Benefits of Insect Pollination in Brassicaceae

Subjects: Entomology | Plant Sciences | Agriculture, Dairy & Animal Science

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Cultivated Brassicaceae attract a wide variety of pollinators. In both self-compatible and self-incompatible crop species, meta-analysis indicates that seed yield (Y), silique set (SQS), number of siliquae/plant (NSQ), and the number of seeds/silique (NSSQ) increase when plants are insect-pollinated compared to when there is no insect pollination. The weight of seeds (WS), however, increased in self-incompatible species but not in self-compatible ones as a result of insect pollination. Overall, the percentage of studies showing a positive effect of insect pollination on yield parameters was higher in self-incompatible than in self-compatible species. It was shown that the ability of self-compatible species to reproduce does not fully compensate for the loss of yield benefits in the absence of insect pollination.

breeding system | insect pollination | pollinators | yield

1. Introduction

Pollinators are essential in food production and plant biodiversity conservation [1][2][3]. More than 78% of angiosperm species are pollinator-dependent [4]. This obligatory and facultative cross-pollination makes insect pollination essential, or at least a positive factor, in maximizing fertilization. Brassicaceae, as most angiosperms, are xenogamous and either require cross-pollination or can be facultatively cross-pollinated [5][6][7][8]. With a few exceptions, flowers in the family Brassicaceae have four sepals, four petals diagonally disposed as a cruciform corolla, two carpels, and six stamens arranged in a tetradynamous pattern (four longer inner ones and two shorter outer ones) [9][10][11]. Except for one species in the genus *Lepidium* [12], plants in the family Brassicaceae have hermaphrodite flowers [13].

Plants in the family Brassicaceae attract a broad diversity of pollinators, including honeybees such as *Apis mellifera* L. (Hymenoptera: Apidae), solitary bees, such as *Andrena* spp. (Hymenoptera: Andrenidae), and hoverflies, such as *Eristalis tenax* L. (Diptera: Syrphidae) [8][14][15]. The family Brassicaceae includes many economically important species, some of which are widely used as vegetables, oils, condiments, or ornamental plants [16][17]. For example, oilseed rape *Brassica napus* L. subsp. *napus*, which is one of the most cultivated oilseed Brassicaceae, has seen the price of its seeds rise by more than 30% in the last three years [18]. To increase crop yield and gross margins in *B. napus*, bee pollination can be more beneficial than pesticide applications [19]. The potential benefit of pollination is most important in cruciferous crops in which the harvest consists of seeds and fruits (i.e., siliquae). Among these are all oilseed Brassicaceae, the most important of which is rapeseed, also known as canola, *B. napus* [20]. Other cruciferous oilseed crops include field mustard *Brassica rapa* L. subsp. *oleifera*, synonymous with *Brassica campestris*; Indian mustard *Brassica juncea* (L.) Czern.; Ethiopian mustard

Brassica carinata A. Braun; camelina *Camelina sativa* L. (Crantz); radish *Raphanus sativus* (L.) Domin; and white mustard *Sinapis alba* L. These oilseed crops can be used for oil, biofuel, and/or lubricant production [21][22][23][24][25][26][27][28]. The seeds of *S. alba* are used for mustard elaboration, and the siliquae of *R. sativus* can be used as a vegetable (**Table 1**). Yield parameters in the family Brassicacae are often measured by seed yield, but other yield parameters such as the number of siliquae/plant and seed oil content are also used [29][30][31].

Table 1. Most common use and breeding system in the cultivated crops of the family Brassicaceae included here. In self-compatible plants, both outcrossing and selfing occurs, while in self-incompatible ones, the main breeding system is outcrossing.

Plant	Most Common Names	Most Common Use	Main Breeding System	References on Breeding System
Brassica carinata A. Braun	Ethiopian mustard	Leaves, seeds for oil	Outcrossing and selfing	[32][33]
Brassica juncea (L.) Czern.	Brown mustard, Indian mustard	Leaves, seeds for oil	Outcrossing and selfing	[32][34]
Brassica napus L.	Rapeseed, canola	Seeds for oil	Outcrossing and selfing	[32][35]
Brassica oleracea L.	Cabbage, broccoli, cauliflower	Leaves, inflorescences	Outcrossing, self-incompatible	[33]
Brassica rapa L.	Turnip, field mustard	Leaves, root, seeds for oil	Outcrossing, self-incompatible	[32][34]
Camelina sativa L. (Crantz)	Camelina, German sesame	Seeds for oil, leaves	Outcrossing and selfing	[32][36]
Eruca sativa Mill.	Arugula, rucola	Leaves	Outcrossing, self-incompatible	[29]
Raphanus sativus (L.) Domin	Radish	Roots, seeds oil	Outcrossing, self-incompatible	[33]
Sinapis alba L.	White mustard	Seeds for table mustard, oil [37]	Outcrossing and selfing	[32][34]

ndance is ducted to examine the effect of insect pollination in yield parameters across the broad spectrum of cruciferous crops, nor have there been meta-analyses examining the effects of insect pollination on yield parameters separately for self-compatible and self-incompatible species. Self-incompatible Brassicaceae species typically have larger flowers than self-compatible ones in order to attract pollinators, with a significantly reduced seed set in the absence of pollinating agents [32][38]. Given the evolutionary advantage of selfing as a reproductive assurance when there is a paucity of pollinators [39], insect pollination is likely to have more marked positive effects on yield parameters in self-incompatible Brassicaceae species than in self-compatible ones.

2. Insect Pollination Effect on Yield Parameters in Cultivated Brassicaceae

Table 2 shows the crops for which the effect (increase, decrease, non-significant) of insect pollination on seed yield parameters was studied in the family Brassicaceae (reports from at least seven studies).

Table 2. Publications were consulted for the main yield parameters (a total of seven or more studies found) which were: seed yield measured as seed weight/(plant, area, or open flower) (Y); weight of seeds (1, 100, or 1000 seeds) (WS); number of siliquae/(plant or area) (NSQ); number of seeds/(silique or open flower) (NSSQ); silique set (SQS); silique length (SQL); number of seeds/(area, plant, or branch) (NSP); seed germination (G); and oil content of seeds (O). An increase, decrease, or neutral effect of insect pollination on yield parameters is shown in red, blue, or green, respectively. Studies included in the meta-analysis for at least one yield parameter are marked with two asterisks (**) in the Note column.

Plant Species	Yield Parameter									References	Note
	Y	WS	SQS	NSQ	NSSQ	SQL	NSP	G	O		
B. carinata					Red					[29]	**
	Red									[40]	
B. juncea	Red			Red	Red	Green				[29]	**
	Red	Red	Red	Red		Red			Red	[41]	**
	Red									[42]	
		Green	Green		Red			Green		[43]	
			Red	Red						[44]	**
	Red									[45]	
	Red	Red	Red	Red	Red	Red		Red	Red	[46]	**
		Red	Red		Red					[47]	
		Red	Red		Red					[48]	
	Red	Green						Green	Green	[49]	
	Red	Red		Red	Red					[50]	
B. napus					Red	Red				[29]	**
		Green				Green	Green			[51]	
	Green	Blue		Green	Red		Green			[52]	Male-fertile line

Plant Species	Yield Parameter									References	Note
	Y	WS	SQS	NSQ	NSSQ	SQL	NSP	G	O		
										[52]	Male-sterile line
										[53]	
										[54]	
										[55]	
										[56]	**
										[57]	**
										[58]	**
										[59]	
										[31]	
										[60]	
										[61]	**
										[62]	**
										[63]	Hybrid
										[63]	Non-hybrid
										[64]	**
	*	*								[65]	**
					*					[66]	
										[67]	
					*					[68]	**
										[69]	Hybrid
										[69]	Non-hybrid
										[70]	
										[71]	
										[72]	
										[73]	Hybrid

Plant Species	Yield Parameter									References	Note
	Y	WS	SQS	NSQ	NSSQ	SQL	NSP	G	O		
										[73]	Non-hybrid
										[74]	
										[75]	
										[76]	**
										[77]	
										[78]	
										[79]	
										[80]	
										[81]	
										[82]	
										[29]	**
B. oleracea										[83]	
										[84]	Cabbage **
										[84]	Cauliflower **
										[85]	
B. rapa										[29]	**
										[86]	**
										[87]	**
										[88]	
										[89]	
										[90]	
										[91]	
										[92]	
										[93]	
										[94]	**

% of crop species benefit from pollinators, contributing to an estimated 9.5% of the value of the world agriculture production devoted to human food [1][139]. Other studies conducting meta-analysis have also shown the benefits of insect pollination for plant reproduction and yield in crops in general [140][141][142], in the plant species of particular natural habitats [143], and in particular crops, such as fava bean [144], oilseed rape [37], and

Plant Species	Yield Parameter									References	Note
	Y	WS	SQS	NSQ	NSSQ	SQL	NSP	G	O		
										[95]	**
.										[96]	
C. sativa										[36]	**
E. sativa										[29]	**
R. sativus										[29]	**
										[97]	**
										[98]	[53][146]
										[99]	**
										[100]	**
										[101]	
										[102]	
S. alba										[29]	
										[103]	

* Most common response when several cultivars, planting dates, or experimental locations were used.

... variety of pollinators attracted to flowers of cultivated Brassicaceae, honeybees, *A. mellifera* and other *Apis* spp., seem to be the dominant reported species. However, other Apidae, such as bumblebees, mining bees (Andrenidae), sweat bees (Halictidae), and hoverflies (Syrphidae) are also commonly reported as pollinators of these crops. Since *A. mellifera* is often the most common floral visitor, the higher frequency of visits can make it a more effective pollinator than other more efficient pollinators that visit flowers less often [15][127][128][129]. Other pollinator families, such as Lepidoptera, were not among the most abundant pollinators found in the studies reviewed. However, lepidopterans such as *Pieris* spp. (Lepidoptera: Pieridae) were sometimes reported among less common pollinators [49][124][132]. Pollinator diversity can also enhance crop pollination and yield [87].

4. Insect Pollinators of Crops of the Family Brassicaceae

The main pollinators reported for these crops are shown in **Table 3**, with the top pollinators for all of them being honeybees (*Apis* spp.), such as *A. mellifera*, *A. cerana*, *A. dorsata*, and *A. florea*, and mining bees (Andrenidae). Additional pollinators often reported for these crops are other Apidae (other than *Apis* spp.), such as bumblebees (*Bombus* spp.), sweat bees (Halictidae), and hoverflies (Syrphidae) for *B. juncea*; other Apidae and Syrphidae for *B. napus*; Halictidae and Syrphidae for *B. oleracea*; Syrphidae, Halictidae, and other Apidae for *B. rapa*; Syrphidae and Halictidae for *C. sativa*; other Apidae and Syrphidae for *E. sativa*; and Halictidae and Syrphidae for *R. sativus*. In the case of *B. napus*, single visit pollen deposition has been shown to be the highest for *Bombus* spp., Andrenidae, and *A. mellifera* (with median pollen grain depositions of 341, 335, and 202, respectively) [93][156], while single visit efficiency in terms of the number of seeds/silique produced was highest for *Halictus* and *Apis* spp. [57]. In *B. napus*, there were no differences in honeybee and bumblebee visits between open-pollinated and hybrid varieties [105], but bee abundance was higher and pollination deficit was lower in conventional compared to genetically modified Roundup Ready plants [106]. In the case of *B. rapa*, efficiency, given by stigmatic pollen grain deposition, by a single visit of an insect to a flower, was highest for *Bombus terrestris* L. [15][107]. In addition to efficiency, the abundance and number of insect visits makes some insects more effective pollinators than others.

The importance of pollinators for yield in Brassicaceae crops makes it paramount to ensure that agricultural practices are compatible with pollinator conservation. Pest management and other agricultural practices can affect the effect of pollination on yield, and this has been shown for *B. napus* [67][71][77][154][155] and *B. rapa* [94][106]. In general, the application of pesticides, if unavoidable, should be performed following practices that minimize the risk of pollinator poisoning, such as using pesticides of low toxicity and not spraying when bees are foraging [104][157]. Unfortunately, some farmers growing cruciferous crops are unaware of the harmful effects that pesticide applications can have on pollinators and other beneficial insects [158][159]. Pollinator conservation practices, such as setting pollinator reservoirs [160][161][162], could also be implemented in the vicinity of Brassicaceae crops to ensure that pollinators can be sustained throughout the year. Pollinator reservoirs can also help in conservation biological control [163][164]. Some of the crops included here, such as *B. rapa* and *S. alba*, have also been used as insectary plants [165]. Proximity to natural habitats with natural vegetation and where wild bees can locate their nests can also

Enhance the abundance of wild bees [96][107][120]. The floral visitor of crucifer crops can also temporarily benefit wild bees because of the food resources that boost [121].

Because of this, A. mellifera will be the most common flower visitor, can be considered a more effective pollinator than less efficient pollinators that visit flowers less often [15]. However, one or two bee flower visits may be sufficient to achieve a full seed set in *B. rapa* flowers [108][109].

In conclusion, it is shown that insect pollination has a positive effect on Y, SQS, NSQ, and NSSQ in both self-compatible and self-incompatible cultivars of the family Brassicaceae. As a result of insect pollination, only the self-incompatible species ... other than the reproductive advantages of self-compatibility in the absence of pollinators, insect pollination could have more positive effects on yield parameters in self-incompatible species than in self-compatible ones. However, among the yield parameters investigated, SW was the only one that did not improve in self-compatible species as a result of insect pollination in Brassicaceae crops. The most reported pollinators are Apidae, Andrenidae, Syrphidae, and Halictidae.

Table 3. Insect pollinators of the family Brassicaceae. Abbreviations for pollinator families are as follows: Apidae of the genus *Apis* (A), other Apidae different than *Apis* spp. (OA), Andrenidae (An), Bombidae (B), Calliphoridae (C), Coccinellidae (Co), Colletidae (Col), Empididae (E), Formicidae (F), Halictidae (H), Megachilidae (M), Muscidae (Mu), Pieridae (P), Scarabaeidae (S), Sesiidae (Se), Stratiomyidae (St), Syrphidae (Sy), Tabanidae (T), and Vespidae (V). Abbreviations for countries are as follows: Australia (A), Bangladesh (B), Belgium (Be), Brazil (Br), China (C), France (F), Germany (G), India (I), Ireland (Ir), Nepal (N), New Zealand (NZ), Pakistan (P), Sweden (S), United Kingdom (UK), and United States of America (US).

Plant	Number of studies reporting main pollinators in a given family																			Countries	References
	A	OA	An	B	C	Co	Coll	E	F	H	M	Mu	P	S	Se	St	Sy	T	V		
B. carinata	3	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I, US	[29][33][40]
B. juncea	14	4	4	-	-	1	-	-	1	3	1	2	-	-	1	-	3	-	1	B, I	[29][33][43][45][47][49][110][111][112][113][114][115][116][117][118]
B. napus	12	8	4	-	1	-	-	1	-	2	1	1	2	-	-	-	4	-	-	Be, Br, C, F, G, I, Ir, UK, P, S	[60][29][31][33][57][58][119][120][121][122][123][124][125]
B. oleracea	8	1	2	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	-	I	[29][83][85][126][127][128][129][130]
B. rapa	11	5	3	-	-	1	2	-	-	3	1	-	-	2	-	1	7	1	-	A, I, N, NZ, P	[15][29][33][89][95][96][107][108][109][112][131][132][133][134]
C. sativa	2	-	1	-	-	-	-	-	-	2	-	-	-	-	-	-	2	-	-	Be, G, US	[36][135][136][137][138]

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Plant	Number of studies reporting main pollinators in a given family																			Countries	References
	A	OA	An	B	C	Co	Coll	E	F	H	M	Mu	P	S	Se	St	Sy	T	V		
E. sativa	3	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	I, P	[29][33][133]
R. sativus	4	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	I, P	[29][33][99][100]
S. alba	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	I	[29][33]
Total	59	19	22	1	1	2	2	1	1	13	3	3	2	2	1	1	20	1	1		

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