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ASSESSING THE RISK OF STIGMA CLOGGING IN STRAWBERRY FLOWERS DUE TO POLLINATOR SHARING WITH OILSEED RAPE

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Abstract—Strawberry and oilseed rape are economically important and co-flowering insect-pollinated crops that may affect each other via shared pollinators. One potential negative effect of pollinator sharing is stigma clogging, i.e. that pollen from one plant species covers the stigma and prevents pollination in the other. We tested if application of oilseed rape pollen on strawberry receptacles reduces pollination with subsequent effects on strawberry weight, number of malformations and ripening time. We simulated real pollination situations by using dead bees mounted on toothpicks to mimic flower-visitation of foraging bees. Six strawberry flowers, usually on different plant individuals, were hand-pollinated sequentially per simulated foraging bout. In half of these foraging bouts, we started with an oilseed rape flower, and in those foraging bouts the proportion oilseed rape pollen was expected to decline with increasing number of visited strawberry flowers. Oilseed rape pollen had no effect on any of the tested variables. Increasing number of previously visited strawberry flowers in the simulated foraging bout enhanced the number of developed achenes, but this was marginally non-significant when accounting for the total number of achenes. Strawberry weight increased and ripening time decreased with increasing number of pollinated achenes, whereas none of the tested factors had any effect on the number of malformations. Our results have implications for strawberry farmers, because shortened ripening time could reduce the risk of yield loss from pests, diseases and unfavourable weather conditions. In addition, we show that oilseed rape pollen is unlikely to disturb pollination success of strawberry flowers.

Keywords: Rapeseed, canola, mass-flowering crops, entomophilous crops, Fragaria, Brassica

INTRODUCTION

Insect-pollinated crops constitute a third of the global agricultural yield (Klein et al. 2007), a share that is steadily increasing (Aizen et al. 2009). Because many of these crops can produce seeds and fruits without insect-pollination, less than 10% of the yield is directly attributable to insect pollination (Aizen et al. 2009). However, pollinators contribute to a large fraction of the non-starch nutrients that humans consume (Eilers et al. 2011) – with vital effects on human health (Smith et al. 2015). Thus, safeguarding pollination services may be crucial in optimizing crop yields (Bommarco et al. 2013) and healthy diets (Eilers et al. 2011; Smith et al. 2015). Crop pollination generally increases with wild pollinator abundance and species richness (Garibaldi et al. 2013), which in turn increase with reduced land management intensity and proximity to natural habitats (Ricketts et al. 2008; Tuck et al. 2014). While densities of managed pollinators can be elevated by placing hives near the flowering crops, management options available to improve crop yields by wild pollinators are associated with a higher uncertainty (e.g. Ricketts et al. 2008).

Increased availability of flowers can benefit crop pollination by wild insects (Blaauw & Isaacs 2014; Carvalheiro et al. 2012), in particular in the absence of natural habitats (Carvalheiro et al. 2011). However, a major obstacle for improving crop pollination by wild pollinators is related to the potential indirect interactions among flowering plants, since co-flowering plants may either compete for pollinators (Brown & Mitchell 2001), or facilitate the pollination of one another by attracting common pollinators (Ghazoul 2006). In addition, pollinator sharing increases the risk of interspecific pollen transfer, i.e. the movement of pollen between plant species. Interspecific pollen transfer can reduce pollination success, by affecting both male and female fitness (Morales & Traveset 2008). When pollen is removed from a flower and deposited on a stigma of another species, the pollen donor may suffer from pollen loss (Morales & Traveset 2008) and the pollen receiver from stigma clogging, i.e. that heterospecific pollen covers the stigma, preventing conspecific pollen from fertilizing the ovules (Brown & Mitchell 2001). In extreme cases, foreign pollen may inhibit pollen germination by producing toxic substances (Kanchan & Chandra 1980). Thus, co-flowering crops that share pollinators can potentially affect each other, either by competition, facilitation or interspecific pollen transfer, but to our knowledge such interactions among co-flowering crops have never been assessed.

Oilseed rape is an economically important insect-pollinated crop with an increasing global production since the 1960s (FAOSTAT 2017). Flowering oilseed rape attracts foraging pollinators (Kovács-Hostyánszki et al.

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2013), thereby reducing pollination of co-flowering plants in nearby grasslands (Holzschuh et al. 2011), and facilitating or having no effect on pollination of adjacent plants (Cussans et al. 2010). Information on how interspecific pollen transfer from oilseed rape to other plants affects pollination is scant. In one study, the proportion of oilseed rape pollen on flowers of wild plants adjacent to the fields constituted around 3% of all pollen grains on the stigma, indicating that concentrations are too low to result in stigma clogging (Stanley & Stout 2014). On the contrary, Klatt (2013) showed that increasing proportion of honeybees correlated negatively with strawberry weight in field borders, where honeybees (but not other bees) carried pollen from both oilseed rape and strawberry crops. In field centers, where bees carried pure strawberry pollen loads, a positive correlation between honeybee densities and strawberry weight was found. This suggests that the reason for the observed pattern is interspecific pollen transfer, but the underlying mechanism remains to be examined.

Strawberry is an entomophilous crop that attracts insects by providing both pollen and nectar (Chagnon et al. 1993). All commercially used strawberry varieties are self-fertilising (Free 1993), but insects promote pollination by dispersing pollen between (Free 1993) and within flowers (Chagnon et al. 1993). The true fruits are the achenes on the strawberry surface (Free 1993), which produce growth hormones and induce strawberry growth and ripening (Nitsch 1950). Consequently, strawberry weight increases with the number of fertilized achenes (Abbott & Webb 1970), and a lack of pollinators can reduce the market value of strawberries by reducing the number of developed achenes or increasing the number of malformations (Klatt et al. 2014).

The aim of this study was to reveal if pollinator sharing with oilseed rape reduces pollination success in co-flowering strawberry crops as a result of stigma clogging. Based on the assumptions that strawberries deriving from flowers with a high number of developed (pollinated) achenes weigh more, have fewer malformations and shorter ripening time, we made several predictions. We predicted that oilseed rape pollen hinders strawberry pollination resulting in a lower number of developed achenes, lower strawberry weight, more malformations, and longer ripening time. On the contrary, we also predicted that increasing amounts of strawberry pollen on the receptacle result in higher numbers of developed achenes, higher strawberry weight, less malformations and shorter ripening time.

MATERIALS AND METHODS

Study design

We sowed spring-sown oilseed rape in a climate chamber, simulating Swedish spring, in February 2014. In April 2014, we acquired 96 strawberry plants with flower buds that had not yet opened, from a grocery store. We used the strawberry variety 'Salsa', which has a moderate insect-dependency compared to other varieties (Klatt et al. 2014). We potted strawberry plants in 1.5 L pots, kept them in a greenhouse and watered them daily. There was no possibility for insects to enter the greenhouse. When the first strawberry flowers started to open, we brought two flowering oilseed rape plants from the climate chamber to the greenhouse, to use as pollen donors.

Each strawberry branch produces several flowers that open sequentially, with the primary flower being the largest, containing most ovules (Free 1993) which results in the largest strawberry (Abbott & Webb 1970) and also the one most dependent on insect-pollination (Chagnon et al. 1989). Plants can produce more than one flower bearing branch, and can thus produce more than one primary strawberry per season (pers. obs.). In this experiment, we only regarded the primary flower/strawberry from the first branch as primary.

Open strawberry flowers were hand pollinated three times each, once per day for the first, second and third open day. We used dead red mason bees (*Osmia bicornis*) for the pollen application. The bees had never visited any flowers because they were frozen directly after they had emerged from the cocoons. The dead bees were attached to toothpicks and hand-pollination was performed by gently rotating the bee around the centre of the flowers, trying to mimic the pivoting flower-visitation behaviour of this and other similarly sized bee species (Albano et al. 2009; Chagnon et al. 1993; pers. obs.). After hand pollination, we cleaned the bees carefully with ethanol, and dried them at ambient temperature during at least 24 h.

We simulated two types of foraging bouts (oilseed rape or control), to mimic real pollination situations in which oilseed rape pollen was either involved or not. Each bee was only used in one type of simulated foraging bout to ensure that no oilseed rape pollen would contaminate the flowers in the control simulated foraging bouts. The oilseed rape foraging bout started with bees "visiting" an oilseed rape flower, after which it continued to six different strawberry flowers. We did not measure the amount of pollen on the bees' body nor how much pollen was transferred, but observed pollen on the bee bodies after the first flower visit (to oilseed rape). In the control simulated foraging bouts, bees visited six strawberry flowers, without first visiting the oilseed rape. The order of which the strawberry flowers were visited was the same during the first, second and third day of hand-pollination treatment. All flowers in the same foraging bout were usually from different plant individuals, but in a few cases we used more than one flower per plant. However, in the analyses we only used primary strawberries, which are the ones that depend most on insect-pollination (Chagnon et al. 1989) and produce the largest strawberries (Free 1993), such that only one flower per plant was analysed.

To avoid mixing up the flower treatments (oilseed rape or control), we used one of the treatments in each pot. To keep track of the position in the foraging bout and the number of hand-pollination treatments each flower within a pot had been through, we colour marked hand-pollinated flowers with one piece of drinking straw (one separate colour for each position in the foraging bout) per performed foraging bout. The first strawberry flowers opened and were hand-pollinated on the 1st May and we continued hand-pollination until the 21st May. A few days there was a lack of flowers, such that we could not accomplish any entire foraging bouts with six visits. When fewer than six flowers were available or when a few flowers remained to be pollinated after all complete simulated foraging bouts had been accomplished, we made shorter simulated foraging bouts.

Measures of strawberry pollination

Ripe strawberries were harvested continuously and were brought to the lab immediately for assessment. Strawberries were considered ripe when they were completely red and could easily be detached from the pedicle. In the lab we took the following measurements on each strawberry: weight, number of malformations (groups of undeveloped achenes), the number of developed and undeveloped achenes and ripening time (number of days from the flower opened until the strawberry was harvested). We continued harvesting until the 19th June, when only two poorly pollinated primary strawberries (and several from later flowers) remained, one control strawberry and one oilseed rape treated. These two strawberries were excluded when we tested weight, malformation and ripening time, but not the number of pollinated achenes, which were easily identified.

STATISTICAL ANALYSES

We used R.3.3.2 for windows and analysed data with general or generalized linear models from the R package 'stats' (R Core Team 2016). We extracted model estimates that we used to plot the results and to calculate effect sizes using package 'effects' (Fox 2003).

Effects of oilseed rape pollen and strawberry pollen

In separate analyses we tested how number of developed achenes, weight, number of malformations and ripening time were affected by an interaction between treatment (i.e. whether the simulated foraging bout was an oilseed rape or a control bout) and the flower's position in the simulated foraging bout (1-6). Because the total number of achenes sets the upper limit for the number of developed achenes and for strawberry weight, we aimed to use this as an offset variable in these two models. However, on four poorly pollinated strawberries (one oilseed rape and three control, all from the first position in the foraging bout) we could not count the total number of achenes, because the undeveloped achenes were embedded in surrounding strawberry tissue. Since accounting for the number of achenes resulted in the exclusion of these strawberries we ran the models both with and without the offset variable. For weight and ripening time we assumed Gaussian distribution of the residuals and for developed achenes and malformations we used quasi-Poisson to handle overdispersion. We removed non-significant ($P \geq 0.05$) terms hierarchically to establish the best model explaining each of our response variables.

Effects of developed achenes on weight, malformations and ripening time

To verify our assumption that well-pollinated strawberries are larger (Abbott & Webb 1970; Nitsch 1950), have fewer malformations and ripen faster than poorly pollinated ones, we performed three additional tests using number of developed achenes as predictor variable and weight, malformations and ripening time, respectively, as response variable. For weight and ripening time we assumed Gaussian distribution of residuals and for malformations we used quasi-Poisson to handle overdispersion.

RESULTS

Effects of oilseed rape pollen

Strawberries had on average (mean ± sd) 138.5 ± 73.5 developed achenes, weighed 13.3 ± 4.2 grams, had 7.0 ± 4.0 malformations and ripened in 32.4 ± 2.3 days. Oilseed rape pollen had no effect on any of these variables, neither via the interaction with the flower's position in the foraging bout (*developed achenes*: $T_{64} = 0.92$; $P = 0.36$/ (with offset) $T_{60} = 1.57$; $P = 0.12$, *weight*: $T_{62} = 1.07$; $P = 0.29$/ (with offset) $T_{60} = -0.31$; $P = 0.76$, *malformations*: $T_{62} = 0.17$; $P = 0.86$, *ripening time:* $T_{62} = -0.95$; $P = 0.35$, Fig. 1), nor as an independently acting factor (*developed achenes*: $T_{65} = 0.69$; $P = 0.49$/ (with offset) $T_{61} = 0.40$; $P = 0.69$; *weight*: : $T_{63} = 1.25$; $P = 0.22$/ (with offset) $T_{61} = -1.23$; $P = 0.22$, *malformations*: : $T_{63} = 0.09$; $P = 0.93$, *ripening time:* $T_{63} = 0.20$; $P = 0.84$, Fig. 1).

Effects of strawberry pollen

When excluding the offset variable, thereby including strawberries with unknown number of achenes, the number of previously visited flowers in the simulated foraging bout (1-6) had a positive effect the number of developed achenes (12% increase per visited flower; $T_{66} = 3.19$; $P = 0.002$, Fig. 1) and strawberry weight (0.87 grams increase per visited flower; $T_{64} = 3.04$; $P = 0.003$, Fig. 1), but this effect became marginally non-significant (*developed achenes*: $T_{62} = 1.95$; $P = 0.056$) or disappeared (*weight*: $T_{62} = -1.24$; $P = 0.22$) when using the number of achenes as offset variable. Increasing number of previously visited flowers in the simulated foraging bout had a negative impact on ripening time (0.44 days shorter per visited flower; $T_{64} = -2.81$; $P = 0.007$, Fig. 1), but no effect on the number of malformations ($T_{64} = -0.84$; $P = 0.41$, Fig. 1).

Effects of developed achenes on other measurements

The number of developed achenes was positively related to strawberry weight (4.2 grams increase per 100 achenes; $T_{64} = 7.92$; $P < 0.001$, Fig. 2), unrelated to the number of malformations ($T_{64} = -0.30$; $P = 0.77$, Fig. 2) and negatively related to ripening time (-1.9 days per 100 achenes; $T_{64} = -5.72$; $P < 0.001$, Fig. 2).

DISCUSSION

Oilseed rape pollen had no effect on strawberry pollination, weight, malformations or ripening time. However, the number of developed achenes increased (significantly or marginally non-significantly so, depending on analysis) with the number of previously visited flowers in the simulated foraging bout, possibly because of higher conspecific pollen loads (Quesada et al. 2001) or higher pollen diversity (Paschke et al. 2002) on the bee body. Increasing number of developed achenes in turn, had a positive influence on strawberry size and reduced the

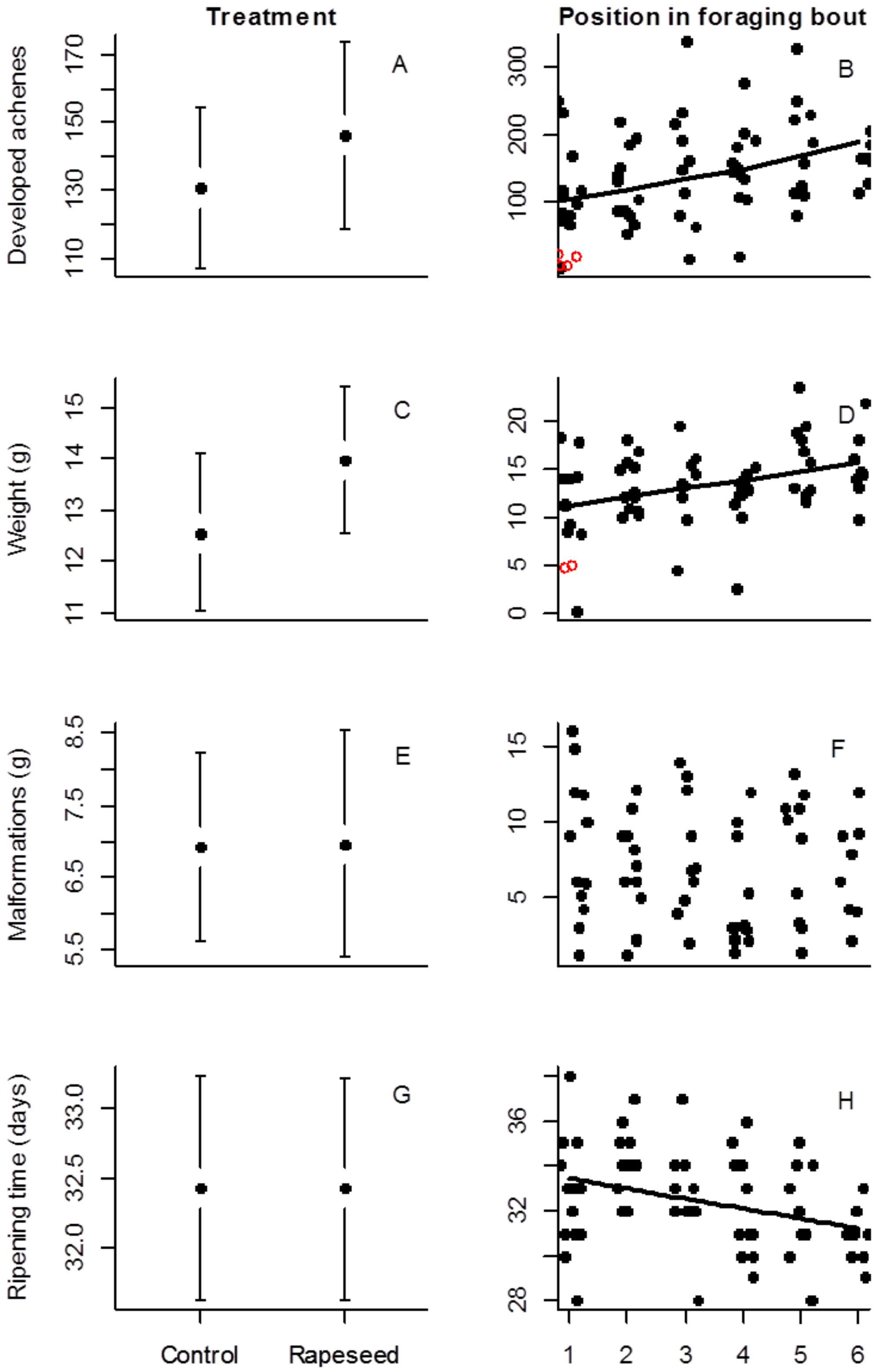

FIGURE 1. The panel shows (A,B) the number of developed achenes, (C,D) strawberry weight, (E,F) number of malformations and (G,H) ripening time in relation to (A,C,E,G) oilseed rape treatment and (B,D,F,H) the flower's position in the simulated foraging bout. In the left column raw mean values for the two treatments are shown with error bars showing 95% confidence intervals. In the right column individual strawberries are shown in black and trend lines are added for significant effects. When accounting for the total number of achenes, the flower's position in the foraging bout had a marginally non-significant effect on number of developed achenes ($P = 0.056$) and no effect on weight ($P = 0.22$). Strawberries that lacked data on the number of achenes, and consequentially were excluded from the latter analyses, are shown as red circles.

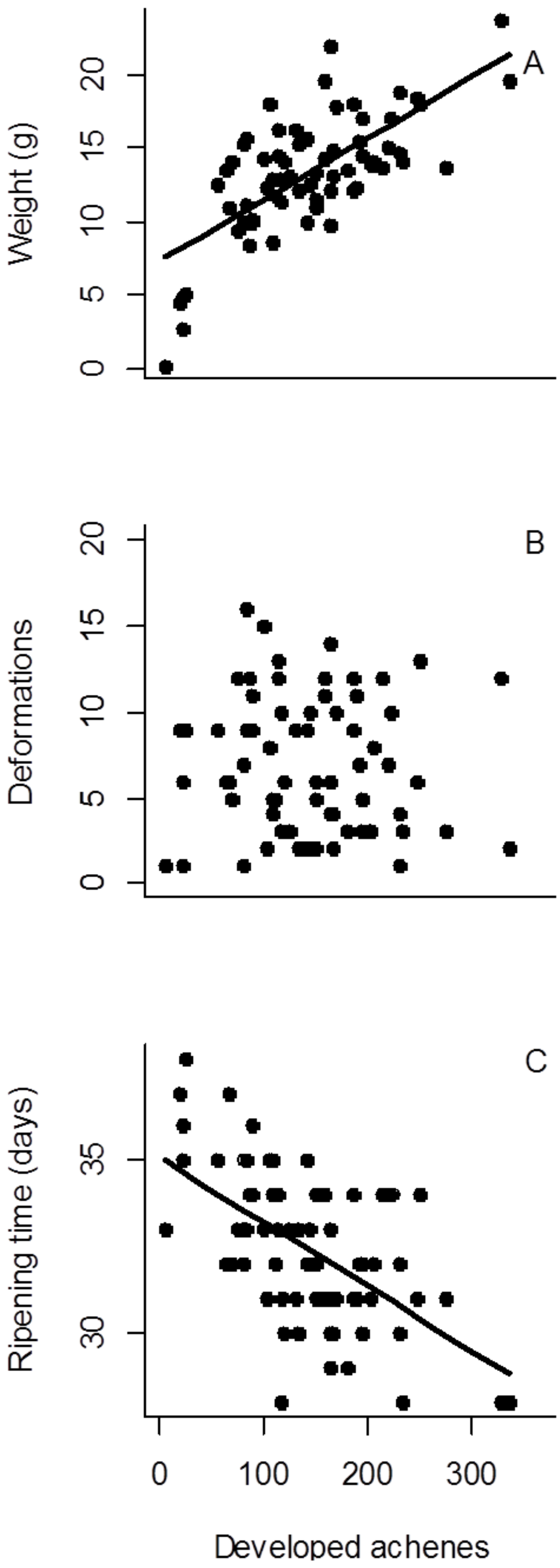

FIGURE 2. (A) Strawberry weight, (B) number of malformations and (C) ripening time in relation to the number of developed achenes. Dots show data on individual strawberries and trend lines are shown if significant.

ripening time, but had no impact on that the number of malformations under these experimental condition.

We found no evidence for oilseed rape pollen to have any negative impact on strawberry pollination, but this does not exclude that oilseed rape increases pollen limitation in strawberry fields by other means. Pollen limitation could occur as a result of competition for pollinators (cf. Holzschuh et al. 2011). We are not aware of any studies showing that competition for pollinators between co-flowering crops reduces yields, but intraspecific competition over pollinators can affect flower-visitation at both field (among coffee plants; Veddeler et al. 2006) and landscape scales (among sunflower fields within 2 km; Riedinger et al. 2014), suggesting that it also affects co-flowering crops, which attract the same pollinators. Pollen limitation could also be the result of pollen loss, i.e. the deposition of pollen on the stigma of a competing species (Morales & Traveset 2008). The effect of losing pollen in this way seems to be of higher importance for pollination than the negative consequences from receiving foreign pollen (Campbell & Motten 1985; Feinsinger & Tiebout 1991). Yet pollen loss is a far less studied phenomenon (Morales & Traveset 2008) and we are not aware of any studies assessing how it affects co-flowering crops.

From a farmer's perspective it may be important to differentiate between pollen limitation caused by lack of pollinators and loss of pollen, because the outcome of potential actions that the farmers commit likely depends on what mechanism is responsible for the effect. Whereas competitive pollinator dilution could be avoided by boosting pollinator densities, pollen loss may instead be aggravated if the same actions are taken and may instead require separation between the two crops. Honeybees can be used to increase pollinator densities, but since they commonly forage more than a kilometer away from the nest (Steffan-Dewenter & Kuhn 2003), spatial separation of the strawberry and oilseed rape fields would be difficult if using honeybees as pollinators. Solitary bees may provide a solution to this problem, because they have shorter foraging ranges than honeybees (Beekman & Ratnieks 2000; Gathmann & Tscharntke 2002), and their nests could possibly be placed to maximize the distance to the oilseed rape (e.g. in the middle of a strawberry field or on a side if the strawberry field where no oilseed rape is grown). Farmers could also grow later flowering strawberry varieties, which flower after the oilseed rape. This would allow the usage of honeybees without risking increased pollen loss and may be particularly beneficial for strawberry yields in landscapes with high proportion oilseed rape where farmers can take advantage of increased bumblebee densities (e.g. Riedinger et al. 2014).

In agreement with previous studies on cloudberry (Kortesharju 1993) and raspberry (Jennings & Topham 1971), we found that well-pollinated strawberries ripened significantly faster than poorly pollinated strawberries. This finding is interesting and should be further investigated, because shorter ripening time means that the critical time when strawberries are exposed to pests and diseases, and the need for water and suitable weather conditions, is minimized.

There are potential shortcomings of this study. First, effects of pollination treatment on the number of pollinated achenes and strawberry weight were only significant when including all strawberries, i.e. without accounting for the total number of achenes. While the estimated effect of pollination treatment on developed achenes remained near-significant ($P = 0.056$) when accounting for the number of achenes and thereby also incidentally excluding some of the less pollinated strawberries, the effect on weight completely disappeared. Increasing amount and diversity of strawberry pollen is likely to have a positive influence on strawberry weight, but if this is not the case, then the lack of effect from oilseed rape pollen should also be carefully interpreted. Second, the fact that no strawberries in our study completely lacked malformations suggest that pollination was generally poor, e.g. because of the low number of "bee visits" or because hand-pollination with dead bees that do not collect pollen actively and do not move around in the same way as living bees do not adequately mimic pollination by live bees. Both these differences could be relevant for the interpretation of the results, e.g. if pollination saturates when the number of pollinator visits increases. Thus, additional studies using live bees in realistic settings are needed. Third, previous studies have shown that insect-pollination reduces the number of malformed strawberries (Free 1993). However, in contrast to our other pollination proxies, the number of malformations in this study was unrelated to the number of developed achenes. A possible reason is that the number of malformations is an unprecise estimate of pollination success; in this study strawberries were generally small and poorly pollinated, and some badly pollinated strawberries had one or a few large malformations instead of many smaller.

Conclusion

Although strawberries are partly self-pollinated (Free 1993), the present and previous studies show that pollinators can increase the value of strawberry yields by several means. Not only does increased pollination result in larger strawberries and higher fruit set (Free 1993), but also in longer shelf-life (Klatt et al. 2014), a more desired fruit shape (Free 1993; Klatt et al. 2014) and, as shown in this paper, shorter ripening time. The present study suggests that foreign pollen from oilseed rape is unlikely to interact with these outcomes, but some caution is needed because increased number of previously visited strawberry flowers also had no significant impact on weight and developed achenes when accounting for the total number of achenes. Other potential effects of oilseed rape on strawberry pollination (e.g. pollen loss and competition for pollinators) still remain to be explored.

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AUTHOR CONTRIBUTIONS

LH and BKK formulated the idea, IG and LH developed the methods with input from HGS, IG and LH collected the data, IG and LH analysed the data, LH and IG wrote the manuscript with contribution from BKK and HGS. LH and IG contributed equally to this work.

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