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Original article

Relationships Among Insect Pollinators, Micro-environmental Factors and Fruit Settings of Teak (*Tectona grandis* L.F.) in Seed Orchards in Thailand

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ABSTRACT

The ecological effects of insects in the tropics have been studied generally in terms of their impact on species diversity and abundance. However, information is very limited regarding the inter-relationship of insects and ecological processes, such as, insect pollinators, environmental variables and fruit settings of teak. Five main teak seed orchards in Thailand were studied. Observations were carried out by walking on line transects and using air-flight malaise traps from tree canopies in each site during the peak flowering season of teak. A total of 63 species in 17 families and three orders (Hymenoptera, Lepidoptera and Diptera) of flower visitors were found. The relationships between insect pollinator composition and environmental factors among the teak seed plantations were significantly different in species composition and some environmental variables. The results of this study showed that micro-environmental factors (temperature and photosynthetic active radiation) significantly affected species diversity and abundance of insect pollinators, especially in their foraging behavior responses to the photosynthetic active radiation variable. We, thus, concluded that some pollinators have different responses to environmental variables that affect their visiting behavior on flowers and also fruit set, and this was associated with visiting periods and habitats.

Keywords: Insect pollination, Visitor, Teak, Microclimate, Tropical forest.

INTRODUCTION

The tropical forest has been characterized by its great diversity of plant and animal species with high levels of interaction, shown by complex ecological patterns and dynamics (Lugo, 1995), for example, pollination mechanisms and breeding systems (Heinrich and Raven, 1972; Bawa and Seidler, 1998; Tangmitcharoen and Owens, 1997a; Ghazoul, 1997). Invertebrates mediate several important ecological processes, interactions between species that contribute to ecosystem function and structure (Ghazoul and McLeish, 2001); including pollination and seed dispersal (Daily *et al*., 2003; Momose *et al*., 1998) are of interest for various reasons in each plant species. Thus, conservation in diversity of insects has importance in natural forests and seed production areas, especially major insect pollinators. The diversity and abundance of insect pollinators may depend on several factors, including geographic and climatic conditions (Herrera, 1995a; Tasen *et al*., 2009).

The tropical hardwood forest tree, teak (*Tectona grandis* L.f.), is one of the most highly desirable tree species in the timber trade. At present, the demand for teak timber and green space is increasing each year. The supply that can be extracted from the remaining natural forests is decreasing and creating a serious problem. One solution to overcome the present shortage is to establish more teak plantations. Teak is a high-priority planting species for plantations in the Asian region, especially in India, Myanmar, Indonesia and Thailand (Kaosa-ard, 1995). Teak planting is still limited; however, this is mostly due to an insufficient quantity and quality of seeds. However, teak seed orchards or seed production areas have been established in order to cope with the increasing demand for high-quality seeds (Wellendorf and Kaosa-ard, 1988) and planting stock for reforestation and afforestation. Some locations have generally shown low fruit-set production (Meekaew, 1992; Pianhanuruk, 1995; Indira, 2003) which has often been attributed to a lack of adequate diversity of pollinating insects (Bryndum and Hedegart, 1969; Tangmitcharoen and Owens, 1997a).

Many studies have reported that insects of the orders Hymenoptera, Lepidoptera and Diptera are major visitors of teak flowers (Bryndum and Hedegart, 1969; Egenti, 1981; Mathew *et al*., 1987; Tangmitcharoen and Owens, 1997a; Tangmitcharoen *et al*., 2006b). These studies showed that insect pollinators play an important role in the reproductive success of teak (Mathew *et al*., 1987; Tangmitcharoen and Owens, 1997a; Tasen *et al*., 2002; Tangmitcharoen *et al*., 2006a). However, different habitats and environmental factors may affect the diversity, abundance and behaviors of pollinators for an individual plant which are linked to the reproductive success of teak. Morphological floral characteristics are an important factor that differentiates the foraging niches among insect visitors (Harder, 1985; Inoue and Kato, 1992), and this is related to specific pollinator species (Sakai *et al*., 1999). Variations in nectar secretion can affect the number and behavior of pollinators that visit the flowers (Burd, 1995; Conner and Rush, 1996; Proctor *et al*., 1996; Cawoy *et al*., 2008). The foraging behaviors of pollinators are related to variations in environment (Stanton and Galen 1989; Herrera, 1995a).

Only a few reports are available on the interrelationships between insect pollinators, floral nectar, and environmental variables and the pollination of teak in different habitats. The objective of this study is to examine the relationships between the composition of pollinator fauna and some environmental factors, and to determine any regional differences. Variations in pollinator abundance and identity (or diversity) do affect pollination services for teak, based on or mediated by the idiosyncratic or specific response of pollinators to some environmental factors.

MATERIALS AND METHODS

Study Sites

The study areas, located in different parts of Thailand, were established in different forest types: 1) Mae Gar Seed Orchard (MG), Phayao province (19° 10′ N, 99° 55′ E, 300-350 m a.s.l.) (Northern part), covering an area of 396 ha and located between dry deciduous forests (DDF), mixed deciduous forests (MDF) and dry evergreen forests (DEF); 2) Mae Tha Seed Orchard (MT), Lampung province (18° 11′ N, 99° 34′ E, 300-350 m a.s.l.) (Northern), covering 528 ha and located between agriculture land and DDF; and 3) Larn Sang Seed Orchard (LS), Tak province (16° 48′ N, 98° 04′ E, 200-220 m a.s.l.) (Northern), covering 127 ha and surrounded by dwarf DDF; 4) Dong Larn Seed Orchard (DL), Khon Kaen province (16° 48′ N, 101° 58′ E, 300-360 m a.s.l.) (Northeastern), covering 408 ha and surrounded by DEF; and 5) Khao Soi Dao Seed Orchard (KD), Chantaburi province (13° 00′ N, 102° 15′ E, 150-200 m a.s.l.) (Eastern), covering 372 ha and surrounded by a moist evergreen forest (MEF). The orchards are mainly managed as teak-seed plantations of Thailand. The plots selected were composed of trees between 31 and 34 years old and grown at 12x12 m spacing.

Data Collection

Observations were made during peak blooming season, between July and August (2008 and 2010), to identify insect visitors to teak flowers, and to determine their abundance, their visitation frequency, and their roles as major visitors. Information on insect pollinators visiting flowers was collected by direct observations in the field from 09:00 to 15:00 hrs. This was done by walking on line transects and making observations and collecting insects from tree canopies at each seed orchard. The peak receptive period was from 11:00-13:00 (Tangmitcharoen and Owens, 1997a). In addition, visitor collection was supplemented by use of a sweep net and air-flight malaise trap. The trap is effective for collecting Hymenoptera and Diptera (Grazoul, 1997) on the teak canopies from 09:00 to 15:00. Fruit settings were collected at ten teak tree canopies randomly selected in each area and counted by recording the number (kg/ tree) of all fruit sets of each tree after fruit matured in February and March, to estimate relative output of trees among seed plantations.

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 to 15:00). The flowers in each inflorescence were bagged before flower opened between 07:00 to 08:00 each day. The bags were then removed for nectar measurements at 09:00, which is starting point of the peak receptive period. Nectar volumes were determined 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).

We also studied the influence of environmental factors affecting pollination in each teak seed orchard in order to investigate the relationships between insect pollinators and environmental factors in the ecosystem influencing seed and fruit production. Measurements of environmental factors (air temperature, relative humidity, photosynthetic active radiation (PAR) and wind speed) were carried out at each plantation, at the observation sites of flower visitors, from 09:00 to 15:00 hrs, and the field data was recorded. The PAR of each seed orchard was measured using an AccuPAR model LP-80 (Decagon Devices, Inc., Pullman WA, USA), a photosensor which measures PAR in the 400-700 nm waveband. At the same time, air temperature, relative humidity, and wind speed were measured using a Kestrel® 4000 Pocket Weather Tracker (Nielsen-Kellerman, Boothwyn Pa USA).

Statistical Analyses

All of data were averaged for each site and the variables were first tested for homogeneity of variance (Levene's test) and normal distribution (Kolmogorov-Smirnov) to meet the requirements of ANOVA. Shannon's diversity index *H′* (Ludwig and Reynolds, 1988) and Margalef's species richness index (Magurran, 1988) were calculated. The Kruskal-Wallis nonparametric test (*H*) was analyzed to test differences in insect species, individuals, Shannon's diversity index and species richness among habitats. Relationships among the parameters on insect pollinator composition, environmental factors and fruit production were tested using Spearman's rank correlation coefficient (r_s) and stepwise multiple linear regression. All the statistical analyses were performed using SPSS® 13.0 for Windows (SPSS Inc. 2005). We used this to calculate the means and standard errors for comparison of all measurements.

RESULTS AND DISCUSSION

Insect pollinator composition

Insect visitors on teak flowers were found to comprise 63 species belonging to 17 families of Hymenoptera (37 species, 65.56% of total visitors), Lepidoptera (18 species, 19.92%) and Diptera (8 species, 14.52%). Differences and proportional relationships of insect pollinators at the species level, and grouped into individual orders, were recorded at each seed orchard. Hymenopterans at each site ranged between 57.14-70.63% of the total number of visitors, while Lepidopterans and Dipterans ranged between 10.42-30.67% and 4.76-19.79%, respectively.

Shannon's diversity (*H′*) index of insect pollinators in the MG seed orchard was higher than in the KD, DL, LS and MT seed orchards (Table 1). Kruskal-Wallis test showed that the *H′* index was significantly different among habitats ($\chi^2 = 19.93$, $P < 0.001$). Margalef's index of species richness was higher in the MG than other orchards. Mean number on species richness of insect pollinators showed a significant response to time period ($\chi^2 = 24.431$, $P < 0.001$), while there were not significant differences among sites ($\chi^2 = 5.347$, $P = 0.254$).

Table 1 Pair-wise comparisons between five seed plantations of Shannon's diversity and species richness of insect pollinator at the flowering season of teak (*F*-values, *represents $P<0.05$, **$P<0.01$, ns= not significant).

	Locations	Shannon's diversity index *(H')*				
		MG	MT	DL	KD	LS
Species richness	MG		9.953**	8.891**	6.662*	6.677*
	MT	2.976^{ns}		5.713*	9.998**	1.081^{ns}
	DL	0.802^{ns}	0.332^{ns}		0.530^{ns}	2.238^{ns}
	KD	0.918^{ns}	0.922^{ns}	0.016^{ns}		2.815^{ns}
	LS	3.940*	0.202^{ns}	1.185^{ns}	1.644^{ns}	

Relationship between micro-environment and insect pollinator composition

Three separate features among the five seed orchards, namely, the levels and relationships of pollinator composition, floral nectar and micro-environmental variables, were calculated. Among microclimate variables, only PAR and temperature were considered (Figure 1), as no significant differences between seed orchards were found for relative humidity and wind speed. Seed orchards were characterized by the sequence and duration of sunlight periods during daytime (09:00-15:00).

The multiple regression coefficient for the relationship between pollinator species composition and micro-environmental variables (R^2 = 0.296) was significant ($F_{2, 32}$ = 6.712, P = 0.004), while that for pollinator species composition and floral nectar variables (R^2 = 0.046) was not significant ($F_{2, 32}$ = 0.770, P = 0.471). The relationships between all of the features were calculated using multiple linear regression. The estimated R^2 for the multiple regression model (0.296) was significant ($F_{4, 30}$ = 3.154, P = 0.028). The partial regression coefficients of insect composition on sugar concentration (0.209) and volume (0.173) of floral nectar were not significant (P = 0.235, P = 0.328, respectively). However, the coefficient of the PAR variable on micro-environmental (0.533) was significant ($F_{1, 33}$ = 13.127, P = 0.001), while that of air temperature was not significant ($F_{1, 33}$ = 1.281, P = 0.266).

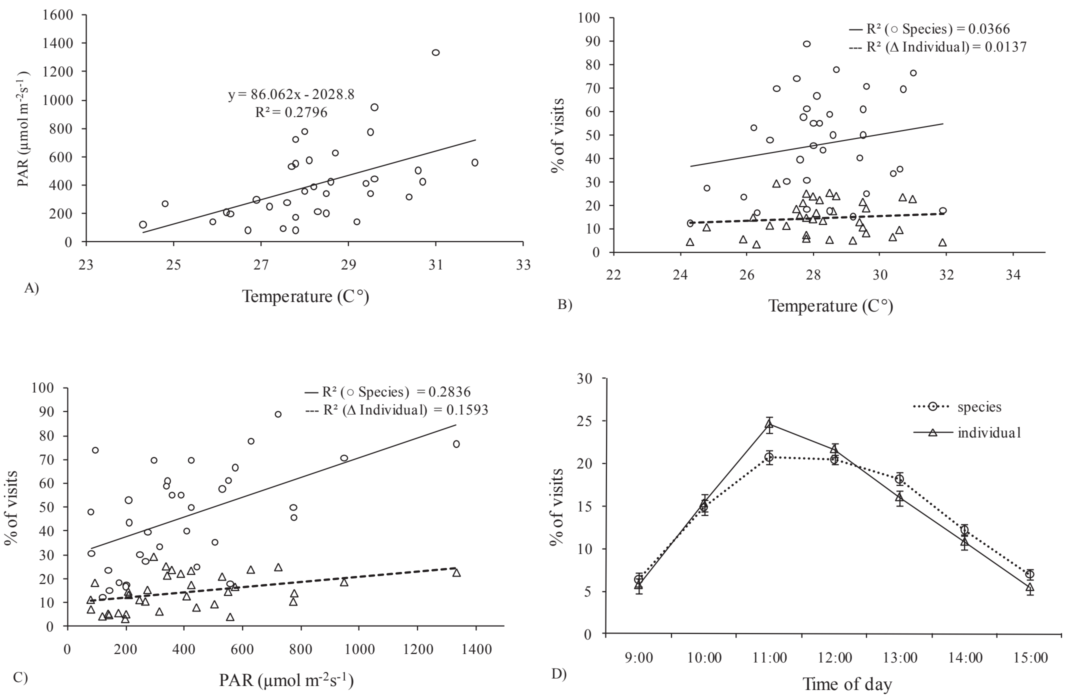

Figure 1 Relationships between PAR and temperature variables (A), separate regression lines are shown for means of environmental variables in visiting period of each site; variation among insect pollinator composition and means of temperature (B); PAR (C); and time of day (D) variables were observed at the point of capture in seed plantations. Separate regression lines are shown for % number of individual and species of insect pollinators visited the flowers.

Relationship between insect pollinator composition and fruit production

Relationship between insect pollinator composition (Shannon's diversity and abundance) and the quality of fruit setting of teak in each site was investigated. Fruit production, recorded as proportion of weight containing fruit setting (kg/ tree), of teak in each seed plantation was significantly different among the habitats (ANOVA, $F_{4, 45} = 9.868$, $P < 0.001$) and there was a positive correlation with abundance of insect pollinator composition ($R^2 = 0.953$, $P = 0.004$) but was not significantly correlated with Shannon's diversity ($R^2 = 0.093$, $P = 0.618$). The fruit setting of trees occurring in Mae Gar site appears, on average, to show more diversity and abundance of insect pollinator composition variables than those of other seed plantations (Figure 2).

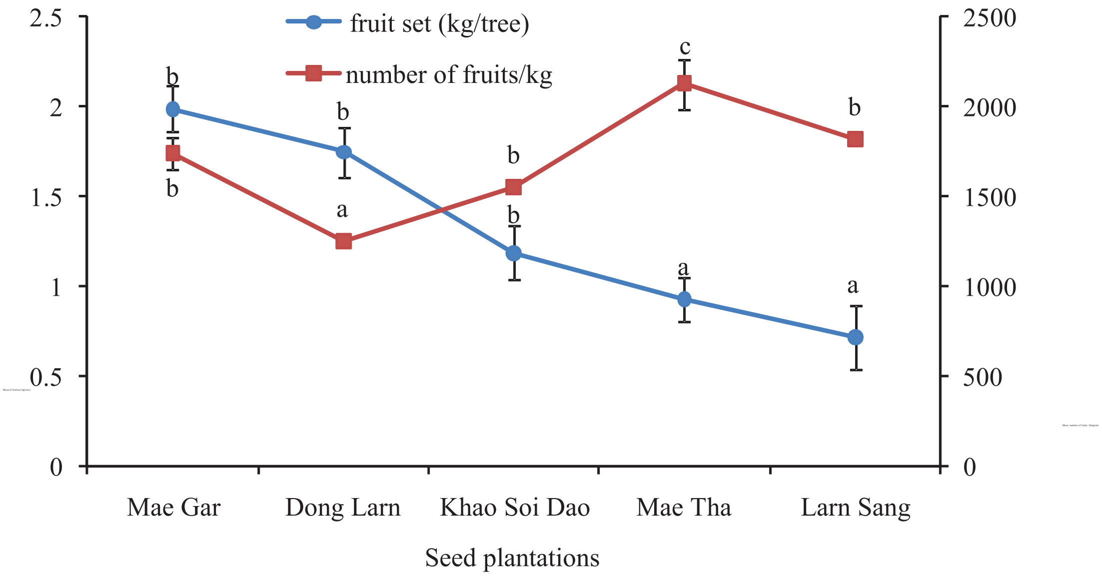

Figure 2 Mean numbers of teak fruit setting as kilograms per tree and number of fruits per kilogram in each seed plantation. The same letters indicate a non-significant difference.

There were significant differences between sites in fruit production of teak measured as number of fruits per kilogram (ANOVA, $F_{4, 45} = 42.561$, $P < 0.001$), but was not significantly correlated with either Shannon's diversity or abundance of pollinator composition ($R^2 = 0.223$, $F_{1, 4} = 0.052$, $P > 0.05$). However, relationship among the macroclimate factors, chemical properties of soil variables and fruit production in each site was not significant ($P > 0.05$), in either kilogram per tree or number of fruits per kilogram. This indicates that the variation of macro-environment factors was sufficient to prevent the growth and appearance of teak trees in five seed plantations.

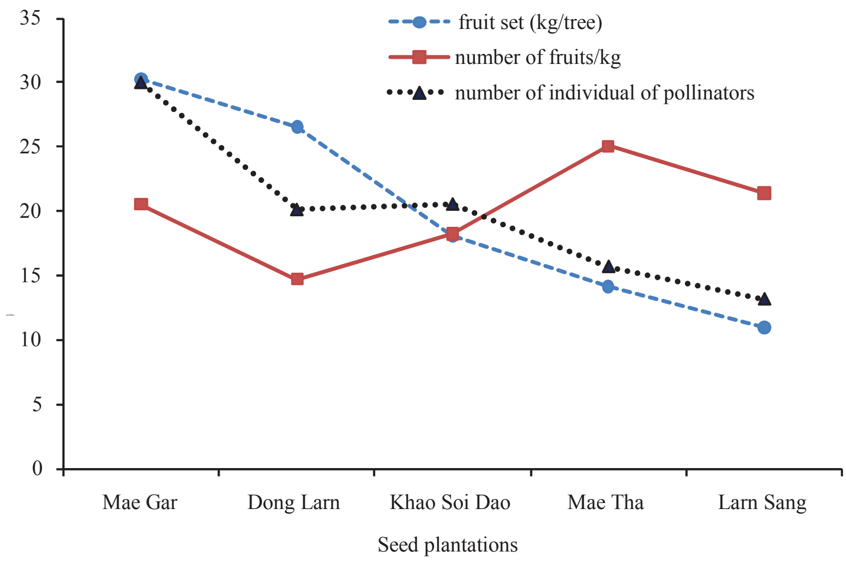

Figure 3 Relationship between percentage of pollinators' abundance, fruit setting in kilograms per tree and number of fruits per kilogram in each seed plantation. The same letters indicate a non-significant difference.

The species diversity and abundance of insect visitors showed a significant difference in each site. The data indicated that Mae Gar seed orchard, located between the three natural forest types (DDF, MDF and DEF), had the highest species numbers and Shannon's diversity index, while the Mae Tha seed orchard near the agriculture land (paddy field about 80%) and DDF, had the lowest. The results from this study showed that the variation within species diversity and richness of insect pollinators was related to habitat types. Table 2 shows that the ten major insect species contributing most flower visits (all sites combined, $n = 475$) were *Trigona collina* (family Apidae), *Apis florea* (Apidae), *Catopsilia pomona hilaria* (Pieridae), *Apis cerana* (Apidae), *Catopsilia pomona pomona* (Pieridae), *Ceratina* spp. (Apidae), *Vespa affinis* (Vespidae), *Chrysomya* sp. (Calliphoridae), *Trigona terminata* (Apidae) and *Episyrphus* sp. (Syrphidae). The orchards surrounded by natural forests have important effects on insect diversity and abundance. However, many reports about biodiversity of fauna in increasing habitat modification found general trends decreasing species richness (Lawton *et al*., 1998). The characteristics of each site may vary among pollinator species and abundance; these may also be dependent on floral production and the extent of habitat fragmentation. Habitat fragmentation is one of the factors affecting species diversity (Saunders *et al*., 1991; Kemper *et al*., 1999), as well as the abundance of particular pollinators and other factors, such as, vegetable cover and the ratio of grass to shrubs (Donaldson *et al*., 2002).

Table 2 Shannon's diversity index, number of species and individuals of 10 major insect pollinators observed on flowers in five teak seed plantations (H = Hymenoptera, L = Lepidoptera and D = Diptera).

	species	Order	Shannon's diversity index *(H')*					Number of individuals
			MG	MT	DL	KD	LS	
1	*Trigona collina*	H	0.34	0.25	0.26	0.23	-	65
2	*Apis florea*	H	0.21	0.25	-	0.27	0.22	40
3	*Catopsilia pomona hilaria*	L	0.10	0.25	-	0.20	0.28	30
4	*Apis cerana*	H	0.19	0.22	0.19	0.15	-	29
5	*Catopsilia pomona pomona*	L	0.16	0.22	0.21	0.13	-	27
6	*Ceratina* spp.	H	0.13	-	0.19	0.13	0.14	20
7	*Vespa affinis*	H	0.03	0.27	0.21	-	-	19
8	*Chrysomya* sp.	D	0.12	-	0.19	0.15	-	17
9	*Trigona terminata*	H	0.12	-	0.13	0.17	-	15
10	*Episyrphus* sp.	D	0.13	0.13	-	0.11	0.14	15

Among the micro-environmental factors of each seed orchard (Table 3), only PAR and temperature variables were significantly different (see Figure 1a), showing that variations among sites in light intensity and sunlight depended on each location. However, each individual location had a characteristic temporal pattern, which Herrera (1995b) implied depended on the duration and timing of direct insolation periods.

Table 3 Differences in mean (± SE) of micro-environmental factors and floral nectar recorded during 09:00 to 15:00 hrs in each seed plantation. The same letters indicate a non-significant difference (*P* < 0.05).

Sites	Micro-environmental factors				Floral nectar	
	PAR (μmol m^{-2} s^{-1})	Humidity (%)	Temperature (°C)	Wind speed (m/s)	% of sugar concentration	Volume (µL/flower)
MG	348.39±86.51^{ab}	83.34±1.33^{c}	26.86±0.50^{a}	0.79±0.10^{b}	35.40±6.22^{a}	0.12±0.03^{b}
LS	360.59±45.21^{ab}	67.59±1.11^{a}	28.71±0.34^{b}	0.75±0.14^{b}	47.11±6.01^{a}	0.04±0.01^{a}
KD	204.33±51.21^{a}	74.94±1.74^{b}	28.76±0.36^{b}	0.34±0.10^{a}	41.23±6.96^{a}	0.07±0.02^{ab}
DL	501.28±77.75^{ab}	75.90±0.95^{b}	28.34±0.37^{b}	0.43±0.07^{a}	43.58±5.58^{a}	0.09±0.03^{ab}
MT	575.56±161.89^{b}	73.20±1.95^{b}	28.94±0.62^{b}	0.44±0.11^{a}	42.02±8.49^{a}	0.08±0.02^{ab}

Variations in the insect pollinator composition and environmental variables among the teak seed orchards differed significantly by species composition and micro-environmental variables. The main finding of this study was that irradiance significantly affected insect pollinator species (see Figure 1b), especially in their foraging responses to the spatio-temporal mosaic of sun and shade patches (Herrera, 1995a). Therefore, the proper microclimate, especially sunlight and temperature, was required to encourage the visiting behavior of certain teak insect pollinators. Insect activity on rainy or cloudy days was less than on sunny days. Temperature is an important factor in determining the effective pollination period, stigma receptivity, and pollen germination (Fernandez-Escobar *et al*. 1983, Burgos *et al*. 1991). However, high temperatures on sunny days may cause drying of the stigmatic surface, resulting in less effective pollination (Tangmitcharoen and Owens, 1997b).

The variations in the pollinator assemblage (rather than adaptation to local environmental conditions) may cause population differentiation. Adaptations of pollinator that may increase visitation frequency and efficiency of pollination in different locations can lead to species divergence and behavior isolation between closely related populations. Different environmental factors can result in adaptation to particular habitats (Hiesey *et al*. 1971, Bennington and McGraw, 1995), while different pollinators may initiate a pattern of floral divergence (Grant, 1993). However, the relationships of entomophilous plants reveal that the plant is influenced by the pollinators more than the pollinators are by the plants (Feinsinger, 1983).

As suggested by many studies (Grant 1993; Herrera 1995b; Lau and Galloway 2004), we expect that other factors in addition to climatic variables or the direct physical environment and plant traits associated with species abundance may have an influence on the composition of insect pollinators in each seed orchard. One further factor that may influence pollinator diversity and abundance at each site is the distribution of nests or hives of certain insects, especially social insects such as honeybees, wild bees and wasps. Nest sites may occur in high densities for some insect species, with differences in fragment size (Gess and Gess, 1993), which can predict the effects of habitat fragmentation on pollination systems and plant reproductive success (Donaldson *et al*., 2002).

CONCLUSION

In conclusion, we have demonstrated that insect pollinator abundance can vary due to floral traits and environmental factors from different time periods and habitats. Our results show that some species of pollinator insects respond to variations of microclimate and floral trait variables. Other studies have found that low fruit sets in some areas may be due to major pollinator scarcity. Insect visitors are necessary for the pollination of teak. Forest buffer conservation and artificial supplementation of efficient pollinators could be an alternative way to improve fruit production, and to ensure the quality of improved seeds in seed orchards. We assume that the selection of particular characteristics of pollinator ability can directly affect the efficiency of the reproductive success of teak.

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