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Insect pollination as an agronomic input: Strategies for oilseed rape production

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Abstract

1. Ecological intensification involves the incorporation of biodiversity-based ecosystem service management into farming systems in order to make crop production more sustainable and reduce reliance on anthropogenic inputs, including fertilizer and insecticides.
2. The benefits of effectively managing ecosystem services such as pollination and pest regulation for improved yields have been demonstrated in a number of studies, however, recent evidence indicates that these benefits interact with conventional agronomic inputs such as fertilizer and irrigation. Despite the important contribution of biodiversity-based ecosystem services to crop production their management is rarely considered in combination with more conventional agronomic inputs.
3. This study combines a number of complementary approaches to evaluate the impact of insect pollination on yield parameters of *Brassica napus* and how this interacts with a key agronomic input, fertilizer. We incorporate data from a flight cage trial and multiple field studies to quantify the relationships between yield parameters to determine whether insufficient insect pollination may limit crop yield.
4. We demonstrate that, by producing larger seeds and more pods, *B. napus* has the capacity to modulate investment across yield parameters and buffer sub-optimal inputs of fertilizer or pollination. However, only when fertilizer is not limiting can the crop benefit from insect pollination, with yield increases due to insect pollination only seen under high fertilizer application.
5. A nonlinear relationship between seed set per pod and yield per plant was found, with increases in seed set between 15 and 25 seeds per pod resulting in a consistent increase in crop yield. The capacity for the crop to compensate for lower seed set due to sub-optimal pollination is therefore limited.
6. *Synthesis and applications*. Oilseed rape has the capacity to compensate for sub-optimal agronomic or ecosystem service inputs although this has limitations. Insect pollination can increase seed set and so there are production benefits to be gained through effective management of wild pollinators or by utilizing managed species. Our study demonstrates, however, that increased insect pollination cannot simply replace other inputs, and if resources such as fertilizer are limiting, then

yield potential cannot be reached. We highlight the need to consider insect pollination as an agronomic input to be effectively managed in agricultural systems.

KEYWORDS

agronomy, *Brassica napus*, crop production, ecological intensification, fertilizer, oilseed rape, pollination, sustainable agriculture

1 | INTRODUCTION

Rising global demand for food has led to widespread uptake of intensive, high-input practices to increase or maintain agricultural output (Tilman, Balzer, Hill, & Befort, 2011). However, concerns about the long-term impacts of intensive agriculture on ecosystems, have prompted the search for alternative methods of intensifying production that are more ecologically and economically sustainable. One approach, referred to as ecological intensification, involves adapting agriculture to more effectively utilize yield-enhancing biodiversity-based ecosystem services in order to partially or totally replace anthropogenic inputs such as fertilizers and pesticides (Bommarco, Kleijn, & Potts, 2013).

Although several studies have demonstrated the benefits of individual ecosystem services on crop yield and quality (Garratt, Breeze, et al., 2014; Klatt et al., 2014), recent studies have indicated that these benefits are affected by interactions among different services (Bartomeus, Gagic, & Bommarco, 2015; Lundin, Smith, Rundlöf, & Bommarco, 2013; Sutter & Albrecht, 2016) and between ecosystem services and anthropogenic inputs such as fertilizer and irrigation (Klein, Hendrix, Clough, Scofield, & Kremen, 2015; Marini et al., 2015; van Gils, van der Putten, & Kleijn, 2016). Despite the potential importance of biodiversity-derived services to contribute directly to yield, only by understanding and quantifying these interactions can effective ecologically intensive management strategies be applied with predictable outcomes for production.

Oilseed rape (*Brassica napus*) is a key crop in arable systems and its production has increased significantly over the last decades, due to its utility as a break crop and through policy support driven by promotion of biofuel crops (Breeze et al., 2014). Oilseed rape crops require high application rates of synthetic fertilizer (Rathke, Behrens, & Diepenbrock, 2006; Rathke, Christen, & Diepenbrock, 2005) and pesticides (Williams, 2010; Zhang et al., 2017) in order to attain maximum yield and quality. However, many varieties also benefit from insect pollination through increased pod set and seed set (Garratt, Coston, et al., 2014; Hudewenz, Pufal, Bogeholz, & Klein, 2013; Jauker, Bondarenko, Becker, & Steffan-Dewenter, 2012; Jauker & Wolters, 2008; Manning & Wallis, 2005; Stanley, Gunning, & Stout, 2013) and improved crop quality parameters such as seed mass or oil content (Bommarco, Marini, & Vaissiere, 2012). The insect pollinator assemblage of *B. napus* is diverse and varies with region, and both wild and managed pollinators are found visiting the crop (Ali, Saeed, Sajjad, & Whittington, 2011; Garratt, Coston, et al., 2014; Rader, Howlett, Cunningham, Westcott, & Edwards, 2012; Stanley et al., 2013; Woodcock et al., 2013). Pollinators are rarely considered as an input to be managed in the same way as insecticides or fertilizers in production of oilseed rape for food or biofuel (Diepenbrock, 2000; Habekotte, 1997; Rathke et al., 2006), with pollinator management typically limited to commercial production of hybrid seed. Pollination can be increased either through utilization of managed species such as honeybees (Manning & Wallis, 2005; Sabbahi, de Oliveira, & Marceau, 2005; Witter et al., 2014) or promotion of wild pollination services (Garibaldi et al., 2013).

In order to better develop ecological intensification strategies, particularly in widespread arable crops, pollination and other biodiversity-based ecosystem services need to be considered and managed as an agronomic input, and a better understanding of the interactions between ecosystem services and other agronomic inputs is essential. This study combines a number of complementary approaches to evaluate the impact of insect pollination on yield parameters of *B. napus* and how this interacts with a key agronomic input, fertilizer. Our approaches include: (1) a flight cage trial manipulating fertilizer application to *B. napus* to understand how this interacts with insect pollination to influence crop yield parameters; (2) a field scale trial manipulating pollination inputs to understand how this affects yield parameters in the field; and (3) the use of data from multiple field studies to characterize the relationship between yield parameters, across *B. napus* varieties and to determine if insufficient insect pollination may limit yield.

2 | MATERIALS AND METHODS

2.1 | Flight cage trial

2.1.1 | Growing conditions

To investigate the response of oilseed rape to fertilizer and insect pollination treatments, a pot experiment was conducted in 2016 at the Crop and Environment Laboratory, University of Reading, UK (51°26′ 10.31″N latitude, 00°56′ 31.98″W longitude) on spring sown *B. napus* (cv. Tamarin). Plants were grown to maturity in plastic pots (180 mm diameter; 4 l volume) containing a low nutrient medium consisting of vermiculite, gravel, sand and compost at a ratio of 4:4:2:1. Three seeds were sown per pot, which allowed thinning to one plant per pot when three leaf pairs were unfolded (BBCH 13; uniform decimal code for plant growth; Lancashire et al., 1991). Plants were supplied with individual drip irrigation which provided water twice a day for the duration of the experiment. All experimental plants were positioned in a randomized block and grown in a single 6 × 3 × 2 m insect-exclusion cage with 1.33 mm aperture polythene mesh ("holding cage"). The pots were positioned on a 20 mm aperture metal mesh *c*. 100 mm above the ground to allow free draining. Plants were moved out of the holding cage to the pollination treatment cages for 2–4 hr, once every 2 days during flowering.

2.1.2 | Fertilizer treatments

During seedling establishment (BBCH 10 to 30), each pot was supplied with 500 ml of liquid feed fertilizer solution with an N:P:K ratio of 1:1:1, applied once per week. At the start of stem elongation (BBCH 30), 20 plants were selected at random and assigned one of four contrasting fertilizer treatments: (1) a "high" dose treatment with a 500 ml solution of fertilizer applied to each of the pots twice per week, (2) a "medium" dose where fertilizer was applied once every 2 weeks, (3) a "low" dose with only two applications applied until maturity, and (4) a "no input" control treatment, where no additional fertilizer was applied. These treatments were randomized across the block of 80 plants and whenever a fertilizer treatment was applied to any pots, an equivalent volume of water was applied to all other pots.

2.1.3 | Pollination treatments

Two pollination treatments were implemented to determine possible interactive effects of pollination and fertilizer on yield, each on a sample of 40 plants such that 10 plants received each combination of fertilizer and pollination treatment in a balanced factorial design. The first pollination treatment involved self-, wind- and insect pollination, referred to hereafter as the "insect pollinated" treatment. From the start of flowering, the 40 plants receiving this treatment were transferred to a flight cage containing a *Bombus terrestris audax* colony with *c*. 50–100 workers (Koppert Ltd Natupol) for 2 to 4 hr once every 2 days. The plants were then allowed to be visited by bumblebees for this period before being moved back to the holding cage. Our previous research has demonstrated that this time period and stocking density is more than sufficient to ensure good levels of visitation to flowers (Garratt, Coston, et al., 2014). The second pollination treatment was a procedural control in which plants were transferred to an empty flight cage, allowing for self- and wind pollination but no insect pollination, hereafter referred to as the "no insect pollination" treatment. Between pollination treatments, all plants were stored in a randomized block in the holding cage and all insect pollinators were excluded. There is evidence that pollinator exclusion netting can potentially reduce wind pollination (Mesquida, 1988; Pierre, Vaissiere, Vallee, & Renard, 2010) although the estimated contribution of wind as a pollen vector in *B. napus* is variable (Ouvrard, Quinet, & Jacquemart, 2017; Williams, 1984). The aim of this experiment was to examine the additional contribution of insect pollination and how it interacted with an agronomic input to shape yield parameters and the insect pollinated and control plants were subject to the same environmental conditions throughout.

2.1.4 | Crop yield measurements

Yield parameters were measured when the study plants had reached maturity (BBCH 90). The total number of pods produced by each plant was recorded, 10 pods were then selected at random from each plant and the total number of seeds per pod was recorded. All pods from a plant were then grouped and dried at 80°C for 24 hr before being threshed using a mechanical thresher and weighed to establish yield in grams of seed per plant. Mean seed number per pod and total pod number per plant were used to estimate total seeds per plant. Plant yield in grams divided by this number was used to determine thousand grain weight (TGW).

2.2 | Pollinator exclusion field trial

To investigate the response of oilseed rape to insect pollination treatments under a typical fertilizer management regime involving the application of mineral nitrogen, phosphorus and potassium at UK recommended rates, a field experiment was conducted in 2015 on conventionally managed winter-sown *B. napus* (cv. Excaliber). The field experiment used three oilseed rape fields at least 1 km apart in Wiltshire, Southern England, UK. Each field contained three 2 × 50 m study plots along a tramline, spaced at least 50 m apart. A series of pollinator manipulation treatments were implemented at 25-m intervals along each study plot so that each treatment was replicated in each study plot. Using large field cages consisting of four plastic posts covered by 2.5-mm aperture polythene mesh, a crop area of 1.5 by 1.5 m was completely excluded from insect pollinators for the duration of flowering. In a second treatment, cages were raised and lowered three times during flowering to restrict insect pollinators visiting flowers for *c*. 50% of the flowering period. In a third treatment, an equivalent area of crop remained open to ambient pollination.

In order to measure the effect of pollination treatments on seed set, three visits were made to the study plots at early, mid and late flowering. On each visit, one raceme with open flowers, on a single randomly selected plant receiving each treatment within each plot was selected and cable ties were placed above and below all open flowers on that raceme and the number of open flowers was recorded. At the end of the season, all plants with marked racemes (three per treatment per study plot) were collected. These marked pods were harvested and the number of seeds per pod was recorded. The whole plant was then dried at 80°C for 24 hr before being threshed using a mechanical thresher to establish total seed yield in grams per plant, total seeds per plant and thousand grain weight. At two of the three field sites, the total number of pods on a single plant from each treatment within each study plot was also recorded.

2.3 | Relationship between yield parameters

Data from the flight cage and field trial indicated clear relationships between yield parameters including seeds per pod and yield, and TGW and seeds per plant. In order to test these relationships across a number of cultivars of *B. napus* in a range of soil, agricultural management and environmental conditions, data from two additional field trials were incorporated into this study. The first dataset (Dataset 1) was from a trial at the University of Reading experimental farm at Sonning (51°28′ 50.8″N 0°54′ 07.3″W) in 2016. In this trial, spring oilseed Rape (*Brassica napus* cv. Tamarin) was grown in four experimental blocks. The oilseed crop was harvested at maturity, five plants from each plot were collected and dried at 80°C for 24 hr. Twenty pods were randomly selected from each plant and the number of seeds per pod was recorded and total plant yield in grams was measured.

The second dataset (Dataset 2) was from 11 fields of conventionally grown winter-sown oilseed rape grown in the Wiltshire/Hampshire area (NW corner 51° 24′ 55.7″ N, 2° 17′ 21.4″ W, SE corner 51° 5′ 13.7″ N 1° 20′ 21.5″ W) season 2013/2014. Seven cultivars were grown: Astrid, DK Camelot (four fields), DK Cabernet, DK Excellium, Fashion, Pioneer 44 and PR46W21 (two fields). Plants at least 8 m away from the crop edge were labelled before the flowering season and collected once the field had been desiccated prior to harvest. From each field between three and nine plants were analysed. The seed number per pod was established for 18 pods from each plant. The seeds were extracted from the rest of the pods by hand, then cleaned and counted using a seed counter to give total seed number per plant and total seed weight per plant and from this TGW was determined.

2.3.1 | Analysis

Analysis of variance was used to investigate effects of fertilizer, pollination and their interaction on yield parameters of *B. napus* plants in the flight cage experiment. Fertilizer and pollination treatments were both treated as categorical variables. Any significant interactions between treatments were interpreted using post hoc Tukey's tests for each fertilizer:pollination treatment combination. To meet model assumptions of normal residuals, yield, pods per plant and total seed number were log transformed prior to analysis. Initial interrogation of the data showed two plants had unusually high yields, falling outside the 3rd quartile by at least 1.5 times the interquartile range, and were removed from subsequent analysis. Linear models were used to quantify the relationship between the yield parameters of seeds per pod and yield, and between TGW and seed number. To investigate whether pollination treatment or fertilizer affected these relationships, both were included in the model.

Linear mixed-effects models were used to investigate effects of the pollination treatment on *B. napus* yield parameters in the pollinator exclusion field trial. Study plot, field site and round (early, mid and late flowering) were included as nested random effects. To characterize relationships between yield parameters in this experiment, linear models were used to compare seeds per pod with yield, and TGW with seed number. To investigate whether pollination treatment affected these relationships, an interaction term with pollination was included in the models and removed if not significant according to a maximum likelihood ratio test ($p > .05$). Yield per plant, pod number, TGW and total seed number were log transformed prior to analysis to ensure they met model assumptions of normal residuals.

To investigate the relationships between seeds per pod and plant yield, and between seed number and TGW in the additional field trials (Dataset 1 and Dataset 2), linear mixed-effects models were used. For Dataset 1, block was included in the model as a random effect and total seed number was log tramsformed before analysis. For Dataset 2, variety was included in the analyses as an interaction term but was found not to be significant and so was removed from subsequent models. Field was included as a random effect and yield and total seed number were log transformed before analysis.

To examine the relationship between yield parameters (yield vs. seeds per pod, seeds per plant vs. TGW) across all the datasets combined, generalized additive models were used. Plant yield parameters varied considerably between field trials and so the relationship could be compared between datasets, yield was standardized by subtracting the dataset mean from each data point and dividing this by the dataset standard deviation (Clark-Carter, 2014). To identify the optimal shape of the relationship between parameters across the datasets the penalized least-squares method of cross-validation was used to automatically select smoothing parameters of the explanatory variable using the mgcv package. Across all models, residuals were checked for normality and heteroscedasticity. Analyses were carried out in R version 3.3.1.

3 | RESULTS

3.1 | Flight cage trial

Brassica napus yield was affected by a significant interaction between fertilizer and pollination treatments ($F_{3\text{-}70} = 3.41$, $p = .022$) (Figure 1a). Yields from insect pollinated plants were significantly greater than plants that did not receive insect pollination at the high fertilizer dose ($t = 3.78$, $p < .01$) with an almost 40% increase in yield per plant. Significant effects of pollination were not seen at any other fertilizer dose.

Several yield parameters of *B. napus* were affected by fertilizer and pollination treatments. There was a greater number of seeds on plants that received higher fertilizer doses and which were insect pollinated (Figure 1b) with a significant interaction effect ($F_{3\text{-}70} = 2.88$, $p = .042$) showing significant differences between insect-pollinated and non-insect-pollinated plants at high ($t = 3.33$, $p = .029$) and low ($t = 3.55$, $p = .016$) fertilizer doses. The number of pods per plant (Figure 1c) was significantly greater at higher fertilizer doses ($F_{3\text{-}74} = 43.95$, $p < .001$) but was not affected by pollination treatment ($F_{1\text{-}73} = 1.70$, $p = .20$), although the interaction between fertilizer and insect pollination ($F_{3\text{-}70} = 2.72$, $p = .051$) was nearly significant. The number of seeds per pod (Figure 1d) was greater with insect pollination ($F_{1\text{-}73} = 76.67$, $p < .001$) and at higher fertilizer doses ($F_{3\text{-}73} = 13.77$, $p < .001$) but these two factors did not interact significantly ($F_{3\text{-}70} = 2.41$, $p = .075$). Thousand grain weight was significantly affected by fertilizer only ($F_{1\text{-}74} = 4.35$, $p = .007$), with heavier seeds at low compared to high fertilizer doses (Figure 1e). No significant

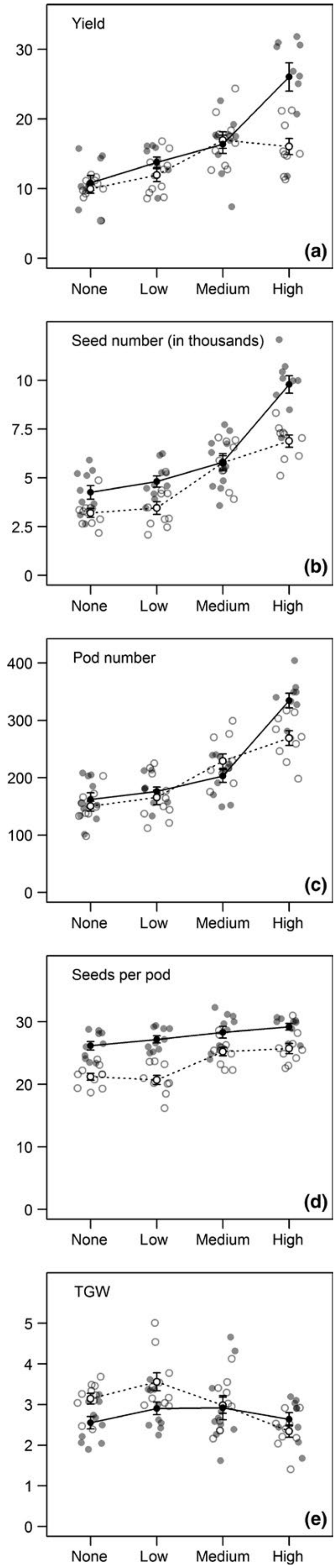

FIGURE 1 Effects of increasing fertilizer dose and insect pollination on yield parameters of *Brassica napus* (a) yield (g/plant) (b) seed number per plant, (c) pod number, (d) seeds per pod and (e) thousand grain weight (TGW) in grams. Values are given as $M \pm SE$. Closed circles show plants receiving insect pollination and open circles show those that have not

effect of insect pollination ($F_{1\text{-}73} = 3.58$, $p = .062$) or a fertilizer–pollination interaction ($F_{1\text{-}70} = 2.65$, $p = .055$) on TGW was observed.

Brassica napus yield showed a significant positive relationship with seeds per pod ($F_{1\text{-}76} = 19.19$, $p < .001$) (Figure S1a) although there was no significant interactive effect of fertilizer ($F_{3\text{-}68} = 2.49$, $p = .068$) or insect pollination on this relationship ($F_{1\text{-}68} = 2.97$, $p = .089$). There was a significant negative relationship between seed number and TGW ($F_{1\text{-}74} = 15.24$, $p < .001$) and there was a significant interactive effect of insect pollination, with a steeper negative relationship seen for insect pollinator-excluded plants ($F_{1\text{-}74} = 9.45$, $p = .003$) (Figure S1b). No interactive effect of fertilizer on this relationship was seen ($F_{3\text{-}68} = 2.32$, $p = .084$).

3.2 | Pollinator exclusion field trial

In the field experiment there was no significant effect of insect pollinator exclusion treatments on yield ($F_{2\text{-}44} = 1.11$, $p = .34$) (Figure 2a). The average number of seeds per pod was significantly greater from plants in open treatments compared to those that had insect pollinators fully or partially excluded ($F_{2\text{-}44} = 4.08$, $p = .020$) (Figure 2d). No significant effect of pollination treatment on the number of pods per plant ($F_{1\text{-}8} = 2.88$, $p = .11$), TGW ($F_{1\text{-}44} = 1.42$, $p = .25$) or seeds per plant ($F_{1\text{-}44} = 1.44$, $p = .25$) was seen.

The relationship between seeds per pod and plant yield was significantly positive ($F_{1\text{-}41} = 17.93$, $p < .001$) and there was also a significant interactive effect of pollination treatment ($F_{1\text{-}41} = 4.72$, $p = .014$) with the steepest positive relationship seen for insect pollinator-excluded plants (Figure S2a). Seed number and TGW were negatively related ($F_{1\text{-}45} = 9.35$, $p = .004$) (Figure S2b) but with no significant interactive effect of pollination treatment ($F_{2\text{-}41} = 0.84$, $p = .44$).

3.3 | Relationship between yield parameters

From the field trial involving spring-sown *B. napus* (Dataset 1) there was a significant positive relationship between seeds per pod and plant yield ($F_{1\text{-}65} = 55.74$, $p < .001$) (Figure S3a) and total seed number and TGW were negatively related ($F_{1\text{-}59} = 44.94$, $p < .001$) (Figure S3b). In the mixed variety trial (Dataset 2), there was also a significant positive relationship between seeds per pod and yield ($F_{1\text{-}45} = 13.57$, $p < .001$) (Figure S4a) and although the relationship between total seed number and TGW appeared negative it was not significant ($F_{1\text{-}45} = 1.11$, $p = .30$) (Figure S4b).

Combining all datasets together across the field trials, the relationship between seeds per pod and plant yield was positive and nonlinear ($F = 9.76$, $p < .001$) and the relationship between seeds per pod and TGW was linear and negative ($F = 25.73$, $p =< .001$) (Figure 3).

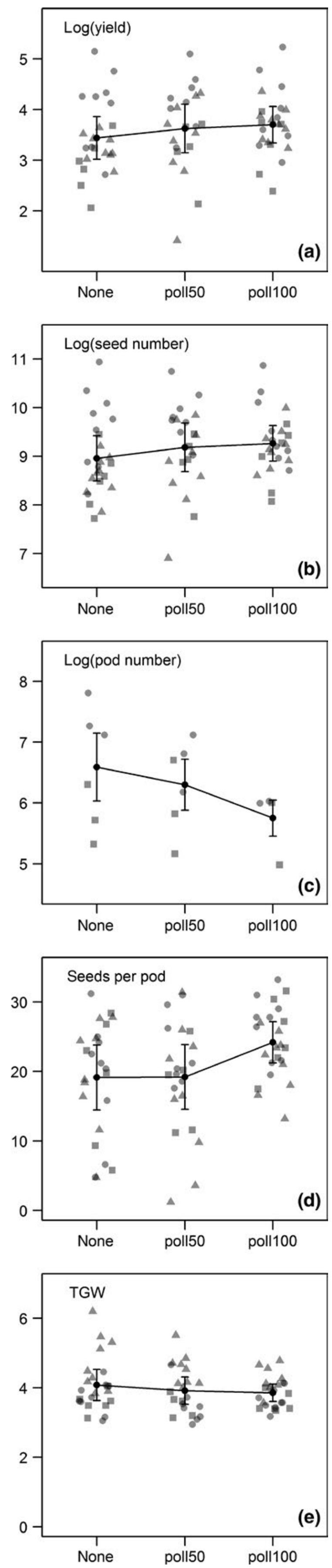

FIGURE 2 Effects of no insect pollination (none), 50% insect pollination (poll50) and ambient pollination (poll100) on yield parameters of *Brassica napus* (a) yield (g/plant), (b) seed number per plant, (c) pod number, (d) seeds per pod and (e) thousand grain weight (TGW) in grams. Values are given as *M* ± *SE*. Point styles indicate the three different field sites in the study

4 | DISCUSSION

This study demonstrates the capacity for *B. napus* to mitigate reduced nutrient availability or lower levels of insect pollination, by modulating resource investment across various yield parameters. However, it is still necessary to ensure that yield is not so limited by one of these inputs that the crop is unable to capitalize on the potential benefits provided by another. For example, in the flight cage trial, the benefits of insect pollination to *B. napus* yield were only realized in the high fertilizer treatment when nutrients such as nitrogen, potassium and phosphorus were not limiting. Also, the compensation mechanism whereby reductions in seed set (e.g., due to reduced insect pollination) are mitigated to some extent by increased individual seed mass is clear. In the field study, insect pollination significantly increased seed set per pod, but plants that did not receive insect pollination were able to compensate and largely bridge the yield gap by producing larger seeds and/or more pods. However, our results demonstrate a nonlinear relationship between seed set per pod and final yield per plant across all the field trials, with increases in seed set between 15 and 25 seeds per pod resulting in a consistent increase in crop yield, while little change in yield occurred at lower numbers of seeds per pod.

Yield of *B. napus* is maximized through a number of factors, including by increasing pod set, increasing seed set per pod or increasing individual seed mass (Habekotte, 1997). Through modulation of any one of these yield parameters, the crop has the capacity to compensate for a shortfall in another to meet its yield potential. Fertilizer management (Rathke et al., 2006), sowing density and breeding (Diepenbrock, 2000) all determine the way that the crop grows and can be optimized for maximum yield under external constraints such as climate, soil and other environmental limitations. Ecosystem services such as insect pollination, however, are rarely considered as a managed input that could be utilized to improve the yield of crops like *B. napus* and meet yield potential. Insect visitation could increase pollination of *B. napus* flowers, either through greater outcrossing, or by increasing levels of self-pollination and can result in increased number of seeds per pod in both conventional and hybrid cultivars (Garratt, Coston, et al., 2014; Hudewenz et al., 2013; Jauker & Wolters, 2008; Jauker et al., 2012; Pierre et al., 2010; Williams, Martin, & White, 1987). The key role of insect pollinators in increasing seeds per pod is further highlighted in this study. It is clear, however, that despite the *B. napus'* capacity to compensate, seed set per pod is related to yield demonstrating that this capacity to compensate for low pollination has limits. Therefore, ensuring adequate insect pollination is likely to result in increased seed set and therefore increased yield. Research has shown that, on average, a single visit per flower from

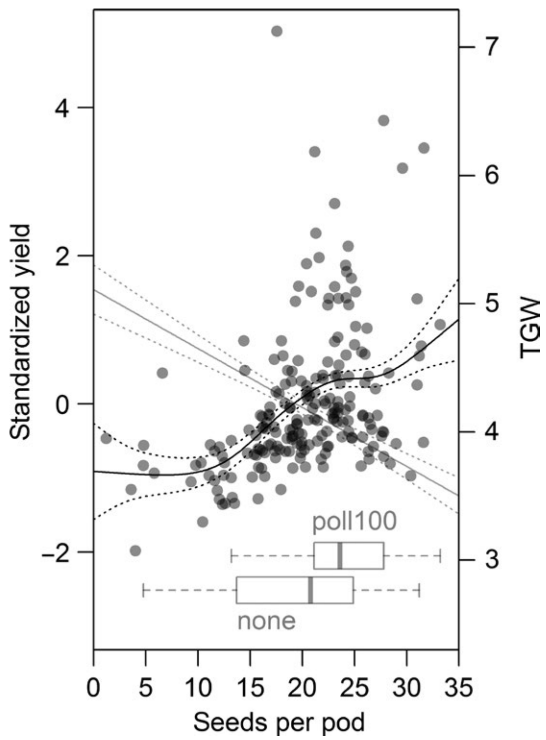

FIGURE 3 Relationship between mean seeds per pod and standardized yield per plant in spring and winter *Brassica napus* varieties across all field studies. The relationship between seeds per pod and thousand grain weight (TGW) in grams is also shown, as well as boxplots representing exclusion (none) and ambient pollination (poll100) effects on seeds per pod. Lines are model estimated *M* ± *SE*. Gray line shows TGW

insects including bees and hoverflies is enough to increase seed set from 15 to more than 20 seeds per pod, and greater numbers of visits increase seed set further (Garratt, Coston, et al., 2014). Increases above 15 seeds per pod in particular elicit a strong positive yield response (Figure 3). The benefits of insect pollination to *B. napus* yield is demonstrated by studies which have supplemented insect visitation through the use of managed pollinators (Manning & Wallis, 2005; Sabbahi et al., 2005).

Although there are benefits of insect pollination to seed set in *B. napus*, the present study shows that increasing insect pollination cannot simply replace an agronomic input such as fertilizer, and that if resources are limiting then the crop cannot exploit the increased seed set potential provided by pollinators. Therefore, for effective ecological intensification, good agronomic practices still need to be maintained with possible opportunities to partially replace conventional inputs with biodiversity-based inputs (Bommarco et al., 2013). The interplay between ecosystem services, such as insect pollination, and agronomic inputs is also likely to be cultivar dependent (Hudewenz et al., 2013; Marini et al., 2015), but the clear relationship between seed set and plant yield, and seed number and TGW across the cultivars investigated in this study does demonstrate a consistent trend.

Brassica napus is a morphologically very adaptable crop and as the plant grows it can respond to external and internal factors and moderate the number of flowers it produces and alter its investment in seed size up until senescence. Some crops may not have this flexibility, particularly those where key quality parameters directly relate to pollination such as size, shape or shelf-life in apples and strawberries (Garratt, Breeze, et al., 2014; Garratt et al., 2016; Klatt et al., 2014). In this case, production of more, lower quality fruit cannot simply compensate for a drop in quality due to the considerable effect of quality on price. Therefore, the contribution of insect pollinators as an agronomic input, and how it interacts with other factors, will vary between different crops and this should be taken into account when insect pollination management decisions are made.

In order to optimize productivity and reduce risks from poor pollination, insect pollination should be considered as an agronomic input for production of oilseed and other entomophilous crops (Klein et al., 2007). Supplying pollination through managed pollinators such as honeybees can be an effective strategy (Manning & Wallis, 2005; Sabbahi et al., 2005). However, relying on a single pollinator presents both agronomic and financial risks from sudden catastrophic losses (Garibaldi et al., 2014). Furthermore, the capacity of current honeybees stocks in the UK and several other EU countries may not be sufficient to meet demand for a widely cultivated crop such as oilseed rape (Breeze et al., 2014) and the benefits to yield may not be large enough to justify the costs of hiring hives. Better utilization of wild pollinator communities is an alternative and more sustainable strategy (Pywell et al., 2015) as a number of taxonomic groups of wild insect pollinators can effectively pollinate oilseed rape (Garratt, Coston, et al., 2014). This study shows that farmers should try to ensure maximum seed set in *B. napus* to avoid a yield penalty. Maintaining areas of uncropped land and semi-natural landscape elements in and around crop fields provides nesting and additional forage resources for insect pollinators and can result in improved pollination service to crops (Garibaldi et al., 2011, 2013). Although the relatively low unit area value of oilseed may not justify the cost of such interventions in terms of pollination services provided to the crop alone, management measures to support insect pollinators may be cost-effective if benefits of other ecosystem services are considered (Morandin, Long, & Kremen, 2016; Ramsden, Menéndez, Leather, & Wäckers, 2015; Wratten, Gillespie, Decourtye, Mader, & Desneux, 2012). Importantly, as this study shows, investment in pollination services can only pay off if other agronomic inputs are not limiting.

5 | CONCLUSIONS

Crop growth is moderated to compensate for limited resources in order to achieve maximum reproductive output, and in turn yield. However, the capacity to compensate is finite, and critical limitations in inputs need to be avoided in order for a crop to achieve its yield potential. In this study, we show that fertilizer and pollination by insects are two such interacting inputs. Insect pollination should be considered as an agronomic factor to be managed in agriculture systems and its capacity to shape yields and meet yield potential should not be taken for granted as an incidental benefit provided by the wider environment.

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AUTHORS' CONTRIBUTIONS

M.G., J.B. and S.R. conceived the ideas and designed methodology; M.G., E.D., R.F.S. and A.S. collected the data; M.G. and J.B. analysed the data; M.G., J.B. and S.G.P. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available through the University of Reading Research data archive https://doi.org/10.17864/1947.141 (Garratt & Degani, 2018). "Dataset2" is available from the Natural and Environment Research Council Data Centre https://doi.org/10.5285/fc219733-a8e8-4ec0-a34e-e0e8115f0d68 (Shaw, Bullock, & Osborne, 2018).

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