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POLLINATION ECOLOGY WITH SPECIAL REFERENCE TO INSECTS-A REVIEW

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Abstract: Pollination is the process of transferring pollens to the stigma of conspecific plant and pollination ecology is the mutual relationship between flowers and pollinators. Pollination is a co-evolutionary process between flowering plants and pollinators, which dates back to millions of years. Insects are the most effective pollinators and have important role in pollination ecology. This review deals with different aspects of pollination ecology with special reference to insects. The effect and relationship of different characteristics of flowers, insect pollinators and environmental factors are discussed. Pollinators are greatly influenced by shape, length, colour, odour, nectar, pollen and other rewards of flowers. Effectiveness of pollination also depends upon vision, olfaction, taste, anatomy, food preference, behaviour and learning ability of the pollinators. Physical factors, i. e. altitude, temperature, light, wind and rainfall also influence the flower visiting, foraging behaviour and effectiveness of pollinators.

Keywords: Insects, pollinators, pollination ecology.

INTRODUCTION

Pollination is the act of moving pollens from the anthers of a flower to stigma, allowing the flowers to develop seeds for reproduction, while pollination ecology deals with relationship between pollination, pollinators and environmental factors. There are numerous agents responsible for pollination such as wind, insects, birds and bats, which act as dispersal agents for pollens, spores and seeds of many plants. Majority of the plants depend upon insects for pollination, which results in increased biodiversity [Anonymous 2003a]. Pollination ecology is a rapidly developing field [Faegri 1978]. Previous work [Baker and Hurd 1968, Faegri and van der Pijil 1978, Key 1978, Kevan and Baker 1983, Price 1984, Yazdani and Agarwal 1997] on pollination ecology has contributed a lot to our knowledge on the subject. This review concentrates mostly on the entomological aspects regarding pollination ecology. We have tried to cover concepts, relevant fields, important factors and insects involved in pollination.

HISTORICAL BACKGROUND

The process of coevolution between flowering plants and pollinators has been proceeding for 225 million years [Leppik 1960, Anonymous 2003b]. It has been established from fossil record that insects were potentially effective pollinators when first flower appeared, which was small (5 mm) [Leppik 1960]. Gradual increase in flower size (10-12 cm) resulted about 140 million years ago [Smart and Hughes 1973]. Aristotle had the idea of relationship between bees and flowers but detailed floral structure and role of insect pollinators was described by Koelleuter Dobb in 1870 [Verma 1990] and explained by Sprengel's theory [Sprengel 1793], i.e. "every peculiarity of plant anatomy and physiology is related to the peculiarity of the structure and behaviour of the insects which visit and pollinate the flowers". Work of Darwin [1887] is helpful for understanding of plant perpetuation and vigour maintenance through cross-pollination.

There are about 250,000 species of angiosperms out of which 70 % of plants rely on insect pollinators and 30 % of our food comes from insect pollinated plants [Anonymous 2003a]. Angiosperms' relationship with insects as pollinators and birds as seed dispersers is source of its dominance [Regal 1977, Anonymous 2003a]. Grasses are also visited by many insects in tropical regions [Soderstrom and Calderon 1971], which elsewhere are anemophilous. Insects are important transporters of pollens [Faegri and van der Pijil 1978] and spores of some mosses [Erlanson 1930] and fungi, especially rust fungi [Alexopoulos 1952], having mutualistic relationship with each other, while birds are seed dispersers [Regal 1977]. Insect pollinators belonging to important insect orders [Proctor and Yeo 1973] depend upon floral characteristics. Important orders of anthophilous insects (feeding on flowers) are Collembolla and Arachnida [Kevan *et al.* 1975], Coleoptera [Muller 1883, Proctor and Yeo 1973], Diptera [Thien 1980], Lepidoptera [Kendall 1981] and the most important one, Hymenoptera [Spradbury 1973, Keeler 1981]. Role of honeybees as efficient pollinators of different cultivated crop plants is discussed by several authors [Kozin 1976, Crane and Walker 1984] because they can be managed in sufficient number and show flower constancy [Yazdani and Agarwal 1997] especially in apple [Dulta and Verma 1987, Verma 1987].

Insect pollination permits a plant species to outcross with others of the same species [Dressler 1968, Heinrich and Raven 1972]. These pollinators are also responsible for long distance seed dispersal and ultimately reduced seed predation and vulnerability to epidemic diseases [Regal 1977], high evolutionary rate [Levin and Wilson 1976] and increase in seed or fruit yield [Deodikar and Suryanarayana 1977]. The study of pollination ecology requires a detailed understanding of floral characteristics, pollinator's characteristics and environmental factors.

CHARACTERISTICS OF FLOWERS

Pollinators, especially bees and other insects are greatly influenced by shape, outline form, length of flowers [Leppik 1956, Kevan 1983], colour, odour, nectar, pollen and other rewards of flowers. Thus, the effectiveness of pollination depends upon floral characteristics.

COLOUR

Floral colour is a very important factor, which restricts the specific pollinators to visit the flowers and affects the general behaviour of pollinators. Pollinators are responsible for the maintenance of polymorphism in plant population, e.g. pollinating butterflies (*Pierus* spp.) and syrphid flies (*Eristalis* spp.) preferred yellow coloured wild radish, *Raphanus raphanistrum,* while bumblebees (*Bombus* spp.) preferred white colour [Key 1978]. Change in colour of flowers with age also affect the foraging behaviour, e.g. brown-centered older inflorescences of ragwort (*Senecio jacobaea*) are ignored by hover flies visiting yellow-centered younger inflorescences [Kugler 1950]. Similarly, fewer bumblebees visit loco weed (*Oxytropis splendens*) flowers, whose petals are faded [Laverty 1980]. To be efficiently pollinated flowers must contrast with its background [Kevan 1979] because flowers growing in shaded areas and dull backdrops tend to be pale while those blooming in open situation and bright backdrops are darker.

Bee pollinated flowers are bright coloured, reflect light in blue to violet portion of spectrum [Eisner *et al.* 1969] having nectar guides with nectar produced during day [Anonymous 2000]. Blue, purple and mauve flowers are more frequently visited by bees depending upon their strong structural adaptation [Kevan and Baker 1983]. Moths and bats-pollinated flowers are bright or light coloured, with appropriate odour and having nectar guides with nectar produced during night [Anonymous 2000]. Red coloured flowers, opened during the day, are more attractive for birds (humming birds], while blue coloured are less preferred [Price 1984, Anonymous 2000]. The association of butterflies with pinkish [Muller 1883] and red flowers [Proctor and Yeo 1973] is well known.

SCENT

Floral scent is also an important character, which is responsible for the attraction of specific pollinators. Insect-pollinated flowers mostly emit fragrances, whereas bird-pollinated flowers are scentless [Price 1984]. For moth pollination, nocturnally blooming plants having characteristically strong and pervasive floral scent are necessary for long distance advertisement [Kevan and Baker 1983]. *Sphinx pinastri* approaches hidden flowers of honeysuckle, *Lonicera periclymenum*, by orienting upwind [Tinbergen 1958]. Floral scents are not strong in diurnally blooming plants. Generally these scents act as attractants to lure landing [Manning 1956] and may be specifically associated with nectar guides [Brantjes and Leenmans 1976]. Bumblebees prefer to visit one morph of an alpine plant, *Polemonium viscosum* with sweet flowers, while flies visit another morph with skunky flowers [Galen and Kevan 1980]. So, pollinators are responsible for maintenance of polymorphism of plants. Mimetic scents are produced by plants to attract pollinators, e.g. dung and carrion scent for certain beetles and flies [Yeou 1973] and fungal scent in mimicking Mycetophylidae [Vogel 1973].

BLOOMING

Synchronous blooming of small flowers of large inflorescences may increase the energetic gain and reduce time and energy required by pollinators [Price 1984]. It may promote outcrossing by attracting pollinators and achieving pollination [Wilson and Price 1977, Wilson and Bertin 1979], while reduces frequency of cross-pollination [Price 1984]. Vertical inflorescences are greatly advantageous for bees because amount of nectar tends to decrease and sugar concentration increase in higher inflorescence [Hocking 1968] and bees tend to start foraging at bottom and go upward [Pyke 1979, Waddington and Heinrich 1979].

FLOWER CONSTANCY

It relates to the foraging pattern of pollinators. Foraging restricts to one plant species during each trip [Anonymous 2003a] due to high floral constancy [Price 1984] by providing specific and optimum reward per plant and minimizing cost [Anonymous 2000]. Floral constancy and local foraging may lead to sympatric and allotropic speciation in orchids, which are pollinated only by male euglossina bee [Dressler 1968, Dodson 1975]. Flower constancy is important for bees because they learn to extract nectar and pollen while visiting the same flower type [Grant 1950]. The constancy of bees can be estimated by examination of pollen types on the body after foraging. *Apis cerana indica* has higher floral fidelity, i.e. carried 5200 pollen load [Choudary 1978] than other foragers, i.e. *A. florae, A. dorsata* and *A. mellifera* [Dhaliwal and Atwal 1986] foraging on alfalfa (*Medicago sativa*).

FLORAL REWARDS TO POLLINATORS

NECTAR

Nectar is very important as a nutritional and energy source for pollinators. It is a complex mixture of sugars [Anonymous 2000], amino acids [House 1974], proteins [Baker and Baker 1975, Anonymous 2000], lipids [Downer 1978, Cobert *et al*. 1979], antioxidants [Chippendale 1978, Anonymous 2000], alkaloids [Baker and Baker 1975], vitamins, organic acids and inorganic materials such as minerals [House 1974, Waddington and Holden 1979]. All of these have significance in pollination [Baker and Baker 1973, Baker 1978]. Small quantity of highly desirable nectar enables the pollinators to visit numerous flowers and increasing the level of out crossing [Heinrich and Raven 1972, Hickman 1974]. Bats, hawk moth and bird- pollinated flowers open and secrete much nectar at night, while bee and butterfly- pollinated flowers do so during the day [Price 1984, Anonymous 2000].

Nectar sugar concentration varies from less than 10 µg per flower to 163 mg per flower as in *Acanthus mollis* [Percival 1965] and pollinator's requirement for nectar sugar also varies from 15 – 75% [Anonymous 2002]. The nutritive value of all nectar sugars is not the same [Haydak 1970]. Some sugars are even toxic to certain insects, e.g. galactose, lactose, and rafinose are toxic to honeybees [Baker and Lehner 1967] but not to other insects, e.g. Diptera [Sotavalta *et al.* 1962]. Nectar or honeydew may also contain protein building amino acids [Baker and Baker 1973, Baker 1978, Anonymous 2000] and small amount of enzymatic proteins [Baker and Baker 1975] required by insects. Significant concentrations of amino acids in nectar improve both foraging and pollinating efficiency [Baker and Baker 1975].

POLLENS

Pollen was probably the first food reward consumed by spore dispersing arthropods; these may have been Collembolla and Arachnida [Kevan *et al.* 1975]. Pollens are also highly nutritive [Stenly and Linskens 1974] and contain essential and quasiessential amino acids [Haydak 1970] and proteins, e.g. Petunia contains 6% amino acid, 6% peptides and 13 % proteins [Stenly and Linskens 1974]. Oils on the outside of pollen grains may act as attractants [Doull 1976] and are responsible for adherence to each other and to the bodies of pollinators. Pollen is a vital food for many insects, especially Apidae (larvae), many beetles, flies, thrips and butterflies. Pollen's reward of 16-30% protein, 1-7% starch, 0-15% sugar and 3-10% fats are critical for bee pollinators [Anonymous 2002]. Lipids in pollen include sterols [Stenly and Linskens 1974], which are important for insect hormone or pheromone producing capabilities. Modes of ingestion differ among insects, e.g. ingestion of whole grains in thrips [Grinfeld 1959] and maceration in beetles.

OTHER REWARDS

Other rewards for which pollinators visit flowers are caloric reward, energetic, protection and oviposition sites. Plants restrict the visit of certain organisms by their caloric reward [Heinrich and Raven 1972], e.g. 100mg bumblebees uses about 0.08 cal per min. while walking on flowers [Heinrich 1973] but 3g sphinx moth and humming bird use 11 cal per min. while hovering [Heinrich 1971]. The energy balance for pollination involves energy intake (food) and energy used by insects during foraging. Body temperature is a reliable indication of energy expenditure, most of which is released as heat. This relationship in bumblebees has been studied in detail by Heinrich [1979a]. Part of energy expended in flight is used in flight preparation or preflight warm-up [May 1979]. Large insects, e.g. Sphinx moth requires more energy and time to warm up [Heinrich 1975, Heinrich 1979a], while butterflies and flies use solar energy and relish in the sun.

Plant blossoms may provide protection to insects such as thrips, beetles and flies. *Colluna vulgaris* provide protection to pollinator, *Taeniothrips ericae*, which spends most of its life in its flowers [Hartling and Plowright 1979]. Mutualism of *Tegiticula* moth and Yucca [Powell and Mackie 1966] and aganoid wasps and fiscus [Janzen 1979, Wiebes 1979] are other examples of protection and breeding place for insect pollinators and pollination advantage for plants.

CHARACTERISTICS OF POLLINATORS

Effectiveness of pollination greatly depends upon certain attributes and characteristics of pollinators, e.g. their vision, olfaction and taste, their anatomy, food preferences, behaviour and learning ability.

VISION

Generally insect's vision extends from ultraviolet at ca 300 nm (UV) to yellow orange at ca 650 nm. *Heliconius* butterflies are long lived, having highly developed visual system, learning ability and strong selection for male *Anguria* plants [Gilbert 1972]. Bee pollinators have spherical shaped compound eyes with 6300 cone-shaped facets and sensitive to blue, yellow and blue-green colour, ultraviolet and polarized light [Anonymous 2003b]. Pollinating bats have large eyes (good vision), good olfaction, long absorbent tongue and digestive modification [Anonymous 2000].

OLFACTION

Honeybee's olfactory capability is estimated to be 40 times better than human being and plays an important role in locating food sources and communication in and outside the nest [Anonymous 2003b]. Trap lining is mostly used for good location by pollinators such as euglossine bees [Janzen 1970], butterfly, *Heliconius ethilla* [Ehrlich and Gilbert 1973] and sphinx moth [Linhart and Mendenhall 1977]. Significance of trap lining to host plant is described by Janzen [Grant 1971]. Specialized floral morphology and floral visibility is less important for outcrossing at low plant densities.

FORAGING BEHAVIOUR

Changes in, or evolution of floral characteristics are closely correlated with the modification of behaviour of insects / pollinators. Factors that influence the foraging behaviour and determine profitability are weather, distance of food source, food quantity and quality. Pollinators have variable foraging range from 3-12 km [Anonymous 2003b] and different foraging rate depending upon flowers. Foraging rates of bumblebees is twice the rate of honeybees [Free 1968], while that of solitary bees is slow depending upon size [Wood 1965]. Sphinx moth forage fairly rapidly than ants and other crawling insects, having very low-energy foraging behaviour [Hickman 1974].

Short distance movement on patches of flowers has been shown in honeybees, syrphid flies, bees, flies, butterflies, hawk moth and other moths [Beattie 1978, Levin 1978, Waddington and Holden1979]. Turning during foraging has also been quantified for honeybees, bumblebees, and butterflies. Bees turn more frequently while foraging in a rich patch of plants with abundant nectar [Pyke 1979]. Returning ability to same locality over a period of time occurs in land marking honeybees and bumblebees [Manning 1956, Heinrich 1979a]. In trap-lining euglossine bees [Janzen 1970, Grant 1971] and in territorial anophilas such as some Syrphidae and bumblebees learn to recognize the individual plant positions and visit them in sequence [Manning 1956], but may repeat parts of same path several times on a single foraging trip [Heinrich 1979a]. Honeybees are known to recognize the reward by colour and scent [Frisch 1967] and learning start two second prior to feeding and fades rapidly [Menzel 1967]. Flower probing in bumblebee is innate but in case of complex flower, they must learn how to exploit them successfully [Laverty 1980].

Many native butterflies and other nectar feeders are attracted to exotic plant species and drink nectar, pollinate them and contribute to their invasion success by less visiting of native plant species. It results in decline of native plant species [Simonson *et al.* 2000]. Broad tailed and rufous humming birds avoid plants and flowers that have recently been visited by nectar robbing bumblebees by using nectar as proximate cue along with spatial and visual cues [Irwin 2000].

ENVIRONMENTAL FACTORS

The physical environment influences the flower visiting, foraging behaviour and effectiveness of pollination. Environmental factors may include attitude, temperature, light, wind and rainfall.

ALTITUDE

Altitudinal gradient affects the pollination and pollinator’s foraging, e.g. humming birds are more effective pollinators at high elevations while bee at middle [Cruden 1972] and moths at middle and low altitudes [Cruden *et al.* 1976]. The initiation of foraging activity of bees, *Apis mellifera* and *Apis cerana* was reported to be delayed and ceased earlier with increasing altitude [Verma and Dulta 1986]. Fragmentation of natural habitat will disrupt the relationship between plants and its pollinators, e.g. two shrub species, *Acacia brachybotrya* and *Eremophila glabra* growing in linear vegetation received less pollen than conspecifics in nearby reserves [Cunningham 2000].

TEMPERATURE

Temperature has profound effect on pollinators, particularly the poikilothermic insects [Heinrich and Raven 1972]. The energy cost of foraging depends partly upon the environmental temperature [Heinrich

1979a]. As temperature declines, the energetic reward is reduced, so the number of flowers visited must increase [Heinrich 1975, Heinrich 1979a] and flowers should provide more caloric reward [Heinrich and Raven 1972]. Foraging activity in the evening starts to decline at slightly higher temperature [Lundie 1925]. The hive bee, *Apis cerana* can forage at lower temperature than *Apis mellifera* [Verma 1968]. Foraging of bee is also greatly affected by changing temperature, e.g. no foraging occurs below 8^o C, some activity between 8-16^o C, optimum activity between 16-32^o C and reduce foraging above 32^o C [Roberts 1979, Anonymous 2003b] but under some circumstances foraging may continue up to temperature of 42-48^o C [Lundie 1925].

Some insects can thermoregulate [May 1979] to generate or capture heat or to lose heat when overheated [Heinrich 1979b]. In some hot deserts, nocturnal pollination is important [Linsley *et al.* 1973, Hurd and Linsley 1975], while perching, bees keep their flight mechanism at flight temperature by maintaining their thoracic temperature at 32 ^{o}C [Heinrich 1979a].

LIGHT

Insect activity is greatly affected by the light due to nocturnal, diurnal, matinal or crepuscular behaviour of insects. Mostly moths and bats are nocturnal or matinal in foraging activity [Linsley *et al.* 1963, Hurd and Linsley 1975]. Honeybees come and go when light intensity is 500 lux or more while below that, their activity decreases and stops at 10 lux [Levchenko 1961]. In the morning, honeybees start to work at lower light intensity than when they stopped in the evening [Schricker 1965]. Verma and Dulta [1986] studied the comparative foraging behaviour of *Apis mellifera* and *Apis cerana* on apple bloom with respect to time and their results are reviewed in Table 1.

Table 1: Foraging data for *Apis cerana* and *Apis mellifera* honeybees on apple flowers at 1350m in northwest Himalaya in April- May.

PARAMETERS	Apis cerana	Apis mellifera
Initiation (day time) of foraging	06.03±0.01	06.27±0.02
Cessation (day time) of foraging	19.13±0.01	18.55±0.01
Duration (h) of foraging activity	13.10±0.002	12.28±0.003
Duration (min) of foraging trip	11.85±0.36	17.29±0.36
Peaking foraging hours (day time)	09.00 – 11.30	11.00 – 13.20
Time(s) on flower (min)	590±0.22	6.63±0.23
No. Stigmas touched per flower	3.09±0.39	3.33±0.32
Weight (mg) of pollen load: 09:00	9.06±0.02	9.24±0.04
12:00	9.26±0.02	12.22±0.04
15:00	8.64±0.06	11.12±0.03

Each mean (± SE) is for eight observations. For times of initiation, cessation and duration of daily foraging activity, duration of a foraging trip and weights of pollen loads, differences between species are significant (P< 0.01); for number of stigmas touched per flower and time spent on flower P> 0.01. [Verma and Dulta 1986].

So, pollinators show restricted foraging times. Similarly, cloudiness may increase the activities of crepuscular and shade loving insects on flowers but may depress the activities of others.

WIND

Wind affects the foraging activity of insects especially the flying ones. Wind velocity of 24-34 km hr^{-1} adversely affects the foraging behaviour of bees [Lundie 1925, Verma 1990]. Downwind movement of floral odour or upwind flight due to wind greatly influenced directional foraging of bumblebees [Woodell 1978]. Light sea breezes below 7-9 km hr^{-1} influence the ability of hawk moth to pollinate *Pancratium maritimum* at dusk [Eisikowitch and Galil 1971]. Pollination may continue under windy conditions if pollinators have strong flight muscles and plants have rigid and dwarf flower stalk [Eisikowitch and Woodell 1975, Eisikowitch 1978].

RAIN /HUMIDITY

Moisture also affects the activities of insect pollinators like any other organism. Chironomid flies *Smittia velutina,* remain underside of flowers of *Saxifraga oppositifolia* using it as a shelter from rain [Kevan 1973] while bumblebees continue foraging during light precipitation [Bruggeman 1958]. Cloudy and rainy environment may restrict the activity of syrphid [Levesque and Burger 1982] and bees [Cruden 1972], respectively.

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