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Insect pollination is the weakest link in the production of a hybrid seed crop

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ABSTRACT

Ecological intensification of farming proposes that more effective use of ecosystem services can, in part, replace external inputs allowing farmers to maintain high crop yields while reducing adverse effects on the environment. However, uptake of ecological intensification among farmers is currently hampered by a lack of realistic studies on the agronomic benefits of enhancing ecosystem services vis-à-vis the benefits of conventional external inputs. Here, we use a full-factorial field experiment to test the relative and interactive effects of fertilisation, irrigation and pollination on crop yield of three parental crop lines of leek (*Allium porrum*) hybrid seed production. In a commercial leek seed production field, we assessed the agronomic performance of plants receiving conventional or 50 % reduced external inputs and that were either continuously accessible to pollinators or only 50 % of the time. For all crop lines, we found that reducing insect pollination had at least two times stronger effects on crop yield than similar reductions in fertilisation or irrigation. Surprisingly, reducing fertiliser inputs by half did not negatively affect crop yield (one line) or even increased crop yield (two lines), suggesting that in this system fertiliser is an over-applied agricultural input. Reducing irrigation did not affect crop yield in two lines but reduced crop yield in the third line. However, there were strong indications that this negative effect of reduced irrigation was due to reduced attractiveness for pollinators. Effects of fertilisation, irrigation and pollination on crop yield were additive, with the exception of pollination effects being influenced by fertilisation level in one of the lines. Under real-world conditions, reductions in insect pollination consistently reduced hybrid leek crop yield while reductions in external inputs did not. This suggests that in this cropping system insect pollination is the weakest link in the agricultural production process. Our findings help explain why the relation between agricultural intensification and yield growth disappears with the dependence of crops on insect pollination. For insect-depended crops, protection or promotion of pollinators in agricultural landscapes is essential for maintaining high yields.

1. Introduction

Intensive agriculture has adverse effects on biodiversity in agricultural landscapes (Donal et al., 2001; Tscharntke et al., 2005) and associated delivery of ecosystem services such as pest control (Karp et al., 2018) and insect pollination (Kremen et al., 2002; Kennedy et al., 2013). These negative environmental impacts have raised concerns about the sustainability of intensive agriculture in meeting rising demand for agricultural products (Godfray et al., 2010). Ecological intensification has been proposed as a more sustainable farming approach to maintain and/or enhance agricultural production while minimizing negative environmental impacts. It encompasses the adoption of management practices to enhance biodiversity-based ecosystem service delivery to supplement or replace external inputs (Bommarco et al. 2013). However, effective uptake of the concept is limited so far (Kleijn et al., 2019), possibly because the agricultural sector does not perceive ecosystem service-providing organisms to be as important for crop productivity as regular agricultural inputs such as fertilisers or pesticides (IPBES, 2016).

While there is a growing body of literature that shows that managing for biodiversity enhances the provision of key ecosystem services supporting agricultural production (Kovacs-Hostyanszki et al., 2017), the evidence base may not yet be convincing enough for the agricultural sector to integrate biodiversity into farm management (Kleijn et al., 2019). A commonly heard argument from growers is that they can improve yields via conventional agricultural inputs more easily than through managing for ecosystem services (Kleijn et al., 2019). However, whether managing for more inputs or enhanced ecosystem

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service delivery is more effective will depend on the contribution of the ecosystem services to crop yield relative to that of agricultural inputs (Fijen et al., 2018).

The most important external agricultural inputs that aim to increase crop yields are fertiliser and irrigation (Tilman et al., 2002, 2011), while pesticides are mainly applied to reduce yield losses (Oerke, 2005). Agricultural intensification has seen a steady rise in agricultural input levels in the last decades, corresponding with increasing yields (Tilman et al., 2002). However, for insect-dependent crops the increase in yields decreases with increasing insect dependency (Garibaldi et al., 2011; Deguines et al., 2014), which suggests that pollination is currently often limiting yield of these crops. Globally, two-thirds of the crops depend at least partly on insect-pollination (Klein et al., 2007; Aizen et al., 2008), with wild pollinators generally contributing most to crop yield (Garibaldi et al., 2013, 2016; Fijen et al., 2018). Recently, several studies have explored whether the relative benefits of insect pollination on crop yield depend on the levels of the agricultural inputs (Garibaldi et al., 2018; Tamburini et al., 2019). Many studies find that pollination and agricultural inputs have additive effects on crop yield, suggesting that both pollination and agricultural inputs need to be optimized to increase yield (van Gils et al., 2016; Garibaldi et al., 2018; Garratt et al., 2018).

However, most of these studies (but see Boreux et al., 2013; Tamburini et al., 2017) have used all-or-nothing levels of, for example, insect pollination (no insect pollination vs open pollination) and fertiliser (no fertiliser vs fertiliser). Such extreme contrasts can provide useful information on the mechanisms regulating the contributions of pollination or fertilisation to crop yield, but they cannot reveal the contribution of pollination at different realistic input levels. For example, Tamburini et al. (2017) found that pollination benefits were optimal under intermediate fertilisation levels for crop yield of sunflower. Even for crops that fully depend on insect pollination (e.g. pumpkin c.f. Hurd et al., 1971) some input of fertilisation and irrigation is still necessary for high yields. Hence, results from all-or-nothing studies are hard to translate into day-to-day practices of farmers. To convince the agricultural sector of the relative importance of insect pollination compared to agricultural inputs, we need studies that use input levels resembling those in real-world systems.

Here we test the reliance of a conventionally managed insect-pollinated crop on pollinators and how this compares to, and possibly interacts with, application of fertilisation and irrigation. We used an experimental approach with a full-factorial, randomized block design in a commercial hybrid leek-seed production field in southern Italy and studied the response of three different crop lines. We compared conventionally managed plants receiving ambient pollinator visitation rates with plants receiving 50 % reduced fertilisation and irrigation levels and whose flowers were accessible to pollinators half of the time. The results of this study can help to inform farmer management decisions on focusing on conventional agricultural inputs, insect pollination, or both, and how this varies between lines of the same crop.

2. Materials and methods

2.1. Study system

We used a commercial leek (Allium porrum) hybrid seed production field (one hectare) in southern Italy as our experimental field. The experimental field (loamy clay) was located in a predominantly flat area, surrounded by agricultural production fields, mainly wheat, and close to a small river. The climate in this region is Mediterranean and described by mild winters and hot and dry summers, with on average 500 − 550 mm of rain, mostly in the winter months.

Because of the hybrid seed production system, the seed producing female parent lines are fully dependent on insects to transport the pollen from the male parent line to the female parent line (Wright, 1980; Brewster, 2008). Leek is an attractive crop for a wide range of insect pollinators and may attract large numbers of pollinators, in particular bees (honeybees, bumblebees, solitary bees) and hoverflies (Fijen et al., 2018, 2019). To increase transferability of results, we selected three different female parent lines with different plant characteristics (Fijen et al., 2018), that are being used for commercial seed production (referred to by BASF as line B, C and F). These crop lines varied in their average seed production and relative pollination contribution, based on an earlier study across commercial fields (Fijen et al., 2018). Leek plants were transplanted into the field in October 2016, and flowered around June 2017 for about 3–4 weeks. Leek forms a primary umbel, and often one or two (up to three) secondary umbels that flower after the primary umbel. For this study we focused on the primary umbel, which yields the majority (> 80 %) of the marketable yield.

2.2. Experimental setup and treatments

We used a full-factorial randomized block design with five replicates, placed within the commercial field. Each block contained eight plots in randomized order (two fertiliser x two irrigation x two pollination levels). Within each plot we placed six female plants of each female line and randomized the relative location of female lines to each other. Plants were planted in double rows, with 20 cm between the rows and 10 cm between the plants. To avoid that a treatment in one plot affected the neighbouring plots (for example during irrigation events), we placed 20 buffer plants between two subsequent plots (Fig. 1). The buffer plants were the male parent line of the commercial field, thereby also ensuring a sufficient and nearby pollen source. These plants also received the treatment of the closest plot of female plants.

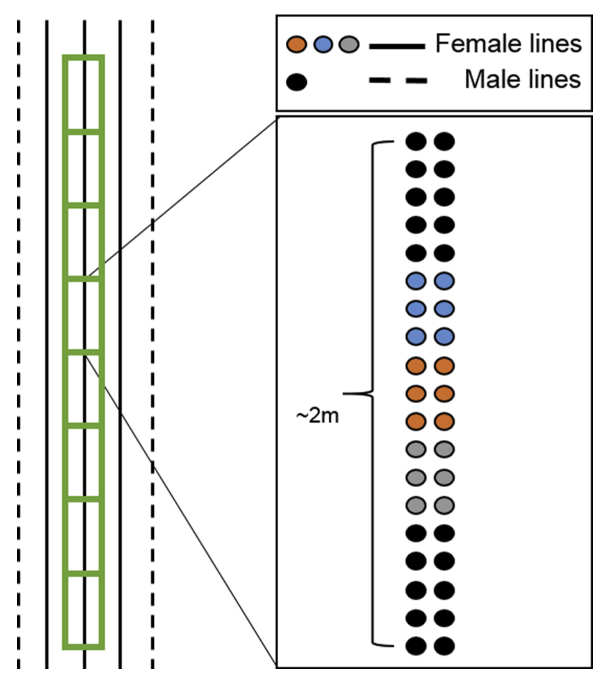

Fig. 1. Schematic diagram of the experimental setup. The experiment was located in the middle bed of female plants (black solid line = bed of female plants, black dashed line = bed of male plants), with approximately one metre between beds. The green rectangle represents one block consisting of eight treatment plots. The inset shows a schematic setup of one plot, with six plants per female line, of which two representative plants were chosen as experimental plants. Each dot represents a single female plant. The order of the female lines within a plot and the treatment per plot were randomized. The male plants represent a buffer zone between plots to ensure a high pollen load and to avoid effects of neighbouring treatments. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

The two treatment levels were 100 % (hereafter standard) and 50 % (hereafter reduced) levels of conventional application rates of fertilisation, irrigation, and of ambient pollination levels.

We based the standard level of fertiliser on the conventional nurturing protocol for leek seed production and adapted it to local growing conditions based on soil type and a soil analysis prior to transplanting (Brewster, 2008). The standard fertiliser treatment corresponded to a total of 200 kg/ha nitrogen (N), 120 kg/ha phosphorus (P), and 10 kg/ha potassium (K) in granular form, applied over several fertilising events (~60 % before transplanting, ~20 % in early spring, and ~20 % before flowering) during the growing season. For the reduced fertiliser level we reduced the NPK amount by 50 % for each fertilising event.

In this crop system, irrigation is applied mostly in spring and summer, with the plants receiving approximately four hours of drip irrigation every three days (standard treatment, approximately 15 mm of water per irrigation event). For the reduced irrigation treatment, we doubled the time between watering events (i.e. six days between events), and not the amount of water per event, as we wanted to be sure that enough water was given to reach the majority of the roots during each event. We only applied the irrigation treatment from the start of flowering until harvest, as this is the period with potential water stress affecting seed production (Brewster, 2008). It did not rain in the period from the start of flowering until harvest, so the irrigation was the only source of water in that period.

For pollination we used open-pollination (managed honey bees and wild pollinators, in order of abundance bumblebees (Apidae), solitary bees (Andrenidae and Halictidae), and hoverflies (Syrphidae) c.f. (Fijen et al., 2018)) as the standard treatment, and for the reduced treatment we bagged the plants with small mesh bags made of bridal gown every other day during the flowering period. In this way we reduced the time that pollinators could visit the plants by 50 %, and we expected that this would effectively reduce pollination success. Stigmatic receptivity of the closely related onion (Allium cepa) is approximately five days, but is highest three days after anthesis (Chang and Struckmeyer, 1976), which suggests that pollination may depend on a plant being bagged that particular day. To remove any potential effect of bagging day, we treated all plants within a block similar (either all bag on, or all bag off), and randomized which block had the bags on or off at the start of the flowering period.

All other agricultural interventions like weeding, addition of micronutrients, or applications of pesticide were applied as in the commercial field. One plot (treatment standard fertiliser, reduced irrigation and reduced pollination) was lost due to the placement of an irrigation pipe, resulting in a total of 39 plots in the experiment.

2.3. Plant, pollinator and yield measurements

Just before crop flowering we visually selected and marked two representative plants per female line per plot as our experimental plants (in total six experimental plants per plot). To facilitate interpretation and explanation of yield effects, we measured several characteristics. Plant size was measured as the basal stem circumference (cm) of the experimental plants just after crop flowering, as this measure correlates well with other plant characteristics, and can be measured throughout the growing period (Fijen et al., 2018). We quantified nectar production as this may influence pollinator visitation rate and can be affected by the fertiliser and irrigation treatments (Gallagher and Campbell, 2017). To this end, we bagged two umbels per line per plot for 24 h to allow nectar to build-up in the florets. After this period, we used 1 μl micro capillaries to measure for each plant the number of florets required to fill one micro capillary with nectar. We then calculated the average amount of nectar per floret per line per plot. Because the bagging of plants for nectar measurements would interfere with the pollination of the main experiment, we selected two additional plants per line per plot. Furthermore, because the bagging for nectar has the same effect as our reduced pollination treatment, we excluded the reduced pollination plots from nectar measurements. We measured nectar production of the plants of a single block per day, and we randomized the order of measurements between plots. Nectar production of each plant was measured on three occasions with on average six days between subsequent measurements.

To see if pollinator visitation rates differed between treatments we determined pollinator visitation rates for each experimental plant six times during the flowering period, with a minimum of three days between observations. Observations within blocks were finished before observing the next block, and the order of observations in and between blocks was randomized. Plants which received a reduced pollinator treatment were effectively observed three times, as the other three times the bags excluded pollinator visitation and we assumed no visitation occurred (in total six observation rounds). We counted all bees and hoverflies that landed on the umbel during 30 min, or until five pollinators had visited the umbel (Fijen and Kleijn, 2017). We then calculated visitation rate (pollinators/minute) for each line in each plot on each observation day, including the bagged days.

To measure seed yield we harvested the umbels of the two experimental plants just before seed shedding in August 2017, and we pooled the umbels per line per plot to avoid pseudo-replication. Umbels were left to dry, and then threshed and cleaned. We counted the number of seeds using a seed counter (Contador, Pfeuffer GmbH). We subsequently assessed seed quality with a vigour test (see also Fijen et al. (2018)). In this test, three sets of 100 randomly selected seeds were sown in suboptimal circumstances and after 18 days, the vigour of the seedlings was assessed by experts in a NAL-authorized test (Naktuinbouw Authorized Laboratory). Vigour scores (%) was categorised as (A) optimal, (B) suboptimal, (C) poor, or (D) did not emerge. For the marketable seed yield we calculated the total amount of good quality seeds (Vigour (%A + %B) * total number of seeds). The average vigour scores (%) were calculated over the three sets.

2.4. Analysis

We separated analyses per line because the sample size ($n = 5$ blocks) was relatively low, and four-way interactions would be difficult to analyse and interpret. Furthermore, to avoid pseudo-replication, we averaged measurements and observations per line per plot. We performed all analyses using linear mixed effect models with block as random factor using the function 'lmer' in R-package lme4 with R-version 3.5.2 (Bates et al., 2015; R Core Team, 2018).

We tested the effects of the treatments on plant size, nectar production, pollinator visitation rate and marketable seed yield in separate models. We constructed a full model with the treatments and their interactions, and assessed significance of treatment effects using backward model simplification based on likelihood ratio tests (Burnham and Anderson, 2002). Because visitation rate could also be affected by plant size (e.g. visual cue) and nectar production (e.g. reward cue), we furthermore tested this in a separate model including plant size, nectar production and the two-way interaction, and block as random factor. We then simplified the model based on the same approach as above. Nectar production (average nectar per floret) and average visitation rate were log-transformed and log+1 transformed, respectively, to improve normality of residuals. As we did not measure nectar production in plots with 50 % pollinator treatment, we excluded this treatment for that analysis. We excluded two extreme outliers in the analyses with visitation rate for line B and F (value > 5 and > 4 SD from mean, respectively).

3. Results

The fertilisation treatment had consistent effects on plant growth (Fig. 2a) with on average 7 %, 11 % and 9 % smaller plants under reduced fertilisation than standard fertilisation in line B (marginally

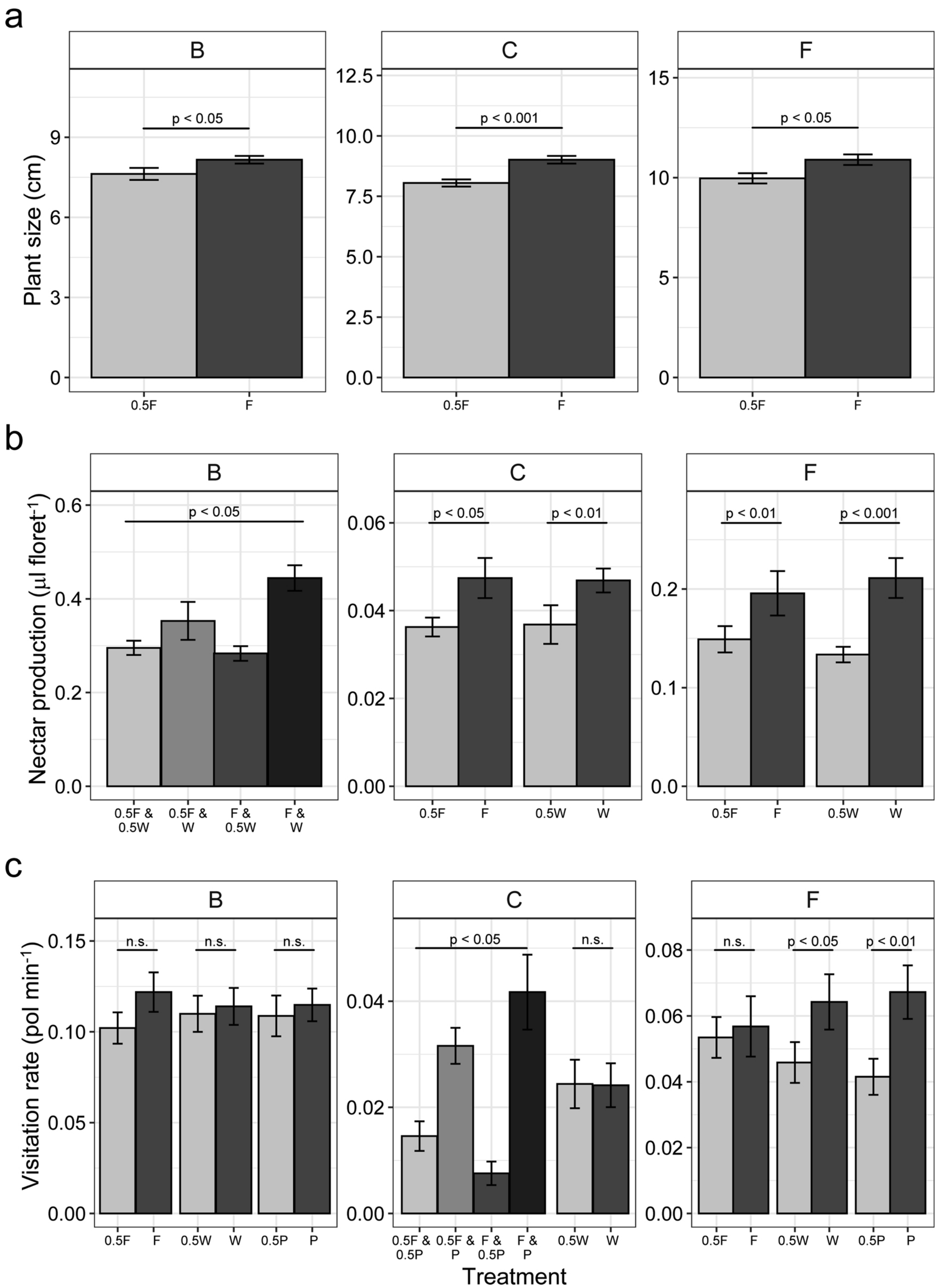

Fig. 2. Treatment effects (F = fertilisation, W = irrigation, P = pollination) on plant characteristics and pollinators. Only treatment effects that are significant for at least one line are shown. (a) Plant size (only fertilisation), (b) nectar production (only fertilisation and irrigation treatments), and (c) pollinator visitation rate per line. Female line identity is indicated above the graphs. Standard treatment levels are indicated in dark grey, reduced levels in lighter grey. Interactions or pairwise significance levels are indicated on top (n.s. = not significant). Bars show average values ± standard errors. Y-axis scale varies for different panels with the same y-axis unit.

significant), C and F respectively (B: $\chi^2(1) = 3.89$, P = 0.048; C: $\chi^2(1) = 17.30$, P < 0.001; F: $\chi^2(1) = 6.38$, P = 0.015; Fig. 2a). Other treatments had no significant effect on plant size, nor were there any significant interaction effects (P > 0.66).

Treatment effects on nectar production differed slightly per line. Reducing fertiliser application lowered nectar production with 24 % in both line C and F (C: $\chi^2(1) = 6.41$, P = 0.011; F: $\chi^2(1) = 7.17$, P = 0.007), while reducing irrigation lowered nectar production with 21 %

and 37 % in line C and F (C: $\chi^2(1) = 7.91$, $P = 0.005$; F: $\chi^2(1) = 16.30$, $P < 0.001$) respectively. In line B, nectar production decreased with decreasing irrigation but the effect was stronger in the standard fertilisation treatment (i.e. significant interaction fertilisation x irrigation; $\chi^2(1) = 6.18$, $P = 0.013$; Fig. 2b).

The pollinator community was dominated by bumblebees (45.6.% of in total 1943 observations), followed by solitary bees (34.5.%), honeybees (14.6.%) and syrphids (5.3.%). The effects of pollination treatments on visitation rate differed considerably between crop lines. The bagging treatment did not affect visitation rates in line B ($P = 0.70$; Fig. 2), even though flowers received zero visitors on the days they were bagged, and received the highest numbers of visitors of all crop lines. Line C plants without bags had about three times as many visitors as plants with bags (Fig. 2c) and this effect was stronger for plants also receiving the standard fertilisation treatment (i.e. significant fertilisation × pollination interaction; $\chi^2(1) = 4.65$, $P = 0.03$). Both the reduced irrigation and the reduced pollination treatment decreased average visitation rate in line F (irrigation: $\chi^2(1) = 4.76$, $P = 0.03$; pollination: $\chi^2(1) = 7.66$, $P = 0.006$; Fig. 2c). Furthermore, we found that in line F, but not in the other lines, visitation rate was significantly lower with increasing plant size ($\chi^2(1) = 4.86$, $P = 0.03$), and that visitation rate increased with increasing nectar production ($\chi^2(1) = 5.99$, $P = 0.014$; Fig. 3).

The treatments affected marketable seed yield differently in each line, but the reduced pollination treatment had a significant negative effect in all of the three lines. For line B, we found a positive interactive effect of fertilisation and pollination ($\chi^2(1) = 8.26$, $P = 0.004$), indicating that pollination increased yield under standard, but not reduced fertilisation rate (Fig. 4). In line C we found that marketable seed yield was 60 % higher under the reduced fertilisation rate ($\chi^2(1) = 14.18$, $P < 0.001$), and that the reduced pollination treatment had only 36 % of the amount of marketable seeds as the standard pollination treatment ($\chi^2(1) = 39.40$, $P < 0.001$; Fig. 4). For line F we found that both the reduced treatments of irrigation (15 % less; $\chi^2(1) = 7.85$, $P = 0.005$) and reduced pollination (27 % less; $\chi^2(1) = 21.38$, $P < 0.001$) yielded significantly less marketable seeds (Fig. 4).

4. Discussion

Our results show that leek marketable seed yield is influenced more by a reduction in insect pollination than reductions in fertilisation and irrigation application rates, but the magnitude of effects differed between the crop lines. Surprisingly, although a 50 % reduction in fertilisation reduced plant size in all three lines, the fertiliser reduction did not reduce seed yield in one of the lines and even increased seed yield in the two other lines. The effects of reducing irrigation were less pronounced, but the results suggest that high irrigation rate may be beneficial for crop yield, and possibly act through the beneficial effects of irrigation on pollination. Treatment effects were mainly additive, but in one line the influence of pollinators became apparent only under standard fertiliser levels. These results indicate that NPK-fertilisers are over-applied, and that pollination is undervalued as an agricultural input in this crop system.

Of all treatments, manipulating pollination levels generally had the strongest effects on marketable seed yield, suggesting that in our study system variation in insect pollination influences crop yield more than variation in fertilisation or irrigation. The magnitude of effects differed between crop lines, however. The yield difference caused by the pollination treatment in lines C and F was around two times larger than the effect of the respective fertilisation and irrigation treatments. In line B the only significant effect on crop yield was caused by reduced pollination but only under the standard fertilisation treatment (i.e. significant interaction). That different lines displayed different yield responses to the pollination treatment is also reflected in the different effects of the pollination treatment on pollinator visitation rate of the crop lines. Plants of line B and F that were bagged every other day were visited by pollinators relatively more frequently on the days when they were not bagged compared to plants that were never bagged (i.e. visitation rate of bagged treatment was more than 50 % of un-bagged treatment, Fig. 2c), thereby reducing the effective difference between pollinator treatments. However, variability in daily pollinator visitation rates in these lines increased substantially, with zero visitors on bagged days, and above average visitors on un-bagged days. These crop lines had relatively high nectar production rates, and this likely made the plants extra attractive on the days they were not bagged. We nevertheless found significant effects of the reduced pollination treatment on marketable seed yield in line B and F, possibly because florets were on average less receptive in the reduced pollinator treatment compared to the standard treatment (Chang and Struckmeyer, 1976; Devi et al., 2015). In contrast, bagged plants of line C were relatively less attractive on the un-bagged days compared to the not-bagged plants, which was reflected in the strong effect of the pollinator treatment on marketable seed yield. Even though the crop lines responded differently to pollination reduction, our results suggest that in this cropping system insect pollination is the weakest link in the agricultural production process.

Unexpectedly, although fertiliser application had clear positive effects on plant size and nectar production, reducing fertiliser inputs by 50 % did not affect crop yields, or even increased crop yield. From a farmer's perspective, it may be understandable why such high levels of fertiliser are generally applied, as higher input levels resulted in larger plants, which can easily be observed in the field. Furthermore, over-application can act as a form of insurance against crop failure (Sheriff, 2005). Nevertheless, crop yields were equally high or even higher with less fertiliser inputs, showing that increasing fertiliser levels in this high-input system is not the most appropriate way to maximize seed yield or reduce risk. A possible explanation for lower crop yields under conventional levels might be that the over-application of fertiliser

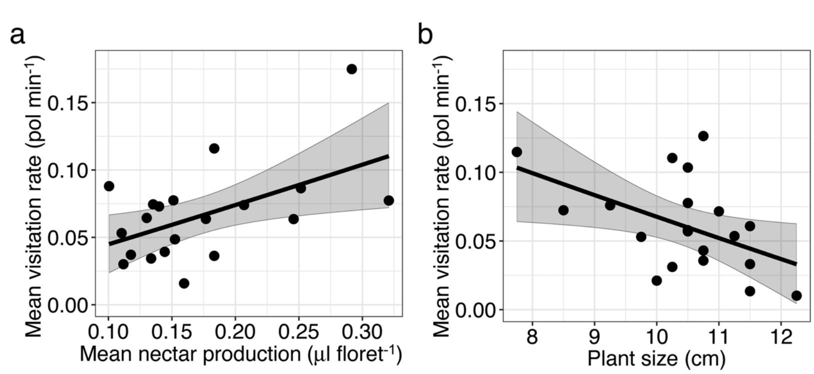

Fig. 3. The relations between mean pollinator visitation rate and (a) mean nectar production and (b) plant size in line F. Relations were not significant for line B and C (see main text). Black points represent back-transformed partial residuals. Grey area indicates 95 % confidence interval.

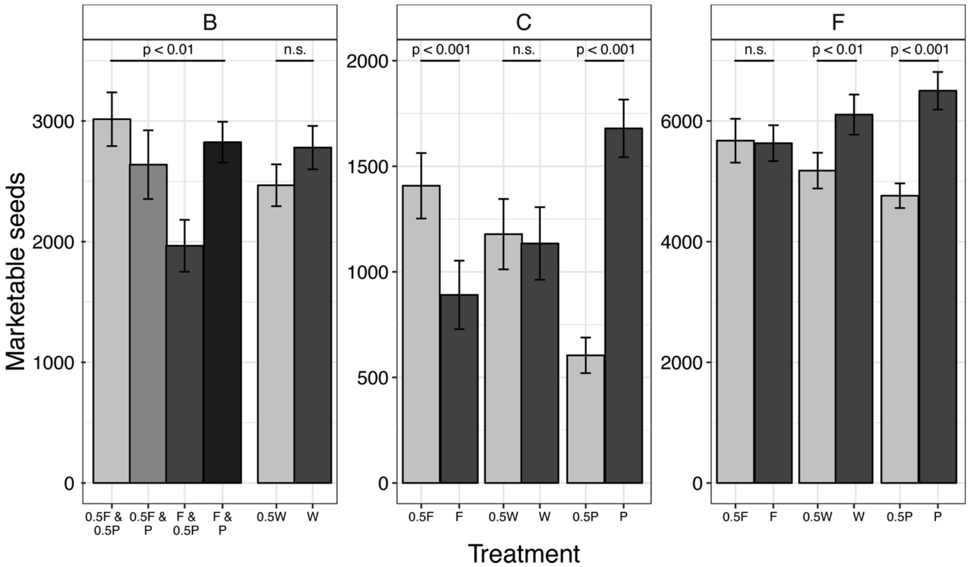

Fig. 4. The effects of treatments (F = fertilisation, W = irrigation, P = pollination) on the total number of high-quality seeds per two female plants. Female line identity is indicated above the graphs. Standard treatment levels are indicated in dark grey, reduced levels in lighter grey. Interactions or pairwise significance levels are indicated on top (n.s. = not significant). Bars show averages ± standard errors). Y-axis scale varies for different panels with the same y-axis unit.

lowered the concentration of other nutrients in the plant that are essential for seed production (Sørensen et al., 1995; Fageria, 2001). For example, reduced boron concentrations may lead to reduced seed quantity or quality (Johnson and Wear, 1967; Dordas, 2006). The over-application of fertiliser may be more common and wide-spread than generally assumed, as it has also been found for the majority of global staple seed crops like wheat, rice and maize (Matson et al., 1998; Ju et al., 2009). This practice is not only pushing up costs of fertiliser application (Matson et al., 1998; Compton et al., 2011; Sutton et al., 2011), but also comes with undesirable high environmental costs (Foley et al., 2005; Kleijn et al., 2009; Vitousek et al., 2009).

Reducing irrigation frequency during the crop flowering period generally had a negative effect on nectar production, but only in line F did it have a significant negative effect on crop yield. Concurrently, line F was also the only line where higher nectar production was positively related to pollinator visitation rate (Fig. 3), suggesting that benefits of irrigation for this line may largely be attributed to higher attractiveness of the plants for pollinators (Gallagher and Campbell, 2017). The reduced nectar production in the two other lines did not significantly affect pollinator visitation rate, nor did it affect crop yield, possibly indicating that nectar quality might play a more prominent role in these lines. Although, across all lines, reduced irrigation had no clear effect on seed yield, it will probably become an increasingly important part of the day-to-day agricultural management under future climate change, with expected longer and more intense periods of droughts (Parry et al., 2004; Dai, 2013). In addition to irrigating crops to promote plant establishment and growth, our results suggests that irrigation during the flowering period of insect dependent crops may act as a tool to increase or maintain high pollinator visitation rates, and thereby maintaining high pollen dispersal.

Our experiment was realistic and representative for the levels of agricultural management in this system, as the levels were comparable to measurements across 36 commercial leek seed production fields in 2016 (Fijen et al., 2018). The plant sizes of all lines in the standard fertilisation treatment corresponded to the median plant size across 36 commercial fields in the aforementioned study, while the visitation rate for the standard pollination treatment was around the average (above median; positively skewed) for these lines (Fijen et al., 2018). Furthermore, the reduced treatments decreased plant sizes and visitation rates (with the exception of line B) so that the levels approached the lowest 25 % percentile of observations across fields in 2016. This suggests that our results are probably representative for other years, albeit absolute yields may differ, for example because of cold weather during the growing season or higher pollinator abundance during flowering.

Whereas fertilisation and irrigation levels have seemed to reached, or overshot, the optimum input levels, there still lies great potential in enhancing crop pollination in more than half of the crop fields (Fijen et al., 2018). Because honeybees are ineffective at pollinating leek (Fijen et al., 2018), crop pollination services are delivered mostly by wild pollinators. If wild pollinators can be effectively promoted, this may potentially close a part of the yield gap, even in this intensively managed agricultural system.

Although the patterns differed subtly between crop lines, our results show that effects of fertiliser application, irrigation and pollination on crop yield were largely additive in this system, making effects of different management strategies rather predictable. A reduction in insect pollination generally resulted in substantially lower crop yields. Contrastingly, a reduction in fertiliser inputs did not lower crop yields, and even increased crop yields in two crop lines. Our findings may explain why previous studies have found that the relation between agricultural intensification and crop yield growth decreases with increasing dependence of crops on insect pollination (Garibaldi et al., 2011; Deguines et al., 2014). A further intensification by means of conventional agricultural inputs may therefore not be a very efficient approach for increasing crop yield of insect-dependent crops. Instead, putting more effort into promoting the abundance and diversity of wild pollinators is more likely to result in higher crop yields (Fijen et al., 2018). Whether doing this is actually cost-effective to a farmer will depend on the opportunity costs of pollinator-enhancing measures (Rundlöf et al., 2018; Sutter et al., 2018; Kleijn et al., 2019), at least in the first couple of years when the investments have not yet been returned (Blaauw and Isaacs, 2014; Pywell et al., 2015; Grab et al., 2018), and on the expected yield increase per crop line. However, in our high revenue crop system a 25 % increase of wild pollinator levels, relative to the median, could increase crop revenue with $17.000 ha^{-1} (Fijen et al., 2018). These high revenue gains allow to set substantial amounts of productive land aside for promoting crop pollinators, while at the same protecting the local pollinator biodiversity (Fijen et al., 2019). Although the promotion of wild crop pollinators currently receives little or no attention in this system, pollination by wild insects is the agricultural input that has the highest potential to improve productivity.

Author contributions

TF, JS, JvR & DK conceived and designed the experimental setup. TF & CV collected data. TF performed analyses and wrote the initial manuscript. All co-authors contributed significantly to improving the manuscript. All authors gave final approval for publication.

Data availability

Data supporting the results will be made publically available upon publication in the Dryad Data Repository.

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Declaration of Competing Interest

None.

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