Insect pollination enhances faba bean yield more than weed removal or fungicide application

Chloé A. Raderschall [a,b,*], Laura G.A. Riggi [a], Ola Lundin [a]

[a] *Swedish University of Agricultural Sciences, Department of Ecology, Uppsala SE-750 07, Sweden*
[b] *Swedish University of Agricultural Sciences, Department of Plant Protection Biology, Lomma SE-234 22, Sweden*

A R T I C L E   I N F O

A B S T R A C T

Insect pollinators provide important crop pollination services but are declining in response to lack of diverse flower resources and exposure to pesticides. Despite increasing evidence that the benefits of insect pollination for crop production depend on other ecosystem services and crop management practices, investigations have mostly been limited to how pollination benefits are affected by insect pest control and soil fertility levels. Here we used a factorial cage experiment in the field to test how pollination by bumble bees, manual weed removal and fungicide application interactively shape faba bean (*Vicia faba*) yield components, and how weed removal and fungicide application affect bumble bee foraging behaviour. We found that insect pollination and weed removal increased faba bean yield components mostly additively, with insect pollination being the most important factor to maximise yield. The fungicide treatment did not affect crop yield, probably due to the low fungal pathogen incidence in the experiment, but instead affected bumble bee visitation behaviour. Bumble bees visited flowers of fungicide-sprayed plants more often than fungicide-free plants. This has potential consequences on bee health that should be further assessed. Guidelines on pesticide use should be improved by weighing benefits to agricultural productivity against risks for pollinators according to integrated pest and pollinator management principles. Our results emphasise that insect pollination can be an important factor for crop yield. The additive benefits of insect pollination and weed removal to crop yield indicates that they are crop production factors which can be managed for independently.

1. Introduction

Agricultural production benefits substantially from a suite of ecosystem services such as insect pollination, biological pest control and nutrient cycling (Losey and Vaughan, 2006). Paradoxically, many ecosystem services are being degraded by conventional agricultural practices using high inputs of pesticides, fertilisers and frequent tillage regimes (Tilman et al., 2011). Bee abundances and richness have declined in accord with the intensification of agricultural management practices, compromising the provision of crop and wild plant pollination (Biesmeijer et al., 2006; Grab et al., 2019; Potts et al., 2016). Exposure to agrochemicals such as insecticides, herbicides and fungicides has been identified as one of the major drivers contributing to bees declining (Dicks et al., 2021). The implementation of ecological intensification aims to manage agroecosystems to enhance ecosystem services such as insect pollination or control of pests - including herbivores, weeds or pathogens - to reduce or even replace harmful agrochemical inputs

(Bommarco et al., 2013). While there is evidence that managing for increased beneficial arthropod or plant diversity can enhance ecosystem services delivery alongside crop production (Dainese et al., 2019; Kovacs-Hostyanszki et al., 2017), effective uptake of the concept by farmers remains limited (Kleijn et al., 2019). To incentivise the adoption of ecological intensification, better knowledge is needed on the combined effects of ecosystem services and conventional management practices on crop production.

Insect pollination does not shape crop yield in isolation. Rather, the contribution of insect pollination to crop yield has to be assessed in the context of other ecosystem services, crop management practices and biotic and abiotic stressors influencing crop yield (Boreux et al., 2013). Interactive effects between ecosystem services, such as insect pollination, soil fertility, and insect pest control, on crop yields are increasingly evident (Garibaldi et al., 2018; Tamburini et al., 2019). To date, interactions between insect pollination and insect pest control have most often been found to shape yields in a neutral-to-synergistic manner, with

the benefit of insect pollination being similar or greater in undamaged plants (Garibaldi et al., 2018; Martinez-Salinas et al., 2022). Synergistic effects between insect pollination and insect pest control on crop yields can be driven by insect pests damaging and reducing plant reproductive structures or by changing the quality of floral rewards, both of which can lead to reduced pollinator visitation and cancel pollination benefits (Sutter and Albrecht, 2016; Tamburini et al., 2019). Pest-induced plant stress can also interfere with plant resource acquisition and allocation to reproduction, and thereby limit the contribution of insect pollination to seed formation (Tamburini et al., 2019). Similar to insect pests, plant pathogens and weeds are biotic stressors inflicting serious crop yield losses worldwide despite crop protection efforts (Oerke, 2006). There is some indication that weeds and plant diseases can limit the crops' ability to respond positively to insect pollination (Melathopoulos et al., 2014; Motzke et al., 2015) similarly to insect pests, but empirical evidence is sparse. It is not well understood whether the insect pollination benefit is inhibited in the presence of weeds or plant pathogens due to physiological constraints e.g. induced weed-crop competition for light, water or nutrients, or indirect effects by interfering with pollinator visitation behaviour.

Fungicides are often used to control fungal plant pathogens while herbicide use and mechanical removal are common methods to manage weeds. Because herbicides and fungicides are not designed to target insects, less research has been dedicated to assess their impact on bees and other insects compared to insecticides (Cullen et al., 2019). In the past few years, however, evidence has been collected that fungicides negatively affect bees and crop pollination (Rondeau and Raine, 2022; Tamburini et al., 2021). One important aspect that affects fungicide exposure and risk for bees is how fungicide use affects flower visitation rates. Thus far, research has, however, shown mixed results with both increased and decreased flower visitation to fungicide-treated plants (Stejskalová et al., 2018; Tarno et al., 2018; Voß et al., 2023). Concerning weed control, irrespective whether through chemical or mechanical means, a main effect on pollinators is the removal of food resources (Bretagnolle and Gaba, 2015). Flowering weeds provide essential alternative nectar and pollen resources when left to persist (Balfour and Ratnieks, 2022; DiTommaso et al., 2016) and can support pollination of flowering crops (Crochard et al., 2022). Weeds and other alternative forage might also alter pollinator foraging behaviour in crops (Raderschall et al., 2022). Interactive effects between insect pollination, weed removal and fungicide treatment on yield need to be understood to optimise crop management and limit yield gaps.

Faba bean (*Vicia faba* L.) is one of the most important grain legume crops worldwide (Karkanis et al., 2018). In central and northern European agricultural landscapes, faba bean provide important late-season food resources for pollinators at times when other flowering resources are sparse (Timberlake et al., 2019), and the flowers are frequently visited by honey bees (*Apis mellifera* L.) and bumble bees (*Bombus* sp.) (Beyer et al., 2020; Lundin, 2023). Even though faba bean plants can produce seeds through autogamy (hereafter auto-pollination), yields generally increase with insect pollination, although the insect pollination benefit varies among cultivars (Bishop et al., 2020; Bishop and Nakagawa, 2021). The insect pollination benefit is also mediated by biotic and abiotic stressors such as insect herbivory or extreme weather events (Bishop et al., 2016; Raderschall et al., 2021a; Riggi et al., 2022). Bee foraging behaviour plays an important role for faba bean pollination, because not all types of flower visits transfer pollen. Bees can visit faba bean flowers legitimately, by entering the front of the corolla and contributing to cross-pollination, or they can rob the flowers for nectar by piercing a hole at the base of the corolla without cross-pollinating, which is less beneficial for yield (Tasei, 1976; Lundin, 2023). Furthermore, faba bean are susceptible to plant diseases such as the chocolate spot disease (caused by *Botrytis fabae*) and faba bean rust (caused by *Uromyces viciae-fabae*), and weeds can reduce yield by up to 50 % due to competition for resources (Frenda et al., 2013). To ensure co-management of pollination and crop protection practices in faba bean

production, a better understanding of the interactions among insect pollination and control efforts against plant pathogens and weeds is needed.

Our aim was to examine how insect pollination, weed removal and fungicide application interactively shape crop yield components in faba bean. We expected faba bean plants that are insect-pollinated, weed-free and sprayed with fungicide to produce the highest yield, because these plants would benefit from cross-pollination by insects and not be affected by weed-crop competition or yield-limiting pathogens. Further, we expected that the benefits from insect pollination on faba bean yield depended on weed removal and fungicide application by interfering with resource acquisition and allocation. To gain insights into potential mechanisms, we explored how the weed and fungicide treatments affected pollinator visitation rates and foraging behaviour.

2. Methods

2.1. Experimental design

We performed a field experiment in a faba bean (cv. Sampo) field of approximately 0.1 ha at Lövsta field station (59°50′30″N, 17°47′19.0″E) outside of Uppsala, Sweden in 2021. Sampo (Boreal Plant Breeding Ltd, Jokioinen, Finland) is a Finnish cultivar grown at higher latitudes because it has a short growing period. We are not aware of any previous information on this cultivar's insect pollinator dependency. We chose this cultivar because unusually late snow melt delayed the sowing until June 9. Upon plant emergence we erected 28 cages, each two by two by two meters covered with a nylon net (Artes Politecnica SRL, Schio, Italy), with a mesh size of 0.35 by 1.6 mm. The net was dug approximately 10 cm into the ground to prevent insects from leaving or entering the experimental plots. Cages were set up such that there were at least 5 m to the closest edge of the faba bean field and 7 m between cages to avoid shading effects (Fig. 1). We used a randomised complete block design replicated in seven blocks for the pollination treatment (i.e insect pollination *versus* auto-pollination) crossed with the weed treatment (i.e. weed-free *versus* weedy). Nested within the block design we used a split-plot design for the fungicide treatment, such that each cage contained two subplots assigned to be either fungicide-sprayed or sprayed with distilled water to serve as control (Fig. 1). In every cage, we marked ten experimental faba bean plants of similar size and bud numbers in each fungicide treatment subplot before the onset of faba bean bloom.

Because of an aphid outbreak inside some of the cages, the nylon nets covering the cages were removed about a week earlier than planned when some plants still had individual flowers (BBCH 69, Weber and Bleiholder, 1990) to allow natural enemies to control the aphids. To make sure that removing the cages did not compromise the pollination treatment, we marked plant stems with a plastic ring at the height of the remaining open flowers, to know, which flowers were potentially insect pollinated in assigned auto-pollinated cages. Across all cages, eight experimental plants that were assigned to be only auto-pollinated produced pods after the cages were removed. Together they yielded 18 pods and 30 beans weighing 3.56 g (0.93 % of total bean dry mass assigned to auto-pollination), which we considered to be negligible. To compare yield components in all plants across the same time period and conditions, we included these pods and beans in the analyses.

2.1.1. Pollination treatment

When faba bean flowers on the first raceme had opened (BBCH 61; 14 July), half the cages were supplemented with one hive of buff-tailed bumble bees (*Bombus terrestris* L.). The buff-tailed bumble bee is the most common and important wild pollinator of faba bean in Sweden (Raderschall et al., 2021b; Lundin, 2023) and is the only bumble bee species that is commercially available in Europe. The hives consisted of approximately ten workers and male brood and were supplemented with sugar water inside the hive (Natupol Seeds; Koppert Biological Systems). Bumble bees were enclosed but able to forage freely on faba bean

Fig. 1. Experimental set-up showing a) the distribution of the four treatments within the faba bean field with pollinator-supplemented cages subject to insect pollination (P), pollinator-free cages subject to auto-pollination (AP), weed-free cages (WF)) subject to weed removal by hand and weedy cages where weeds were left to grow (W), and b) illustrating the four treatments contained in each of the seven blocks: insect-pollinated (bumble bee icon), auto-pollinated (no bumble bee icon), weed-free (light blue) and weedy (light green). Within each of the four treatments, plants in one half of the cage were sprayed with fungicide (F, dark green), while the other half was sprayed with distilled water and served as a control (C, brown). The photos show a weedy subplot (bottom left) and a bumble bee legitimately visiting a faba bean flower (bottom right).

flowers and weeds within the cage, and in addition were provided with pollen outside the hive to counteract unrealistically high faba bean flower visitation rates. Bumble bee hives were kept in the field until harvest - even after the cages were removed and faba bean flowering had ended.

2.1.2. Weed treatment

We relied on the local weed community for our weedy treatment. The field was previously conventionally managed but was not treated with herbicides in the year we conducted the experiment. Weeds in the entire field were only mechanically controlled once the day before faba bean seeds were sown by harrowing, which removes the soil from around the roots of the weeds, and helps the germination of the faba bean seeds. Once the cages were erected, weed-free cages were checked weekly and any emerging weeds manually removed to prevent weed-crop competition. Care was taken not to touch or shake the experimental plants when removing any weeds. Weeds in the weedy cages were left to grow.

During crop maturation (BBCH 85; early August), when weeds reached peak biomass, and faba bean had stopped flowering, we collected the aboveground biomass of each weed species in each subplot per cage by cutting the plants just above the soil surface. Weeds were oven dried at 65 degrees C over 48 hours and dry biomass was weighed.

2.1.3. Fungicide treatment

In each cage, a subplot of faba bean plants was sprayed with 0.5 kg per hectare of the fungicide Signum © (BASF; 267 g/kg boscalid + 67 g/kg pyraclostrobin) at the onset of faba bean bloom (BBCH 60; July 11). The other half of the cage was sprayed with the same amount of distilled water instead of fungicide to serve as control. We used two 5 l handheld pressure sprayers for the application; one for each treatment, that had a nozzle, which was pointed directly at the plants to avoid contamination of the control treatment with fungicide.

Chocolate spot and faba bean rust caused by the common fungal pathogens *B. fabae* and *U. viciae-fabae*, respectively was estimated on three randomly selected plants per subplot in all cages at the end of the growing season (BBCH 88; mid-September) by estimating the percentage of leaf area covered with lesions. Only faba bean rust and no chocolate spot or symptoms of other fungal diseases were, however, found. In two cages, all plants in one subplot each were wilted due to aphid damage and it was not possible to estimate the percentage of leaf area covered with pathogen lesions.

2.1.4. Pollination visitation behaviour

During faba bean bloom (BBCH 61–68), we observed bumble bees every afternoon between July 15 - July 23 over 14 minutes in each cage supplemented with bumble bee hives. One experimental fungicide-sprayed plant was damaged on July 17 and removed from the experiment for the remaining observation. We observed bumble bees over seven minutes in each subplot and counted the number of visits made to the marked plants. The order in which each fungicide treatment was observed was alternated among cages and reversed between visits. For each bumble bee visit we noted the plant identity and whether the bumble bee was visiting legitimately or was robbing nectar. Visits to extra-floral nectaries were also noted but because it was difficult to count the exact number of visits made, and because extra-floral nectary visits do not contribute to pollination, we excluded these visits from further analyses. At the end of each observation period we counted the number of open flowers on each of the marked plants. In addition to the end-of-season disease assessment conducted in all cages (see above), and to more closely link any presence of plant disease to pollinator foraging behaviour, we also inspected all marked plants in each fungicide treatment of the pollinator-supplemented cages multiple times per week during faba bean bloom for plant diseases. We graded chocolate spot and faba bean rust by estimating the percentage of leaf area covered with lesions. Only faba bean rust, and no chocolate spot or symptoms of other fungal diseases were, however found on any of the plants.

2.1.5. Yield and yield components

When pods reached maturity (BBCH 89; late September), we estimated plant density by counting the number of faba bean plants within a 0.36 m^2 quadrat randomly placed in each subplot. Subsequently, we manually harvested experimental plants from both fungicide treatment subplots in each cage (ten fungicide-sprayed and ten control plants) by cutting the plants just above the soil surface and storing them in individual paper bags. In the laboratory, plants were oven dried at 65℃ for 48 hours. After drying, we counted pods per plant and beans per pod and weighed aboveground plant biomass (including leaves, stems and pod husks) and beans separately. Individual bean weight was calculated by dividing total bean weight per pod with the number of beans per pod. To provide a measure of agronomic relevance, yield was calculated by multiplying the average bean mass per plant in each subplot with crop plant density per quadrat, and then recalculated and expressed as kg dry bean mass per hectare. Due to the small scale of the cage experiment, care should, however, be taken when comparing this yield measure to on-farm harvested yields.

2.2. Statistical analyses

Statistical analyses were done using (generalised) linear effects models in R version 4.2.0 for Windows (R Core Team, 2022). Linear mixed effect models were analysed with the *lmer* function (package: *lme4* (Bates et al., 2015)) and generalised linear mixed effect models were analysed with the *glmmTMB* function (package: *glmmTMB* (Brooks et al., 2017)). The amount of variances that contributed to a sample by the different treatment factors was analysed with a type 2 ANOVA (package: *car* (Fox and Weisberg, 2019)). All models included treatment interactions as fixed effects as defined below. We did not simplify models because treatment interactions were an inherent part of the experimental design. We visually examined the residuals of each model to assure that model assumptions were met (package: *DHARMa* (Hartig, 2022). The 95 % confidence intervals were extracted using the *emmeans* function (package: *emmeans* (Lenth, 2023)) and results plotted using the *geom_boxplot* function in *ggplot2* (package *ggplot2*, (Wickham, 2016)).

2.2.1. Weed biomass and species richness

Weed biomass and weed species richness were summarised per subplot in weedy cages (N = 14). Weed biomass was analysed with a normal distribution and weed species richness with a Conway-Maxwell Poisson error distribution with a log link to account for underdispersion (Huang, 2017). As fixed effects we added the pollination and fungicide treatment and their two-way interaction to verify that weed effects were balanced across all treatments. Block, and cage identity nested within block identity were added as random effects.

2.2.2. Plant diseases

The percentage of leaf area with faba bean rust lesions was averaged across the three experimental plants per subplot and analysed with a normal distribution. As fixed effects we added the pollination, fungicide and weed treatment and their two-way and three-way interaction, to test if disease severity of bean rust was affected by treatments. Block, and cage identity nested within block identity were added as random effects.

2.2.3. Faba bean yield and yield components

To analyse faba bean yield, yield components and aboveground crop biomass, we used bean yield per hectare, bean mass per plant, individual bean weight, number of pods, number of beans and aboveground crop biomass (stalks, leaves and pod husks, excluding beans) as response variables. We aggregated data of all variables across the ten experimental plants in each fungicide treatment subplot prior to analyses. We used a normal distribution for analysing the average yield per hectare, bean mass per plant, individual bean weight and aboveground crop biomass, and a Conway-Maxwell Poisson error distribution, to analyse the total number of pods and beans. For the number of pods we added the log-transformed number of plants per subplot as an offset to effectively analyse pods per plant, while for the number of beans we added the log-transformed number of pods as an offset to effectively analyse beans per pod (Reitan and Nielsen, 2016). Yield per hectare and bean mass per plant were square root transformed to meet model assumptions. We included the pollination, weed and fungicide treatment and their two- and three-way interaction as explanatory variables in all models. Block, and cage identity nested within block identity were included in all models as random effects.

Late during the flowering period, black bean aphid (*Aphis fabae* Scopoli) colonies started to spread among many of the experimental plants inside the cages. While many cages were affected, one cage in particular (cage 14, P/WF) was heavily affected causing almost complete yield loss. To test whether this cage stood out among all cages, such that it would justify analysing yield and yield components without cage 14, we extracted the random effects of the model estimated yield per hectare using the *ranef* function (package: *lme4* (Bates et al., 2015)). The results showed that cage 14 deviated the most from the estimated yield, with a much lower yield than expected, and could be considered an outlier (Fig. S1, Table S1). As a result, we analysed yield and yield components without cage 14, but show the results including cage 14 in the Supplementary materials.

2.2.4. Pollinator visitation behaviour

Flower abundance, pollinator visitation rate for both legitimate visits and nectar robbing, and plant diseases during flowering were analysed for all cages containing bumble bee hives (N=14). We summed flower and pollinator visitation data across the ten marked plants for each subplot and sampling day. To analyse the number of open flowers per plant, we used a model with a Poisson error distribution and a log link with the number of open flowers as response variable and the log-transformed number of plants per subplot as an offset. To analyse the number of legitimate and nectar robbing visits per flower, we used a model with a Conway-Maxwell Poisson error distribution with a log link with the number of visits as response variable and the log-transformed number of open flowers as an offset. To analyse plant diseases, we averaged the percentage of leaf area with faba bean rust lesions over the entire observation season. As fixed effects we added fungicide treatment and weed treatment and their two-way interaction in all models. Block, and cage identity nested within block identity were added as random effects, and in the models for flowers and pollinator visitation also sampling day nested within cage identity and block identity.

3. Results

3.1. Weed treatment

We identified 13 weed species that spontaneously grew among our 14 weedy cages and on average four weed species were found per cage subplot (Table S2). All species except for an unidentified grass (<1 % of the weed biomass) produced flowers. Two species, wild mustard (*Sinapis arvensis*) (59.9 %) and white goosefoot (*Chemopodium album*) (35.7 %) were dominating the weed community in terms of aboveground biomass (Table S2), and both species were flowering at the same time as faba bean and regularly visited by the bumble bees (C. Raderschall, pers. obs.). Weed dry biomass per cage subplot was on average 55.0 g but varied among cages (range: 8.2–218.4 g, Fig. S2). We found no difference in weed biomass or species richness between the pollination or fungicide treatments (Table S3).

3.2. Fungicide treatment

Plant disease severity was very low in all subplots. We found no chocolate spot symptoms on any of the plants, and disease severity of faba bean rust was limited in both fungicide treatments (mean: 4.4 %, range: 0–12.5 %). There was a tendency of higher faba bean rust pressure in fungicide-sprayed subplots than in control plots (Table S4, *p=0.087*).

3.3. Faba bean yield and yield components

Faba bean yield (kg per hectare) and bean mass per plant were 164 % and 169 % higher, respectively, in insect pollinated compared to auto-pollinated cages (Table 1, Fig. 2a, c), and 64 % and 78 % higher, respectively, in weed-free compared to weedy cages (Table 1, Fig. 2b, d). Individual bean weight was not explained by any of the treatments (Table 1). The number of pods per plant was explained by an interaction between the pollination and the weed treatment (Table 1, Fig. 2e). Post-hoc tests revealed that the number of pods per plant was 45 % lower in weedy cages compared to weed-free cages, but only in auto-pollinated cages *(p=0.0014)*. In insect-pollinated cages the number of pods did not differ between weedy and weed-free cages *(p=0.36)*. Insect pollination increased the number of pods by 81 % in weedy cages and 75 % in weed-free cages. The number of beans per pod was 19 % higher in insect-pollinated compared to auto-pollinated cages (Table 1, Fig. 2f).

Table 1
Results from (generalised) linear mixed effects models excluding cage 14 for: yield (kg per hectare), bean mass per plant (grams), individual bean weight (grams), the number of pods per plant, the number of beans per pod and aboveground plant biomass (grams) with respect to the pollination (P), weed (W) and fungicide (F) treatments and their two-, and three-way interaction. Shown are test statistics (F or χ2), (denominator, d) degrees of freedom (DF) and p-values (p) for the respective treatments. Model error distributions (compois – Conway-Maxwell Poisson) are also listed.

Variable		P	W	F	P*W	P*F	W*F	P*W*F	model
Yield	F	**21.21**	**5.77**	0.13	0.62	0.034	<0.01	0.48	normal
	dDF	**17**	**17**	23	17	23	23	23	
	p	**<0.001**	**0.028**	0.72	0.44	0.86	0.99	0.50	
Bean mass per plant plant (g)	F	**26.07**	**9.05**	0.37	0.080	0.018	<0.01	0.66	normal
	dDF	**17**	**17**	23	17	23	23	23	
	p	**<0.001**	**0.0078**	0.55	0.78	0.90	0.94	0.43	
Ind. bean weight (g)	F	0.45	2.95	3.27	0.050	0.63	3.61	0.095	normal
	dDF	17	17	23	17	23	23	23	
	p	0.51	0.10	0.084	0.83	0.44	0.070	0.76	
Number of pods per plant	χ2	**48.33**	**7.49**	0.037	**4.50**	<0.01	1.19	1.45	compois
	DF	**1**	**1**	1	**1**	1	1	1	
	p	**<0.001**	**0.0062**	0.85	**0.034**	0.97	0.28	0.23	
Beans per pods	χ2	**42.80**	0.39	1.74	0.021	1.87	0.018	01.83	compois
	DF	**1**	1	1	1	1	1	1	
	p	**<0.001**	0.53	0.19	0.89	0.17	0.89	0.18	
Crop biomass (g)	F	0.094	**9.43**	1.16	1.35	0.53	2.31	0.90	normal
	dDF	17	**17**	23	17	23	23	23	
	p	0.76	**0.0068**	0.29	0.26	0.48	0.14	0.35	

Aboveground crop biomass was 25 % higher in weed-free cages compared to weedy cages (Table 1, Fig. 2g). None of the yield components were affected by the fungicide treatment (Table 1).

Keeping cage 14 (P/WF) in the analyses despite its severe aphid attack influenced the interpretation of the weed treatment. With cage 14, yield per hectare (Fig. S3a) and bean mass per plant (Fig. S3b) were only influenced by the pollination but not the weed treatment. The effects of treatments on other yield components did not change qualitatively by including cage 14 (Table S5, Fig. S3).

3.4. Pollinator visitation behaviour

Over the entire experimental season we counted 11304 open flowers and observed 811 legitimate bumble bee visits and 1455 nectar robbing visits. The number of open flowers per faba bean plant was explained by an interaction between the weed and the fungicide treatment (Table 2, Fig. 3a). Post-hoc tests revealed that the number of open flowers per faba bean plant tended to be higher in fungicide-sprayed subplots compared to control subplots, but only in weed-free cages (p=0.071). In weedy cages, the number of open flowers per plant did not differ between fungicide-sprayed and control subplots (p= 0.10). The number of legitimate flower visits made by bumble bees tended to by higher in fungicide-sprayed than in control subplots (Table 2, Fig. 3b, p=0.052). Bumble bees robbed nectar from flowers in fungicide-sprayed subplots more often than control subplots (Table 2, Fig. 3c). Plant diseases during the flowering period were low in all subplots with no signs of disease except for faba bean rust (mean 1.48 %, range 0.66–1.73 %). The percentage of fungal infection did not differ among the treatments (Table 2).

4. Discussion

We found that insect pollination and weed removal both increased yields as expected, whereas fungicide treatment did not affect yield. Against our expectation insect pollination and weed removal shaped faba bean yield and yield components mostly additively. In accord with the additive effects, we did not find any effect of weed removal on pollinator foraging behaviour. However, in conventionally managed fields, weeds are often controlled using herbicides, which can have negative effects on bumble bees (Straw et al., 2021; Weidenmüller et al., 2022). As such, weed removal using herbicides might influence pollinator visitation rate and behaviour and cause interactive effects between the weed and the pollination treatment on yield that were not explored here. Pollinators unexpectedly visited fungicide-sprayed plants more frequently than control plants, in particular when they were robbing nectar.

Insect pollination increased faba bean yield (+164 %), bean mass per plant (+169 %), beans per pod (+19 %) and pods per plant (+81 % in weedy and +75 % in weed-free cages) substantially compared to auto-pollinated plants and was the most important factor to maximise yield. The importance of insect pollination in our experiment is in accord with research in leek, watermelon and cucumber production systems, which found that insect pollination was the most yield-limiting factor (Fijen et al., 2020; Leach and Kaplan, 2022; Motzke et al., 2015). In faba bean, yield benefit from insect pollination varies greatly among cultivars, experiments and sites (Bishop et al., 2020) but a meta-analysis has shown that there is an 80 % chance of some yield increase from insect pollination (Bishop and Nakagawa, 2021). The insect pollination benefit in the cultivar Sampo we used here, has not been studied earlier and was found to be comparably high. We here quantified the insect pollination benefit on yield components by comparing bumble bee to auto-pollinated flowers in cages where both pollination treatments are somewhat exaggerated with bumble bees visiting faba bean flowers more often than what has been observed in an open field (Lundin, 2023), and with control plants receiving no visits. However, we did not find evidence that over-visitation compromised yield, whereas in field experiments, we did not find evidence that faba bean yields are pollen-limited by insufficient insect pollination under open-pollinated field conditions (Lundin and Raderschall, 2021). Hence we can confirm that insufficient insect pollination is a large potential yield-limiting factor in the absence of any pollinators, whereas it is likely a smaller realised yield-limiting factor in faba bean farming (but see: Cunningham and Le Feuvre, 2013).

Weed removal also benefited faba bean yield and bean mass per plant (+ 64 and 78 %, respectively) but to a lesser extent than insect pollination. Considering that the weed pressure was low in our experimental site, we can expect that yield losses due to weed infestation could be more severe in fields with a higher weed seed bank of competitive weed species. The fungicide treatment did not have any effect on yield but we also did not observe any chocolate spot disease, despite this being a plant disease of major concern in faba bean in northern Europe (Bankina et al., 2021; Olle and Sooväli, 2020; Stoddard et al., 2010), and the disease severity of faba bean rust was low. This shows that even major yield-limiting factors such as plant disease in faba bean are heterogeneous and can be practically absent even during a growing season that was not unusually dry or otherwise unsuitable for these plant diseases.
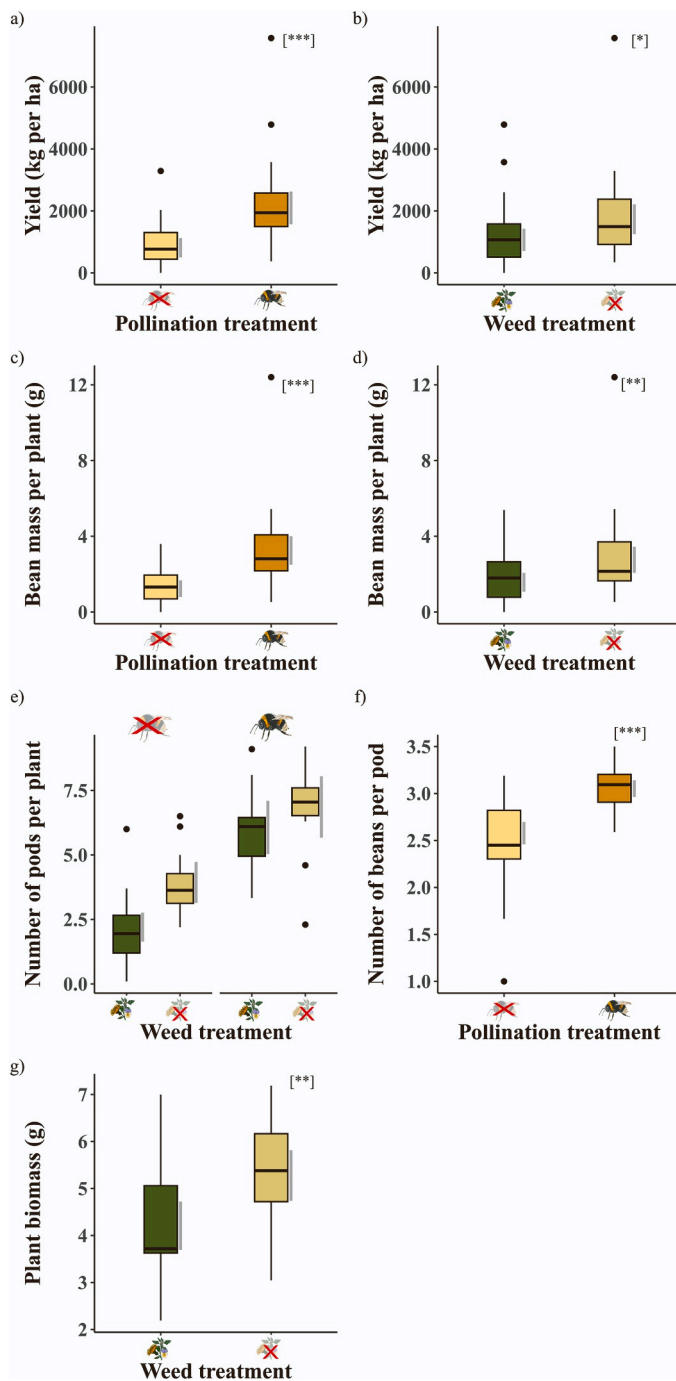
Fig. 2. Boxplots of yield components without cage 14 showing a, b) yield (kilogram per hectare), c,d) bean mass (grams) per plant, e) number of pods per plant, f) the number of beans per pod (grams) and g) above ground plant biomass (grams) in respect to the pollination treatment or the weed treatment. Auto-pollinated plants (crossed-out bumble bee icon, light yellow), insect-pollinated plants (bumble bee icon, dark yellow), weed infested plants (plant icon, dark green), weed-free plants (crossed-out plant icon, light green). Boxplots show the 25th, 50th (median) and 75th percentiles and whiskers extend 1.5 the interquartile range. Grey bars indicate 95 % confidence intervals extracted from the models. Asterisks indicate alpha-levels of the p-values of main effects: ***=p<0.0010, ** =p<0.010, *=p<0.050.

The number of pods per plant was the only yield component that was shaped by an interaction between the pollination and the weed treatment. The negative effect of weeds on the number of pods was less pronounced in insect-pollinated compared to auto-pollinated plants,

Table 2

Results from (generalised) linear mixed effects models for: average number of open flowers per plant, frequency of legitimate bumble bee visits per flower and frequency of nectar robbing per flower with respect to the weed (W) and fungicide (F) treatments and their two-way interaction. Shown are Chi-square values ($\chi 2$), p-values (p) and (denominator, d) degrees of freedom (DF) for the respective treatments. Model error distributions (compois – Conway-Maxwell Poisson) are also listed. Values in bold indicate significance at an alpha-level of 0.05.

Variable		W	F	W*F	model
Open flowers per plant	$\chi 2$	0.85	<0.01	**6.00**	Poisson
	p	0.36	0.94	**0.014**	
	DF	1	1	**1**	
Legitimate visits per flower	$\chi 2$	0.069	3.77	0.11	compois
	p	0.79	0.052	0.75	
	DF	1	1	1	
Robbing per flower	$\chi 2$	<0.012	**12.07**	2.42	compois
	p	0.97	**<0.001**	0.12	
	DF	1	**1**	1	
Plant disease	F	0.012	1.69	0.014	normal
	p	0.92	0.22	0.91	
	dDF	6	12	12	

suggesting that insect pollination might buffer the negative effects of weed-crop competition. This result is in contrast to what has been found in cucumbers, where weed control increased yields more in insect-pollinated cucumber plants than in auto- and self-pollinated plants (Motzke et al., 2015). In general, such synergistic interactions among ecosystem services are more common than antagonistic interactions (Garibaldi et al., 2018). This is probably because lack of crop protection practices - be it targeting weeds, pathogens or insects - usually reduces the number of flowers or flower rewards, which subsequently reduces pollinator visitation and yield (Motzke et al., 2015). In our experiment, there was no indication that the weed treatment affected the number of faba bean flowers nor pollinator visitation behaviour. It is possible that under the experimental conditions with few weed flowers and high pollinator densities, potential effects of the weed treatment on pollinator visitation behaviour to faba bean flowers were masked because pollinators were forced to visit less attractive or rewarding faba bean flowers, despite being supplemented with sugar water and pollen. The antagonistic interaction between pollination and weeds on pod set might have been caused by differential resource allocation. Insect-pollinated faba bean plants might have been able to allocate more resources into pod production to compensate for the yield loss induced by weed-crop competition, while auto-pollinated plants might have allocated resources into seed formation and away from pod production and aboveground biomass to compensate for the lack of insect pollination. One indication that weeds might induce a shift in the allocation of resources away from crop biomass production and into physiological responses to weeds (Horvath et al., 2023) is the lower above-ground faba bean plant biomass in weedy cages. Whichever the mechanism, the interactive effect on pod set did not manifest in bean yield.

Bumble bees visited faba bean flowers in fungicide-sprayed subplots more often than in unsprayed control subplots. Particularly pollinators that were robbing for nectar showed a preference for robbing from fungicide-sprayed flowers. The lack of quantifiable effects on any major plant diseases makes it less likely that the pollinators' preference for fungicide-sprayed plants was due to pollinators avoiding pathogen-infected plants. A similar effect of fungicides has been described in sunflowers and coffee, where bumble bees and honey bees, respectively, visited flowers sprayed with fungicide more often than flowers in the control treatment (Stejskalová et al., 2018; Tarno et al., 2018). This preference for fungicide-sprayed flowers in bumble bees is concerning considering that fungicide exposure can hamper body size development, colony growth and pollination (Tamburini et al., 2021; Wintermantel et al., 2022). Contrary to our finding, bumble bees visited flowers less frequently following fungicide application in strawberry (Voß et al.,
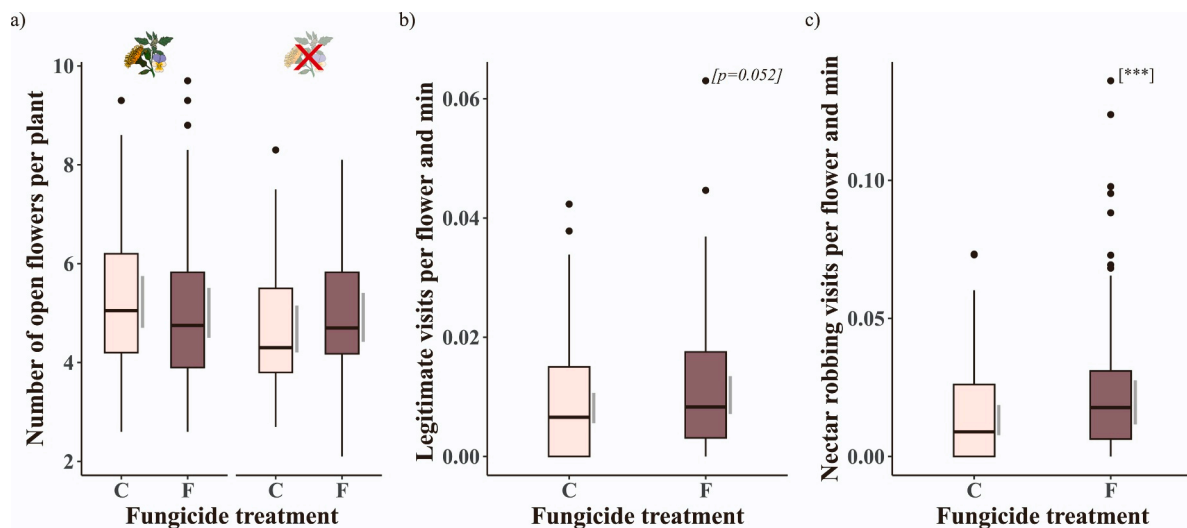
Fig. 3. Boxplots showing a) the number of open flowers per plant, b) the frequency of legitimate pollinations visits per flower and minute and c) the frequency of nectar robbing visits per flower and minute in respect to the weed and fungicide treatments: Weedy (plant icon), weed-free (crossed-out plant icon), control plants (light pink, C), and fungicide-sprayed.(dark pink, F). Boxplots show the 25th, 50th (median) and 75th percentiles and whiskers extend 1.5 the interquartile range. Grey bars indicate 95 % confidence intervals. Asterisks indicate alpha-levels of the p-values of main effects: [***] = p<0.0010.

2023). It is possible that the effect of fungicides on bee visitation differs depending on the fungicide's active ingredients. The active ingredient in both our study and that on sunflower (Stejskalová et al., 2018) was boscalid, whereas the study in strawberry was on cyprodinil and fludioxonil or copper (Voß et al., 2023). Despite its potential attractive effects on bumble bees, chronic exposure to field-realistic doses of boscalid can lead to lethal toxicity in honey bees (Simon-Delso et al., 2018), and thus also provide risks to bumble bees. Higher visitation to pesticide-treated plants can, however, be both positive and negative for bee populations depending on the relative effects on additional resources gained and increase in risk from pesticide exposure (Knapp et al., 2022). The mechanisms underlying the higher attraction of bumble bees to fungicides-sprayed plants are unclear. It is, however, likely not a direct effect of the fungicide but rather due to changes in plant volatiles or floral resource quality due to interference with leaf-, root- or nectar-associated fungal communities (Cahill et al., 2008; Voß et al., 2023). There was a tendency that fungicide-sprayed plants produced more flowers in weed-free cages. But considering that we analysed bumble bee visitation rate per flower, flower abundance is likely not driving the preference for visiting fungicide-sprayed plants in our study.

For our cage experiment, we experimentally introduced two pollination treatments but relied on the field baseline for the pathogen and weed infestation. Future experiments addressing similar questions could complement our approach with open field experiments, where each treatment is more variable and it is harder to isolate treatment combinations compared to the more controlled cage studies (Schmitz, 2008), but which allow for multi-site replication.

5. Conclusions

We have reconfirmed the importance of insect pollination in faba bean by showing that it enhances yield substantially compared to auto-pollination, with weed removal playing a secondary role and fungicide use not affecting yield in our experiment, where plant disease severity was low. The benefits of insect pollination and weed removal for yield components were mostly additive, indicating that they can be managed for independently. Only the number of pods per plant was shaped by a negative interaction suggesting that insect pollination can buffer the negative effects of weeds on pod development. Pollinators are in decline due to several factors such as loss of habitat and floral resources,

pesticides and pathogens (Dicks et al., 2021). While the risk of insecticide use for pollinators is well documented, fungicides are often the pesticide type that pollinators are most exposed to (McArt et al., 2017) yet their effects on non-target organisms such as pollinators are poorly understood (Cullen et al., 2019). The result that fungicide-sprayed plants were visited more frequently by bumble bees than control plants is therefore concerning because it could have detrimental effects for bumble bee populations. Access to diverse flower resources can offset the negative effects of fungicide and insecticide use on bee fitness (Klaus et al., 2021; Wintermantel et al., 2022). We therefore recommend to avoid routine sprays against pests, whereby pollinators are unnecessarily exposed to agrochemicals and weed eradication exacerbates the lack of diverse flowering resources. Agricultural policy should improve guidelines on pesticide use by weighing benefits to agricultural productivity against risks for pollinators according to integrated pest and pollinator management (IPPM) principles (Egan et al., 2020; Lundin et al., 2021).

CRediT authorship contribution statement

Chloë A. Raderschall: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Conceptualization, Formal analysis. **Laura G.A. Riggi:** Writing – review & editing, Methodology, Conceptualization. **Ola Lundin:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, 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.

Data Availability

The data that support the findings of this study are openly available via the Swedish National Data Service at: https://doi.org/10.5878/z69q-bf06.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2024.109159.

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