Path analysis and correlation coefficient of environmental factors influencing foraging behaviour of four honeybee species pollinating litchi flowers (*Litchi chinensis* Sonn.)

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Summary: Honeybee species *Apis dorsata* F; *A. mellifera* L; *A. cerana* F. and *A. florea* F. were the most important and efficient pollinators of litchi flowers *(Litchi chinensis* Sonn.) in India. They constituted more than 65% of the total pollinating insects. The ecological threshold for commencement and cessation of flight activity of each honeybee species varied from one another. In general, 15.5-18.5°C temperature, 600-1700 lx light intensity, 9-20 mW/cm^2 solar radiation appeared to be the minimum ecological conditions for commencement of flight activity in *Apis* species. Cessation of activities in all the honeybee species was governed mainly by decline in values of light intensity and solar radiation irrespective of other factors.

In between commencement and cessation, the activity of all honeybee species followed the same general pattern as temperature (T), light intensity (LI). Solar radiation (SR). Nectar sugar concentration (NSC) and inversely with relative humidity (RH). Path analysis revealed that all the honeybee species differed in their responses to environmental factors prevailing under similar set of conditions depending upon physiological adaptation of each honeybee species. Of all the factors studied; temperature, light intensity and solar radiation were the three important factors whose influence on foraging population was more pronounced.

Key words: Litchi, honeybees, environmental factors, pollination, path analysis

Introduction

Litchi *(Litchi chinensis* Sonn.) is one of the important fruit crop known for its delicious juicy fruit, high nutritive value, good taste and pleasant flavour. It originated in China where it has been cultivated for over 3000 years from where it spread to tropical and subtropical areas of the world. In India, litchi is cultivated in an area of 23 442 ha and about 50 cultivars are grown in different states *(Pande & Sharma*, 1989). As litchi cultivation yields a lucrative income there has been a keen interest for its increased multiplication to boost production. Among the various factors which regulate its production, self-sterility in some of the cultivars is mainly responsible for its failure in fruit set in absence of pollinating insects (*Free*, 1993). *Uji* (1987) observed that inflorescences isolated from insect visits failed to produce any fruit, thereby indicating that insect pollination is essential for fruit production in litchi. The present study was therefore, conducted to determine the spectrum of pollinating insects and their foraging behaviour in relation to some meteorological variables such as air temperature, relative humidity, light intensity, solar radiation and nectar sugar concentration. The results obtained are presented in this paper.

Material and method

The study was conducted in litchi orchard located at Regional Horticultural Research Station, Udheywala of Sher-e-Kashmir University of Agricultural Sciences and Technology, Jammu located at a distance of 5 km from Jammu city (Longitude 70.5 ° East and latitude 32.39° North and 300 m M.S.L.) The climate of the experimental area is typically subtropical. Relative abundance of insects was recorded right from the commencement till the end of the flowering. For this purpose, five panicles of uniform size were randomly selected and number of insect pollinators of each species recorded by visual counting method at the beginning of each hour for five minutes from 0800–1700 h on all the days of observation. The mean of these observations constituted reading for each hour. Simultaneously, air temperature and relative humidity were recorded with dry and wet bulb thermometer. Light intensity (LI) was recorded with a lx meter (model lxomet-300) and solar radiation (SR) with a solarimeter (model, lxomet-300). Total dissolved sugars in the nectar were estimated with the help of pocket refractometer (Erma type, Japan make). The recorded data were analysed for simple correlation and path analysis as per method described by *Dewey and Lu* (1959).

Table 1 Taxonomic status and pollinating efficiency of insect species, visiting litchi flowersa

Order	Family	Species	Pollinator rating		
Hymenoptera	Apidae	*Apis dorsata*	+++		
		A. mellifera		+++	
		A. cerana			+++
		A. florea			+++
	Anthophoridae	*Xylocopa fenesterata*	+		
		S. aestuans		+	
	Halictidae	*Halictus* spp.		++	
		Nomia spp.			+
	Vespidae	*Vespa orientalis*			*
		V. cincta			+
		Polistes hebraeus		+	
	Megachilidae	*Megachile lanata*		+	
	Formicidae	*Camponotus compressus*		+	
Diptera	Muscidae	*Musca* spp.		++	
	Syrphidae	*Eristalis tenax*		++	
		Eristalis spp.			
		Sporophoria indiana		++	
		Metasyrphus corollae		++	
		Melanostoma univitatum		++	
		Episyrphus balteatus		++	
Lepidoptera	Lycaenidae	*Horage* spp.	*		
Coleoptera	Coccinellidae	*Coccinella septumpunctata*	+		
		C. septumpunctata var *divaricata*		+	
		Menochilus sexmaculata		+	
		Coleophora sanzeti		+	
		Leia spp.			+
Hemiptera	Scutelleridae	*Chrysocoris partricius*	+		
Thysanoptera	Thripidae	Thrips	*		

Explanation:
+++ Most efficient
++ Moderate
+ Less efficient
* Accidental pollinator

Results and discussion

The studies revealed that litchi flowers attracted insects belonging to 6 orders, 12 families, 22 genra and 29 species *(Table 1)*. Of all these insects, honeybees *Apis dorsata, A. mellifera, A cerana* and *A. florea* were the dominant flower visitors and comprised more than 65% of the total flower visiting insects. Their abundance was in the order: *A. dorsata > A. mellifera > A cerana > A. florea (Figure 1)*. The other important insects frequenting litchi flowers were *Musca* sp. and *Syrphus* sp; the latter group of insects mostly collected nectar and were not considered as the reliable pollinators. The detailed investigations were, therefore, carried out on honeybees which frequented litchi flowers in large numbers throughout the day and fully equipped with anatomical modifications suitable for pollen collection. In most of the earlier studies also, *Apis* spp have been reported as important and efficient pollinators of litchi (*Pande and Yadav*, 1970; *Uji* 1987; *Badiyala and Garg* 1990; *Kakutoni et al.* 1990).

Commencement and cessation of foraging activity: Each bee species was found to have its specific ecological threshold below which activity does not occur. The time of commencement of bee activity varied from one day to another which depended upon attainment of minimum threshold conditions for their foraging activity *(Table 2)*. In general, 16 °C temperature, 74 per cent RH, 600 lx LI and 10 mW/cm^2 SR for *A. dorsata;* 16°C temperature, 75 per cent RH, 800 lx LI, 10 mW/cm^2 SR for *A. mellifera;* 15.5° C temperature, 76 per cent RH, 600 1x LI, 9 mW/cm^2 SR for *A. cerana* and 18.5 °C temperature, 64 per cent RH, 1700 1x LI and 20 mW/cm^2 SR for *A. florea* appeared to be minimum threshold condition for initiation of flight activity. The cessation of activities in all the honeybee species was governed mainly by the decline in values of light intensity and solar radiation which were appreciably low at cessation than at the commencement. It is further evident that cessation of foraging activity occurred, even before the temperature dropped to the values, required for commencement of field activity. The results are in accordance with *Kapil & Kumar* (1974) who reported 15–18 °C as the minimum threshold temperature for commencement of field activities in honeybees. In a similar study, *Osgood* (1974) reported that ambient temperature is the predominant factor governing the morning flight of *Megachile rotundata* while cessation of activity is governed by LI.

Diurnal trends in bee activity in relation to various environmental factors: The data presented in *Figure 2* show that bee abundance followed air temperature, LI, SR and fluctuations in NSC but was inversely related to RH. In general, maximum foraging populations of all the honeybee species were observed between 1100–1300 hour when the air temperature ranged between 23–34 °C; RH between 65–87 per cent, LI between 2700–6700 lx, SR between 24–35 mW/cm^2 and NSC between 40-68 per cent. However, on cloudy/ overcast days the pattern was altogether different. There was no well defined peak. Foraging populations were generally low in numbers and activity occurred only when ecological conditions within which foraging occurs were attained. *Szabo & Smith* (1972) reported that greatest foraging activity of *M. rotundata* occurred at 30 °C in bright sunshine and declined at higher temperature in Hungary. *Kapil & Brar* (1971) recorded peak activity of *A. florea* on toria between 21–25 °C temperature and 50–57 percent relative humidity during November. In general suitability of optimum bee activity vary from season to season, depending upon the geographical regions, time of the year, melliferous crops or species of bees.

Table 2 Temperature, relative humidity, light intensity and solar radiation in relation to the commencement and cessation of flight activity of *Apis mellifera* L. and Apis cerana indica F. on litchi bloom, during April, 1998.

Date of observation	Commencement						Cessation				
	Time (h)	Temp. (°C)	Relative humidity (%)	Light intensity Remarks	(lx)	Solar radiation (mW/cm²)	Time (h)	Temp. (°C)	Relative humidity (%)	Light intensity (lx)	Solar radiation (mW/cm²)
A. mellifera April, 1998											
9	06.50	18.0	90.00	0800	15.00	17.20	27.0	80.0	0700	7.5	Clear
12	07.00	16.0	75.00	1700	18.00	17.30	25.0	60.0	0700	12.5	Clear
15	08.50	18.0	76.00	1500	16.00	17.20	25.0	62.0	950	15.0	Cold, cloudy & windy
18	07.30	16.5	88.00	1600	25.00	17.20	26.0	86.0	1100	13.5	Clear
21	07.00	20.5	78.00	1100	22.50	17.00	30.0	80.0	1400	12.0	Clear
24	07.20	19.0	92.00	1300	24.00	17.00	28.5	86.0	800	8.0	Clear
27	07.10	18.5	85.00	1200	10.00	17.05	28.5	82.0	800	9.0	Clear
30	07.30	19.0	88.00	1500	15.00	17.20	29.5	84.0	900	9.0	Clear
Apis cerana indica April, 1998											
9	06.00	16.5	92.00	0600	14.50	17.30	27.5	80.0	0630	6.0	Clear
12	06.45	15.5	80.00	1500	16.50	17.20	25.0	76.0	1000	12.5	Clear
15	08.30	16.5	76.00	1200	23.50	17.50	23.0	65.0	800	13.5	Cold, cloudy & windy
18	06.00	15.5	91.00	1400	22.50	17.10	25.0	86.0	900	13.0	Clear
21	06.30	20.0	77.00	1100	22.00	17.40	28.5	83.0	600	11.0	Clear
24	06.40	18.5	90.00	1450	26.00	17.35	28.0	81.0	1130	7.0	Clear
27	06.50	18.0	83.00	1000	9.00	17.50	28.0	85.0	550	6.0	Clear
30	06.40	18.5	90.00	1200	9.00	17.40	28.0	86.0	650	6.0	Clear
Apis dorsata April, 1998											
9	06.00	16.5	90.00	600	15.00	18.20	27.0	76.0	200	5.5	Clear
12	07.00	16.0	75.00	1700	18.50	18.10	27.0	74.0	250	6.5	Clear
15	09.00	18.0	74.00	1400	26.50	17.30	25.0	60.0	230	5.0	Cold cloudy & windy
18	07.20	16.5	90.00	1700	23.50	18.00	26.5	85.0	340	6.5	Clear
21	06.30	20.0	78.00	1100	22.00	18.30	30.0	81.0	380	7.0	Clear
24	06.45	18.5	90.00	1500	27.00	18.30	29.5	82.0	240	5.4	Clear
27	07.00	20.0	82.00	1100	10.00	18.40	30.0	83.0	300	6.0	Clear
30	06.30	18.5	90.00	1200	9.00	18.20	28.5	85.0	450	8.0	Clear
A. florea April, 1998											
9	09.00	20.0	78.00	2200	35.00	16.30	29.0	73.0	1100	13.0	Clear
12	10.30	21.0	64.00	3300	43.00	16.50	28.5	70.0	1800	18.5	Clear
15	09.30	20.0	70.00	1700	28.00	16.40	27.0	58.0	1700	20.5	Cold cloudy & windy
18	09.40	19.5	68.00	2700	35.00	17.00	26.5	85.0	1200	15.0	Clear
21	08.50	21.5	84.00	2300	34.00	17.10	29.5	82.0	1300	10.0	Clear
24	09.10	20.0	83.00	2100	27.00	16.40	30.0	80.0	1400	11.0	Clear
27	09.40	18.5	76.00	1800	21.00	16.25	32.0	78.0	1100	13.0	Clear
30	09.50	19.5	67.00	3300	37.00	16.40	30.0	80.0	1200	9.0	Clear

Relationship of foraging population with environmental factors: Correlation co-efficient matrix *(Table 3)* between bee activity and different environmental factors indicated that foraging populations of *A. dorsata*, *A. mellifera*, *A. cerana* and *A. florea* correlated significantly and positively with air temperature, LI, SR, NSC and negatively with RH.

Similar results were obtained by Cirudarescu (1971) who found that the number of insect visitors on lucerne varied directly with temperature and inversely with RH. *Benedek & Prener* (1972) found that air temperature significantly affected the foraging activities of honeybees. They further reported that flower visiting rate increased with increasing air temperature. *Nunez* (1977) reported that morning activity

Table 3 Correlation coefficient matrix exhibiting interrelationship of different environmental factors influencing pollination activity of insects visiting litchi flowers

Factors	Relative humidity	Light intensity	Solar radiation	Nectar sugar conc.	*A. dorsata*	*A. mellifera*	*A. cerana*	*A. florea*
Temperature	–8.27**	0.364**	0.732**	0.600**	0.510**	0.566**	0.542**	0.684**
Relative humidity	–0.439**	–0.758**	–0.481**	–0.518**	–0.661**	–0.674**	–0.640**	–
Light intensity	0.349**	0.486**	0.552**	0.751**	0.660**	0.506**		
Solar radiation	0.512**	0.822**	0.440**	0.576**	0.787**			
Nectar sugar conc.	0.392**	0.475**	0.386**	0.687**				

* $P < 0.05$, df = n-2 = 78
** $P < 0.01$, df = n-2 = 78
ns= Non-significant

of *A. mellifera* was related to nectar flow, while the afternoon, with the photoperiod.

Furthermore, the interrelationship among the independent variables were often highly significant. For example, NSC was highly and positively correlated with temperature, LI and SR and significantly and negatively with RH. Similarly, SR was significantly and positively correlated with temperature, LI, NSC and significantly and negatively with RH. These interrelationship indicate that all the environmental factors are interrelated among themselves. Thus, a need was indicated for further analysis by the path coefficient technique to ascertain the more important factors influencing bee flight activity. For this purpose, correlations were further analysed by path coefficient technique. This technique involves the partitioning of the apparent association of different factors into direct (unidirectional pathways P) and indirect effects (alternate pathways through factor interaction, pathway, P x Correlation coeffi-cient, r) and thus facilitates the more precise deter-mination of relative importance of each factor. With the correlation coefficients partitioned into direct and indirect effects, one clearly sees the quantum of actual contribution by each factor, to the bee activity. Bee activity was considered as the resultant variable and air temperature, RH, LI, SR and NSC as causal variables. Path coefficients were obtained by the solution of simultaneous equations through the method of least squares as given by *Dewey & Lu* (1959) and *Sokal & Rholf* (1981). The path coefficient analysis of inter-relationships of temperature, RH, LI, SR and NSC with bee activity is shown by a schematic model *(Fig. 3)*. The double arrowed lines indicate the mutual association as measured by simple correlation coefficient analysis and single arrowed lines represent the direct effects in one direction only, as measured by path coefficients. the residual factors unaccounted for, were considered independent of other variables and are shown P x 6.

Direct and indirect effects of different environmental factors on bee activity: The data presented in Table 4 show that in case of *A. dorsata,* the direct effect of LI (0.3162), temperature ((0.3012) and SR (0.2018) were pronounced and positive, while the direct effect through RH (–0.1882) was negative and low in magnitude. The direct effects through NSC were negligible (–0.052). Total correlation between temperature and bee activity was high and positive (r = 0.510). This was due to a moderately high and positive direct effect of LI (0.2108) and SR (0.1600). The negative indirect effect of RH (–0.2524) was counter balanced by very low and positive indirect effects of NSC. Similarly, the total correlation between bee visits and LI (r = 0.552) was very high and positive. It developed mainly from its positive direct effect (0.3162) and favourable interactions with other factors. The relationship between bee visits and SR was highly significant and positive. It mainly resulted from positive direct effect of SR itself and positive interaction with other factors. The direct effect of NSC was negligible but its positive interactions with temperature, LI, SR were largely responsible to strengthen its overall positive association with bees (r = 0.392). The direct effect of RH was negative (–0.1882) but its strong negative interactions with temperature, LI, SR and NSC were largely responsible for its overall significant negative association with bees (r = –0.598). Thus, it appears from the above analysis that air temperature, LI, SR were the three environmental factors whose influence on foraging population was direct and pronounced.

In case of *A. mellifera (Table 4)*, the direct effect of LI was more pronounced and positive (0.2206) followed by temperature and solar radiation while the direct effect of RH was negative and that of NSC was negligible. The overall significant positive or negative association with bee visits largely developed through favourable or unfavourable interactions with other factors. Evidently, T, LI and SR directly and positively and RH directly and negatively influenced and foraging populations. In case of *A. florea,* the direct effects of SR and LI were pronounced and positive, while the RH directly and negatively influenced the bee activity. The direct effect of temperature was also negative. The direct effect of NSC was negligible. The ultimate significant positive or negative association with bee visits were largely, determined by positive or negative indirect effects of simultaneously operating factors. The analysis clearly reveals that in case of *A. florea,* SR directly and positively and RH directly and negatively influenced the flight activity. In case of *A. cerana,* the direct effect of LI was pronounced and positive while the direct effect of other

Table 4 Direct and indirect effects of various environmental factors on the flight activity of *A. mellifera* and indica visiting litchi flowers

Factors	Temp. humidity	Relative intensity	Light radiation	Solar sugar conc.	Nectar with bee activity	Coefficient of correlation
A. mellifera						
Temperature	0.2108	–0.2204	0.3010	0.1720	0.1020	0.566
Relative humidity	–0.2200	–0.2025	–0.0120	–0.2082	–0.0192	–0.661
Light intensity	0.2206	–0.2030	0.2206	0.3018	0.0202	0.751
Solar radiation	0.1123	–0.0940	0.2360	0.1084	0.0780	0.440
Nectar sugar conc.	0.1430	–0.0440	0.2484	0.1087	0.0189	0.475
Residual						0.170
A. cerana indica						
Temperature	0.1140	–0.2101	0.4200	0.1568	0.620	0.542
Relative humidity	–0.2400	–0.1506	–0.0520	–0.2481	–0.0160	–0.661
Light intensity	0.1807	–0.2140	0.3481	0.3120	0.0400	0.660
Solar radiation	0.1368	–0.0187	0.3220	0.0421	0.0940	0.576
Nectar sugar conc.	0.2444	–0.2926	0.3102	0.2068	0.082	–0.386
Residual						0.140
A. florea						
Temperature	–0.1874	–0.5012	0.1530	0.1563	0.0609	0.684
Relative humidity	–0.2305	–0.5012	–0.1519	–0.1184	–0.1000	–0.641
Light intensity	–0.0940	0.1140	0.3496	0.0583	0.079	0.506
Solar radiation	–0.1899	0.1810	0.3162	0.5429	–0.0631	0.787
Nectar sugar conc.	–0.0810	0.1922	0.2312	0.3429	–0.0881	0.687
Residual						0.21
A. dorsata						
Temperature	0.3012	–0.2524	0.2108	0.1600	0.0910	0.510
Relative humidity	–0.2028	–0.1882	–0.2162	–0.0200	–0.0410	–0.598
Light intensity	0.1012	0.0156	0.3162	0.1052	0.0140	0.552
Solar radiation	0.3102	0.1098	0.1208	0.2018	0.0800	0.882
Nectar sugar conc.	0.2608	–0.2508	0.3004	0.1836	–0.052	0.442
Residual						0.130

Figures underlined denote direct effects

factors were low in magnitude negative or negligible. Overall, significant positive or negative association with foraging populations as revealed by simple correlation analysis was largely due to favourable or unfavourable interactions with interacting environmental variables. An overall examination reveals that in case of *A.dorsata* temperature, LI, SR; in case of *A. mellifera,* T, LI, SR and RH; in case of *A. cerana* LI and in case of *A. florea* SR and RH were the important factors.

Comparative analysis of the data by simple correlation and path coefficient analysis revealed that the latter technique gave a somewhat different picture of effects from that which could be anticipated by the use of former analysis as has been done by several investigators (*Cirudarescu* 1971; *Szabo & Smith* 1972; *Nunez* 1977; *Corbet* 1978 a, b; *Bailey* et al., 1983; *Burill & Dietx* 1981; *Lerer* et al., 1983). For example, the widely held contention that changes in NSC are reflected by the spectrum of flower visitors (*Corbet*, 1978 a; *Nunez* 1977) and also revealed by simple correlation analysis in present studies *(Table 3)*, is not supported by this analysis. Path analysis, however clearly revealed that NSC has very little concern with bee activity since its direct effect was negligible. The observed correlation with bee visits was largely due to its favourable interaction with temperature and SR *(Table 4)*. Simple correlation analysis revealed that activity of *A. florea (Table 3)* is significantly and positively correlated with temperature (r = 0.684) which implies that with the increase of temperature bee activity will increase. The path coefficient analysis, however, demonstrated that direct effect of temperature was negative and the resultant correlation was strengthened through favourable interactions with other factors. This analysis clearly revealed that SR and RH were the governing factors in case of *A. florea* while the direct effects of other factors were negligible. This analysis has clearly established that interrelated factors like temperature, LI, SR and RH exerted the greatest influence directly and indirectly on the flight activity of the bees. At the behavioural level, *Lindauer* (1955) and others have shown that bees gather more dilute nectar in hot dry weather- a form of negative feed back which could be reflected in a negative correlation between bee activity and relative humidity. The direct effects of temperature, LI and SR were pronounced and positive. This is because of the fact that all these factors are measures of the same basic parameter. The temperature and radiations are responsible for heating of the biosphere and light intensity for illumination. This is evident from their mutual relations as well as significant correlations with bee activity. Thus, the direct effect of NSC was negligible. This may be due to the reason that NSC, a biotic factor, like bee activity, is influenced by temperature and radiation as is evidenced from a high and significant correlation between them. Thus path coefficient analysis provides a different pattern of effects and better explanation than could be anticipated from simple scatter diagrams or simple correlations, as were earlier used by *Szabo & Smith* (1972), *Cirudarescu* (1971)and *Burill & Dietz* (1981). In both these instances, the contradiction between two analysis is due to the fact that the total correlation simple measures mutual association without considering the causation, whereas path coefficient analysis species the basic causes and measures their relative importance.

It is therefore, essential that when number of simultaneously operating and interrelated factors are taken into consideration, as a supplement to simple correlation analysis, the path coefficient analysis should be used to ascertain true nature of interactions and cause effect relationship of different factors, affecting bee activity.

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