-value	**0.003**	**< 0.001**
Nodulation (%)	X^2	0.52	0.19
	p-value	**0.002**	0.657
Cropping system* Pollination treatments	X^2	-	7.67
	p-value		**0.005**
Cropping system* Nodulation	X^2	-	4.01
	p-value		**0.045**
Pollination treatments * Nodulation	X^2	8.90	18.86
	p-value	**0.002**	**< 0.001**
Cropping system * Pollination treatments * Nodulation	X^2	-	4.34
	p-value		**0.049**

differentiation between the two crops (Fig. 1). Alternatively, root exudates such as *Rhizobia*-promoting flavonoids might have enhanced nodulation, similar to what has been observed in cereal-legume intercropping systems (Li et al., 2016; Liu et al., 2017). Whether root exudates play a role in faba bean-pumpkin intercropping systems should be further investigated. While nodule mass and proportion of active nodules were higher in strip-intercropped plants, the number of nodules was not affected by the cropping system. It has been reported that nodule mass, rather than nodule number, correlates with BNF (Martins et al., 2022). Possibly, plants invest their energy in existing nodules rather than forming new nodules, since nodule formation is an energy intensive process (Li et al., 2022). Future research should relate nodule mass, nodule number and active nodule mass with BNF, to elucidate the relationship between different nodulation parameters and BNF.

Nodule mass, nodule number and root dry mass decreased by 20 %, 2 % and 11 %, respectively in self-pollinated plants compared to insect-pollinated plants (Fig. 5b). As far as we know, we are the first to report an effect of pollination treatment on roots and nodulation. Lack of pollination has been reported as a stressor resulting in altered plant resource allocation (Adamidis et al., 2019; Fairhurst et al., 2022) and increased faba bean pod abortion (Riggi et al., 2022). Possibly, faba bean plants responded to the absence of insect pollination by allocating more resources into producing new flowers to maximise reproductive success and away from roots and nodules (López-Bellido et al., 2005). While flowering was not assessed, we observed that several bagged plants prolonged flowering compared to open-pollinated plants (personal observation; no data obtained). An alternative mechanism could be that insect-pollinated plants required enhanced nodulation to supply the higher number of developing seeds with nitrogen. No effect of pollination treatment was found on the proportion of active nodules, possibly due to a time lag between when nodules become active and nodulation assessment. Future assessments of the effect of pollination on source-sink dynamics in faba bean, including data on faba bean flowering, belowground symbioses and standardized root traits assessments are required to test these hypotheses. Furthermore, building on previous findings of *Rhizobia*-symbioses affecting flower numbers, positively or negatively depending on the plant species (Barber and Soper Gorden, 2015), future work should simultaneously assess the relations between nodulation, flower traits and pollinator visitation. This may provide an additional mechanism by which soil bacteria interact with aboveground organisms to affect legume biomass and yield.

4.2. *Cropping system and pollination treatment increased faba bean yield*

All yield components were higher in plants at the strip edge of the intercrop compared to the monocrop (Fig. 5a). This is in line with previous findings of increased faba bean yield in cereal intercropping systems (Li et al., 2016, 2009; Mei et al., 2021). However, no effects as well as negative effects of intercropping on faba bean yield have also been reported (De Long et al., 2023). In our study, faba bean plants at the strip edge likely benefitted from above- and belowground resource complementarity. Aboveground, faba bean plants at the strip edge likely benefitted from increased light interception because they are taller than pumpkin (Wang et al., 2017), which in turn could benefit the amount of photosynthetic products that can be used to invest into nodule formation (Li et al., 2022). Belowground, enhanced nodulation, likely benefited the amount of available N in the plant to invest in faba bean yield parameters (Allito et al., 2021; Zhong et al., 2024). While we did not find

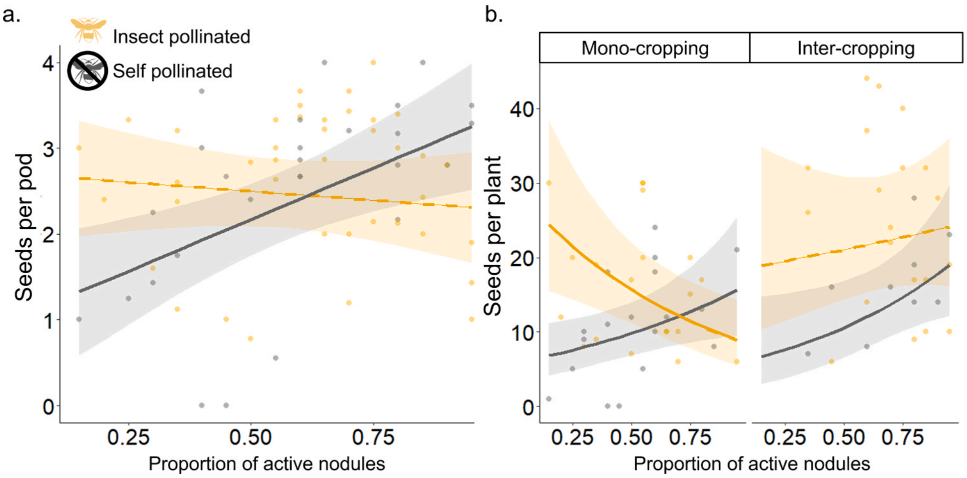

Fig. 4. Model predictions for faba bean yield components in relation to the proportion of active nodules and (a) seeds per pod per pollination treatment and (b) total seeds per plant per pollination treatment and per cropping system. Bands represent 95 % confidence intervals, solid lines indicate significant trends and points show the raw data distribution.

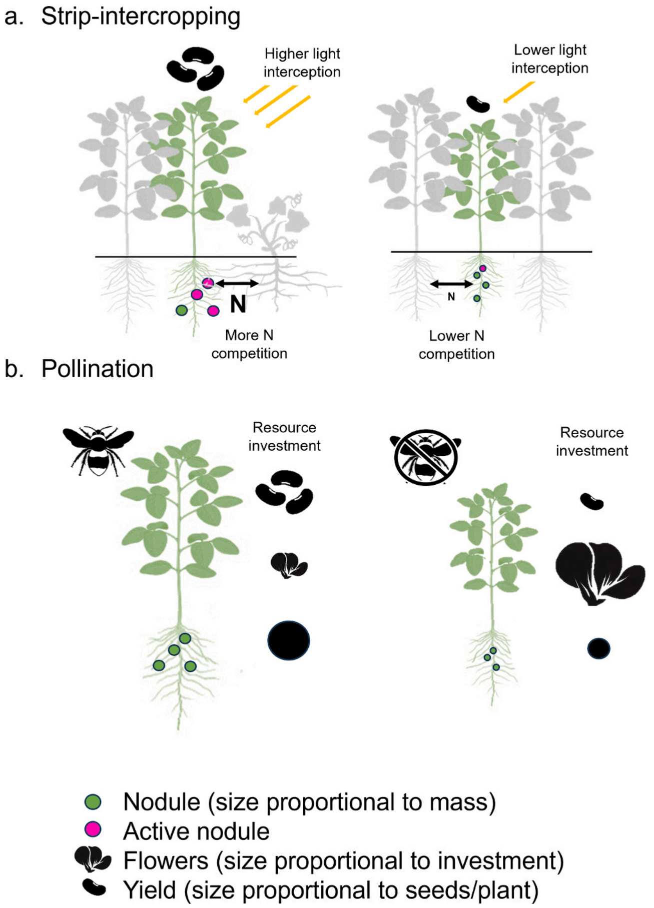

Fig. 5. Schematic summary figure illustrating the effects of (a) cropping system and (b) pollination on yield, biomass and nodulation parameters. Shown are hypothesized mechanisms of intercropping via changes in resource availability (light and nutrient (N)) and of pollination via shifts in resource allocation between yield, flowers and nodules. Note that flowers have not been measured in our study, this represents hypothesized mechanisms that should be further investigated. In addition, we found that some yield parameter (e.g. seeds per plant and per pod) increased with proportion of active nodulation in plants that were self-pollinated, but not under insect-pollination.

strong correlations between leaf N content and nodulation parameters (Figure SD.1), the origin of the N in the leaves remains unclear. Future studies could more precisely determine the proportion of biologically fixed N by applying stable isotope techniques (Li et al., 2009). We found a negative relationship between pollination treatment and leaf N and P content, likely due to nutrient reallocation toward reproductive structures at the expense of leaves Wenk et al., 2025). Positive effects of the strip-intercropping on both nodulation and yield parameters were observed at the strip edge but not at the centre of the strip (1.5 m from the edge, Supplementary material B). This finding suggests that using narrower strips or row intercropping may better utilize complementarity effects in intercropping systems (Wang et al., 2020), however, this might be difficult to implement due to current limitation in farming machinery size.

As expected, several faba bean yield parameters were enhanced by insect pollination treatment (Fig. 5b). In self-pollinated conditions, we found an average faba bean yield loss of 37 % compared to insect-pollinated conditions. Our findings are in line with a previous meta-analysis by Bishop and Nakagawa (2021), reporting on average 32.9 % faba bean yield loss in the absence of insect pollination. Reduced yield in self-pollinated plants was mainly due to insect pollinated plants having more pods and seeds per plant. This could have been driven by self-pollinated plants having reduced pod set or increased pod abortion. In contrast to earlier studies, self-pollinated plants did not have fewer seeds per pod nor higher individual seed weight compared to insect-pollinated plants (Lundin and Raderschall, 2021). While we cannot disentangle the mechanisms leading to increased yield in insect pollinated plants, our findings strengthen the case for insect pollinator management in faba bean production, which will become more urgent in the future given the rapid pollinator decline in agroecosystems (Dicks et al., 2021).

4.3. Interaction between pollination treatment and nodulation affect faba bean yield

We describe a novel relation by which pollination treatment indirectly affects crop yield via nodulation by moderating faba bean fertilization rate. The number of seeds per pod and seed per plant increased with increasing active nodulation in plants that were self-pollinated but not in insect-pollinated plants. This suggests that in plants that have a low proportion of active nodules the number of seeds per pod and hence crop yield is limited in self-pollinated plants, but this yield gap was closed in plants with higher active nodulation, via boosting the number of seeds per pod. As a result, at high levels of active nodulation, the yield gap between pollination treatments closed. The interaction only occurred between pollination treatment and active nodules – no interactions with nodule mass nor nodule number on yield parameters were found. Possibly, higher proportion of active nodules directly benefits available N for the plant, which is not necessarily the case for higher nodule mass or numbers as these can partly be inactive or senescing (Puppo et al., 2005). Previously, pollination in faba bean was found to interact with heat stress (Bishop et al., 2016), herbivory (Raderschall et al., 2021b) and presence of semi-natural habitats (Raderschall et al., 2021a) in shaping faba bean yield. As far as we know, this is the first record of an interactive effect between nodulation and pollination on faba bean yield. We also found complex interactions between cropping system, pollination treatments and nodulation. In self-pollinated plants, the number of seeds per plant was positively related to the proportion of active nodules in both monocropping and intercropping systems. In insect pollinated plants, on the other hand, the number of seeds per plant was independent of nodulation in intercropping systems but decreased with increasing nodulation in monocropping systems suggesting that plants in monocropping systems face a trade-off between seed production and BNF (Fig. 4b). Care should be taken in interpreting these interactions as not all plants might have been at the same developmental stage, depending on the cropping system or pollination treatments (or other unknown confounding factors). For example, the most productive, insect-pollinated monoculture plants might have already past their peak nodulation activity at the time of sampling. While more in depth investigation including direct assessment of fertilization rate, plant growth (e.g. distribution of pods per node) and flowering are needed to disentangle effects, these interactions highlight the combined benefit of increasing crop diversity and of supporting pollinator populations for faba bean production. Future research could further explore these interactions using a minirhizotron as a non-destructive method to assess nodulation (Gray et al., 2013) to make inferences about nodulation and yield on the same plant, which was not possible in our experiment.

5. Conclusions

Here we show that fully realizing the benefits of crop diversification - such as enhanced BNF and higher yields - relies not only on diverse cropping arrangements but also on supporting pollinator populations, for example by embedding diversified systems in pollinator-friendly landscapes. In addition, to the already known benefits of crop diversification and insect pollination on crop yields, we show for the first time that insect pollination positively affects activity of N fixing nodules. Our results indicate an interactive effect between pollination treatments and nodulation, where active nodules positively related to yield in self-pollinated but not in insect-pollinated plants. Future studies exploring plant resource allocation and the interactions between above- and belowground mutualisms are essential to uncover underlying mechanisms, which are important for the transition to more sustainable cropping systems. Nevertheless, these findings reveal a pathway through which pollination might indirectly influence yield by modulating fertilization rate and belowground plant-microbe interactions. Leveraging on natural processes to reduce dependency on synthetic inputs by maximizing synergies between above- and below-ground crop plant mutualists could support legume yields, particularly in low input systems.

CRediT authorship contribution statement

Riggi Laura Gianna Agnes: Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **van Apeldoorn Dirk F:** Writing – review & editing, Resources, Methodology. **Anna Edlinger:** Writing – review & editing, Methodology. **Raderschall Chloé A:** Writing – review & editing, Methodology. **Pibbe Dirkson:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109889.

Data availability

The data collected for this experiment will be made available on Zenodo online repository upon publication.

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