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The effects of honeybees Apis mellifera L. and leafcutter bees
Megachile rotundata (F.) on outcrossing between different
cultivars of faba beans (Vicia faba L.) in caged plots.

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ABSTRACT

The effectiveness of honey bees and leafcutter bees in cross pollinating two cultivars of faba beans within cages was assessed. Both honey bee and leafcutter bee positive-foragers crossed laterally between rows more often than along rows. The bees crossed to rows with different cultivars more frequently than to rows with the same cultivar. However, the direction and type of crossing did not differ significantly between the two species of bees.

Honey bees foraged in greater numbers, and on more flowers per bee than did leafcutter bees. The amount of crossing also varied with the cultivars that were used. Few bees crossed between the cultivars that diffed greatly in appearance and growth habit (Aladin and 15025). The amount of crossing between the cultivars Aladin and CM4 was much higher, ranging from 27 to 43 % in honey bees and 22 percent in leafcutter bees.

Introduction

Our laboratory has been involved in a collaborative research program with the International Center for Agricultural Research in Dry Areas (I.C.A.R.D.A.) at Aleppo, Syria where it is important, in breeding programs, to identify pollinating insects which are suitable for use within cages for cross-pollinating faba beans. Previous research, where various species of bees have been used to pollinate crops in cages or green houses, has been reviewed by several authors (e. g. Free, 1970; Szabo and Smith, 1970; Mc Gregor, 1976; and Torchio, 1976). Studies involving the use of honey bees or bumble bees to pollinate faba beans in cages have also been reviewed (Bond and Poulsen (1983); Stoddard and Bond (1987)).

In the present study, the effectiveness of honey bees and leafcutter bees for cross-pollinating two faba bean cultivars within a cage was assessed. The amount of outcrossing between faba bean cultivars was determined indirectly through observation of bee behavior and directly through the use of seed coat color and resistance to Ascochyta fabae (Leaf Spot) as genetic markers in the caged plots.

Methods

Two lines (2N740 and CM4) that had purple seed coat and two inbred lines (14434 and 15025) that were resistant to Ascochyta fabae (Leaf Spot) were planted in cages with the cultivar Aladin (that is susceptible to leaf spot).

The faba bean plots were seeded in rows at a depth of 5.1 cm, with 7.6 cm between plants and 30.5 cm between rows in both

1985 and 1986. In 1985, faba bean plots were planted in 3.05X6.09 m cages with 8 rows of plants 4.87 m long in each plot. One half of each row was planted with Aladin and the other half with one of the marker cultivars. The position of the two cultivars was reversed in alternate rows so that adjacent (rows of) plants consisted of different cultivars. Four caged plots were planted, one with each of the four lines. Honey bees were enclosed in the cage with the purple seed coat marker (line CM4) and leafcutters were enclosed in both cages with the Ascochyta resistant marker (lines 14434 and 15025). In 1986, the arrangement of the marker cultivars and Aladin in the cages was the same as in 1985 but, 3.05X3.05 m cages were used with 4 rows of plants 2.44 m long in each plot. Twelve caged plots were used, 6 plots with the seed coat marker (line CM4), and 6 plots with the resistant Ascochyta marker (line 15025). In 1986, the cultivar 15025, was also seeded one week later than Aladin to synchronize the bloom. Honey bees or leafcutter bees were each enclosed within two cages on both of the marker cultivars.

Colonies of honey bees (Apis mellifera L.) were housed in single chamber Langstroth hives and placed within the cages at ground level. The colonies were managed so that they contained uncapped brood and young foragers. In both 1985 and 1986 the colonies were replaced in the cages after about 10 days.

Nests of leafcutter bees (see Richards, 1984) (Megachile rotundata (F.)) 30.5 X 91.5 cm that contained approximately 1500 bees, were placed in the cages at crop height. In 1985, the nest was replaced after 5 days. In 1986, new nests were rotated every 4-5 days, the bees were also fed sugar syrup and buckwheat was

planted in the cages to provide leaf material for the bees.

The foraging behavior of both honey bees and leafcutter bees, and the amount of outcrossing that occurred between cultivars in cages, was observed in 1985 and 1986. Individual bees were followed and the type of forage collected, the number of flowers and plants visited, the length of visits and the amount of crossing that occurred between and within rows were recorded. The bees were observed for as long as possible or until they stopped foraging. The bees in the cages were observed throughout the day from the time foraging activity began until foraging ceased. The foraging behavior of honey bees was observed in the cages containing CM4 and Aladin for 7 days in 1985 and for 5 days in 1986. Leafcutter bee behavior was observed in the cages that contained CM4 and Aladin, for 3 days in 1986. The foraging behavior of bees in the cages that contained 15025 and Aladin was observed for 3 days in leafcutters, in 1985, and for 4 days in honey bees, in 1986.

To estimate the amount of crossing in cages with Ascochyta resistant cultivars and Aladin, the plants were harvested, and the seeds from the cultivar Aladin were planted in field plots the following season. The plants were inoculated with Ascochyta fabae at the four to six leaf stage. After inoculation the plants were watered and enclosed in plastic cages overnight. Plants were scored approximately fifteen days later to determine the percentage of plants that showed resistance to Ascochyta.

The amount of crossing in the cages with the purple seed coat marker gene (CM4) was estimated by growing the seed

harvested from the marker plot to maturity to obtain crossing rates.

Comparisons between leafcutter bees and honey bees for the average number of plants and flowers that each bee foraged on and the speed of visits were made using analysis of variance. The frequency and direction of crossing were analyzed using the log-linear model method for categorical data (Bishop *et al.*, 1975).

Results

The number of bees observed, the total number of plants visited, the total number of flowers visited and the mean number of flowers visited per minute for honey bees and leafcutter bees on each treatment are shown in Tables 1 and 2 respectively. Honey bee foragers were more abundant in the cages and tended to forage for longer periods than did leafcutter bees (Tables 1 and 2). Honey bees also visited more plants/bee ($p<0.001$) and flowers/bee ($p<0.001$) than did leafcutters (Tables 1 and 2). The speed of visits (flowers/minute) did not differ significantly between honey bees or leafcutter bees but there was a significant interaction ($p<0.05$) between the time of day that bees foraged and the year when the experiments took place. In 1985, the number of flowers visited per minute was higher in the afternoon than in the morning but in 1986, the number of visits/min. was higher in the morning than in the afternoon.

The percentage of honey bees that were positive foragers and crossed between rows of CM4 and Aladin, decreased from 65 % in 1985 to 40 % in 1986. However, the number of times that bees crossed between different rows did not vary significantly with

the species of bee, the time of day or the cultivar.

Both honey bees ($p<0.001$) and leafcutters bees ($p<0.009$) crossed laterally between rows of the same or different cultivars, more frequently than they crossed along a row (i.e. within a row, or vertically, to a different cultivar in another row containing the same or a different cultivar) (Tables 3 to 7). In honey bees the direction of crossing varied significantly ($P<0.007$) between the two cultivars and at different times of the day ($p<0.055$) (Tables 4 and 5). In the cultivar 15025, the proportion of bees that crossed laterally was higher than the proportion that crossed along a row in the morning, but this trend was reversed in the afternoon (Table 5). The cultivar, and the time of day had no effect on the direction of crossing in leafcutter bees (Tables 6 and 7).

Honey bees did not show floral constancy when foraging in the cages that contained CM4 and Aladin (Tables 3 and 4). The majority of the honey bees that were positive foragers crossed between rows of Aladin and CM4 and not between different rows of the same cultivar. The type of cross that occurred did not vary with the type of forage collected or with the time of day when forage was collected, but did vary between years ($p<0.004$) (Table 3 and 4). In 1986, honey bees were not observed crossing from rows of Aladin to other rows with Aladin (Table 4).

Leafcutters, that were positive foragers, also crossed more often between different rows of Aladin and CM4 than between different rows of the same cultivar (Table 6). The pattern of crossing was not significantly different from that observed in honey bees and did not vary with the time of day or the type of

forage that was collected.

The responses of both honey bees and leafcutter bees was significantly different ($p<0.0001$) in the cages that contained the cultivars 15025 and Aladin (Tables 5 and 7). Both honey bees and leafcutter bees tended to forage and cross mostly between different rows of the same cultivar (Aladin). Few honey bees and no leafcutter bees that were positive foragers were observed crossing between rows of Aladin and 15025.

Intra-plot outcrossing rates correlated with the observations of bee activity in the cages that contained Aladin and CM4. Outcrossing rates between Aladin and CM4 were highest in cages that contained honey bees and were much lower in cages with either leafcutters or no bees (Table 8). In the cages that contained Aladin and 15025 only 2.3 % (N=218 plants) of the plants confined with honey bees and 5.0 % (N=202 plants) of the plants confined with leafcutter bees showed resistance to Ascochyta indicating that little crossing occurred.

Table 1. Observations on the foraging behavior of honey bees in caged plots that contained alternating rows of two cultivars of faba beans.

Cultivars	Day	Time of observed	Number		Total # plants	Total # flowers	Mean # flowers/ visited
			of bees ved	Total time(min.) observed			
ALADIN+ CM4(1985)	a.m.	21	1777	58	111	4.4+.4	
	p.m.	70	5733	218	385	5.3+.4	
ALADIN+ CM4(1986)	a.m.	13	1578	30	65	3.5+.8	
	p.m.	42	4282	105	186	2.9+.2	
ALADIN+ 15025(1986)	a.m.	17	1810	37	85	3.1+.3	
	p.m.	41	4304	90	147	2.3+.2	

Table 2. Observations on the foraging behavior of leafcutter bees in caged plots consisting of two cultivars of faba beans.

Cultivars	Day	Time of observed	Number		Total # plants	Total # flowers	Mean # flowers/ visited
			of bees ved	Total time (min.) observed			
ALADIN+ 15025(1985)	a.m.	38	1880	89	135	4.9+.6	
	p.m.	3	109	4	4	5.5+1.2	
ALADIN+ CM4(1986)	a.m.	32	1697	51	70	3.9+.5	
	p.m.	32	2035	47	65	2.9+.4	

Table 3. Observations on the foraging behavior of honey bees in caged plots of faba beans that contained alternating rows of the cultivars Aladin and CM4, in 1985.

Time of Day	Type of Forage gathered	Number of bees observed	1 Number				2		3		4		5			
			Frq of Crossing 0	1	2	>3	N	Lateral	Vertical	AA	AR	RA	RR			
a.m.	pollen	4	.25	.25	.25	.25	4	.50	.50	.50	.25	.00	.25			
a.m.	nectar	3	.33	.67	.00	.00	2	1.00	.00	.50	.50	.00	.00			
a.m.	mixed	14	.40	.28	.16	.16	15	.91	.09	.27	.40	.27	.06			
a.m.	extrafl	49	.19	.42	.28	.11	64	.84	.16	.05	.48	.42	.05			
p.m.	pollen	14	.28	.34	.28	.00	16	.91	.09	.06	.37	.44	.13			
p.m.	nectar	25	.43	.31	.09	.17	23	.85	.15	.13	.39	.48	.00			
p.m.	mixed	31	.26	.43	.17	.14	36	.88	.12	.11	.31	.47	.11			
p.m.	extrafl	11	.27	.27	.27	.19	14	.90	.10	.00	.57	.43	.00			

1 Bees collecting pollen, nectar or pollen and nectar (mixed) that crossed over the stigma were positive foragers. Bees on extrafloral nectaries and did not cross over the stigmas were negative foragers.

2 The frequency with which bees crossed between rows

3 N=number of times that bees crossed to different rows

4 The direction of the row to which bees crossed. Laterally- to a row of the same or a different cultivar. Vertically- either within the same row to a different cultivar or, vertically, to a row of the same or a different cultivar.

A=ALADIN, R=CM4) AR-indicates a cross from a row with Aladin to a row with CM4.

Table 4. Observations on the foraging behavior of honey bees in caged plots of faba beans that contained alternating rows of the cultivars Aladin and CM4, in 1986.

Time of Day	Type of Forage gathered	Number of bees observed	1 Number				2		3		4		5			
			Frq of Crossing	0	1	2	>3	N	Lateral	Vertical	Type of Cross	AA	AR	RA	RR	
a.m.	pollen	2	.50	.50	.00	.00		1	1.00	.00		.00	.00	.00	1.00	
a.m.	nectar	1	1.00	.00	.00	.00		0	-	-		-	-	-	-	
a.m.	mixed	10	.70	.00	.30	.00		6	.64	.36		.00	.17	.33	.50	
a.m.	extrafl	42	.42	.22	.26	.10		42	.71	.29		.05	.35	.31	.29	
p.m.	pollen	24	.50	.25	.25	.00		18	.92	.08		.00	.28	.39	.33	
p.m.	nectar	9	.89	.00	.00	.11		3	1.00	.00		.00	.33	.33	.33	
p.m.	mixed	9	.40	.23	.23	.14		9	.65	.35		.00	.45	.33	.22	
p.m.	extrafl	62	.15	.37	.38	.10		90	.81	.19		.06	.37	.32	.25	

1 Bees collecting pollen, nectar or pollen and nectar (mixed) that crossed over the stigma were positive foragers. Bees on extrafloral nectaries and did not cross over the stigmas were negative foragers.

2 The frequency with which bees crossed between rows

3 N=number of times that bees crossed to different rows

4 The direction of the row to which bees crossed. Laterally- to a row of the same or a different cultivar. Vertically- either within the same row to a different cultivar or, vertically, to a row of the same or a different cultivar.

A=ALADIN, R=CM4) AR-indicates a cross from a row with Aladin to a row with CM4.

Table 5. Observations on the foraging behavior of honey bees in caged plots of faba beans that contained alternating rows of the cultivars Aladin and 15025, in 1986.

1 Number

Time Day	Type of Forage	Type of bees observed	Frq. of Crossing				N	Direction		Type of Cross			
			0	1	2	>3		Lateral	Vertical	AA	AR	RA	RR
a.m.	pollen	2	.00	1.0	.00	.00	2	.17	.83	1.00	.00	.00	.00
a.m.	nectar	9	.44	.33	.23	.00	7	.44	.56	1.00	.00	.00	.00
a.m.	mixed	6	.82	.06	.06	.06	0	-	-	-	-	-	-
a.m.	extrafl	11	.09	.18	.64	.09	19	.52	.48	.63	.11	.26	.00
p.m.	pollen	8	.75	.00	.25	.25	5	.75	.25	.21	.21	.37	.21
p.m.	nectar	20	.73	.15	.05	.00	5	.42	.58	1.00	.00	.00	.00
p.m.	mixed	13	.46	.46	.08	.00	8	.72	.28	1.00	.00	.00	.00
p.m.	extrafl	43	.54	.21	.10	.15	36	.69	.31	.78	.11	.08	.03

1 Bees collecting pollen, nectar or pollen and nectar (mixed) that crossed over the stigma were positive foragers. Bees on extrafloral nectaries and did not cross over the stigmas were negative foragers.

2 The frequency with which bees crossed between rows

3 N=number of times that bees crossed to different rows

4 The direction of the row to which bees crossed. Laterally- to a row of the same or a different cultivar. Vertically- either within the same row to a different cultivar or, vertically, to a row of the same or a different cultivar.

5 (A=ALADIN, R=15025) AR--indicates a cross from a row with Aladin to a row with 15025.

Table 6. Observations on the foraging behavior of leafcutter bees in caged plots of faba beans that contained alternating rows of the cultivars Aladin and CM4, in 1986.

Time Day	Type of Forage Gathered	Type of bees observed	1 Number				2		3		4		5			
			0	1	2	>3	N	Lateral	Vertical	AA	AR	RA	RR			
a.m.	pollen	14	.86	.14	.00	.00	2	.50	.50	.00	.50	.50	.00			
a.m.	nectar	16	.66	.20	.14	.00	7	.94	.06	.14	.29	.43	.14			
a.m.	mixed	2	1.00	.00	.00	.00	0	-	-	-	-	-	-			
a.m.	extrafl	0	-	-	-	-	-	-	-	-	-	-	-			
p.m.	pollen	3	1.00	.00	.00	.00	0	-	-	-	-	-	-			
p.m.	nectar	29	.67	.28	.05	.00	10	.86	.14	.10	.40	.40	.10			
p.m.	mixed	0	-	-	-	-	-	-	-	-	-	-	-			
p.m.	extrafl	0	-	-	-	-	-	-	-	-	-	-	-			

1 Bees collecting pollen, nectar or pollen and nectar (mixed) that crossed over the stigma were positive foragers. Bees on extrafloral nectaries and did not cross over the stigmas were negative foragers.

2 The frequency distribution showing the number of times that bees crossed to different rows

3 N=number of times that bees crossed to different rows

4 The direction of the row to which bees crossed. Laterally- to a row of the same or a different cultivar. Vertically- either within the same row to a different cultivar or, vertically, to a row of the same or a different cultivar.

A=ALADIN, R=CM4) AR-indicates a cross from a row with Aladin to a row with CM4.

Table 7. Observations on the foraging behavior of leafcutter bees in caged plots of faba beans that contained alternating rows of the cultivars Aladin and 15025, in 1985.

Time of Day	Type of Forage Gathered	Type of bees observed	1 Number				2		3		4		5			
			Frq of Crossing				N	Direction		Type of Cross						
			0	1	2	>3		Lateral	Vertical	AA	AR	RA	RR			
a.m.	pollen	17	.58	.42	.00	.00	7	.81	.19	1.00	.00	.00	.00			
a.m.	nectar	6	.50	.50	.00	.00	3	.38	.62	1.00	.00	.00	.00			
a.m.	mixed	15	.64	.27	.09	.00	6	.93	.07	1.00	.00	.00	.00			
a.m.	extrafl	51	.64	.29	.07	.00	19	.53	.47	.90	.05	.05	.00			
p.m.	pollen	1	1.00	.00	.00	.00	0	-	-	-	-	-	-			
p.m.	nectar	2	1.00	.00	.00	.00	0	-	-	-	-	-	-			
p.m.	mixed	0	-	-	-	-	-	-	-	-	-	-	-			
p.m.	extrafl	56	.57	.36	.07	.00	28	.78	.22	.92	.04	.00	.04			

1 Bees collecting pollen, nectar or pollen and nectar (mixed) that crossed over the stigma were positive foragers. Bees on extrafloral nectaries and did not cross over the stigmas were negative foragers.

2 The frequency with which bees crossed between rows

3 N=number of times that bees crossed to different rows

4 The direction of the row to which bees crossed. Laterally- to a row of the same or a different cultivar. Vertically- either within the same row to a different cultivar or, vertically, to a row of the same or a different cultivar.

5 (A=ALADIN, R=15025) AR-indicates a cross from a row with Aladin to a row with 15025.

Table 8. Inter-plot outcrossing rates between cultivars of faba beans in caged plots that contained honey bees, leafcutter bees or no bees.

<u>Cultivars in Cages</u>	<u>Treatment</u>	<u>Number of Cages</u>	<u>N</u>	<u>Percent** Crossing</u>
ALADIN+CM4(1986)	No bees	2	220	11.6
ALADIN+CM4(1985)	Honey bees	1	10476*	43.4
ALADIN+CM4(1986)	Honey bees	2	275	26.8
ALADIN+CM4(1986)	Leafcutter bees	2	303	21.7

N Total number of plants from which crossing was estimated

* Crossing was estimated from the number of seeds

** Crossing was estimated between Aladin and CM4 by using seed coat color.

Discussion

Honey bees that foraged on the faba beans were more abundant and foraged for longer periods of time than did leafcutter bees (Tables 1 and 2). In 1985, leafcutter bees actively foraged for pollen and nectar from the first to the second day after their nests were moved into the cages. However, after 2 days they foraged mostly on extrafloral nectaries (Table 7). Many leafcutter bees got "stuck" in the flowers and died while trying to obtain nectar. Therefore, in 1986, the bees were fed sugar syrup and buckwheat was planted in the cages to provide leaf material for nesting. A greater number of leafcutters were positive-foragers on faba beans in 1986 were larger than in 1985 and leafcutter bees were not observed foraging on the extrafloral nectaries (Table 6).

In this study, the honey bees foraged on extrafloral nectaries more frequently (in cages) (Tables 3 to 5) than in similar open plot studies (Jay et al., 1987). Honey bees usually visit extrafloral nectaries before flowering, during flowering (when no holes have been made by robbing bees) and towards the end of the flowering period (Stoddard and Bond, 1987). The extrafloral nectaries are thought to "maintain the interest" of bees in the crop (Stoddard and Bond, 1987). In this study, the honey bees collected extrafloral nectar in the early morning and late afternoon, shifting to the collection of floral pollen and nectar in the afternoon. Similar daily shifts in honey bee foraging behavior occur in open plots (Bond and Poulsen, 1983).

The honey bees actively foraged under a wider range of environmental conditions than did leafcutter bees. We observed

that at temperatures below 17°C and at high humidities the leafcutter bee activity in the cages ceased while honey bees continued foraging. Leafcutters generally do not start pollinating until temperatures reach 18°C Richards (1984). Leafcutters (foraging on cucumber) in cages and greenhouses are most efficient at temperatures of 30°C and high light intensities (Szabo, 1969). In this study, the daily temperatures inside the cages when bees could forage was fairly low, ranging from 10 to 30°C. The activity of leafcutter bees foraging on faba bean may be greater in areas with higher mean daily temperatures and light intensities.

The speed of positive visits for honey bees on faba beans (Tables 1) were similar to those reported by Bond and Poulsen (1983) and did not differ significantly from that of leafcutter bees (Table 1 and 2). However, the foraging speed and activity of leafcutters is affected by factors such as temperature, blossom height and light intensity and thus can differ significantly from that of honey bees (Szabo, 1969).

Both honey bees and leafcutter bees had similar crossing patterns (Tables 4 to 7) and tended to cross laterally between rows (to different cultivars), more frequently than along a row (to either the same or a different cultivar) even though the distance between rows was greater than the distance between plants. The alternation of rows used in this study resulted in large proportions of bees crossing between cultivars given the row spacing that was used. However, if the rows are wider apart this may not apply. Honey bees usually show a strong tendency to

work along rather than across rows when the distance between plants is less than the distance between rows (Bond and Poulsen, 1983).

The proportion of honey bees that crossed between cultivars was lower in 1986 than in 1985 (Tables 4 and 6). This may have been due in part to the weather conditions or the stage of development of the crop on the specific days when bees were observed. However, the percentage of crossing in the plants (Table 8) at the end of the season was also lower and thus the reduction in crossing was probably related to weather conditions over the entire season.

Leafcutters tended to "rest" on the sides of the cages after foraging on only one or two flowers. Thus, crossing in leafcutters may have been underestimated because the "resting bees" may have subsequently returned to a different cultivar at a later time without having been recorded. However, this did not appear to be a significant problem as the plant crossing estimates correlated with those of bee observations.

Few honey bee, and no leafcutter bee, positive-foragers crossed between the cultivars 15025 and Aladin (Tables 5 and 7). This low level of crossing was also reflected in the percentage of plants that showed resistance to Ascochyta (2.5 and 5 % for honey bees and leafcutter bees respectively). In 1985, there were problems with the synchronization of bloom in the cages with Aladin and 15025. However, in 1986 planting dates were staggered to help synchronize the bloom but the crossing was still very low (Table 5). These low levels of crossing (in Aladin and 15025 cages) may have been due to differences in the

growth habit of the two cultivars. The cultivars Aladin and CM4 were very similar in appearance, however the inbred cultivar 15025 was quite a bit smaller and more "spindly" than Aladin and did not appear to be as "attractive" to the bees. Foraging bees do tend to show some constancy to plant type; differences in growth habit, floral structure and color are known to affect outcrossing rates (Bond and Poulsen, 1983).

In this study inter-plot outcrossing rates correlated well with observed bee activity and with expected values in the literature that range from 4-84% (mean approximately 35%). Plant survival rates, the method of calculating crossing (i.e. total crossing rates etc.), disease, and stress are factors that can alter estimates of crossing thus the estimates vary widely between studies and only measure a "function" of the amount of cross breeding (see, Bond and Poulsen 1983). There was some crossing in the cages with no bees. This may indicate that some wind pollination, mechanical pollination or pollination from other insects (e.g. thrips) may have occurred.

Acknowledgments

The authors thank the International development Research Center of Canada for providing the funds to conduct this study, Dr. G.H. Hawtin for his direction in establishing priorities in this study, and Rheal La Frenier for his technical assistance. We also thank Dr. C.C. Bernier and Dr. K. Rashid of the Dept. of Plant Science, University of Manitoba for their co-operation and facilities and Sandra Fuller for her technical assistance.

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