Tropical Ecology **45**(2): 263-270, 2004 ISSN 0564-3295

Intensity and diversity of flower-visiting insects in relation to plant density of *Zizyphus mauritiana* Lamk.

R.M. MISHRA, PUSHPLATA GUPTA & G.P. YADAV

School of Environmental Biology, A.P.S. University, Rewa (M.P.) 486 003, India

Abstract : The floral syndrome of *Zizyphus mauritiana* Lamk. (Rhamnaceae) reflects its adaptation to insects. We examined the blossom visitor assemblage of *Z. mauritiana* in relation to plant density. Results indicate that flowers of this plant species are visited by 86 species of insects which consisted 32 species of wasps, 30 flies, 18 butterflies and 6 bees. Pollinators exhibited temporal fluctuations in their visits. More number of insect species visited the flowers with lower intensities (1 to 10 visits m^{-2} h^{-1}). It is observed that intensity of pollinators species increases with increased plant density. Number of pollinators species and their individuals showed significant difference among the blossoms of three patches of plant density. Similarly, the diversity of pollinators was maximum on dense population and minimum on isolated plant.

Resumen: El síndrome floral de *Zizyphus mauritiana* Lamk. (Rhamnaceae) refleja su adaptación a los insectos. Nosotros examinamos el ensamble que visita las flores de *Z. mauritiana* en relación con la densidad vegetal. Los resultados indican que las flores de esta especie vegetal son visitadas por 86 especies de insectos, los cuales incluyeron 32 especies de avispas, 30 de moscas, 18 de mariposas y 6 de abejas. Los polinizadores exhibieron fluctuaciones temporales en sus visitas. Un mayor número de especies de insectos visitaron las flores que tenías menores densidades (1 a 10 visitas m^{-2} h^{-1}). Se observó que la intensidad de las especies de polinizadores aumenta con el incremento de la densidad de plantas. Los números de especies de polinizadores y sus individuos mostraron que hay diferencias significativas entre las flores de tres manchones de densidad vegetal. Asimismo, la diversidad de polinizadores fue máxima en poblaciones densas y mínima en las plantas aisladas.

Resumo: O sindroma floral na *Zizypphus mauritiana* Lamk (Rhamnaceae) reflecte a sua adaptação aos insectos. Examinámos os visitantes nos botões florais na Z. *mauritiana* em relação à densidade das plantas. Os resultados indicam que as flores desta espécie são visitadas por 86 espécies de insectos dos quais 32 espécies são de vespas, 30 de moscas, 18 borboletas e 6 abelhas. Os polinizadores exibiram flutuações temporais nas suas visitas. Maior número de espécies de insectos visitou as flores com menor intensidade (1 a 10 visitas m^{-2} h^{-1}). Foi observado que a intensidade das espécies polinizadoras aumentou com o aumento da densidade das plantas. O número de espécies polinizadoras e as suas hospedeiras mostraram diferenças significativas entre os botões florais de três manchas de densidade de plantas. Semelhantemente, a diversidade dos polinizadores era máxima nas populações densas e mínima em plantas isoladas.

Key words: Diversity, intensity, plant density, pollinators.

Introduction

Pollination results in the production of dispersal units (fruits and seeds) which permit colonization of new sites. The large majority of tropical trees rely exclusively on animals to transfer their pollen. Most of the tropical plant species have evolved relationships with a variety of animals, ranging from tiny thrips and midges to bees and large bats, to shuttle pollen between trees. These relationships can be quite specific, with one type of insect being solely responsible for pollinating the flowers of a particular plant species.

Many recent studies have demonstrated that most of the plant species are pollinated by a diverse assemblage of pollinators (Bawa 1994; Herrera 1988, 1996; Thompson 2001; Waser *et al.* 1996; Wilson & Thompson 1991). Both size and density of a plant species are known to affect pollination and subsequent reproductive performance (Bosch & Waser 1999; Feinsinger *et al.* 1991; Klinkhamer & De Jong 1990; Kunin 1993, 1997; Mustajarvi *et al.* 2001; Sih & Baltus 1987).

Zizyphus mauritiana Lamk. (Rhamnaceae) is a medium size tree, grows commonly within villages of central India. This species produces disciflorous flowers, where the disc on the thalamus serves as a nectar producing organ. The nectar smeared disc in open sunlight gives an impression of exposed sugar drop, which serves to attract a great variety of pollinators, creating a polyphilic system. The present paper provides data on foraging activities and diversity of flower visiting insects (pollinators) in relation to plant density of *Z. mauritiana*.

Materials and methods

This study was conducted in the campus of A.P.S. University, Rewa (M.P.). It lies between latitude 24°-20′ N and 81°-20′ E and 616 meters above MSL. The mean annual total rainfall of this region is 1019.60 mm, with maximum and minimum average temperatures being 31.4°C and 19.2°C respectively.

Field studies were carried out during October 2001. Ten plants of *Z. mauritiana* were marked and observations were made at one-week interval for phenological traits such as appearance of flower buds, flower anthesis, completion of flowering, and duration of flowering. Five twigs, each of 15 cm length from tip of the branch, having 8-10 axillary flower clusters of different stages of flower development, were brought to the laboratory in closed polythene bags. Samples were brought in polythene bags to avoid their drying before study. The axillary clusters were analysed for average number of buds and flowers. Flowers were further analysed for their sexual stages of development, i.e. maleness or femaleness. From such data sex ratios based on number were determined (Yadav 1990).

Visual fields of 1 m^2 (3 for isolated, 14 for intermediate, and 21 for dense plants) area were marked by threads on flowers bearing branches of lower heights. The blossoms in these fields were observed for the period of 15 minutes at each hour between 0600 to 1800 hrs. Insects making visits to the blossom were recorded at each observation for species and their individual numbers. This study was carried out for seven days during peak flowering period (09 October to 15 October 2001) of the plant species. Some individuals of each insect species were collected and brought to the laboratory, and identified with the help of previous collections. Those, which could not be identified, were sent to the Commonwealth Institute of Entomology, London for systematic identification.

The intensity of insects was studied in relation to three grades of plant density (Levin & Kerster 1969); (i) isolated plant (1 plant), (ii) intermediate (patch of 7 plants), and (iii) dense (patch of 21 plants). Temperature records were kept at each hour throughout the study period. We also calculated the Shannon Wiener species diversity index ($\bar{H}$) of blossom visiting pollinators in relation to time and three density classes of *Z. mauritiana* (Shannon-Weaver 1949). The insects were sampled at three times in a day; morning (08.00 hr), afternoon (14.00 hr) and early evening hours (17.00 hr). This sampling was done during the peak period of flowering of plant species. The relative abundance for each species, making visits to blossoms, was determined (Yadav 1990).

Results

Flowering phenology and floral biology

Zizyphus mauritiana is a post-monsoon bloomer. Flower buds appeared during the second week of the September and started opening by the last week of the same month. The flowering came to an end during the first week of November. Thus the flowering lasted for about one month. The flowers are hermaphrodite and reveal protandry (dichogamy). Anthesis occurs during noon and the floral span of this species is 16.30 hr. The species exhibits a definite female bias in its numerical sex ratios. Flowers are greenish-cream in colour and give aminoid smell during hot and dry days. The nectar quantity seems to be very less but swollen floral disc deceitfully created impression of nectar drop, which shines in the light, creating sufficient stimulus to attract a number of insect species.

Flower-visiting insects

A total of 86 species of insects were recorded on the blossom of *Z. mauritiana* during seven days period. This insect community consisted 30 species of flies, 32 wasps, 18 butterflies and 6 bees. Thus wasps contributed maximum (37.20%) to the pollinator guild (Fig. 1) followed by flies (34.88%), butterflies (20.93%) and bees (6.97). Results reveal that flowers of this plant are predominantly visited by flies and wasps. The relative abundance of different insects species varied among four pollinator types. Of 32 species of wasps, *Cerceris tristis, C. albopicta, C. pictiventris, C. pulchra, C. suphureus, Tachytes erythopoda, Oxybellus squamosus, Rhynchium molleryii, Sceliphron madraspatanum,* and *Ammophila nigripes* were numerically abundant. Among the flies, the abundant species were *Syritta pipiens, Antherogona nudiseta, Musca conducens, Daucus cucurbitae, Antherogona oreintalis, Musca sorbens, Physiphora aenaea, Ischiodon scutellaris, Myospila lenticeps* and *Paragus serratus*. Comparatively higher values of relative abundance, recorded for butterflies, were *Zizera gaika, Tarucus theophrastus, Tarias hecabe, Precis almana, P. brassiceae, Spindasis natalensis, Euploea coreta* and *Atelta phalantha.* The abundant bees were *Crocisa ramosa*, *Halictus sp., Apis florea* and *Apis indica.*

Pollinator intensity and species incidence in relation to plant density

The blossom visiting insects of *Z. mauritiana* started their visits early in the morning (between 0600 to 0700 h) and tended to increase in their numbers upto 10.00 h (Fig. 2). However, there was a sharp decline in the species number and their individuals afterwards upto 1500 h. An increased insect activity resumed again during 15.00 to 16.00 h which tended to decline during the subsequent hours. It is observed that blossom visiting insects species (no. $m^{-2}h^{-1}$) and their individuals (m^{-2} h^{-1} sp^{-1}) increased with increase in plants density (Fig. 2). Comparatively higher number of pollinator species (Fig. 3) were recorded on dense plants (average, 45.16 m^{-2} h^{-1}) to be followed by intermediate (average, 32.16 m^{-2} h^{-1}) and isolated

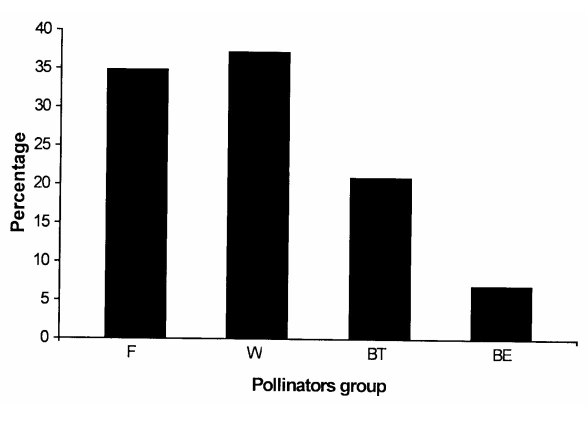

Fig. 1. Percentage contribution of different groups to the pollinators guild of *Zizyphus mauritiana* (F = Flies; W = Wasps; BT = Butterflies, BE = Bees).

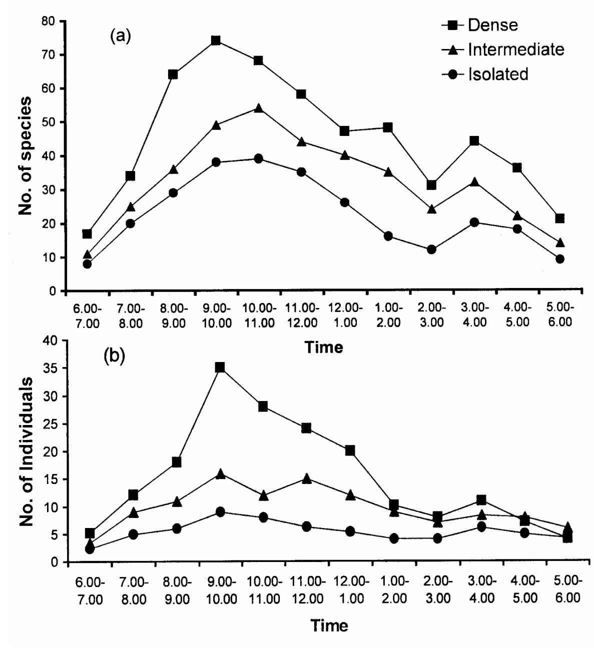

Fig. 2. Pollinators intensity (no. $m^{-2}h^{-1}$) in relation to time and plant density of *Z. mauritiana*; (a) Total insect species, (b) Total individuals.

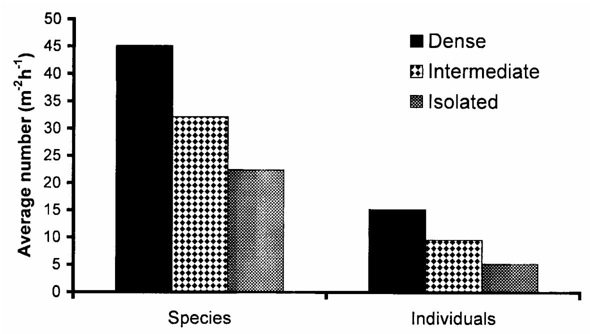

Fig. 3. Average number of pollinator species ($m^{-2}h^{-1}$) and per species individuals ($m^{-2}h^{-1}sp^{-1}$) in relation to plant density of *Z. mauritiana*.

plants (average, 22.5 m^{-2} h^{-1}). Similarly, the average number of individuals per species was recorded to be higher for dense plants, (15.17 m^{-2} h^{-1}) and lower for isolated plant (5.30 m^{-2} h^{-1}). There was significant difference between the number of pollinator species (F=7.36, d.f. 2, 33; P>0.01) and individual numbers (F=7.86, d.f. 2, 33; P<0.01) on the blossoms of three grades of plant density.

Although, intensities of pollinator visits declined with decreased plant densities, their patterns i.e. temperature dependent initiation of visits, periods of peak visits and decline did not get upset. There are temporal fluctuations in pollinator intensities but visits do not stop totally throughout the day. However, two peaks of insect intensities have been observed. The first was observed between 09.00 to 11.00 h and the second peak between 15.00 to 16.00 h. These are the peaks when maximum number of pollinators visited the blossoms.

Distribution of pollinator species number in different intensity classes reveals that more species of pollinators visited the blossoms during the noon and lesser during the evening hours. Also, highest number of species was recorded in the lowest intensity class (1 to 10 visits m^{-2} h^{-1}) and similar trend was observed for all the three classes of plant density. Very few species visited the flowers with high intensity (50-60-visit h^{-1})

Pollinators incidence in relation to temperature

Pollinator incidence on blossom in relation to temperature has been investigated (Table 1). The incidence was measured in terms of number of species and mean number of individuals for four groups of blossom visitors. Diurnal temperature variation ranges from 22ºC to 38ºC. Results show that bees and butterflies did not make their visits to the blossom during the lower temperature range (15ºC to 25ºC). This temperature range, however, is marked by the visits of wasps and flies. The most favourable temperature range was 25ºC to 35ºC for the visits of pollinators. Wasps, flies, bees and butterflies visited maximum during this temperature range.

Pollinators diversity

High pollinator diversity was observed on dense patch of the plant species and low on isolated plant. Higher values of species diversity were recorded for the afternoon samples, followed by morning and early evening samples for all the three categories of plant density (Fig. 4).

Table 1. Incidence and intensity (no. $m^{-2}h^{-1}$) of pollinator species of *Zizyphus mauritiana* in relation to deil temperature intervals.

Class of blossom visitors	Temperature					
	15° - 25°C		25° - 35°C		35° - 45°C	
	Species	Average no. of individuals	Species	Average no. of individuals	Species	Average no. of individuals
Wasps	1	7.2 ± 0.00	30	98.589 ± 2.006	23	17.63 ± 4.618
Bees			6	46.4 ± 0.104	4	6.00 ± 0.166
Flies	5	6.72 ± 0.312	12	161.2 ± 2.289	8	12.30 ± 0.258
Carrion and dung flies	6	4.8 ± 0.51	9	158.166 ± 2.08	8	10.2 ± 0.561
Hover flies	5	3.84 ± 0.26	10	92.14 ± 0.365	4	10.8 ± 0.165
Butterflies			18	42.4 ± 3.001	10	7.68 ± 0.49
Total	17		85		57	

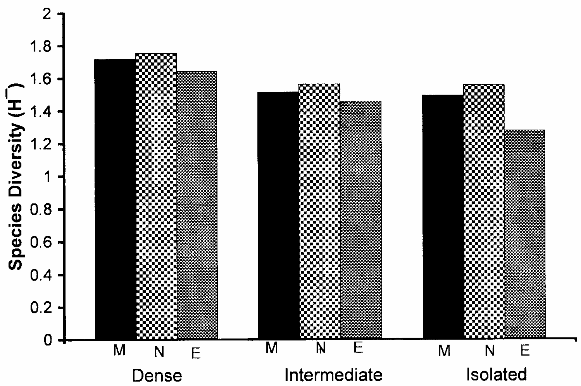

Fig. 4. Pollinators species diversity in relation to time and plant density of *Z. mauritiana* (M = Morning; N = Noon; E = Early evening).

Discussion

Angiosperms have a broad range of reproductive strategies, and the morphology and phenology of the flower influence the behaviour of the pollinators. Because of the differences in reward presentation, visitors may be differentially attached to flowers in a particular stage of development, and visitors may handle flowers differentially depending on the rewards that they are seeking. Pollination is accomplished during pollen and nectar foraging by visitors.

The flowers of *Z. mauritiana* are simple, small, greenish-cream, in short axillary cymose clusters, and with exposed nectar on floral disc and aminoid smell. To ensure pollination, flowers possess adaptations to the sensory abilities, mobility, and morphology of pollinators (Faegri & van der Pijl 1979). Flowers of different species often converge in the characteristics (syndrome) that they present to attract particular guild of pollinators. For instance, flowers visited by insects are, in general, small, scented and contain small amount of nectar. "Ornithophilous" flowers are usually large, orange or yellow and contain large amount of dilute and unscented nectar (Faegri & van der Pijl 1979). Judging from this description, the flowers of *Z. mauritiana* are primarily adapted for insects for their pollination. The flower characteristics of this species are usually associated with entomophilous syndrome.

Flower-visiting insect taxa of this plant species includes 32 species of wasps, 30 flies, 18 butterflies and 6 bees. Yadav (1990) has reported that flies and wasps are the chief pollinators of this species. The flies have also constituted the important pollination group of some other entomophilous plants of the tropical forests (Bawa 1990; Forster 1992). Visit of wasps, bees and butterflies in combination with flies to the blossom of *Z. mauritiana* is in line with the findings of other studies. House (1989) and Jones & Crome (1990) are of the opinion that visitation and pollination by flies, often in combination with pollination by Hymenopteran insects, forms a dominating trait amongst entomophilous plants.

Since the role played by each group of pollinator in effective pollination (pollen transfer) was not a part of this study, it is very difficult to assign any group as an effective pollinator and also to draw an inference of effective pollination from floral traits. It is recognized that inferences of pollination effectiveness base solely on floral traits can be suspect (Bawa 1994; Fishbein & Venable 1996; Waser *et al.* 1996). Herrera (1996) suggested that specialization for one particular pollinator for one syndrome may not occur if the most consistent pollination results from visits from diverse pollinators. However, the floral traits of *Z. mauritiana* partly implies the flies-pollination syndrome (Faegri & van der Pijl 1979). Since flies with shorter tongue do not probe deep and feed on exposed nectar, they usually prefer cymose umbelloid inflorescence. Further flies increase their number by exploiting decaying debris and animal litter, pollination of monsoon and post monsoon flowering plants by them is a natural coincidence (Bhatnagar 1989).

Results reveal the abundance of wasps on the blossom of *Z. mauritiana* (Fig. 1). Some other ecological studies also provide data on wasps as flower visitors of different plant communities (Heithaus 1979; Petanidou & Ellis 1993; William & Adam 1995). Wasps visited the flower for nectar, and the insect body does not have adaptations for the collection of pollen. In place of pollen, wasps collect larvae and adult insect as the source of protein. Since all wasps land on blossom surface as they visit flowers, the blossom must provide sufficient horizontal landing surface. This is provided by umbelloid inflorescence of *Z. mauritiana*. Further studies on wasps, as an effective pollinator of this plant species are needed. *Z. mauritiana* neither reveal syndrome for melittophily (pollination by bees) nor for psychophily (pollination by butterflies). The swollen floral disc which deceitfully created impression of nectar drop might have created sufficient stimulus to attract the wasps, bees, butterflies and flies.

There is temporal variation in pollinator visits on the blossom. More number of insects visited the flower during late morning hours followed by a sharp decline afterwards the noon. The increased insect activities resumed again during early evening hours which tended to decline during subsequent hours (Fig. 2). The most favourable range of temperature has been 25ºC to 35ºC for the visits of pollinators on the blossom of *Z. mauritiana* (Table 1). The establishment of precise activity thresholds is difficult because responses depend on a combination of factors that include not only weather variables, but also the physiological and behavioral state of insects, as well as floral resource availability (Stone 1994). Temperature can have considerable influence on pollinator systems, both by affecting the activity of insects or by altering the volatilization of attractants and nectar flow (Williams & Williams 1983). This study implies that insect activity initiation is limited by temperature, and activity termination is determined either by a decline in light intensity or possibly, by a decline in pollen-nectar availability (Abrol 1988; Vicens & Bosch 2000). Standing crops of pollen and nectar may condition daily activity rhythms, and mask the effect of weather factors, specially in endothermic species (Stone *et al.* 1998).

This study clearly shows a significant effect of plant density on species composition of the visitor community. Maximum number of pollinator species visited the dense plants, as compared to intermediate and isolated plant (Fig. 2). This result is in agreement with the findings of Bosch & Waser (1999), Feinsinger *et al.* (1991) and Kunin (1997). It is suggested that larger populations of plants are likely to be more attractive to pollinators resulting in higher visitation rate and therefore pollination success (Agren 1996; Sih & Baltus 1987), whereas small populations may suffer from insufficient pollen transfer and consequently lower seeds set (Fischer & Matthies 1998; Lamont *et al.* 1993). Optimal foraging theory (Charnov 1976) predicts that in sparse populations, pollinators will switch between plants less often and visit more flowers on a plant when plant density is low (Cresswell 1997; Heinrich 1979; Klinkhamer & De Jong 1990; Zimmerman 1981). This is possibly the reason for increased number of pollinator species on blossoms of dense plants in *Z. mauritiana.* De Jong *et al.* (1993) have stated that plant density probably affects the behaviour of pollinators which are more likely to move between the individuals in dense population, where flight distances are shorter than in sparse population where increased visits within a plant may favor within-plant pollen transfer (geitonogamy). Dense populations might experience some benefits from the greater cross-pollination rate (Mustajarvi *et al.* 2001).

As in earlier studies (Aizen & Feinsinger 1994; Mustajarvi *et al.* 2001), pollinators diversity increased with increasing plant density (Fig. 4). Since the blossom pollinators community is maintained against single resource, the diversity of blossom visiting fauna might have generated on account of nectar resource. Further, this diversity might be an outcome of a passive competition, which is described as scrambling (Nicholson 1957). The species in such a system exploit a resource according to their individual capacities, without any contest or interference.

Acknowledgements

Authors are thankful to Prof. R.N. Shukla, Head, School of Environmental Biology, APS University, Rewa for encouragement and providing facilities in the department. We also express our gratitutes to Prof. S. Bhatnagar, Retd. Professor of the department for his constant guidance.

References

Abrol, D.P. 1988. Effect of climatic factors on pollination activity of *Alfalfa*-pollinating subtropical bees *Megachile nana* Bingh and *Megachile flavipes* Spinola (Hymnoptera : Megachilidae). *Acta Oecologia Genera* **9**: 371-377.

Agren, J. 1996. Population size, pollinator limitation, and seed set in the self-incompetible herb *Lythrum salicaria. Ecology* **77**: 1779-1790.

Aizen, M.A. & P. Feinsinger. 1994. Habitat fragmentations, native insect pollinators and feral honey bees in Areentine Chaco Serrano. *Ecological Applications* **4**: 378-392.

Bawa, K.S. 1990. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecological Systematics* **21**: 399-422.

Bawa, K.S. 1994. Pollinators of tropical dioecious angiosperms: a reassessment? No, not yet. *American Journal of Botany* **81**: 456-460.

Bhatnagar, S. 1989. Plant animal interactions with special reference to strategies of growth, phenology and pollination. pp. 252-270. *In*: J.S. Singh & B. Gopal (eds.) *Perspective in Ecology*. Jagminder Book Agency, New Delhi.

Bosch, M. & N.M. Waser. 1999. Effects of local density on pollination and reproduction in *Delphinium muttaliawum* and *Aconitum columbianum* (Rannunculaceae). *American Journal of Botany* **86**: 871-879.

Charnov, E. 1976. Optimal foraging: the marginal value theorem. *Theoretical Population Biology* **9**: 129-136.

Cresswell, J.E. 1997. Spatial heterogeneity, pollinator behaviour and pollinator mediated gene flow: bumblebee movements in various aggregated rows of oil-seed rape. *Oikos* **78**: 546-556.

De Jong, T.J., N.M. Waser & P.G.L. Klinkhamer. 1993. Geitonogamy: the neglected side of selfing. *Trends in Ecology and Evolution* **8**: 321-325.

Faegri, K. & L. van der Pijl. 1979. *The Principles of Pollination Ecology*. Pergamon, Oxford.

Feinsinger, P., H.M. Tiebout & B.F. Young. 1991. Do tropical bird-pollinated plants exhibit density-dependent interactions? Field experiments. *Ecology* **72**: 1953-1963.

Fischer, M. & D. Matthies. 1998. Effects of population size on performance in the rare plant *Gentianella germanica*. *Journal of Ecology* **86**: 195-204.

Fishbein, M. & L. Venable. 1996. Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology* **77**: 1061-1073.

Forster, P.I. 1992. Insects associated with the flowers of *Marsdenia cymbulosa*. Benth. (Asclepiadaceae) and their possible role in pollination. *Australian Entomological Magzine* **19**: 45-47.

Heinrich, B. 1979. Resource heterogeneity and patterns of movement in foraging bumble bees. *Oecologia* **40**: 235-245.

Heithaus, E.R. 1979. Community structure of neotropical flower visiting bees and wasps: diversity and phenology. *Ecology* **60**: 190-202.

Herrera, J. 1988. Pollination relationship in southern Spanish Mediterranean shrub lands. *Journal of Ecology* **76**: 274-287.

Herrera, C.M. 1996. Floral traits and plant adaptations to insect pollinators: a devil advocate approach. pp. 65-87. *In*: D.G.B. Lloyd & S.C.H. Barrett (eds.) *Floral Biology*. Chapman & Hall, New York, U.S.A.

House, S.M. 1989. Pollen movement to flowering canopies of pistillate individuals of three rainforest tree species in tropical Australia. *Australian Journal of Ecology* **14**: 77-94.

Jones, R.F. & F.H.J. Crome. 1990. The biological web-plant/animal interactions in the rainforest. *In*: L.J. Webb & J. Kikkawa (eds.) *Australian Tropical Rainforests*. CSIRO, Australia.

Klinkhamer, P.G.L. & J. De Jong. 1990. Effects of plant size, plant density and sex differential nectar reward on pollinator visitation in the protandrous *Echium vulgare* (Boraginaceae). *Oikos* **57**: 399-405.

Kunin, W.E. 1993. Sex and single mustard: population density and pollinator behaviour effects on seed-set. *Ecology* **74**: 2145-2160.

Kunin, W.E., 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology* **85**: 225-234.

Lamont, B.B., P.G.L. Klinkhamer & E.T.F. Witkowski. 1993. Population fragmentations may reduce fertility to zero in *Banksia goodii* – a demonstration of the allee effect. *Oecologia* **94**: 446-450.

Levin, D.A. & H.W. Kerster. 1969. The dependence of bee mediated pollen and gene disersal upon plant density. *Evolution* **23**: 560-571.

Mustajarvi, K., P. Shkamari, S. Rytkonen & A. Lammi. 2001. Consequences of plant populations size and density for plant-pollinator interactions and plant performance. *Journal of Ecology* **89**: 80-87.

Nicholson, A.J. 1957. The self adjustment of populations to change. cold spring. *Harbor Symposia on Quantitative Biology* **22**: 153-173.

Petanidou, T. & W.N. Ellis. 1993. Pollinating fauna of a phryganic ecosystem: composition and diversity. *Biodiversity Letter* **1**: 9-22.

Shannon, C.E. & W. Weaver. 1949. *The Mathematical Theory of Communication*. Urbans University, Illinois Press.

Sih, A. & M.S. Baltus. 1987. Patch size, pollinator behavior, pollinator limitations in *Catnip*. *Ecology* **68**: 1679-1690.

Stone, G.N. 1994. Activity patterns of the solitary bee *Anthophora plumupes* in relation to temperature, nectar supplies and body size. *Ecological Entomology* **19**: 177-189.

Stone, G.N., P.G. Williams & R.A. Rowe. 1998. Partitioning of pollinators during flowering in a African *Acacia* community. *Ecology* **79**: 2808-2827.

Thompson, J.D. 2001. How do visitation patterns vary among pollinators in relation to floral display and floral design in a generalist pollination system? *Oecologia* **126**: 386-394.

Vicens, N. & J. Bosch. 2000. Weather dependent pollinator activity in an apply orchard, with special reference to *Osmia cornuta and Apis mellifera* (Hymnoptera: Megachilidae and Apidae). *Environmental Entomology* **29**: 413-420.

Waser, N.M., L. Chitaka, M.V. Price, N.M. Williams & J. Ollerton. 1996. Generalization in pollination systems, and why it matters. *Ecology* **77**: 1043-1060.

Williams, G. & P. Adam. 1995. Records of aculeate wasps from flowering subtropical rainforest trees. *Australian Entomologist* **22**: 51-58.

Williams, G.A. & T. Williams. 1983. A list of Buprestidae (Coleoptera) of the Sydney basin, New South Wales, with adult food records and biological notes on food plant associations. *Australian Entomological Magzine* **9**: 81-93.

Wilson, P. & J.D. Thompson. 1991. Heterogeneity among floral visitors leads to a discordance between pollen removal and pollen deposition. *Ecology* **72**: 1503-1507.

Yadav, G.P. 1990. *Studies of Pollination Ecology of Some Species of Genus* Zizyphus *(Rhamnaceae).* Ph.D. Thesis, A.P.S. University, Rewa (M.P.), India.

Zimmerman, M. 1981. Patchiness in the dispersion of nectar resources: probable causes. *Oecologia (Berlin)* **49**: 154-157.