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# Nocturnal pollination is equally important as, and complementary to, diurnal pollination for strawberry fruit production

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ABSTRACT

Declining insect populations and their associated pollination services to crops raise concerns for global food security. While most studies focus on the contribution of diurnal pollinators to crop yields, nocturnal pollination receives little attention. In this study, we used a randomised block design (n = 6) in the open ground to determine the relative contribution of nocturnal and diurnal pollination to strawberry yield. We found that, on average, there was no effect of insect pollination (nocturnal, diurnal, or both) on total number of fruits and total weight of fruits harvested per plant. However, when plants produced many fruits, night-pollinated and open-pollinated plants increased total fruit weight per plant, compared to plants that received no pollinators. Furthermore, compared to the no-pollinators treatment, individual fruit weight (g) was significantly higher in night-pollinated plants (27% higher) and open-pollinated plants (46% higher), whereas the day-pollinated treatment (17% higher) did not significantly differ from no-pollinators and night-pollinated plants. Fruit diameter (mm) followed a similar pattern. Fruit sweetness (%total soluble solids) was highest in the no-pollinated treatment, and other treatments did not differ from each other. The average fruit shape was of significantly poorer quality in the no-pollinators treatment than any of the other treatments, which did not significantly differ from each other, but did show a trend of fewer poorly shaped fruits. Overall, nocturnal pollination was at least equally important as, and highly complementary to diurnal pollination for determining strawberry fruit quality. However, we do not know the identity of the nocturnal pollinators. Nevertheless, nocturnal pollination seems to be an important, but overlooked part of the contribution to insect pollination to crop yield.

## 1. Introduction

The combination of large scale insect declines (Potts et al., 2010; Hallmann et al., 2017) and the pollination services that they deliver to three-quarter of our global crops is raising concerns about global food security (Klein et al., 2007, but see Aizen et al., 2022). The majority of insect crop pollinators discussed in literature are the diurnally active (wild) bees and (hover)flies (Rader et al., 2016; Requier et al., 2022). Nocturnally active insects, such as moths and beetles, can significantly contribute to crop pollination too (Cutler et al., 2012; Alison et al., 2022) but receive much less attention than diurnal pollinators (Macgregor and Scott-Brown, 2020; Requier et al., 2022). To fully understand how to conserve and manage crop pollination, we need to understand the relative contribution of nocturnal and diurnal pollinators to crop yield.

In temperate regions, relatively few plant species rely solely on nocturnal pollinators for pollination (e.g. *Lonicera* sp.), and none of them are being cultivated extensively (Buxton et al., 2022). However, as nocturnal pollinators visit flowers to feed on nectar of pollen, it should not come as a surprise that they can significantly contribute to crop pollination too. Many crop species might be nocturnally pollinated, in addition to diurnal pollination, as flower morphology does not seem to play a major role and many nocturnal pollinators are generalists (Macgregor and Scott-Brown, 2020). In an experiment on lowbush blueberry (*Vaccinium angustifolium*; bell-shaped flowers) in Canada, nocturnal pollination contributed to about one-third of the total ripe berries (Cutler et al., 2012). More recently, Alison et al. (2022) showed that nocturnal moth visits comprise about one-third of all flower visits to red clover (*Trifolium pratense*; complex flowers) in Switzerland, thereby increasing seed set compared to no-pollination. In the more open flowers of apple (*Malus domestica*) in Arkansas, USA, it was found that nocturnal

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pollination increased fruit set by approximately 10% (Robertson et al., 2021). These previous studies suggest that nocturnal pollination contributes substantially to crop pollination, albeit less than diurnal pollination, but more studies are required to establish how important nocturnal pollinators are.

The relative contribution of nocturnal pollinators to crop yield is particularly important in the face of crop pollinator management and conservation. Nocturnal pollinators are affected by other environmental changes than diurnal pollinators. For example, artificial light at night can have a detrimental effect on the pollination of plants (Knop et al., 2017), and the activity of moths when visiting flowers (van Langevelde et al., 2017). If nocturnal pollinators contribute substantially to crop yield, then farmers can take their contribution into account, for example by reducing light pollution (Grubisic et al., 2018).

Strawberry (*Fragaria x ananassa*) is a globally important and valuable crop with a 43% increase in global production between 2004 and 2013 (Simpson, 2018). Many studies have shown the contribution of insect pollination on fruit set but also on fruit quality such as size, shape and sweetness (Klatt et al., 2014; Wietzke et al., 2018; Castle et al., 2019; Bänsch et al., 2020). Strawberries are known to produce higher quality fruits when allogamous pollen is deposited on the stigma compared to autogamous or geitonogamous pollen (Dung et al., 2021). Different pollinators deposit different ratios of these pollen origins on the stigmas as a result of their behaviour and size (MacInnis and Forrest, 2019). However, the contribution of nocturnal pollination to both fruit quantity and quality has not been investigated. Here, we use a controlled field experiment to answer the research question: what is the relative contribution of nocturnal pollination and diurnal pollination to strawberry fruit production.

## 2. Methods

### 2.1. Study system

As our model system we have used strawberry (*Fragaria x ananassa* Elsanta), cultivated outdoors in the soil. Elsanta is a popular commercial variety that is strongly insect-dependent for proper pollination (Klatt et al., 2014). The experimental site was located near Etten-Leur (N51.55, E4.64), Noord Brabant, The Netherlands, on a commercial farm for strawberry plants (i.e. a strawberry multiplier) and at-the-door strawberries. The area is located on sandy soils, and surrounded by grasslands and small forests. Strawberries are technically a pseudocarp but here the terms fruit and fruit quality refer to the whole pseudocarp, as conventional for strawberries.

### 2.2. Experimental design

To test the relative contribution of nocturnal and diurnal pollination on strawberry yield, we placed full-grown plants from their overwintering site in polytunnels into a randomised block design in open ground on April 12th 2022. Plants were growing in potting soil and were put in the open ground where we only loosened up the potting soil and roots. The randomised block design (replicated six times; n = 6) consisted of four treatments: a negative control (no access by pollinators), a night-pollinated (not accessible to diurnal pollinators), a day-pollinated (not accessible to nocturnal pollinators), and an open-pollinated treatment. The plants were arranged in a double-row system, with 60 cm between the plants of both rows, and 90 cm between the double-rows. One single row comprised one block, with each treatment randomly assigned within the block. To increase accuracy of the yield measurements, we placed seven plants within each treatment within each block, so that each block consists of 28 plants (total 168 plants; Fig. 1). Throughout the experiment, we irrigated the plants using drip-irrigation when required.

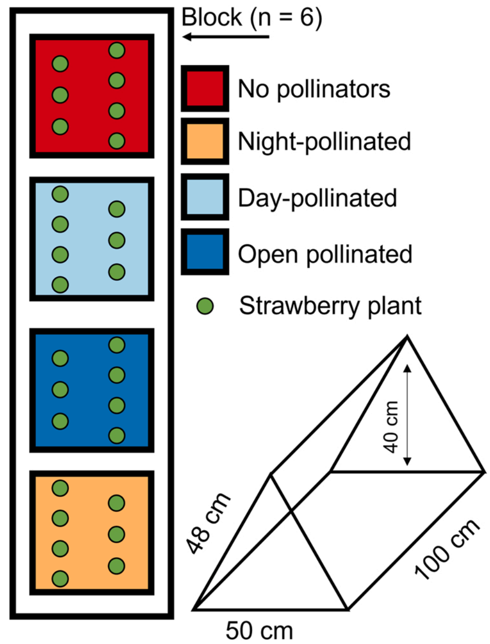


**Fig. 1.** Experimental setup of the experiment. The cages (right below) covered the whole plot of a treatment, and were only open at the bottom.

### 2.3. Pollination treatments

To exclude pollinators, we built twelve triangular cages with a wooden frame (l*w*h = 100 *500 *40 cm; Fig. 1). All but the bottom sides were covered with fine insect mesh (mesh size 1.35 mm) to exclude insects.

We started the pollination treatments directly after starting the experiment. The no-pollinators treatment was permanently covered by a cage. For the night-pollinated and day-pollinated treatments, we switched the cages from the night-pollinated to the open-pollinated treatments and vice-versa every day at sunset and sunrise, respectively. The treatments were continued up to the 20th of May, when the majority of strawberries were harvested in all treatments.

### 2.4. Harvesting and yield measurements

All ripe strawberries were harvested during three harvesting events (13th, 17th and 20th of May), where we noted down from which plants these were harvested. Each strawberry was weighed (g) using a precision scale (mg accuracy), and the diameter was measured using a digital calliper to the nearest 0.1 mm. We furthermore assessed fruit quality by measuring the total soluble solids (TSS, °Brix/% total soluble solids) of the juice with a handheld refractometer (Eclipse 45–81 Brix 50 low volume) as a proxy for sweetness (Chen et al., 2021), and by scoring the shape according to the commercial shape standards (Grade 1 = perfect shape, Grade 2 = minimal deformations, Grade 3 = deformed) of each strawberry (Klatt et al., 2014; Bänsch et al., 2020).

### 2.5. Statistical analyses

To calculate the relative contribution of nocturnal and diurnal pollination to strawberry crop yield, we used mixed-effects models to account for the nestedness of the experimental design. Yield quantity was assessed using the total number of strawberries, and the total weight (g) harvested per plant. We excluded 21 plants that died or did not produce flowers. Yield quality (individual fruit weight (g), fruit diameter (mm), and fruit sweetness (%TSS)) were assessed on the individual harvested strawberries. We analysed fruit shape on the plant level (average scores per plant as continuous variables), because we are not aware of frequentist functions for ordinal data with multiple random effects. We used linear mixed effect models with the function 'lmer' (Bates et al., 2015) in R 4.2.1 (R Core Team, 2022), where the yield parameter was the response variable, pollinator treatment the explanatory variable, and our random structure plot nested within block (1|block/plot) for the yield quantity models and the fruit shape model. For the other yield quality models we used the same model structure, except we added one level into our random structure: plant nested within plot, nested within block (1|block/plot/plant). To meet the normality of residuals, the total number of strawberries per plant, and the individual fruit weight were sqrt-transformed, and the fruit sweetness was log10-transformed. Differences between groups were assessed using a Tukey test with the function 'glht' from the package multcomp (Hothorn et al., 2016).

The ideal outcome for farmers is to have high production rates, but the summed weight of many smaller fruits can be larger than that of fewer larger fruits. We therefore explored the relationship between the total number of fruit produced per plant and total weight of fruit harvested per plant, and whether this relationship differed between the treatments (e.g. nocturnal pollinators could set many incompletely pollinated fruits). We separated the dataset into plants with low ($<=4$ fruits/plant) and high ($>4$ fruits/plant) fruit production, with the median number of fruits produced per plant as cut-off (median = 4 fruits). We then used a linear mixed effect model with total weight per plant as our response, fruit production (low/high), treatment and their interaction as our explanatory variables, and (1|block/plot) as our random structure. Significance of the interaction was assessed using a likelihood ratio test (Zuur et al., 2009), and the differences between groups were assessed as described above.

## 3. Results

In total, we harvested 626 strawberries, of which 167 in non-pollinated, 181 in night-pollinated, 142 in day-pollinated, and 136 in open pollinated treatments. Both the average total number, and the total harvested fruit weight per plant did not significantly differ between the pollinator treatments (Fig. 2A-B). However, the average individual fruit weight of strawberries was lowest for the non-pollinated plants (mean $\pm$ se: 12.7 $\pm$ 0.48 g), and significantly higher in night-pollinated plants (16.1 $\pm$ 0.44 g; 27% higher) and open-pollinated plants (18.5 $\pm$ 0.49 g; 46% higher). Average individual fruit weight of the day-pollinated treatment (14.8 $\pm$ 0.45 g; 17% higher) differed only significantly from the open-pollinated treatment (Fig. 2 C). Because individual fruit weight and diameter were highly correlated (Pearson's r = 0.92, $p < 0.001$), the average diameter followed the same pattern, with 28.9 $\pm$ 0.41 mm, 31.4 $\pm$ 0.36 mm (8% larger), 30.6 $\pm$ 0.37 mm (6% larger), 33.3 $\pm$ 0.36 mm (15% larger) as respective means $\pm$ se of the no-pollinators, night-pollinated, day-pollinated and open-pollinated treatments (Fig. 2D). The sweetness of the fruits (%TSS) was highest in the no-pollinators treatment (7.7 $\pm$ 0.10%), lowest in the night-pollinated treatment (6.6 $\pm$ 0.10%; 14% lower), followed by the open-pollinated treatment (6.8 $\pm$ 0.13%; 12% lower), and day-pollinated treatment (7.2 $\pm$ 0.13%; 6% lower). The day-pollinated treatment did not statistically differ from any of the other treatments (Fig. 2E). The average scored shape of the fruit was significantly poorer in the no-pollinators treatment (1.51 $\pm$ 0.06) than any of the other treatments (night-

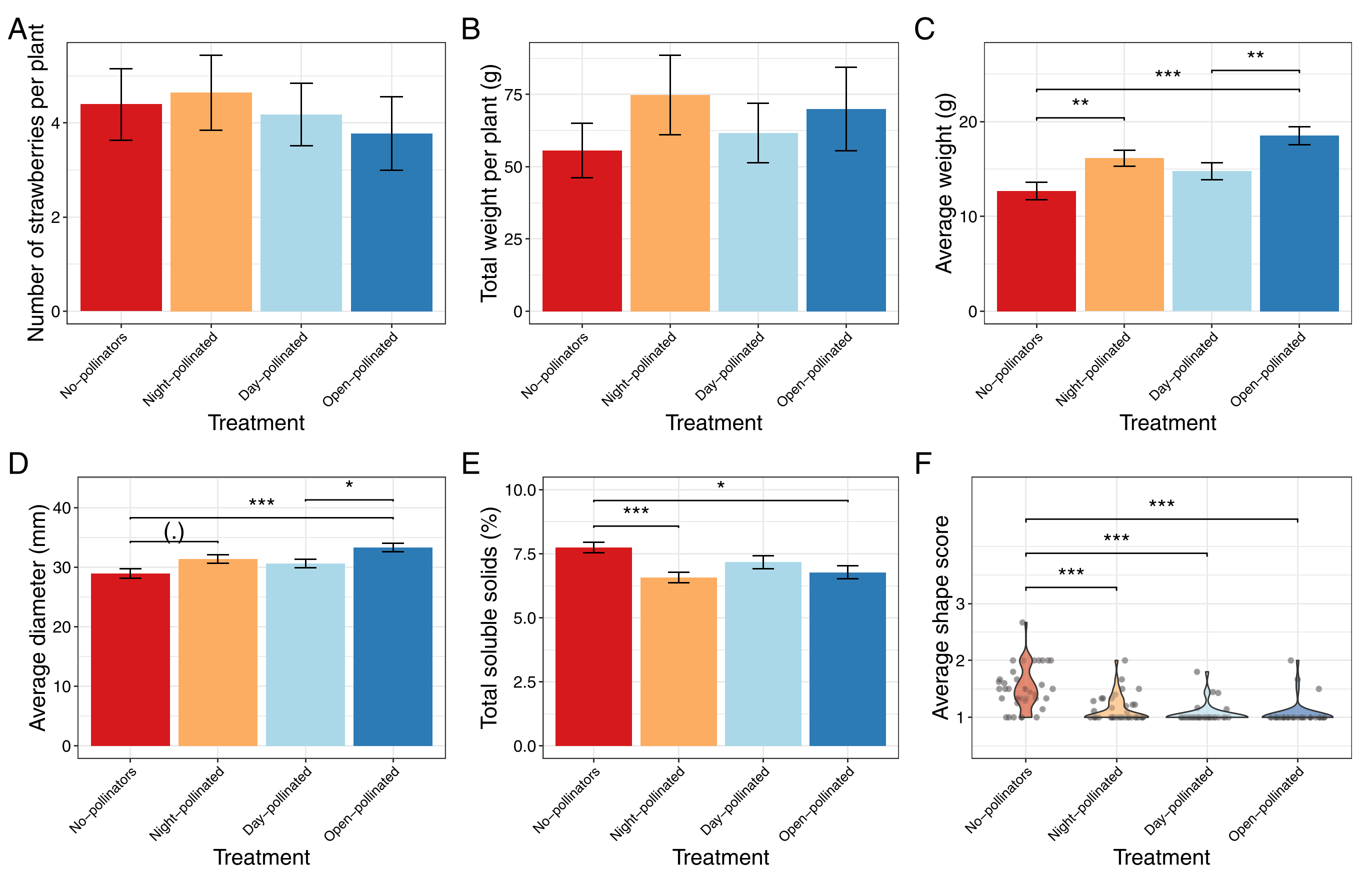


**Fig. 2.** The effect of no-pollinators (red), night-pollinated (orange), day-pollinated (light blue) and open pollinated (darker blue) treatments on (A) the number of strawberries per plant; (B) the total harvested berry weight per plant (g); (C) the average weight of a single strawberry (g); (D) the average diameter (mm) at the widest point; (E) the average total soluble solid contents (%); and (F) the average shape category. Panel A-E show means + 95% confidence interval of the raw data. Panel F shows a distribution of the average shape scores in a violin plot, as well as average shape scores per plant as overlayed points (jitter applied for illustrational purposes). Significant differences between treatments are indicated with the brackets, where (.) = $p < 0.10$, * = $p < 0.05$, * * = $p < 0.01$, and * ** = $p < 0.001$.

pollinated 1.14 ± 0.04; day-pollinated 1.06 ± 0.03; open-pollinated 1.06 ± 0.04), which did not significantly differ from each other.

The relationship between a low or high total number of fruit harvested and the total fruit weight per plant harvested depended on the treatment (i.e. significant interaction low/high fruit production * treatment; $\chi^2(3) = 15.83$, $p = 0.001$; Fig. 3). There were no significant differences for plants that produced below median number of fruits (=<4 fruits/plant), but did differ for plants with high fruit production (>4 fruits/plant; Fig. 3). Plants in the night-pollinated and open pollinated treatments had higher harvested fruit weight/plant than the no-pollinators treatment, whereas the day-pollinated treatment only differed significantly from the open-pollinated treatment.

## 4. Discussion

Here, we found that nocturnal pollination, and the combined nocturnal and diurnal insect pollination (i.e. open pollination) contributes significantly to total yield, but only when plants produce many fruits (>4 per plant). Furthermore, we found that nocturnal and diurnal pollination equally and complementarily contribute to single fruit quality, notably fruit size and shape. To our knowledge, this is one of the few studies teasing apart the contribution of nocturnal and diurnal pollination to crop production in the temperate region (Cutler et al., 2012; Robertson et al., 2021), and the first for strawberry.

While on average we found no effect of pollination treatment on the total harvested yield per plant, these effects became apparent for plants that produce relatively many fruits. The fact that this pattern only appears under high fruit production rates suggests that strawberry plants are able to partly compensate lower fruit production by increasing the fruit weight, similar to raspberry (Chen et al., 2022a, 2022b) and apple (Geslin et al., 2017). This partial compensation (or also called resource allocation trade-offs; Geslin et al., 2017) can also be observed in the strawberry sweetness: treatments with on average smaller strawberries, were on average sweeter and vice versa. Insect pollination plays an important role in fruit set of strawberries (Lata et al., 2018b), and here we show that under productive growing conditions, nocturnal and diurnal pollinators contribute more or less equally to strawberry.

The contribution of insect pollination is generally most noticeable in fruit size of single strawberries (Klatt et al., 2014), and our results show that the contribution of nocturnal and diurnal pollinators was highly complementary. If we add the contribution of nocturnal pollination (night-pollinated – no-pollinator) to individual fruit weight and fruit diameter to that of the diurnal pollination (day-pollinated – no-pollinator), we found that the sum of the contribution of nocturnal and diurnal pollination matches the open-pollinated treatment. This strongly supports our finding that nocturnal pollination contributes strongly to strawberry yield quality, and that our exclusion treatments (not applied in the open-pollinated treatment) had little unwanted side-effects. Remarkably, as in the previous studies (Cutler et al., 2012; Robertson et al., 2021; Alison et al., 2022), the contribution of nocturnal pollinators was not significantly different from the diurnal pollination, nor from the open pollination. Nocturnal pollination seems therefore to be equally important as, and complementary to, diurnal pollination fruit production.

Timing of pollination is known to play an important role in strawberry, with flowers pollinated at the time of maximum stigma receptivity, at anthesis, producing more (Lata et al., 2018a) and 13–58% heavier than those pollinated before or after this time (Skrebtsova, 1958). Having both diurnal and nocturnal pollinators visiting the plants will therefore result in a larger percentage of the flowers pollinated shortly after anthesis.

The identity of the nocturnal pollinators is, however, still unclear. In ad-hoc observations at night (not included here), we only found two ants on flowers on a single occasion. The nocturnal pollinator community is likely diverse, with moths, flies and coleoptera most likely the most abundant (Knop et al., 2017; Macgregor and Scott-Brown, 2020; Requier et al., 2022). Future studies should also focus on observing and identifying the nocturnal flower visitors of strawberry and other crops.

Overall, we find that nocturnal pollination is an overlooked part of the total insect pollination contribution to many crops, and that their contribution is probably frequently ascribed to diurnal pollinators, such as bees and hoverflies. While this does not mean that the contribution of insect pollination to crops is actually higher or lower, it does mean that there are additional groups of insects that should be studied in order to improve predictions of crop pollination services (Lonsdorf et al., 2009). On top of that, more focus and attention should be given on the facilitation and conservation of nocturnal pollinators in agricultural landscapes (Grubisic et al., 2018; Macgregor and Scott-Brown, 2020).


## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.


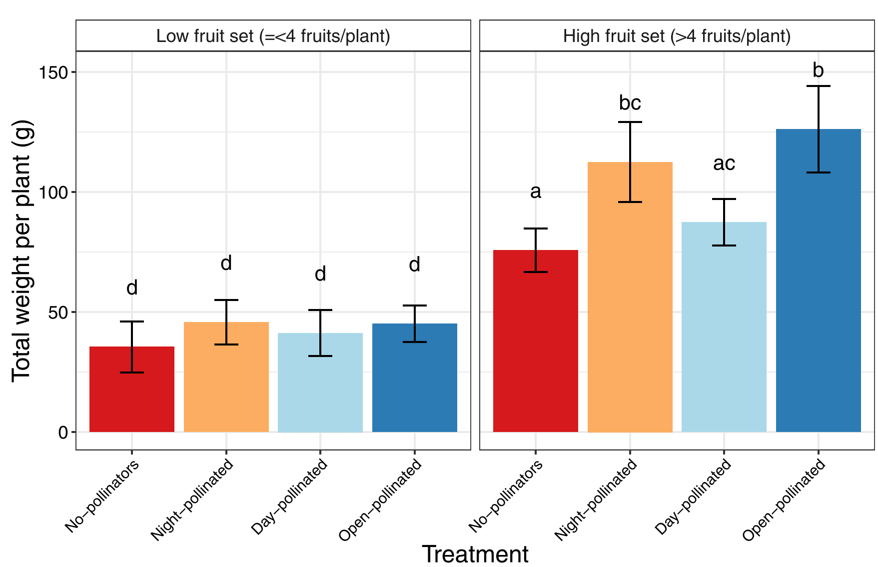


**Fig. 3.** The effect of low and high numbers of fruit produced on the total weight of harvested strawberries per plant for the different pollination treatments. Median number of strawberries per plant was 4. Letters indicate significant subgroups ($p < 0.05$). Bars represent mean values, and error bars the 95% confidence interval.

## Data Availability

Added as supplementary information.


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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108475.

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