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Effects of Some Environmental Factors on Species of Major Insect Pollinators in the Teak (*Tectona grandis* L.f.) Flowering Season

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ABSTRACT: Insect pollinators were studied together with floral nectar and micro-environmental variables at the five main teak seed orchards in Thailand. Observations were carried out by walking on line transects and by using air-flight malaise traps in tree canopies in each seed orchard during the peak blooming season. The relationships between insect species and environmental variables were established for three groups. For group I, the spread of data regarding insect species and visiting periods on the ordination was positively correlated with photosynthetic active radiation and ambient temperature variables. In group II, a positive correlation was found with solar irradiance and relative humidity. In group III we found a negative correlation with all seven factors considered (two factors regarding floral nectar, and five micro-environmental variables, including the three mentioned above). Some major insect species in groups I and II that responded to photosynthetic active radiation, temperature and relative humidity were found to infrequently visit teak flowers, changing their foraging behavior due to sunlight variation throughout the day. We suggest that species in group III that did not show the same variations in behavior be considered for selection as suitable candidates for the introduction of new insect visitors into some seed plantations which lack sufficient pollinators or have irregular micro-environmental variables.

KEY WORDS: insect pollinator, teak, plantation, environmental factors, Thailand

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INTRODUCTION

In recent years, high native species diversity has been reported to be declining in tropical rain forests. Most studies have quantified the human impact on diversity of fauna species (e.g. Chey *et al*., 1997; Watt *et al*., 1997; Thompson et al., 2002). Forest modification and human activities have negative impacts on biodiversity (Bawa and Seidler, 1998; Mayfield *et al*., 2005). Species diversity and abundance may be inconsistent across different habitat types and locations (Mayfield et al. 2005). Differences in the diversity and species composition of fauna may be affecting the function of pollinators and dispersers at each site (e.g. mammals: Daily *et al*., 2003; insects: Tangmitcharoen *et al*., 2006b). Habitat types and some environmental factors may affect the diversity and activity of insects that visit flowers (Inoue and Kato, 1992; Herrera, 1995b).

Teak (*Tectona grandis* L.f.) is one of the most important commercial timber species in many countries of the world, e.g. in Asia (Thailand, Mynmar, Indonesia, Sri Lanka, Bangladesh and China); in West Africa (Ghana, Nigeria, Ivory Coast, Senegal, Togo and Benin); in East Africa (Sudan and Tanzania); in Central America (Trinidad and Tobago, Puerto Rico, Panama and Costa Rica); and in South America (Brazil and Ecuador) (FAO, 1957, 2001; Kaosa-ard, 1981,1995; Keogh, 1996, Pérez Cordero and Kanninen, 2003). Teak is a highly self-incompatible species (Hedegart, 1973). Palupi (2005) concluded that this high self-incompatibility was considered to be the major cause of the low fruit set. Hedegart (1973) reported that an insufficient number of pollinators was the reason for low fruit setting. Teak has a hermaphroditic flower. It is predominantly an outcrossing species (Bryndum and Hedegart, 1969; Kjaer *et al*., 1996; Tangmitcharoen and Owens, 1997), and also entomophilous (Cameron, 1968; Bryndum and Hedegart, 1969; Egenti, 1974; Kedarnath, 1974).

Many studies have reported that insects are frequent visitors to teak flowers (Bryndum and Hedegart, 1969; Egenti, 1981; Mathew *et al*., 1987; Tangmitcharoen and Owens, 1997; Tangmitcharoen *et al*., 2006b). Those studies showed that insect pollinators play a significant role in the reproductive success of teak (Mathew *et al*., 1987; Tangmitcharoen and Owens, 1997a; Tangmitcharoen *et al*., 2006a). Insect visitors vary with regard to pollination efficiency and in their preferences for floral traits (Lau and Galloway, 2004). Reasons for the restriction of foraging behaviors, at least for some periods of time, and for some specific species of flowers are known to vary (Heinrich, 1975). The efficiencies and foraging behaviors of pollinators may be affected by the spatial distance between individuals and the population, and by the population of plants and flowers (Stout *et al*., 1998; Richards *et al*., 1999; Townsend and Levey, 2005; Fried *et al*., 2005). This study aims to examine how insect pollinator species respond to variations in environment factors, and to determine the time periods involved and regional differences. The study was carried out to investigate the effects of environmental factors on each of the major species of insect pollinators during the teak flowering period.

MATERIALS AND METHODS

Study Sites

Five clonal seed orchards of teak, located in different parts of Thailand, were selected: Mae Gar Silvicultural Research Station (19° 10′ N, 99° 55′ E), Phayao province, ranges from 300-350 metres above mean sea level, (asl) and covers an area of about 396 ha; Mae Tha Silvicultural Research Station (18° 11′ N, 99° 34′ E), Lampang province, ranges from 300-350 metres asl. and covers an area of about 528 ha; Larn Sang Silvicultural Research Station (16° 48′ N, 98° 04′ E), Tak province, ranges from 200-220 metres asl. covereing an area of about 127 ha; Dong Larn Silvicultural Research Station (16° 48′ N, 101° 58′ E), Khon Kaen province, ranges from 300-360 metres asl. covereing an area of about 408 ha and Khao Soi Dao Silvicultural Research Station (13° 00′ N, 102° 15′ E), Chantaburi province, ranges from 150-200 metres asl. and covers an area of about 372 ha. The orchards are mainly managed as teak seed plantations, with trees grown at 12x12 m spacing. The age of teak trees in the selected plots ranged from 31 and 34 years old.

Data Collection

The insects visiting teak flowers were observed during the peak of the flowering period from July to August (2008 and 2009). The direct observation was be done by line transects marked between towers at each site. Because the peak of the receptive flower period is between 9:00am-15:00pm, all observations were conducted during these times on sunny days. The peak period for teak pollination is from 11:00am-13:00 pm (Tangmitcharoen and Owens 1997). In addition, supplementary collection of visiting insects was carried out using air-flight malaise traps, which are effective for collecting Hymenoptera and Diptera (Grazoul, 1997) in the teak canopies. The number of flower visitors and their behaviors were recorded for a 20 min period every hour. The number of individuals and the species of visitors in ten inflorescences were recorded in the first 10 min; while the visitor behaviors, including mean time of visits and frequency of flower visits (number of visitors and anthesis of flowers), were recorded in the second 10 min.

To investigate the quantity of nectar production by individual flowers, nectar volumes and sugar concentrations were directly measured at the study site once each hour (09:00 am to 15:00 pm). Nectar volumes were measured by inserting a 2 μL capillary tube down to the base of each flower. Because of the small amount of nectar produced by each flower, fresh nectar from several flowers was pooled in order to measure nectar concentration using a hand-held refractometer (Nippon Optical Works, Tokyo, Japan).

Measurements of environmental factors were carried out at the same time as visiting insect observations (9:00 am-15:00 pm) at each seed plantation, in order to investigate the relationships between insect pollinators and environmental factors in the ecosystem influencing seed and fruit production. The PAR (photosynthetic active radiation, 400-700 nm wavebands) and LAI (leaf area index) were measured using a photosensor of AccuPAR model LP-80 (Decagon Devices, Inc., Pullman WA, USA). At the same time, the air temperature, relative humidity, and wind speed were measured using a Kestrel® 4000 Pocket Weather Tracker (Nielsen-Kellerman, Boothwyn Pa, USA).

Statistical Analyses

Data was processed and analyzed using SPSS® 13.0 for Windows (SPSS Inc., 2005). Analysis of variance (ANOVA) was used for the comparative means between insect pollinator species composition, floral nectar and micro-environmental variables in each the times of visiting insect observation at each seed plantation.

Relationships between insect pollinator species and environmental variables were examined by canonical correspondence analysis (CCA) using PC-ORD version 5.10 for Windows (McCune and Mefford, 2006). We then interpreted the results using multivariate analysis of response data with consideration of explanatory variables (Ter Braak and Prentice, 1988; Ter Braak, 1992). CCA ordinations for insect species were shown separately per hour (09:00 am-15:00 pm) at five different sites. The CCA was performed using a primary data matrix of log-transformed numbers of individual insect visitors whose individuals visited at least two habitats. A secondary data matrix was analyzed, consisting of seven environmental variables: two factors regarding floral nectar (sugar concentration and volume of nectar) and five factors of micro-environmental variables (PAR, LAI, temperature, relative humidity and wind speed). These biplots graph information on floral nectar and micro-environmental variables, pollination period times and insect species, relative to their scores, on the two main axes of the ordination. If lines representing floral nectar and micro-environmental variables point in the same direction they are positively correlated; if they point in opposite directions, they are negatively correlated. A longer line indicates the greater confidence in the inferred correlation.

RESULTS

Diversity of Insect Pollinators

A total of 63 species were collected, belonging to 17 families from three insect orders; Hymenoptera, 37 species; Lepidoptera, 18 species and Diptera, 8 species. Variations in insect pollinator composition were calculated from individual values and statistical variability at the species and order levels. Most pollinator insect species occurred infrequently and did not appear in our census. The study was restricted to the 10 major species of insect pollinators that each contributed more than 3% of the total visits to flowers (Table 1). The difference in pollinator composition was statistically significant at both the species level ($F_{9, 40}$ = 2.22, P = 0.041) and the order level ($F_{2, 12}$ = 4.17, P = 0.042) in each teak seed orchard. The ten major insect species contributing most flower visits (all seed orchards combined, n = 475) were *Trigona collina* (family Apidae), *Apis florea* (Apidae), *Catopsilia pomona hilaria* (Pieridae), *Apis cerana* (Apidae), *Catopsilia pomona pomona* (Pieridae), *Ceratina* sp. (Apidae), *Vespa affinis* (Vespidae), *Chrysomya* sp. (Calliphoridae), *Trigona terminata* (Apidae) and *Episyrphus* sp. (Syrphidae).

Table 1. Summary and percentage of visits of 26 insect pollinators were recorded on flowers in five teak seed orchards (H = Hymenoptera, L = Lepidoptera and D = Diptera).

no.	Species (abbreviation)	Order	% of pollinator visits on teak flowers: Mae Gar	Mae Tha	Dong Larn	Khao Soi Dao	Larn Sang	% of total (n)
1	*Trigona collina* (colli)	H	23.78	12.00	12.50	10.20	-	13.68 (65)
2	*Apis florea* (flore)	H	8.39	12.00	-	13.27	9.52	8.42 (40)
3	*Catopsilia pomona hilaria* (hilar)	L	2.80	12.00	-	8.16	14.29	6.32 (30)
4	*Apis cerana* (ceran)	H	6.99	9.33	7.29	5.10	-	6.11 (29)
5	*Catopsilia pomona pomona* (pomon)	L	5.59	9.33	8.33	4.08	-	5.68 (27)
6	*Ceratina* spp. (cerat)	H	4.20	-	7.29	4.08	4.76	4.21 (20)
7	*Vespa affinis* (affin)	H	0.70	13.33	8.33	-	-	4.00 (19)
8	*Chrysomya* sp. (chrys)	D	3.50	-	7.29	5.10	-	3.58 (17)
9	*Trigona terminata* (termi)	H	3.50	-	4.17	6.12	-	3.16 (15)
10	*Episyrphus* sp.(episy)	D	4.20	4.00	-	3.06	4.76	3.16 (15)
11	*Rhinia* sp. (rhini)	D	2.10	6.67	6.25	-	-	2.95 (14)
12	*Nomia clypeata* (clype)	H	2.80	-	5.21	-	3.17	2.32 (11)
13	*Asarcina aegrota* (aegro)	D	1.40	-	3.13	3.06	-	1.68 (8)

Table 1. Continued...

no.	Species (abbreviation)	Order	% of pollinator visits on teak flowers					% of total (n)
			Mae Gar	Mae Tha	Dong Larn	Khao Soi Dao	Larn Sang	
14	*Vespa velutina* (velut)	H	2.80	4.00	-	-	-	1.47 (7)
15	*Trigona ventralis* (ventr)	H	2.10	-	-	4.08	-	1.47 (7)
16	*Pseudapis* sp. (pseua)	H	-	2.67	-	-	6.35	1.26 (6)
17	*Parasarcophaga* sp. (paras)	D	2.10	-	-	2.04	-	1.05 (5)
18	*Hypolymnas bolina* (bolin)	L	2.80	-	-	-	1.59	1.05 (5)
19	*Anthena emolus* (emolu)	L	-	2.67	-	-	4.76	1.05 (5)
20	*Tachina* sp. (tachi)	D	-	-	3.13	2.04	-	1.05 (5)
21	*Troides aeacus* (aeacu)	L	0.70	1.33	-	2.04	-	0.84 (4)
22	*Xylocopa aestuans* (aestu)	H	1.40	2.67	-	-	-	0.84 (4)
23	*Polistes stigma* (stigm)	H	0.70	-	-	-	3.17	0.63 (3)
24	*Pachliopta aristolochiae* (arist)	L	0.70	1.33	-	1.02	-	0.63 (3)
25	*Euploea core godartii* (godar)	L	-	1.33	-	-	3.17	0.63 (3)
26	*Braunsapis* sp. (braun)	H	0.70	-	1.04	-	-	0.42 (2)

Variation in Floral Nectar and Micro-Environmental Factors

Relationships between floral nectar and micro-environmental variables during the times of visiting insect observations (09:00am-15:00pm) were investigated at each site. Differences in nectar volume per flower and the observed times of insect visits did not differ significantly between the sites ($P > 0.05$). The sugar concentration of nectar did not differ significantly for all sites, but the visiting times of insects observed were significantly different ($F_{1, 34} = 187.33$, $P < 0.001$). Variation of micro-environmental factors in each seed plantation differed significantly in means of PAR ($F_{1, 69} = 3.161$, $P = 0.028$), LAI ($F_{1, 69} = 4.085$, $P = 0.009$) and air temperature ($F_{1, 69} = 2.64$, $P = 0.042$) but did not differ in relative humidity and wind speed. Only the PAR differed significantly ($F_{3, 32} = 7.53$, $P < 0.01$) in each observation time. Differences between seed plantations in the means of PAR, LAI and temperature variables were highest during the 11:00 am to 13:00 pm period of the day.

The relationship between floral nectar and micro-environmental factors (PAR, LAI, temperature and relative humidity) are expressed in Figure 1. This figure shows site-dependent variation in sunlight intensity occurring during the day at each site.. Only the air temperature affected the sugar concentration and volume of nectar significantly ($F_{2, 33} = 24.353$, $P<0.001$; $F_{2,33}=27.024$, $P<0.001$, respectively). This indicated that the concentration of nectar depended on the duration of nectar exudation in the daytime.

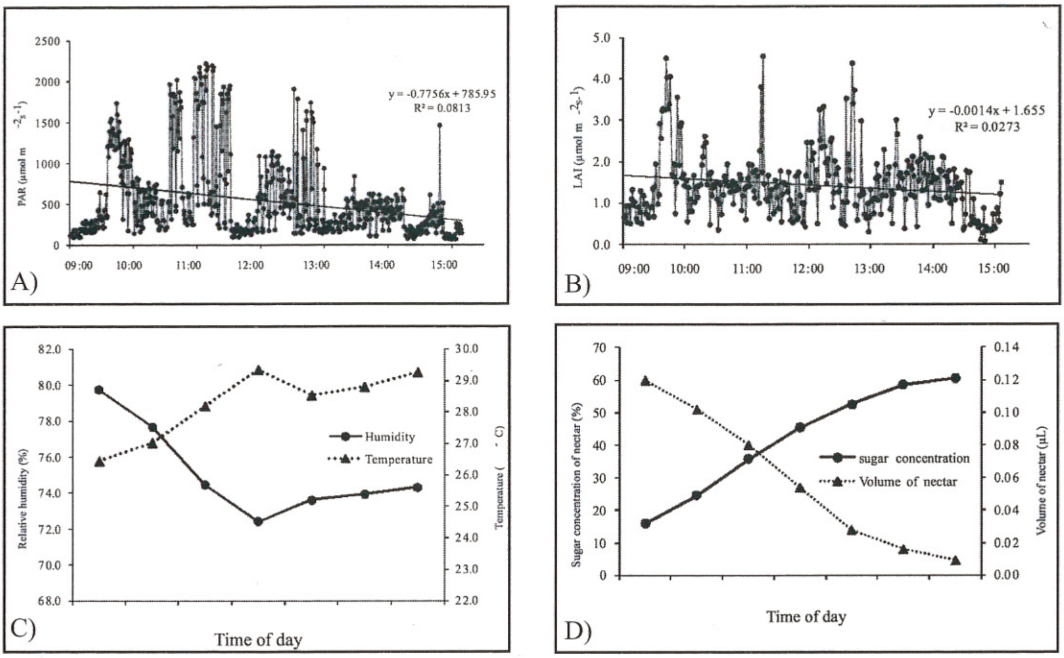

Figure 1. A-B; Variation in mean of PAR (photosynthetic active radiation) and LAI (leaf area index), C-D; relationships between relative humidity, temperature, % sugar concentration and volume of nectar during 09:00am to 15:00pm period in the flowering season of teak in seed plantations.

Relationships Between Species of Insect Pollinators and Environmental Factors

The correlation of the different environmental factors was identified and analyzed for each insect species, pollinating time period and location. The relationships between insect species and environmental variables, which were analyzed with CCA ordination, were significantly identified by seven factors: two factors involving floral nectar (sugar concentration and volume of nectar); and five factors of micro-environmental (PAR, LAI, temperature, relative humidity, and wind speed). Kendall (rank) correlations between sample scores for an axis derived from the species data and the sample scores are linear combinations of the environmental variables (the first and second axes are 0.644 and 0.526, respectively).

The first two CCA axes explain the variation in species data sets (7.4% and 6.2%, respectively). Both the first and second axes had higher loadings of mean PAR, temperature and humidity than other factors – a finding which allows greater confidence in the inferred correlation (see Table 2). Figure 2 showed that the insect pollinators were distinguished as three groups of species in the visiting period in each area. Group I (between the graph line of temperature) included several common insect species (e.g. *Apis florea*, *Pseudapis* sp., *Xylocopa aestuans, Troides aeacus*, *Catopsilia pomona hilaria*, and *Euploea core godartii*). This group had a high correlation with temperature variations indicating that the foraging behaviors of many species of insect pollinators are similar. Group II (between the graph lines of PAR and humidity) were significantly correlated with PAR and humidity variables. Visiting insect species in group II included *Apis cerana, Trigona ventralis*, *Trigona terminata, Vespa velutina, Hypolimnas bolina*, *Cirrochroa tyche* and *Episyrphus* sp.

Group III (between the graph lines of humidity and temperature) differ markedly from the other groups, and form a group relating to an ordination that was negatively correlated with PAR and other factors. The presence of insect pollinators (e.g. *Catopsillia pomona pomona*, *Asarcina aegrota*, *Chrysomya* sp., *Rhinia* sp., *Ceratina* spp., *Trigona collina* and *Nomia clypeasis*) in this group was not strongly related with most of the micro-environmental variables, especially the PAR, but was highly correlated with sugar concentration.

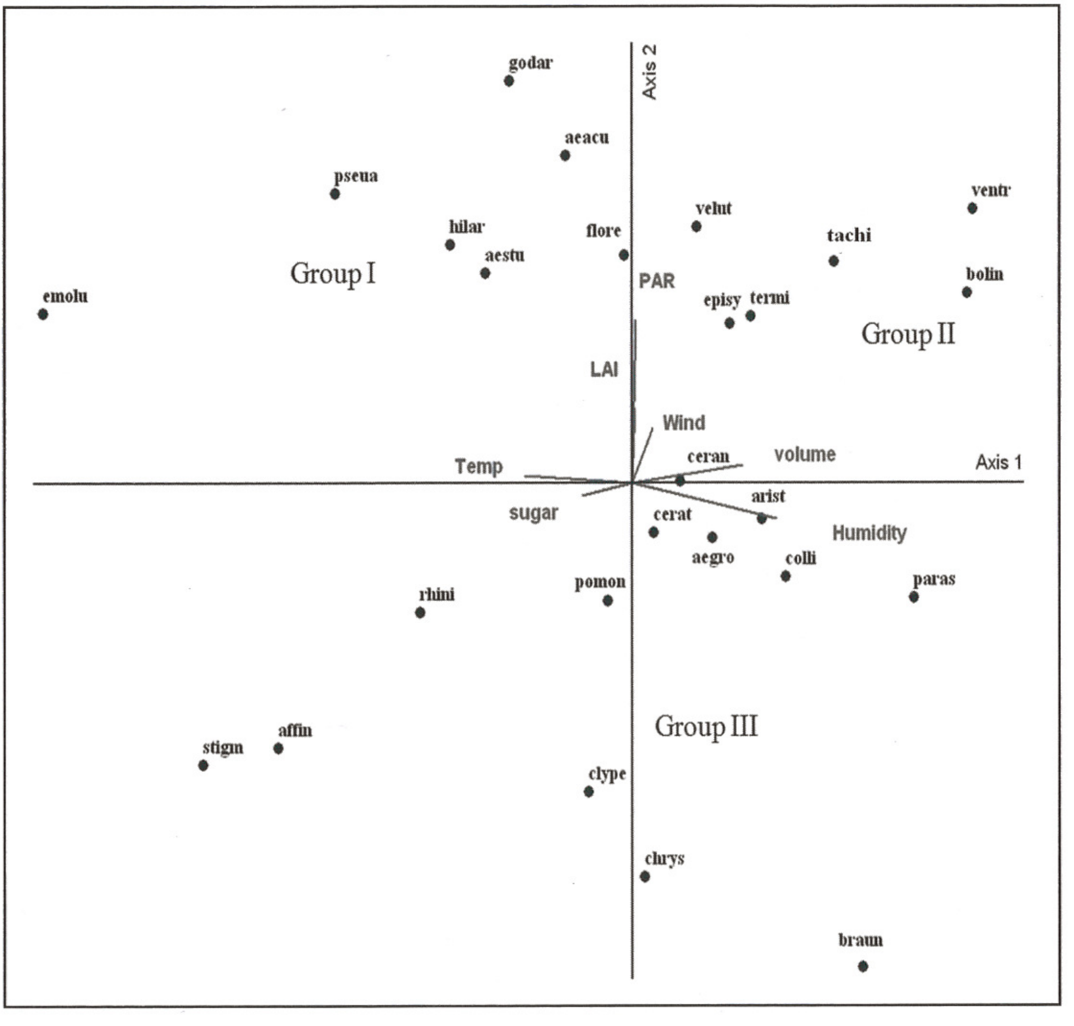

Figure 2. Canonical correspondence analyses (CCA) ordination of insect pollinators in teak seed plantations, showing the relationships of the seven significant explanatory variables. Solid cycles refer to 26 species (for abbreviations see Table 1) of insect pollinators. Lines refer to the environmental variables: PAR - photosynthetic active radiation; LAI - leaf area index; Temp - temperature; Humidity - relative humidity; Wind - wind speed; Volume - nectar volume and Sugar - sugar concentration of nectar. The lines of each factor represent the direction and relative strength of these canonical variables

Table 2. Axis summary statistics of the canonical correspondence analysis, the relationships between environmental variables and first and second axes, performed with a matrices of the log-transfer numbers of insect pollinator and seven environmental variables and their canonical coefficients

	Canonical axes and coefficients	
	Axis 1	**Axis 2**
Eigenvalue	0.16	0.135
% of variance in species data explained	7.4	6.2
Cumulative % of variance in species data explained	7.4	13.6
Pearson Correlation, Species- Environment variable	0.851	0.695
Kendel (Rank) Correlation, Species- Environment variable	0.644	0.526
Environmental variables		
- Micro-environmental variables		
Photosynthetic active radiation (PAR)	-0.632	-0.528
Leaf area index (LAI)	-0.029	0.250
Relative humidity	-0.157	0.377
Temperature	0.438	0.177
Wind speed	-0.035	-0.020
- Floral nectar variables		
Sugar concentration of nectar	-0.018	0.105
Volume of nectar	0.003	0.149

DISCUSSION

The results from this study showed that the variations within populations of insect pollinators were a limited factor at the species level. For the time period of our study we selected the peak of the flowering season, an important period for pollination success also mentioned by Tangmitcharoen and Owens (1997). We focused on groups of major insect pollinators rather than the number of species visiting the flowers. The results reflected a difference among individual locations in species diversity and abundance patterns. This report does not cover in detail all of the species found during the teak flowering period; however, almost all of the major pollinators were studied. Tangmitcharoen *et al.*, (2006b) found almost 700 morphospecies of insects on teak flowers in natural forest and plantation canopies, but of these only ten percent were considered to be potential pollinators.

This study has detected possible evidence of direct selection on floral nectar and micro-environmental factors by some pollinators. Differences in microclimate conditions (Sedgley and Annells, 1981; Burgos et al., 1991) among orchards have been found to affect pollinator behaviors. Herrera (1989, 1995a) did find that this kind of micro-environmental difference could be important in reducing the likelihood of pollinators acting as selective pressures. Herrera (1989) did not analyze the effect of the environment on pollination. Many studies have shown the effects of efficient pollinators on plant fitness and floral preferences (e.g. Herrera, 1995b; Galen, 1996; Lau and Galloway, 2004). Habitat modification is one of the factors affecting species diversity (Lawton *et al.*, 1998; Schulze *et al.*, 2004) and the abundance of particular pollinators, together with other factors such as vegetable cover and the ratio of grass to shrubs (Donaldson *et al.*, 2002).

The seed plantations are surrounded by natural forest that has important effects on insect diversity and abundance, e.g. in Mae Gar seed orchard both the species diversity and abundance were greater than at other sites, because it is located between three natural forest types: deciduous dipterocarp, mixed deciduous, and dry evergreen. Conditions and floral morphology in each habitat are important factors that differentiate the foraging niches among insect visitors (Harder, 1985; Inoue and Kato, 1992 Herrera, 1995b), related to specific pollinator species (Sakai *et al.*, 1999).

The CCA indicates that insect pollinators in the first and second groups, which are responsive to PAR, were found to infrequently visit teak flowers, and changed their foraging behavior due to sunlight variation throughout the day while solar irradiance-indifferent insect visitors (e.g. *Trigona collina*, *Ceratina* spp. and *Chrysomya* sp.) very often visited teak flowers, and their foraging behaviors remained consistent all day. Two varieties of bees (*Trigona collina* and *Ceratina* spp.) are reported to be important pollinators at the Saraburi and Phayao seed orchards (Bryndum and Hedegart, 1969; Tangmitcharoen and Owens, 1997, Tasen *et al.*, 2002; Tangmitcharoen *et al.*, 2006a; Tangmitcharoen *et al.*, 2009).

Figure 2 indicates that insect species in group III obviously show significant differences from the first two groups with negative correlation to micro-environmental factors. The quantity of floral nectar production depends on environmental factors, especially temperature. The results showed that the percentage of sugar concentration of nectar increased in the afternoon while the volume of nectar was distinctly lower (see Fig. 1D). When the relationship between floral nectar and micro-environmental factors was examined, it was found that only temperature affected both sugar concentration and the volume of nectar in teak flowers. Thus, temperature tended to be an important factor in determining the effective pollination period, excretion of nectar, stigma receptiveness and pollen germination (Fernandez-Escobar *et al.* 1983; Burgos *et al.* 1991; Alekseyeva and Bureyko, 2000). Teak flowering occurs during the rainy season. At midday (11:00 am - 13:00 mp) the stigma of teak flowers is most receptive (Tangmitcharoen and Owen 1997). Micro-environmental factors, especially sunlight and temperature increase the visiting activity of teak insect pollinators. In contrast, insect activities on a rainy day or cloudy day were less than on a sunny day. We can conclude that insects in group III may be suitable teak pollinators, because during some periods of the teak blooming (rainy) season there is limited direct sunlight in some geographical regions.

This study suggests that some pollinators have distinctively less response to environmental variables when visiting teak flowers. We suggest that these species be considered for selection as suitable candidates for the introduction of new insect visitors into some teak seed orchards which lack sufficient pollinators or have irregular micro-environmental variables.

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