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REVIEW

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Fruit set is moderately dependent on insect pollinators in strawberry and is limited by the availability of pollen under natural open conditions

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ABSTRACT

Modern strawberry (*Fragaria ×ananassa* Duch.) cultivars are hermaphrodite and have fertile flowers, with the anthers releasing viable pollen. Cultivars are self-compatible and do not require cross-pollination. Studies supporting managed or wild insects are based on a few reports and there are problems with the methods used to assess pollination. This review examined the role of pollination in strawberry. The mean (± s.d. or standard deviation) pollinator dependence (PD) for yield (self-pollination versus open- or insect-assisted pollination) was 0.36 ± 0.26 ($P < 0.001$, $N = 52$ studies). The yields of plants exposed to supplementary insects were higher than those exposed to pollinators under natural open conditions, with a calculated pollen limitation (PL) of 0.20 ± 0.17 ($P < 0.001$, $N = 20$ studies). Fields close to semi-natural habitats, wildflowers, grass or hedges can have more pollinators and a greater diversity of pollinators than fields further away. However, a greater abundance of pollinators does not always lead to higher fruit set. Yield is dependent on insect pollinators (moderate pollinator dependence) and is limited by the availability of pollen under natural open conditions (moderate pollen limitation).

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Introduction

Strawberry (*Fragaria ×ananassa* Duch.) is cultivated around the globe under a range of growing systems and climates (Hancock, 2008, 2020; Hernández-Martínez et al., 2023; Schattman et al., 2022). Total production is 14 million tonnes, with China producing 41% of the crop (Lei et al., 2021) and the United States 19% of the crop (Samtani et al., 2019). High-yielding cultivars are crucial for viable production, with land, labour and marketing expensive in many areas (Guthman & Jiménez-Soto, 2021)

Modern cultivars are hermaphrodite and have fertile flowers, with the anthers releasing viable pollen (Ashman et al., 2015; Ashman, 2003; Free, 1968a, 1968b, 1993). Cultivars are self-compatible and do not require cross-pollination (Du et al., 2021a, 2021b; Hortyñski et al., 1972). Individual flowers can be fertilised by pollen released from within the flower through the assistance of gravity and wind. However, the arrangement of the stamens within the flower (often below the stigmas) and the large number of stigmas in each flower (up to 500 or more per flower) lead to inadequate fruit growth in the absence of pollinators (Free, 1993; Connor & Martin, 1973; McGregor, 1976; Yoshida et al., 1991a, 1991b). The role of pollinating insects in production is unclear, with a range of methods used across experiments and a range of responses recorded.

This paper examines the importance of pollination on strawberry production. The dependence on pollinators for yield or fruit weight (pollinator dependence or PD) was assesses across studies. The relationship between fertility and self- and cross-pollination was assessed from previous literature. Data were examined to determine if yield is limited by the supply of pollen under natural conditions (pollen limitation or PL). Information was collected on the insects associated with pollination and how they are best managed for production. The review provides recommendations for future research.

Economics of pollination

There are several studies highlighting the economic benefits of pollinators for strawberry. The bulk of these reports are from the United States (Barfield et al., 2015; Calderone, 2012; Chopra et al., 2015; Jordan et al., 2021; Koh et al., 2016; Losey & Vaughan, 2006; Southwick & Southwick, 1992; Robinson et al., 1989a, 1989b) or Europe (Breeze et al., 2021; Carrek & Williams, 1998; Martin et al., 2019; Picanço et al., 2017; Richards, 2001; Zych & Jakubiec, 2006). There are also analyses from Australia and New Zealand (Cunningham et al., 2002), Brazil (Giannini et al., 2015), India (Chaudhary & Chand, 2017), Japan

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(Konuma & Okubo, 2015; Oguro et al., 2019) and China (An & Chen, 2011; Mashilingi et al., 2021).

Some authors have examined economics across the globe (Aizen & Harder, 2009; Aizen et al., 2008, 2009, 2019; Dainese et al., 2019; Gallai et al., 2009; Garibaldi et al., 2015; Klein et al., 2007; Lautenbach et al., 2012; Lippert et al., 2021). The value of bee pollination for crop production is higher than for honey and beeswax production (e.g. Levin, 1983 in the United States).

Calderone (2012) reported on economics in the United States. The value of the strawberry industry was US$2.245 billion, with honeybees contributing US $0.045 billion and other insects US$0.404 billion. Pollinators contributed to 25% of the value of the industry and wild insects were more important than honeybees. Lautenbach et al. (2012) indicated that pollination for strawberry in the top ten countries was worth US$1.690 billion. Klatt et al. (2014) conducted an analysis of yield and pollination in the European Union. Pollination contributed US$1.6 billion to the industry, equivalent to US$14,968 per ha. Breeze et al. (2021) estimated that pollination in the United Kingdom between 2014 and 2016 was worth an average of ₤150 million each year.

Mallinger et al. (2021) reviewed the importance of pollination to agriculture in Florida. Insects contributed to a mean of 38.4% of the value of strawberry cultivated on 9,499 ha, with the contribution ranging from 27 to 56% across various scenarios. The relative contribution of managed and wild insects was not provided.

Agricultural and wild plants vary in their dependence on pollinators for seed or fruit set (Basualdo et al., 2022; Baylis et al., 2021; Breeze et al., 2016; Carr & Davidar, 2015; Freimuth et al., 2022; Hein, 2009; Melathopoulos et al., 2015; National Research Council, 2007; Porto et al., 2020; Sáez et al., 2018). The dependence on pollinators ranges from zero (fertility not dependent on pollinators) to one (fertility completely dependent on pollinators). Dependency varies over time and with populations of a species (Rech et al., 2021) and across geographical areas (Leme da Cunha et al., 2023). A review of human nutrition and pollination demonstrated that poor pollination resulted in a global loss of 4.7% of fruit, 3.2% of vegetables and 4.7% of nuts (Smith et al., 2022).

The method used to assess the importance of pollinators affects estimates of PD (Mallinger et al., 2021). Pollination-exclusion experiments can be conducted to compare seed set from flowers open or closed to insects. However, the results from these experiments are dependent on the abundance, diversity and efficiency of the pollinators at the site. The results of this research indicate realised pollinator contributions not maximum contributions. The importance of pollinators for fertility can be assessed by comparing seed set after self- or cross-pollination. However, this technique does not include the contribution of insects to self-pollination, potentially overestimating insect pollination.

Values of PD for strawberry range from 0.10 to 0.80 and are mostly from 0.20 to 0.30 (see citations above). These values are based on a few original reports and many of the studies do not include data on yield (e.g. Allen-Perkins et al., 2022; Ashworth et al., 2009; Barfield et al., 2015; Borneck & Merle, 1989; Chacoff et al., 2010; Chagnon et al., 1993; Chagnon, 2008; Chisel, 2015; Chopra et al., 2015; Delaplane & Mayer, 2000; Delaplane, 2021; Gallai & Vaissière, 2009; Connor & Martin, 1973; Maeta et al., 1992; Malagodi-Braga & Kleinert, 2004; Pless et al., 2021; Żebrowska, 1998). The relationship between yield and pollination in strawberry is unclear. It is not known if PD varies between different cultivars and different growing locations and between protected and open field environments. Pollination dependence varies across cultivars within a species (e.g. apple as shown by Garratt et al., 2021) and the method used to assess self- and insect-pollination. A survey of 1,174 flowering plants indicated that a third of the species produced no seeds without pollinators and half suffered at least an 80% reduction in fertility (Rodger et al., 2021).

Description of the flowers and fruit

The two outer whorls of the strawberry flower are sterile and do not contribute directly to fertility (Ariza et al., 2015). In contrast, the two inner whorls contain the fertile male and female parts of the flower. At anthesis, the flowers have a two-whorled calyx, with twelve alternating sepals (Figure 1). A single-whorled corolla, with five white petals is present interior to the sepals. There are two whorls of twenty stamens surrounding a central receptacle. Each stamen has an anther which contains microsporangia and a short or long filament. The stamens are collectively called the androecium. There is an innermost whorl with several hundred carpels or free pistils. Each carpel consists of a stigma, a style, an ovary and one ovule. The carpels are imbedded in the epidermis of the receptacle in a spiral pattern. The pistils are collectively called the gynoecium.

The strawberry berry is an aggregate fruit originating from the receptacle tissue, with a number of ovaries. These develop into one-seeded fruit or achenes (Figure 2). In some reports, the achenes refer to the seed and ovary tissue (gynoecia) which originate at the base of each pistil (Feng et al., 2019; Kang et al., 2013). In other reports, the achenes refer only to the seed (Pi et al., 2021; Yao et al., 2022). Each berry has 20 to 500 achenes, depending on the cultivar and growing conditions. The base of the flower is called the receptacle and develops into the edible part of the berry. The

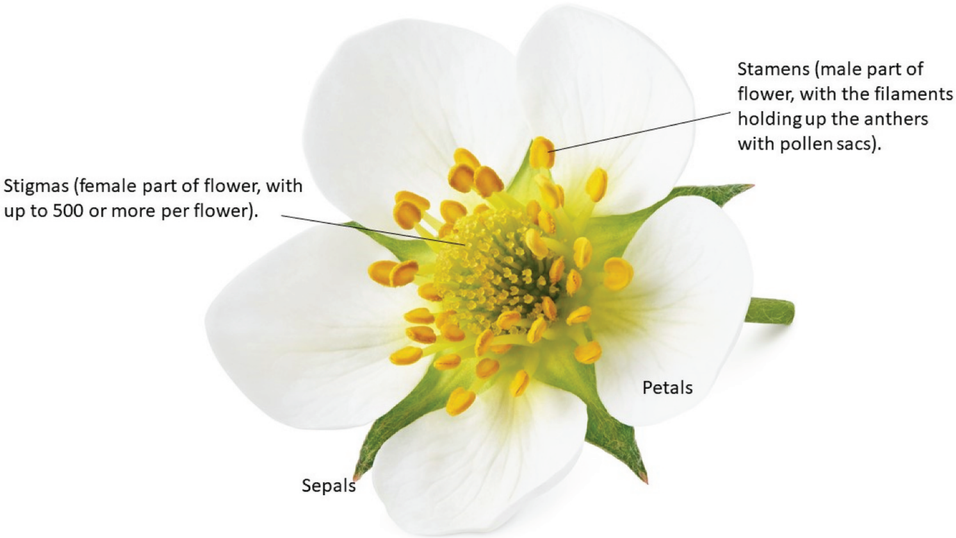

Figure 1. The main parts of the strawberry flower. Source of photograph was Berries Australia (https://berries.net.au; Roman Samokhin).

Figure 2. Strawberry flowers and immature fruit showing different stages of achene development.

percentage of ovules setting a seed is usually high (87% with Hulewicz & Hortyński, 1972; and 80% with Connor & Martin, 1973). Fertility is much higher than in some other crops (e.g. 1% of flowers in avocado as shown by Alcaraz & Hormaza, 2021; and 5 to 6% of flowers in olive as shown by Dölek Gencer et al., 2023).

The physiology of pollination and fertilisation

Seed set in angiosperm plants is dependent on successful pollination and fertilisation. The process begins with the pollen grains adhering to the stigmas of the flowers, followed by the hydration and germination of the grains and then the growth of the pollen tube (Adhikari et al., 2020; Chen et al., 2020; Erbar, 2003; Lord & Russell, 2002). The pollen tube cells elongate on an active extra-cellular matrix in the style and are guided by signals from the style and embryo sac (Lord & Russell, 2002). Eventually, two sperm cells from one pollen tube fuse to produce two distinct tissues. The first sperm cell fuses to produce the zygote and embryo, while the second fuses to produce the endosperm.

Information is available on the physiology of pollination and fertilisation in strawberry. Cui et al. (2022) described seven stages of anther and pollen development, including the sporogenous cell, microspore mother cell, tetrad, free microspore, vacuolated microspore, bicellular pollen and mature pollen. The pistils enlarged and elongated rapidly in the free microspore stage, accompanied by expansion of the ovary. There are variations in fertility in parts of the flower (Zini et al., 2023). There is a higher incidence of immature gametophytes in the apical pistils and a higher incidence of unviable gametophytes in the basal pistils. Fertility is reduced under extreme temperatures (Cui et al., 2021; Pipattanawong et al., 2009).

When the flower is fully developed, further development is blocked and dependent on hormonal signals from the developing seed (Liu et al., 2020). These hormones are primarily auxins and gibberellins and stimulate the growth of the seedcoat and fruit (Guo et al., 2022). Self-fertilisation leads to lower fruit set than open- or hand-pollination, smaller berries and lower concentrations of auxins in the developing fruit (Wietzke et al., 2018).

Relationship between fertility and the stamens

There are variations in the structure of flowers, depending on the species, cultivar and plant (Ariza et al., 2015; Hollender et al., 2012). The anthers on the stamens carry the pollen used to pollinate the ovaries. Ashman (1999, 2000) studied the biology of the wild strawberry, *F. virginiana* in the United States. The stamens from the female flowers were shorter (1.28 to 1.66 mm) than those from the hermaphrodite flowers (4.01 to 4.55 mm). There was a weak correlation between the amount of pollen removed from the hermaphrodite flowers and the height of the stamens above the base of the flowers ($P < 0.05$, $r = 0.38$). More pollen was removed from flowers with long stamens than those with short stamens.

There are mixed reports on the relationship between fertility and the height of the stamens. The results of some studies suggest that long stamens favour fruit set. In contrast, the results of the others suggest that short and long stamens provide similar fruit set.

Connor (1972) and Connor and Martin (1973) examined the fertility of cultivars in Michigan. There was a moderate relationship between the percentage of ovules setting seed and the mean height of the stamens above the base of the flower ($P = 0.007$, $R^2 = 0.52$, $N = 11$). The height of the stamens above the base of the flowers ranged from 2.0 to 5.2 mm and the percentage of ovules setting ranged from 35 to 78%.

Bagnara and Vincent (1988) conducted similar work with eight cultivars in Canada. There were no relationships between fruit weight and the height of the stamens above the base of the flower ($P = 0.843$), the height of the receptacle ($P = 0.879$) or the ratio of the two measures ($P = 0.887$). The stamens were 7.2 to 8.9 mm long, the receptacles rose 9.4 to 10.3 mm from the base of the flowers and the fruit weighed 6.8 to 8.2 g. Lata et al. (2018) collected data on the performance of 16 cultivars over two years in India. There were no relationships between the percentage of flowers setting fruit or the percentage of misshapen fruit, and the height of the stamens above the base of the flower ($P = 0.174$ or 0.188). The stamens were 2.1 to 3.9 mm long, the percentage of flowers setting ranged from 37 to 71% and the percentage of misshapen fruit ranged from 31 to 58%. The receptacles rose 2.3 to 5.9 mm from the base of the flowers.

Żebrowska (1998) reported on pollination and fertility in five cultivars in Poland. There were weak correlations between yield per inflorescence and the height of the stamens after self- ($P < 0.01$, $r = 0.35$), wind- ($P < 0.01$, $r = 0.54$) or open-pollination ($P < 0.01$, $r = 0.36$). There were similar correlations between fruit weight and the height of the stamens ($P < 0.01$, $r = 0.27$, 0.59 or 0.33). These results suggest that fertility was associated with long stamens, irrespective of the mode of pollination.

The relationship between fertility and the height of the stamens above the base of the flowers is mixed. Further research is required to determine whether cultivars with long stamens are more productive than those with short stamens.

Relationship between fruit growth and achene production

The achenes represent only a small proportion of the fruit, but they have a strong effect on the development of the receptacle (Aragüez et al., 2013; Pi et al., 2021). Fruit growth stops once the achenes are removed (Nitsch, 1950). Achene density and viability influence the shape, uniformity and size of the fruit (Li et al., 2020).

There is a strong relationship between fruit weight and achene production (Table S1). Fruit weight increases as the number of achenes per fruit increases (Hulewicz & Hortyňski, 1972; Øydvin, 1984). Some authors also include information of the density of achene production. Fruit weight decreases with the number of achenes per cm^2 of fruit surface area (Abbott & Webb, 1970; Abbott et al., 1970; Webb et al., 1974, 1978).

The relationship between fruit weight and achene production varies in experiments. There are different relationships across species, hybrids and cultivars and across primary, secondary, tertiary or quaternary fruit. The linear relationship between fruit weight and the number of achenes per fruit was assessed (Table S1, $N = 42$; Figure 3, $N = 35$). The mean (± s.d. or standard

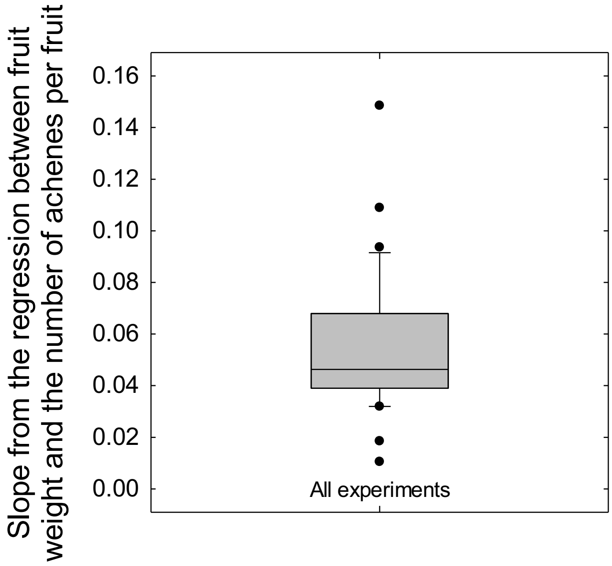

Figure 3. Box plot showing the distribution of the slopes (*b*) from the linear regression between fruit weight (g) and the number of achenes per fruit in strawberry cultivars ($N = 34$). Data are from the various authors shown in Table S1.

deviation) slope (*b*) from the regressions was 0.0548 ± 0.0263 g FW and ranged from 0.0105 to 0.1485 g FW (Figure 3). There were variable, but strong relationships between fruit weight and the number of achenes per fruit. An example of the relationship between fruit weight and achene production is provided (Figure 4).

Insects associated with pollination

There have been numerous investigations on the insects associated with pollination in strawberry (Table S2). Information has been compiled on the number and diversity of insects collected in pan-traps or nets along transects in fields ($N = 10$). In other research, data were collected on the number of insects visiting the flowers ($N = 53$). There are a few studies where information was collected on the amount of pollen deposited on the flowers or the source of the pollen on the insects identified ($N = 4$). Finally, some authors have measured fruit set after exposing the flowers to potential pollinators ($N = 42$). The fertility of the flowers with insects was compared with those not exposed to insects and dependent on gravity and wind.

A range of insects are associated with pollination (Table S2). Honeybees are common ($N = 74$), along with wild bees ($N = 36$), bumblebees ($N = 25$) and flies ($N = 16$), while other insects are less common ($N = 5$). The importance of specific pollinators

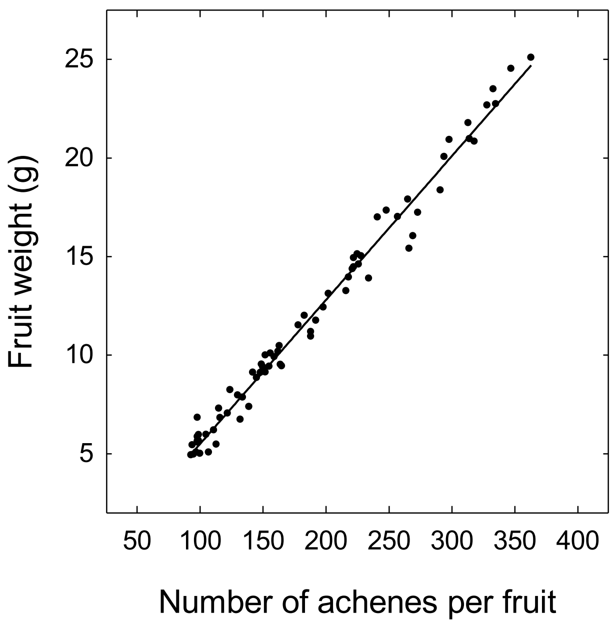

Figure 4. Relationship between fruit weight and the number of achenes per fruit in strawberry. Fruit weight (g) = Intercept + 0.0734 × No. of achenes ($P < 0.001$, $R^2 = 0.98$, $N = 71$). Fruit were sampled from different positions on the inflorescence or cyme. Data are from Webb et al. (1978).

varies, possibly due to differences in the diversity of insects across agricultural and natural landscapes (Reilly et al., 2020). Some of the research is difficult to interpret because not all pollinators were assessed. Strawberry has fewer pollinators than other crops such as apple, bean and oilseed rape and a greater variation in total flower visits over time (Hutchinson et al., 2022). A study in The Netherlands demonstrated that insects visiting during the night were as important as those visiting during the day (Fijen et al., 2023).

The most common pollinators are from the Hymenoptera (Apidae, Melittidae, Halictidae and Megachilidae) and the Diptera (Syrphidae and Calliphoridae) (Table 1). Species from the Coleoptera and Lepidoptera are less common. Rader et al. (2020) indicated that the pollinators of strawberry came from five Orders of insects and seventeen Families.

The following examples demonstrate the variety of insects associated with pollination in strawberry.

O'Connor et al. (2019) set up pan traps in eight fields in the United Kingdom and counted the number of insects visiting the flowers. Thirty-two species were noted, including twelve bumblebees, fourteen solitary bees, five hoverflies and the Western or European honeybee. The most common insects collected in the pan traps were solitary bees (mean ± s.e. of 33.7 ± 4.5), followed by bumblebees (16.5 ± 6.3), honeybees (3.5 ± 1.6) and hoverflies (2.4 ± 0.5). The most common insects visiting the flowers were bumblebees (65.4 ± 9.4), followed by honeybees (8.7 ± 2.0), solitary bees (1.9 ± 0.6) and hoverflies (1.2 ± 0.4). More insects were found visiting the flowers (especially bumblebees) than were collected in the traps. Bumblebees were drawn away from the traps to hunt out the flowers.

Castle et al. (2019) assessed pollination in Germany, with potted plants placed in various locations near arable fields, grasslands or forests. The most common insects visiting the flowers were from Coleoptera (including Families Nitidulidae and Cerambycidae), with 134 visitors. The next most common insects were from Diptera (Families Empididae, Rhagionidae and Syrphidae), with 212 visitors. Insects from Hymenoptera, including honeybees and bumblebees were less common, with 21 visits.

Wei et al. (2021) grew potted plants of 'Mara Des Bois', 'Albion', 'Portola' and 'San Andreas' in Pennsylvania and counted the number of insects visiting the flowers. The most common visitors were true bugs (Hemiptera with about 50% of total), bees (Hymenoptera, 20%) and flies (Diptera, 20%). Beetles (Coleoptera, 5%) and butterflies (Lepidoptera, 2%) were less important.

Methods used to study pollination

Various methods have been used to study pollination, making it difficult to compare the results (Tables S1 to S3). Variations in the responses could be due to different growing conditions and cultivars. Extremes of temperature affect flower development and reduce pollination and fertilisation (Cui et al., 2021;

Table 1. Main insects associated with pollination in strawberry. Data are summarised from Table S2.

Order	Family	Species	Common name	Distribution
Hymenoptera	Apidae	*Apis mellifera*	Western or European honeybee	Widely-distributed.
		Apis cerana	Eastern or Asian honeybee	Southern, eastern & south-eastern Asia.
		Apis dorsata	Giant honeybee	Southern & south-eastern Asia.
		Apis florea	Dwarf honeybee	Southern & south-eastern Asia.
		Bombus terrestris	Buff-tailed bumblebee	Europe.
		Bombus lapidarus	Red-tailed bumblebee	Central Europe.
		Bombus lucorum	White-tailed bumblebee	Europe.
		Bombus pascuorum	Common carder bee	Most of Europe.
		Bombus atratus	Bumblebee	South America.
		Anthophora plumipes	Hairy-footed flower bee	Europe & Asia.
		Nannotrigona testaceicornis	Stingless bee	Neotropical America.
		Trigona minangkabau	Stingless bee	Central & southern America.
		Tetragonisca angustula	Stingless bee	Mexico, central & southern America.
		Trigona spinipes	Dog bee (stingless bee)	Brazil.
		Hypotrigona sp.	Stingless bee	Africa.
		Plebeia nigriceps	Small bee (stingless bee)	Mexico to Argentina.
Hymenoptera	Melittidae	*Dasypoda hirtipes*	Hairy-legged mining bee	United Kingdom to China.
Hymenoptera	Halictidae	*Lagioglossum calceatum*	Sweat bee	Northern Europe.
Hymenoptera	Megachilidae	*Osmia bicornis*	Red mason bee	Europe & the Middle East.
Diptera	Syrphidae	*Eupeodes latifasciatus*	Hoverfly	Widely-distributed.
		Eupeodes corollae	Hoverfly	Europe, northern Africa & Asia.
		Episyrphus balteatus	Marmalade hoverfly	Europe, northern Asia & northern Africa.
		Melanostoma sp.	Hoverfly	Widely-distributed.
Diptera	Calliphoridae	*Lucilia sericata*	Green bottle fly	Europe, Africa & Australia.

Karapatzak et al., 2012; Ledesma & Kawabata, 2016; Ledesma & Sugiyama, 2005). Some cultivars are more dependent on insects than others (Blasse & Haufe, 1989; Connor, 1972). Bishop et al. (2020) demonstrated that the effect of insects on the yields of faba bean depended on the method used to exclude pollinators.

Researchers have grown the strawberry plants under a range of environments, including greenhouses, plastic tunnels and open-field plots (Ariza et al., 2012; Bänsch et al., 2020; Witter et al., 2012). Insects need to be introduced into protected cropping environments to achieve satisfactory yields, whereas plants in the open have access to pollinators (Ariza et al., 2012; Hall et al., 2020; Saridaş et al., 2021).

Different strategies have been used to exclude insects from the flowers, including bagging of individual flowers or inflorescences or the use of insect-proof screens around the plants (Bänsch et al., 2020; Klatt et al., 2014; Connor & Martin, 1973; Moore, 1969). Paper bags exclude wind pollination, whereas mesh bags allow wind pollination. The paper bags must exclude foreign pollen, but not interfere with the health of the flowers. McGoey et al. (2017) described individual chambers for assessing the fertility of wind-pollinated plants.

Studies using plants are better than those using flowers or inflorescences. Perrot et al. (2019) found that pollinators increased the yields of sunflower by 40% on a field-scale and by 31% on a plant-scale. They recommended that studies should be conducted on a field scale. Webber et al. (2020) examined the effect of pollination in apple in the United Kingdom. At an inflorescence scale, fruit set was 13% of normal levels when insects were excluded. It was 75% and 79% of normal levels at the branch and tree scales. Supplementary pollination led to fruit set of 218%, 172% and 117% of normal rates at the inflorescence, branch or tree scales. Bishop and Nakagawa (2020) proposed that simple experiments comparing the yield of open-pollinated and caged plants provide reliable information on the benefits of insects.

Cages covered with screens reduce light levels above the plants and this affects yields. Some authors have included a treatment where the top of the cage has been enclosed to determine whether there is impact of the enclosure on yield. Goodman and Oldroyd (1988) used shade cloth to reduce solar radiation levels by 50%. The shaded plants had 79% of the yields of the plants in the open. Petersen (1983) covered all the plots with screens to have uniform light levels in open and insect-excluded plots. Antonelli et al. (1988) found that plots shaded and given similar light levels to plants under cages had 84% of the yields of open plots in Washington (2.03 and 2.39 kg per plot). Bagnara and Vincent (1988) indicated that screens reduced solar radiation levels at noon by 16% compared with open plots and average wind speed by 45%. Temperatures in the two environments were similar.

Researchers have used different methods to measure fertility. These include the percentage of flowers setting fruit, the number of fertilised achenes per fruit and the weight of achenes per fruit (Colbert & de Oliveira, 1992; Ferrante et al., 2022; Hulewicz & Hortyñski, 1972; Van Oystaeyen et al., 2022). The proportion of stigmas fertilised and producing a viable achene can be used to calculate the rate of pollination (Moore, 1964; Thompson, 1971). Fruit weight and the proportion of misshapen fruit can be used (Moore, 1969). Most of these measurements are poor proxies for yield (Goodman & Oldroyd, 1988).

Classical pollination experiments

The results of research conducted mostly in the 1960s and 1970s highlight the importance of pollination. In some of the experiments, bees were excluded by bagging the flowers or by placing insect-proof screens over the plants. In the others, mesh bags were placed over the flowers to allow for wind movement and the passage of foreign pollen. In some of the experiments, bees were placed in cages to evaluate the effect of insects. Finally, the effect of hand-pollination with pollen from other cultivars was investigated.

Hulewicz and Hortyñski (1972) examined modes of pollination in a glasshouse in Poland. Fruit growth and achene development were better with cross- or open-pollination than with self-pollination (Table 2). Żebrowska (1998) conducted similar experiments to those conducted by Hulewicz and Hortyñski (1972). Data were collected on fruit weight, yield and the incidence of misshapen fruit. Self- and wind-pollination were better than self-pollination, and self-, wind- and insect-pollination were better than self- and wind-pollination (Table 3).

Connor and Martin (1973) investigated the effect of pollination in Michigan. Self- and bee-pollination, self-, wind- and bee-pollination, and self-, wind- and all insect-pollination gave heavier fruit than self-pollination and self- and wind-pollination (Table 4). Wind, bees and other insects increased achene development compared with self-pollination. Moore (1969) grew plants in Arkansas using insect-proof cages to exclude bees and other pollinators. Plants in the open had higher yields than those under the cages, larger fruit and fewer misshapen fruit (Table 5). The benefits of insects were apparent.

Free (1968b) grew plants in the United Kingdom in cages with and without bees and compared their performance with plants in the open. The plants in the open and those in cages with bees had more flowers setting fruit than those in the cages without bees (Table 6). The plants in the open and those in cages

Table 2. Effect of pollination on fruit weight and achene development in strawberry in Poland. Means in a column followed by a common letter are not significantly different by the Fisher's least significant test at 5% level of significance. Data from Hulewicz and Hortyñski (1972).

Treatment	Fruit weight (g)	Percentage of achenes that were fully developed
Autogamy (self-pollination with pollen from the same flower using cloth bags)	4.5 a	46 a
Geitonogamy (pollination with pollen from another flower using cloth bags)	6.8 bc	66 b
Pollination within a clone	5.3 ab	61 b
Cross-pollination (different clone)	7.5 bc	64 b
Open pollination	9.7 c	87 c

Table 3. Effect of pollination on yield, fruit weight and the incidence of misshapen fruit in strawberry in Poland. Means in a column followed by a common letter are not significantly different by the Fisher's least significant test at 5% level of significance. Data are from Żebrowska (1998).

Treatment	Yield (g per inflorescence)	Fruit weight (g)	Percentage of misshapen fruit
Self-pollination (linen bags)	17.2	2.1	72.3
Self + wind pollination (netted bags)	28.2	4.6	34.0
Open pollination with insects	40.0	6.7	7.4

Table 4. Effect of pollination on fruit weight and achene development in strawberry in Michigan. Means in a column followed by a common letter are not significantly different by the Fisher's least significant test at 5% level of significance. Data are from Connor and Martin (1973).

Treatment	Fruit weight (g)	Percentage of achenes that were fully developed
Self-pollination (plastic screen)	5.5 a	51 a
Self + wind pollination (netted cages)	5.8 a	62 b
Self + insect pollination (plastic screen + bees)	7.2 b	68 c
Self + wind + bee pollination (netted cages + bees)	7.2 b	71 c
Open pollination with bees	7.3 b	80 d

with bees had larger fruit and fewer misshapen fruit. There were only small differences in the performance of the plants in the open and those in the cages with bees. The benefits of bees and other pollinators were demonstrated.

The importance of self- and insect-pollination varies across cultivars. Blasse and Haufe (1989) examined the effect of pollination on the yields of four cultivars over three seasons in Germany. Half the plants were grown in insect-proof cages, while the other half were grown in the open. The plants in the cages were dependent on gravity and wind, whereas those in the open had access to honeybees. The plants in the open had higher yields than those in the cages in four out of twelve comparisons ($P < 0.05$, Table 7). The relative yields of the plants in the cages compared with those in the open ranged from 0.58 to 1.22.

Hulewicz and Hortyñski (1972) investigated the effect of pollination on the performance of eleven cultivars in a glasshouse in Poland. In the first group of plants, the flowers were covered with small cloth bags to exclude wind and insects (self-pollination). In the second group, the flowers were exposed to insects (open pollination). The fruit in the open had more well-developed achenes than those in the bags in four out of eleven comparisons ($P < 0.05$, Table 8). The fruit in the open were larger in eight cases.

Hortyñski et al. (1972) grew seven cultivars in a glasshouse in Germany and examined the effect of cross-pollination on fruit growth. All combinations of female (♀) and male (♂) parents were used, including selfing. Cross-pollination had a mixed effect on fruit weight (Table 9). Overall, 'Red Gauntlet' and 'Talisman' were the best ♀ parents and 'George Solwedel' was the best ♂ parent. Cross-pollination resulted in heavier fruit than self-pollination in 'Red Gauntlet', 'Senga Sengana' 'Talisman' and 'Brandenburg'.

The results of research indicate variations in the response across experiments and cultivars. Open pollination with insects was better than self-pollination with gravity and wind. Cross-pollination gave mixed results.

Pollinator dependence

Experiments can measure fertility using self-pollination, open pollination, hand pollination, cross-pollination, and supplementary pollination with insects

Table 5. Effect of pollination on yield, fruit weight and the incidence of misshapen fruit in strawberry in Arkansas. Means in a column followed by a common letter are not significantly different by the Fisher's least significant test at 5% level of significance. Data are from Moore (1969).

Treatment	Yield (t per ha)	Fruit weight (g)	Percentage of misshapen fruit
Self-pollination (insect-proof cages)	16.3 a	9.1 a	48 b
Open pollination with insects	24.1 b	11.0 b	14 a

Table 6. Effect of pollination on fruit set, fruit weight and the incidence of misshapen fruit in strawberry in the United Kingdom. Means presented with standard errors (s.e.). Data are from Free (1968b).

Treatment	Percentage of flowers setting fruit	Fruit weight (g)	Percentage of misshapen fruit
Self-pollination (insect-proof cages)	56 ± 1	6.7 ± 0.4	49 ± 2
Self + bee pollination (cages with bees)	65 ± 2	8.3 ± 0.3	21 ± 2
Open pollination with insects	60 ± 3	8.4 ± 0.03	15 ± 1

Table 7. Effect of pollination on the yield of strawberry cultivars in Germany. The caged plots excluded insects. Paired mean yields without a superscript are not significantly different by the Fisher's least significant test at 5% level of significance. General means (± s.e. or standard error) also presented. Data are from Blasse and Haufe (1989).

			Yield (g per plant)		Relative yield
Year of planting	Fruiting season	Cultivar	Caged plot	Open plot	Caged/Open
1984	Second	Red Gauntlet	208	268	0.78
		Red Gauntlet	194	264*	0.73
		Gorella	195	160	1.22
		Senga Sengana	217	312*	0.70
1985	First	Red Gauntlet	175	234	0.75
		Tenira	185	246	0.75
		Senga Sengana	161	276*	0.58
1986	Second	Red Gauntlet	164	161	1.02
		Tenira	106	114	0.93
		Tenira	216	294*	0.73
		Senga Sengana	192	179	1.07
Mean (± s.e.)			*183* ± 9	*228* ± 19	*0.84* ± 0.06

(Delaplane, 2021; Garratt et al., 2021; Mallinger & Prasifka, 2017; Thomson, 2001). The results of these studies indicate how much a plant depends on insects for successful pollination (pollinator dependence) or if a shortage of pollen limits productivity (pollen limitation). These studies can determine if productivity is better after cross-pollination with foreign pollen.

The dependence of strawberry on pollinators (pollinator dependence or PD) was assessed from the literature (Table S3). Fertility with self-pollination (SP) was compared with open pollination under natural conditions (OP) or with supplementary insects (SUPP) ($PD = 1 - (Yield_{SP}/Yield_{OP}$ or $1- (Yield_{SP}/Yield_{SUPP})$). A value of PD of one indicates that a crop is highly dependent on pollinators, while a value of zero indicates that a crop is independent of pollinators. Two-sided *t-tests* were used to determine if the PD for yield or fruit weight was significantly ($P < 0.05$) lower or higher than zero. The null hypothesis that PD equals zero was then rejected. Open or insect pollination was better than self-pollination, indicating a moderate pollinator dependence (Figure 5).

In the experiments, the flowers were bagged to exclude insects or the plants grown in insect-proof cages, tunnels or greenhouses. Two types of bags were used. Paper bags prevented pollination by insects and the wind. Mesh bags prevented pollination by insects, but allowed for pollination by the wind. The other treatments included open pollination under natural conditions or with supplementary insects.

The mean (± s.d. or standard deviation) PD for yield was 0.36 ± 0.26 (Figure 5; $N = 52$, $P < 0.001$).

Table 8. Effect of pollination on the number of well-developed achenes and fruit weight in strawberry cultivars in Poland. The bagged flowers excluded insects. Paired mean yields without a superscript are not significantly different by the Fisher's least significant test at 5% level of significance. General means (± s.e. or standard error) also presented. Data are from Hulewicz and Hortyñski (1972).

	No. achenes per fruit		Relative no. of achenes	Fruit weight (g)		Relative fruit weight
Cultivar	Bagged flowers	Open flowers	Bagged/Open	Bagged flowers	Open flowers	Bagged/Open
Red Gauntlet	56	197*	0.28	8.1	13.8	0.58
Cambridge Princess	116	200	0.58	3.6	12.0*	0.30
Senga Gigana	156	219	0.72	6.7	11.3*	0.60
George Soltwedel	62	219*	0.28	2.3	11.0*	0.21
Purpuratka	84	203	0.41	5.3	9.1	0.59
Senga Sengana	73	170*	0.33	1.8	8.4*	0.21
Sparkle	80	158	0.50	3.2	8.2*	0.39
Regina	67	216*	0.31	2.4	7.9*	0.30
Dixiland	89	148	0.60	3.7	7.8*	0.47
Redcoat	83	122	0.68	3.8	6.6	0.58
Ananas	64	170	0.37	3.8	6.3*	0.61
Mean (± s.e.)	*85* ± 8	*184* ± 9	*0.47* ± 0.04	*183* ± 9	*9.3* ± 0.7	*0.44* ± 0.05

Table 9. Effect of cross-pollination on fruit weight (g) in seven strawberry cultivars in Poland. Means in the extreme column and row without a superscript are not significantly different by the Fisher's least significant test at 5% level of significance. Means in a row without an asterisk are not significantly different from the selfed plant by the Fisher's least significant test at 5% level of significance. Data are from Hortyñski et al. (1972).

	♂ Parent							
♀ Parent	George Solwedel	Red Gauntlet	Senga Sengana	Senga Gigana	Talisman	Brandenburg	Ville de Paris	*Mean*
George Solwedel	3.8	2.3	3.8	6.6	5.5	2.7	3.8	*4.1 a*
Red Gauntlet	11.6*	5.8	6.3	10.4*	6.8	8.5	5.2	*7.8 d*
Senga Sengana	6.1	3.7	3.7	2.0	2.6	6.1	3.5	*4.0 a*
Senga Gigana	9.4*	3.8	4.4	4.9	7.3	7.2	9.7*	*6.7 cd*
Talisman	8.7*	5.8	9.7*	5.9	4.5	9.1*	6.3	*7.2 d*
Brandenburg	8.5*	4.8	7.1*	7.6*	6.4	3.2	1.5	*5.6 bc*
Ville de Paris	7.2	5.7	3.3	3.1	6.1	6.9	3.8	*5.2 ab*
Mean	*7.9 c*	*4.5 a*	*5.5 ab*	*5.8 ab*	*5.6 ab*	*6.2 bc*	*4.8 a*	

The null hypothesis was rejected. The mean PD for fruit weight was 0.29 ± 0.22 (Figure 5; $N = 55$, $P < 0.001$). The incidence of misshapen fruit was 3.20 ± 1.89 higher in the plants not exposed to insects (Table S3; $N = 40$, $P < 0.001$). The benefit of insect pollinators is clear. Differences in the response could be due to variations in the abundance of pollinators in the local environment (Mallinger et al., 2021). The difference in fertility of flowers exposed or not exposed to insects would be small if there is a shortage of pollinators in the experiment. Crops that have a high rate of self-pollination have similar yields when they are caged or exposed to potential pollinators (e.g. Gazzoni et al., 2022 with soybean in Brazil). Modern strawberry cultivars have a moderate rate of self-pollination.

Differences in fruit weight and the percentage of misshapen fruit between self- and open-pollinated plants did not reflect differences in yield (Table S3). The relationships between relative yield, and relative fruit weight ($P = 0.076$, $R^2 = 0.08$) or the relative percentage of misshapen fruit ($P = 0.155$, $R^2 = 0.04$) were weak. Fruit weight and the percentage of misshapen fruit are poor proxies for yield.

Cross-pollination

Cross-pollinated flowers (CP) set more fruit than self-pollinated flowers (SP) (CP/SP = 1.08 ± 0.11, $N = 38$, $P < 0.001$) and produced larger fruit (CP/SP = 1.19 ± 0.48, $N = 93$, $P < 0.001$) (Table S4; Figure 6). In contrast, the weight of achenes per fruit (CP/SP = 0.96 ± 0.21, $N = 40$, $P = 0.272$) and the incidence of misshapen fruit (CP/SP = 0.81 ± 0.36, $N = 16$, $P = 0.055$) were similar in the two groups. These studies compared the fertility of flowers that were hand-pollinated using pollen from the same cultivar or hand-pollinated

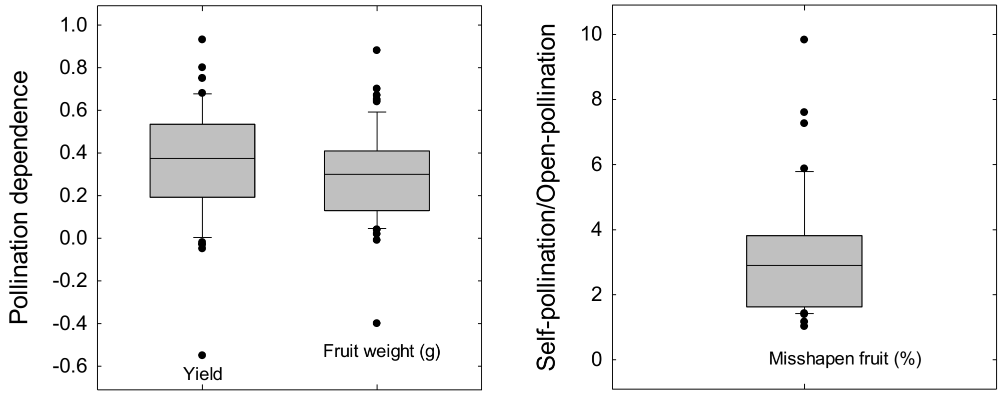

Figure 5. Box plots showing the effect of pollination on yield ($N = 52$), fruit weight ($N = 55$) and the percentage of misshapen fruit in strawberry cultivars ($N = 39$). The flowers were self-pollinated (SP) or pollinated under natural open conditions (open pollination or OP) or with supplementary insects (SUPP). For yield or fruit weight, pollinator dependence or PD = 1 - ($Value_{SP}/Value_{OP}$ or 1-($Value_{SP}/Value_{SUPP}$). For the percentage of misshapen fruit, data are presented as the ratio of misshapen fruit with SP/OP, etc. Data are from the various authors shown in Table S3.

using pollen from a different cultivar. The comparison does not include the contribution of insects to self-pollination, potentially underestimating the contribution of pollinators to self-pollination (Mallinger et al., 2021).

There are mixed effects of cross-pollination on fertility suggesting that self-pollination can limit the productivity of some cultivars. Hudewenz et al. (2014) indicated that the benefit of cross-pollination varied amongst cultivars of oilseed rape in Germany. Yield was better in two out of four cultivars with hand pollination than with self-pollination.

Kämper et al. (2022) explored the relationship between fertility and cross-pollination in 'Red Rhapsody' and 'Sundrench' strawberry in Queensland, Australia. They found that 98% of the seeds on the fruit were from self-pollination, even when the two cultivars were planted only 1 m apart. In 'Red Rhapsody', fruit were similar after self- (24.1 ± 0.7 g) or cross-pollination (24.0 ± 0.5 g). In 'Sundrench', fruit were larger after self-pollination (26.0 ± 0.9 g versus 19.9 ± 0.7 g). It was concluded that cross-pollination was not important in commercial fields. Dung et al. (2023) conducted a similar experiment to that of Kämper et al. (2022), with flowers of 'Redlands Joy' self-pollinated or pollinated using pollen from 'Rubygem'. Fruit produced after cross-pollination were 4.2 to 7.5% heavier than those produced after self-pollination.

Pollen limitation

Pollination in strawberry is better with insects than with wind or gravity (see above). In some plants, the availability and transfer of pollen limit seed or fruit set (Ashman et al., 2004; Knight et al., 2005; Layek et al., 2020, 2022; Li et al., 2022b; Vansynghel et al., 2022a). Pollen limitation (PL) or pollination deficit varies across populations of wild and crop plants and with the methods used to assess seed or fruit set (Bennett et al., 2018; Garratt et al., 2023; Holland et al., 2020; Larson & Barrett, 2000; Olhnuud et al., 2022). Low values of pollen limitation are associated with abundant pollinators and frequent visits of pollinators to the flowers (Hegland & Totland, 2008).

Pollen limitation can be estimated by comparing the fertility of plants with and without supplementary insects (Benjamin & Winfree, 2014; Delaplane, 2021; Garratt et al., 2021; Thomson, 2001). Alternatively, it can be estimated by comparing the fertility of hand- and open-pollinated flowers (Andrzejak et al., 2022; Campbell & Halama, 1993; Li et al., 2022a; Stanley et al., 2013; Stoner, 2020). There are issues with both methods. Hand-pollination can damage the flowers or apply excessive pollen to the stigmas. The response to supplementary pollination depends on the abundance of native pollinators at the site. The density of the pollinators in cages is often higher than that in the natural environment.

There are few studies comparing the two methods used to estimate pollen limitation. Layek et al. (2021) examined the effect of pollination on the fertility of watermelon. Fruit set was lower when pollinators were excluded from the flowers (self-pollination), intermediate with open pollination and higher with hand-pollination or when pollination was supplemented with stingless bees or honeybees. Estimates of PL were lower with bees (0.18 or 0.21) than with hand-pollination (0.27). Layek et al. (2022) conducted similar work with fennel. Estimates of PL were lower with stingless bees (0.13) than with hand-pollination (0.18). These results suggest that PL is underestimated using supplementary pollination with insects.

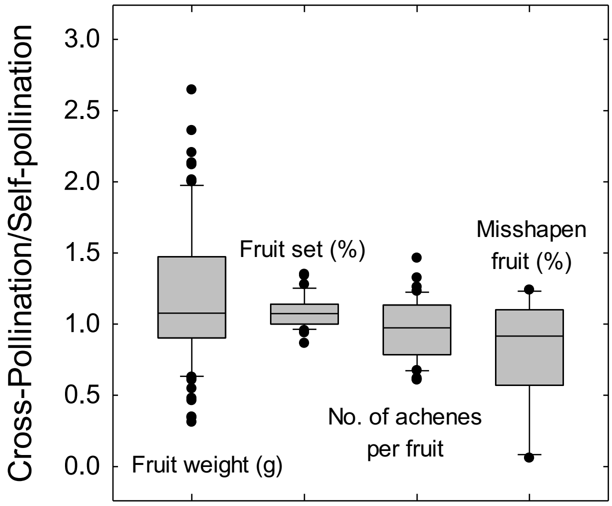

Figure 6. Box plots showing the effect of cross-pollination on fruit weight ($N = 93$), the percentage of flowers setting fruit ($N = 38$), number of achenes per fruit ($N = 40$) and the percentage of misshapen fruit in strawberry cultivars ($N = 16$). The flowers were self-pollinated (SP) or cross-pollinated (CP) by hand. Data are from the various authors shown in Table S4.

Pollen limitation is higher in self-incompatible than in self-compatible plants, higher in non-autogamous than in autogamous plants and higher in flowers with multiple carpels than those with single carpels (Larson & Barrett, 2000). In some cases, pollen limitation is due to poor pollen quality rather than to inadequate pollen supply (Aizen & Harder, 2007). Some authors used the term 'pollinator-limited' to indicate a shortage of pollinators to transfer pollen (Ai et al., 2013; Pan et al., 2012).

The relationship between fertility and pollen in strawberry was assessed across studies (Table S5). The fertility of flowers that were exposed to supplementary insects was compared with that under natural open pollination. Pollen limitation (PL) was calculated as $PL = (P_s - P_o)/P_{Max}$, where P_s is the yield or fruit weight after supplementary pollination, P_o is the yield or fruit weight from the control treatment (open pollination) and P_{Max} is the larger of the two values (Baskin & Baskin, 2018; Ryniewicz et al., 2022). Two-sided *t-tests* were used determine if PL was significantly ($P < 0.05$) lower or higher than zero. The null hypothesis that the mean ratio equals zero was then rejected.

Mean (± s.d.) pollen limitation for yield was 0.20 ± 0.17 ($N = 20$, $P < 0.001$), with the null hypothesis rejected. There was a moderate, but variable pollen limitation across the experiments (Figure 7). There was a different response when estimates of pollen limitation were based on fruit weight. Mean pollen limitation was 0.06 ± 0.18 ($N = 25$, $P = 0.106$). Seed set after supplementary pollination should be higher or at least equal to seed set under natural conditions (zero or positive values of PL). Negative values of PL reflect experimental error or excessive pollen loads (Garratt et al., 2021; Petersen et al., 2014). In some studies, negative values of PL are set to zero in the analyses (Lázaro et al., 2014).

Managed or wild bees or other insects improve the productivity of some plants compared with open pollination. A second analysis was conducted to estimate pollen limitation based on a comparison of hand- and open-pollination (Table S6). Different indices were used, including fruit weight, fruit width and the number of achenes per fruit. Mean pollen limitation was 0.03 ± 0.11 ($N = 11$, $P = 0.307$), suggesting a small and variable pollen limitation.

Case and Ashman (2009) examined the fertility of the wild strawberry, *F. virginiana* in the United States. Pollen limitation was determined by measuring the proportion of seeds produced per ovule in a hand-pollinated clone minus seed set in an open-pollinated clone. They found no evidence for pollen limitation in the hermaphrodite plants ($P > 0.05$). Burd (1994) found pollen limitation at some time or at some sites in 159 out of 258 species (62%). Bennett et al. (2020) reviewed seed and fruit set across 1,247 species around the globe. They found that there was a 63% increase in reproduction following supplementary pollination compared with open pollination. Sáez et al. (2022) assessed the productivity of 30 crops and reported that hand pollination increased yield by 34% compared with open pollination, suggesting a significant pollen limitation.

Pollinator exclusion experiments indicate the degree to which a plant depends on insects for pollination (Koch et al., 2020). In contrast, pollen supplementation (supplementary insect pollination or hand pollination) indicates the degree to which reproduction is limited by the availability of pollen (Knapp & Osborne, 2017). Some plants can be dependent on pollinators, but not limited by the availability of pollen (Knapp & Osborne, 2017; Koch et al., 2020), while

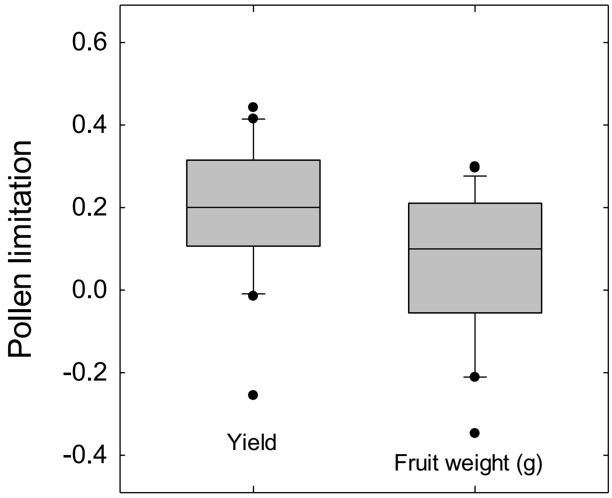

Figure 7. Box plots showing the effect of supplementary pollination on yield ($N = 20$) or fruit weight ($N = 25$) in strawberry cultivars. The flowers were exposed to supplementary pollinators such as bees (SUPP) or exposed to insects under natural conditions (OP). Pollen limitation (PL) was calculated as $PL = (P_s - P_o)/P_{Max}$, where P_s is the number of seeds, etc. from the supplementary pollination treatment, P_o is the number of seeds from the control treatment (open pollination) and P_{Max} is the larger of the two values (Baskin & Baskin, 2018; Ryniewicz et al., 2022). Data are from the various authors shown in Table S5.

others are dependent on pollinators and limited by the availability of pollen (Amorin et al., 2021; Gazzoni & Barateiro, 2023; Newstrom & Robertson, 2005; Rodger & Ellis, 2016; Urbanowicz et al., 2018). A small pollen deficit can have a strong impact on the profitability of a high-value crop such as courgette, where a 3% pollen limitation reduced profitability (Knapp & Osborne, 2017).

Relationship between fertility and the pollinator community

The success of pollination in plants is related to visits by individual or groups of insects (Garibaldi et al., 2016; Garratt et al., 2016; Geslin et al., 2017; Guzman et al., 2023; Haedo et al., 2022, 2023; Rollin et al., 2019; Simpson et al., 2022; Tan et al., 2023; Vansynghel et al., 2022b). In some plants, pollination is dependent on rare and sometimes declining species (Genung et al., 2023). Different measures of the insect community can be used to classify the pollinators. Abundance refers to the number of individual insects visiting a field, while species richness refers to the number of species, genera or taxonomic groups (Garibaldi et al., 2014; Wu et al., 2021).

Two other terms are used to characterise the complexity of the pollinator community. These are related to the types of insects visiting the flowers and how well they and their traits are distributed in the community. Indices of functional diversity are often based on the morphology and feeding niche of the pollinators (Woodcock et al., 2019). Functional evenness reflects the distribution of certain traits within the insect community (Zhang et al., 2021). There are different ways to estimate diversity, which can influence the interpretation of the results (Thompson et al., 2021; Roswell et al., 2021). There are disagreements about which measurement best characterises a community and how the measurements relate to each other (Kral O'Brien et al., 2021; Locey & White, 2013).

The main insects associated with pollination in strawberry include honeybees (*A. mellifera and A. cerana*), bumblebees (*B. terrestris* and others), numerous native bees (Hymenoptera: Apidae, Halictidae, Melittidae and Megachilidae) and flies (Diptera: Syrphidae and Calliphoridae). Reports on the effectiveness of the species are mixed (Table S7). In some cases, honeybees were better than bumblebees and gave heavier fruit, while in the others, the reverse was true. Silva et al. (2020) found that flowers exposed to many insects produced larger fruit than those exposed to single insects. Herrmann et al. (2019) exposed plants in cages to orchard bees (*Osmia cornuta*) or green bottle bees (*Luciana sericata*). Fruit growth was similar after one or both species visited a flower. Horth et al. (2018) demonstrated the flowers exposed to mason bees (*Osmia lignaria*) produced larger fruit than those exposed to mixed pollinators (Table S7).

There were mixed effects of abundance and species richness on pollination (Table S7). There were significant relationships between fruit weight or yield, and the number of insects visiting the flowers ($N = 11$ out of 25 studies) and species richness ($N = 2$ out of 7 studies). There were insufficient data to determine the relationship between fertility and functional diversity ($N = 2$ studies) or evenness ($N = 2$ studies). Often the data were variable, making it difficult to determine the relationship between pollination and pollinators.

It is estimated that 78% of temperate plants are pollinated by animals, including insects (Ollerton et al., 2011). This figure rises to 94% for tropical species. The importance of honeybees and other bees varies across ecosystems and crops (Aizen et al., 2020; Badenes-Pérez, 2022; Garibaldi et al., 2021; Hung et al., 2018; Liu et al., 2023; Moreira & Freitas, 2020). Some authors consider that the importance of honeybees or bees in general for crop production is overstated (Batra, 1995; Borchardt et al., 2021; Diller et al., 2022; Mashilingi et al., 2022; Mateos-Fierro et al., 2022; Norfolk et al., 2016; Pfiffner & Müller, 2016; Requier et al., 2023; Senapathi et al., 2021; Spivak et al., 2011; Smith & Saunders, 2016; Thakur, 2012; Torchio, 1990).

There is debate about the importance of *Apis* and non-*Apis* species for the pollination of agricultural and wild plants (e.g. Aebi & Neumann, 2011; Aebi et al., 2012; Arachchige et al., 2023; Baena-Díaz et al., 2022; Corbet, 1991a, 1991b; Cusser et al., 2021; Iwasaki & Hogendoorn, 2022; Kilpinen et al., 2022; Morse, 1991; Muñoz et al., 2021; Ollerton et al., 2012; Schmidlin et al., 2021; Vaidya et al., 2023; Weekers et al., 2022b).

Burns and Stanley (2022) demonstrated that honeybees, bumblebees, solitary bees and hoverflies contributed to pollination of apple in Ireland. Junqueira et al. (2022) reported that *Apis* and non-*Apis* bees were essential for crop production. Yields were greater with bees than without bees ($P < 0.001$). El Abdouni et al. (2022) surveyed the insects in agroecosystems, including 22 crop plants in Morocco over two years. They recorded a total of 53,361 insect pollinators in all agroecosystems, among which 37,091 visited the crop flowers. Bees were the most abundant group visiting the crops. Honeybees represented 49% of crop visitors, followed by wild bees at 33%. Three genera (*Lasioglossum*, *Andrena* and *Xylocopa*) represented 53% of the total abundance of the wild bees visiting the crops.

Managing the pollinator community

Agricultural and wild plants are pollinated by managed and wild insects (Bohart, 1972; Cavigliasso et al., 2020; Kevan et al., 1990; Khalifa et al., 2021; Mazi et al., 2023; Muschett & Fontúrbel, 2022; Nene et al., 2022; Pardo & Borges, 2020; Peña & Carabali, 2018; Potter & Mach, 2022; Potts et al., 2016; Mallinger et al., 2019; Splitt et al., 2022). Managed pollinators are universally social bees such as *A. mellifera* and *Bombus* spp., with some exceptions, including *Osmia cornuta* (European orchard bee), *O. lignaria* (mason bee) or *Megachile rotundata* (alfalfa leaf-cutting bee) (Pitts-Singer & Cane, 2011; Robinson et al., 2023).

Semi-natural habitats have mixed effects on the abundance, species richness or functional diversity of pollinators in agricultural fields and other landscapes (Campbell et al., 2022; Ahrenfeldt et al., 2015; Aslan et al., 2022; Blasi et al., 2021; Bottero et al., 2021; Carvalheiro et al., 2011; Centeno-Alvarado et al., 2023; Clausen et al., 2022; Ferrante et al., 2023; Herbertsson et al., 2021; Lowe et al., 2021; Millard et al., 2021; Monasterolo et al., 2022; Rahimi et al., 2022; Ramírez-Mejía et al., 2023; Ratto et al., 2022; Ricketts et al., 2008; Rydhmer et al., 2022; Shackelford et al., 2013; St. Claire et al., 2022; Zurbuchen et al., 2010). Eeraerts (2023) collected data on wild pollinators in 22 cherry orchards in Flanders, Belgium. He proposed that a minimum of 15% semi-natural habitat facilitated wild pollinator (27 species) visits to the flowers.

The effect of mixed crops, organic culture, conservation tillage, wildflowers, natural margins, hedgerows, green spaces, etc. can be variable (Allasino et al., 2023; Bencharki et al., 2023; McCullough et al., 2021; Cusser et al., 2023; Donkersley et al., 2023; Fountain, 2022; Image et al., 2023; Jacobs et al., 2023; Kirsch et al., 2023; Kuppler et al., 2023; Nel et al., 2017; Sentil et al., 2022; Toivonen et al., 2021; Zamorano et al., 2020). Most of this research has been conducted in Europe and North America with fewer reports from Asia, Africa and South America (Archer et al., 2014).

The benefits of semi-natural and artificial habitats on the pollinator community varies with the crop and with individual pollinators (Delphia et al., 2022; Jaumejoan et al., 2023). In some studies, there is no increase in the abundance of pollinators or no increase in pollination of the crop (Azpiazu et al., 2020; Burkle et al., 2017; Delphia et al., 2019; Bishop et al., 2023; Gervais et al., 2021; Pardo et al., 2020; Sardiñas & Kremen, 2015; Toukem et al., 2023).

There is an interplay between pollinators across agricultural and natural habitats. Some authors indicate that honeybees decrease the abundance of bumblebees and/or wild bees, while others indicate no or mixed effects (Bernauer et al., 2022; Bommarco et al., 2021; Briggs et al., 2019; Herbertsson et al., 2016; Lindström et al., 2016; Sapir et al., 2017; Vergara et al., 2023). Mallinger et al. (2017) reviewed the impact of managed bees on wild bees in agricultural and natural habitats. They indicated that 53% of studies reported that managed bees had a negative effect on wild bees, 28% of studies reported no effect and that 19% of studies reported mixed effects. Equal numbers of studies reported positive (36%) and negative (36%) effects on plant communities, with the remainder reporting no or mixed effects. The results depended on whether managed bees were in their native or non-native range. Managed bees within their native range were less competitive than those outside their native range.

The effect of semi-natural habitats, wildflowers, etc. on the pollinator community in agricultural fields can depend on the size of the field relative to rest of the landscape (Botzas-Coluni et al., 2021; Kirchweger et al., 2020; McGrady et al., 2021; Schoch et al., 2022). In some scenarios, the benefits of natural landscapes only apply to the margins of the fields (Szitár et al., 2022; Tschanz et al., 2023). There is debate on this issue across pest species and pollinators, with some authors suggesting that large fields harbour more pest species than small fields and fewer pollinators (Kennedy & Huseth, 2022; Marini et al., 2023; Perrot et al., 2022; Rosenheim et al., 2022, 2023). Magrach et al. (2023) examined the productivity of agriculture in Spain over two decades. They found that small fields and a diversity of crops provided the highest yields across 54 crops of which 41% were dependent on pollinators for reproduction.

Experiments have been conducted to determine whether semi-natural habitats, wildflowers, grass or hedges improve the pollinator community in strawberry (Table S8). There have also been experiments to determine whether mass-flowering crops draw away pollinators from strawberry flowers. Fields close to semi-natural habitats had more insect visitors in 15 out of 24 studies. Fields close to wildflowers, grass or hedges had more insect visitors in eight out of thirteen studies. Fields close to mass-flowering crops had fewer pollinators in six out of eight studies. Increases in the abundance, species richness or functional diversity of the pollinators increased the fertility of the strawberry plants in 16 out of 33 studies (Table S8).

Connelly et al. (2015) examined the effect of the semi-natural habitats and agriculture on pollinators and pollination in 14 strawberry fields in the United States. The proportion of agriculture varied from 0.09 to 0.60 across the sites. The abundance and species richness of wild bees decreased as the proportion of agriculture in the landscape increased. Fruit weight increased with the abundance of bees ($P = 0.002$, $R^2 = 0.86$), but not with species richness ($P > 0.05$). Orford et al. (2016) demonstrated that the abundance, species richness and functional diversity of pollinators in the United Kingdom increased with increasing biodiversity of grass sown next to the fields. Fruit weight increased with the species richness ($P = 0.022$) and functional diversity of the pollinators ($P = 0.012$).

McCullough et al. (2022) demonstrated that diverse landscapes, but not wildflowers increased crop yields across 22 farms in the United States. In strawberry, the percentage of fertilised achenes was associated with the proportion of semi-natural habitat at a 1,000 m scale ($P = 0.036$). Marketable yield increased with the proportion of semi-natural habitat ($P = 0.002$). Image et al. (2022) studied the pollinator community in a range of crops in the United Kingdom. They found that there was no relationship between the abundance of several species of bumblebees and ground-nesting solitary bees in strawberry and natural landscapes. They concluded that this probably because most strawberry fields in the United Kingdom are not close to natural habitats.

Sciligo et al. (2022) investigated the effect of natural habitats and agricultural diversification on the pollinator community in 16 fields in California. The farms had different proportions of natural land cover in the surrounding landscape and had either mono-culture or poly-culture. Information was collected on the pollinator community in the fields and on the performance of the plants. During the experiment, the authors collected 2,422 honeybees, 1,699 native bees and 2,399 non-bee visitors to the fields. There were more native bees in the farms with poly-culture than with mono-culture and more native bees when the fields were close to natural cover. In contrast, native habitat and farm culture had no effect on the number of honeybees or non-bee visitors. Landscape and culture had no effect on fruit weight or the percentage of misshapen fruit. It was concluded that there were enough honeybees in the fields for adequate fertility.

Bänsch et al. (2021) studied the effect of mass flowering on pollinators in Germany. The abundance of honeybees and bumblebees decreased with the amount of flowering in oil-seed rape crops in the adjacent fields. In contrast, the abundance of solitary bees increased. Honeybees represented 46.5% of the community, followed by bumblebees with 29.9% and solitary bees with 23.6%. Fruit weight in one cultivar ('Honeoye') increased with increasing abundance of bees, but not in the other cultivar ('Sonata'). Horth et al. (2018) examined the effect of supplementary pollination on the performance of nine fields in the United States. The introduction of mason bees (*Osmia lignaria*) to parts of the fields increased fruit size compared with areas without mason bees.

The results of the experiments on the management of pollinators in strawberry are mixed. The abundance and diversity of pollinators are often higher in fields close to semi-natural habitats, wildflowers or grass. However, these changes do not always lead to better fertility.

Effect of pollinators on yield

The effect of insects on pollination can be assessed by measuring the fertility of individual flowers, plants or plots (DeVetter et al., 2022; Bishop et al., 2020). Experiments conducted in a field are preferred to those conducted on individual flowers or plants (Ouvrard & Jacquemart, 2019). Colonies of managed pollinators can be introduced into fields and the yields of plots with managed bees compared with those without managed bees and dependent on local pollinators.

Angelella et al. (2021) found that the yields of strawberry were 18% lower across all farms with honeybee hives in north-east United States compared with those without hives ($P < 0.05$; Figure 8). These results suggested that the managed bees had a negative effect on pollination by wild bees. Lindström et al. (2016) indicated that honeybees affected the yield of oilseed rape in Scandinavia, but the response depended on the cultivar ($P = 0.04$). The yields of open-pollinated cultivars were

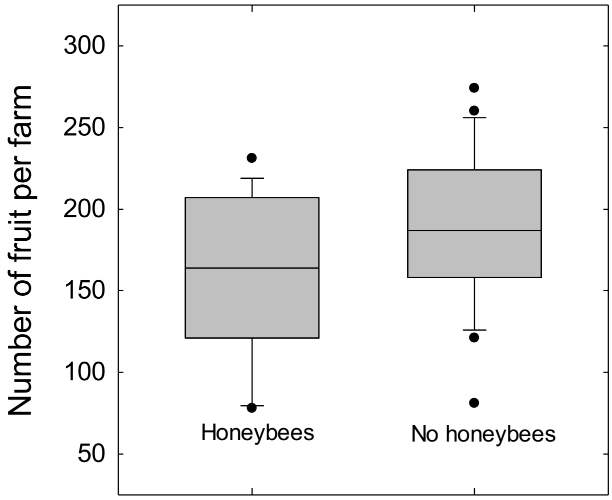

Figure 8. Box plots showing the effect of honeybees on the yield of strawberry in the United States. The farms were supplemented with honeybees ($N = 17$) or not supplemented with honeybees ($N = 21$). Data are from Angelella et al. (2021).

11% higher with hives than without hives. Hybrid cultivars had similar yields with and without hives. Pitts-Singer et al. (2018) investigated the effect of pollinators on the performance of nine almond orchards in California. They indicated that overall, fields managed with honeybees and blue orchard bees (*Osmia lignaris*) had similar yields as those managed with only honeybees.

Petersen et al. (2013) investigated the effect of insects on the productivity of pumpkin in New York, United States. The fields were supplemented with honeybees or bumblebees or not supplemented (control). The average yield was similar across the three treatments ($P = 0.770$). It was concluded that supplementary pollination did not improve yields, with sufficient pollinators in the local environment. A total of 2,390 bees were recorded visiting the flowers in the first season and 2,709 bees in the second season. Three species accounted for 97.7% of visits, including *Peponapis pruinosa* or the Eastern cucurbit bee ($N = 1{,}382$ and 1,272), *A. mellifera* ($N = 695$ and 765) and *B. impatiens* ($N =$ 241 and 628). The Eastern cucurbit bee is native to North America from the East to the West Coast of the United States and into Mexico.

Miñarro et al. (2023) examined pollination in three fruit crops in Spain. They found that pollination in rabbiteye blueberry was dependent on managed pollinators within the orchard. In contrast, pollination in kiwifruit and highbush blueberry was dependent on pollinators from the surrounding landscape. Weekers et al. (2022a) demonstrated that the yields of apple across 22 locations in Europe were mainly driven by landscape management practices, without any evidence for a superior contribution by managed honeybees.

There is limited data on the pollination of strawberry under protected cultivation. Cao et al. (2023) demonstrated the best yield and fruit quality were obtained with about one honeybee per plant in a greenhouse in China.

Research is required to determine the role of managed and wild bees in strawberry in different environments. The studies mentioned above are a guide to the set-up of the experiments and the data to collect.

Conclusion

Insect pollination provided higher yields than self-pollination in strawberry. Plants exposed to supplementary insects had higher yields than those exposed to pollinators under natural open conditions. In contrast, differences in the fertility of the flowers after self- or cross-pollination were small.

Honeybees are over-represented, with less interest in wild bees, bumblebees and flies. Strawberry fields close to semi-natural habitats, wildflowers, grass or hedges have more pollinators and a greater diversity of pollinators than fields further away. However, a greater abundance of pollinators does not always lead to higher fruit set. Comparisons across studies are complicated because of the use of different proxies to assess yield, which may not be equivalent. Research conducted in a field can help determine whether managed or wild insects provide the best yields, and how the pollinator community can be optimised. Fruit set is dependent on insect pollinators (moderate pollinator dependence) and is limited by the availability of pollen under natural open conditions (moderate pollen limitation).

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Data availability statement

The author confirms that the data supporting the findings of this study are available within the supplementary materials published online with this paper or available from the author on reasonable request.

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