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POLLINATION DEFICITS IN UK APPLE ORCHARDS

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Abstract—Apple production in the UK is worth over £100 million per annum and this production is heavily dependent on insect pollination. Despite its importance, it is not clear which insect pollinators carry out the majority of this pollination. Furthermore, it is unknown whether current UK apple production, in terms of both yield and quality, suffers pollination deficits and whether production value could be increased through effective management of pollination services. The present study set out to address some of these unknowns and showed that solitary bee activity is high in orchards and that they could be making a valuable contribution to pollination. Furthermore, fruit set and apple seed number were found to be suffering potential pollination deficits although these were not reflected in apple quality. Deficits could be addressed through orchard management practices to improve the abundance and diversity of wild pollinators. Such practices include provision of additional floral resources and nesting habitats as well as preservation of semi-natural areas. The cost effectiveness of such strategies would need to be understood taking into account the potential gains to the apple industry.

Keywords: Apples, Pollination, Deficits, Pollinators, United Kingdom

INTRODUCTION

Apples are typically self-incompatible and require pollen transfer from another "polliniser" cultivar to set fruit in marketable quantities (Delaplane & Mayer 2000). Wind and self pollination are not significant in apples and therefore insects such as bees and hoverflies are the predominant pollination vector and their activity in orchards is essential for apple production worldwide (Free 1964; Delaplane & Mayer 2000; Klein et al. 2007). Historically, honey bees, which are effective pollinators of apples (Stern et al. 2001), have been utilised to pollinate orchards (Carreck et al. 1997). Recent research, however, has shown that both solitary bees (Vicens & Bosch 2000; Ladurner et al. 2004; Matsumoto et al. 2009) and bumblebees (Thomson & Goodell 2001) can also be effective apple pollinators. Given the rising costs of honey bee hire and ongoing decline in their numbers across Europe (Potts et al. 2010b), the importance of wild insect pollinators for apple production may be increasing (Breeze et al. 2011).

2010 (DEFRA 2012). It is unknown which insect pollinators are currently most active in UK orchards during flowering, and importantly, which are contributing to apple pollination. Furthermore, it is not known whether present insect pollination in orchards is adequate or whether apple

In the UK, apple production was worth £103 million in

yield and quality is limited and there are pollination deficits. Although studies on pollination deficits in cultivated crops are not common (Thomson 2001), evidence showing deficits in tree crop production systems exist (Brookfield et al. 1996; Volz et al. 1996; Pritchard & Edwards 2006; Holzschuh et al. 2012).

In the face of rising demand for apple pollination services and potential wild and managed pollinator declines (Potts et al. 2010a), it is becoming increasingly necessary to understand the ecology of apple pollination in the UK. Is the true value of wild pollinators to apple production currently underestimated? Is orchard management necessary to arrest local pollinator declines to maintain apple production at current levels? Could yield and production value of apples in the UK be increased through improved wild and domestic pollinator management?

To answer these important questions the aims of this study were to: I. Establish which pollinators are active on blossoms in UK apple orchards; 2. Establish if there are pollination deficits in UK orchards and if yield and quality could be improved; 3. Determine if pollination deficits are linked to insect pollinator activity.

MATERIALS AND METHODS

Sites

In 2011, eight Cox apple orchards were selected in the top fruit growing region of Kent, UK. All orchards were conventionally managed, of varying tree age and surrounded by plantations of other varieties of apple. All orchards were at least 2 km apart and I ha in size.

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Pollinator surveys

At each orchard, two centrally located tree rows were selected for pollinator surveys. Surveys were done during apple flowering, which in 2011, occurred in the last two weeks of April. The time taken for surveys and the locations of the orchards enabled 4 orchards to be surveyed in any one day, thus 4 full days of surveys were carried out and each orchard was visited for an am and pm survey during flowering. On all survey days, temperatures exceeded 15°C, were predominantly clear and with minimal wind. Surveys involved 6 timed tree observations, each 50m apart, 3 along each tree row. For each observation, a Im by Im area of blossoms was marked out and observed for a period of 15 minutes with all flower visiting insects, as well as the number of visits they made, recorded. Visitors were categorised as bumblebees, honey bees, solitary bees, hoverflies or other (which included Lepidoptera, other Diptera, Coleoptera and other Hymenoptera). The number of open blossoms in the observation area was also noted.

Pollination treatments

At each of the eight orchards, 5 randomly selected trees along each of the two tree rows involved in pollinator surveys were selected. Approximately two weeks before flowering, three branches on each experimental tree were randomly selected, meaning 240 branches in total were involved in the study. One was to receive a hand pollination treatment, one was to remain pollinated by the natural insect community and the remaining branch was to have insect pollinators excluded entirely. A PVC mesh bag with a mesh size of I.2mm sq and wind and rain permeable, was placed over between I and 3 closely associated inflorescences on the hand pollinated and insect excluded branches. At peak flowering (late April), each orchard was visited and, on hand pollinated inflorescences, the bag was removed and all open flowers were pollinated using a paint brush. For each orchard, pollen was taken from dehist anthers on flowers located on the polliniser trees at each site; these were either planted within rows, between rows or in neighbouring orchard blocks. The polliniser varieties also varied between orchards and included Cameo, Spartan and Malus varieties. The number of flowers on hand pollinated, insect excluded and open pollinated inflorescences was also recorded. When flowering had finished at all sites, bags were removed and experimental inflorescences were marked with coloured cable ties and string so they could be located for apple harvest.

Fruit set measurements

Prior to commercial thinning which was carried out on some of the orchards (late July), a visit was made to each site. For each experimental branch, the number of apples which had developed on experimental inflorescences was recorded. The apples on each branch, which included any experimental apples, were then thinned according to the industry practice. Any apples removed from experimental inflorescences were stored and taken back to the laboratory for seed number analysis.

Quality measurements

All apples from experimental inflorescences were collected one day to a week before commercial harvest at

each of the orchards (late August). Apples were bagged individually by treatment, tree, row and orchard and taken back to the laboratory for quality assessment. Within 10 days of harvest, all quality measures had been taken.

Quality measures included; fresh weight, taken on a Mettler Toledo balance sensitive to the nearest milligram; maximum width, measured using callipers sensitive to 0.05 mm; firmness in kg/cm, taken using a Silverline penetrometer; brix, using a Hanna refractometer and; seed number. Additional data on the seed number per apple was also taken from apples removed on the visit made to orchards for apple thinning.

Statistical analysis

A linear mixed effects model was used to investigate which pollinators most frequently visited apple flowers. Using the number of flowers counted during each tree observation, the time period for each observation and the number of visits made by some important groups of pollinators (bumblebees, honey bees, solitary bees, hoverflies and others), visits per flower per minute (v/f/m) was calculated. An average for the six observations at each site was analysed with pollinator group and survey round included in the model as fixed effects and site as a random effect. Prior to analysis v/f/m was $\log +1$ transformed.

To investigate pollination treatment effects on fruit set and seed number, generalised linear mixed effects models were used. Pollination treatment was a fixed effect and trees nested within rows, nested within orchards were random effects. Seed number is a count so a poisson error structure was defined, and fruit set is a proportion so a binomial error structure was used.

A linear mixed effects model was used to analyse treatment effects on width, weight, firmness and brix with the same fixed and random effects as for the fruit set and seed number analysis. Weight was square root transformed and firmness was log transformed prior to analysis.

In order to establish a link between the extent of pollination deficits, for those apple measures that showed a deficit, and pollinator activity, regression analysis was carried out between the average per tree deficit for each site and the average per observation v/f/m for bumblebees, honey bees, solitary bees, hoverflies and others. Deficits were calculated as the percentage difference between hand and open pollination treatments for whatever measure of apple yield or quality was being considered. Any negative deficits i.e. where open treatments were greater than hand treatments, were considered as a zero deficit. Deficit is thus a percentage value and so was arcsine transformed prior to analysis. All analysis was carried out in R version 2.14.1.

RESULTS

Pollinator Surveys

Flower visitation rates varied significantly between pollinator groups ($F_{4.468} = 3.98$, P = 0.0035). Visitation

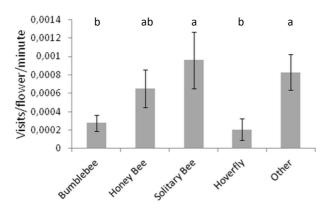


FIGURE 1. Flower visitation rate for some important groups of pollinators to Cox blossoms in UK orchards, Mean \pm standard error. Bars with different letters are significantly different according to a linear mixed model $P \leq 0.05$.

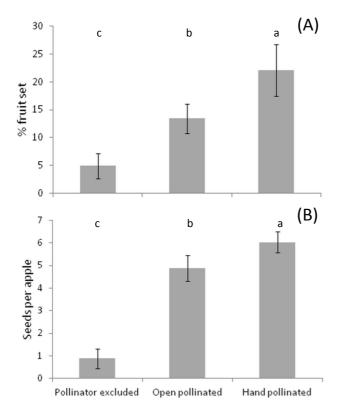


FIGURE 2. The effect of pollination treatment on (A) the fruit set and (B) the number of seeds of Cox apples, Mean \pm standard error. Bars with different letters are significantly different according to a generalised linear mixed model P < 0.05.

rates by solitary bees and other insects were significantly higher than visitation by bumblebees and hoverflies (Fig. I). There was no significant effect of survey round ($F_{1.467} = 3.26$, P = 0.0718) on visitation rate or a pollinator:survey round interaction ($F_{4.463} = 0.50$, P = 0.733).

Fruit Set and seed number

There was an effect of pollination treatment on fruit set (Fig. 2A) with significantly more fruit set on hand pollinated branches compared to open pollinated branches (Z=3.74, P<0.001), which in turn set significantly more fruit than pollinator excluded branches (Z=6.24, P<0.001). The same pattern was seen for seed number per apple with hand greater than open (Z=3.47, P<0.001) and open greater than pollinator excluded treatments (Z=8.83, P<0.001) (Fig. 2B).

Apple quality

Apple width was not affected by pollination treatment (Tab. I). Open pollinated apples were significantly heavier and contained more sugar than those that developed from pollinator excluded flowers. Pollinator excluded apples were significantly firmer than both hand and open pollinated apples.

Linking Deficits with Pollinators

Apple fruit set and seed number showed a significant pollination deficit so the influence of pollinator activity on these was analysed. There was found to be no significant correlation between the activity of any of the pollinator groups and pollination deficit (Tab. 2). There was a near significant negative relationship between bumblebee visitation rate and seed number deficits.

DISCUSSION

Apple pollinators

With the highest visitation rates, the pollinator surveys showed that solitary bees could be particularly important apple pollinators in the orchards studied. Visitation rate will not always reflect a pollinator's true contribution to flower pollination (Ne'eman et al. 2010); that will also depend on the tendency to deposit pollen during floral visits and importantly for apple orchards, foraging flights between trees to increase transmission of viable pollen from polliniser varieties. Research has shown that *Osmia cornuta* can be an effective apple pollinator (Ladurner et al. 2004), is active at

TABLE I. Effect of pollination treatment on Cox quality measures (means \pm standard error). F and P value from linear mixed effects models shown.

Measure	Pollinator exclusion	Open pollinated	Hand pollinated	n	F value	P value	Significant differences
Width (cm)	62.I ± I.8	64.8 ± 1.7	63.7 ± 1.6	2-89	2.00	0.141	
Weight (g)	108.5 ± 6.8	121.6 ± 9.3	112.9 ± 6.7	2-89	3.13	0.049	Open > Closed
Sugar (%)	11.0 ± 0.4	11.3 ± 0.3	11.2 ± 0.4	2-89	3.36	0.039	Open > Closed
Firmness (kg/cm)	12.4 ± 1.4	10.8 ± 0.6	10.8 ± 0.2	2-89	3.79	0.026	Hand, Open < Closed

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	App	Apple fruit set deficit			Apple seed number deficit			
Pollinator	n	F value	p value	n	F value	p value		
Bumblebee	8	0.16	0.70	8	4.88	0.07		
Honey bee	8	2.75	0.15	8	0.51	0.50		
Solitary bee	8	0.53	0.49	8	0.02	0.89		
Hoverfly	8	0.31	0.60	8	0.004	0.95		
Other	8	0.23	0.65	8	I.47	0.27		

TABLE 2. Statistical outcome following regression analysis between the visitation rate of some pollinator groups and the extent of pollination deficits for apple fruit set and apple seed number.

lower temperatures than honey bees (Vicens & Bosch 2000) and Osmia cornifrons was shown to retain apple pollen on its body well (Matsumoto et al. 2009). This data shows that the contribution of solitary bees to apple production in the UK may have been underestimated. The pollination efficiency of those species found visiting apple flowers, however, would need to be established. None of the growers involved in the study brought in honey bees to supplement pollination, yet activity of honey bees across the orchards was evident with approximately 20% of visits. So despite the absence of deliberate management, honey bees still play a role in the pollination of the orchards involved in the present study.

With no significant effect of survey round on apple blossom visitation rate, pollinator activity did not appear to change significantly during the flowering season. However, there is potential for inter-annual variation in the activity and the relative importance of different pollinators (Alarcon et al. 2008), particularly given the short period of flowering in apples. Studies to identify the most important insect pollinators of apples would benefit from surveys over multiple years.

Pollination deficits

The importance of insect pollination for fruit set, seed set, increased apple weight and sugar content in Cox apples is clearly demonstrated when open and closed pollination treatments are compared. That fruit set and seed set could be significantly increased through optimisation of pollination indicates there may also be potential yield and quality deficits. Our data shows that fruit set could have been increased by up to 8% on average across the orchards. The number of fruit is not the only measure of apple production and the quality of those fruit produced is important. In some situations high fruit set can have negative implications for fruit quality with high fruit loads meaning apples do not develop to their maximum size and weight (Volz et al. 1993), factors important for desert apples. When measuring pollination deficits it is important to consider both yield and quality, although excess fruit set can be remediated by chemical or mechanical blossom removal or apple thinning prior to harvest. High levels of insect pollination are still required to ensure good quality in those fruit that remain however, and evidence for many apple varieties shows that increased seed number in fruit can increase size, evenness of shape and improve mineral concentrations (Brookfield et al. 1996; Volz et al. 1996; Buccheri & Di Vaio 2004; Matsumoto et al. 2012). The data from the present study shows there are clear potential pollination deficits with regards to seed number. The pollination treatment impacts on seed number in the present study are, however, not matched by impacts on apple size or weight suggesting that this link between seed number and quality does not exist for Cox. The good weight and size of many apples that developed on pollinator excluded branches in the absence of any seed development is testament to this. There may be additional effects on mineral content, which was not measured in this study, and ripening as the treatment effect on sugar and firmness suggest.

These results show that there is a potential yield but perhaps not a quality deficit in these Cox orchards, but it is important to consider varietal differences and pollination deficits in quality would be extensive for varieties where apple growth is linked to seed set.

Deficits and pollinators

Fruit set and seed number deficits varied between orchards by 0-75% and 0-56% respectively so there is clear scope for improvement in both these parameters. If solitary bees are indeed important apple pollinators in UK orchards then there are numerous management options growers could implement to reduce deficits. Planting additional floral resources which will flower before or after apple flowering has been shown to improve the reproductive success of apple visiting solitary bees and could establish active populations for subsequent seasons (Sheffield et al. 2008). Preservation of natural or semi-natural areas in or around orchards could also increase the abundance and diversity of wild apple pollinators. Such benefits have been seen in other fruit crops as well as apples (Chacoff & Aizen 2006; Garibaldi et al. 2011; Watson et al. 2011; Holzschuh et al. 2012). The negative correlation between bumblebee visitation and seed number deficits was the only close to significant relationship found between deficits and pollinator activity. That bumblebees may be effective apple pollinators and thus increase seed set follows findings by Thomson and Goodell (2001) who recorded that bumblebees deposited more pollen following visits to apple blossoms than honey bees. The indication of this correlation between bumblebees and deficits despite bumblebees showing low visitation rates further highlights their potential as effective apple pollinators. Once again, management of orchards could be adapted accordingly to support greater bumblebee populations (Carvell et al. 2011; Pywell et al. 2011), although the practicality of such measures in orchards would need to be considered. It is not only by managing pollinators that pollination deficits could be addressed. The variation in fruit set and seed set deficits in this study could partly be

explained by the varying distributions of polliniser varieties within and around our experimental orchards as well as their compatibility to Cox. Improving the distribution and abundance of compatible polliniser trees in orchards will invariably improve fruit and seed set by increasing the chance of visiting pollinators carrying viable pollen. However, the negative effects of this on reducing the number of preferred varieties and the increased impracticality of apple harvest limit the way growers can distribute polliniser trees. Any orchard management to maintain or improve effective pollination services must consider management of both the insect pollinators and the availability of viable polliniser trees.

Conclusion

The community of insects visiting Cox apple blossoms in Kent includes representatives from several potentially important pollinator groups but solitary bees were the most active. There is evidence of pollination deficits for both yield and apple seed number in Cox although this is not reflected in the quality of apples produced in terms of size, weight, sugar content and firmness. Deficits in quality may be evident for varieties where seed number directly influences quality. There is a clear need for continued research on UK apple pollination ecology to determine the true value of insect pollination, particularly in terms of apple quality for different varieties. This understanding of pollinator value can then underpin future orchard management so appropriate investment in managing pollination services can be made.

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REFERENCES

- Alarcon R, Waser NM, Ollerton J (2008) Year-to-year variation in the topology of a plant-pollinator interaction network. Oikos 117-1796-1807
- Breeze TD, Bailey AP, Balcombe KG, Potts SG (2011) Pollination services in the UK: How important are honeybees? Agriculture, Ecosystems & Environment 142:137-143.
- Brookfield PL, Ferguson IB, Watkins CB, Bowen JH (1996) Seed number and calcium concentrations of 'Braeburn' apple fruit. Journal of Horticultural Science 71:265-271.
- Buccheri M, Di Vaio C (2004) Relationship among seed number, quality, and calcium content in apple fruits. Journal of Plant Nutrition 27:1735-1746.
- Carreck NL, Williams IH, Little DJ (1997) The movement of honey bee colonies for crop pollination and honey production by beekeepers in Great Britain. Bee World 78:67-77.
- Carvell C, Osborne JL, Bourke AFG, Freeman SN, Pywell RF, Heard MS (2011) Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality. Ecological Applications 21:1760-1771.

- Chacoff NP, Aizen MA (2006) Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. Journal of Applied Ecology 43:18-27.
- DEFRA, 2012. Orchard Fruit Survey. http://www.defra.gov.uk/statistics/files/defra-stats-foodfarm-landuselivestock-orchard-timeseries-120531.xls. (accessed Feb 2013)
- Delaplane KS, Mayer NF (2000) Crop Pollination by Bees. CABI Publishing, Wallingford.
- Free JB (1964) Comparison of the Importance of Insect and Wind Pollination of Apple Trees. Nature 201:726-727.
- Garibaldi LA, Steffan-Dewenter I, Kremen C, Morales JM, Bommarco R, Cunningham SA, Carvalheiro LG, Chacoff NP, Dudenhöffer JH, Greenleaf SS, Holzschuh A, Isaacs R, Krewenka K, Mandelik Y, Mayfield MM, Morandin LA, Potts SG, Ricketts TH, Szentgyörgyi H, Viana BF, Westphal C, Winfree R, Klein AM (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters 14:1062-1072.
- Holzschuh A, Dudenhöffer J-H, Tscharntke T (2012) Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. Biological Conservation 153:101-107.
- Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences 274:303-313.
- Ladurner E, Recla L, Wolf M, Zelger R, Burgio G (2004) Osmia cornuta (Hymenoptera Megachilidae) densities required for apple pollination: a cage study. Journal of Apicultural Research 43:118-122.
- Matsumoto S, Abe A, Maejima T (2009) Foraging behaviour of Osmia cornifrons in an apple orchard. Scientia Horticulturae 121:73-79.
- Matsumoto S, Soejima J, Maejima T (2012) Influence of repeated pollination on seed number and fruit shape of 'Fuji' apples. Scientia Horticulturae 137:131-137.
- Ne'eman G, Jürgens A, Newstrom-Lloyd L, Potts SG, Dafni A (2010) A framework for comparing pollinator performance: effectiveness and efficiency. Biological Reviews 85:435-451.
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010a) Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25:345-353.
- Potts SG, Roberts SPM, Dean R, Marris G, Brown MA, Jones R, Neumann P, Settele J (2010b) Declines of managed honey bees and beekeepers in Europe. Journal of Apicultural Research 49:15-22.
- Pritchard KD, Edwards W (2006) Supplementary pollination in the production of custard apple (Annona sp.) - the effect of pollen source. Journal of Horticultural Science & Biotechnology 81:78-83.
- Pywell RF, Meek WR, Hulmes L, Hulmes S, James KL, Nowakowski M, Carvell C (2011) Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. Journal of Insect Conservation 15:853-864.
- Sheffield CS, Westby SM, Smith RF, Kevan PG (2008) Potential of bigleaf lupine for building and sustaining Osmia lignaria populations for pollination of apple. The Canadian Entomologist 140:589-599.
- Stern RA, Eisikowitch D, Dag A (2001) Sequential introduction of honeybee colonies and doubling their density increases cross-pollination, fruit-set and yield in 'Red Delicious' apple. Journal of Horticultural Science & Biotechnology 76:17-23.

- Thomson JD (2001) Using pollination deficits to infer pollinator declines: Can theory guide us? Conservation Ecology 5:1-12.
- Thomson JD, Goodell K (2001) Pollen removal and deposition by honeybee and bumblebee visitors to apple and almond flowers. Journal of Applied Ecology 38:1032-1044.
- Vicens N, Bosch J (2000) Weather-Dependent Pollinator Activity in an Apple Orchard, with Special Reference to Osmia cornuta and Apis mellifera (Hymenoptera: Megachilidae and Apidae). Environmental Entomology 29:413-420.
- Volz RK, Ferguson IB, Bowen JH, Watkins CB (1993) Crop load effects on fruit mineral-nutrition, maturity, fruiting and tree

- growth of Cox Orange Pippin apples. Journal of Horticultural Science 68:127-137.
- Volz RK, Tustin DS, Ferguson IB (1996) Pollination effects on fruit mineral composition, seeds and cropping characteristics of 'Braeburn' apple trees. Scientia Horticulturae 66:169-180.
- Watson JC, Wolf AT, Ascher JS (2011) Forested Landscapes Promote Richness and Abundance of Native Bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin Apple Orchards. Environmental Entomology 40:621-632.