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Pollination biology of fruit-bearing hedgerow plants and the role of flower-visiting insects in fruit-set

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- *Background and Aims* In the UK, the flowers of fruit-bearing hedgerow plants provide a succession of pollen and nectar for flower-visiting insects for much of the year. The fruits of hedgerow plants are a source of winter food for frugivorous birds on farmland. It is unclear whether recent declines in pollinator populations are likely to threaten fruit-set and hence food supply for birds. The present study investigates the pollination biology of five common hedgerow plants: blackthorn (*Prunus spinosa*), hawthorn (*Crataegus monogyna*), dog rose (*Rosa canina*), bramble (*Rubus fruticosus*) and ivy (*Hedera helix*).
- *Methods* The requirement for insect pollination was investigated initially by excluding insects from flowers by using mesh bags and comparing immature and mature fruit-set with those of open-pollinated flowers. Those plants that showed a requirement for insect pollination were then tested to compare fruit-set under two additional pollination service scenarios: (1) reduced pollination, with insects excluded from flowers bagged for part of the flowering period, and (2) supplemental pollination, with flowers hand cross-pollinated to test for pollen limitation.
- *Key Results* The proportions of flowers setting fruit in blackthorn, hawthorn and ivy were significantly reduced when insects were excluded from flowers by using mesh bags, whereas fruit-set in bramble and dog rose were unaffected. Restricting the exposure of flowers to pollinators had no significant effect on fruit-set. However, blackthorn and hawthorn were found to be pollen-limited, suggesting that the pollination service was inadequate in the study area.
- *Conclusions* Ensuring strong populations of insect pollinators may be essential to guarantee a winter fruit supply for birds in UK hedgerows.

Key words: Blackthorn, bramble, *Crataegus monogyna*, frugivorous birds, hawthorn, *Hedera helix*, hedgerows, ivy, insect pollination, *Prunus spinosa*, *Rubus fruticosus*, *Rosa canina*.

INTRODUCTION

The flowers of fruit-bearing hedgerow plants provide a succession of forage for insects for much of the year. The fruits of plant species found in British hedges provide a winter food resource for small mammals (Pollard *et al.*, 1974) and form a large part of the winter diet of resident and migratory frugivorous birds on farmland (Snow and Snow, 1988). Loss of hedgerows in UK farmland (Barr *et al.*, 1986, 1991) will have reduced the availability of hedgerow fruit. Many farmland birds have declined in recent decades (Gregory *et al.*, 2004; Baillie *et al.*, 2007), but it is unclear whether changes in availability of hedgerow fruit have contributed to this.

The flowers of blackthorn (*Prunus spinosa*), hawthorn (*Crataegus monogyna*), dog rose (*Rosa canina* agg.), bramble (*Rubus fruticosus* agg.) and ivy (*Hedera helix*) are visited for pollen or nectar (or both) by several insect species, mainly Aculeate Hymenoptera (bees and wasps), Diptera (true flies) and Lepidoptera (moths and butterflies) (Knuth, 1908; Pollard *et al.*, 1974; Yeboah Gyan and Woodell, 1987*a*; Guitián and Fuentes, 1992; Guitián *et al.*, 1993; Proctor *et al.*, 1996). It is likely that these visits result in pollination, seed set and fruit-set, but the importance of insects for hedgerow fruit-set depends on the reproductive system of the plant.

The aim of the present study was two-fold: (1) to investigate the role of insect pollination for a range of fruit-bearing hedgerow plants; and (2) for those that are insect pollinated, to establish whether pollination services limit fruit-set in a selection of British hedges. Pollen limitation is observed as a common phenomenon in plants (Burd, 1994; Ashman *et al.*, 2004; Knight *et al.*, 2005) and supplemental pollination experiments have demonstrated its occurrence for several plant species (Bierzychudek, 1981; Pflugshaupt *et al.*, 2002; Ward and Johnson, 2005). Factors that could contribute to sub-optimal fruit- or seed-set are the delivery of incompatible pollen (Campbell and Motten, 1985; Hessing, 1988; de Jong *et al.*, 1993) or the delivery of insufficient numbers of pollen grains due to low pollination services (Gross and Werner, 1983; Morandin and Winston, 2005). Resource limitation can also reduce seed- and fruit-set and can operate in conjunction with pollen delivery to influence seed-set or fruit size (Zimmerman and Aide, 1989; Campbell and Halama, 1993; Casper and Niesenbaum, 1993). If fruit-set is reduced in the absence of insects and pollen limitation is occurring it might be predicted

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TABLE 1. *Experimental treatments and possible routes of pollination*

Year	Treatment	Mesh type & gauge	Insects	Wind	Self	Supplemented by hand
2005	BG	Muslin/nylon 0·7 mm	No	Very little (3–5 % of open pollination)	Yes	No
2005	OP	–	Yes	Yes	Yes	No
2007	M100	Muslin 0·7 mm	No	Very little (3 % of open pollination)	Yes	No
2007	T100	Tulle 1·2 mm	No	Yes (less) (40 % of open pollination)	Yes	No
2007	T50	Tulle 1·2 mm	Yes (50 %)	Yes	Yes	No
2007	OP	–	Yes	Yes	Yes	No
2007	HP	–	Yes	Yes	Yes	Yes

that reducing the time of exposure of flowers to insects would have an effect on fruit-set. For example, Benedek *et al.* (1994, 2000, 2006) found that even partial exclusion of pollinators resulted in a decrease in fruit yield in both self-incompatible and self-fertile cultivars of orchard trees.

Experiments were performed to establish whether five common hedgerow plants require flower visits from insects to set fruit, by excluding insects from flowers using mesh bags. The pollination biology of plants that showed reduced fruit-set in the absence of flower-visiting insects was examined further to determine (1) whether fruit-set was pollen-limited by supplementing open-pollinated flowers by manual cross-pollination and (2) what would happen to fruit-set if flowers received restricted exposure to flower-visiting insects.

MATERIALS AND METHODS

Hedges containing blackthorn (*Prunus spinosa* L.), hawthorn (*Crataegus monogyna* Jacq.), dog rose (*Rosa canina* agg.), bramble (*Rubus fruticosus* agg.) and ivy (*Hedera helix* L.) were located at Rothamsted Research and neighbouring farms (Hertfordshire, UK, 51°48·9′N, 0°21·5′W, Ordnance Survey ref: TL1314) and at The Game & Wildlife Conservation Trust's 'Allerton Project' farm (Loddington, Leicestershire, UK, 52°36·5′N, 0°49·9′W, UK Ordnance Survey ref: SK7902).

A preliminary insect exclusion experiment was performed in 2005 to establish the requirement for insect pollination for fruit-set and to identify plant species for studying in more detail. At Rothamsted and Loddington, groups of buds from blackthorn, hawthorn, dog rose, bramble and ivy on one or more hedges were selected before anthesis. Two treatments were applied according to a randomized block design within each hedge: (1) BG, 'bagged' using muslin or nylon (more resilient than muslin to thorns, and therefore used for dog rose and bramble) to exclude flower-visiting insects; and (2) OP, 'open pollination' – flowers were left open to flower-visiting insects.

Plant species that showed reduced fruit-set when insects were excluded in 2005 were studied in more detail, at Rothamsted in 2007, to test for pollen limitation and the effects of restricting exposure to flower-visiting insects on fruit-set. In addition, a tulle mesh bag treatment was used alongside the nylon or muslin mesh bag treatment to provide a better assessment of the contribution of wind-pollination. Tulle is sufficiently fine to prevent insects from reaching flowers, but has a coarser weave (1·2 mm) than nylon or muslin (0·5–0·7 mm), allowing more airborne pollen to pass through, whilst still being insect-proof. A small-scale experiment was done to assess the quantity of airborne pollen entering the different bags. Slides coated with a thin layer of petroleum jelly were placed inside bags next to flowering blackthorn for 5 d. The number of pollen grains on bagged slides were compared with the number present on uncovered slides. Muslin allowed 3 % of airborne pollen through, nylon allowed 5 % through and tulle allowed the greatest amount through (40 %) (Table 1).

Groups of buds were selected before anthesis and five treatments (Table 1) were applied according to a randomized block design: (1) M100, buds enclosed in muslin bags for the whole duration of flowering; (2) T100, buds enclosed in tulle bags for the duration of flowering (allowing a comparison with muslin); (3) T50, buds enclosed in bridal tulle bags for 50 % of the duration of flowering (bags removed for 5 d and replaced for 5 d in a continuous cycle); (4) OP, 'open pollination' – flowers freely exposed to insect visitors; and (5) HP, 'hand cross-pollination' – flowers supplemented with pollen by hand from a different hedge every 2 d to test for pollen limitation. Sample sizes of experiments with results presented in this paper are listed in Table 2, together with a list of crops growing in the fields adjacent to the hedges. The majority of hedges were located adjacent to fields without mass-flowering crops such as winter oilseed rape. This was because mass-flowering crops are attractive to pollinators and could potentially influence pollinator visitation rates and hence pollination and fruit-set of hedgerow plants. When hedges were located next to a mass-flowering crop, efforts were made to ensure a similar number of hedges were located next to a cereal crop.

For all pollination treatments, groups of flower buds were marked before anthesis using weather-proof enamel paint. Those assigned to the bagged treatments (BG, T50, M100, T100) were covered with a wire frame, and a mesh bag was placed over the frame and secured with a labelled twist tie. The end of the bag was sealed onto the branch using insulating tape to prevent insects from crawling inside. The wire frame avoided the likelihood of contact between the bag and the reproductive organs of the flowers, and prevented stigmas protruding through the bag.

Flowers in the HP treatment in 2007 were supplemented with pollen from flowers collected from a different hedge, less than 1 h previously, as pollen viability declines over time and can affect the success of hand cross-pollination (Stone *et al.*, 1995). Dehisced anthers from donor flowers were wiped over the stigma of the recipient flower, coating the stigma surface. All flowers in the HP treatment were cross-pollinated by hand every other day to maximize pollen

TABLE 2. *Experimental sample sizes in a randomized block design (final replication in graphs may differ as groups of buds were occasionally missing on return to the hedges)*

Species	Year	Site	Adjacent crop types	No. of hedges	No. of groups of buds per treatment (blocks per hedge)	No. of buds per group
Dog rose	2005	Rothamsted	Cereal/winter oilseed rape	3	8 –10	~3
	2005	Loddington	Winter oilseed rape	1	10	~3
Bramble	2005	Rothamsted	Cereal/winter oilseed rape	3	10	Unknown
	2005	Loddington	Cereal/winter oilseed rape	3	8 –10	Unknown
Blackthorn	2007	Rothamsted	Cereal/field beans (not in flower)/pasture	6	5 –10	~30
Hawthorn	2007	Rothamsted	Cereal/grassland	6	11	~15
Ivy	2007	Rothamsted	Bare field/crop at seedling stage	3	6	~30

delivery when stigmas were receptive. Each group of treatments (block) was positioned at intervals of at least 3 m along the hedge, along a height band of approx. 0·5–2 m above the ground (determined by ease of access to the buds).

After flowering, bags were removed to avoid shading of the developing fruits. A few days later, the numbers of immature fruits (i.e. small, unripe fruits) were counted in all treatments. This provided information on initial levels of pollination, whether through self-pollination or cross-pollination. In fruit-producing plants, abscission of unfertilized immature fruits (which may be due to inadequate pollination) occurs soon after flowering (Jackson, 1999; Tromp and Wertheim, 2005). Mature fruits that had been successfully pollinated, fertilized and retained by the plant were counted later in the season, shortly before ripening, i.e. before birds were attracted to them as a food source. In ivy, fruit ripening is highly asynchronous, and inflorescences were covered with netting to prevent bird predation before mature fruits had been counted.

Statistical analysis

For the 2005 experiment, the mean proportion (P) of flowers that set (1) immature and (2) mature fruits was compared for the bagged (BG) and open-pollinated (OP) treatments using ANOVA in GenStat (Payne *et al.*, 2007). As some groups of buds set no fruits, the original proportion was first adjusted using $P_{adj} = (r + 0{\cdot}5)/(n + 1)$, where r is the number of fruits and n the number of buds. These adjusted proportions were transformed to the logit scale before analysis. Back-transformed means and confidence intervals are presented. When experiments were done at both Rothamsted and Loddington, the site main effect and the interaction between site and treatment (i.e. bagged or open-pollinated flowers) were included as fixed effects in the model. The nested blocking structure of the ANOVAs according to the notation of Wilkinson and Rogers (1973) was as follows: SITE/HEDGE/POSITION or 'positions within hedges within sites' where the symbol / is the nesting operator ($A/B = A + A{\cdot}B$). This analysis could not be applied to data for bramble, which produces flower buds over a long period, making it difficult to obtain an accurate count of the number of buds bagged. Bramble fruit-set was therefore measured according to the presence/absence of fruit on each treatment group of buds, and these data were analysed using a χ^2 test.

For the 2007 experiment, the mean proportion of flowers that set (1) immature and (2) mature fruits for the bagged (T50, M100, T100), open-pollinated (OP) and supplementally pollinated (HP) treatments were also compared for each plant species using ANOVA in GenStat (Payne *et al.*, 2007). The overall treatment effect was partitioned into four specific 1 d.f. contrasts:

(1) bagged flowers (M100, T100, T50) vs. open flowers (OP and HP);
(2) open-pollination (OP) vs. hand cross-pollination (HP);
(3) continuously bagged flowers (M100, T100) vs. flowers bagged for half of flowering (T50);
(4) flowers bagged with muslin (M100) vs. flowers bagged with tulle (T100).

Comparison of confidence intervals was used to examine differences between open pollination (OP) and the bagging treatments (BG, M100, T100, T50). Back-transformed means and confidence intervals from the models are presented (except for treatments where no fruits were set).

RESULTS

Insect exclusion experiments, 2005

In 2005, experiments showed that dog rose and bramble flowers set fruits in the absence of insects. Initial immature fruit-set and final mature fruit-set of dog rose flowers was very high with more flowers setting immature fruits within the bags (mean immature fruit-set ± s.e. for $OP = 0{\cdot}76 \pm 0{\cdot}19$ and $BG = 0{\cdot}92 \pm 0{\cdot}17$, $F_{1,33} = 12{\cdot}70$, $P = 0{\cdot}001$). This trend was also found for mature fruit-set ($OP = 0{\cdot}73 \pm 0{\cdot}06$, $BG = 0{\cdot}84 \pm 0{\cdot}05$), although the difference between treatments was not statistically significant at the 5 % level (OP vs. BG: $F_{1,33} = 3{\cdot}62$, $P = 0{\cdot}066$). Experiments were done at both Rothamsted and Loddington, and there was no significant interaction between site and treatment. As it appeared that insect pollination is not necessary for fruit-set, no further experiments were done on dog rose.

Bramble set mature fruits in 92·3 % of inflorescences that had been bagged compared with 77·3 % of inflorescences that were left open to insect visitors ($\chi^2_1 = 3{\cdot}54$, $P = 0{\cdot}06$). As there was no statistically significant effect of insects on bramble fruit-set, no further experiments were done on this plant.

Experiments from 2005 showed that blackthorn, hawthorn and ivy fruit-set was significantly reduced when insects were excluded ($P < 0{\cdot}001$ for all plants). Consequently, these three plants were selected for further study. Results of more detailed experiments done in 2007 are presented below.

Blackthorn

Initial fruit-set in blackthorn was high in all treatments, but many of these fruits abscised and did not reach maturity. Flowers that were supplemented with pollen by hand (HP) initiated more fruits than open-pollinated (OP) flowers (Table 3, Fig. 1A). Flowers that were bagged for only 50 % of the flowering period (T50) set more immature fruits than those that were bagged for 100 % of the flowering period (M100 + T100; Table 3, Fig. 1A). Immature fruit-set was higher in the tulle bags (T100) compared with the muslin bags (M100; Table 3, Fig. 1A).

No mature fruits were set in either of the treatments where flowers were bagged for the whole of the flowering period (M100, T100; Fig. 1A). The mature fruit-set of blackthorn was substantially lower than immature fruit-set, but there was still evidence of pollen limitation as flowers that were supplemented with pollen (HP) set more mature fruits than open-pollinated (OP) flowers (Table 3, Fig. 1A).

Hawthorn

Immature fruit-set was greater than mature fruit-set, but both showed similar trends according to treatment (Fig. 1B). Flowers that were supplemented with pollen (HP) set more immature and mature fruit than open-pollinated (OP) flowers (Table 3, Fig. 1B). With the two meshes, immature fruit-set was higher in flowers that were bagged with tulle, but mature fruit-set was similar irrespective of the mesh used (Table 3, Fig. 1B). Flowers in the T50 treatment set more fruits than those that were bagged for 100 % of the flowering period (Table 3, Fig. 1B).

Ivy

Immature fruit-set was greater than mature fruit-set, but the trends were fairly similar across treatments (Fig. 1C). There was no difference between flowers that were supplemented with pollen (HP) and those that were open-pollinated (OP) in terms of both immature and mature fruit-set (Table 3, Fig. 1C). Initial immature fruit-set of flowers bagged with muslin and tulle was similar, but final mature fruit-set was higher in flowers that were bagged with tulle (Table 3, Fig. 1C). Flowers in the T50 treatment set more fruit than those bagged for the whole flowering period (Table 3, Fig. 1C).

DISCUSSION

Blackthorn, hawthorn and ivy all showed a significantly reduced proportion of flowers setting fruit when insects were excluded from flowers, confirming that insects provide a pollination service for these plants. Dog rose and bramble did not show a significant reduction in fruit-set with insect exclusion.

Dog rose

With regard to dog rose, there are three to four types in the UK and many hybrids between *R. canina* and other *Rosa* species (Graham and Primavesi, 1993). Knuth (1908) proposed

TABLE 3. *Results of pollination treatment contrasts for immature and mature fruit-set of blackthorn, hawthorn and ivy*

	Blackthorn		Hawthorn		Ivy	
Contrasts	Immature fruit-set	Mature fruit-set	Immature fruit-set	Mature fruit-set	Immature fruit-set	Mature fruit-set
OP vs. HP (pollen limitation)	$F_{1,188} = 32{\cdot}80$, $P < 0{\cdot}001$	$F_{1,185} = 173{\cdot}88$, $P < 0{\cdot}001$	$F_{1,241} = 22{\cdot}53$, $P < 0{\cdot}001$	$F_{1,241} = 44{\cdot}85$, $P < 0{\cdot}001$	$F_{1,68} = 0{\cdot}60$, $P = 0{\cdot}442$	$F_{1,66} = 0{\cdot}67$, $P = 0{\cdot}416$
M100, T100 vs. T50 (continuously bagged vs. bagged for half of flowering)	$F_{1,188} = 4{\cdot}81$, $P = 0{\cdot}03$	No fruit-set in M100 and T100 treatments	$F_{1,241} = 30{\cdot}09$, $P < 0{\cdot}001$	$F_{1,241} = 33{\cdot}38$, $P < 0{\cdot}001$	$F_{1,68} = 26{\cdot}79$, $P < 0{\cdot}001$	$F_{1,66} = 72{\cdot}68$, $P < 0{\cdot}001$
M100 vs. T100 (self- vs. wind-pollination)	$F_{1,188} = 4{\cdot}70$, $P = 0{\cdot}031$	No fruit-set in M100 and T100 treatments	$F_{1,241} = 4{\cdot}85$, $P = 0{\cdot}029$	$F_{1,241} = 2{\cdot}52$, $P = 0{\cdot}114$	$F_{1,68} = 0{\cdot}91$, $P = 0{\cdot}345$	$F_{1,66} = 6{\cdot}01$, $P = 0{\cdot}017$

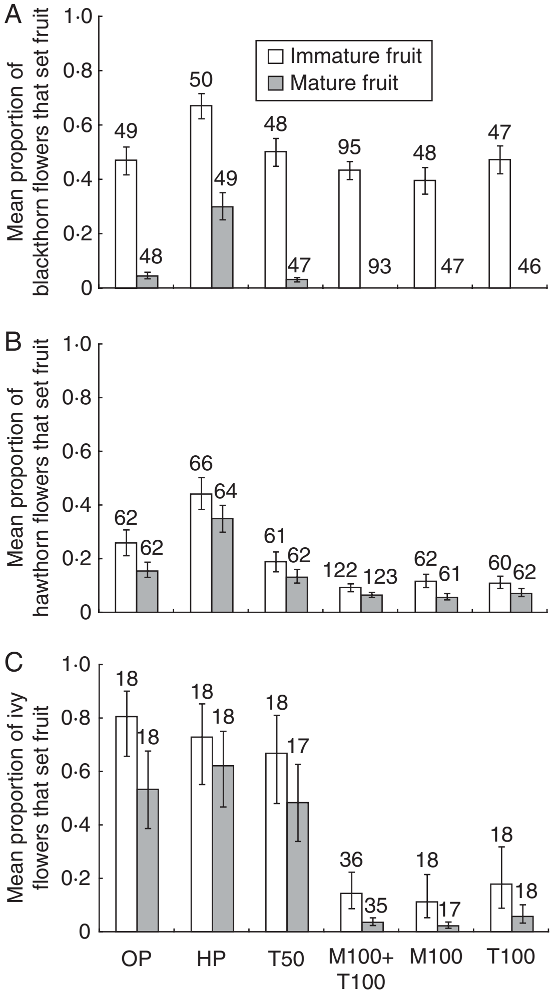

FIG. 1. Back-transformed mean proportions of (A) blackthorn, (B) hawthorn and (C) ivy flowers setting immature fruit and mature fruit (± 95 % confidence intervals) for five treatments (in 2007): open-pollinated (OP), supplemental cross-pollination (HP), bagged with muslin for 100 % flowering (M100), bagged with tulle for 100 % flowering (T100) or bagged with tulle for 50 % flowering (T50). Values above columns are number of groups of buds.

that self-pollination was possible, Jones (1939) suggested that flowers were self-incompatible, and a study of a UK population of dog rose showed that fruit-set was reduced when insects were prevented from visiting the flowers (Yeboah Gyan and Woodell, 1987*b*). More recent work has demonstrated that dog roses may be able to produce seeds through apomixis and self-pollination, although not as readily as through cross-pollination (Wissemann and Hellwig, 1997). The current findings showed that insect visits were unnecessary for fruit-set of the dog rose plants in this study, although the effect of insect exclusion on seed number was not assessed here.

Bramble

With regard to bramble, in the British Isles, *R. fruticosus* is a species aggregate of approximately 300 microspecies (Edees and Newton, 1988; Newton and Randall, 2004). Some *Rubus* species are able to set seeds and fruit in the absence of insects, and their breeding systems include pseudogamy, self- and cross-pollination, and vegetative reproduction (Nybom, 1985, 1988; Yeboah Gyan and Woodell, 1987*b*; Proctor *et al.*, 1996; Kollmann *et al.*, 2000). Both dog rose (Graham and Primavesi, 1993) and bramble (Edees and Newton, 1988) are taxonomically complex and may exhibit variable modes of reproduction, ranging in self-fertility and the degree to which they require insect pollinators for fruit-set. Some *Rubus* species have been documented as self-compatible, but the arrangement of their anthers determines the extent to which they self-pollinate (Nybom, 1985).

The proportion of flowers initiating fruit was higher than the proportion maturing for blackthorn, hawthorn and ivy. Among these species, blackthorn flowers showed the highest fruit initiation, but many of these were not retained to maturity. According to Stephenson (1981), immature fruits that are most likely to mature are those that (1) set first, (2) have the most seeds or (3) result from outcrosses. Self-pollination was the likely cause of abscission of many immature fruits, particularly those that were set from flowers that were bagged.

Blackthorn

Blackthorn flowers earliest in the season so it is of use to insects emerging from hibernation that are looking to establish nests, such as bumble-bee queens and solitary bees, and it may help honeybee colony development after the winter. Knuth (1908) reported that blackthorn can self-pollinate if insect visits are in short supply, although this was not based on empirical evidence. Subsequent research indicates that it is self-incompatible and sets no, or very few, fruits in the absence of insect visits (Guitián *et al.*, 1993), which supports the present findings. There was no mature blackthorn fruit in either type of bag, suggesting insects are the main pollen vectors in blackthorn and that their visits are essential for fruit-set.

Hawthorn

According to Clapham *et al.* (1989), hawthorn is self-incompatible, and it has been shown to set very few fruits through self-pollination (Bradshaw, 1971; Guitián and Fuentes, 1992). Some authors have described *Crataegus* spp. as having apomictic forms, with seeds developing without fertilization (Muniyamma and Phipps, 1979). In the Rosaceae subfamily Maloideae (of which *Crataegus* is a member), apomixis is usually associated with polyploidy (Campbell *et al.*, 1991) and it is unlikely that apomixis occurs in Britain, as *C. monogyna* is diploid (Dickinson and Campbell, 1991). However, one study of a British hawthorn population found that fruits were set in the absence of insects, indicating self-pollination or apomixis for those plants (Yeboah Gyan and Woodell, 1987*b*). The contrast between bagged flowers and flowers in the open-pollinated treatment was strong, with lower fruit-set when insects were excluded, suggesting insect pollination to be important. Reduced fruit-set of hawthorn in the absence of pollinators supports the majority of previous studies (Bradshaw, 1971; Guitián and Fuentes, 1992; but see Yeboah Gyan and Woodell, 1987*b*).

Ivy

Ivy is a native climber and because it flowers late in the season it is a useful resource for insects preparing for hibernation, such as bumble-bees, butterflies and queen wasps. Little is known of the mode of reproduction of ivy; anecdotal evidence that insect flower visits are required for pollination and fruit-set is provided by Wittrock (in Knuth, 1908), who noted that ivy flowering in a greenhouse did not produce fruit. In the present study, fruit-set was reduced when insects were prevented from visiting flowers, suggesting insect pollination is important. This study provides the first empirical evidence that ivy fruit-set requires insect visitors.

Pollen limitation

In the present study, blackthorn and hawthorn flowers that were hand cross-pollinated set more fruits than those flowers that were unbagged and open to insects, providing evidence of pollen limitation in plants at the study sites. In contrast, there was no difference in fruit-set between open-pollinated flowers and hand cross-pollinated flowers in ivy, suggesting that this plant species was not pollen-limited at the study sites. Pollen limitation occurs more frequently in woody plant species than in herbaceous species, which Larson and Barrett (2000) propose may be due to larger floral displays reducing the number of pollinator visits received by each flower. Despite a large floral display, and contrary to the results here, blackthorn was not pollen-limited at a Spanish site, suggesting that pollinators were more abundant or more effective at this site (Guitián *et al.*, 1993). Yeboah Gyan and Woodell (1987*b*) studied hawthorn at a UK site and, again in contrast to the results of the present study, found no evidence of pollen limitation, although the plants in their study showed similar fruit-set in bagged flowers to unbagged flowers, suggesting that there is variation in the reproductive system of hawthorn. Despite ivy showing reduced fruit-set in the absence of pollinators, it was not pollen-limited at these study sites in these years.

Pollen limitation in blackthorn and hawthorn may be a result of inadequate quantity or quality of pollen delivery to flowers (Aizen and Harder, 2007). If pollinator activity is too localized within a patch of flowers it may restrict the delivery of outcrossed pollen and increase geitonogamy (pollination between flowers on the same plant), which can compromise seed-set (Hessing, 1988; de Jong *et al.*, 1993). In the case of blackthorn, which readily reproduces vegetatively, a hedge could potentially contain areas dominated by genetically identical clones. Yeboah Gyan and Woodell (1987*b*) found that blackthorn fruit-set on open-pollinated branches was extremely low, which they suggest was due to their study population being largely clonal, thus restricting fruiting. Other researchers have demonstrated that fruiting or seed production can be restricted by the population structure of clonal plants (Eriksson and Bremer, 1993; references within Charpentier, 2002; Åigner, 2004; Honnay *et al.*, 2006). For plants that have a degree of self-incompatibility, large distances between plants can reduce outcross pollen deposition (Duncan *et al.*, 2004) and consequent seed- and fruit-set (Eriksson and Bremer, 1993; Kunin, 1993; Gibbs and Talavera, 2001). The number of individual plants within a hedge could also affect fruit-set, as seed- and fruit-set can be lower in small populations (i.e. with low numbers of individual plants) than in large populations (Kéry *et al.*, 2000; Jacquemyn *et al.*, 2002; Zorn-Arnold and Howe, 2007).

Wind-pollination

The use of different mesh bags provides some indication of the relative importance of selfing, wind and insects as pollen vectors. The muslin bags allowed the passage of only a small amount of airborne pollen (3 %), resulting in self- plus a little wind-pollination. Tulle bags allowed a greater quantity of airborne pollen grains to enter (40 %), resulting in some wind-pollination. If wind were an important vector of pollen, there should be a difference between treatments M100 (muslin) and T100 (tulle). Estimation of wind-pollination using the tulle bag treatment results is limited by the fact that 60 % of airborne pollen is still excluded, but it was the most practical solution to prevent insect visits and assess wind-pollination simultaneously.

There was no mature blackthorn fruit in either type of bag, suggesting that for blackthorn in this study, wind was not an important vector of the 'out-cross' pollen required for fruit-set. There was a small proportion of mature fruit-set in bagged hawthorn flowers, indicating either some self-fertility or some wind cross-pollination. The proportion of fruit-set for hawthorn was similar in tulle bags and muslin bags, suggesting little additional wind-pollination took place. Similarly, there was a small proportion of mature fruit-set in bagged ivy flowers, indicating either some self-fertility or some wind cross-pollination. The proportion of fruit-set was higher in tulle bags for ivy compared with muslin bags, which may be indicative of wind-pollination, but at a very low level.

Reducing the exposure of flowers to insects

Although no formal tests were done, excluding flower-visiting insects for half the duration of flowering partially to reduce the exposure of flowers to pollinators did not have a detrimental effect on the fruit-set of blackthorn, hawthorn or ivy. This may seem surprising, as supplementing flowers with 'out-cross' pollen increased fruit-set for blackthorn and hawthorn (providing evidence of pollen limitation in the open-pollinated controls), and excluding pollinators for the duration of flowering significantly reduced fruit-set in all three species. However, the relationship between pollen deposition and fruit-set is not necessarily linear, and mature fruit-set of flowers that were bagged for half of flowering in both hawthorn and blackthorn was intermediate between open and permanently bagged treatments, which is consistent with the conclusion that pollination is limiting in these plant species.

Understanding the links between insect pollinators, fruits and frugivorous birds is important for determining whether habitats for pollinators in agricultural areas need to be maintained or improved (through farmland management) to ensure a strong population of pollinators, and consequently a plentiful winter food resource for birds. This study has shown that blackthorn, hawthorn and ivy in British hedges require flower visits from insect pollinators to provide fruits, and it provides evidence that for two of these plants, blackthorn and hawthorn, pollinator abundance may limit fruit-set. It is now important to establish which flower-visiting insects are the most effective pollinators in these plants, by measuring insect visitation rates, pollen deposition and fruit-set parameters directly. It is also appropriate that improved management of farmland for insect pollinators (e.g. provision of 'pollen and nectar' flower strips along field margins; Carvell *et al.*, 2007) should be investigated as a means of increasing available fruit supply for farmland birds. Of course other factors such as hedgerow management also greatly affect the availability of some fruits (Sparks and Martin, 1999; Maudsley *et al.*, 2000; Croxton and Sparks, 2002), but sensitive hedge management and the provision of habitats for pollinators on farmland should help ensure a winter fruit supply for birds.

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