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Floral visitors and the importance of honey bee on buckwheat (*Fagopyrum esculentum* Moench) in central Belgium

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SUMMARY
Visitors to buckwheat (*Fagopyrum esculentum* Moench) flowers were studied in central Belgium during 2 months (July and September) over 2 years (2001–2002). Forty-nine different insect species, belonging to 18 families, were recorded. Over both years, species from the orders Diptera and Hymenoptera were the principal visitors. Hymenoptera were mainly represented by honey bees (*Apis mellifera* L.; 18.5 – 51.8% of total visitors), while Diptera were represented by syrphid flies and several other families. Variation in the visitor guild occurred at the beginning and the end of both Summers, as the proportion of honey bees was significantly higher in July than in September. No variation was detected in the relative abundance of insects between years. Honey bees appeared to be the most numerous visitors. Some syrphids and other Diptera species could, however, act as co-pollinators because of their high relative frequency and activity. In experimental cages, the effectiveness of honey bee pollination was good as these insects deposited compatible pollen on a majority (90 – 93%) of flowers without any discrimination between floral morphs.

Buckwheat (*Fagopyrum esculentum* Moench; Polygonaceae) is an annual, herbaceous plant that has been cultivated for centuries in Asia, North America and Europe for human and cattle consumption. Low seed-set constitutes a major constraint to buckwheat cultivation in the main growing countries. The causes of this reduced fertility remain essentially unknown, although environmental stresses (high temperatures, water stress), resource limitations, inadequate pollination or fertilisation problems (defective reproductive organs, failure of fertilisation due to self-incompatibility or seed abortion) have all been investigated (Marshall and Pomeranz, 1982; Björkman, 1995a; Goodman *et al*., 2001; Taylor and Obendorf, 2001; Halbrecq *et al*., 2005).

Buckwheat is a sporophytic self-incompatible distylous species pollinated by insects (Nagatomo and Adachi, 1985). The flowers are organised in racemes of cymes, and plants flower over a long period (Quinet *et al*., 2004). Individual flowers are open for less than 1 d, however, and contain only one ovule. They have five petaloid perianth segments and eight stamens that occur in an inner whorl of three, closely surrounding the styles, and an outer whorl of five (Free, 1993; Quinet *et al*., 2004). The eight nectaries alternate with the filaments of the stamens. The inner whorl of stamens dehisces outwards and the outer whorl dehisces inwards, so that an insect probing for nectar is dusted with pollen on both sides. The “pin” flowers develop long styles that project 2-3 mm above the anthers. The “thrum” flowers present short styles reaching to about the middle of the stamen filaments. Fewer pollen grains are produced in thrum than in pin flowers (Ganders, 1979; Namai and Fujita, 1995) and the pollen grains of thrum flowers are larger than those of pin flowers (Marshall and Pomeranz, 1982; Samborska-Ciania *et al*., 1989; Namai and Fujita, 1995). As in many other distylous species, thrum and pin plants are found at equal frequencies (Quinet *et al*., 2004).

Cross-pollination (transfer of pollen between the two different flower morphs) results in fertilisation less than 1 h after pollen deposition (Björkman, 1995a, b, c). Following self-pollination (intra-morph pollination), pollen tube growth is inhibited at two-thirds of the style-length in the long styles of pin flowers, and at the junction between the stigma and the style in the short styles of thrum flowers. The saturating pollen load for fruit initiation occurs at about ten pollen grains per flower (Björkman, 1995c). Anther sacs are normally emptied within 2 h, after which time there is little further pollen deposition (Björkman, 1995a). As no seed-set has been found in the absence of insect pollination, wind pollination is considered to be insignificant in this species (Björkman and Pearson, 1995).

Buckwheat is visited by a diverse fauna, including Hymenoptera: honey bees (*Apis mellifera* L.), bumble bees, solitary bees and wasps; Diptera: Syrphidae and others; and Lepidoptera, and other orders (Hedtke and Pritsch, 1993; Ogasahara *et al*., 1995; Lee and Choi, 1997; Wang and Li, 1998; Goodman *et al*., 2001; Carreck and Williams, 2002). In some countries, such as Germany, Poland, Korea, the USA and Australia, honey bees are the main pollinators (McGregor, 1976; Hedtke and Pritsch, 1993; Björkman, 1995a, c; Lee and Choi, 1997; Goodman *et al*., 2001). Accordingly, agronomists

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recommend the introduction of bee-hives to ensure satisfactory seed yield (McGregor, 1976; Wang and Li, 1998; Dalby, 2000; Goodman *et al*., 2001). Of the total floral visitors, however, honey bees represented only 5% in Japan, 35% in China and 37% in Russia (McGregor, 1976; Ogasahara *et al*., 1995; Wang and Li, 1998). In Belgium, a precise pollinator guild description for buckwheat has been lacking.

Björkman and Pearson (1995) attributed the variable and relatively low seed production to inadequate insect pollination (selfed and too few pollen deposits) or to maternal infertility. Honey bees may not be well-adapted to buckwheat pollination if they deliver too few pollen grains per visit, or deliver non-compatible pollen due to sequential visits to one morph. Their effectiveness still needs to be assessed.

The objectives of our study were: (1) to determine the guild of floral visitors to buckwheat in central Belgium; (2) to compare pollinator behaviour under field conditions; and (3) to test the effectiveness of honey bees at pollination in field cages.

MATERIALS AND METHODS

Plant species and study site

Buckwheat cultivar 'La Harpe' was planted using registered seed from Agri Obtentions (Guyancourt, France) on 6 June 2001 and 30 May 2002 in 1,100 m^2 plots at a density of 40 kg ha^{-1}. The plots were located around the Ferme Expérimentale de Marbaix, Chaumont-Gistoux (50°40'20" N; 4°38'00" E). In 2002, the plot was surrounded by diverse flowering species during the Summer; whereas in 2001, the plot was more isolated, in a maize field.

Floral visitors: diversity, frequency and foraging behaviour

To compare visitor guilds, the study was carried out at the beginning (July) and at the end (September) of two flowering seasons (i.e., 23–26 July 2001, 14–16 September 2001; and 21–23 July 2002, 3–6 September 2002). We made quantitative collections by capturing and killing all insect visitors within 1 m^2 quadrats of plants during 10 min periods. In total, sampling was spread over 7 d (total 22 h) in 2001, and 7 d (total 14 h) in 2002, on sunny days (temperature > 20°C).

On the same days, we also examined insect foraging behaviour on the flowers and on the plants (foraging for nectar, for pollen, or resting). The number of each visiting insect, the time spent per inflorescence, per plant and per quadrat, and the number of flowers visited were also recorded. In order to describe the pattern of insect foraging behaviour during the day, observations were pooled in three periods: < 11.30 h, 11.30 – 13.00 h, and > 13.00 h. For estimations of pollinator behaviour, the main floral visitors were described as belonging to one of the three main categories: honey bees, syrphids or Diptera other than syrphids.

Effectiveness of honey bee pollination

In July 2001, before flower set, three visitor exclusion cages were erected over the buckwheat plot. The cages (12.6 m^2) were made of a metallic frame covered by a white polyester windbreak net. One honey bee colony

TABLE I
Insect visitors to the flowers of buckwheat in central Belgium

Species	2001	2002
Coleoptera		
(a) Cantharidae		
Cantharis sp.	1	0
Ragonicha fulva	9	0
(b) Chrysomelidae		
Oulema sp.	1	0
Diptera		
(a) Calliphoridae		
Calliphoridae undet.	2	1
Lucilia caesar	16	5
(b) Muscidae		
Dasyphora sp.	0	1
Graphonia sp.	0	1
Musca autumnalis	10	0
Musca sp.	12	0
Muscidae undet.	2	8
(c) Sarcophagidae		
Sarcophaga carnaria	5	1
(d) Stratiomyidae undet.	1	0
(e) Syrphidae		
Episyrphus balteatus	14	2
Eristalis arbustorum	0	9
Eristalis nemorum	2	6
Eristalis pertinax	4	0
Eristalis tenax	4	12
Eumerus strigatus	1	0
Helophilus trivittatus	0	4
Lejogaster metallina	0	1
Melanostoma mellinum	4	3
Metasyrphus corollae	9	1
Metasyrphus luniger	2	0
Myatropa florae	2	1
Platycheirus peltatus	0	1
Scaeva pyrastri	0	1
Sphaerophoria scripta	3	8
Syrita pipiens	21	10
Syrphus ribesii	7	0
Volucella pellucens	0	1
Heteroptera		
Miridae undet.	4	4
Hymenoptera		
(a) Andrenidae		
Andrena undet.	0	19
Andrena bicolor	1	0
Andrena dorsata	10	0
Andrena flavipes	3	0
(b) Apidae		
Apis mellifera	NC	NC
Bombus lucorum	0	1
Bombus pascuorum	0	1
Bombus terrestris	8	0
(c) Halictidae		
Halictus rubicundus	1	0
Halictus sp.	1	0
Lasioglossum calceatum	1	0
(d) Tenthredinidae undet.	1	1
(e) Vespidae		
Vespula germanica	1	0
Vespula vulgaris	1	4
Lepidoptera		
(a) Pieridae		
Pieris rapae	1	1
(b) Plutellidae undet.	1	0
Mecoptera		
Panorpidae		
Panorpa communis	0	1
Neuroptera		
Chrysopidae		
Chrysoperla carnea	1	1
Total of different species	37	30

Values based on 10 min capture censuses in field trials, in 2001 and 2002. Undet. = undetermined. Numbers of honey bees were not indicated as these insects were not caught (NC).

TABLE II
Seasonal variation in the visitor guild of buckwheat

Season	Year	n	Honey bee visits (%)	Syrphid visits (%)	Diptera other than syrphid visits (%)
July	2001	44	49.1 ± 5.3†	16.4 ± 3.8	34.5 ± 5.3
	2002	6	51.8 ± 5.6	25.5 ± 7.2	22.7 ± 10.3
September	2001	14	18.5 ± 4.9	69.6 ± 4.7	11.8 ± 4.0
	2002	17	23.6 ± 4.2	49.9 ± 4.9	26.5 ± 4.2
Between seasons	*F*		15.63	55.27	4.19
	P		0.0002	< 0.0001	0.0441
Between years	*F*		2.64	6.69	0.22
	P		0.1084	0.0116	0.6432

Values based on 10 min observations in 1 m^2 quadrats in buckwheat fields, central Belgium in 2001 and 2002.
†Data presented as means ± standard errors.
n = number of observations.

(CARI, Louvain-la-Neuve, Belgium) of approx. 10,000 bees was introduced into each cage 2 d after they were erected, and remained inside until the end of the experiment.

At the end of the day (> 19.00 h), we collected ten flowers (8th node) per morph from each cage. These flowers were preserved in FAA [1:1:8 (v/v/v) formaldehyde, acetic acid, ethanol] and used to observe pollen grains and pollen tube growth in the styles. The styles were placed in 1.0 M NaOH for 1 h to soften them. They were then rinsed in distilled water and crushed in 0.1% (v/v) aniline blue solution in 1.0 M KH_2PO_4 pH 9.0, before being observed by fluorescence microscopy (Nikon Y FL, Analis, Belgium).

Statistical analyses

All statistical analyses were performed using the SAS statistical package (SAS Institute Inc., 1993). Proportions were arcsine square-root transformed before analysis. Analyses of variance in normally distributed data were performed with the general linear method procedures in SAS. Means are given with their standard errors.

RESULTS

Diversity and frequency of floral visitors

We identified 49 species of insects, belonging to 18 different families, from a total of 277 individuals captured on buckwheat flowers at the study sites (Table I). Three species of bumble bees among a total of 13 different species of Hymenoptera were recorded. Syrphids were the most diverse group, with 18 different species (mainly *Eristalis* spp., *Episyrphus balteatus*, *Sphaerophoria scripta*, and *Syrita pipiens*).

Only insects collected during quantitative sampling periods were used to assess the relative frequency of each visitor group. Over the 2 years, Diptera and Hymenoptera were the principal visitors. Hymenoptera were mainly represented by honey bees (18.5 – 51.8% of total visitors), while Diptera were represented by syrphid flies and other families. Variation in the visitor guild occurred between months (Table II). For example, honey bee proportions were significantly higher in July than in September ($F = 15.63$; $P = 0.0002$), whereas no difference was detected between years ($F = 2.64$; $P = 0.1084$). In September 2001 and 2002, honey bees represented only 18.5 – 23.6% of visitors, and syrphids were the principal visitors (49.9 – 69.6%).

Foraging behaviour of the main floral visitors

Honey bees and Diptera other than syrphids spent more time on a per quadrat or per plant basis than did syrphids (Table III). Honey bees visited more flowers than syrphids, and foraged systematically on many flowers in a single inflorescence. Honey bees visited in higher numbers in the morning, and their abundance decreased after 13.00 h. They spent a similar time per inflorescence, plant or quadrat, but visited fewer flowers after 13.00 h (Table IV).

Diptera other than syrphids spent more time per plant and per inflorescence than other visitors. No differences were observed in the time spent on inflorescences, plants or quadrats, or on the number of flowers visited among the different periods of the day (Table IV). They seemed to visit flowers for nectar, their probosces exploring the bottom of the corollas.

The foraging activity of syrphids was markedly less than that of other insects. Indeed, these flies were more stationary on an inflorescence, foraging for a longer period on a single flower, and also spending long periods on inflorescences without foraging. Only 23.3% of syrphids visited more than one flower per quadrat (*vs.* 79.9% of honey bees and other Diptera species). Contacts with stigmas were less frequent, and occurred mainly when the insects moved onto the inflorescence, especially for small species such as *Episyrphus* spp., *Platycheirus* spp., *Syrita* spp., or *Syrphus* spp. Active individuals visited fewer flowers and spent less time per inflorescence and per plant after 11.30 h (Table IV).

TABLE III
Foraging behaviour of the three main groups of insect visitors to buckwheat

Category	Honey bees	Syrphids	Diptera other than syrphids	*F*; *P*
Foraging time (s) per 1 m^2 quadrat	22.0 ± 2.1a†	9.9 ± 2.2 b	23.1 ± 2.8 a	2.89; 0.0213
Foraging time (s) per plant	8.3 ± 0.6 b	5.1 ± 1.1 c	14.9 ± 1.3 a	22.27; < 0.0001
Foraging time (s) per inflorescence	4.6 ± 0.3 b	3.7 ± 0.6 b	8.2 ± 0.6 a	24.98; < 0.0001
Number of flowers visited	6.9 ± 0.5 a	2.4 ± 0.3 b	5.6 ± 0.5 a	11.41; < 0.0001
n	228	49	117	

Values are based on 10 min observation censuses in 1 m^2 quadrats in July 2001, central Belgium.
†Data are presented as means ± standard errors. Values in a row followed by a different lower-case letter are significantly different.
n = number of observations.

TABLE IV
Evolution of the foraging behaviour of the three main groups of insect visitors to buckwheat, in relation to periods of the day

Visitors	Parameter	Morning	Mid-day	Afternoon	*F*; *P*
Honey bees	Time per quadrat (s)	25.0 ± 3.4†	20.7 ± 2.6	9.7 ± 2.0	2.19; 0.1100
	Time per plant (s)	8.3 ± 0.9	8.3 ± 0.8	8.6 ± 1.7	0.02; 0.9795
	Time per inflorescence (s)	4.3 ± 0.4	4.6 ± 0.4	6.3 ± 0.3	2.14; 0.1202
	Number of flowers visited	7.8 ± 0.7 a	6.8 ± 0.7 a	3.5 ± 0.5 b	4.27; 0.0151
	n	113	90	25	
Syrphids	Time per quadrat (s)	16.2 ± 4.9	8.9 ± 3.2	3.6 ± 0.6	3.31; 0.0462
	Time per plant (s)	8.6 ± 2.4 a	3.3 ± 1.0 b	2.5 ± 0.4 b	3.98; 0.0260
	Time per inflorescence (s)	5.7 ± 1.4 a	2.6 ± 0.5 b	2.4 ± 0.3 b	3.75; 0.0313
	Number of flowers visited	3.3 ± 0.6 a	2.6 ± 0.6 a,b	1.3 ± 0.2 b	3.86; 0.0282
	n	18	13	18	
Diptera other than syrphids	Time per quadrat (s)	37.1 ± 12.0	22.1 ± 3.6	18.2 ± 2.2	3.20; 0.0465
	Time per plant (s)	15.7 ± 4.1	12.0 ± 1.8	15.9 ± 1.7	0.80; 0.4509
	Time per inflorescence (s)	9.1 ± 1.8	7.8 ± 1.3	8.2 ± 0.6	0.25; 0.7814
	Number of flowers visited	6.4 ± 1.7	5.6 ± 1.0	5.4 ± 0.6	0.20; 0.8152
	n	27	16	74	

Values are based on 10 min observation censuses in 1 m^2 quadrats, in July 2001, central Belgium.
Morning refers to < 11.30 h, mid-day to 11.30h – 13.00 h, and afternoon to > 13.00 h.
†Data are presented as means ± standard errors. Values in a row followed by different lower-case letters are significantly different.
n = number of observations. Times are expressed in seconds.

Effectiveness of honey bee pollination

In the experimental cages, 90% (± 5.8%; n = 30) of pin flowers and 93% (± 3.3%; n = 30) of thrum flowers were fertilised at the end of the day. It is noteworthy that some flowers received no pollen at all (pin: 6.7 ± 6.7%; and thrum: 6.7 ± 3.3%). Only one pin flower out of 30 showed incompatible pollen. All fertilised flowers had more than ten compatible pollen grains.

DISCUSSION

Any examination of pollination systems must consider both the composition of the visitor guild and the effectiveness of each flower visitor (Herrera, 1988). In this study, buckwheat attracted a variety of visitors, mainly honey bees and Diptera. As we observed 49 different visitor species, but with only a fraction of the visitors having the potential to be effective pollinators, buckwheat may be described as a “moderate generalist” species (Herrera, 1988; Mahy *et al*., 1998; Olesen and Jordano, 2002). Small syrphids, Coleoptera or episodic visitors such as Lepidoptera or Neuroptera are unlikely to be efficient pollinators. The open and small flowers in buckwheat allow many unspecialised insects to visit for pollen and/or nectar, so diverse visitor assemblages are thus to be expected between different geographical regions or seasons.

Our study indicates that the visitor guild differed between the beginning and the end of the Summer, with a greater proportion of honey bees in July (buckwheat in full bloom) and a greater proportion of syrphids in September. The decrease in honey bee abundance in September could be linked to a decrease in nectar production (Naumkin, 1998; Alekseyeva and Bureyko, 2000). Variation in the composition of visitors to buckwheat has already been observed (Lee and Choi, 1997; Carreck and Williams, 2002). Hymenoptera (*Apis*, *Bombus*, *Halictus*, *Vespula*) and syrphids (*Episyrphus balteatus*, *Eristalis* sp., *Sphaerophoria scripta*) were also predominant in buckwheat fields in China and the UK (Wang and Li, 1998; Carreck and Williams, 2002).

With their high activity, and their foraging and prospecting behaviour that promote frequent contacts with stigmas, honey bees appeared to be the most effective pollinators of buckwheat at our study sites. As in other studies (McGregor, 1976; Free, 1993; Alekseyeva and Bureyko, 2000; Goodman *et al*., 2001), honey bees visited flowers predominantly between 09.00 – 12.00 h each day during our field trials. According to our observations, an individual honey bee visited an average of 20 flowers min^{-1}, and worked buckwheat for 4–5 h d^{-1}. These observations were similar to those in other studies with a mean of 14–15 flowers min^{-1} (Free, 1993; Hedtke and Pritsch, 1993). Moreover, like Björkman (1995b), in our experimental cages we did not detect any differences in the deposition of compatible pollen by honey bees between the two floral morphs.

Because of the wide range of cultivation conditions used for buckwheat, such a flexible insect assemblage could be beneficial to seed yield. We suggest that it could be useful to consider the availability of pollinators such as honey bees before choosing the location of buckwheat fields. More data are needed to determine whether honey bees, under field and open pollination conditions, are effective pollinators and whether buckwheat is affected by pollen limitation.

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