



RESEARCH PAPER

The effect of pollination on the growth and reproduction of oilseed rape (*Brassica napus*)

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Received 29 November 2021; accepted 17 June 2022

Available online 18 June 2022

Abstract

Phenotypic plasticity is an organism's ability to alter its development and life history in response to environmental conditions. In plants, biotic and abiotic factors drive the distribution of resources between growth and reproductive traits. One such biotic factor is pollination. Studies show that wind and insect pollination enhance oilseed rape (*Brassica napus*) yield. However, the impact of pollination on resource allocation towards growth and reproduction is less understood. We conducted a controlled experiment to assess the effect of pollination on growth and functional reproductive traits. We compared two simulated supplementary pollen deposition methods (representing wind and insect pollination) alongside a non-supplementary control. Pollinated plants allocated resources towards growth and reproduction similarly, irrespective of deposition method. Plants receiving no supplementary pollination produced fewer seeds, allocating resources to growth, more prolific and persistent flowering, and heavier seeds. Pollinated plants had a reduced flowering period and were shorter, indicating resources were allocated to seed production rather than growth or the production of additional flowers. This allocation of resources from growth and flowering metrics can increase yield directly through increased seed production and indirectly through shorter plants and a reduced flowering period with seeds that mature earlier (agronomically beneficial traits).

Wind and insect pollination can enhance and stabilise oilseed rape yield under various environmental conditions by acting in complementary ways. Since pollination limits yield in oilseed rape, it must be considered an input that can be actively managed. Successful management of pollination services requires growers to detect pollination deficits. Inadequately pollinated oilseed rape plants exhibit apparent morphological changes (e.g. taller plants that flower for longer), acting as an early warning to growers. Equipping growers with this knowledge provides them with a means of detecting deficits and thus enables them to take positive action to restore pollination services by introducing honeybees or enhancing wild pollinators.

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Keywords: Agronomic traits; *Brassica napus*; Plant growth; Plant development; Flowers; Phenotypic plasticity; Pollination; Reproduction; Resource allocation

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Introduction

Organisms alter their development and life history in response to their environment (Schlichting, 1986; Sultan, 2000). A combination of genetic traits, environmental conditions (e.g. temperature, humidity and soil pH) and available resources (e.g. sunlight, water availability and nutrients) drive these responses. A central theme in life-history strategy is distributing these resources between the functional traits for developmental growth and reproduction—any misallocation of resources influences plant development (Kozłowski, 1992). For example, redirecting resources from developmental growth traits to those responsible for reproduction too early in its life cycle may considerably affect a plant's chance of survival (Lacey, 1986). Similarly, overinvesting resources in flowering and growth may leave plants with insufficient resources for future seed investment (Pyke, 1991).

Phenotypes, the displayed traits impacting an organism's fitness and success, are dependant on both genetic and environmental factors. Phenotypic plasticity is a strategy used by individuals of a given genotype to adjust their phenotype according to their surroundings (Bradshaw, 2006; West-Eberhard, 2003). Plasticity can be expressed through changes in behaviour, morphology and/or physiology (Price, Qvarnström & Irwin, 2003) and is fundamental for an organism to cope successfully with challenging environments.

Phenotypic plasticity is common in plant species (Dudley, 2004; Schlichting, 1986; Sultan, 1987), with impacts observed on biomass allocation, morphological and architectural structure, physiology and phenology (Chapin, 1991; Freschet, Violle, Bourget, Scherer-Lorenzen & Fort, 2018; Kozłowski & Wiegert, 1986; Nicotra et al., 2010). Once stimulated, these responses may become permanent (e.g. the thickening of tree branches when exposed to persistent high winds: Watt, Moore and McKinlay (2005)), or they may be short-lived (e.g. the effect of light on photosynthetic chemistry: Pacini, Nepi and Vesprini (2003)). Studies addressing plant responses to environmental change have primarily focused on abiotic factors, such as soil nitrogen concentration and light limitation (Freschet et al., 2018). However, biotic interactions, such as defence chemistry in response to herbivory (Baldwin, 1999), also offer an essential insight into phenotypic plasticity. One biotic interaction with considerable importance is insect pollination, which can have an overwhelming effect on reproduction (Obeso, 2002, 2004). Despite this, research on pollination has focussed extensively on reproductive metrics (e.g. seed weight and number). Studies evaluating the impact on growth metrics, or indeed the relative allocation of resources between growth and reproductive metrics, are less common (Bartomeus et al., 2014; Bommarco, Marini & Vaissière, 2012). As an ecosystem service, animal pollination is vital to the reproduction of more than 87% of flowering plant species (Ollerton, Winfree & Tarrant, 2011) and 75% of the

world's leading crops (Klein et al., 2007). Pollinator declines, therefore, have severe consequences for both the conservation of (semi)-natural habitats and global food production (Biesmeijer et al., 2006; Bommarco, Lundin, Smith & Rundlöf, 2012; Deguines et al., 2014; Potts et al., 2010; Powney et al., 2019).

Oilseed rape (*Brassica napus*; OSR) is an economically important crop and the dominant mass-flowering crop in Europe, cultivated on 36 million hectares in 2020 (USDA, 2021). Primarily grown as a source of oil, prevalence is increasing to meet biofuel demands (Van Der Velde, Bouraoui & Aloe, 2009). With such importance, seed companies continually develop new cultivars, each with unique characteristics adapted to specific environmental conditions. Cultivars are bred either conventionally, traditionally crossing the most desirable genotypes, or as restored hybrids, using selected inbred lines (Friedt & Snowdon, 2009). Oilseed rape plants show a high degree of phenotypic plasticity, responding to abiotic and biotic interactions. For example, plant stem diameter and biomass increase with distance from the nearest conspecific neighbour (Von Wettberg & Weiner, 2004), and plants can adjust flower production in response to planting density (Cresswell, Hagen & Woolnough, 2001) and insect visitation (Mesquida, Renard & Pierre, 1988).

OSR can be cross-pollinated by utilising abiotic (e.g. wind) and biotic (e.g. insects) vectors or self-pollinated. Vectors assist with self-pollination, primarily through geitonogamy (fertilisation by pollen from another flower of the same plant). However, the flower structure of OSR, particularly the inward-facing anthers, also lends itself to autogamy (fertilisation by pollen from the same flower; Fig. 1); therefore, pollination is possible in OSR with little external assistance (Eisikowitch, 1981).

Nevertheless, OSR flowers offer high quantities of nutrient-rich floral resources, particularly sticky pollen grains, suggesting OSR is more suitable to direct insect pollination than indirect wind pollen deposition (Cresswell et al., 2004; Fairhurst et al., 2021). Indeed, studies indicate that insect visitation benefits OSR yield in terms of both seed production and seed quality (i.e. seed weight, which strongly relates to oil content) (Bartomeus et al., 2014; Bommarco et al., 2012; Hudewenz, Pufal, Bøgeholz & Klein, 2014; Lindström, Herbertsson, Rundlöf, Smith & Bommarco, 2016; Sabbahi, De Oliveira & Marceau, 2005). With the increased demand for OSR, the economic implications caused by pollinator decline remains a concern to growers.

Agricultural intensification, resulting in larger field sizes and loss of semi-natural habitat (Rundlöf, Nilsson & Smith, 2008; Steffan-Dewenter, Nzenberg, Rger, Thies & Tschardtke, 2002; Tschardtke, Klein, Krüss, Steffan-Dewenter & Thies, 2005), alongside the increased use of agrochemicals (Kevan, 1975; Robinson & Sutherland, 2002; Tilman et al., 2001) are identified as primary drivers of insect pollinator declines. These declines continue in Europe despite the EU Common Agricultural Policy's increasing

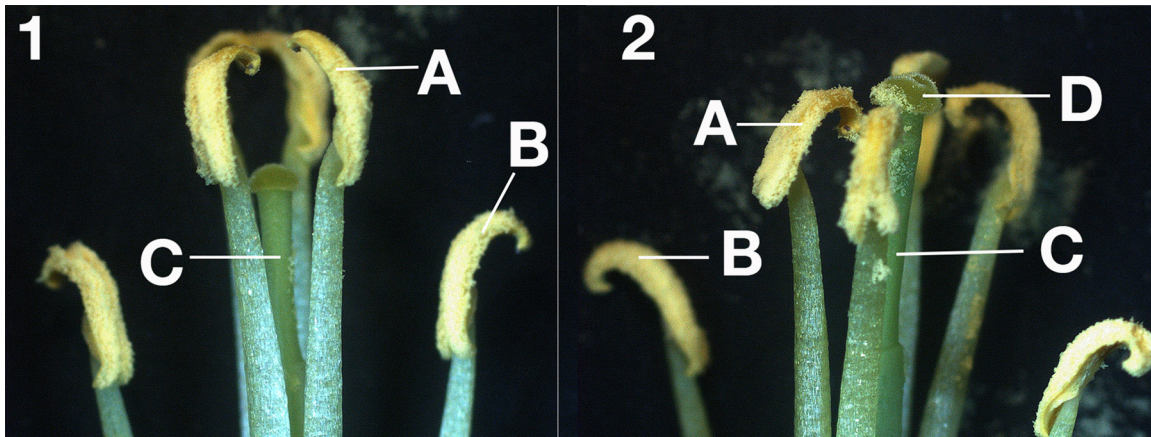


Fig. 1. *Brassica napus* flower with petals removed. **1:** Male structures are arranged in two sets. Four long stamens (A) encircle the female style (C), with a shorter pair located outside (B). Anthers of the short stamens dehisce towards the centre of the flower and rely on insect visitors as a vector for pollen transfer. **2:** The anthers of the long stamens dehisce outwards, although the curvature of these anthers positions them close to the stigma (D), allowing for pollen transfer when the style extends.

commitment to environmental protection (Powney et al., 2019). Since current agri-environment schemes fail to provide all resources pollinators require in sufficient quantities (Cole et al., 2020), there is an urgent need to explore novel means of protecting insect pollinators. Mass-flowering crops such as OSR can provide a pulse of food at a critical point in the season, filling hunger gaps and complementing agri-environment measures such as flower-rich field margins (Carvell, Meek, Pywell, Goulson & Nowakowski, 2007; Stanley & Stout, 2013).

This study assessed the ‘pollination effect’ on OSR vegetative growth and reproduction and the differences between breeding systems. We explored how OSR allocates resources to growth, flowering, and yield metrics under pollen limitation, wind simulated pollination, and insect simulated pollination. We expected OSR plants to display phenotypic plasticity in response to different pollination treatments by altering resources allocated to growth metrics (i.e. plant height and biomass), flowering metrics (i.e. flowering duration and the number of flowers) and yield metrics (i.e. fruit set, seed set and seed weight). We predicted a trade-off between growth and reproduction metrics in response to pollination treatment. Furthermore, we predicted that plants experiencing a pollination deficit would increase seed weight to compensate for a reduction in seed production, highlighting a trade-off between seed quantity and quality. This research sheds light on the capacity of OSR to respond to changes in biotic and abiotic pollination and buffer pollination deficits through phenotypic plasticity.

Materials and methods

Plant material

Eight cultivars of commercially available oilseed rape (OSR; *Brassica napus*), comprising four conventionally

bred and four hybrid cultivars, were grown under insect-free, environmentally controlled conditions in the glasshouses at Scotland’s Rural College, Edinburgh (55°55′18.3″ N, 03°10′43.7″ W). Anonymised at AHDB’s request, cultivars were selected from those undergoing regional, in-field testing for inclusion on the 2016/17 AHDB Recommended List for cereals and oilseeds (North UK region). For a fair representation of available cultivars, selected cultivars covered a range of agronomic characteristics, gross output results (both high- and low-performers), and disease resistance scores obtained from previous Recommended List trial data (AHDB, 2019).

Experimental design

In August 2017, seeds were sown in modular trays containing a 50/50 mixture of peat and washed horticultural sand (1.87 g/L lime and 0.75 g/L Osmocote Exact fertiliser). At the 3–4 true leaf stage, seedlings were vernalised at 5 °C for eight weeks in 24-hour light conditions to stimulate the flowering process. Post-vernalisation, 144 plants (18 plants per cultivar) were re-potted into 4 L pots and moved to an insect-free glasshouse with a 16-hour light / 8-hour dark photoperiod. During the light period, minimum illuminance was 15 kg lux, equivalent to full daylight but not direct sun (Schlyter, 2009). Glasshouse heating maintained a daytime (07:00 – 19:00) mean temperature of 20.0 °C (SD ± 1.8 °C) and night temperature of 16.1 °C (SD ± 2.4 °C), and relative humidity was maintained at 52% (SD ± 7%). Plants were watered daily and organised into a 3-block, randomised block design at a density of 8 pots per m².

At the onset of flowering, six plants per cultivar were allocated to one of the following three treatments:

- 1 Insect-pollination: cross-pollination by insects was simulated by hand-pollinating flowers using a size 8, ‘Filbert-style’ artist’s paintbrush,

with pollen collected from the anthers of another plant of the same cultivar. All open flowers were hand-pollinated until flowering ended.

- 2 Wind-pollination only: self-pollinated by the wind was simulated by gently shaking the plant stem for 10 s. Shaking duration was determined through a pilot study, where shaking was conducted for different durations. Ten seconds was found to dislodge sufficient pollen without causing stem damage. Before shaking, plants were carefully removed from the glasshouse compartment to prevent filling the compartment with airborne pollen. Post-shaking, plants remained separated for 30 min before being carefully returned.
- 3 Pollen-limited: flowers were left untreated as a control. Pollen-limited plants were not disturbed during the experiment. Care was taken to avoid any contact that could dislodge pollen, limiting flowers to autogamous pollination only.

Each of the three randomised blocks contained 48 plants (i.e. 8 cultivars, 3 pollination treatments, two repeats).

As *Brassica* pollen retains some viability for at least 72 h (Bots & Mariani, 2005; Rosa, Blochtein, Ferreira & Witter, 2010), wind- and insect-pollination treatments were performed every other day throughout the flowering of each plant.

Harvesting

Flowering and maturing rates varied across cultivars. Plant harvest was standardised to control for early flowering cultivars benefitting from an extended maturation period or fruits from late-flowering cultivars having insufficient time to mature. Each cultivar was harvested 56 days after the mean flowering end date for all plants. Plants were then cut at the soil surface and dried in the glasshouse for 14 days before all seed pods were removed.

Resource metrics

To distinguish between the allocation of resources towards growth and reproduction, metrics were broadly divided as follows:

- Growth and biomass: To determine the effect of pollination on vegetative growth, we measured each plant's final height and total above-ground dry biomass (Table 1).
- Reproduction: To measure reproductive resource allocation, we recorded metrics related to flowering and reproductive success (Table 1).

Data analysis

Linear mixed-effects models were used to analyse the effect of pollination treatment on vegetative and reproduction metrics. For response variables involving count data, i.e. flowering period, number of flowers, number of seeds per plant, generalised linear mixed-effects models (GLMMs), drawn from a Poisson distribution, were used. For continuous data (i.e. plant height, biomass, and seed

Table 1. Measurement methods for vegetative and reproductive metrics of oilseed rape (*Brassica napus*).

Metric	Method of measurement
<i>Growth and biomass</i>	
Plant height	Measured post-flowering
Biomass	Weight of all above-ground vegetation, excluding seeds
<i>Flowering</i>	
Flowering period	Number of days between the first and final day of flowering
Number of flowers	Sum of all seed pods and flower abscission scars
<i>Reproduction</i>	
Fruit set	Number of seed pods / (number of seed pods + abscission scars)
Number of seeds	Seeds were manually removed from pods and counted.
Seed weight	Seed biomass per pod

weight), linear mixed-effects models (LMMs) were used. Reproductive success was determined by flowers developing into seed pods, and a GLMM, drawn from a binomial distribution, was used with 'reproductive success' and 'reproductive failure' as response variables. All models included 'cultivar' as a random effect to consider the data's hierarchical structure. Fixed effects of 'pollination treatment', 'breeding system', 'block' and the interaction between 'treatment' and 'breeding system' were used to determine if growth and reproductive metrics were influenced by pollination treatment and breeding system and whether treatment effects were consistent between breeding systems. The Bayesian information criterion (BIC) was used to identify the most parsimonious models. All models were fitted using Residual Maximum Likelihood (REML) with the LME4 package (Bates, Maechler, Bolker & Walker, 2015). Spearman's rank correlation explored the relationship between seed number and weight. All analyses were undertaken using R version 3.6.1 (R Core Team, 2019).

Results

Effect of pollination on growth and biomass

Plant height was consistent between breeding systems (see Appendix A: Table 1), but a significant effect of pollination treatment was detected (Table 2). Plants receiving supplementary pollination were significantly shorter than untreated plants (Fig. 2A), and these effects were consistent between breeding systems. Dry biomass was not influenced by the breeding system or pollination treatment (Table 2; Fig. 2B).

Table 2. Results of the mixed-effects models for the effects of pollination treatment, interaction with breeding system and block (where significant) on vegetative, flowering, and reproductive metrics of oilseed rape. No direct effect of breeding system was found, and this information is omitted from the table. Significant results are highlighted in bold.

Response variable	Predictors (df)	F	P
<i>Growth and biomass</i>			
Plant height	Treatment (2, 125)	21.53	<0.001
Dry weight above-ground biomass	Treatment (2, 123)	0.36	0.699
	Block (2, 123)	7.31	0.001
<i>Flowering</i>			
No. days in flower	Treatment (2, 125)	31.44	<0.001
No. of flowers per plant	Treatment (2, 118)	198.44	<0.001
	Block (2, 118)	18.83	<0.001
<i>Reproduction</i>			
Fruit set	Treatment (2, 118)	452.33	<0.001
No. of seeds per plant	Treatment*breeding system (2, 123)	122.80	<0.001
	Block (2, 123)	165.49	<0.001
No. of seeds per pod	Treatment (2, 123)	31.05	<0.001
Seed weight per plant	Treatment (2, 123)	4.60	0.012
	Block (2, 123)	5.11	0.007
1000 seed weight	Treatment (2, 123)	4.38	0.015

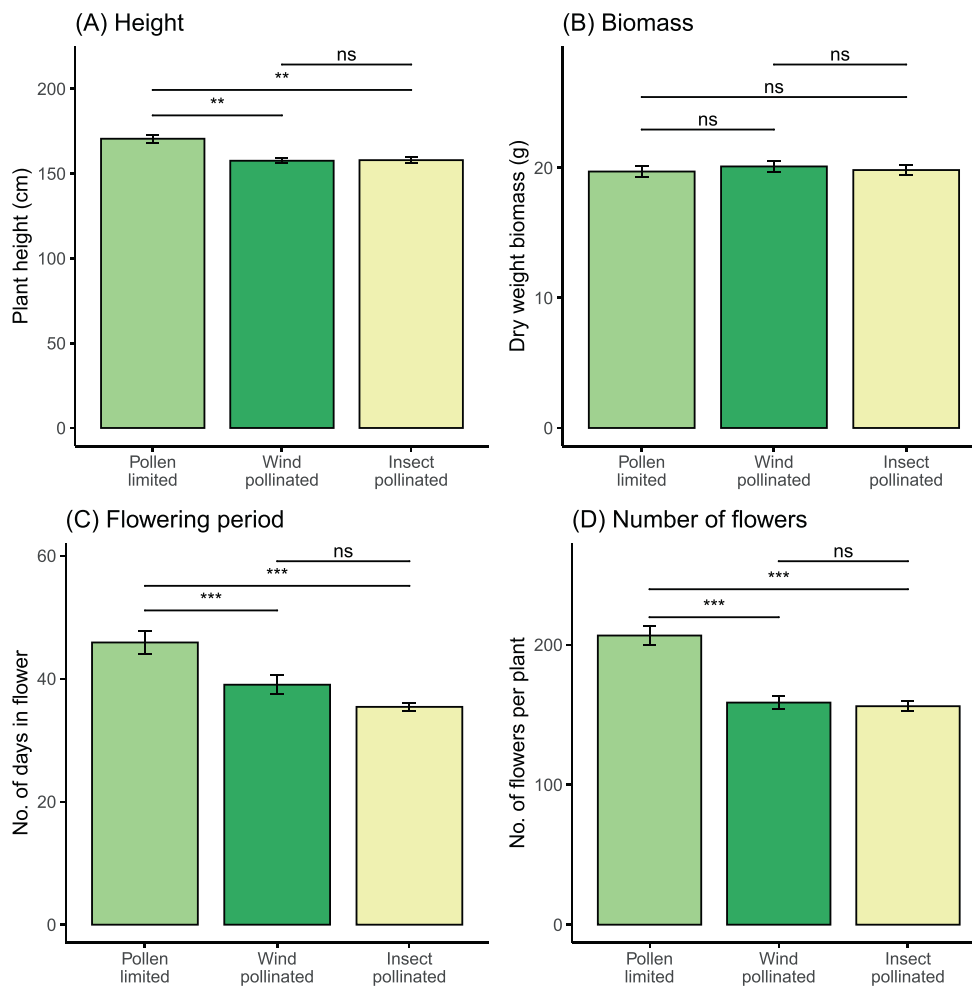


Fig. 2. The effects of pollination treatment on vegetative growth and flowering ($n = 48$ per treatment). Error bars \pm SE. Significance: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

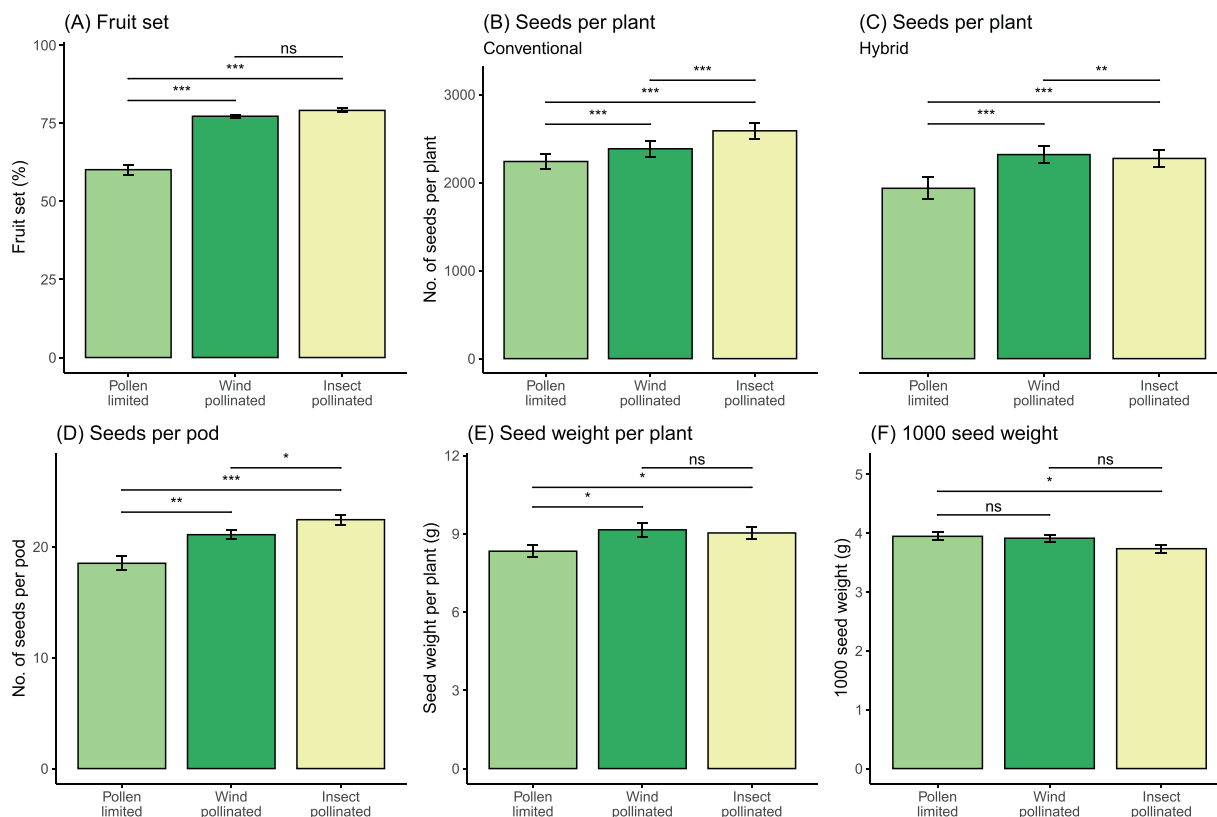


Fig. 3. The effects of pollination treatment on reproductive metrics ($n = 48$ per treatment). Seeds per plant had a significant interaction between treatment and breeding system. Error bars \pm SE.

Significance: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$.

Effect of pollination on flowering

The flowering duration and number of flowers per plant were consistent across breeding systems but were significantly affected by pollination treatment (Table 2). Plants subjected to supplementary pollination flowered for a significantly shorter duration (Fig. 2C) and produced significantly fewer flowers (Fig. 2D; See Appendix A: Fig 1) than those plants left untreated. There was no significant difference between simulated wind or insect pollination.

Effect of pollination on reproduction

Breeding system did not significantly influence any reproductive metrics under investigation. However, significant effects of pollination treatment were detected for all reproductive metrics (Table 2). These effects were consistent between breeding systems, except for the number of seeds per plant, where a significant interaction was detected ($P < 0.001$; Table 2). In conventional varieties, insect-pollinated plants produced significantly more seeds than wind-pollinated plants. However, the opposite was true for hybrid varieties, with wind-pollinated plants producing significantly

more seeds than insect-pollinated plants, although this difference was small (Fig 3B and 3C).

Supplementary pollination also significantly increased fruit set (Fig. 3A), seeds per pod (Fig. 3D), and seed weight per plant (Fig. 3E) when compared to pollen-limited plants. The effects of simulated wind and insect pollination on reproductive metrics were similar except for 1000 seed weight, with insect-pollinated plants having lower seed weights (Fig. 3F).

Discussion

Overview

By considering the effects of pollination on OSR plant growth metrics, this study expands beyond existing research that focuses on reproductive metrics (Adamidis, Cartar, Melathopoulos, Pernal & Hoover, 2019; Steffan-Dewenter, 2003; Williams, Martin & White, 1986). OSR plants showed phenotypic plasticity in response to pollination treatment, altering how they allocated photosynthate towards plant growth, flowering, seed set and seed weight. Plants receiving supplementary pollination were shorter, produced fewer flowers over fewer days, showed a higher fruit set and yielded a significantly greater number of seeds

per plant. Plants subjected to pollen limitation compensated by increasing flower production and extending the flowering period. This highlights that OSR can somewhat mitigate a reduction in pollination service delivery through phenotypic plasticity. Despite pollen-limited OSR plants compensating for pollination deficits through extending the duration and extent of flowering and increasing the weight of individual seeds, a yield gap (i.e. a decline in total seed weight per plant) was still detected, highlighting the importance of safeguarding pollination services to optimise yield.

Impact of pollination on growth and flowering

Oilseed rape plants exposed to supplementary pollination allocated fewer resources to plant growth and flowering, both in terms of the number of days in flower and the number of flowers produced. Instead, these resources were directed toward reproductive metrics (i.e. the number and weight of seeds). When pollination is limited, oilseed rape continued to grow and produce flowers for a significantly extended period, producing, on average, 32% more flowers and flowering, on average, nine days longer than pollinated plants. The difference in the flowering period between pollinated and pollen-limited plants might suggest that oilseed rape has a ‘maximum carrying capacity’, as defined by Williams et al. (1986). This may relate to fulfilling the plant’s pollination requirements through the number of ovules fertilised, with lack of fertilisation triggering extended flowering (Bell & Cresswell, 1998; Herrera, 1995; Sabbahi, De Oliveira & Marceau, 2006). Our findings support this hypothesis. Although plants subject to pollen limitation produced more flowers per plant, the number of pods per plant was similar to those given supplementary pollination. Extending the flowering period and increasing the abundance of flowers will increase the likelihood of both insect visitation and wind pollination (Primack, 1985). With foraging in many pollinating species constrained by temperature (Corbet et al., 1993), phenotypic plasticity in flowering traits in response to pollen limitation is likely to help stabilise and maintain OSR yields under fluctuating environmental conditions.

The shorter flowering period of adequately pollinated plants will likely drive earlier maturation, enabling seeds to ripen evenly, allowing for earlier harvest. When the turnaround between harvesting and sowing the following crop is tight (e.g. sowing of winter cereals), earlier harvests build flexibility within the rotation. Plants receiving supplementary pollination also direct fewer resources into growth, resulting in shorter plants (Adamidis et al., 2019). Shorter above-ground growth reduces the risk of lodging (i.e. the plant’s permanent displacement from its vertical position). Lodging yield losses are substantial and estimated at £47–£120 million per annum in the United Kingdom (Kendall, Holmes, White, Clarke & Berry, 2017). Furthermore, pollination treatment did not influence plant biomass, indicating that pollinated plants are shorter in height and more structurally dense, increasing their robustness (e.g. to

excessive wind). The production of shorter, more robust plants that mature earlier highlights that wind and insect pollination can have additional indirect agronomic benefits as well as direct yield benefits.

Impact of pollination on yield

Previous studies of oilseed rape under controlled conditions confirm that fruit set is increased with pollination (Williams et al., 1986) by honeybees (Sabbahi et al., 2005), wild bees and hoverflies (Jauker, Bondarenko, Becker & Stefan-Dewenter, 2012), agreeing with our finding that pollinated plants converted more flowers to fruit (i.e. 79% and 77% in insect- and wind-pollinated plants versus 60% in pollen-limited plants). This higher fruit set increased yield by 8% and 10% for insect- and wind-pollinated plants, respectively. This result is modest compared to other studies where yield increased between 18% (Bommarco et al., 2012) and 46% (Sabbahi et al., 2005). Nevertheless, this is still a substantial increase for growers from an economic standpoint.

Pollination deficits can reduce yield by impacting the fruit set, the number of seeds per pod, and/or seed weight (Bommarco et al., 2012; Stanley & Stout, 2013). In this study, pollination deficits resulted in reduced fruit set and fewer seeds per pod (e.g. pollen-limited plants produced 21% and 14% fewer seeds per pod than insect- and wind-pollinated plants, respectively). However, plants compensated for lower seed production by investing more resources into each seed, and seeds from pollen-limited plants were 5% heavier than insect-pollinated plants. This is contrary to field studies that found pollination deficits resulted in lighter seeds (Bommarco et al., 2012). This discrepancy is possibly due to resources being more limited in a glasshouse environment (e.g. due to the constraints of pot size). As such, insect-pollinated plants with a greater fruit and seed set had insufficient resources to invest in seed weight. This is supported by field investigations indicating that pollination and soil properties/nutrient availability interactively impact yield (Bartomeus, Gagic & Bommarco, 2015; Garratt et al., 2018). With seed weight strongly related to oil concentration, a quality measure in OSR (Bommarco et al., 2012), there may be a trade-off between seed production and quality when resources are constrained. Despite pollen-limited plants allocating more resources to growth and flowering and increasing seed weight, yield deficits were still observed.

Differences between insect and wind simulated pollination

Vegetative or reproductive metrics associated with seed weight did not differ between wind- or insect-simulated pollination. This highlights that in a controlled environment, the mode of pollination delivery is less important than the occurrence. A similar performance in wind- and insect-

pollinated OSR indicates that similar yields can be achieved without insect pollination. However, these results may be explained by pollen delivery efficiency. Clumping can occur if the pollen load is too large, leading to stigma clogging and reduced yield (Thomson, 1989). While increasing pollen load can positively affect OSR seed set initially, there is an optimum pollen loading of 100–200 grains (Lankinen, Lindström & D’Hertefeldt, 2018). Regular hand-pollination may have increased pollen deposition beyond this optimum, adversely affecting yield, or damaged the stigmas.

Contrary to field experiments, our pollen-limited plants did not have lower total seed weights (Bartomeus et al., 2015; Bommarco et al., 2012; Jauker et al., 2012). Our treatments focussed on limiting either wind or insect pollination, whereas field investigations typically compare wind pollination (i.e. through excluding pollinators) and open-pollinated treatment (i.e. subjected to both wind and insect pollination). Therefore, discrepancies between field and controlled environment studies may highlight that a combination of wind and insect pollination can maximise yield. With pollinators typically preferring to forage in warm, still weather, wind and insect pollination may complement each other. For example, in windy conditions, the curtailment of insect pollination could be stabilised by more effective wind pollination. Furthermore, in this study, wind-simulated pollination focused on transferring pollen within a single plant, whereas wind pollination would result in both self and cross-pollination in a field situation.

Pollen limitation clearly adversely affects yield, although these impacts are somewhat mitigated by prolonging the flowering period and increasing seed quality. With the low probability of windborne pollen finding a receptive stigma (Langridge & Goodman, 1982; Ouvrard, Quinet & Jacquemart, 2017), wind and insect pollination could complement each other, stabilising yields under different environmental conditions.

Conclusions

This study demonstrates the impact of pollination on oilseed rape and how, through phenotypic plasticity, plants alter functional traits in response to pollination. Resource allocation between growth and flowering metrics can increase and stabilise yields, either directly (i.e. through increased fruit set and the number of seeds) or indirectly (i.e. producing shorter plants and reducing flowering time). Despite OSR altering how resources are allocated when pollen is limited (e.g. prolonging flowering and producing heavier seeds), negative impacts on yield were still detected. For oilseed rape to produce more stable yields under varying environmental conditions, a combination of wind and insect pollination offers the best opportunity. When environmental conditions affect one delivery system's efficiency, the other can mitigate potential pollen restrictions.

Alongside agri-environment schemes providing habitat and resources for pollinators, mass-flowering crops provide pulses of forage in intensive agricultural landscapes helping to fill hunger gaps (Timberlake, Vaughan, Memmott & Requier, 2019; Westphal, Steffan-Dewenter & Tschamntke, 2009). Since pollen-limited plants display clear changes in morphology (e.g. taller growth, greater flowering, and more prolonged flowering), such trait changes could act as an early warning of pollination deficits. Equipping growers with the ability to detect a deficit in pollination services raises awareness of the importance of insect pollinators and empowers them to take remedial action to restore pollination services (e.g. introducing managed honeybees or planting floral-rich field margins to enhance wild pollinators). By detecting pollination service deficits and managing pollination as an agricultural input, growers can exploit the valuable ecosystem service offered by insect pollinators to increase economic output well into the future.

Author contribution statement

SMF, LJC and GJ conceived the ideas and designed the methodology; SMF collected the data; SMF, LJC and GJ analysed the data; SMF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability statement

The data presented in this study will be openly available in Edinburgh DataShare [<https://datashare.ed.ac.uk>] (doi and reference number to be forwarded once accepted).

Declaration of Competing Interest

The authors declare no conflict of interest.

Acknowledgements

This work was supported by a studentship from the Natural Environmental Research Council (NERC) E³ Doctoral Training Partnership (Grant number: [NERC NE/L002558/1](#)).

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