Palynology

The study of external morphological features of mature pollen grains is referred to as palynology. Since the first use of the term palynology by Hyde and Williams in 1845, several significant contributions have been made in this area, and it has emerged as an important discipline of fundamental and applied interests. In India, the chief centres of research in this field are: National Botanical Research Institute (Lucknow), Birbal Sahni Institute of Palaeobotany (Lucknow), Osmania University (Hyderabad) Bose Institute (Kolkata), French Institute of Pondicherry and Gondwana University (Godchiroli).

Pollen grains are initially formed in groups of four (tetrads). Each pollen grain has two poles (Fig. 5.1) at opposite ends of what is commonly described as the polar axis. The proximal pole (p.p.) is at the centre of the proximal face (toward the centre of the tetrad), whereas the distal pole is at the centre of the distal face (away from the centre of the tetrad). The polar axis must always be perpendicular

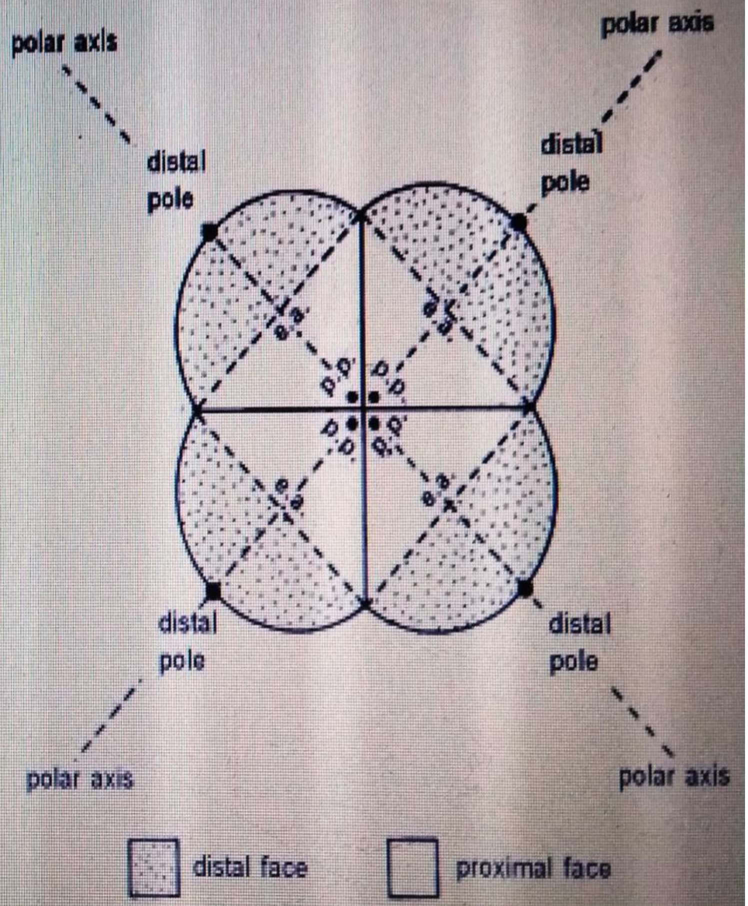

Fig. 5.1 Diagram of a pollen tetrad (all the pollen are in the same plane), showing the polar axis, one equatorial axis (*e. a.*) of the equatorial plane, the distal face, the proximal face, the distal pole, and the proximal pole (*p.p.*) of each pollen grain in the tetrad. (*after* Walker, 1976)

with the distal pole at the apex and proximal pole at the base. The pollen grains are said to be heteropolar if their two faces are different, and isopolar if similar. In heteropolar grains one face has an aperture while the other has none. The equator runs round the surface of isopolar pollen grains midway between the poles. In order to illustrate the pollen grains in a uniform way and to facilitate comparison these terminologies and their definitions are essential. A schematic illustration (Fig. 5.1) of a pollen grain is called 'Palynogram'.

Apertures

An aperture is any weak area on the pollen surface which is directly or indirectly associated with its germination. Long apertures are called colpi, and short ones pores. The apertures may be simple or compound. Pollen grains with simple apertures are either colpate (with colpi) or porate (with pores). A compound aperture consists of a central region called oral, and an outer region called colpal in colporate pollen (with compound colpi), and poral in pororate pollen (with compound pores).

NPC-System

NPC refers to Number (*N*), Position (*P*), and Character (*C*) of apertures (Fig. 5.2). Under this system the usage of the term 'treme' has been recommended in place of 'aperture' for the purpose of preparing key for the classification of pollen grains (Fig. 5.2). Pollen grains without aperture are called atreme, also represented as N_0. Depending upon the number of apertures the pollen are monotreme (N_1), ditreme (N_2), tritreme (N_3), tetratreme (N_4), pentatreme (N_5) or hexatreme (N_6). Pollen grains with more than 6 apertures (7 or more) are said to be polytreme and represented as N_7. When the apertures, irrespective of their number, are irregular or irregularly spaced, the pollen grains are described as anomotreme (N_8).

Fig. 5.2 The NPC-System. Diagram showing number (*N*), position (*P*), and character (*C*) of apertures. For details *see* text. (*after* Erdtman, 1969)

With regard to the position (*P*) of apertures, there are seven ($P_0 - P_6$) groups (Fig. 5.2). The pollen are designated as catatreme (P_1) when the aperture is on the proximal face, and anatreme if it is on the distal face (P_3). When the centres of apertures are located on the equator, the pollen grains are referred to as zonotreme (P_4). The condition is said to be pantotreme when the apertures are more or less uniformly distributed all over the pollen surface (P_6).

The character-groups (Fig. 5.2), like the position-groups, are also seven (C_0-C_6). Pollen are designated C_0 (0 stands for a query) when the character of the aperture is not known. C_1 pollen have an aperture-like thin area, or leptoma. Pollen with one leptoma are called monolept. They may be catalept (leptoma on proximal face), or analept (leptoma on distal face). The grains with a 3-slit colpus belong to C_2 category, and are called trichotomocolpate. The remaining characters viz., C_3, C_4, C_5 and C_6 comprise colpate, porate, colporate, and pororate pollen grains, respectively.

Shape and Size

The shape of pollen grains can vary from very flat (peroblate), where equatorial diameter is more than twice the length of the polar axis, to very elongate (perprolate) where the diameter is less than half the length of the polar axis. Although the variations in the shape of pollen are quite characteristic for taxonomic and phylogenetic considerations, these are less important than apertures.

The size of pollen grains varies from nearly 10 µm in *Myosotis* to as much as 200 µm in some Cucurbitaceae and Nyctaginaceae.

SCOPE OF PALYNOLOGY

The palynological research can be either basic or applied (*see* also Agashe, 2006). To the basic aspects belong the pollen morphology in relation to taxonomy and to the applied aspects belong geopalynology (fossil pollen grains), aeropalynology (pollen found in atmospheric air), iotropalynology (medical aspects such as hayfever, criminology, etc.), and melittopalynology (study of pollen in honey).

Applied Aspects of Palynology

The distribution of spore genera and species in coal is an important tool to investigate stratigraphical problems like correlation of coal seams and oil fields. It also helps in determining the age of rocks. The maximal use of applied palynology is in oil geology. Since many pollen and spore types serve as index fossils, these have helped in exploring oil-bearing strata. In fact, the most well-equipped palynological laboratories are those established by oil companies.

Aeropalynology is a subject of great importance because of its application in medicine, forestry, and palaeobotany. It is now established that airborne pollen cause allergies like hayfever and seasonal asthma. Information on the type of pollen in the air has been of great help in determining the allergens. Most of the plants that cause hayfever belong to weeds and grasses. Some of the allergenic taxa occurring in India are *Amaranthus spinosus, Artemisia scoparia, Chenopodium album, Cynodon dactylon, Prosopis juliflora, Ricinus communis,* and *Sorghum vulgare.* Seed production in forest trees is also closely linked with the occurrence of pollen in the air.

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Pollen grains, to a great extent, reflect the vegetation of an area and its surroundings. In several cases it has been possible to locate the site of crime by studying pollen in the samples collected from dirt under the nails, and from mud stuck to shoes, clothes, etc.

Pollen samples from the stomach contents, or excrements, have provided a clue to several deaths in Brazil. The deaths were ascribed to the use of poisonous honey. The pollen of a poisonous plant, *Serjania lethalis* (Sapindaceae), were found in the stomach contents of one of the victims who died after taking poisonous honey.

There are several reports regarding the useful properties of certain pollen tablets, tonics, creams, etc. The pollen tablets have been used in the treatment of prostatitis which has been confirmed by repeated experiments.

Plants are a source of both pollen and nectar collected by the honey-bee for making "bee-bread" (Nair, 1966). The pollen not only provides vitamins,

minerals, and amino acids in the honey, but also information about the plants from which the nectar and pollen have been gathered. It also helps detect adulteration in the honey, and keeps in check the unscrupulous traders. Nair (1963) made an extensive study of Indian honeys collected from various places. Such an analytical study has provided useful data about pollen, and nectar-yielding plants. A trained melittopalynologist can easily distinguish between honey from two different localities. He can also tell the time when the particular honey was prepared.

Honey is said to be "unifloral" if it is dominated (50 per cent or more) by pollen of only one plant and "multifloral" if it contains various types of pollen in considerable percentages (Sharma and Nair, 1965). Seventy-six samples of Indian honey, examined microscopically showed the presence of pollen belonging to the following plants: *Eugenia*, *Nephelium*, *Sapindus*, *Putranjiva*, *Citrus*, *Plectranthus*, *Brassica* (all nectar-yielding plants), *Holoptelea*, *Alnus*, *Borassus* and other palms (all pollen-yielding plants; Nair and Chaturvedi, 1974). Such an analytical study provides useful data about pollen and nectar-yielding plants of a locality which should be helpful in establishing apiary gardens (Nair and Chaturvedi,1974).

Pollenkitt

The pollenkitt is an oily layer forming a thick viscous coating over the pollen grain surface of many insect-pollinated species. The stickiness, odour and colour of the grains are because of the pollenkitt. Pollenkitt material is contributed by the tapetal cells and is later transferred to the pollen surface. It comprises chiefly of carotenoid or flavonoid pigments which impart the characteristic yellow or orange colour to the pollen. The pollenkitt or the surface pollen cement also contains glycoproteins, lipids, glycolipids and monosaccharides which are responsible for its sticky nature (Clarke *et al.*, 1979).

Hesse (1979) made a detailed study of the nature and function of pollenkitt in entomophilous and anemophilous species of *Acer*, and some other families. According to him, in the insect-pollinated species, the pollenkitt is electron-dense and homogeneous forming a coating on the exine rendering the pollen sticky. On the other hand, in the anemophilous taxa, the pollenkitt is electron-transparent and not homogeneous, and is in much less quantity. It becomes inactive in the pollen locule and settles into exine perforations, thus rendering the pollen powdery and non-sticky.

The biological function of the pollenkitt is not clear. However, it may be contributing in the following ways:

1. Acting as an insect-attractant.
2. Protecting the pollen against the damaging effect of ultraviolet radiation.
3. Acting as an adherent to the insect body, because of the sticky nature.
4. Being hydrophobic, it might even be associated with the dispersal of pollen.
5. Functioning as the pollen-borne substances involved in sporophytic incompatibility.

POLLINATION

The transferral of pollen grains from the opened anther of the stamen to the receptive stigma of the carpel is called pollination. It is of two types— self pollination and cross pollination (Fig. 9.1) :

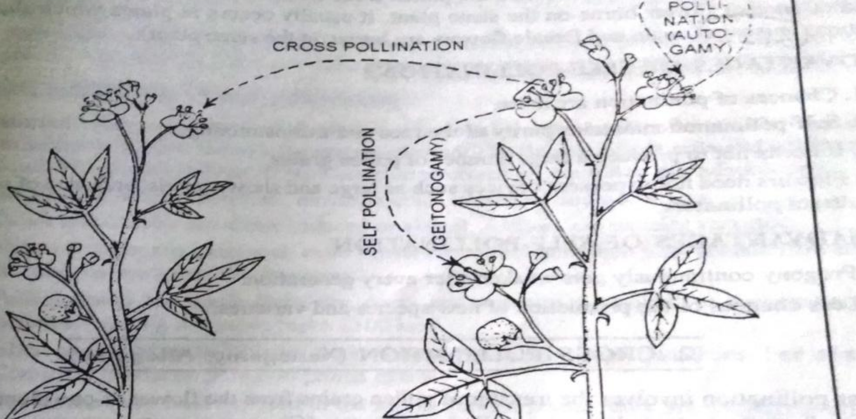

FIGURE 9.1.
Diagram explaining self and cross-pollination.

1. SELF POLLINATION

Self pollination involves the transfer of pollen grains from the anthers of a flower to the stigma of the same flower or genetically similar flower. It is of two types —

(A) AUTOGAMY (Gk. *autos* = self, *gamos* = marriage)

It is a kind of pollination in which the pollen from the anthers of a flower are transferred to the stigma of the same flower. It occurs by three methods :

(*a*) **CLEISTOGAMY** (Gk. *Kleisto* = closed, *gamos* = marriage). Some plants never open to ensure complete self-pollination. This condition is called cleistogamy, *e.g.*, *Commelina bengalensis*, *Oxalis*, *Viola*, etc. The cleistogamous flowers are bisexual small, inconspicuous, colourless and do not secrete nectar.

Chasmogamous – open flowers

(*b*) **HOMOGAMY.** Anthers and stigma of the bisexual flowers of some plants mature at the same time. They are brought close to each other by growth, bending or folding to ensure self pollination. This condition is called homogamy, *e.g.*, *Mirabilis* (Four O, clock), *Catharanthus* (= *Vinca*), Potato, Sunflower, etc.

(*c*) **BUD POLLINATION.** Anthers and stigma of the bisexual flowers of some plants mature before the opening of the buds to ensure self-pollination, *e.g.*, Wheat, Rice, Pea, etc.

(B) GEITONOGAMY (Gk. *geiton* = neighbour, *gamos* = marriage)

It is a kind of pollination in which the pollen from the anthers of one flower are transferred to the stigma of another flower borne on the same plant. It usually occurs in plants which show monoecious condition (unisexual, male and female flowers are borne on the same plant).

ADVANTAGES OF SELF-POLLINATION

1. Chances of pollination are more.
2. Self-pollination maintains purity of the race and avoids mixing.
3. It needs not to produce a large number of pollen grains.
4. Flowers need not to possess devices such as large and showy petals, presence of scent and nectar, etc. to attract pollinators.

DISADVANTAGES OF SELF-POLLINATION

1. Progeny continuously gets weaker after every generation.
2. Less chances of the production of new species and varieties.

2. CROSS POLLINATION (Xenogamy, Allogamy)

Cross pollination involves the transfer of pollen grains from the flower of one plant to the stigma of the flower of another plant. It is also called **xenogamy** (Gk. *xenos* = strange, *gamos* = marriage) or **allogamy** (Gk. *allos* = other, *gamos* = marriage). The main floral characteristics which facilitate cross pollination are — (*i*) **Herkogamy.** Flowers possess some mechanical barrier on their stigmatic surface to avoid self-pollination, *e.g.*, presence of gynostegium and pollinia in *Calotropis*. (*ii*) **Dichogamy.** Pollen and stigma of the flower mature at different times to avoid self-pollination. It is of two types — **protogyny** (when gynoecium matures earlier than androecium, *e.g.*, Bajra, *Aristolochia*, etc.) and **protandry** (when androecium matures and shed pollen before gynoecium, *e.g.*, Maize). (*iii*) **Self incompatibility.** In some plants, the mature pollen fall on the receptive stigma of the same flower but fail to bring about self pollination. It is called self incompatibility. Under such conditions, the cross pollination is the only option. (*iv*) **Male sterility.** The pollen grains of some plants are not functional. Such plants set seeds only after cross pollination. (*v*) **Dioecism.** Cross pollination always occurs when the plants are unisexual and dioecious, *i.e.*, male and female flowers occur on separate plants, *e.g.*, Papaya, some cucurbits, etc. (*vi*) **Heterostyly.** The flowers of some plants have different lengths of stamens and styles so that self pollination is not possible, *e.g.*, *Primula, Linum*, etc.

POLLINATION

- Self Pollination
  - Autogamy (Same flower)
  - Geitonogamy (Different flowers of the same plant)
- Cross Pollination (Xenogamy or Allogamy) Flowers from different plants of the same species.
  - Abiotic agencies
    - 1. Anemophily (Wind)
    - 2. Hydrophily (Water)
  - Biotic agencies
    - 1. Entomophily (Insects)
    - 2. Ornithophily (Birds)
    - 3. Chiropterophily (Bats)

Myrmecophily (ants)
4 Malacophily (snail) eg Lemna
5 Ophiophily (snake) eg – Sandal
6 Anthophily (man)

The agents (or vectors) responsible for cross pollination in angiosperms have been grouped into two main categories — (*i*) **Abiotic** (such as wind current, gravity, water, etc.) and (*ii*) **Biotic** (animal pollinators).

(A) ANEMOPHILY (Wind pollination)

Anemophily (Gk. *anemos* = wind, *philein* = to love) is a mode of pollination or transfer of pollen grains from anther to stigma through the agency of wind. The flowers which are wind pollinated are called anemophilous. The anemophilous flowers are characterized by the following adaptations :

(*i*) Flowers are small colourless, inconspicuous, odourless and nectarless.

(*ii*) Calyx and corolla are either reduced or absent. Anthers are usually versatile.

(*iii*) When flowers are unisexual, male flowers are more abundant than female flowers. In bisexual flowers, the stamens are generally numerous.

(*iv*) Pollen grains are small, light, dry, dusty and sometimes winged (or saccate) so that they are easily blown away to long distances (upto 1300 km).

(*v*) Pollen grains of anemophilous flowers are produced in huge quantities. For example, a single flower of *Cannabis* produces 5,00,000 pollen grains.

(*vi*) The flowers are well exposed in the air. In certain plants, they are produced above the foliage before the appearance of new leaves.

(*vii*) The stigmas are large, well-exposed, hairy, feathery or branched to catch the air-borne pollen grains.

(*viii*) In some plants (*e.g., Urtica*), the anthers burst suddenly to throw the pollen grains into the air (gun- powder mechanism).

The common examples of wind pollinated flowers are — grasses, sugarcane, bamboo, coconut palm, date palm, cannabis (bhang), maize (Fig. 9.2), etc.

(B) HYDROPHILY (Water pollination)

Hydrophily (Gk. *hydro* = water, *philein* = to love) is a mode of pollination or transfer of pollen grains from anther to stigma through the agency of water. The hydrophilous flowers are characterized by the following adaptations :

(*i*) Flowers are small, colourless, inconspicuous, odourless and nectarless.

(*ii*) Calyx, corolla and other floral parts are unwettable.

(*iii*) Pollen grains and stigma are generally unwettable.

(*iv*) The stigma are long and sticky.

Hydrophily is not very common and occurs only in a few aquatic plants, *e.g.*, *Vallisneria* (Fig. 9.3), *Zostera*, *Ceratophyllum*, *Hydrilla*, etc.

In *Zostera marina*, a totally submerged marine angiosperm, the pollen grains are long, elongated (upto 2500 μ*m*), needle-like and without exine. They float below the surface of water because they have the same specific gravity as that of water. When they touch the long stigmas, they coil around later and germinate.

In *Ceratophyllum demersum*, a totally submerged fresh water plant, the male flower bears 30-45 stamens. The mature anthers abscise at the base, rise upwardly, reach to the surface of water and dehisce. The liberated pollen grains germinate and sink. While sinking in water, they come in contact with long and sticky stigmas of female flowers to effect pollination.

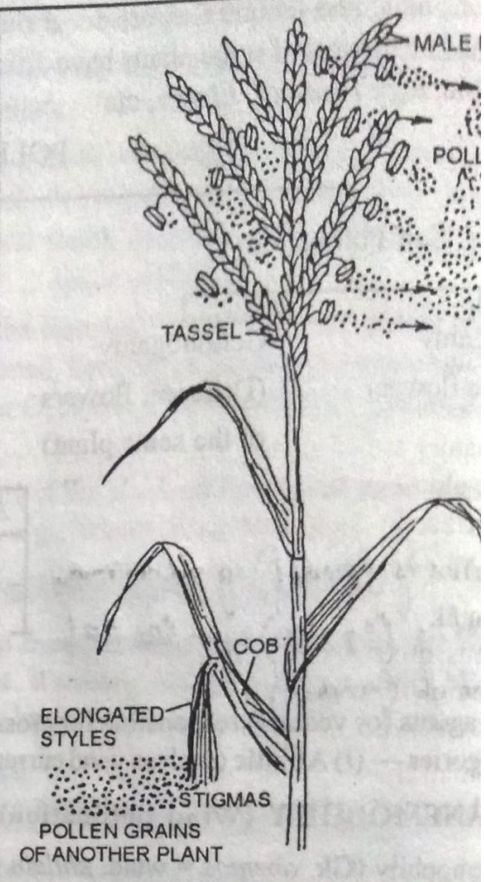

FIGURE 9.2.
Wind pollination in maize.

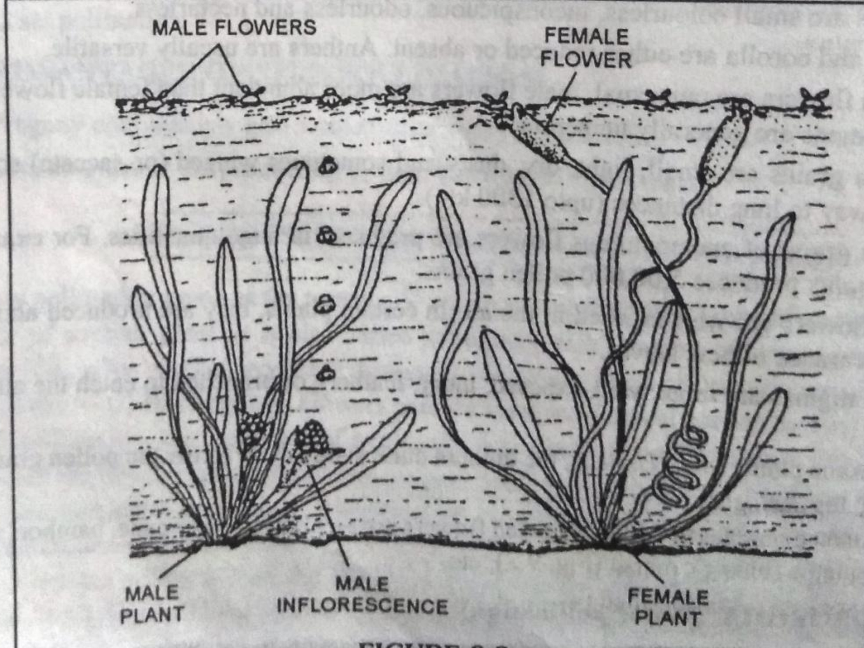

FIGURE 9.3.
Pollination in *Vallisneria*.

In *Vallisneria*, a submerged fresh water hydrophyte, is a dioecious plant, *i.e.*, the male flowers borne on male plants and female flowers are borne on female plants. Mature male flowers are abscised from the spadix and float on the surface of water. The mature female flowers also float on the water surface, but remain attached to the female plants with the help of long stalks. The floating female flowers have large sticky trifid stigmas. While floating, the male flowers come close to female flowers where anthers burst to release the pollens. Pollination occurs on the surface of water. After fertilization, the female flowers are pulled down inside the water by the coiling of the flower stalks.

(C) ENTOMOPHILY (Insect pollination)

Entomophily is a mode of pollination or transfer of pollen grains from anther to stigma through the agency of insects. The flowers which are insect pollinated are called entomophilous. The most common insect pollinators are — moths, flies, butterflies, wasps, bees, beetles, etc. The beetles (Coleoptera) are probably the oldest group of insects which pollinated the ancient angiosperms. The entomophilous flowers are characterized by the following adaptations —

(*i*) The flowers are usually large, conspicuous, brightly coloured and showy to attract insect pollinators.

(*ii*) Usually the petals of entomophilous flowers are large and attractive. When they are small and inconspicuous, other parts of the plant enlarge and become attractive. For example — leaves of *Poinsettia*, in the region of flowers, become wholly or partly coloured. Similarly, bracts in *Bougainvillea*, single sepal in *Mussaenda* and spathes in arioids are attractive.

(*iii*) Small flowers bloom in bunches to attract the insects. Sometimes, they are condensed together to form a head (*e.g.*, Sunflower). Under such condition, a single insect pollinates a large number of flowers.

(*iv*) Different colours of flowers attract different insects. White colour of flowers attracts moths. Red colour attracts butterflies and wasps. Bees are colour-blind for red. They use ultra-violet radiation for observation. The red colour appears black in UV radiation.

(*v*) Entomophilous flowers usually blossom at a specific time when the particular insect pollinator is available. For example, moths visit flowers which open after sunset. Similarly bees, flies and beetles visit flowers which open in the day time.

(*vi*) Entomophilous flowers usually produce specific odours to attract specific insects. For example, flies are attracted by the unpleasant smells of flowers such as *Rafflesia* (smell of rottening meat to attract Carrion flies), *Arum* (human dung), *Aristolochia* (decaying tobacco), etc. Some flowers produce pleasant smell and sweet fragrance to attract insects from long distances (*e.g.*, Jasmine, Rose, Rangoon creepers, etc.). Generally moth-pollinated flowers blossom at or after dusk. They produce heavy fragrance to guide the moths.

(*vii*) Pollen grains of certain flowers (*e.g.*, *Rosa, Clematis, Magnolia*, etc.) are edible. Many insects visit these flowers to eat their pollens or to carry them for their brood of larvae.

(*viii*) Nectar, secreted from nectaries, is an important source of food for certain insect pollinators. Usually the nectaries are positioned in floral parts in such a way that the insect visitor touches both the anthers and stigmas during the extraction of nectar. Some flowers even possess special markings on petals for guiding the insect to nectaries (*e.g. Viola*).

(*ix*) The outer surface of pollen grains may be rough, spiny or sticky. Angiospermous pollen also possess yellow sticky substance called pollenkitt which acts as insect-attractant and as an adherent to the insect body.

Among insects, bees are the most common pollinators which pollinate about 80 per cent of the total insect pollinated flowers. They visit flowers to collect their food (pollen and nectar) in their pollen baskets.

A detailed study of the inter-relationship between the structure of flower and insect pollinators clearly indicates that some angiospermous plants are dependent upon a particular type of insect for pollination. Some classic examples are as follows :

(*a*) **POLLINATION IN SALVIA** (Fig. 9.4). The genus *Salvia* belongs to family Labiatae (Mint family) in which the gamopetalous corolla is two-lipped (bilabiate). The lower lip provides platform for the visiting insect and the upper lip is just like a hood which protects the floral organs. The flowers are **protandrous.** Each flower has two epipetalous stamens located anterio-lateral in position. Each stamen has a short filament and an elongated curved connective. The anther has two parts — one half is sterile and another half is fertile. Both the parts of anther are separated apart due to elongation of connective. The elongated connective has two unequal arms. The upper arm is long and curved. It bears the fertile lobe of anther. The lower arm of connective is short and bears the sterile lobe of anther. The two sterile lobes jointly form a sterile plate of tissue which is placed at the mouth of corolla tube and partly blocks the path of the visiting insect. The upper fertile lobes are sheltered in the upper lip of corolla. As a bee visits the young flower and moves inward in search of nectar, its head pushes the sterile plate which brings down the fertile anther lobes to strike against its back. The pollen grains are deposited upon the back of the bee. When the pollen-dusted bee visits older flower (with protruded bilipped stigma), its back rubs against the mature stigma bringing about the pollination. Since the bisexual flowers of *Salvia* are protandrous (anthers mature earlier than the gynoecium), cross pollination occurs only when pollen-dusted bee visits older flowers with mature gynoecium.

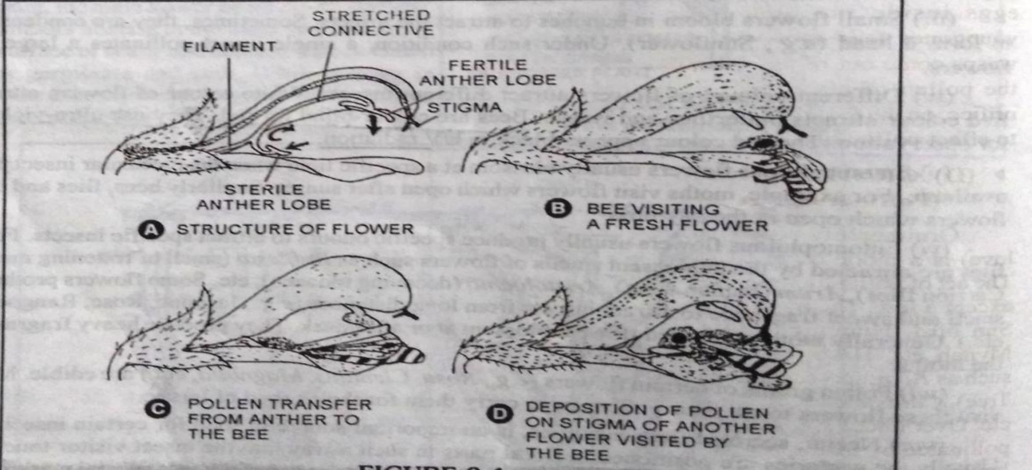

FIGURE 9.4.
Pollination in *Saliva* (see text for explanation).

resembling the female of a wasp—*Colpa aurea*.

▸ (D) ORNITHOPHILY
(Pollination by birds) (Fig. 9.6) :

Ornithophily (Gk. *ornis* = bird, *philein* = to love) is a mode of pollination performed by birds. The act of pollination is not performed by all the birds except a few. The most common bird pollinators are Sun bird, Humming bird, Crow, Bulbul, Parrot, Mynah, etc. The birds visit a large variety of flowers such as *Bombax* (Red Silk Cotton), *Erythrina* (Coral Tree), *Callistemon* (Bottle Brush), *Bignonia*, *Agave*, etc. Over about 100 species of Australian plants are pollinated by birds. Humming bird pollinates while hovering over the flowers and sucking nectar. The bird can derive about half of its body weight of nectar in a single day. The nectar is chiefly made of sugars and provides a sweet drink to the bird.

The ornithophilous flowers are characterized by the following adaptations —

(*i*) The flowers are usually large in size. They have tubular or funnel-shaped corollas.

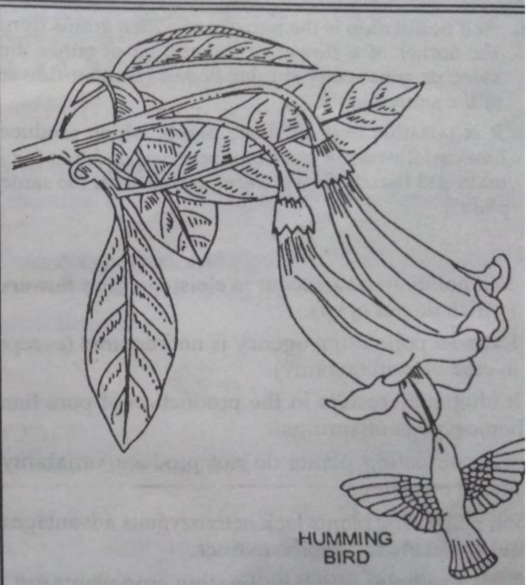

FIGURE 9.6.
Bird pollination (Ornithophily).

(*ii*) The flowers are brightly coloured (such as red, yellow, orange, blue, etc.) which attract the birds from long distances.

(*iii*) The flowers produce abundant watery nectar.

(*iv*) They are usually scentless.

(E) CHIROPTEROPHILY (Bat Pollination)

Chiropterophily (Gk. *cheir* = hand, *pteros* = wing, *philein* = to love) is a mode of pollination performed by bats. The bats are nocturnal flying mammals which move swiftly and transport pollen grains to long distances, sometimes over 30 kms. The flowers they visit are large, dull-coloured and have a strong scent. Chiropterophilous flowers produce abundant pollen grains and secrete more nectar than the ornithophilous flowers. Some of the common chiropterophilous plants are — *Kigelia pinnata* (Sausage Tree), *Adansonia* (Baobab Tree), *Bauhinia megalandra, Anthocephalus* (Kadam Tree), etc. Each flower of *Adansonia* (Baobab Tree) has 1500—2000 stamens.

ADVANTAGES OF CROSS POLLINATION

1. Cross pollination brings about genetic recombination and production of new varieties (variations).
2. Cross pollination results in healthy and stronger offsprings due to phenomenon of hybrid vigour.
3. Several crop plants (such as Mustard, Safflower, Sunflower, Clover, Cucurbits, Almonds and Pomes) give significantly higher yields if bees are available and cross pollination is allowed to occur.
4. Variations caused due to cross pollination may result in production of disease resistant plants.
5. Cross pollination results in the production of seeds in **self-sterile plants** (*i.e.*, Pollen grains fail to grow on the stigma of the same flower).

Differences between Self Pollination and Cross Pollination :

SELF POLLINATION
CROSS POLLINATION
5. Cross pollination ...
grow on the stigma of the same flower).
Differences between Self Pollination and Cross Pollination :

SELF POLLINATION	CROSS POLLINATION
1. Self pollination is the transfer of pollen grains from the anther of a flower to the stigma of either the same or genetically similar flower (another flower of the same plant).	1. Cross pollination is the transfer of pollen grains from the anther of a flower to the stigma of genetically different flower.
2. It is possible only in those plants which produce bisexual flowers or have monoecious condition (*i.e.*, male and female flowers are produced on the same plant).	2. It is possible in all unisexual plants which are dioecious (*i.e.*, possess male and female flowers in different plants). It may also occur in those plants which produce bisexual flowers under conditions of dichogamy, prepotency, self sterility, heterostyly or herkogamy.
3. Self pollination can occur in cleistogamous flowers (which do not open).	3. Cross pollination can occur only when the flowers open.
4. External pollinating agency is not required (except in case of geitonogamy).	4. External pollinating agency (such as wind, water, birds, insects, animals, etc.) is required.
5. It ultimately results in the production of pure line homozygous offsprings.	5. It results in the production of zygotes with a higher degree of heterozygosity.
6. Self pollinating plants do not produce variability among offsprings.	6. Cross pollinating plants produce offsprings having variations among themselves.
7. Self pollinating plants lack heterozygous advantages and are likely to become extinct.	7. Cross pollinating plants reduce evolutionary stagnation of the population.
8. A few examples of self pollinating crop plants are : Wheat, Rice, Barley, Pea, Ground nut, Tomato, Potato, Brinjal, Jute, Peach, Citrus, etc.	8. A few examples of cross pollinating crop plants are : Maize, Rye, Bajra, Cabbage, Cauliflower, Turnip, Carrot, Cucumber, Apple, Banana, Grapes, Papaya, Coconut, Sugar cane, etc.

DISADVANTAGES OF CROSS POLLINATION

1. Cross pollination is not economical. The plants waste a lot of energy and food materials in unnecessary adaptations and devices to bring about pollination.

2. Cross pollination is uncertain because a factor of chance is always involved.

3. It involves addition of some undesirable character or loss of some important character.

POLLEN-PISTIL INTERACTION

Pollination assists transfer of the required pollen grains from anthers to the receptive surface of the carpel. Further development *i.e.*, the germination of pollen grains on the stigma and growth of pollen tube through the style upto the embryo sac, needs favourable physical and chemical conditions. It depends on the favourable pollen-pistil interaction.

The angiosperm pollen grains have exine which is composed of sporopollenin. The cavities present in the exine layer are filled with specific proteins (mainly enzymes), glycoproteins, lipids and certain allergens derived from the anther tapetum during sporogenesis. Since these chemicals are mainly derived from tapetum, they carry some specific sporophytic recognition factors. The intine, on the other hand, consists of proteins and polysaccharides of haploid spores. They are, therefore, gametophytic in origin. The stigmas of some angiosperms are wet while those of others are dry. Wet stigmas possess proteins, amino acids and lipids in the form of free-floating secretion. The dry stigmas, on the other hand, possess a hydrated layer of proteins, carbohydrates and lipids. The chemicals are also of sporophytic origin. Thus, there is an interaction between the chemicals of pollen grains and those present on the surface of stigma. These interactions determine whether a pollen grain will germinate (by giving out a germ tube) or not.

SELF-INCOMPATIBILITY : Most of the angispermous plants possess a capability to inhibit germination of pollen grains and further growth of pollen tube so as to avoid inbreeding and help out breeding. This chemical control of an individual plant is called self incompatibility. It is achieved by the interaction of chemical substances produced by the male gametophyte and the tissue of style.

SELF-INCOMPATIBILITY

A large number of flowering plants are outbreeders, which means that they are successfully fertilized only by the pollen of other plants of the same species and not by their own. In nature different floral adaptations, such as dichogamy, herkogamy and unisexuality (*see* page 115) have evolved to prevent self-pollination but the most widespread and effective natural device to enforce outbreeding is self-incompatibility, which refers to the inability of a plant producing functional male and female gametes to set seeds when selfpollinated. Self-incompatibility has been reported in 116 families ((Cruz-Garcia and McClure, 2001). Morphologically, self-incompatibility is of two types:

1. HETEROMORPHIC. It is characterized by the occurrence of two (distyly) or three (tristyly) morphologically distinct mating types* within a species, which can be easily recognized without a breeding test. The differences in the mating types are generally with respect to the relative lengths of the stamen and style (*see* Chapter 8). In these systems the incompatibility reaction may be controlled by one gene with two alleles, as in dimorphic species (*Primula*), or by two genes with two alleles each, as in tristyly (*Lythrum*). Other features of heteromorphic incompatibility are:

(a) the incompatibility reaction is determined sporophytically;
(b) the growth of incompatible pollen tubes is inhibited in the style; *Armeria maritima* is an exception where inhibition occurs on the surface of the stigma (Baker, 1975); and
(c) dominance between alleles of the incompatibility genes is expressed both in the pollen and the style.

Heteromorphic self-incompatibility occurs in 25 families (Cruz-Garcia and McClure, 2001)

2. HOMOMORPHIC. In this category all the mating types within a species are morphologically indistinguishable and require proper breeding tests for their recognition. A species with this type of incompatibility has numerous mating types. Homomorphic self-incompatibility which is more common than heteromorphic self-incompatibility has been described in 91 families.

families.

Depending on the origin of factors determining the mating types on the pollen side two categories of self-incompatibility have been recognized:

(i) *GAMETOPHYTIC SELF-INCOMPATIBILITY(GSI)*. The incompatibility process is determined by the genotype of male gametophyte (pollen) itself, *e.g.*, Liliaceae, Poaceae, Solanaceae, *Trifolium*.

(ii) *SPOROPHYTIC SELF-INCOMPATIBILITY(SSI)*. The incompatibility process is controlled by the genotype of the sporophytic tissue of the plant from which the pollen is derived, *e.g.*, Asteraceae, Brassicaceae.

GENETIC BASIS OF SELF-INCOMPATIBILITY

Incompatibility is a gene-physiological process. Therefore, before dealing with the physiological aspects of the phenomenon, it would be appropriate to acquaint ourselves with the genetics of self-incompatibility.

The most popular hypothesis about the genetic control of self-incompatibility is the one of "opposition S-alleles", first proposed by East

*Mating type refers to a group of individuals showing similar breeding behaviour. In the present context, legitimate pollination can occur only between two individuals belonging to different mating types; pollinations within a mating type would not favour seed-set.

and Mangelsdorf in 1925. According to this, incompatibility reactions are controlled by a single gene, called S-gene, which has several alleles. Pollen grains that possess the S-allele common to anyone of the two alleles present in the cells of the pistil will not be functional on that particular pistil. To illustrate it further, let us consider a plant having S_1S_2 alleles in its sporophytic cells, including the pistil (Fig. 10.1). During microsporogenesis such a plant will produce two types of pollen, one-half carrying the S_1 allele and the other half S_2 allele. According to the oppositional S-allele concept, neither of these pollen types (S_1 or S_2) would be able to bring about fertilization in the style of this particular plant (Fig. 10.1A) because both the alleles are present in the stylar cells. On the other hand, if this plant is pollinated with the pollen from a plant of S_2S_3 genotype, 50 per cent pollen grains, carrying S_3 allele, would be functional whereas the remaining 50 per cent, carrying S_2 allele, would be non-functional (Fig. 10.1B). However, every pollen grain from a S_3S_4 plant would be functional on the pistil of a S_1S_2 plant (Fig. 10.1C) as none of the alleles is common between these two plants. It should be emphasized at this stage that in all the situations described so far it is the S-allele of the pollen or the male gametophyte which determines the incompatibility reaction (GSI). This is true for Gametophytic self-incompatibility.

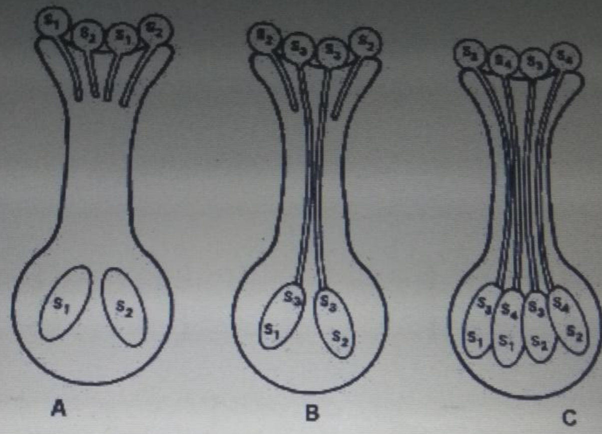

Fig. 10.1 Response of pollen on a pistil of S_1S_2 plant, showing gametophytic self-incompatibility. **A.** None of the pollen from a S_1S_2 plant is able to effect fertilization. **B.** From a S_2S_3 plant only S_3 pollen succeed in fertilizing the ovules. **C.** All the pollen from S_3S_4 plants bring about fertilization.

In SSI-systems all the pollen of a plant behave similarly, irrespective of the S-allele they carry. For instance, from a plant carrying S_1S_2 alleles the pollen carrying S_1 or S_2 allele would behave as S_1 if S_1 is dominant, or as S_2 if S_2 is dominant; if there is no dominance both will behave as S_1 plus S_2. In other words, the presence of even one of the alleles of the stylar tissue in the sporophytic tissue of the male parent would render all the pollen of that plant non-functional with respect to that particular style (Fig.10.2). An S_1S_2 plant

would, therefore, be completely incompatible to plants carrying S_1S_2 (Fig. 10.2A), S_1S_4, S_1S_5 or S_2S_3 (Fig. 10.2B), S_2S_4, S_2S_5, and so on, but would show 100 per cent compatibility with a plant carrying S_3S_4 (Fig. 10.2C), S_3S_5, and so on.

Grasses exhibit two-locus or bifactorial GSI, and the two genes, termed S and Z, are polyallelic. There appears to be co-operation between S and Z in the pollen but they act independently in the pistil (McCubbin and Dickinson, 1997). These bifactorial GSI-systems differ from other GSI-systems in having 3 nucleate pollen and the rejection reaction on the stigma, as in the SSI-systems.

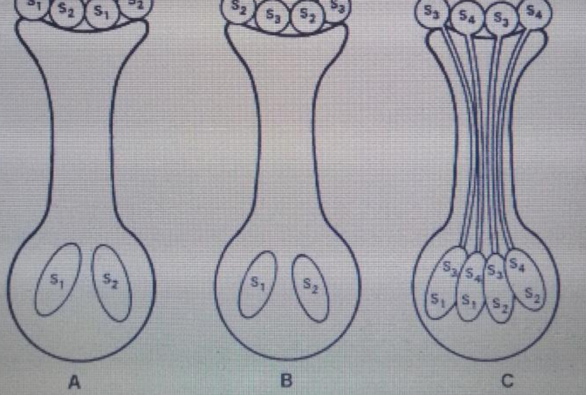

Fig.10.2 Response of pollen on a pistil of S_1S_2 plant, showing sporophytic self-incompatibility. None of the pollen from a S_1S_2 (**A**) or S_2S_3 (**B**) plant can bring about fertilization, but every pollen of a S_3S_4 plant is capable of it (**C**).