Pollen development, biology and function

Rozwój, biologia i funkcja pyłku

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The Navajo Indian once said:
"The symbol for life and productivity,
for peace and prosperity, is pollen.
Pollen symbolizes light".
Stephen C. Jett, 1967

Abstract

The paper presents the role of pollen in multiplication of plants, discussing in particular the structure and function of certain parts of pollen.

Pollen grains contain many different kinds of proteins, but even a small amount of them may cause allergic reactions. These proteins are localized within the cell wall and cytoplasm of pollen grains.

Pollens are transported with the help of animals, wind and water. The author discusses different ways of migration of pollen grains taking into account their size and weight.

Key words: *pollen, development, biology, function, transport.*

Streszczenie

W pracy przedstawiono rolę pyłku w rozmnażaniu roślin i szczegółowo omówiono budowę i funkcję poszczególnych jego części.

Ziarna pyłku zawierają dużą ilość różnego typu białek, natomiast niewielka ich ilość może wywołać reakcje alergiczne. Białka te zlokalizowane są m.in. w błonie komórkowej i cytoplazmie.

W pracy opisano także drogi przenoszenia pyłków (przez zwierzęta, wodę i wiatr), uwzględniając ich rozmiar i wagę.

Słowa kluczowe: *pyłki, rozwój, biologia, funkcja, transport.*

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Introduction

Pollen is the male gametophyte which cells take part in the fertilization process in seed plants. Pollen grains are produced in the male organs of the flower – anthers. However, its life is independent from the parent plant body after flowering. It respirates, germinates, grows and dies. Pollen has unique physiological activities different from those of other cells.

Two or three cells constitute the pollen grain, which are encapsulated in the protecting, decay resistant pollen wall. These structures form the reduced male gametophyte in spermatophytes. Pollen wall consists of two parts: intine and exine.

The major chemical component of the exine is sporopollenin, polymers of carotenoids and carotenoid esters. Sporopollenin is broken down at 500°C with sooty flame, but the unoxidized sporopollenins are remarkably stable and resistant against various chemicals such as aqua regia and sulfuric acid.

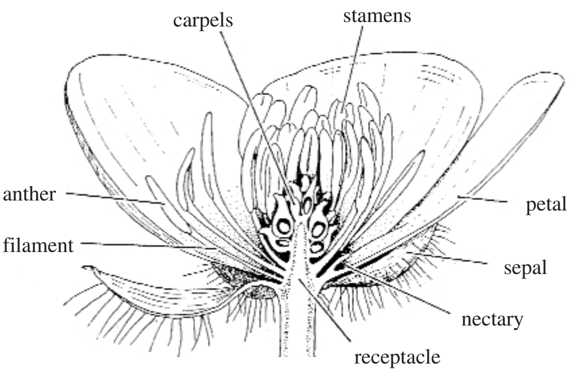
Pollen grain contains the genetic information, which must be transmitted to the stigma in sexual reproduction. The different transport system has developed for pollen grains. Wind, water, insects, birds and other animals are pollen vectors.

The pollen grain has also another function – it is an attractant and food for the flower – visiting insects. It is the packet of concentrated food because of its high protein content 16–35%, 1–10% fats, 1–37% carbohydrates, 1–7% mineral elements, many vitamins: A, B_1, B_2, B_6, C, D, K and others.

Pollen is particularly important to the bees as food for the youngest larvae. For the sake of the special structure of the exine and other features, pollen grains are of interest to the cytologist, the systematist, the paleobotanist, the archeologist, the geologist, the climatologist, the beekeeper and the allergy researcher.

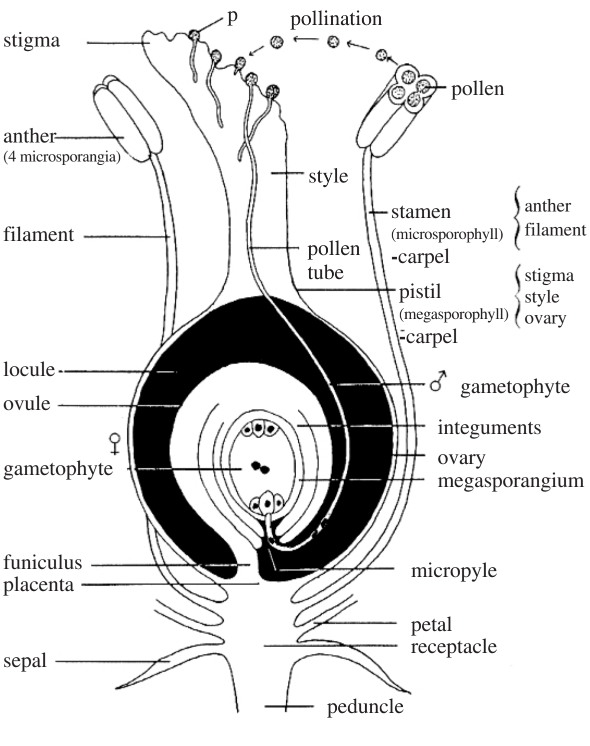
Flower – reproductive organ of plant

The flower is a shoot termination serving for sexual reproduction of plants. All parts of the flower evolved from leaves in the process of angiosperm evolution: sepals making up the calyx; petals forming the corolla, stamens (androecium) and pistil (gynoecium). The shape of the flower is species specific and one of the best criteria for species classification.



(After Proctor et al. 1996)

Fig. 1.



(After Bold, 1973)

Fig. 2.

The most important parts for reproduction are pistils and stamens in which female and male gametes are generated. The pistil consists of three parts: stigma, style and ovary. The stigma placed at the tip of the pistil has branches – or hairlike structures and secretes fluid to receive pollen grains. The ovary contains ovule or ovules with the egg cell in the embryo-sac. After fertilization the ovule can develop into a seed.

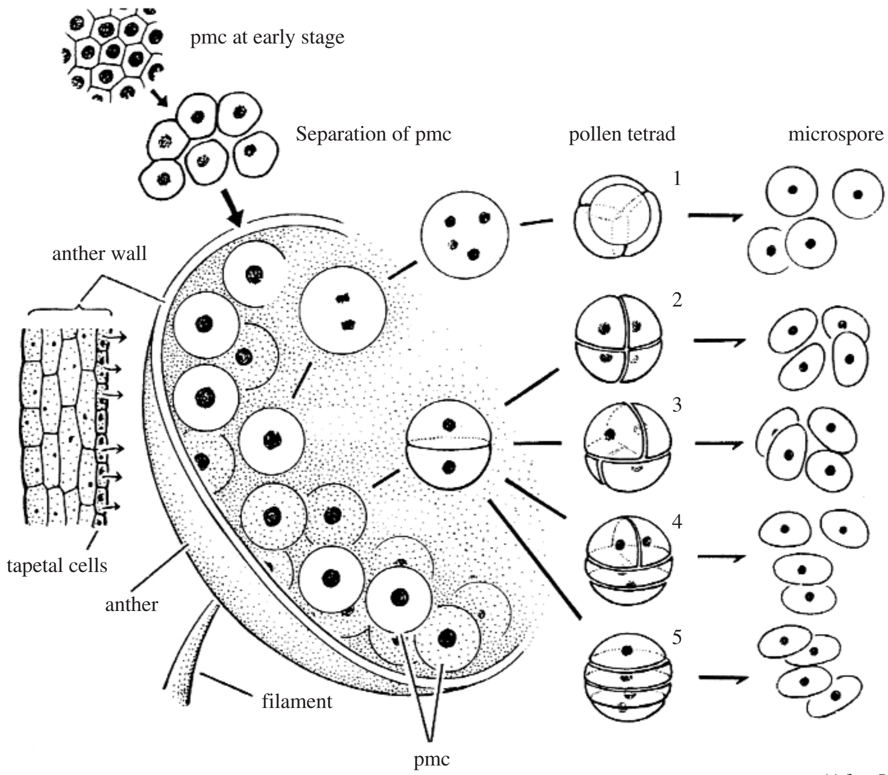
Each stamen consists of a filament bearing an anthers with four elongated thecae, which produce pollen grains with the mail gamete cells. From the phylogenetic point of view the stamen may be called microsporophylly, the anther – microsporangium and pollen grains – microspores. The number of ovules in the ovary is relatively small, compared with the number of the pollen grains. The stamens produce abundant pollen to increase the probability of mating of female gamete. The process of pollination, that is, the transfer of pollen grains to the stigma, is the first step to fertilization of the embryo-sac in the ovule and the development of the ovule into a seed.

If the stigma is receptive to a pollen grain, the pollen produces pollen tube, which grows through the pistil tissues to the egg in the embryo-sac, where fertilization takes place by one of the two male gametes. The fertilised egg develops to form the embryo of the future seed. In Angiosperm flowering plants, a second male gamete of the pollen tube unites with the diploid fusion nucleus in the embryo-sac, producing triploid endosperm tissue which stores nutrients for the developing seed.

Genesis of pollen grains

The wall of the anther consists of some layers: epidermis, endothecium, middle layers and tapetum. In the early stages of the development of anthers, archesporial cells inside them form sporogenous tissue which is enclosed by the tapetum – a nutritive cellular layer. Sporogenous cells differentiate to the pollen mother cells (pmc, microsporocytes). These cells are poorly attached to each other by plasma connections. The pollen mother cells become spherical during growth and separate from each other. A thick callose layer (amorphous cell-wall substance) is formed surrounding the pollen mother cells.

The pollen mother cells undergo meiosis to produce tetrads of haploid cells, which are called microspores. The cells of the tetrad become separated from one another by a callose wall which is connected with the callose surrounding the entire tetrad. The tetrad stage is



(After Ivanami et al. 1988)

Fig. 3. Genesis of microspore; pmc – pollen mother cell; 1-5 – five orientations of pollen tetrad

important in the development of the pollen grain. The surface features of the mature grain are clearly related to the original orientation of the microspore within the tetrad (apertures). Within each microspore, peripheral elements of the endoplasmic reticulum are fixed which polymerize sporopollenin to form the sexine matrix on its surface. At that time the sexine structure is established, the callose disappears.

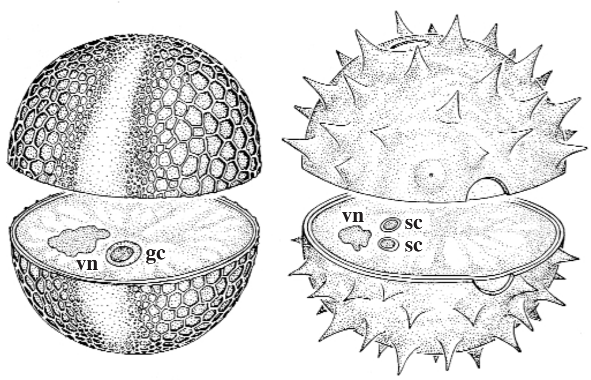
Later, the sexine thickens without changing its structure. Each microspore differentiates into a pollen grain. These four cells then detach from each other to become microspores.

The nucleus of a microspore cell undergoes nuclear division (first pollen mitosis) to form a vegetative and a generative cell. Pollen grains of some taxa reach this stage (dinuclear pollen), in others, the generative cell undergoes a further mitotic division (second pollen mitosis) to form two male gametes (trinuclear pollen).

Function of the tapetum

The tapetum, the innermost layer of the anther wall, is important because all the food material for the developing pollen mother-cells must pass through it.

Two main types of tapetum are recognized depending upon the development associated with sporogenesis: secretory and ameboid. In the secretory type of tapetum, the tapetal cells maintain a continuous position but become disorganized, eventually undergoing autolysis. In the amoeboid tapetum, tapetal cell walls break down at an early stage, forming plasmodium which is associated with the developing pollen grains. Secretory tapeta are reported more frequently in angiosperm families then amoeboid tapeta.



(After Ivanami et al. 1988)

Fig. 4. Dinuclear pollen (left) and trinuclear pollen (right); vn – vegetative nucleus, gc – generative cell, sc – sperm cells

The major function of the tapetum is to provide food precursors to microspores and young pollen grains. Other functions:

- Breakdown of callose layer around microspore and tetrads
- Take part in formation of pollen exine
- Production of orbicules on the inner locular face which may influence pollen dispersal.
- Control of endothecial wall thickening.
- Covering of mature pollen grains of sticky materials or coat substances: pollenkitt and tryphine.

Localization of allergenic pollen proteins

Pollen grains contain many different types of proteins. Only a small number of them are allergenic. Allergen proteins are located in the various parts of pollen grain:

- in the exine: in the surface depressions and in the cavities between the bacuale;
- in the intine: mostly concentrated near the germopore, in the form of radially arranged tubules with protein inclusions;
- in the cytoplasm: in cytosol, starch granules, ER cisternae, Golgi body and mitochondria.

Allergenic proteins of pollen grains have a molecular mass similar to that of most enzymes, 10-70 kDa. Some of these aeroallergens are proteolytic enzymes. They are released rapidly from pollen grains after moistening, usually after several minutes.

Apertures in the exine allow for the germination of pollen tube and movement of water and proteins after hydration.

The major pollen allergen from timothy grass, Phl p 1, has been shown to occur in the cytoplasm and intine, but is absent from the exine. In comparison, a major allergen from rye grass pollen, Lol p 5, is localized within intracellular starch granules. After contact with rainwater, osmotic shock has been shown to burst pollen grains releasing these granules into the atmosphere. On days following rainfall it was noticed a fiftyfold increase of these starch granules in the atmospheric concentration.

Intine proteins are producted in pollen cytoplasm (the male gametophyte). Exine proteins are synthesized in the cells of the adjoining tapetum (the sporophytic tissue).

Pollen – stigma interaction

The stigma of the pistil has developed mechanism to recognise compatible pollen grains, which can grow in the pollen tubes. Stigma reactions are physiological changes, which occur as a result of pollination. Pollen grains stimulate cells of the stigma to be activated. Pollen can secrete amylase, cutinase and pectinase to hydrolise external stigmatic substrates.

Proteins occurring in the exine and intine of the pollen grain are important in ‘sporophytic’ self – incompatibility mechanism of the pistil. Biological function of these proteins is that of pollen-stigma recognition, incompatibility reactions or pollen germination (compatibility).

Studies have revealed that these proteins leave the pollen surface almost instantly (usually within seconds or minutes) on contact with water. These same pollen proteins are responsible for pollinosis in people.

After water absorption pollen cells grow heterotrophically obtaining energy sources exogenously by absorbing sugars and amino acids from stigma. Distinctive characteristic of pollen is that it initiates germination within a short period of time (2–40 minutes) and grows by elongating a pollen tube which is hundreds of times larger than its original size.

Migration of pollen grains

Pollen grains are transported with the help of animals, wind and water.

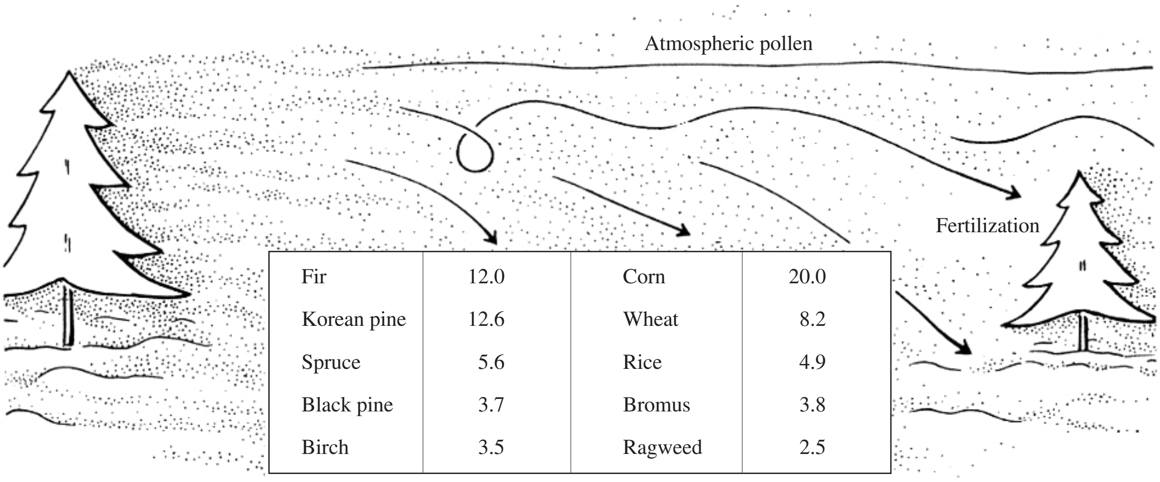
1. **Water pollination (hydrophily)** is relatively rare. Flowers and pollen grains are adapted to float. Stigmas of water – pollinated plants are rigid and simple in outline, though often elongated. In many cases pollen grains are elongated too and they have a tendency to stick together in space – filling rafts in the surface film, or loose, submerged, fluffy or gelatinous masses. Pollen grains are often thin wall, without exine and have reduced apertures. One of the largest pollen grains is that of *Zostera marina*, having a long thread – like structure, 2–3 mm in length and 8 μm in width.

2. **Insect pollination (entomophily)** occurs mainly in temperate clime.

Insects obtain food from the flowers, usually in the form of pollen or nectar. The interrelations between the adaptations of insect-pollinated flowers and those of the flower-visiting insects are a classic instance of co-evolution. Insect-pollinated flowers are attracted by the colour and scent. Their pollen grains are of very varied sizes (5–200 μm), sticky (pollenkitt) and often highly ornamented. Often they are dispersed sticking together in larger groups.

3. **Bird pollination (ornithophily)** is important in many parts of the world (tropics, subtropics). Features of the bird – pollinated flowers are: a big resistant corolla, tubular or nodding; vivid colours, often red, yellow, violet; scent absent; stamen – filaments stiff or united; anthers relatively great; nectar abundant; flower opening in the early morning; sticky pollen.

4. **Bat – pollination (chiropterophily)** occurs mainly in tropics. The floral syndrome: flower – opening takes place late in the day; white colour, creamy or shades of green; scent nocturnal, strong, fruity, sour, musty or



Fir	12.0	Corn	20.0
Korean pine	12.6	Wheat	8.2
Spruce	5.6	Rice	4.9
Black pine	3.7	Bromus	3.8
Birch	3.5	Ragweed	2.5

Migration speed (cm/sec under no wind) of pollen grains in anemophilous plants

(After Ivanami et al. 1988)

Fig. 5. Migration speed (cm/sec under no wind) of pollen grains in anemophilous plants

suggestive of fermentation; large quantity of pollen and dilute nectar; pollen and nectar are available at night.

5. **Wind pollination (anemophily)** occurs mostly in plants of temperate climates. The structures of wind pollinated flowers are relatively simple, with reduced or absent perianth, without smell and nectar.

Anemophilous plants, typically maximise the probability of pollination by increasing the size of stigmas, which are often finely divided and plumose. The stamens are usually large too, often hanging freely on elongated filaments or collected in drooping (pendulous) catkins. The stigmas and stamens are well exposed. The amount of pollen grain produced by a flower varies with species as well as the plants age and climatic conditions.

Anthers of wind – pollinated flowers produce very large amounts of pollen. They open only during warm and dry weather. It has been calculated that a single birch flower produces 22300 pollen grains, catkin about 5,5 million and a hazel catkin nearly 4 million. In the case when the total annual pollen rain may amount to 30,000 grains/cm^2, pollen deposition can be several tons per square kilometre.

Migration speed (cm/s) of pollen grains in various species is different. Rates of fall of wind – borne pollen grains in still air are from 2 cm/s for the smallest and lightest (*Ambrosia*), to about 40 cm/s for the largest and heaviest. Very large grains (*Abies*, *Zea*) with the high rate of fall are limited in dispersal.

The pollen grains of wind pollinated flowers are small and light. The size is commonly 25–40 µm in diameter in angiosperms and 30–60 µm in conifers. The surface of these pollen grains is relatively smooth and non sticky. Consequently they are dispersed singly or in non large groups. Airborne pollen grains have small apertures protecting against desiccating in the air.

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