Project title: Cucurbit Pollination: Mechanisms and Management to Improve Field Quality and Quantity

Project number: CP118

Project leader: Professor Juliet Osborne, University of Exeter

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Location of project: Cornwall, United Kingdom

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The results and conclusions in this report are based on an investigation conducted over a one-year period. The conditions under which the experiments were carried out and the results have been reported in detail and with accuracy. However, because of the biological nature of the work it must be borne in mind that different circumstances and conditions could produce different results. Therefore, care must be taken with interpretation of the results, especially if they are used as the basis for commercial product recommendations.

AUTHENTICATION

We declare that this work was done under our supervision according to the procedures described herein and that the report represents a true and accurate record of the results obtained.

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Contents

GROWER SUMMARY

Headlines

- All parthenocarpy-promoting techniques (genetic modification, hormone application and selective breeding) significantly increased fruit quantity and quality in 18 pollinator-dependent crop species (not including seed and nut crops as parthenocarpy causes seedlessness)' – findings from a meta-analysis desk study (Knapp et al., 2016 Journal of Applied Ecology).
- Pollinators contribute approximately £2.7 million to the value of UK courgette production - findings from 2015 and 2016 field seasons.

Background

The principal focus of this research project is to improve our understanding of the mechanisms which underpin fruit set in cucurbits. Generally, cucurbits require pollen to be transferred from male flowers to female flowers for successful pollination and fruit set (Delaplane et al. 2000).

Preliminary results from 2015 showed that whilst pollination increased the size, weight, and growth rate of courgettes, natural parthenocarpy (fruit set in the absence of pollination) meant that many fruits were able to reach marketable size without any pollination at all. This inspired a meta-analysis of studies across the world which had explored the effect of parthenocarpy promoting techniques (genetic modification, selective breeding, and hormone application) for increasing yield in different horticultural crops.

In the meantime, data on the effect of pollination on courgette yield were collected at additional sites in 2016. This was to calculate a more robust estimate of courgette dependence on pollinators and an economic estimate for the value of pollinators to UK courgette production.

Nonetheless, whilst pollination clearly affects cucurbit yield, there are many other environmental factors which contribute to fruit set such as soil quality, water availability and weather conditions (Boreux et al., 2013; Bos et al., 2007; Klein et al., 2014; Motzke et al., 2015). As a result, the productivity of insect pollinated crops are dependent on the presence of high functioning ecosystems that support pollinator populations, regulate disease, purify and cycle water, and nutrients (Figure 1). The spatial and temporal variation of pollinators, the resources which support their populations and other factors which influence fruit formation formed the basis of an observational experiment in 2016. During this field season I surveyed nine different courgette fields in three counties, three times in a season - the results of which are currently being analysed.

A simple breakdown of the progress of each data chapter (and its related funding objectives) follows:

Chapter	**Title**	**Funding Objective**	**Progress**
1	Re-evaluating strategies for pollinator-dependent crops: how useful is parthenocarpy?	In addition	*Accepted in Journal of Applied Ecology, September 2016*
2	Courgette production: pollination demand, supply, and value	2	*Submitted to Agriculture, Ecosystems and Environment, November 2016*
3	Influence of pollinators, floral resources, nutrients, and farm intensity for determining courgette yield	5 and 6 (updated)	In progress - specimens are currently being identified in the lab (estimated completion March 2017)
4	An intensively managed, mass flowering crop: a resource for pollinators?	3 and 4	Field work to take place in 2017
Report/ factsheet	Most effective wild pollinators of courgette in the South West	1	Data collected in 2015 and 2016. More field work will take place in 2017

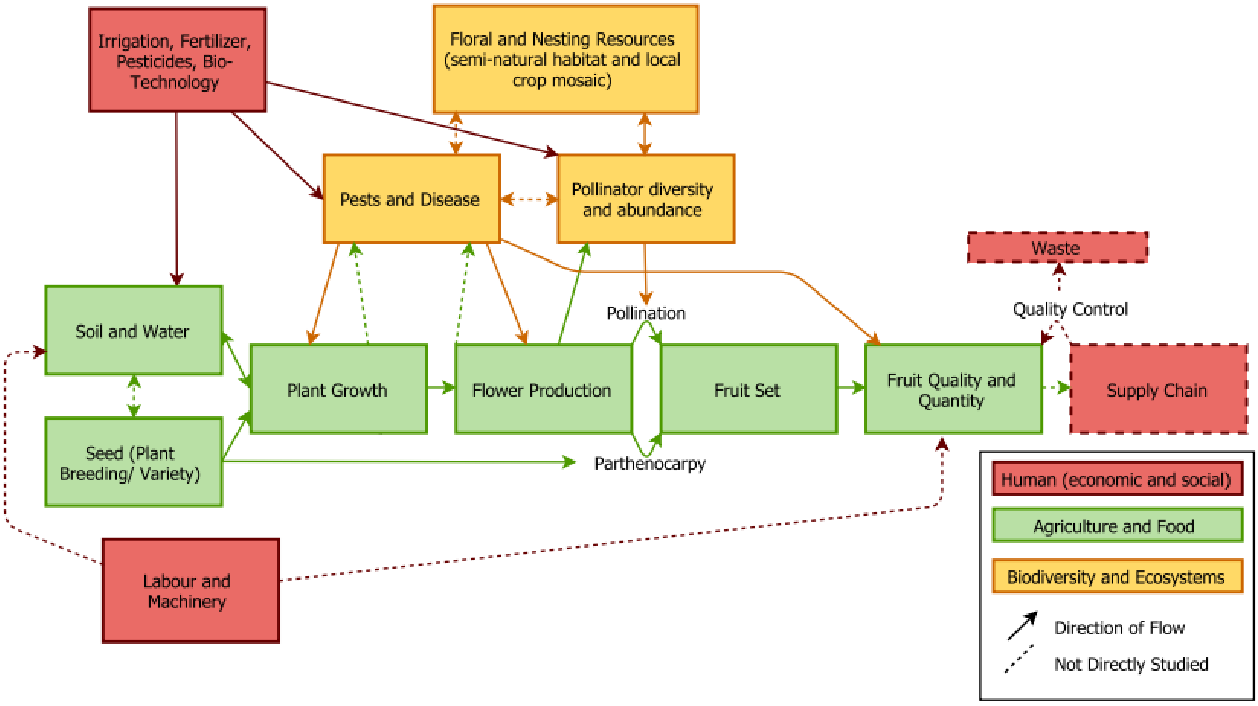

Figure 1. Conceptual framework of the human (economic and social), agricultural and food, and biodiversity and ecosystems which effect fruit set in pollinator dependent crops. Dashed and full lines distinguish between observed and experientially tested relationships during the course of this project.

All empirical work uses the popular courgette variety 'Tosca', a high yielding, compact variety, notably tolerant to powdery mildew which makes it a popular choice for commercial production.

Summary

- All parthenocarpy-promoting techniques (genetic modification, hormone application and selective breeding) significantly increased fruit quantity and quality in 18 pollinator-dependent crop species (not including seed and nut crops as parthenocarpy causes seedlessness).

Whilst most studies reviewing the reliance of global agriculture on insect pollination advocate increasing the 'supply' of pollinators (wild or managed) to improve crop yields, there has been little focus on altering a crop's 'demand' for pollinators. Parthenocarpy (fruit set in the absence of fertilisation) is a trait which can increase fruit quantity and quality from pollinator-dependent crops by removing the need for pollination.

I conducted a meta-analysis (Knapp et al., 2016) of studies examining the extent and effectiveness of parthenocarpy-promoting techniques (genetic modification, hormone application and selective breeding) currently being used commercially, or experimentally, on pollinator-dependent crops in different test environments (no pollination, hand pollination, open pollination).

All techniques significantly increased fruit quantity and quality in 18 pollinator-dependent crop species (not including seed and nut crops as parthenocarpy causes seedlessness). The degree to which plants experienced pollen limitation in the different test environments could not be ascertained, so the absolute effect of parthenocarpy relative to optimal pollination could not be determined.

Parthenocarpy has the potential to lower a crop's demand for pollinators, whilst extending current geographic and climatic ranges of production. Thus growers may wish to use parthenocarpic crop plants, in combination with other environmentally considerate practices, to improve food security and their economic prospects.

- Courgettes require pollination to improve fruit growth and weight, but natural parthenocarpy means that many can reach marketable length without pollination - findings from 2015 and 2016 field seasons

The importance of pollinators to courgettes is demonstrated through a significant reduction in fruit size and weight under **no pollination conditions**. Consequently, percentage fruit set, the size and weight, but not sugar content, of courgettes were significantly increased with pollination. As all sites experienced the same environmental conditions and pollination treatments, the observed reduction in fruit set (for non-pollinated and open pollinated flowers) was due to the absence of pollen. The relatively high fruit set of hand pollinated flowers (98%) suggests that resources (such as nutrient and water availability) were unlikely to be limiting courgette growth and fruit set in Cornwall, and demonstrates the quality and quantity of courgettes under optimal pollination conditions. Unfortunately it was impossible to identify any inter-variety differences in pollinator dependence within courgette as data from this study are only available for one courgette variety.

Nonetheless, it is of industrial and ecological interest that non-pollinated flowers were still able to reach marketable size and shape without any pollination at all. This is due to the natural parthenocarpic tendency of courgettes, previously observed in Tosca (Martínez et al., 2013) and other courgette varieties (Robinson and Reiners, 1999).

- In Cornwall, open pollination levels were high but this is likely to vary spatially and temporally in the landscape - findings from 2015 and 2016 field seasons

The level of open pollination at the study sites in Cornwall was very high, evidenced by no statistical difference in yield (length grown, circumference, and weight) of open- and hand-pollinated crops. Our experiments showed that different sites influenced pollinator abundance and yield, likely due to the spatial and temporal variation in the landscape surrounding each study site. However, yield (length grown, weight and °Brix) of open pollinated courgettes did not decrease with increasing distance into the crop. This is most likely because smaller (than average) field sizes in Cornwall mean that yield measurements were taken at just 50m from the crop edge which might not be far enough from natural or semi-natural habitat (such as hedgerows) to detect differences in pollinators. Nonetheless, this may affect larger fields such as those in Cambridgeshire where the average distances to the centre of field is around 200m (average field size of 16.5 ± 3.1 ha).

High levels of open pollination observed at these study sites are attributed to a high abundance, but not diversity, of pollinators. This highlights that only a few abundant species, rather than high species richness (contrary to a previous study on pumpkins (Hoehn et al., 2008) and watermelons (Kremen et al., 2002)), are able to deliver the pollination requirements for a whole crop (Kleijn et al., 2015; Winfree et al., 2015). Fortunately, these species are generally widespread, resilient to agricultural expansion and can be encouraged through simple conservation measures (Kleijn et al., 2015). These pollinator observations and fruit set experiments also show that *B. terrestris/ B. lucorum* and *A. mellifera* are able to fulfil the pollination requirements of courgette, without squash and gourd bees (belonging to the genera *Peponapis* and *Xenoglossa*) which have previously been regarded as the most important pollinators of Cucurbita crops in North America (Hurd et al., 1974).

- Pollinators contribute approximately £2.7 million to the value of UK courgette production - Calculated from dependency estimates from 2015 and 2016 field seasons

Pollination experiments demonstrate that 41% of courgette fruit set is dependent on natural pollination. Based on one hectare of courgettes being worth over £8,000 to the grower in market value and around 808ha grown, we estimate that pollinators contribute approximately £2.7 million to the total economic value of courgettes in the UK.

Financial Benefits

Based on economic calculations, growers could receive an additional £166 per ha by maximising pollination.

Action Points

- Analyses are still underway so no action points confirmed yet

SCIENCE SECTION

Completed Work

Data Chapter 1

Re-evaluating strategies for pollinator-dependent crops: how useful is parthenocarpy? Taken from (Knapp et al., 2016). Work is in addition to funding objectives.

Introduction

Globally, agricultural land is continuing to expand and agricultural practices continue to intensify to meet rising food demands (Bommarco et al., 2013). It is argued that sustainably maximising agricultural yield requires ecosystem services to be optimised through improved soil quality, water efficiency and management of beneficial insects for pest control and pollination (Bommarco et al., 2013; Tilman et al., 2002). Insect-mediated pollination (the transfer of pollen within or between flowers via an insect) is a key regulating service for many crops and wild plants (Klein et al., 2007; Wilcock and Neiland, 2002). Thus any detrimental impact on pollination services, for example from habitat loss, introduced pests and diseases, and practices associated with intensive agriculture, could have a negative effect on crop yields and farmers' profits (Goulson et al., 2015; Potts et al., 2010; Steffan-Dewenter et al., 2005). Observed losses of pollinator species combined with our dependence on their contribution to food security, has led to a widespread concern that we are facing a 'pollinator crisis' (Steffan-Dewenter *et al*. 2002; Potts *et al*. 2010; although see Ghazoul 2005). However, whilst the plethora of recent reviews and studies on this subject come to similar conclusions that improving habitat and environmental conditions for pollinators will have a positive impact on crop production by increasing the 'supply' of pollinators (wild or managed); none of these studies consider the alternative option of reducing 'demand' for crop pollinators via technological innovation or management of crops. This can lead to a narrow (and potentially out-dated) perspective given that, in the meantime, plant breeders and farmers are finding ways of short-circuiting the need for pollination by developing and using new varieties which can set fruit without pollen vectors (Pandolfini et al., 2009).

The need for insect pollination in crops is usually measured in two ways: 1) **Pollinator dependence** is quantified by comparing the yield of open-or hand-pollinated crops with the yield of crops from which pollinators have been excluded. However, this is often only done for single cultivars in particular environmental conditions; 2) **Pollination deficit** estimates the additional pollination needed to achieve maximum yields in a particular context by comparing open-pollinated with hand-pollinated crops (Vaissière, 2010). This technique has identified pollination deficits in a range of pollinator dependent crop species (See Table S1 in Supporting Information), and is a vital step to evidence the need to implement management interventions to promote pollinator populations. Realistic estimates of the 'value' of insect pollination to global agriculture need to account for not only the variability in pollination deficit that might result from variable pollinator densities and environmental conditions, but also the variability in pollinator dependence between varieties of single crop species, for which there is currently little good evidence (Melathopoulos et al., 2015). In the wider context, discussion and strategies for improving horticultural crop production (in particular) need to incorporate evidence on the variety of options available for increasing fruit and seed set by manipulating pollination systems, and not just assume that the only way to do this is by maximising pollination. To improve estimates of pollinator dependence in crops, and to widen the debate about how to guide farmers in improving seed and fruit production, we present a meta-analysis of studies inducing **parthenocarpy** in horticultural crops.

Parthenocarpy (fruit set in the absence of fertilisation) is a trait which has the potential to make many 'pollinator dependent' species produce fruit without pollination (Vardi et al., 2008). Parthenocarpy is thought to increase fruit quantity as plants are able to set fruit in conditions adverse for fertilisation, for example due to poor pollen maturation or few pollinating species, typically seen in greenhouses or during periods of poor light and cold temperatures (Pandolfini, 2009). Without parthenocarpy, and under these conditions, growers would ordinarily experience high rates of fruit abortion due to an insufficient number of pollen grains delivered to stigmas (Pandolfini, 2009).

Parthenocarpy also has the potential to improve fruit quality as seedlessness (caused by no pollination and therefore fertilisation) can be a desirable trait. This is different to stenospermocarpy, where seedlessness is achieved by seeds being aborted after fertilisation (and therefore pollination) such as with triploid watermelons (Varoquaux et al., 2000). For example, it is thought to extend shelf-life in some species, such as reduced browning in aubergine (Acciarri et al., 2002), is advantageous in fruit processing, such as tinned tomatoes (Pandolfini et al., 2002), and is generally favoured by consumers for convenience in preparation and consumption (Vardi et al., 2008). However, evidence suggests that some parthenocarpic plants may still produce a greater quantity and quality (including higher sugar content (Hayata et al., 2000; Shin et al., 2007)) of fruits when pollinated by insects (Martínez et al., 2013; Nicodemo et al., 2013; Robinson and Reiners, 1999).

Fertilisation of the ovules and seed/ fruit development is co-ordinated by various phytohormones, including auxins, gibberellins, and cytokinins which originate from the developing embryos (Gillaspy et al., 1993). Phytohormones, present in developing seeds are vital for regulating fruit growth and development (Gillaspy et al., 1993). However, in parthenocarpic (and therefore seedless) fruit set, endogenous phytohormones are elevated, suggesting that phytohormones from sources other than developing seeds can regulate fruit growth (Gustafson, 1936). Consequently, parthenocarpy may be initiated through exogenous application of phytohormones. Auxins, gibberellins, and cytokinins or mixtures of these have all been proven to be effective in inducing fruit development in the absence of fertilization and have been shown to increase productivity in various horticultural crops (Reviewed in Pandolfini 2009). However, little is known about the effect of these hormones on the environment and implementation is expensive and labour-intensive (Saito et al., 2009). Consequently, scientists are increasingly finding ways to exploit genetic parthenocarpy.

Traditionally, approaches to genetic parthenocarpy have largely focused on selective breeding programs for seedlessness (reviewed in Vardi *et al*. 2008 and Varoquaux *et al*. 2000). For example, selective breeding of parthenocarpic sweet pepper (Honda et al., 2012; Tiwari et al., 2007), papaya (Rimberia et al., 2007), and summer squash (Kurtar, 2003; Robinson and Reiners, 1999) varieties have all been shown to increase productivity. More recently, scientists have focused on genetic engineering approaches for parthenocarpic fruit set, through modification of auxin synthesis (iaaM), auxin sensitivity (rolB), auxin content (Aucsia), auxin signal transduction (iAA9 or ARF8), and gibberellin signal transduction (DELLA) (reviewed in Pandolfini 2009). For example, the chimeric auxin synthesising DefH9-iaaM gene has been shown to increase productivity in aubergine (Acciarri et al., 2002; Donzella et al., 2000; Rotino et al., 1997), tomato (Molesini et al., 2009; Pandolfini et al., 2002), cucumber (Yin et al., 2006), strawberry (Mezzetti et al., 2004), and raspberry (Mezzetti et al., 2004). Auxin-synthesis parthenocarpy is facultative, meaning that it is seedless in conditions adverse for pollination/ fertilisation and seeded (although much reduced in number (Rotino et al., 2005)) in conditions where pollination occurs (Pandolfini et al., 2009). Breeding for genetic parthenocarpy also has the potential to combine multiple desirable traits. For example, parthenocarpy, female-flowering time, improved fruit quality and disease resistance have been combined in cucumbers (Kushnereva, 2008).

Using parthenocarpy to promote fruit set under unfavourable environmental conditions could improve the quality and quantity of pollinator dependent crops by reducing the number of poorly formed fruits caused by insufficient pollination (Pandolfini, 2009). This could extend current geographic and climatic agricultural ranges of production, simultaneously improving food security and the economic prospects of commercial growers. Methods to induce parthenocarpy should therefore be taken into account when calculating the contribution of pollinators to fruit set, to avoid over-estimating our dependence on them. Klein et al. (2007) provide the most comprehensive review of global crop pollinator dependence, and they acknowledge that their results are often based on studies from single cultivars and/or single regions because of the difficulty of finding comprehensive evidence. However, their data have been used to subsequently estimate the global value of pollination (Breeze et al., 2011; Gallai et al., 2009) and consequently justify the prediction of a ‘pollination crisis’(Potts et al., 2010; Steffan-Dewenter et al., 2005) without substantiated information at the individual crop level, as highlighted by Melathopolous et al. (2015).

In this paper we aim to go beyond previous reviews of parthenocarpy (Gorguet et al., 2005; Pandolfini, 2009; Pandolfini et al., 2009; Vardi et al., 2008; Varoquaux et al., 2000) by using meta-analysis techniques to review and synthesise the literature on the extent of parthenocarpy promoting techniques currently being used commercially or experimentally on pollinator dependent crops across the world. Systematically reviewing plant science literature and applying it to pollination biology provides a broader perspective on the pollinator debate. We specifically investigate the following questions: (1) Does artificial or genetic parthenocarpy increase the quantity and quality of fruits in (normally) pollinator dependent crop species? (2) Which method for conferring parthenocarpy: selective breeding, genetic modification or growth hormones, is most effective for parthenocarpic fruit set?

Materials and Methods

Data Collection

We searched the ISI Web of Science, SCOPUS, Science Direct, Directory of Open Access Journals, AGRICOLA databases, and, Google Scholar, for studies that investigated the effect of genetic and artificial parthenocarpy on the quantity or quality of yield in pollinator dependent crops as defined by Klein et al. (2007), where pollinator dependence is classified as ‘essential’, ‘great’, ‘modest’ or ‘little’ (Table S1). Searches were conducted from 1945 to March 2016 using the search terms: (Parthenocarp*) AND (genetic mod* OR GM OR genetic* engineer* OR chimeric gene* OR selective breed* OR artificial selection OR hormone) AND (yield OR weight OR Brix). To avoid possible publication bias, patents were included and authors were emailed for relevant reports and unpublished studies (Koricheva et al., 2013).

Studies were included that met all the following criteria: (1) They were a pollinator dependent horticultural crop species; (2) presented an effect of induced parthenocarpy on yield; (3) reported the sample size; (4) reported the mean, and if possible, the standard deviation for each treatment (for independent categorical variables). Methods to induce parthenocarpy were selective breeding or genetic modification (genetic parthenocarpy), or application of growth hormones (artificial parthenocarpy). Each intervention was compared to its own (negative) control. So, selective breeding compared parthenocarpic varieties with non-parthenocarpic varieties (SB), growth hormones compared application with no application (HA), and genetic modification compared modified with non-modified plants (GM). Effectiveness was measured in terms of crop quantity (e.g. weight per plant, or yield) and quality in terms of sugar content (e.g. ° Brix where one degree Brix is 1 gram of sucrose in 100 grams of nectar).

Authors of the original studies quantified the effect of parthenocarpy (i.e. compared parthenocarpic treatment with non-parthenocarpic control) within different 'test environments' which can be broadly classified into hand pollination (this includes one example of experimental flowers being 'selfed', i.e. fertilised by pollen from the same plant (Molesini et al., 2009)) (hereafter, HP), no pollination, (hereafter, NP), or open pollination (hereafter, OP). In both OP and HP conditions only pollen from plants of the same genetic material were used. Conditions for which the plants were open pollinated vary between studies, from glasshouses supplemented with *Bombus terrestris* colonies to 'open field' conditions. The ecological complexity, i.e. availability of pollinators at these 'open fields' was not provided. These test environments thus have differing background levels of potential pollination, and were therefore included as a fixed effect in the analysis. The reasons for this were twofold: (1) to see if NP conditions resulted in larger effect sizes (due to non-parthenocarpic controls setting no fruit) and likewise smaller effect sizes in OP and HP conditions for the opposite reason (due to non-parthenocarpic controls setting fruit), and (2) to ensure that test environment did not influence treatment effectiveness. For OP and HP conditions to be included in the meta-analysis, authors had to evidence parthenocarpic fruit set through either a much reduced number of seeds or that fruit set occurred in conditions adverse for pollinators (Pandolfini, 2009).

Calculation of Effect Sizes

Within individual studies different plant species, varieties and pure bred lines may be tested to determine which one has the best parthenocarpic potential for industrial development. Therefore, each genetic line was considered to be independent and thus included as separate cases in the dataset. As a result, many studies contributed more than one entry to the dataset. If a study examined multiple years or more than one treatment level of hormone concentration, then the largest sample size, or in cases with equal sample sizes the treatment level with the greatest effect, was selected.

Hedges' *d* was used as a measure of effect size in our meta-analysis. This measure is not affected by unequal sample sizes and includes a correction factor for small sample sizes (Koricheva et al., 2013). Hedges' *d* was calculated for each treatment-control pair in the dataset (see Table S2), based on the mean, standard deviation and sample size using the ‘metafor’ R package (Viechtbauer, 2010).

We used bootstrapped analyses to fill in missing standard deviations (22 quantity samples and 4 quality samples), using 1000 resampled data sets following 'hot deck' imputation, outlined in Koricheva et al. (2013). We also include Forest plots showing effect sizes using only complete data (without bootstrapping) in Figures S1- S3.

Meta-analyses

Within a single attempt at inducing parthenocarpy, for example with multiple concentrations of hormones, the concentration which resulted in the greatest effect size (measured by hedges’ *d*) was selected. This was done to be representative of how these experimental studies would inform industry, i.e. only the best lines and methods would be put forward for development.

All effect sizes were normalised for their positive skew using a real-solution cube-root transform (following Tukey’s ladder of powers). To assess the importance of parthenocarpy-inducing methods on crop quality and quantity, one sample two-tailed t-tests were used. The relative effectiveness of parthenocarpy-inducing methods and the effect of different test environments were investigated with analysis of variance (ANOVA). Possible interactions between these two effects were investigated with generalised linear models, using backward stepwise model selection (Crawley, 2012).

Results

Following a key word search of the literature, 161 studies investigated the effect of parthenocarpy in 33 pollinator dependent crop species. Of these, 35 did not supply full-text, 8 were not in English, and 78 used a study design unsuitable for inclusion (Table S1). The remaining database included 184 effect sizes from 40 studies. Following our selection of the most effective treatments from each experiment (to reflect those which would be taken forward for development) our final sample size was 69 effect sizes (29 for genetic modification, 31 for hormone application, and 9 for selective breeding) (Table S2).These techniques had been used experimentally and/ or commercially on 18 pollinator dependent crop species, of which 3 have an ‘essential’ need, 6 have a ‘great’ need, 3 have a ‘modest’ need, and 3 have a ‘little’ need for insect-mediated pollination (3 pollinator dependent species were unclassified) (Klein et al., 2007). Tomato was the most commonly studied species (16 studies), followed by aubergine (4 studies) and sweet pepper (3 studies). There was a notable absence of seed and nut crops; this was to be expected given that parthenocarpy causes seedlessness, an undesirable trait in these species. Likewise, an additional 14 pollinator dependent species showed no evidence of experimental or commercial parthenocarpy in the literature (Table S1).

All methods to induce parthenocarpy significantly increased fruit quantity (t_{50} = 8.41, p < 0.001) (Fig. 1a) and quality (t_{17} = 3.57, p = 0.002) (Fig.1b). However, there were no significant differences in the effectiveness of genetic modification, selective breeding, or hormone application for increasing fruit quantity (F_{48} = 0.41, p = 0.666) or quality (F_{16} = 0.86, p = 0.367) (Fig. 2). Test environment was shown to influence how effective treatments were on fruit quantity (F_{48} = 8.35, p < 0.001, with 'no pollination' environments having the largest effect size (Fig. 3). However, test environment did not influence the effectiveness of parthenocarpy-inducing methods on fruit quality (F_{15} = 0.391, p = 0.683). Notably, there was no interactions between treatments and test environment (F_{43} = 1.63, p = 0.197), showing that the influence of test environments on treatment effectiveness was not biased against any particular parthenocarpy-inducing method.

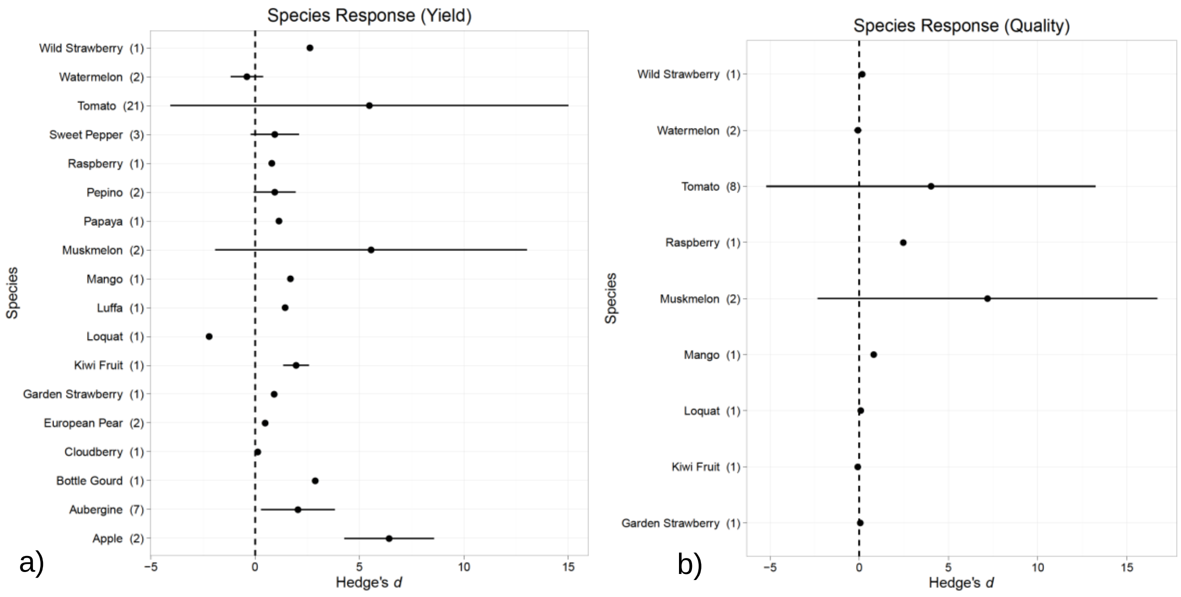

Figure 1. Mean effect sizes for all methods combined to induce parthenocarpy (genetic modification, hormone application, and selective breeding) split by crop species (y axis) for (a) fruit quantity (b) fruit quality. Error bars represent standard deviations. Sample size (number of effect sizes) are given in parentheses.

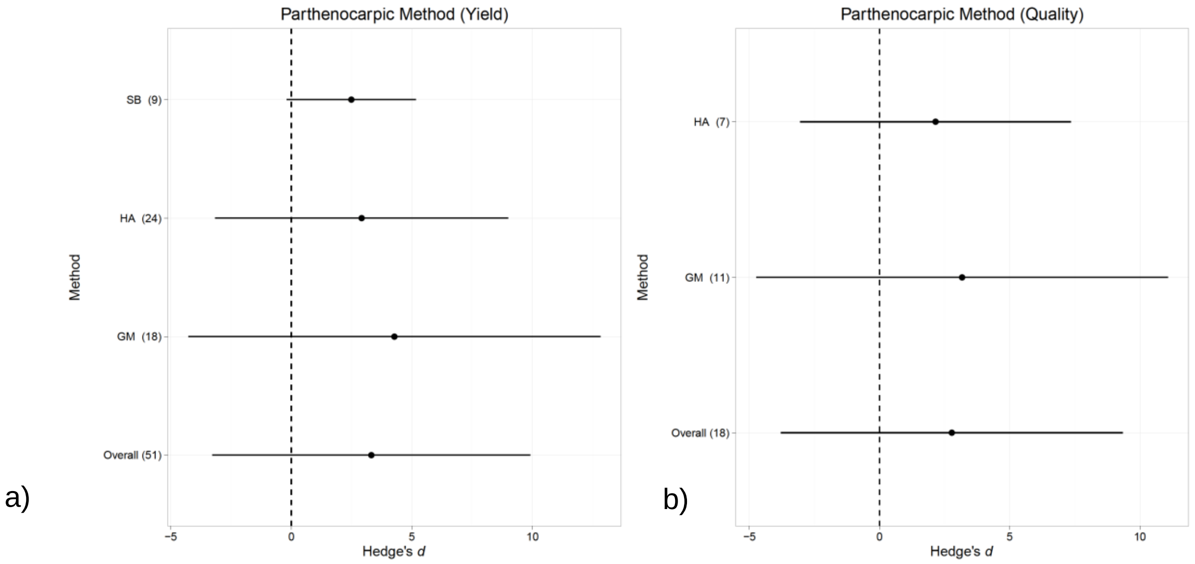

Figure 2. Overall mean effect sizes and effect sizes of methods to induce parthenocarpy (genetic modification (GM), hormone application (HA), selective breeding (SB)) (y axis) for (a) fruit quantity and (b) quality for all crop species. Error bars represent standard deviations. Sample size (number of effect sizes) are given in parentheses.

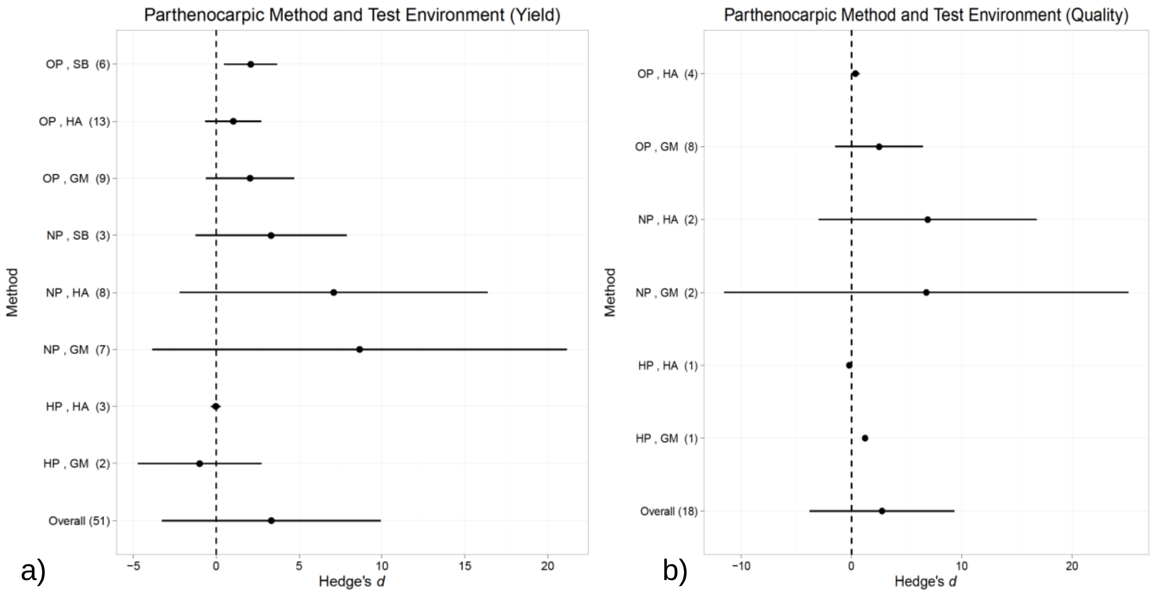

Figure 3. Overall mean effect sizes and effect sizes of methods to induce parthenocarpy (genetic modification (GM), hormone application (HA), selective breeding (SB)) and test environment (NP, OP, and HP) (y axis) for (a) fruit quantity (b) fruit quality for all crop species. Error bars represent standard deviations. Sample size (number of effect sizes) are given in parentheses.

Discussion

Artificial and genetic parthenocarpy have proven to be successful at increasing fruit quantity (Fig. 1a), without negatively affecting quality in all crop species studied (Fig. 1b). This is vitally important for commercial acceptance of parthenocarpy as it is only valuable to growers if there are no adverse effects on fruit quality. For example, damaging normal vegetative growth (other than a reduced number of seeds), or a reduction in sugar and nutritional content (Pandolfini, 2009). In this study °Brix was used as a measure of quality as this was the only metric consistently recorded in studies.

The most studied method for inducing parthenocarpy is hormone application, which was shown to positively increase crop quantity and quality (Fig. 2a, 2b). This method is currently the most widely used by commercial growers, and although usually used prophylactically could be a very good temporary practice for periods of unfavourable environmental conditions.

Selective breeding (creating F1 hybrids) could provide a longer-term solution for inducing parthenocarpy, which despite being investigated in fewer studies, still proved very successful at increasing yield (Fig. 2a, 2b). This complements yield trials not included in this meta-analysis (see Table S1) which have found evidence of genetic parthenocarpy in pollinator dependent species. For example, 66 per cent of sweet pepper varieties (Honda *et al*. 2012) and 33 per cent of squash varieties examined (Robinson and Reiners 1999) were found to set parthenocarpic fruit. Although an effective method, selective breeding has its limitations. Principally, that crop species can only be crossed with ones that they can sexually reproduce with, and undesirable traits may be inherited alongside desirable ones during crossing. Likewise, selective breeding of varieties is expensive and time consuming, with varieties taking 5-10 years to be released (De Vries et al., 1997). This is because pure lines need to be maintained over many years to ensure their quality, and hybridisation of pure lines often needs to be done by hand. Likewise, seeds grown from F1 hybrids often produce inferior yields to parental crops and consequently growers will need to purchase new F1 seeds each year (Tripp, 1994).

Genetic modification for parthenocarpy could speed up this process by removing the need for back crossing and has been shown to be the most effective method in this meta-analysis (Fig. 2a, 2b). This is supported by Donzella et al. (2000) who showed genetic modification to be more effective than hormone spraying at increasing yield. The authors concluded that genetic modification enabled a 10 per cent reduction in production costs (less labour needed for the hormonal sprays) and increased profit from improved quality following the genetic modification. Interestingly genetic modification in strawberry and raspberry (Mezzetti et al., 2004), and tomato (García-Hurtado et al., 2012; Medina et al., 2013) has been shown to increase the number of flowers per plant, demonstrating the role that phytohormones also play in fecundity. Therefore, yield per plant may be greater than yield per fruit. Genetic methods could also use alternative methods of genetic engineering such as cisgenesis. This could increase the likelihood of regulatory and consumer acceptance by transferring genes between organisms that could otherwise be conventionally bred (Telem et al., 2013; Tester and Langridge, 2010).

The range of effect sizes observed in this study (Fig. 2a, 2b) demonstrates the negative effects that unsuccessful parthenocarpy attempts can have on yield, alongside the highly positive effects that successful parthenocarpic treatments can have, for example those shown in tomato and muskmelon (Fig 1a, 1b). The variation in the strength of these responses is primarily due to species-specific responses to growth hormones (both applied and genetically modified). For example, if the expression of auxin coding transgenes (in genetically modified) or auxin concentration (from hormone application) is too high, then fruit may appear malformed, particularly in auxin sensitive species (Gorguet *et al*. 2005; Gemici *et al*. 2006). Likewise relationships between different phytohormones are complex and vary greatly depending on species. This demonstrates the need for continued, multi-treatment experiments to test the most effective strengths and types of hormones, tailored to individual crop species.

Investigating fruit quality and quantity in different test environments can allow us to assess how useful parthenocarpy could be in the total absence of pollination and fertilisation. In the example of genetically modified aubergine, Acciarri et al. (2002) found a 30 to 35 per cent increase in productivity, without any effect on quality under both greenhouse and open field conditions. In both test environments the fruit was always seedless therefore, positively influencing fruit quality and the economic value of production. Larger effect sizes in no pollination conditions (Fig. 3a, 3b), demonstrate the greater effect that parthenocarpy will have in conditions where fruit set would ordinarily be very low. Consequently in conditions where hand pollination is required for improved fruit set, artificial and genetic parthenocarpy could be a cost effective alternative (Allsopp et al., 2008; Niu et al., 2015). Conversely effect sizes tend to be smaller in open and hand pollinated environments where pollen is available (Fig. 3a, 3b). This is likely to be because in these conditions the non-parthenocarpic controls are successfully pollinated to some extent. However, in all test environments plants may have experienced some pollination deficit (i.e. if plants were selfed, pollinated from just one donor plant, or if experiments were conducted in areas with low pollinator abundance). It is not possible to ascertain the degree of pollination deficit in the HP and OP test environments, and to what extent these limitations represent real world growing conditions. So, these results may over-estimate the effect of parthenocarpy compared to yield resulting from open pollination in an environment where pollinators are not limiting, and natural pollination is thus optimal.

Nonetheless, parthenocarpy could still be useful in open pollination environments, where it can minimise the potential for pollination deficits whilst improving fruit uniformity caused by stochastic poor pollination (Pandolfini, 2009). Therefore, parthenocarpy could be advantageous to all crops, whether or not they are experiencing a pollination deficit. In return, these parthenocarpic crops can continue to provide valuable nectar and pollen resources for our wild and managed bees, and other flower-visiting insects. However, there is no information available as to how the quality and quantity of nectar and pollen varies between parthenocarpic and non-parthenocarpic plants, or how selective breeding for parthenocarpy will affect a plant's nectar and pollen production over time. It is also worth remembering that parthenocarpic fruit set and therefore seedlessness is not always desirable, such as crop species where seeds are the edible part and for creating of seed stock.

Incomplete routes of communication between the plant breeding industry, ecologists, and apiculturists have resulted in a mixed and potentially inaccurate message about the extent of our dependence on pollinators for food production (Ghazoul, 2005; Kleijn et al., 2015; Melathopoulos et al., 2015). Studies which value the contribution of insects to pollination are based on pollinator dependence, i.e. the extent that a plant depends on pollinators for fruit set. However, this metric assumes that dependence is constant within a single crop (Gallai et al., 2009; Klein et al., 2007). In reality pollinator dependence is strongly dependent on variety, the spatial and temporal context of the surrounding landscape, and the responses of farmers, consumers and technological innovation to pollinator decline. Therefore, we highlight that there may be over-estimation of pollinator dependence if studies overlook research and development currently underway to reduce the need for pollination. We found evidence for studies inducing parthenocarpy in four out of 13 of the global crops for which pollination is considered essential (according to Klein *et al*. 2007); and 13 out of 30 of the crops for which the need for pollination is considered great. This indicates that research into reducing *demand* for pollination has occurred in 40% of the crops for which ecologists are currently primarily only advocating an increase in *supply* of pollinators as the solution to improving crop yields and quality (Carvalheiro et al., 2013; Garibaldi et al., 2011). Indeed there are three crop species in the top twenty crops for global production (Mt/yr in Klein *et al*. 2007) which benefit from insect pollination and appear in this meta-analysis of parthenocarpy studies (tomato #12; watermelon #15; apple #19). It is not surprising that, if a crop is showing a yield deficit, then different routes are explored to solve the problem; but it is surprising that evidence of the effectiveness of different approaches is not brought together more comprehensively to build an accurate picture for a crop. Single successes presented in this meta-analysis could lead to profound changes in production of certain crops, for example nearly all bananas on the global market are of the Cavendish variety, selectively bred to be parthenocarpic.

Data are not currently available to assess variety choice by farmers, or the level of parthenocarpy in the varieties that they choose. The results of this meta-analysis support the conclusions of Klein et al. (2007) and Melathopoulos et al. (2015) that to get a more complete picture, varietal information is required – both in terms of pollinator dependence, but also in terms of choices that farmers are making.

Synthesis and Applications

Parthenocarpy may be able to reduce the need for pollinators in many horticultural crops but should not be used as a panacea for agricultural success. Biodiversity decline in agricultural landscapes is often an indicator of poor ecosystem health, which can also cause poor fruit set. Thus agricultural growers should carefully consider causes of poor fruit set and ideally use parthenocarpic species (which can still provide an important nectar and pollen source for pollinator species) in addition to other environmentally considerate practices. Likewise, parthenocarpy could further the pollinator crisis by removing the imperative for conserving pollinators as our ‘dependence’ on them is reduced (Brown *et al.* 2016). This could affect pollination of non-parthenocarpic pollinator dependent crops as well as wild plants. Ultimately, widespread implementation of these practices will be limited to countries that have access to, and can afford skilled personnel and equipment. Thus free communication of resources and capabilities from developers to users is essential for the benefits of parthenocarpy to reach the areas of the world that are most in need of its benefits.

This study shows that genetic and artificial parthenocarpy has a great potential to improve fruit quantity, without affecting quality in a range of horticultural crops. Potentially the most promising method for inducing parthenocarpy is genetic modification; the most effective for increasing fruit quality and quantity, whilst being the quickest to implement. However, whilst acceptance for genetic modification, particularly in Europe, remains equivocal, selective breeding may be a more attainable way for achieving genetic parthenocarpy. This method is also relatively cost-effective for many horticultural growers already growing hybrid varieties. Although currently a popular choice, hormone application remains an expensive and un-sustainable option for many horticultural growers. Nonetheless, any additional costs for agricultural growers associated with implementing genetic and artificial parthenocarpy could be offset by increasing the quality and quantity of crops. Unfortunately, no studies have directly compared the cost of parthenocarpy to traditional methods of supplemented pollination, such as introduced honeybee hives and hand pollination. Climate change could also increase pressure to develop parthenocarpic crop species as changes in pollinator distributions or declines in their populations are likely to be detrimental to food production (Kerr et al., 2015). Thus parthenocarpic crop plants could allow producers to extend their growing seasons in otherwise adverse climatic and environmental conditions, furthering their economic advantage, increasing agricultural resilience, and improving food security.

Work in Progress

Data chapter 2

Courgette production: pollination demand, supply, and value

- Submitted to a scientific journal. Further details will be circulated in the final report.

Agricultural **intensification is thought** to be a primary driver in reported declines of wild bee populations. Crop producers often assume that introducing managed pollinator species will enhance natural pollination levels and fulfil their pollination needs. However, this is often done irrespective of wild pollinator species richness or assessment of available food and nesting sites which may support their populations. Over two years, pollination experiments were carried out in Cornwall, UK, to explore pollinator dependence (the crop's 'demand' for pollinators) and pollination deficit (the 'supply' of pollinators relative to maximal pollination) in courgette (*Cucurbita pepo*).

In 2015 and 2016 fruits were harvested 10 days post-anthesis, weighed, measured (length and circumference (circumference only in 2015)), and their sugar content (°Brix) recorded (only in 2016). Experimental fruits were classed as 'aborted' if they did not meet minimum commercial standards (Ellis Luckhurst, personal communication 24th June 2015), i.e. they were less than 14 cm long, 30 mm wide (at the mid-point), and over 5° in curvature, or showed any obvious signs of bacterial damage, such as blossom end rot.

Open pollination resulted in high fruit set, and there was a surprisingly low pollination deficit. The high economic value of courgettes means that pollinators contribute approximately £2.8 million to the total value of UK courgette production, which under maximal pollination could earn growers an additional £166 per Ha. However, spatial and temporal fluctuations in pollinator populations mean that this monetary value is likely an under-estimate (as open pollination in Cornwall was high) hence it may still be beneficial for growers to improve pollination services.

Interestingly, over half of fruit was able to reach marketable size and shape without any pollination. This parthenocarpic trait (the ability to set fruit without fertilisation) can increase yield in conditions usually adverse for pollination - potentially extending current geographic and climatic ranges of production. Understanding a crop's requirement for pollinators can aid growers in their decision making about what varieties and sites should be used. In areas with lower visitation rates, growers may wish to increase their pollination services (via pollinator-supportive land management or managed bees), or use parthenocarpic varieties. In doing so they may increase their agricultural resilience and further their economic advantage.

Data chapter 3

‘Influence of semi-natural habitat, field size, and pollinator species diversity and abundance for predicting courgette yield’ - Updated objectives 5 and 6

- Fieldwork is complete. Identification of solitary bee species is currently underway, with plans to have the work submitted to a scientific journal in spring 2017. Further details will be circulated in the final report.

Increasing the abundance and diversity of flowering plants can increase the availability of food and nesting sites which are vital for maintaining healthy bee populations (Roulston and Goodell, 2011). At a farm scale, floral resources can be increased by planting wild flower strips, allowing areas to be naturally colonised by wild flowers, and by maintaining hedgerows. If correctly managed these practices will provide resources for different pollinator species in space and time (beyond the focal crop) (Carvell et al., 2015, 2007). However, the effectiveness of pollinator-supportive practices are often variable and greatly depend on the complexity of the habitat surrounding a crop field (Batáry et al., 2011; Heard et al., 2007), with more simplistic landscapes showing greater yield increases than ones which already have good floral resources. This is because, at a landscape scale, evidence suggests that proximity to, or quantity of (semi-) natural habitat can increase pollinator populations in the focal crop as they spill-over from natural habitats (Garibaldi et al., 2011; Kremen et al., 2004; Petersen and Nault, 2014).

This study explores the relative importance of pollinators, floral resources (for determining their populations (at a farm and landscape scale)), and other environmental factors important for determining fruit set, such as, prevailing weather conditions, nutrient availability and farming practices, to provide a novel exploration of interactions between different ecosystem processes required for successful fruit set.

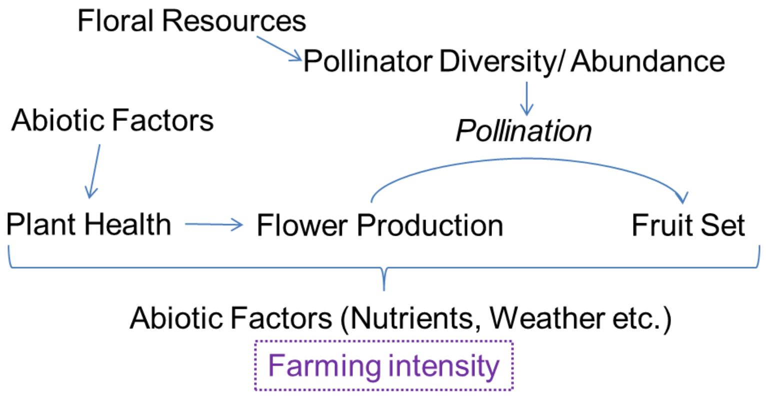

Figure 4. Concept of data chapter 3

Nine different sites (minimum distance of 3 km apart (to avoid the same pollinators being recorded at multiple sites)) were selected in three geographic regions: Cornwall, Worcester and Cambridgeshire to represent courgette production across England. All growers grew *C. pepo*, var. Tosca and were asked to complete a questionnaire regarding land use at each site. Species richness of pollinators and flowers were assessed using timed transects and pan traps (pollinators only) in the margin and production area of each field. Pollinators, flowers and soil nutrients were recorded three times within a growing season (beginning, middle, and end) whilst rainfall and temperature were averaged from daily observations recorded by a local weather station. Quantity of (semi-) natural habitat and mass flowering crops within a 1km radius of each site were calculated from maps produced by the Centre for Ecology and Hydrology (2016). All yield data was provided by growers and was calculated as the quantity of marketable fruits (kg) picked per Ha at the end of the season.

Knowledge and Technology Transfer

- Presented a poster at the AHDB Student Conference 2015 and 2016
- Presented a poster at the Royal Entomological Society Annual Conference
- Presented my work to the Outdoor Cucurbit Growers Group event at NIAB, Cambridge 2015
- Presented my work to the Penryn Campus bioscience department
- Co-produced two lesson packs on ecology and land management which included lesson plans, PowerPoint presentations, extension worksheets, a bespoke board game, short film, and a structured town hall style debate with props.

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Appendices from Knapp et al., (2016)

Table S1 Pollinator dependent crops, as defined by Klein et al. (2007) and studies (identified by the key word search) which investigate methods to induce parthenocarpy.

Crop species with no references demonstrate current areas where parthenocarpy has not been used commercially or experimentally. References in bold are included in the meta-analysis, references in black were identified in the systematic review but not included in the meta-analysis (i.e. they did not fulfil all of the search requirements), and references in blue only had an abstract available.

Species were pollinator dependent if animal pollination was shown to increase production (fruit set, fruit weight and/or quality, seed number and/or seed quality, and/or increased pollen deposition (an indirect measure)) for at least one variety per crop (Klein et al., 2007). Only crop species with essential, great, modest, and/or little dependence on pollinators were included in analyses. Essential = pollinators essential for most varieties (production reduction by ≥ 90% comparing experiments with and without animal pollinators. Great = great production increase/ animal pollinators are strongly needed (40 - <90 % reduction). Modest = modest production increase/ animal pollinators are clearly beneficial (10 -<40 % reduction) (Klein et al., 2007).

Seed and nut crops are absent from this table as parthenocarpy (therefore, seedlessness) would not be a desired trait. Entries are alphabetically ordered by genus.

		From Klein et al 2007		Studies which promote the effect of parthenocarpy on yield identified found from the systematic review of the literature. Studies in bold were included in the meta-analysis.		
Crop species	**Crop name**	**Requirement for animal pollination**	**Rank# in list of top global crops Mt/yr**	**Selective breeding**	**Genetic engineering**	**Growth hormones**
Abelmoschus esculentus	Okra	modest	#56			
Actinidia deliciosa	Kiwifruit	essential				**Iwahori *et al.* 1988** Ohara et al. 1997
Annona squamosa	Atemoya, Cherimoya, Custard apple	essential			Lora *et al.* 2011	
Asimina triloba	Pawpaw, Indiana banana	essential				
Averrhoa carambola	Carambola, Starfruit	great				

Capsicum annum, C. frutescens	Chilli pepper, Red pepper, Bell pepper, Green pepper, Allspice, Pimento	little	#33	Carrizo 2011 Honda *et al.* 2012 **Tiwari *et al.* 2007**		Balakbir *et al.* 1998 Gustafson 1936 Heuvelink & Korner 2001 Thanopoulos *et al.* 2013 **Tiwari *et al.* 2012** **Wien & Zhang 1991**
Carica papaya	Papaya	little	**#52**	**Rimberia *et al.* 2007**		
Citrullus lanatus	Watermelon	essential	#15			**Hayata *et al.* 1995** Huitrón *et al.* 2007 Kwon *et al.* 2006 **Maroto *et al.* 2005** Sedgley *et al.* 1977 Hayata et al. 1994 Hikosaka et al. 2015 Newbury et al. 1977 Pak 1993 Miguel et al.2000

Citrus spp. *parthenocarpy listed as one of breeding mechanisms	Bergamont, Chinotto, Citron, Clementine, Grapefruit, Kumquat, Lemmon, Lime, Manderine, Orange, Pomelo, Tangerine	little	#13	Mesejo *et al.* 2013		García-Martínez & García-Papí 1979 Guardiola *et al.* 1993 Talon et al. 1992
Cucumis melo	Cantaloupe, Melon	essential	#29			**Hayata *et al.* 2000** Risser 1976 Masuda 1990
Cucumis sativus	Cucumber, Gherkin	great	#24	Kushnereva 2008 Li *et al.* 2014 Shaw *et al.* 2007 Sun *et al.* 2006 Yan *et al.* 2012 Dean et al. 1983 Dennijs et al. 1991	Yin *et al.* 2006	Fu *et al.* 2008 Hikosaka & Sugiyama 2015 Kim *et al.* 1992 Shin *et al.* 2007

Cucurbita maxima, C. mixta, C. moschata, C. pepo	Pumpkin, Squash, Gourd, Marrow, Courgette	essential	#36	Kurtar 2003 Martínez *et al.* 2014 Nogueira *et al.* 2011 Robinson & Reiners 1999		Martínez *et al.* 2013 Yu 1999
Durio zibethinus	Durian	great				
Eriobotrya japonica	Loquat, Japanese plum, Japanese mediar	great			Tao et al. 2015	(Mesejo et al., 2010) Ding 1988
Fagopyrum esculentum	Buckwheat	great				
Feijoa sellowania	Feijoa	great				
Ficus carica	Fig	modest				Blondeau and Crane 1949 Crane 1964 Crane et al. 1948
Fragaria spp.	Strawberry	modest			(Mezzetti et al., 2004)	Mudge et al. 1981

Lagenaria siceraria	Bottle gourd	Not in Klein et al. 2007				(Yu, 1999)
Luffa acutangula	Luffa	Not in Klein et al. 2007				(Bisaria, 1977)
Malus domestica *parthenocarpy listed as one of breeding mechanisms	Apple	great	#19	(Watanabe et al., 2008)	(Yao et al., 2001)	(Watanabe et al., 2008) Bangerth 1994 Bangerth et al. 1994 Bukovac 1963 Goldwin et al Goldwin et al 1989 Greene 1980 Williams 1980 Luckwill 1960
Mangifera indica	Mango	great	#30		(Ogata et al., 2010)	Ogata 2009 Perez-Barraza et al. 2015
Manilkara zapota	Sapodilla	essential				

Passiflora edulis	Passionfruit	essential				
Persea americana	Avocado	great				
Prunus armeniaca	Apricot	great				Crane et al. 1960
Prunus avium	Sweet cherry	great				Crane et al. 1960
Prunus cerasus	Sour cherry	great				Crane et al. 1960
Prunus domestica, P. spinosa	Plum, Greengage, Mirabelle, Sloe	great	#48			Crane et al. 1960 Hartmann 1984 Jackson 1968
Prunus persica	Peach, Nectarine	great	#42			Crane et al. 1960
Psidium guajava	Guava, Guayaba	modest				
Punica granatum	Pomegranate	modest				

Pyrus communis	Pear	great	#37	(Nishitani et al., 2012)		(Lafer, 2008) (Niu et al., 2015) (Yarushnykov and Blanke, 2005) (Zhang et al., 2008) Luckwill 1960 Yamada et al. 1991
Ribes nigrum, R. rubrum,	Black currant, Red currant	modest				
Rosa spp.	Rose hips, Dogroses	great				
Rubus ideaus, R. fruiticosus, R. chamaemorus, R. flagellaris, R. trivalis	Raspberry, Blackberry, Cloudberry, Northern Drewberry, Southern Drewberry	great			(Mezzetti et al., 2004)	(Junttila et al., 2002)

Solanum lycopersicum *parthenocarpy listed as one of breeding mechanisms	Tomato	little	#12	(Baggett et al., 1997) (Charbeonboonsit et al., 1985) (Costa et al., 1992) (Dutta et al., 2013) (Fos et al., 2003) (Gorguet et al., 2005) (Habashy et al., 2004) (Mazzucato et al., 1998) (Mohamed, 1998) Philouze et al. 1986 Sugahara et al. 2002 Tang et al. 2015	(Barg and Salts, 2000) (Carmi et al., 2003) (Carrera et al., 2012) (Ficcadenti et al., 1999) **García-Hurtado *et al.* 2012** Goetz *et al.* 2007 Ingrosso *et al.* 2011 Marti *et al.* 2007 **Medina *et al.* 2013** **Molesini *et al.* 2009** Pandolfini *et al.* 2002 **Rotino *et al.* 2005** Schijlen *et al.* 2007 **Shabtai *et al.* 2007**	Fos *et al.* 2003 **Gemici *et al.* 2006** **Goetz *et al.* 2007** Gustafson 1936 **Karapanos *et al.* 2013** **Nandwani *et al.* 2014** **Ramin 2003** Rounis *et al.* 2015 **Serrani *et al.* 2008** Aguero et al. 2007 Alabadi et al. 1996 Alabadi et al. 1998 Ampomah-Dwamena et al. 2002 Bunger-Kibler et al. 1982 Costa et al 1985 El-Habbasha et al.1999

						Gorecka et al. 1987 Gustafson 1960 Mapelli et al. 1987 Mariotti et al. 2011 Matsuo et al, 2012 Mazzucato et al. 1999 Mignolli et al. 2012 Shinozaki et al. 2015 Sjut 1982 Sjut 1984 varga et al 1986 Gelmesa et al. 2013
Solanum melongena	Aubergine	modest	#27	Kikuchi *et al.* 2008 Mori *et al.* 2013 **Saito *et al.* 2009** Boyaci 2009 Takeshi et al. 2010	**Acciarri *et al.* 2002** **Donzella *et al.* 2000** **Rotino *et al.* 1997**	Boyaci *et al.* 2011 Gustafson 1936 Sarma et al. 1997 Sidhu 2007

Solanum muricatum	Pepino dulce, Sweet cucumber	Not in Klein et al. 2007		Nuez et al. 1998 Prohens et al. 2002 Prophens and Nuez 2000 Rodriguez-Burruezo et al 2011		**Ercan & Akilli 1996** Maroto *et al.* 1997
Solanum quitoense	Naranjillo	great				
Sorbus aucuparia	Rowanberry	essential				
Vaccinium corymbosum, V. angustifolium, V. ashei, V. myrtillus	Highbrush blueberry, Lowbrush blueberry, Rabbiteye blueberry, Bilberry	great				Junttila et al. 2002
Vaccinium macrocarpon, V. oxycoccus	American cranberry, European cranberry	great				Devlin & Demoranville 1967

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Table S2 Final dataset used in the meta-analysis, alphabetically ordered by genus

Species	**Method to induce Parthen-ocarpy**	**Test environment**	**Measure**	**Effect Size**	**Variance**
Actinidia chinensis	HA	NP conditions	Sugars	-0.082	0.021109
Actinidia chinensis	HA	NP conditions	Yield	1.996201	0.245295
Capsicum annuum	SB	OP conditions	Yield	1.836082	0.028712
Capsicum annuum	HA	NP conditions	Yield	1.33715	0.005758
Capsicum annuum	HA	HP conditions	Yield	-0.34255	0.012835
Carica papaya	SB	OP conditions	Yield	1.136643	0.003864
Citrullus lanatus	HA	HP conditions	Sugars	-0.20544	0.006123
Citrullus lanatus	HA	HP conditions	Yield	0.155029	0.006113
Citrullus lanatus	HA	OP conditions	Sugars	0.051341	0.021092
Citrullus lanatus	HA	OP conditions	Yield	-0.92558	0.007337
Cucumis melo	HA	NP conditions	Sugars	13.91252	0.159346
Cucumis melo	HA	NP conditions	Yield	10.83453	0.099127
Cucumis melo	HA	OP conditions	Sugars	0.460481	0.006492
Cucumis melo	HA	OP conditions	Yield	0.275551	0.006385
Eriobotrya japonica	HA	OP conditions	Sugars	0.086106	0.001266
Eriobotrya japonica	HA	OP conditions	Yield	-2.20575	0.002034
Fragaria ananassa	GM	OP conditions	Sugars	0.057971	0.002531
Fragaria ananassa	GM	OP conditions	Yield	0.91286	0.001397
Fragaria vesca	GM	OP conditions	Sugars	0.164231	0.006346
Fragaria vesca	GM	OP conditions	Yield	2.621295	0.003919
Lagenaria siceraria	HA	NP conditions	Yield	2.876362	0.003216
Luffa acutangula	HA	OP conditions	Yield	1.4368	0.007957
Malus pumila	HA	NP conditions	Yield	4.924251	0.012747
Malus pumila	SB	NP conditions	Yield	7.911708	3.269794
Mangifera indica	HA	OP conditions	Sugars	0.81371	0.006848
Mangifera indica	HA	OP conditions	Yield	1.687746	0.008576
Pyrus communis	HA	OP conditions	Yield	0.582146	0.001236
Pyrus communis	HA	OP conditions	Yield	0.393657	0.001201
Rubus chamaemorus	HA	HP conditions	Yield	0.121166	0.004547
Rubus idaeus	GM	OP conditions	Sugars	2.470727	0.005575
Rubus idaeus	GM	OP conditions	Yield	0.798029	0.001707

Solanum lycopersicum	SB	OP conditions	Yield	5.113391	0.003374
Solanum lycopersicum	GM	OP conditions	Sugars	0.440201	0.006922
Solanum lycopersicum	GM	OP conditions	Yield	0.605605	0.007052
Solanum lycopersicum	GM	HP conditions	Sugars	1.283145	0.005336
Solanum lycopersicum	GM	HP conditions	Yield	1.650157	0.006492
Solanum lycopersicum	GM	NP conditions	Sugars	15.43655	131.9856
Solanum lycopersicum	GM	NP conditions	Yield	10.62201	12.64204
Solanum lycopersicum	HA	NP conditions	Yield	3.61653	0.015346
Solanum lycopersicum	SB	NP conditions	Yield	3.204817	0.013882
Solanum lycopersicum	GM	OP conditions	Sugars	1.425102	0.01586
Solanum lycopersicum	GM	OP conditions	Yield	1.991905	0.009461
Solanum lycopersicum	GM	OP conditions	Sugars	3.43146	0.031267
Solanum lycopersicum	GM	OP conditions	Yield	1.070159	0.00723
Solanum lycopersicum	HA	OP conditions	Yield	1.336772	0.007737
Solanum lycopersicum	GM	NP conditions	Yield	2.094612	0.001646
Solanum lycopersicum	SB	OP conditions	Yield	0.484457	0.004744
Solanum lycopersicum	HA	OP conditions	Yield	3.244583	0.185242
Solanum lycopersicum	GM	OP conditions	Sugars	11.85771	0.234966
Solanum lycopersicum	GM	OP conditions	Yield	8.835926	0.136094
Solanum lycopersicum	GM	HP conditions	Yield	-3.62953	0.014606
Solanum lycopersicum	GM	NP conditions	Yield	36.08369	1.093537
Solanum lycopersicum	HA	OP conditions	Yield	1.186435	0.038214
Solanum lycopersicum	GM	NP conditions	Yield	2.020992	0.009014
Solanum lycopersicum	HA	OP conditions	Yield	4.556189	0.631613
Solanum lycopersicum	GM	OP conditions	Sugars	0.210216	0.000111
Solanum lycopersicum	GM	OP conditions	Yield	0.143855	0.00317
Solanum lycopersicum	HA	NP conditions	Yield	28.83752	0.829705

Solanum lycopersicum	GM	NP conditions	Sugars	-1.42147	0.001866
Solanum lycopersicum	GM	NP conditions	Yield	1.739234	0.006145
Solanum melongena	GM	OP conditions	Yield	1.444628	0.070885
Solanum melongena	SB	OP conditions	Yield	1.761513	0.01627
Solanum melongena	GM	NP conditions	Yield	3.679541	1.106564
Solanum melongena	HA	NP conditions	Yield	2.399622	0.121138
Solanum melongena	SB	NP conditions	Yield	-1.19352	0.016926
Solanum melongena	GM	NP conditions	Yield	4.184441	1.306233
Solanum melongena	SB	OP conditions	Yield	2.084884	0.007034
Solanum muricatum	HA	OP conditions	Yield	1.662862	0.037947
Solanum muricatum	HA	OP conditions	Yield	0.237487	0.004253

Figures S1-S3 Forest plots showing effect sizes only from studies with complete data, i.e. without bootstrapping for missing standard deviations

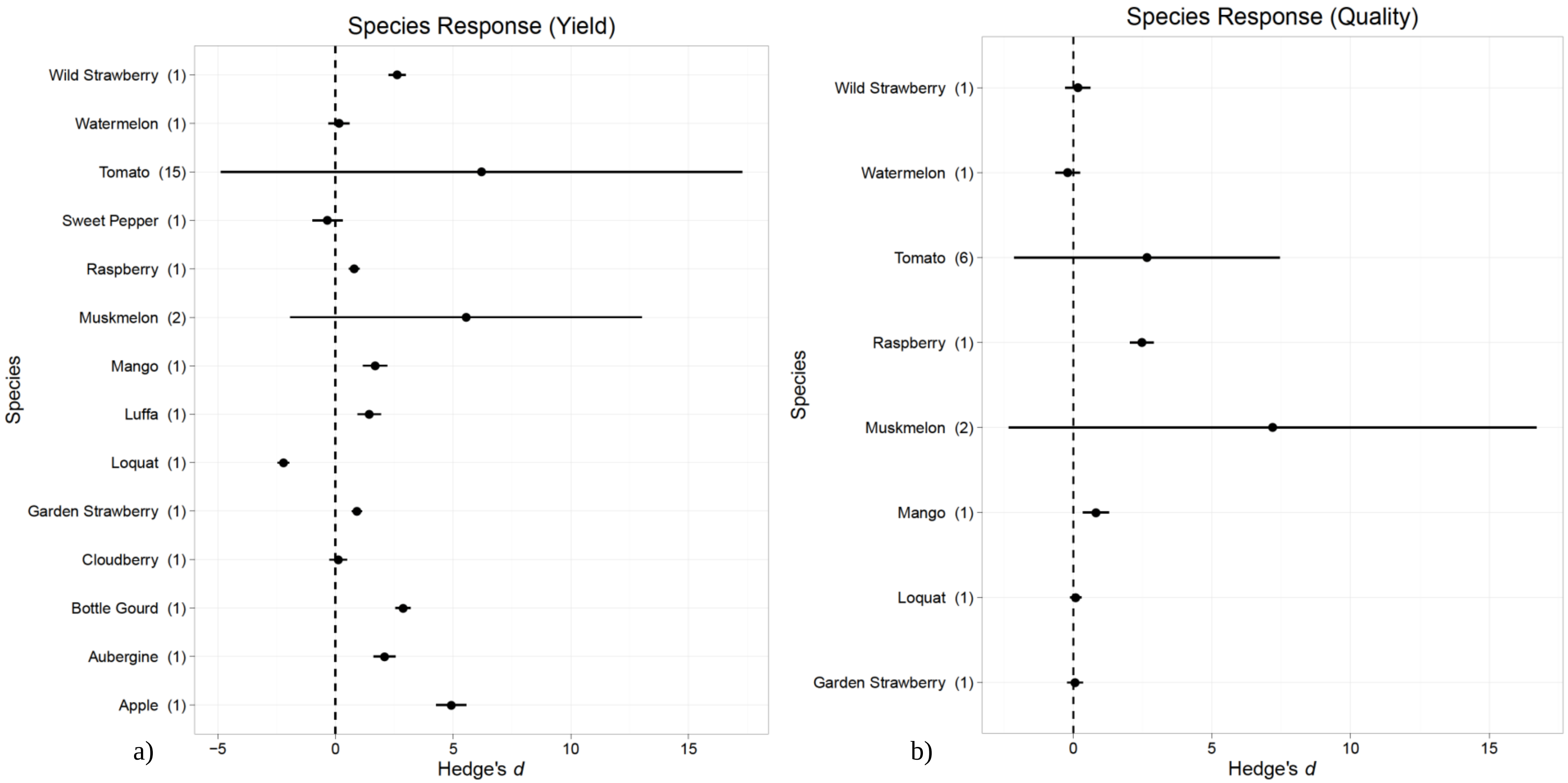

Figure S1. Mean effect sizes for all methods combined to induce parthenocarpy (genetic modification, hormone application, and selective breeding) split by crop species (y axis) for (a) fruit quantity (b) fruit quality. Error bars represent standard deviations. Sample size (number of effect sizes) are given in parentheses.

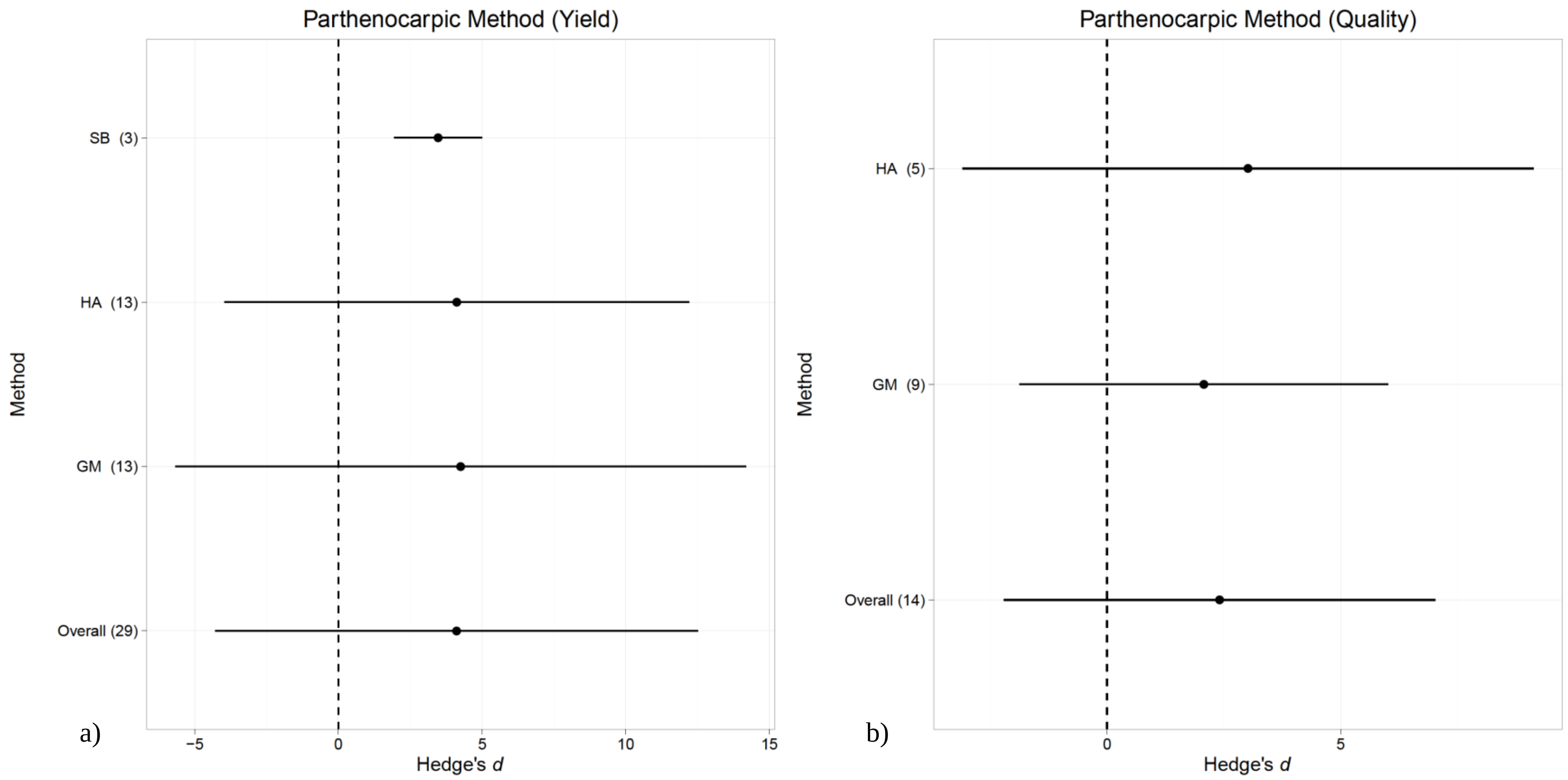

Figure S2. Overall mean effect sizes and effect sizes of methods to induce parthenocarpy (genetic modification (GM), hormone application (HA), selective breeding (SB)) (y axis) for (a) fruit quantity and (b) quality for all crop species. Error bars represent standard deviations. Sample size (number of effect sizes) are given in parentheses.

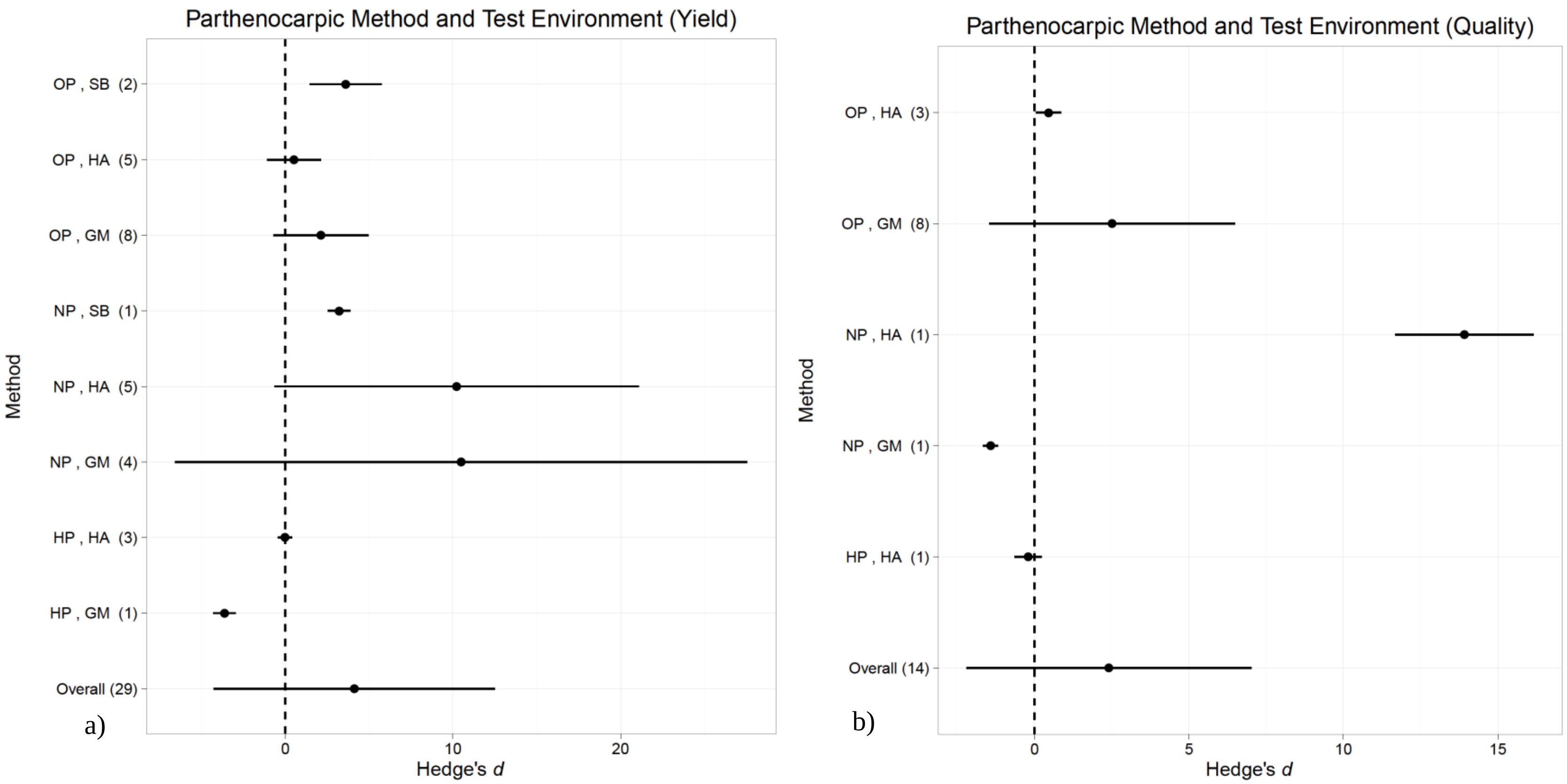

Figure S3. Overall mean effect sizes and effect sizes of methods to induce parthenocarpy (genetic modification (GM), hormone application (HA), selective breeding (SB)) and test environment (NP, OP, and HP) (y axis) for (a) fruit quantity (b) fruit quality for all crop species. Error bars represent standard deviations. Sample size (number of effect sizes) are given in parentheses.