

Diversity of Pollinator Insects in Relation to Seed Set of Mustard (*Brassica rapa* L.: Cruciferae)

TRI ATMOWIDI^{1*}, DAMAYANTI BUCHORI², SJAFRIDA MANUWOTO²,
BAMBANG SURYOBROTO¹, PURNAMA HIDAYAT²

¹Department of Biology, Faculty of Mathematics and Natural Sciences, ²Department of Plant Protection,
Faculty of Agriculture, Bogor Agricultural University, Darmaga Campus, Bogor 16680, Indonesia

Received August 29, 2007/Accepted December 5, 2007

Pollinators provide key services to both natural and agricultural ecosystems. Agricultural productivity depends, in part, on pollinator populations from adjacent seminatural habitats. Here we analysed the diversity of pollinator insects and its effect to seed set of mustard (*Brassica rapa*) planted in agricultural ecosystem near the Gunung Halimun-Salak National Park, West Java. At least 19 species of insects pollinated the mustard, and three species, i.e. *Apis cerana*, *Ceratina* sp., and *Apis dorsata* showed a high abundance. The higher abundance and species richness of pollinators occurred at 08.30-10.30 am and the diversity was related to the number of flowering plants. Insect pollinations increased the number of pods, seeds per pod, seed weights per plant, and seed germination.

Key words: diversity, pollinator insects, social bees, solitary bees, seed set, *Brassica rapa*

INTRODUCTION

Pollinators provide key of ecosystem services to both natural and agro-ecosystems. Almost all flowering plant species in tropical lowland rain forests are pollinated by animals (Bawa 1990). Positive relationships between the richness and abundance of floral resources and pollinator diversity and activity have been found at the landscape level (Steffan-Dewenter *et al.* 2002; Klein *et al.* 2003). On sunflowers, wild bees may contribute more pollination services through enhancement than that of direct pollination, due to they concentrate on male flowers rather than female ones. Bees visiting only male flowers make no direct contribution to its pollination but do contribute through enhanced pollination (Greenleaf & Kremen 2006).

Animal pollinators are thought to contribute in 15 up to 30% of global food production (McGregor 1976; Roubik 1995) and bees are recognised to be the most important pollinating taxon (Delaplane & Mayer 2000). Farmers obtain adequate pollination services by bringing large numbers of honey bees to crop fields (Greenleaf & Kremen 2006). Single plant species, both wild and crops, may also receive a pollination service of higher quality and quantity as a result of this increased pollinator activity (Klein *et al.* 2003; Potts *et al.* 2004). In addition to the honey bee, *Apis mellifera* L., which is often advocated as the only practical pollinator, the use of solitary bees and flies has been proposed (Delaplane & Mayer 2000). Pollination is an ecosystem service of major economic and societal value, which is endangered by recent declines in pollinators (Daily 1997). Destruction and fragmentation of habitats adversely affect the diversity and abundances of

solitary wild bees and bumblebees (Kremen *et al.* 2002; Steffan-Dewenter *et al.* 2002).

In this study, we used mustard species *Brassica rapa* L.: (Cruciferae). This species is an important crop in Asia (Rubatzky & Yamaguchi 2000). Flowers of *B. rapa* are formed in the stem elongates after the leaf stop growing. The stem has many branches, small leaves, and bright yellow flower. Each flower has four petals and six stamens of which two stamens are shorter than the style but four others are longer. There is a single stigma at the tip of the style. Nectar is excreted at the bases of the short stamens and ovary. The flower is open for three days. Approximately, 95% of species of Crucifers require cross-pollination, although some cauliflower varieties are self-fruitful. Wind is not a good pollinator in *Brassica* spp. and bees play an important role in pollen vectors. Selfing in the absence of cross pollination generally reduces seed yield, seed size, and yield in subsequent generation (Delaplane & Mayer 2000). Two species of Cruciferae, *B. rapa* (syn. *campestris*) and *B. oleraceae* were identified as plants with Sporophytic Self-incompatibility (SSI) (Takayama & Isogai 2005). Self-incompatible plants require pollen transfer from plant to plant (Wallace *et al.* 2002). Earlier studies on the effects of pollinator insects to seed set of Cruciferae had been reported. In male sterile oilseed rape (*B. napus*), yields of the species were increased by honey bee pollination (Westcott & Nelson 2001; Steffan-Dewenter 2003). Similarly, in sarson (*B. campestris*), insects pollination increase the seed yield, caused formation of well-shaped, larger grain, and more viable seed (Khan & Chaudory 1995).

Here, we analysed the diversity of pollinator insects in relation to seed set of mustard (*B. rapa*). The diversity of pollinator insects was observed in relation to time and flower phenology. Effects of pollinator insects on reproductive success of *B. rapa* were quantified by measuring the number of pods, seeds, and seed viability.

*Corresponding author. Phone/Fax: +62-251-622833,
E-mail: atmowidi@ipb.ac.id

MATERIALS AND METHODS

Study Area. The study was conducted from December 2006 up to May 2007 in an agricultural landscape located in Cipeuteuy village, Kabandungan, Sukabumi District, West Java, in the margin of Gunung Halimun National Park at an elevation of approximately 845 m asl.

Observation of Pollinator Visitation. One hundred plants of mustard were planted in agricultural landscape for studied the pollinator diversity. Plants were planted three times, i.e. November 30, 2005, January 26, 2006, and March 16, 2006. The plants were fertilized by biofertilizer and no insecticide applications. Observations of pollinator insects were carried out using scan sampling (Martin & Bateson 1993) for 15 min per hour, starting from 07.30 h until 14.30 h on sunny days to measure abundance and species composition of floral visitors. Insect observations were conducted on January 12-February 9 (21 days), March 1-24 (16 days), and April 11-May 8 (16 days), 2006, respectively. Observations of flower-visiting insects were conducted from the start of flowering until approximate 95% of the flower faded. Samples of insect visitors were caught by sweep netting for species identification in the laboratory.

Measuring the Effects of Pollinator Insects to Seed Set. To measure the effects of pollinator insects on reproductive success of mustard, before flowering started, 100 plants of mustard were caged by insect screen of which pollinators had no access to flowers, and 100 plants were exposed to pollinators. Caging of plants was replicated three times. After the end of the fruiting period, we harvested 50 plants and counted the number of pods per plant, seeds per pod, seeds per plant, and seed weights per plant for each treatment. Seed viability was measured using the percentage of germinated seeds. One hundred of seeds were germinated in watered

cotton in the plastic pans. Measurements were replicated 60 times for each treatment and the percentage of seed germination was measured.

Data Analysis. The number of species and individual of pollinator insects related to time of observation and the number of flowering plants were shown in graphics. Student's t test and Analysis of variance (ANOVA) were used to test for differences between two or more groups and group differences were established using the Scheffe test at the 95% level.

RESULTS

Diversity of Pollinator Insects. A total number of 5,955 pollinator insects associated with *B. rapa* were observed. They were belonged to 19 species and 4 orders (Hymenoptera, Lepidoptera, Coleoptera, and Diptera, for 95, 2.17, 2.07, and 1%, respectively). Three species of flower-visiting insects showed a high abundance i.e. *A. cerana* (43.1%), *Ceratina* sp. (37%), and *A. dorsata* (8.4%). Additionally, six species of Lepidoptera (*Nyctemera* sp., *Parnara guttata*, *Eurema hecabe*, *Potanthus* sp., *Jamides virgulatus*, and *Neptis hylas*), and one species of Coleoptera (*Papilia biguttata*) and Diptera (*Shyrphus balteatus*) visited mustard flowers, but they all accounted for less than 3% of the total number of observed pollinators (Table 1).

Diversity of Pollinator Insects Related to Time and Flower Phenology. Species richness of pollinator insects increased from 07.30 h and the highest species richness occurred at 10.30 h and subsequently decreased. The number of individual pollinators reached the peak at 08.30 h and decreased subsequently (Figure 1). Flowering of *B. rapa* were lasted for 20-25 days, and the peak flowering occurred at 10-15th days. The number of species relatively constants to the density of flowers (Figure 2), but the number of individual

Table 1. Species and individual number of pollinator insects on mustard flowers

Taxon	Species	Individual number				Percentage (%)			
		Jan-Feb	March	Apr-May	Total	Jan-Feb	March	Apr-May	Total
Hymenoptera	<i>Apis cerana</i>	1,468	733	366	2,567	50.57	46.16	25.00	43.11
	Apidae, subfamily Apinae								
	<i>Apis dorsata</i>	5	493	0	498	0.17	31.05	0.00	8.36
	<i>Trigona</i> sp.	8	0	1	9	0.28	0.00	0.07	0.15
	Apidae, subfamily Xylocopinae								
	<i>Xylocopa caerulea</i>	37	27	5	69	1.27	1.70	0.34	1.16
	<i>X. confusa</i>	28	21	20	69	0.96	1.32	1.37	1.16
	<i>X. latipes</i>	7	2	6	15	0.24	0.13	0.41	0.25
	<i>Ceratina</i> sp.	1,072	207	923	2,202	36.93	13.04	63.05	36.98
	Colletidae, subfamily Hylaeinae								
	<i>Hylaeus</i> sp.	32	13	62	107	1.10	0.82	4.23	1.80
	Halictidae, subfamily Nomiinae								
	<i>Nomia</i> sp.	67	0	21	88	2.31	0.00	1.43	1.48
	Scoliidae								
	<i>Compsomeris lindenni</i>	0	1	0	1	0.00	0.06	0.00	0.02
Lepidoptera									
	Arctiidae								
	<i>Nyctemera</i> sp.	25	0	2	27	0.86	0.00	0.14	0.45
	Pieridae								
	<i>E. hecabe</i>	7	3	1	11	0.24	0.19	0.07	0.18
	Lycaenidae								
	<i>J. virgulatus</i>	0	4	1	5	0.00	0.25	0.07	0.08
	Nymphalidae								
	<i>N. hylas</i>	0	1	0	1	0.00	0.06	0.00	0.02
	Hesperiidae								
	<i>P. guttata</i>	12	7	1	20	0.41	0.44	0.07	0.34
	<i>Potanthus</i> sp.	10	0	3	13	0.34	0.00	0.20	0.22
Coleoptera									
	Scarabaeidae								
	<i>P. biguttata</i>	42	39	48	129	1.45	2.46	3.28	2.17
Diptera									
	Syrphidae								
	<i>S. balteatus</i>	82	37	4	123	2.82	2.33	0.27	2.07
	<i>M. argyrocephala</i>	1	0	0	1	0.03	0.00	0.00	0.02
Total number		2,903	1,588	1,464	5,955	100	100	100	100

Jan: January, Feb: February, Apr: April

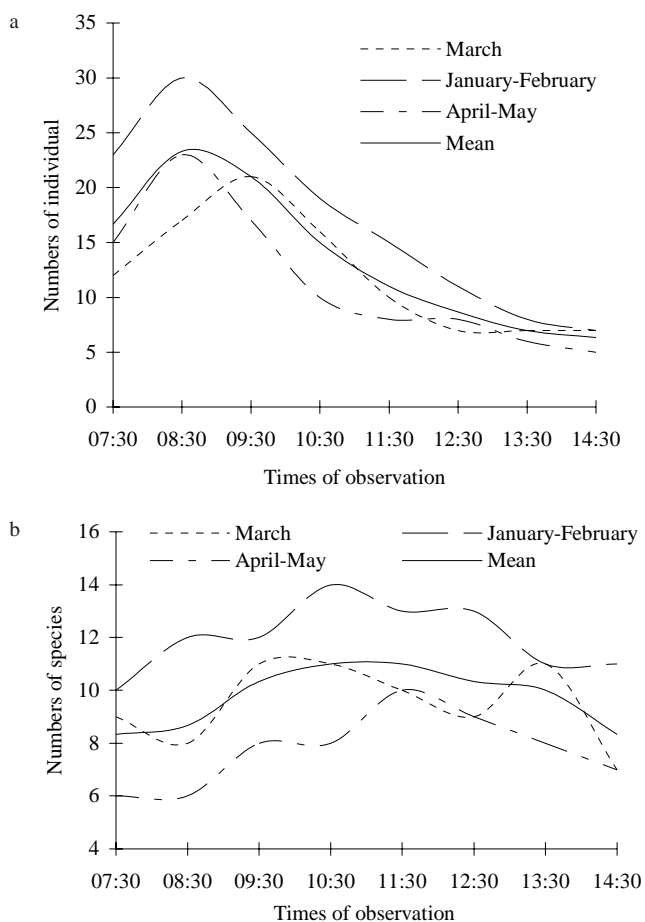


Figure 1. Number of individual pollinators (a) and number of species pollinators (b) found in *B. rapa* flowers at different time (7.30 am-14.30 pm) and month (January-May) observations.

pollinators increased with increasing number of flowering plants ($y = 1.555x + 29.121, r^2 = 0.396$) (Figure 3).

Fruit Set of *B. rapa* Related to Pollinator Diversity.

Diversity of pollinator insects affected to reproductive success of mustard. The number of pods, seeds per pod, and seed weight per plant was higher in non-caged plants (14.9 pods, 12.8 seeds, and 6.4 g, respectively) than those in caged plants (5.4 pods, 6.5 seeds, and 0.6 g, respectively). When plants were exposed to pollinators, the number of pods, seeds per pod, seeds per plant, and seed weight increased by 178.8, 98.2, 932.5, and 931.9%, respectively (Table 2). Additionally, insect pollinations also increased *B. rapa* seed germinations. Seed germination was higher in non-caged plants (92.72%) than that in caged-plants (90.3%) (Table 3). The number of seed set of *B. rapa* increased with the increasing individual number of pollinators (Figure 4).

DISCUSSION

Diversity of Pollinator Insect. Our result showed that bees (95% of total pollinator number) were the main pollinators in *B. rapa*. All other pollinators, such as Coleoptera, Diptera, and Lepidoptera were only of minor importance (5%). Three

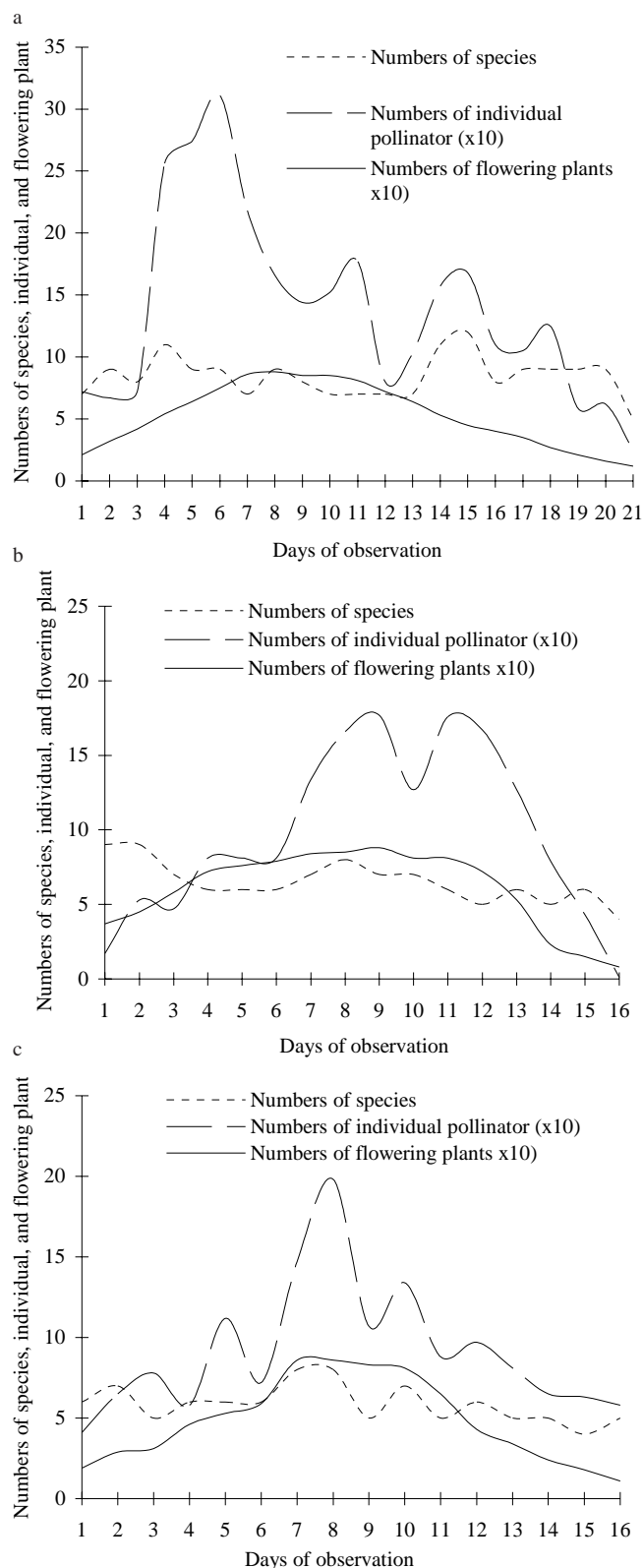


Figure 2. Number of species and number of individual of pollinator insects related to the number of flowering plants at different observation times (a: January-February, b: March, and c: April-May).

species of bees (Apidae: Hymenoptera), *A. cerana*, *A. dorsata*, and *Ceratina* sp., were found dominance (5,267 individuals,

Table 2. Differences of *B. rapa* reproductive success between plants accessible by pollinators and plants which were caged

Plant reproductive success	January-February		March		April-May		Average		Increased yield (%)
	Opened	Caged	Opened	Caged	Opened	Caged	Opened	Caged	
Plant height	120.9	120.9	117.6	112.9	103.3	115.2	113.9a	116.3a	-
Number of racemes per plant	33.0	19.1	9.6	6.0	7.1	4.9	16.6a	10.0b	65.6
Number of pods per plant	13.5	3.2	21.8	6.3	9.5	6.6	14.9a	5.4b	178.8
Number of seeds per pod	13.9	5.2	14.2	7.2	10.4	7.1	12.8a	6.5b	98.2
Number of seeds per plant	6220.0	373.2	2936.5	274.3	802.4	317.1	3319.7a	321.5b	932.5
Seed weights per plant (gr)	13.0	0.9	4.8	0.5	1.3	0.5	6.4a	0.6b	931.9

Different letter(s) in the same row indicated significant difference among means based on two-sample t test.

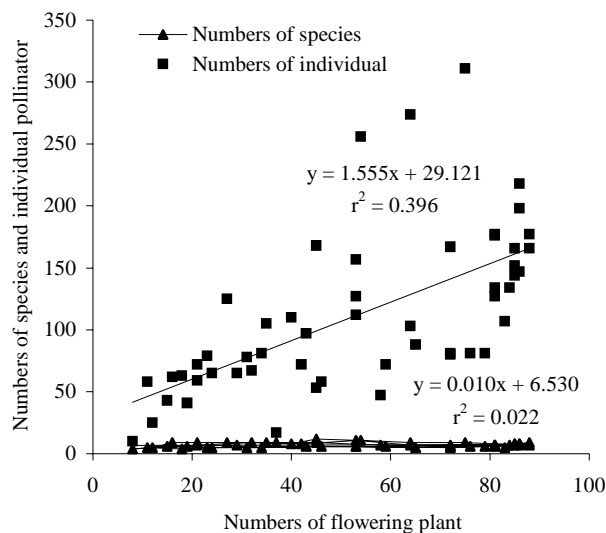


Figure 3. Relationships between the number of individual pollinators, number of species and number of flowering plants of *B. rapa*.

Table 3. Seed germination (%) of mustard from caged and opened plants

Plant experiment	Seed germination (average % \pm st.dev)			
	Jan-Feb	March	April-May	Average
Opened	90.2a \pm 3.11	94.35a \pm 3.92	93.60a \pm 3.52	92.72a \pm 3.92
Caged	88.6a \pm 2.41	90.45b \pm 3.89	91.85a \pm 3.08	90.30b \pm 3.41

Different letter(s) in the same row indicated significant difference among means based on two-sample t test.

88.45%). *A. cerana* and *A. dorsata* are social bees and *Ceratina* sp. is solitary bee (Michener 2000). The number of *A. cerana* workers in a colony ranges from several to twenty-five thousands (Sasaki *et al.* 1995). Its distribution range from tropical Asia across China as far as Siberia. The vast natural distribution is covering a wide range of climatic zones and therefore is responsible for the diverse associations between honey bees and flora of wild plants and cultivated crops (Sihag & Mishra 1995). Unlike *A. cerana*, *A. dorsata* (giant honey bee) generally build nests in the forest. A third species of pollinator bee that has a high abundance is *Ceratina* sp. (Ceratinini: Xylocopinae). Ceratinini are traditionally regarded as solitary bees whose females never meet their progeny, but in many species female work through the completed cell series and sometimes female work in same nest with division of labor (Michener 2000).

Most of social bees were found in higher densities within and near the forest than at greater distance from forest,

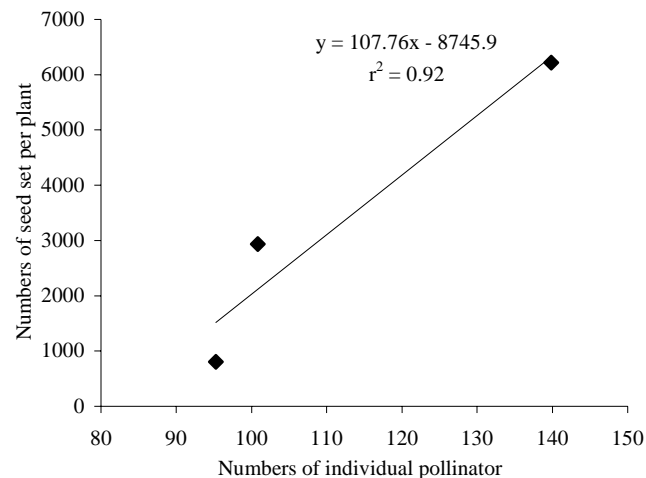


Figure 4. Relationships between the number of individual pollinators and seed set of *B. rapa*.

presumably because forest offer a wealth of suitable nesting sites for the colonies of honey bees and stingless bees foraging into the adjacent land-use system. In contrast, most of solitary bees built nest outside the dense forest, preferring less shaded and less humid agroecosystem that offered open areas for the many ground-nesting species and herbaceous plants for pollen and nectar resources. Solitary bees profited from land-use intensity, because increasing land-use intensity led to more nesting sites for ground-nesting solitary bees and possible competition between social and solitary bees (Klein *et al.* 2002). Social bees (*A. cerana* and *A. dorsata*) were found in higher abundant at *B. rapa* flowers than solitary bee (*Ceratina* sp.). Dense flower patches of *B. rapa* in this study was more attractive for social bees, because social bees prefer mass-flowering crops (Steffan-Dewenter & Tschamtkke 1999). Klein *et al.* (2003) reported that when coffee flowers are abundant, social bees are attracted in large numbers. Solitary bees were more abundant at times when only single flowers were blooming, with correspondent to the declining of social bees.

Other pollinator species as shown in Table 1, have a lower frequent visitation (less than 3%). A lower frequent visitation of these species suggest as being less important pollinators. Although, *Pieris rapae* (Lepidoptera) and several species of stingless bees were reported as efficient pollinators on other plants (Amano *et al.* 2000; Kandori 2002). Two pollinator species, i.e. *P. bigutata* (Coleoptera) and *S. balteatus* (Diptera) were relatively the more frequent visitations (2.17 and 2.07%) (Table 1).

On *B. rapa* flowers, pollinator insects visited early morning (before observation time) and at the end of observation (14.30 h) we still found those insects. But, the peak abundance of those insects occurred between 08.30 and 09.30 am (Figure 1a). A higher abundance of pollinator insects in 08.30-09.30 am were due to higher abundance of two Hymenopteran pollinators species (*A. cerana* and *Ceratina* sp.). Similar visitation were showed by two pollinators (*T. carbonaria* (Apidae) and *Leiopcoctus speculiferus* (Colletidae) that visited *Persoonia virgata* (Proteaceae) between 09.00 and 11.00 h (Wallace *et al.* 2002).

Visitation time of pollinator insects, generally occur in the morning, related to plant resources, especially pollen and nectar availability. Most probably, both availability of pollen and nectar are higher in the morning than in the afternoon and evening. Most bees (Hymenoptera: Apoidea) collect nectar, which provides energy, and pollen, which supplies the protein for larval growth. Pollen and nectar are essential resources for bees because both are required for survival, and one cannot be completely substituted for the other (Plowright *et al.* 1993). Despite this joint requirement and the concurrent production of pollen and nectar by many plant species, bees do not often collect pollen and nectar simultaneously. This behaviour implies that the criteria affecting preferences for plant species depend on nectar whether pollen or nectar is the focus of a bee's foraging (Rasheed & Harder 1997). In *B. napus*, Pierre *et al.* (1999) reported the highest nectar secretion was observed at the beginning of flowering with a mean temperature of 12.1 °C and the lowest nectar secretion the day after when the temperature was only 9.1 °C, the second lowest nectar secretion occurred at the end of flowering, despite warm weather (19.9 °C). Nectar resource diversity is not the only factor that is important in structuring communities of pollinator insects (Potts *et al.* 2004). Several other important components were the flower morphology (Neal *et al.* 1998) and the combination of sugars in the nectar (Hainsworth & Hamill 1993).

Abundance of pollinator insects on *B. rapa* were related to flowers abundance (Figure 2). Similarly, abundance of pollinator insects increased during flowering season of the temperate grassland (Kandori 2002; Hegland & Todland 2005) and abundance of *A. mellifera* on *Erythronium umbilicatum* were varied greatly among sites and years (Kandori 2002). Dense flower patches seem to be the more attractive resource for many different bee species at smaller spatial scales (Veddeler *et al.* 2006). In *Phacelia* sp., Westphal *et al.* (2006) also reported mass-flowering fields represent more rewarding resources and bumblebees could collect more rewards per unit time than the ones in the environments with sparse resources, which presumably had longer search and travel times. Once a bumblebee has discovered a rewarding foraging site, it will memorise the location, and exploit the site as long as it will be rewarding (site and flower constancy). Thus, on future foraging trips it will spend less time for searching.

Fruit Set of *B. rapa*. Seed set of *B. rapa* could be increased significantly by the number of pollinator insects. The number of pods, seeds per pod, and seed weight per plant increased in non-caged plants. In non-caged plants, the number of pods and seeds per pod increased almost three and two times, respectively. The number of seeds and seeds weight per plant in non-caged plants increased more than ten times compared with caged plants (Table 2). Insect pollinations also increased the seed germinations of *B. rapa*, although it was not clearly different (Table 3). The high yields of *B. rapa* in non-caged plants are mostly caused by cross-pollination by insects. Population of cross-fertilising plants contains a large number of heterozygous genes. Obviously, heterozygosity was advantageous for the plants. Heterozygosity gives plants of high growth efficiency and yield. The breeding of cross-fertilising plants is now based on the heterosis effect (Mohr & Schopfer 1995).

Brassica rapa belongs to Sporophytic Self-incompatibility (SSI) as reported by Takayama and Isogai (2005) that require pollen transfer from plant to plant. This indicates that pollinators must be regularly transferring pollen between plants (Wallace *et al.* 2002). In the self-incompatible plants of this family, pollen tubes do not develop properly on the stigma that express the same *s*-haplotypes as the pollen's parent. Self-pollen rejection results in abrogated pollen hydration, or a rapid arrest of the pollen tube growth at the stigma surface (Takayama & Isogai 2005). Insect pollination leads to earlier cessation of flowering, and more synchronous pod and seed ripening, thereby possibly increasing the weight of seed harvest (Westcott & Nelson 2001).

The number of individual pollinators affected seed set of *B. rapa*. Seed set and abundance of pollinator insects was positively related (Figure 4). Also Wallace *et al.* (2002) reported for *P. virgata* that natural pollinators can be extremely efficient in pollinating flowers and thereby increasing the fruit set. Steffan-Dewenter (2003) reported in male-sterile oilseed rape (*B. napus*) that insect pollination can positively affect several yield components. However, these effects depend on cultivar and growing conditions and total yields are often not increased due to the considerable compensatory capacity of oilseed rape (Westcott & Nelson 2001). Insect pollination is one factor influencing the seed set. Other factors are nutrient availability (Juenger & Bergelson 1997), genetic variability (Oostermeijer *et al.* 1994), patch size (Agren 1996), flower and leaf herbivory (Herrera 1995), and interactions between herbivores and their natural enemies (Thies & Tschardtke 1999). Combination of several complementary pollinator species differing in flower-visiting behaviour could be of more importance for high fruit set than only pollinator abundance (Klein *et al.* 2003). But overcrowding in cages with different species may result in over exploitation of pollen and damage of flowers, thereby possibly lowering the fruit set (Mesquida *et al.* 1988).

In conclusion, this study provides insights into the importance of pollinator insects to help plant pollination, included mustard, an importance crop in the tropic. Our results indicate a diversity and abundance of pollinator

insects, especially bees, plays a significant role in fruit set of mustard. Enhancement of pollinator insects as part of crop management should be considered by farmers. This could be done by a reduced use of pesticides, providing nesting sites for solitary bees, and improving pollen and nectar availability for bees.

ACKNOWLEDGEMENT

We greatly thanks to Sih Kahono, Rosichon Ubaidillah, Yayuk Rahayuningsih, Woro Nurjito, and Pudji Aswari from Zoological Museum, Indonesian Institute of Science, for their assistance in identification of the pollinator insects. We also thanks to Tuani Z. Rambe for his field assistance. We are grateful to the two anonymous referees for the comments on this manuscript. For financial support we thanks to Graduate Scholarship Program (BPPS), Directorate General of Higher Education, Ministry of National Education of Indonesia and Center for Conservation and Insect Study (PEKA Indonesia).

REFERENCES

- Agren J. 1996. Population size, pollinator limitation, and seed set in the self-incompatible herb *Lythrum salicaria*. *Ecology* 77:1779-1790.
- Amano K, Nemoto T, Heard TA. 2000. What are stingless bees, and why and how to use them as crop pollinator? *A Rev JARQ* 34:183-190.
- Bawa KS. 1990 Plant-pollinator interactions in tropical rain forests. *Ann Rev Ecol Syst* 21:399-422.
- Daily GC. 1997. *Nature's service: social dependence on natural ecosystem*. Washington: Island Pr.
- Delaplane KS, Mayer DF. 2000. *Crop pollination by bees*. Oxon: CABI Publ.
- Greenleaf SS, Kremen C. 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *PNAS* 37:13890-13895.
- Hainsworth FR, Hamill T. 1993. Foraging rules for nectar: food choices by painted ladies. *Am Nat* 142:857-867.
- Hegland SJ, Totland O. 2005. Relationships between species' floral traits and pollinator visitation in a temperate grassland. *Oecologia* 145:586-594.
- Herrera CM. 1995. Floral biology, microclimate, and pollination by ectothermic bees in an early blooming herb. *Ecology* 76:218-228.
- Juenger T, Bergelson J. 1997. Pollen and resource limitation of compensation to herbivory in scarlet gilia, *Ipomopsis aggregata*. *Ecology* 78:1684-1695.
- Kandori I. 2002. Diverse visitors with various pollinator importance and temporal change in the important pollinators of *Geranium thunbergii* (Geraniaceae). *Ecol Res* 17:283-294.
- Khan BM, Chaudory MI. 1995. Comparative assessment of honey bee and other insects with self-pollination of sarson (*Brassica campestris*) in Peshawar, Pakistan. In: Kevan PG (ed). *The Asiatic hive bee: Apiculture, Biology and Role in Sustainable Development in Tropical and Subtropical Asia*. Ontario: Enviroquest Ltd. p 147-150.
- Klein AM, Steffan-Dewenter I, Buchori D, Tscharntke T. 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conserv Biol* 16:1003-1014.
- Klein AM, Steffan-Dewenter I, Tscharntke T. 2003. Fruit set of highland coffee increases with the diversity of pollinating bees. *Proc R Soc B* 270:955-961.
- Kremen C, Williams NM, Thorp RW. 2002. Crop pollination from native bees at risk from agricultural intensification. *PNAS* 99:16812-16816.
- Martin P, Bateson P. 1993. *Measuring Behaviour: an Introductory Guide*. 2nd ed. Cambridge: Cambridge Univ Pr.
- McGregor SE. 1976. *Insect Pollination of Cultivated Crop Plants*. Washington: US. Department of Agriculture-Agricultural Research Service.
- Mesquida J, Renard M, Pierre JS. 1988. Rape seed (*Brassica napus* L.) productivity: the effect of honey bees (*Apis mellifera* L.) and different pollination conditions in cage and field tests. *Apidologie* 19:51-72.
- Michener DM. 2000. *The Bees of the World*. Baltimore: Johns Hopkins Univ Pr.
- Mohr H, Schopfer P. 1995. *Plant Physiology*. Berlin: Springer-Verlag.
- Neal P, Dafni A, Giurfa M. 1998. Floral symmetry and its role in plant-pollinator systems: terminology, distribution and hypotheses. *Ann Rev Ecol Syst* 29:345-373.
- Oostermeijer JGB, van Eijck MW, den Nijs JCM. 1994. Offspring fitness in relation to population size and genetic variation in the rare perennial plant species *Gentiana pneumonanthe* (Gentianaceae). *Oecologia* 97:289-296.
- Pierre J, Mesquida J, Marilleau R, Pham-Delegue MH, Renard M. 1999. Nectar secretion in winter oilseed rape, *Brassica napus* quantitative and qualitative variability among 60 genotypes. *Plant Breeding* 118:471-476.
- Plowright RC, Thomson JD, Lefkovitch LP, Plowright CMS. 1993. An experimental study of the effect of colony resource level manipulation on foraging for pollen by worker bumble bees. *Canad J Zool* 71:1393-1396.
- Potts SG et al. 2004. Nectar resource diversity organises flower-visitor community structure. *Entomol Exp et Appl* 113:103-107.
- Rasheed SA, Harder LD. 1997. Economic motivation for plant species preferences of pollen-collecting bumble bees. *Ecol Entomol* 22:209-219.
- Roubik DW. 1995. *Pollination of cultivated plants in the tropics*. Rome: FAO.
- Rubatzky VE, Yamaguchi M. 2000. *Sayuran Dunia: Prinsip, Produksi dan Gizi*. Bandung: Penerbit ITB.
- Sasaki M, Ono M, Yoshida T. 1995. Some biological aspects of the north-adapted eastern honey bee, *Apis cerana japoniva*. In: Kevan PG (ed). *The Asiatic Hive bee: Apiculture, Biology, and Role in Sustainable Development in Tropical and Subtropical Asia*. Ontario: Enviroquest. p 59-78.
- Sihag RC, Mishra RC. 1995. Crop pollination and *Apis cerana*. In: Kevan PG (ed). *The Asiatic Hive bee: Apiculture, Biology, and Role in Sustainable Development in Tropical and Subtropical Asia*. Ontario: Enviroquest Ltd. p 129-134.
- Sola E, Widyaningrum IK, Mulyati S. 2005. *A photographic Guide to the Common Insects of Gunung Halimun-Salak National Park*. Bogor: VSO, JICA, TNGHS.
- Steffan-Dewenter I. 2003. Seed set of male-sterile and male-fertile oilseed rape (*Brassica napus*) in relation to pollinator density. *Apidologie* 34:227-235.
- Steffan-Dewenter I, Munzenberg U, Burger C, Thies C, Tscharntke T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83:1421-1432.
- Steffan-Dewenter I, Tscharntke T. 1999. Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121:432-440.
- Takayama S, Isogai A. 2005. Self-Incompatibility in Plants. *Ann Rev Plant Biol* 56:467-489.
- Thies C, Tscharntke T. 1999. Landscape structure and biological control in agroecosystems. *Science* 285:893-895.
- Veddeler D, Klein AM, Tscharntke T. 2006. Contrasting responses of bee communities to coffee flowering at different spatial scales. *Oikos* 112:594-601.

Wallace HM, Maynard GV, Trueman SJ. 2002. Insect flower visitors, foraging behaviour and their effectiveness as pollinators of *Personia virgata* R. Br. (Proteaceae). *Austral J Entomol* 41:55-59.

Westcott L, Nelson D. 2001. Canola pollination: an update. *Bee World* 82:115-129.

Westphal C, Steffan-Dewenter I, Tschardt T. 2006. Foraging trip duration of bumblebees in relation to landscape-wide resource availability. *Ecol Entomol* 31:389-394.