Project title:	Cucurbit Pollination: Mechanisms and Management to Improve Field Quality and Quantity
Project number:	CP 118
Project leader:	Professor Juliet Osborne, University of Exeter
Report:	Annual, December 2015
Previous report:	Not Applicable
Key staff:	PhD student: Jessica Knapp Professor Juliet Osborne; Dr Frank Van Veen
Location of project:	Cornwall, United Kingdom
Industry Representative:	Ellis Luckhurst, P.E. Simmons and Son, Gwinear Road, Cornwall
Date project commenced:	01/01/2015
Date project completed (or expected completion date):	[01/01/2018]

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DISCLAIMER

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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Professor Juliet Osborne

Research Supervisor, Chair in Applied Ecology

Environment and Sustainability Institute, University of Exeter, Cornwall, TR10 9FE

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Contents

GROWER SUMMARY

Headlines

- Natural parthenocarpy ('virgin' fruit production resulting in fruit without seed) means that courgettes can reach marketable length without the need for pollination. However pollination improves fruit growth and weight.
- Findings so far are that under good conditions, courgettes in Cornwall do not experience a pollination deficit. The courgette fields that were studied were visited by a range of pollinating insects.

Background

The principal focus of this research project is to improve our understanding of the mechanisms which underpin fruit set in cucurbits. Cucurbits are a large plant family which over centuries have been domesticated for their fleshy fruits, roots, leaves, shoots, seeds and flowers for food and commodity goods (Bates et al. 1990). Generally, cucurbits require pollen to be transferred from male flowers to female flowers for successful pollination and fruit set (Delaplane et al. 2000).

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 (Bos et al. 2007; Boreux et al. 2013; Klein et al. 2014; Motzke et al. 2015). As a result, the productivity of insect pollinated crops is dependent on the presence of high functioning ecosystems to support pollinator populations, regulate disease, purify and cycle water and nutrients. Thus any impact (particularly anthropogenic (Winfree et al. 2009)) on the wider ecosystem can have a detrimental impact on multiple ecosystem services; crop yields and farmers profits (Potts et al. 2010; Steffan-Dewenter et al. 2005; Goulson et al. 2015).

This PhD studentship is structured around a series of complementary studies, with each focused on a different aspect of the agricultural system which affects fruit quality and quantity (Figure 1). The project is broken down into the following chapters:

- 1 - Quantity and quality of parthenocarpic fruit set in *Cucurbita pepo* (2015-2016)
- 2 - Yield and pollination deficits in field grown *Cucurbita pepo*: influence of semi-natural habitat, field size and species diversity/ abundance (2015-2016)
- 3 - Interaction between nutrients, fungicides and pollination in promoting fruit set of *Cucurbita pepo* (2016)
- 4 - An intensively managed, mass flowering crop: a resource for pollinators? (2017)

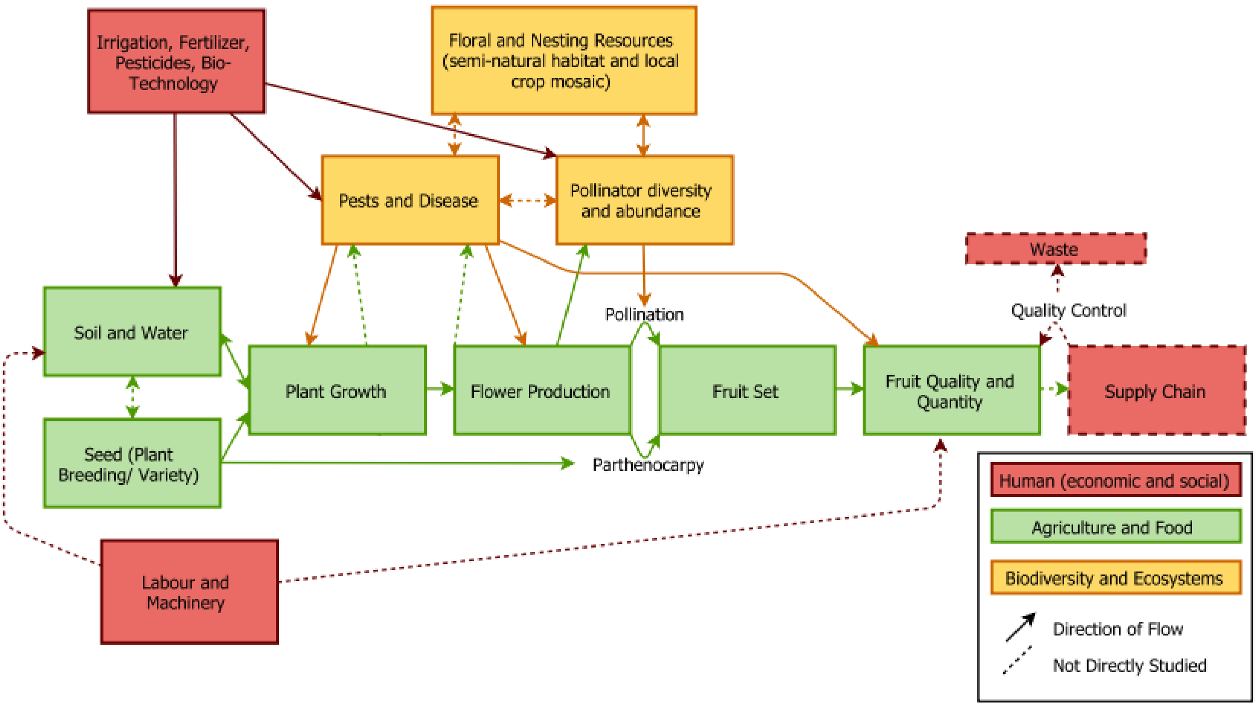

Figure 1 Conceptual framework integrating human (economic and social) systems, agricultural and food systems and biodiversity and ecosystems which effect fruit set in pollinator dependent crops.

As a model species for cucurbit crops field grown courgettes *Cucurbita pepo* of the variety Tosca) were studied.

Summary

Parthenocarpic fruit set

Parthenocarpic fruit set is of economic interest because it is an efficient way to produce fruits under environmental conditions adverse for pollination and/or fertilisation. This is because pollen maturation and fertilisation are affected by environmental factors such as light, temperature, and relative humidity (Pandolfini 2009). Parthenocarpy is a useful trait for pollinator dependent crops grown for extended harvest seasons, under protected conditions and beyond the extent of their natural ranges (Pandolfini 2009). Under these conditions growers would ordinarily experience high rates of fruit abortion, due to an insufficient number of pollen grains delivered to the stigmas.

Promoting fruit set of pollinator dependent crops under unfavourable environmental conditions is vitally important for commercial growers, and consequently food security as a whole. Seedlessness (caused by the absence of fertilisation) can also improve the quality of fruits such as in aubergines, watermelons and industrial tomatoes; potentially increasing profit. Although hybrid crops are expensive to implement, growers could offset their costs by increasing the quality and quantity of their crops, and by extending growing seasons, which would strengthen their market advantage.

Experiments from the first field season have shown that pollinated courgettes grow faster, to a greater weight and have a greater number of seeds compared to when they are grown in the absence of pollination. Fruit set was higher with 100% of hand pollinated flowers setting fruit compared to 65% of non-pollinated fruits. Nonetheless, bagged flowers were still able to set fruit of marketable size even in the complete absence of pollination (and therefore fertilisation) which is evidence of parthenocarpy (Figure 2).

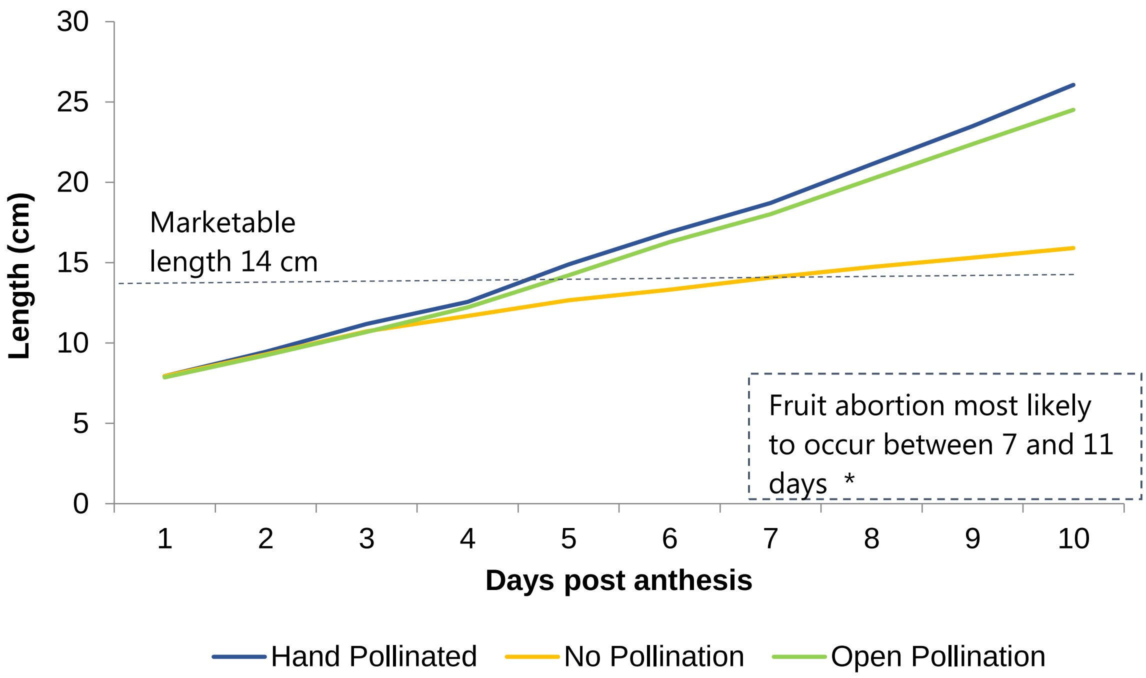

Figure 2 Average daily growth of courgettes grown in open field conditions. Dashed lines show standard marketable length and the number of days where fruit abortion is most likely to occur in Cucurbita pepo. *(Stephenson et al. 1988)

Yield and pollination deficits

Accordingly, crop producers may need to provide floral resources and nesting sites suitable for pollinators. Introduced species such as *A. Mellifera* and *B. terrestris* can greatly enhance yield. However, combined evidence suggests that crops could also experience greater yields in more diverse habitats; where increased species richness can improve pollination services (Hoehn et al. 2008; Garibaldi et al. 2011), provide insurance against any pollinator loss (Shuler et al. 2005) and reduce the spread of disease and pathogens (Kremen & Miles 2012). Enhancing wild pollinators can take several years but can provide a cost-effective alternative to introduced species. In the UK, farm stewardship schemes provide guidance on hedgerow and field margin management, particularly favoured by bumblebee species (Osborne, Martin, Shortall, et al. 2008; Wood et al. 2015). Any costs can be directly offset by increased profit from improved quality and quantity of yields, and indirectly from increased abundance of other beneficial insects. Pollinator-supporting practices will vary depending on the context in which they are implemented. For example, wild flower strips are often most effective in homogeneous landscapes (Batáry et al. 2011) and natural habitat may be more important at determining pollinator diversity and abundance than large scale practices such as conventional versus organic (Kremen et al. 2004).

In this study there was little difference in the growth rate, weight, and number of seeds between natural and maximum (hand pollination) pollination levels (Figure 2). This suggests that natural pollination levels are already high in Cornwall. This is most likely because the study sites were in relatively small fields with a high proportion of semi-natural habitat, known to provide floral and nesting resources for pollinators (Garibaldi et al. 2013). However, this is unlikely to be true for other sites in the United Kingdom as many agricultural systems are isolated from natural habitats.

Resource for pollinators

Generally, cucurbits must receive adequate pollination for their fruit to be large and well-formed and can consequently offer great quantities of nectar and pollen as floral rewards to visiting insects such as solitary bees, bumblebees and honeybees (Tepedino 1981). In particular, the North American squash and gourd bees belonging to the genera *Peponapis* and *Xenoglossa* are thought to rely exclusively on *Cucurbita* pollen to rear their offspring (Tepedino 1981) and were previously believed to be the most important pollinators of *Cucurbita* crops (Hurd et al. 1974). Although these specialist bees do not occur in the UK, it is highly likely that other pollinator species will rely heavily on cucurbits for nectar and pollen. Consequently, mass flowering pollinator dependent crops such as courgettes have the potential to provide vital food and nesting resources for pollinators and other biodiversity. Estimating the distance of pollinator flights in courgette systems can allow us to gain a valuable insight into forage resource use and the potential for pollen transfer within and between plant species. By understanding how our native and managed pollinators use agricultural systems (spatially and temporally) it is possible to optimise pollination services to improve crop yields whilst simultaneously protecting our pollinator species.

Financial Benefits

Findings from studies on courgette crops in Cornwall are that insect pollination increases courgette yield by up to 31%. Increasing the level of pollination could also improve yields.

Action Points

- None to date.

SCIENCE SECTION

Introduction

Globally, agricultural land is continuing to expand and intensify to meet rising food demands (Bommarco et al. 2013). The artificial replacement of many biological functions and the spread of agricultural land is a great threat to biodiversity (Bommarco et al. 2013). Sustainably maximising agricultural output requires ecosystem services to be optimised through increased crop yields, soil quality and implementation of ecologically-based management practices (Tilman et al. 2002; Bommarco et al. 2013). In doing so, producers can act to reduce negative impacts from agriculture such as: habitat loss, nutrient runoff, and pesticide poisoning of non-target species (Tilman et al. 2002; Zhang et al. 2007; Power 2010;).

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; with 75 per cent of global crop plants requiring insect pollination for fruit set. As agriculture intensifies and habitat conversion to farmland continues, crop producers are frequently relying on managed pollinator species to fulfil their pollination needs. Increasing the abundance of species such as *Apis mellifera* and *Bombus terrestris* can interrupt the damaging cycle of lower yields from reduced diversity and abundance of wild pollinators caused by losses in (semi-) natural habitat (Garibaldi et al. 2014). Honeybees are often favoured to perform this task as they form large colonies, forage on a wide variety of food sources, are easy to transport and have the further economic advantage of producing honey (Delaplane and Mayer 2000).

Areas of semi-natural habitat and/or improved habitat heterogeneity can increase the diversity of food and nesting resources available to both managed and wild pollinators. This is important for ‘door step foragers’ such as *B. muscorum*, *B. pascuorum* and *B. lapidarius* which are known to forage close to their nests (Walther-Hellwig & Frankl 2000; Darvill et al. 2004; Knight et al. 2005) and is likely to be why several species such as *B. terrestris* and *A. mellifera* (known for their longer flight distances) are found in high abundance in large, intensively farmed fields (Osborne, Martin, Carreck, et al. 2008). Likewise, increasing phenological diversity by promoting higher plant species richness will help to fulfil the requirements of different species in space and time. This is vital for both managed and unmanaged pollinators who often require resources beyond that of the focal crop.

Observed losses of pollinator species, and our dependence on them for their contribution to food security, has led to a widespread concern that we are facing a ‘pollinator crisis’ (Ghazoul 2005). Despite this alarm, temporal trends have shown an increase in the yields of pollinator-dependent crops in both the developed and developing worlds (Aizen et al. 2008). The use of commercial pollinators are largely thought to be responsible for these trends, but it is also possible to selectively breed, artificially induce, and genetically modify plants to produce fruit without pollination and fertilisation, a process known as parthenocarpy (Vardi et al. 2008).

Cucurbits

Cucurbitaceae (Cucurbits or gourds) are a large plant family which include major food plants such as *Cucurbita* (squash, pumpkin, courgette), *Cucumis* (cucumber, melon), and *Citrullus* (watermelon) (Bates et al. 1990). Over centuries cucurbits have been domesticated for their fleshy fruits, roots, leaves, shoots, seeds and flowers for food and commodity goods and are consequently of great economic importance (Bates et al. 1990).

Generally, cucurbits must receive adequate pollination for their fruit to be large and well-formed and can consequently offer great quantities of nectar and pollen as floral rewards to visiting insects such as solitary bees, bumblebees and honeybees (Tepedino 1981). In particular, the North American squash and gourd bees belonging to the genera *Peponapis* and *Xenoglossa* are thought to rely exclusively on *Cucurbita* pollen to rear their offspring (Tepedino 1981) and were previously believed to be the most important pollinators of *Cucurbita* crops (Hurd et al. 1974).

However, a small number of cucurbit cultivars are parthenocarpic; setting fruit in the absence of fertilisation (Vardi et al. 2008).

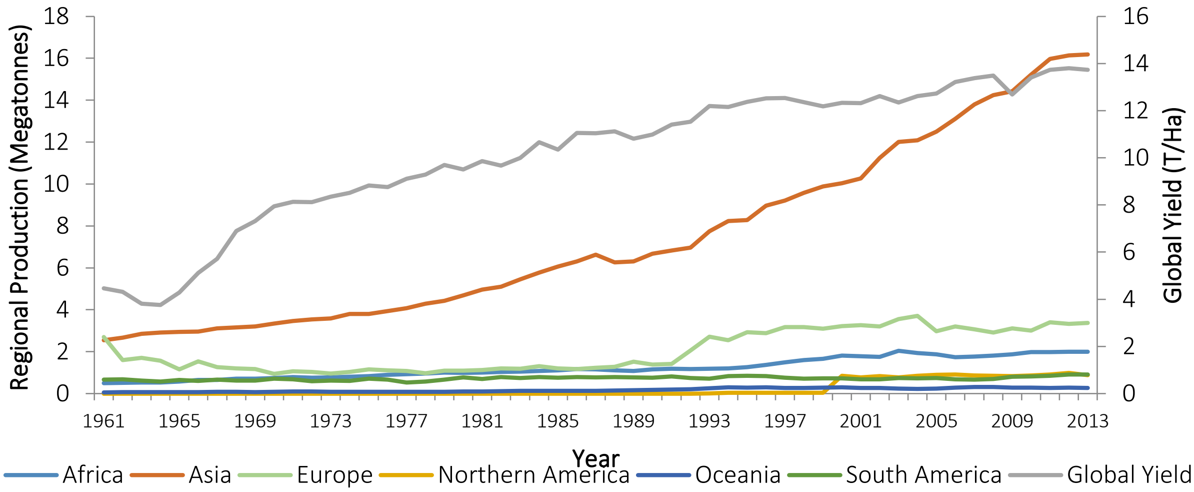

Figure 3 Regional production of and average global yield of Cucurbita species from 1961 to 2013. Data source: FAOSTAT (Aggregate, may include official, semi-official, estimated or calculated data).

As the yield of cucurbit crops increases per hectare (Figure 3), many questions of how to best grow these crops in an ecologically sustainable way remain open. This information is important, because different cucurbit species and varieties may vary in their extent of dependence on pollinators (Klein et al. 2007). This is particularly true in Asia where pioneering technological advancements and genetic improvements, especially with seedless varieties, have advanced cucurbit production worldwide (Figure 3) (McCreight et al. 2013).

Quantifying pollination systems is needed to deliver optimum pollination services to ensure regular crop production. This is vitally important to commercial growers trying to gain a competitive advantage by improving the quality and quantity of fruits. Therefore it is vital to understand the pollination requirements of Cucurbita pepo for optimum fruit set.

Research Questions

Literature Review

Meta-analysis techniques will be used to review and synthesise the literature on the extent of natural and artificial parthenocarpy in 'pollinator dependent crops', as described in Klein *et al*. (2007).

The following will be investigated:

(1) whether the quality and quantity of fruit set from parthenocarpic varieties (grown in protected conditions) is equivalent to pollinator dependent varieties (grown in open field conditions);

(2) if the quantity and quality of fruit set from parthenocarpic varieties can be improved by insect pollination and;

(3) whether selective breeding, genetic modification or growth hormone application is more effective at setting parthenocarpic fruit.

New pollinator dependency estimates which take into account selective breeding, regular application of growth hormones and genetic modification to promote parthenocarpywill be produced from this novel analysis.

Data Chapter 1

The growth rate and fruit set of *Cucurbita pepo* var. Tosca (a marketed non-parthenocarpic variety) grown in open field and control temperature environments was investigated to find out if parthenocarpy occurs in UK commercial varieties of *C. pepo* and investigations also aimed to find out if there was pollination deficit in UK field grown *C. pepo*.

Studying the quality and quantity of parthenocarpic fruits grown in controlled and open field environments aimed to answer the questions:

- to what extent does hand pollination, i.e. optimal pollen load, improve yield quality and quantity?
- to what extent does this differ between varieties?

Data Chapter 2

The aim of this study is to determine if the abundance and/or diversity of pollinators acts in combination with site and landscape variables to influence *C. pepo* yields.

To answer this question pollinators using courgette fields will be identified and whether pollinator activity is more important than landscape at influencing yields will be determined.

Materials and methods

Across all studies Cucurbita pepo var. Tosca were studied. All fields were subject to the same standard applications of fungicides, molluscicides, and fertilisers.

Site Selection

Eleven fields were studied in Cornwall, UK. The growing season was divided into two separate 'plantings', each around 80 ha from April to June and June to September. Within each planting, fields were separated into two geographically distinct 'blocks'. Each field block and planting was geographically independent of each other, and therefore varied in their surrounding landscapes.

Figure 4 a Map showing pan trap and transect arrangement in a single block of three courgette fields. b) Eleven field sites across Cornwall (sites in close proximity to each other are obscured due to scale).

Pollinator Surveys

At each of the 11 fields, pollinator visitation was assessed weekly for four weeks by using a combination of transects and pan traps (Figure 4). Within each field three 50 m x 2 m transects were walked in 10 minutes to record all wild bee and honeybee visits to courgette flowers. The majority of species recorded during transects were identified to species level on the wing. Where this was not possible specimens were collected and frozen for further identification in the laboratory.

Pan traps were made from plastic cereal bowls sprayed with yellow UV paint (to attract pollinators) and filled with soapy water (soap was used to break up the surface tension in water). These were set up at five equally spaced locations on the diagonal of each field and placed at each location upon arrival and collected again three days later. All bee and hoverfly species were identified to species level in the laboratory.

Using this combination of survey techniques allowed for a better representation of overall species richness. All fields within each planting were surveyed on the same day.

Site and Landscape Variables

TinyTag © data loggers were placed in the centre of each field to record the temperature (°C) every three minutes in order to calculate the daily minimum and maximum temperature. One data logger was also used to record relative humidity in a single field. Before each pollinator survey the wind speed (m/s) and sunlight (klx) were recorded. Yield was calculated as the quantity of fruits (kg) picked per field by labourers at the end of each day.

Landscape Characterisation

To characterise the environment in a one kilometre radius of each field, how the land was being used and the proportion of semi-natural habitat was determined. Land use was assessed by visiting each field on foot (via public rights of way) and recording whether the land was pastoral, arable or set-aside. All arable fields had their crop species recorded. The proportion of semi-natural habitat and field boundaries were calculated from Ordnance Survey Maps downloaded from Digimap in ArcGIS 10.1.

Pollination Deficit

Within each planting, one field was selected to investigate *Cucurbita pepo* dependence on pollinators. There were three treatments: hand pollinated (n=30), open pollinated (n=30) and no pollination (n=30). Thus 180 pistillate flowers, each from separate plants, were studied. The no pollination treatment was initiated the day before expected anthesis by securing PVC mesh bags with cable ties to female flowers. Bags had a mesh size of 0.2mm, which were designed to be permeable to the wind and rain yet exclude any pollinators. On the first day of anthesis, half of the open flowers received a hand pollination treatment, whereby pollen was provided from a male donor flower, transferred using a paint brush, the remaining half of the flowers were left for the open pollination treatment. Pollination deficit was calculated by comparing the difference in fruit set between hand pollinated and open pollinated flowers.

Each experimental plot was located within one field per planting, 25m away from a corner of a field. The location was chosen to minimise edge effects caused by field margins which are thought to enhance the availability of floral and nesting resources and therefore increase the abundance of pollinators. The same distance in each field also reduced any possible influences of field size, as large and small fields would differ from their central point to the nearest field margin.

Controlled Temperature (CT) Room Experiment

- *Cucurbita pepo* plants will be grown in a CT room from November 2015 to February 2016 to explore inter-variety differences in fruit set in the absence of pollination. 33 plants of three varieties: Tosca, Cavili and Partenon (11 plants of each) will be grown in 50 litre grow bags under conditions simulating a British summer, i.e. 14 hours of sunlight, maximum temperature 22°C.
- Unlike the open field experiment, the CT rooms will have a total absence of pollinators which will negate the need for pollinator exclusion bags. This will mean that half of the female flowers will be left open for the no pollination treatment, whilst the remaining half will receive a hand pollination treatment (using the same method as in the open field experiment).

Fruit Set and Quality Measurements

In both the open field and CT room experiments, all experimental flowers were individually marked with flagging tape. Fruit length was measured daily from the first day of anthesis to 10 days post-anthesis. All fruits were then harvested, weighed, and their sugar content (°Bx) measured using a refractometer. The numbers of seeds in each fruit was recorded, and seed size graded (out of 4) for each fruit.

Statistical Analysis - Pollination Deficit

Linear mixed effects models were used to investigate the effect of pollination on fruit length, circumference, and weight. Pollination treatment was a fixed effect and planting a random effect, to account for any potential variation between fields. Mann-Whitney *U* tests were performed on seed number and seed size (parametric assumptions were not met).

Statistical Analysis - Influence of Semi-natural Habitat, and Species Diversity/ Abundance on Yield/Ha

General linear models will be used to investigate the effect of species diversity, species abundance, temperature and field size on yield. The same design will also be used to investigate the effect of pollinator visitation, geographic location and proportion of semi-natural habitat on the percentage pollination deficit at each site.

Results - Analysis still underway

Field Grown Courgettes

In open field conditions 100% of hand pollinated flowers set fruit compared to 96% from open pollinated flowers and 65% from bagged flowers (no pollination). Hand and open pollinated fruits grew at a similar rate throughout the experiment, whilst non-pollinated fruits grew at a similar rate for the first three days before slowing down.

The number of the seeds per fruit (p = < 0.001) and seed size (a measure of quality) increased with hand pollination (p = 0.02).

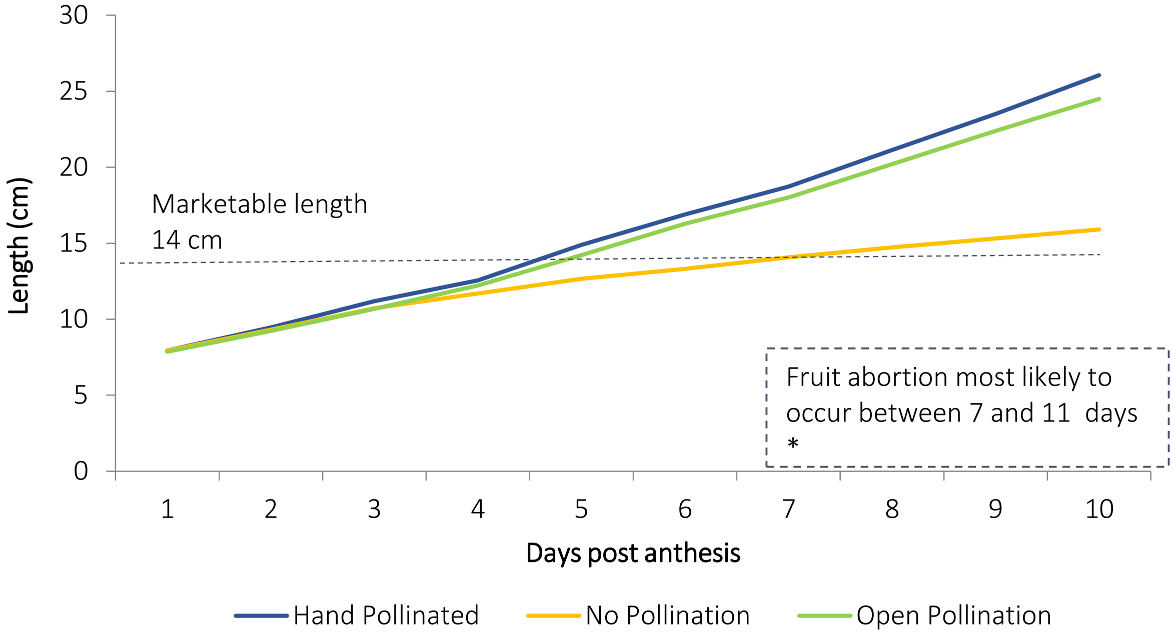

Figure 5 Average daily growth of courgettes grown in open field conditions. Dashed lines show standard marketable length and the number of days where fruit abortion is most likely to occur in *Cucurbita pepo*. *(Stephenson et al. 1988)

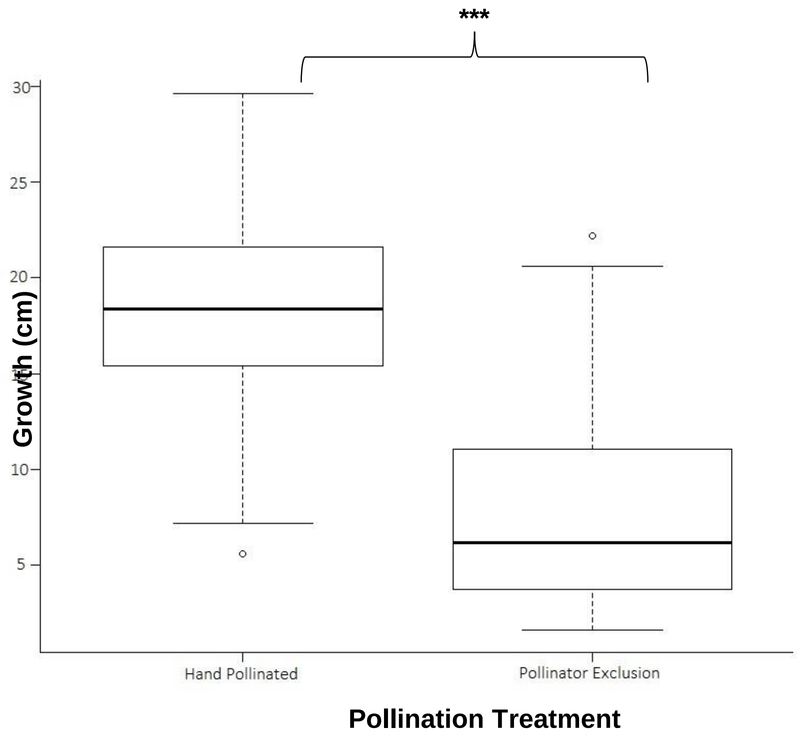

Figure 6 Effect of pollination treatment on courgette growth (difference in length between 1 and 10 days post anthesis).

Table 1 Effect of pollination treatment on field grown courgette quality measures (means ± standard error). F and P values from linear mixed models shown.

Measure	Pollinator exclusion	Open Pollinated	Hand pollinated	n	df	*F*-value	*P*-value	Significant differences
Fruit length (cm) after 10 days	15.9 ± 0.7	16.7 ± 0.9	22.2 ± 0.4	90	178	72.78	<0.0001	Hand > Exclusion
Fruit circumference (cm)	15.0 ± 0.5	18.5 ± 0.7	17.4 ± 0.5	90	178	56.7	<0.0001	Hand > Exclusion
Fruit weight (g)	300 ± 21.9	459.8 ± 32.3	431.1 ± 25.2	90	178	42.71	<0.0001	Hand > Exclusion
Number of seeds	778.4 ± 100.2	1235.2 ± 49.7	1268 ± 28.8	30	-	-	-	-
Seed quality (graded 1 - 4, 1 being best)	3.1 ± 0.1	2.1 ± 0.1	1.7 ± 0.1	30	-	-	-	-

Discussion

The 100% maximal fruit set of hand pollinated flowers suggests that there were no resource limiting factors (such as pollen, nutrient and water availability) effecting courgette growth and fruit set. As all plants (subject to all pollination treatments) were grown at the same site and under the same environmental conditions the observed reduction in fruit set (for non-pollinated flowers) is due to the absence of pollen.

Results showed that courgettes (in Cornwall) are experiencing a very small pollination deficit, but this was not significant. The average pollination deficit across both sites was 4% (the difference in fruit set between hand and open pollinated flowers). This relatively small pollination deficit found in Cornwall cannot be compared to other sites without replication at a landscape scale. Nonetheless, courgettes do require pollination to improve fruit set, this was shown by an increase in fruit set of 35% (the difference between non- and open-pollinated flowers).

Tosca has previously been described as non-parthenocarpic, due to the variety showing an increase in the production of ethylene around three days after anthesis (Martínez et al. 2013). This burst of ethylene is thought to cause early fruit abortion in non-pollinated flowers and may explain the slower growth rate around three days post anthesis in the non-pollinated flowers (Figure 5). Nonetheless many non-pollinated fruits were still able to reach a marketable size, on average just 1-2 days behind hand pollinated ones. This demonstrates the natural parthenocarpic potential of this courgette variety.

The observed fruit set in non-pollinated flowers owing to parthenocarpy is supported by their seeds being significantly smaller in size than those from hand-pollinated fruits (Robinson & Reiners 1999). Any seeds in non-pollinated fruits was because of ‘empty seeds’ caused by seed abortion due to the absence of fertilisation (Deunff & Sauton 1994; Pandolfini 2009).

Hybrid crops, selected for parthenocarpic traits have the potential to improve fruit set especially under adverse environmental conditions as they the crop species will be less pollinator dependent. Selective breeding programmes can also combine economically useful traits such as parthenocarpy with disease resistance and improved fruit quality (Kushnereva 2008). Although hybrid crops are expensive growers could offset their costs by increasing the quality and quantity of their crops, and by extending growing seasons, strengthening their market advantage in a global economy. This will be vitally important for commercial growers, and consequently food security as a whole.

These results suggest that even non-parthenocarpic varieties have a great potential to supplement pollination, particularly in conditions adverse for pollinators. Even in the total absence of pollination, a significant proportion of fruits were able to meet marketable size, on average just 1-2 days behind hand pollinated ones.

Promoting fruit set of pollinator dependent crops under unfavourable environmental conditions is vitally important for commercial growers, and consequently food security as a whole. Selective breeding programmes can combine economically useful traits such as parthenocarpy with disease resistance and improved fruit quality (Kushnereva 2008). Although hybrid crops are expensive growers could offset their costs by increasing the quality and quantity of their crops, and by extending growing seasons, strengthening their market advantage in a global economy.

Whilst parthenocarpy is a useful trait for crops grown under glass and out of season, it is believed that parthenocarpic fruit set in pollinator dependent crops may still be of a greater quantity and quality (including higher sugar content (Shin et al. 2007)) when pollinated by insects (Martínez et al. 2013; Robinson & Reiners 1999; Nicodemo et al. 2013).

More experimental work is needed to test the effectiveness of pollinator supporting habitats on yield, particularly in cucurbits. Nonetheless, conserving biodiversity for pollination services will enhance other ecosystem services vital for agricultural production such as natural pest control and soil cycling, increasing the functioning of the agricultural system (Kremen & Miles 2012; Palm et al. 2014). It is most likely that the synergistic effects of multiple regulating and supporting services (rather than pollination on its own) will be the most important factor effecting yield.

As many agricultural systems are isolated from natural habitats, crop producers may need to provide floral resources and nesting sites suitable for pollinators. In the UK, farm stewardship schemes provide guidance on hedgerow and field margin management, particularly favoured by bumblebee species (Osborne, Martin, Shortall, et al. 2008; Wood et al. 2015). Alternatively, costs can be directly offset by increased profit from improved quality and quantity of yields, and indirectly from increased abundance of other beneficial insects.

Although specific to cucurbits, these examples are relevant to all insect pollinated crops, in different agricultural systems and geographic regions.

Conclusions

Parthenocarpy is an efficient way to produce fruits under environmental conditions adverse for pollination and/or fertilisation. This is because pollen maturation and fertilisation are affected by environmental factors such as light, temperature, and relative humidity (Pandolfini 2009). This is a very useful trait for pollinator dependent crops grown for extended harvest seasons, under protected conditions and beyond the extent of their natural ranges (Pandolfini 2009). Under these conditions growers would ordinarily experience high rates of fruit abortion, due to an insufficient number of pollen grains delivered to the stigmas.

Promoting fruit set of pollinator dependent crops under unfavourable environmental conditions is vitally important for commercial growers, and consequently food security as a whole. Seedlessness can also improve the quality of fruits such as in aubergines, watermelons and industrial tomatoes; potentially increasing profit. Although often expensive to implement, growers could offset their costs by increasing the quality and quantity of their crops, and by extending growing seasons, which would strengthen their market advantage.

Nonetheless, evidence suggests that parthenocarpic fruit may still produce a greater quantity and quality (including higher sugar content (Shin et al. 2007; Hayata et al. 2000)) of fruits when pollinated by insects (Martínez et al. 2013; Robinson & Reiners 1999; Nicodemo et al. 2013). Likewise in closed conditions (i.e. no pollinators) parthenocarpic fruit set is often significantly lower than under open pollinated conditions (Robinson & Reiners 1999).

Consequently, both natural and artificial parthenocarpy may be of the greatest benefit in open pollinated conditions, where parthenocarpy can minimise any potential yield gaps whilst improving fruit uniformity. In return, these crops can continue to provide valuable nectar and pollen resources for our wild and managed bees.

Introduced pollinators, selective crop breeding, and growth hormones are clear examples of how our understanding of plant-pollinator interactions can contribute to global food security. Continuing to support pollinator populations is essential for seed and fruit set in many wild plants, as well as in crops where seeds are the edible parts. Consequently we must not let practices which reduce our dependence on pollinators undermine our wider efforts to conserve and promote biodiversity in agricultural systems.

Knowledge and Technology Transfer

- Presented a poster at the AHDB Student Conference
- Presented a poster at the Royal Entomological Society Annual Conference
- Presented my work to the Outdoor Cucurbit Growers Group event at NIAB, Cambridge
- Presented my work to the Penryn Campus bioscience department
- Presented my work to students at Mullion High School

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Appendix A - Pollination Biology of Cucurbita pepo

Cucurbita pepo is monecious (Figure 1) and self-compatible. Staminate flowers form first and are gradually taken over by pistillate flowers until they predominate. Both flowers begin to open at 06:00 am and close around 12:00 pm on the same day and do not open again. Flower opening and closing varies slightly depending on the climate but is not affected by climatic events such as rainfall. Pollen viability is around 92% in a newly open flower (07:00 am) this is reduced to around 75% when the flower closes (Nepi, Massimo and Pacini 1993). Viability quickly decreases over the afternoon until it reaches about 10% the next morning. Germination on the stigma begins 3 - 5 minutes after pollination (Nepi, Massimo and Pacini 1993).

Figure 1 Pistillate (left) and staminate (right) flowers of C. pepo

Figure 2 Bombus terrestris leaving a pistillate flower

Pollinators vary in the way that they travel to collect nectar in staminate and pistillate flowers because the nectar is located in different places (Figure 3). For example in staminate flowers, bees are forced into a vertical position to gather nectar which means that pollen adheres to the bee's backs, with only one individual able to access the flower at a time. Once out of the staminate flower, bees tend to sit on a flower or leaf and clean excess pollen grains from themselves using their back legs. This usually happens in the first hour of anthesis when pollen grains are plentiful. Nonetheless, many pollen grains will remain on the bees. Once inside a pistillate flower, bees unload their pollen grains on to the stigma as they make their way to the base of the corolla. Here, two to three bees may collect nectar at the same time and continue to release more pollen grains as they move symmetrically around the whole circumference of the corolla (Figure 3). By the end of anthesis, the stigma is thought to receive 827 ± 143 pollen gains (Nepi, Massimo and Pacini 1993). Pollinators are thought to visit pistillate flowers more often and for longer than staminate flowers. This is because the nectary of a pistillate flower is thought to be harder to access, yet able to produce more, and more concentrated nectar (Nepi, Massimo and Pacini 1993).

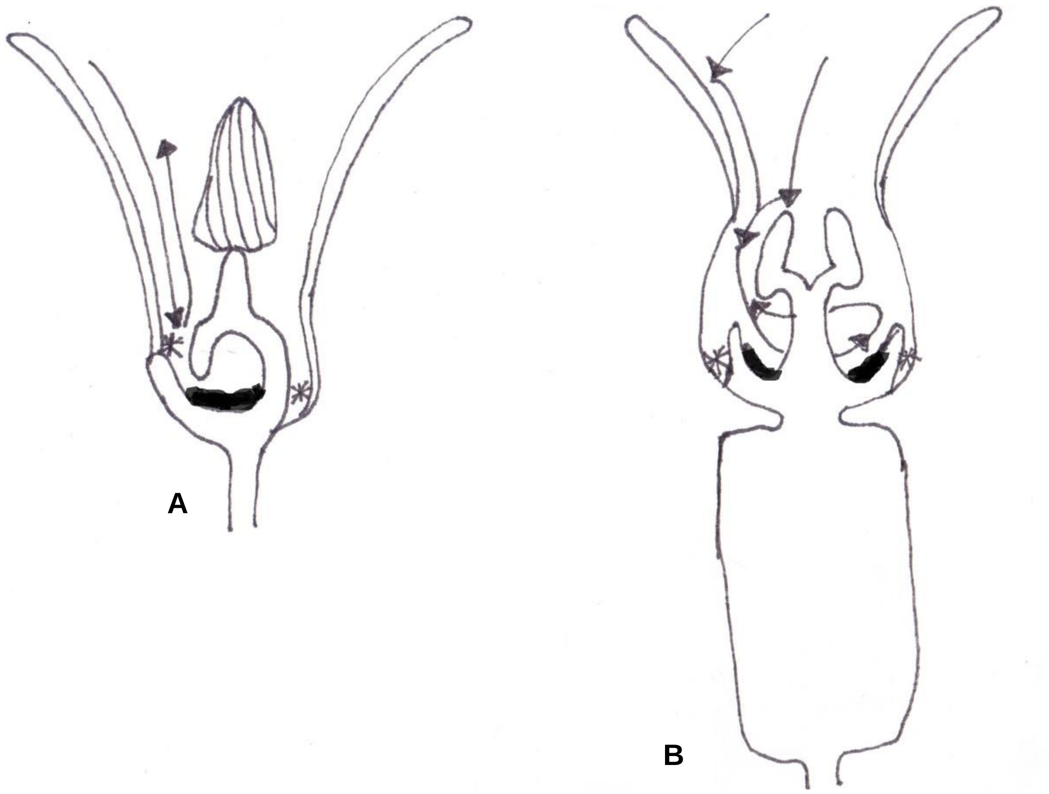

Figure 3 Morphology of staminate (A) and pistillate (B) flowers. The nectaries are shown in black, arrows show the path of bees collecting nectar, and * where pollen accumulates. Diagram modified from (Nepi, Massimo and Pacini 1993)**.**

C. pepo is thought to be dependent on pollinators as many pollen grains must be deposited or seeds formed for their fruit to be regular in shape and therefore of commercial value. However pollinators may not be so crucial for fruit set in *C. pepo* as courgettes are immature fruits. Nonetheless, pollination will be essential for seed production.

Appendix B - Example Landscape Classification Map

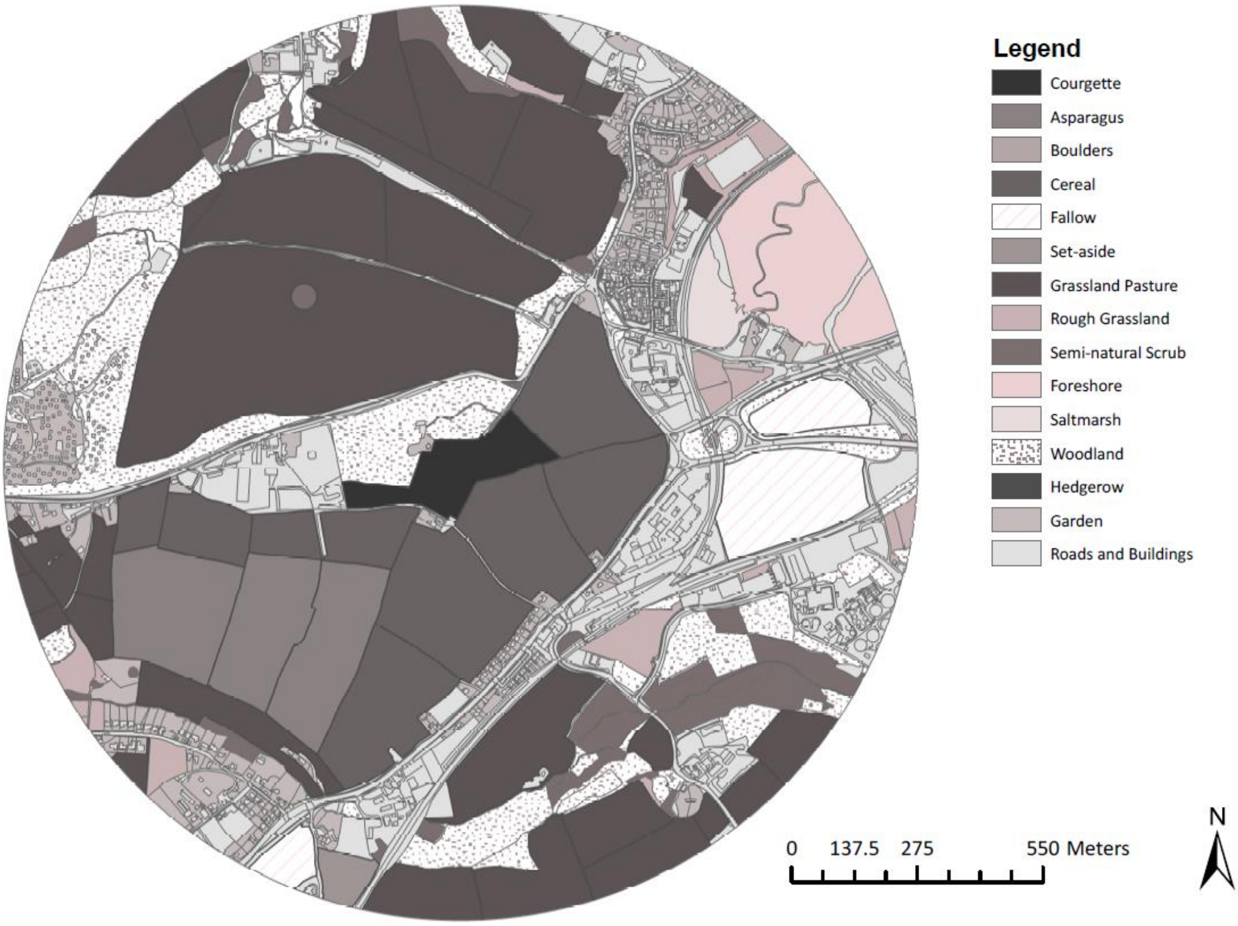

Figure 4 Example landscape map output for field 7. Land use was assessed by visiting each field on foot (via public rights of way) and recording whether the land was pastoral, arable or set-aside. All arable fields had their crop species recorded. The proportion of semi-natural habitat and field boundaries were calculated from Ordnance Survey Maps downloaded from Digimap in ArcGIS.

