Plant Reproduction

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Introductory article

Article Contents

Plants reproduce asexually and sexually. Asexual plant reproduction includes offspring arising from plant parts and by apomixis. Sexual plant reproduction allows for the exchange of genetic material, increasing diversity among the offspring, and consists of the fusion of gamete cells to form the new plant.

Introduction

The generation of new individuals of a species – reproduction – presents unique problems to organisms. The number of solutions is bewildering. While most animal reproduction involves two individuals contributing gender-specific reproductive cells that fuse, plants are not as limited. Plants are able to reproduce asexually, or clonally, so that the 'offspring' are the exact genetic copy of the parent; or sexually, producing offspring with contributions from both parents in their genetic code. Although when animals reproduce sexually, two individuals are usually involved, plants can forego finding a mate and self-fertilize in sexual reproduction. This feature is unique to plants and some lower animals.

Unlike animals, plants are mostly immobile and when the search for a mate is on, plants need other ways to exchange reproductive cells.Wind, insects or animals can transport reproductive cells to their targets over long distances. Such a feat requires copious production of reproductive cells, of which pollen is an example.

A broad overview of the major means of plant reproduction is presented. First, the genetic material, mitosis and meiosis, is reviewed. Second, asexual reproduction is discussed. Finally, sexual plant reproduction is presented. Within each section, 'reference' or model plants are presented to illustrate the mechanisms of plant reproduction. Further information can be found in the references in the annotated bibliography, from which much of this information is presented, as well as other entries within the encyclopedia.

How to Make a Reproductive Cell (Gamete)

With the exception of viruses, cells are the building blocks of all living organisms. They are the 'unit' of life; they harbour the genetic material, usually in the form of deoxyribonucleic acid (DNA). The building blocks of DNA, the nucleotides, are ordered to encode the information a cell needs to synthesize the proteins that are the building blocks and maintenance factors of the cell itself. Chromosomes are composed of long strands of DNA tightly packed with protein molecules. An organism's total genetic material may be spread over many chromosomes. Haploid cells have only one copy of each chromosome, while organisms that carry two copies of each chromosome, each pair being said to be homologous, are diploid. In plant sexual reproduction, the single-cell gametes are haploid. When two haploid gametes fuse and combine their genetic material, a single diploid cell is formed.

A challenge for a cell is making daughter cells that have exact copies of the parental genetic material. In mitosis, cells duplicate their chromosomes; they divide in half by cytokinesis, allocating a set of chromosomes to each daughter cell. In sexual reproduction, however, each parent makes cells that have half the genetic information (that is, one set of chromosomes instead of two); these special cells are the haploid gametes and are produced by meiosis. Mitosis results in the production of two cells from a single cell, whereas meiosis produces a total of four cells. Most diploid cells and some haploid cells can undergo mitosis to replicate themselves, but only specialized diploid cells can undergo meiosis. Genetic contributions from each parent produce novel combinations that may have advantageous traits from each parent. The phenomenon of genetic recombination, where homologous chromosomes exchange genetic information, further increases the mixing of genetic material. The frequent combining of genetic material in sexual reproduction ensures that no two individuals are exactly alike. The advantages of maintaining diversity in a species are evolutionarily manifested in an ever-changing environment. If an organism is perfectly suited for its immediate environment and the environment were constant, then sexual reproduction would be wasteful. But the environment is always changing, both on small and large scales.

Cloning Yourself: Asexual (Vegetative) Reproduction and Apomixis

Definitions

Asexual reproduction in plants occurs when new individuals arise from a single individual and are the exact genetic copies of their parent. Asexual reproduction may be apomixitic, involving flower parts, or vegetative, involving non-flower parts of the plant. Vegetative reproduction often, although not always, results in offspring that grow near the parent plant. Asexual reproduction is evolutionarily advantageous for a plant's perpetuation if a particular individual is especially well suited for the environmental niche in which it finds itself.

Examples of asexual reproduction

Vegetative

The repertoire of means of vegetative reproduction is surprisingly vast; almost every plant part can generate a new individual. One familiar method includes the generation of offspring from roots or root-associated or-derived structures. These include runners (stolons), which emanate from the body of the plant at the soil surface. These grow above ground and periodically set down roots to give rise to offspring, creating rows of genetically identical plants. Strawberry plants are a well-known example. Rhizomes grow below ground; they may be mistaken for roots or bulbs. Tulips, irises and potatoes are familiar examples, the actual potato being an enlarged tip of a rhizome, forming a tuber. Suckers are shoots that sprout from the roots of fruit trees and some shrubs.

Roots are not the only parts of plants that can propagate. Leaves themselves can give rise to new individuals. Such an example can be found in the maternity plant (*Kalanchoe daigremontiana*) (**Figure 1**) where plantlets arise from the leaf margins. The miniature plantlets, complete with developed root systems, establish themselves in the soil when they are knocked off the mother plant. Another similar mechanism can be found in the walking fern (*Asplenium rhizophyllum*). As the fronds (the leaves of ferns) unfurl, the frond can extend to such a point that the tip contacts the ground, from which new plants may arise.

The means by which plants can vegetatively reproduce extends beyond these familiar examples. The water-dwelling photosynthetic diatoms (phylum *Bacillariophyta*; **Figure 2**) have to overcome unusual physical constraints in reproduction put on them by their unique cell walls. These creatures are encased in exquisite glass-like walls, the frustules, that have two halves joined together, one smaller than the other. Asexual reproduction is accomplished by mitosis and cytokinesis. Each division results in daughter cells that have half a frustule inherited from the parent, the other new half of the frustule is smaller. Thus half the daughter cells are smaller than the parent. The frustule is unable to expand, disallowing cell growth. If left unchecked, populations of diatoms would become so small as to divide themselves out of existence! However, when the cells reach a critical small size or if environmental conditions are conducive, diatoms will undergo sexual reproduction.

Volvox, a green alga, has an interesting means of asexual propagation. This organism consists of 500 to 60 000 individual 'vegetative' cells that form a living, motile sphere. Within this is often another mitotically dividing daughter colony, which hatches from the mother sphere.

Bryophytes include the liverworts (phylum *Hepatophyta*), hornworts (phylum *Anthocerophyta*) and mosses (phylum *Bryophyta*). Liverworts and mosses are capable of two means of asexual reproduction. Small, 'leafy-like' flat plants, they can reproduce by simple fragmentation of their body parts or via the production of gemmae, multicellular entities that are splashed out from gemma cups by the rain and give rise to new individuals. Hornworts can asexually reproduce by fragmentation.

Apomixis

Although flowers are usually the sites of sexual reproduction, they can also produce progeny. In apomixis, unfertilized flowers produce offspring. Some citrus plants, orchids, grasses (Kentucky bluegrass) and dandelions will undergo apomixis. Parthenocarpy is the production of fruit in the absence of fertilization.

Creating Diversity: Sexual Plant Reproduction

Definitions

Sexual plant reproduction occurs when two haploid cells, formed through meiosis, fuse to form a diploid zygote that will form the diploid embryo, which may be encased in seeds. Sexual reproduction may be oogamous or isogamous. Oogamous reproduction may be heterosporous or homosporous. Heterospory, found in all seed plants, features a female gamete, the egg, that is large and nonmotile (the megaspore), while the male sperm (microspore) is often much smaller and mobile. Homosporous plants produce only one type of spore, that is, bisexual spores, characteristic of horsetails and most ferns. After germination, the gametophyte produces both male antheridia and female archegonia. All vascular plants undergo oogamous reproduction. Isogamous reproduction, found in some algae, features gametes that have no obvious morphological distinction, despite the gametes being of different mating type (e.g. male or female, or sometimes '+' and '−').

Figure 1 Examples of plants that use different modes of reproduction. (a) *Kalanchoe daigremontiana*. Note the young plantlets growing on the leaf margins. (b) *Selaginellaceae* sp., a moss. (c) *Marchantia* sp., a liverwort. (d) *Polypodium* sp., a fern. The under side of the frond is shown; the brown, circular structures are the sori. (e) *Zamia* sp., a cycad. A female plant is pictured. (f) *Gingko biloba*, gingko (maidenhair) tree, showing the fruits. *Zamia* and *Gingko* are examples of gymnosperms.

Evolutionary advantage

Sexual reproduction affords a plant many advantages over asexual reproduction. This advantage is realized because the offspring are slightly different from either parent. Whereas asexually derived individuals are genetically identical to the parent from which they arose, offspring of sexual-mediated reproduction are the consequence of two parents. If a plant can self-fertilize, differences arise because the gametes are slightly different through genetic recombination that occurs during meiosis. Because of this 'mixed' genetic background, there is more chance that the resulting individuals will be different from each other. This may benefit the offspring that find themselves in different environmental conditions; some of these differences may help the plant to adapt, giving it an evolutionarily important selective advantage.

Another advantage for sexual reproduction is the 'packaging' of the new individuals, whether in spores or seeds. Both offer some degree of protection from the environment, and unlike vegetatively reproduced offspring, growth can be delayed for some time in anticipation of favourable growing conditions.

Alternation of generations

In animals, the haploid gametes are single cells: sperm and eggs. In sexual plant reproduction, the haploid phase can be a multicellular plant in its own right. Two generations, or plant types, exist: the gametophyte, which is haploid, and may have male-and female-specific components, and the sporophyte that is formed by the fusion of gametes that occurs in the gametophytic generation. The sporophyte produces new gametes, which germinate and form the gametophytic generation. This phenomenon is known as alternation of generations. Either generation may dominate, depending on the plant species. In flowering plants

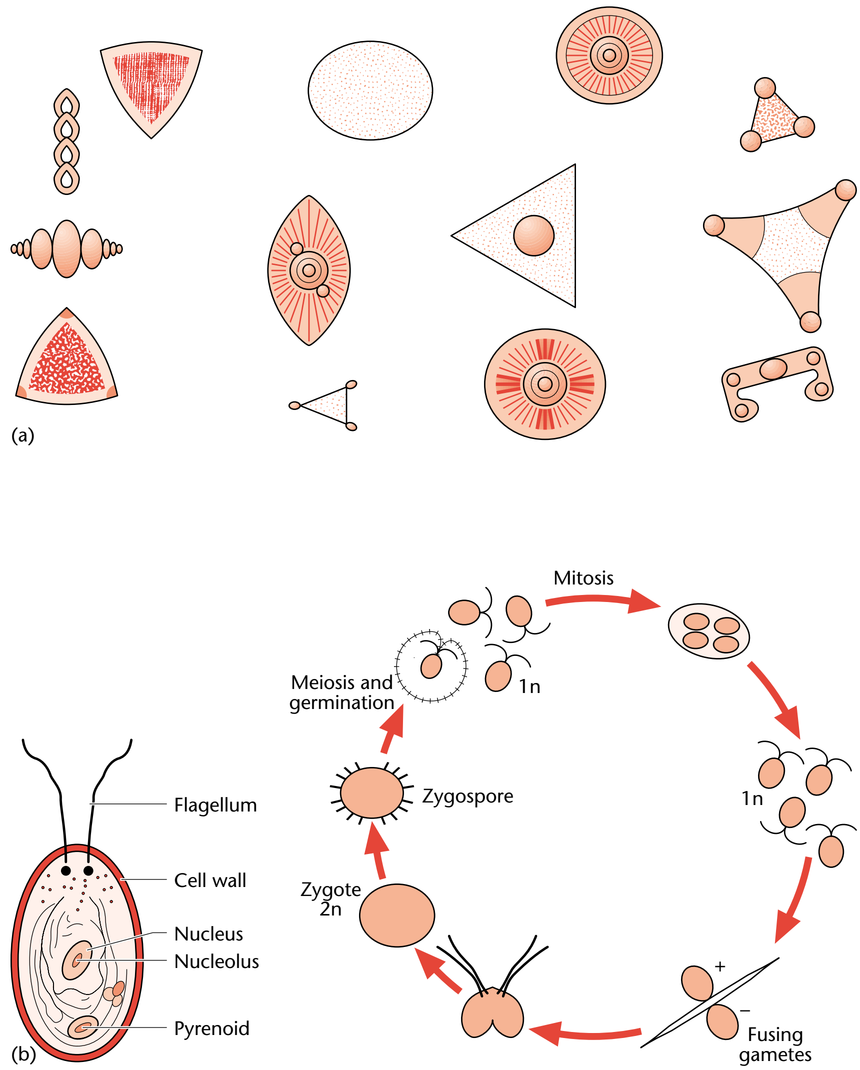

Figure 2 (a) Drawings of diatoms (phylum *Bacillariophyta*) showing the range of different shapes. (b) *Chlamydomonas reinhardti* structure and diagram of *Chlamydomonas* life cycle.

the sporophytic generation dominates, and the gametophytic generation grows inside sporophytic tissues. In bryophytes, such as mosses, the familiar 'plant' is actually the haploid gametophyte; the sporophytes are often only a few cells, and may grow on the tips of the gametophyte leaf blades.

Sexual Reproduction in Seedless Plants

Chlamydomonas reinhardti, a unicellular green alga

A well-understood example of sexual reproduction in the algae comes from the unicellular green alga *Chlamydomonas reinhardti* (**Figure 2**). The haploid vegetative phase can be found swimming through ponds and puddles, propelled by two flagella, whip-like structures that emanate from the front of the cell. This organism has two mating types: mt + and mt −, much like male and female but identical in appearance, and thus is an example of isogamous reproduction. When a signal consisting of light and food deprivation is processed, vegetative cells differentiate into gametic cells. The gametic cells are able to withstand long periods of nutrient deprivation and mate with gametes of the opposite mating type. When gametes of opposite mating types happen upon each other, a series of events is triggered which leads to their fusion. The two cells adhere via their flagella, almost as if they were dancing. The two cells then fuse, creating a diploid zygote with four flagella. These flagella are absorbed, and a thick wall is deposited around the circumference of the fused cells, forming a zygospore. In this state, the zygospore is not only capable of withstanding nutrient deprivation, but also dehydration. When environmental conditions become favourable, the zygospore is relieved from this dormant state, which then hosts one round of meiosis. Four haploid vegetative cells hatch from the zygospore, completing the cycle. Thus *Chlamydomonas* vegetative cells that had thrived in an environment but that is no longer favourable undergo sexual reproduction, mixing their genetic material. When conditions for growth become favourable, the potential for the offspring to succeed in a subsequent, most likely different environment, is maximized.

Bryophytes (mosses, hornworts and liverworts)

The bryophytes, including mosses, hornworts and liverworts (**Figure 1**), are distinguished from more advanced vascular plants in that the haploid gametophytic generation dominates and is free-living; the sporophyte is small and depends on the gametophyte. A distinguishing characteristic of the bryophytes is the lack of a 'true' vasculature (such as leaf veins, or more specifically xylem and phloem). While these plants reproduce asexually by fragmenting the gametophyte or by gemmae, they also reproduce sexually. In this realm, they share some characteristics with their more advanced relatives, such as the presence of male and female reproductive structures: the antheridia comprising the male and the archegonia housing the female gametes. Gametophytes may be male or female, producing only antheridia or archegonia respectively.

The small antheridia of a prototypical moss, propped on a stalk at the tips of the leafy shoots, are enclosed in a single-cell-thick layer called a jacket and house spermatogenous cells. A spermatogenous cell divides by mitosis to yield two sperm. Unlike *Chlamydomonas* cells, only the bryophyte male gametes possess flagella. The archegonia are flask-shaped structures; the venter – stomach – contains the egg borne on a neck consisting of canal cells. Although the neck arises as a solid mass of tissue and initially bars access to the waiting egg cell, the canal cells eventually disintegrate, releasing sperm-attractant chemicals and leaving a fluid-filled canal in which the spermatogenous cells swim.

After the spermatogenous and egg cell nuclei fuse, fertilization is accomplished, and a zygote is formed. The zygote undergoes numerous cell divisions and matures into a sporophyte. Interestingly, no cell connections are maintained between the developing embryo and the gametophyte; instead, a placenta-like structure facilitates transport of necessary nutrients along the cell walls. As the embryo grows, the venter expands to house the developing sporophyte. Upon maturation, the sporophyte produces spore cells by meiosis. These spores are then dispersed from the formed sporangium. When environmental conditions are favourable, the spores germinate to form juvenile developmental forms known as protonemata (singular, protonema), a thread-or plate-like juvenile structure that will eventually give rise to mature gametophytes.

The release of spores from the sporangium can be quite dramatic. In peat mosses, *Sphagnum*, the sporophyte capsules are elevated on a stalk from the gametophyte, and capped with a lid. As the sporangium dries, pressure builds within the capsule until the lid is blown off with a 'pop', propelling a cloud of spores. In some mosses, a ring of 'teeth' that acts as a 'gate' lines the lid structures. When dry, the teeth pull up, opening the sporangium and allowing the spores to be blown by the wind; when moist, the teeth curl back, thus ensuring that spores are released under conditions conducive to wide dispersion.

Seedless vascular plants

Vascular plants that produce spores represent an evolutionary step forward in plant reproduction. Ferns are common examples, but other seedless vascular plants are relatively familiar. These include the horsetails (*Equisetum*), the leafless and rootless *Psilotum* (phylum *Psilotophyta*), and the club mosses (phylum *Lycophyta*).

Like all vascular plants, the reproductive systems of the seedless plants are oogamous, with immobile eggs and sperm that propel themselves through water with flagella. In seedless vascular plants, unlike in the bryophytes, the sporophyte generation dominates. As in the bryophytes, the spores are haploid, but they may be homospores or heterospores.

Fern reproduction

Fern reproduction is an excellent example of seedless vascular plant reproduction. Sori (singular, sorus; **Figure 1**) are sporangia that form underneath the leaf of the adult sporophyte, commonly referred to as a fern plant, and produce spore cells by meiosis. A released spore germinates to form the young gametophyte, called a prothallus, which is small and unremarkable to the unaided eye. Set into the gametophytic tissue are archegonia, which house the waiting eggs, and antheridia, which produce flagellated sperm cells. When adequate moisture is available, sperm swim to and enter the archegonia, fusing with the eggs to form diploid zygotes, which immediately divide. Although several eggs may be fertilized, only one new adult plant usually emerges per prothallus. The zygote develops a primary root, a first leaf, and the beginnings of a stem. After a short time, the developing sporophyte becomes nutritionally independent of the gametophyte, and the gametophyte disintegrates. An adult sporophyte, or recognizable fern, emerges.

Sexual Reproduction in the Gymnosperms and Angiosperms

Differences between seedless and seed plants

The male–female gametophytic interaction is different

The production of a seed changed how male and female gametophytes interact. Instead of being produced in nearby antheridia and swimming in puddles of water, the male gametophyte is delivered to the female gametophyte as a package: the pollen grain. The pollen grain is transferred to the female gametophyte by any number of means depending on the plant, from simple passive transport by wind, insects or animals. The deposition of pollen on to a receptive female surface is called pollination, not to be confused with fertilization, which occurs when sperm and egg nuclei fuse. Water is not required for the sperm to swim to the egg; thus a humid exterior aqueous interior environment is not required. Instead, the male gametophyte grows towards the waiting eggs to deliver the sperm.

The gametophytes are different

The pollen grain is an interesting, specialized cell designed to withstand harsh environmental conditions. As in *Chlamydomonas* zygotes and bryophyte spores, a major constituent of the outermost protective wall, the *exine*, is a lipid-and carotenoid-derived substance called sporopollenin. The protective capability of sporopollenin is remarkable. It is so resistant to environmental abuse that pollen grains thousands of years old can be found intact, although dead. Sporopollenin contributes to the formation of the intricate lattice structure of the exine, characteristic to each plant, which can be smooth, spiky or net-like. The exine surrounds a second wall, called the intine.

Pollen grains come in a wide range of shapes and sizes. They may be so small as to easily blow about in the wind, or so large that individual grains are distinguishable with the naked eye, such as in lilies or petunias. They can be released as tetrads, triads or dyads. In some cases, such as some orchids, pollen grains are massed to form what looks like one enormous grain.

The female gametophyte is also changed. A megasporocyte, or megaspore mother cell, undergoes meiosis, but usually only one of those meiotic products, the megagametophyte, is functional. An opening in the ovule between the tips of the integuments, called the micropyle, allows pollen tube and sperm entry.

The structure of the seed provides an evolutionary advantage

The most significant difference between seedless and seed plants is that the embryo is enclosed in a seed. The seed is a great evolutionary advance. Efficiently packed in an environmentally protected casing, the seed coat, and supplied with a substantial food source, the young sporophyte embryo is poised to succeed where spore-derived individuals would fail. Not only does the seed coat protect the young embryo, but the accompanying food also provides nourishment during dormancy, prolonging viability, and during the critical early stages of germination.

Seed structure is simple. From the exterior to the interior: a seed coat surrounds stored food that nourishes the embryo proper, the new sporophyte. These structures directly arise from the female gametophyte: the integument gives rise to the seed coat, the megasporangium (nucellus) contains a single functional megaspore that fuses with a sperm nucleus to give rise to the embryo, and the endosperm arises from the fusion of a sperm nucleus with the two nuclei of the female central cell.

Sexual reproduction in the gymnosperms

The first seed-bearing plants to appear were the gymnosperms, of which the conifers (cone-bearing, phylum *Coniferophyta*) trees are familiar, including the pines. However, the gymnosperms also include such striking plants as palm-like cycads (phylum *Cycadophyta*) and the phylum *Gingkophyta*, which today has a sole living representative, the maidenhair tree, *Gingko biloba* (see Figure 1). 'Gymnosperm' means 'naked seed', which refers to a seed that is not enclosed in an ovary, commonly referred to as a fruit, as is angiosperm seed.

The life cycle of a pine tree will serve as a paradigm for gymnosperm reproduction. Microsporangia giving rise to the pollen, and megasporangia giving rise to the female egg cells, develop in separate cones, called strobili, on the same tree. The microsporangia house the diploid microsporocytes that undergo meiosis. The haploid microspores divide twice mitotically to give rise to a four-celled pollen grain, consisting of two prothallial cells, a generative cell and a tube cell. At this point, further development of the male gametophyte is arrested until delivered to the female gametophyte, which is usually accomplished by the wind.

Each ovule of the megasporangia contains a single megasporocyte, the megaspore mother cell, which undergoes meiosis. These meiotic products, megaspores, all die except for the cell furthest from the micropyle, which survives to serve as the egg. Interestingly, the megasporocyte does not undergo meiosis until after pollination.

The process of pollination, fertilization and seed development is especially protracted in pines, encompassing two seasons. Interactions between the two gametophytes begin when pollen grains stick to a pollination 'drop' secreted from micropylar canals. This drop dries, and 'sucks' the pollen grains into the micropyle, where the grain germinates to form the pollen tube. As the pollen tube penetrates and feeds off the nucellus, the surviving megaspore nucleus undergoes many rounds of mitotic division, producing thousands of nuclei. Approximately 15 months post-pollination, cell walls separate the nuclei, and several archegonia form. Meanwhile, the generative nucleus of the pollen tube has undergone mitosis to produce a stalk cell and a body cell. The body cell (the spermatogenous cell) divides, resulting in two sperm. After the long voyage, the pollen tube reaches the egg cell in the archegonia, bursts, and delivers most of its cytoplasm. One of the sperm nuclei fuses with the waiting egg cell, the other dies. Because more than one pollen tube can enter an ovule, all of the eggs can be fertilized. This phenomenon is called polyembryony; under most circumstances, only one embryo survives, although rarely two or even three embryos will form, and consequently will germinate from a single seed.

The gymnosperm seed consists of tissues of different ploidy: the seed coat and the embryo are diploid, while the remaining female gametophyte tissue, which nourishes the embryo, is haploid.

Sexual reproduction in the angiosperms (the flowering plants)

Evolutionary advantages

Angiosperms comprise almost every kind of plant with which most people are familiar and are of great economic and health importance, supplying food, pharmaceuticals, fibres and construction materials. The evolutionary success of the angiosperms is bespoken by their dominance: they are the largest group of photosynthetic organisms.

Angiosperm means ‘seed enclosed’. The angiosperms are classified into two classes, the eudicots and the monocots, referring to the number of seed leaves, or cotyledons, of the young sporophytes. The monocots sport one such leaf, while the eudicots have two. Other characteristics distinguish the two classes: eudicots have flower parts that come in groups of four or five, the monocots in groups of three. The pollen grains of monocots have only one pore from which the pollen tube will emerge; eudicots have three. Another characteristic is leaf venation: monocots have parallel venation, such as celery, corn and other grasses, while eudicots exhibit web-like venation, such as sycamore leaves or spinach. One characteristic that all angiosperms share is the phenomenon of double fertilization and an ovary enclosed in a specialized floral structure, the carpel.

Flower anatomy

Angiosperms are characterized by the presence of flowers. Flower parts are arranged in four whorls: starting from the base of the flower, sepals, petals, male stamens, and the female carpels. Sepals form the calyx, while the sum of the petals is known as the corolla. Together, the corolla and calyx are known as the perianth.

Most often the stamens consist of two distinct parts: an anther born on a slender stalk, the filament. Within the anther, the microspores (pollen grains) are borne within two lobes containing four microsporangia, or pollen sacs. These organs make up the androecium, the ‘house of man’. The gynoecium, or ‘house of woman’, gives rise to the megaspores (eggs). The gynoecium comprises the sum of carpels in a given flower. A carpel consists of a stigma, the receptive surface upon which pollen lands, often a style, a solid mass of tissue that divides the stigma from the ovary, and the ovary proper, housing the ovule(s) containing the egg cells.

This description depicts an ideal flower structure; in nature, the variation is great. Plants may fuse different floral organs, or flowers may be male-or female-specific, and thus lack female or male organs, respectively. Individuals within a given plant may bear only male flowers, while others bear female blooms; these plants are dioecious (‘two houses’). If male and female flowers are borne on the same plant, then they are monoecious (‘one house’). If, however, both male and female organs are found within the same flower, then the flower is called perfect; lacking stamens or carpels, they are termed imperfect. Therefore, flowers are perfect or imperfect, but individual plants are monoecious or dioecious. Bracts are modified leaves that may look like petals; both may be coloured any of an amazing number of hues. In addition, the structure of a flower may be adapted to encourage specific pollinators or to keep out other less productive pollinators.

Pollen development

The structure of angiosperm pollen is determined during microsporogenesis. Four groups of cells give rise to the pollen mother cells, or microsporocytes, which in turn divide meiotically to form the pollen grains (microspores), within each anther. The haploid microspores then divide mitotically, forming a large generative cell and a smaller tube cell; a cell wall does not divide these cells. Finally gametogenesis is complete when the generative nucleus divides once more to produce the sperm nuclei, giving rise to a total of three nuclei in the male gametophyte. Some plants shed pollen that have only two nuclei, wherein the generative nucleus does not divide until some time after pollination, while other plants release trinucleated pollen. Like gymnosperm pollen, angiosperm pollen contains an exine and an intine. Interestingly, the origins of these two cell walls are different: the intine is deposited by the developing, haploid microspore, while nonmeiotic, diploid nutritive cells, the tapetum, mostly form the exine. Sometimes embedded between exine projections, a pollen coat, or tryphine, is deposited. Like the exine, diploid tissues contribute this lipid and protein-rich structure.

Female gametophyte

In flowering plants, megasporogenesis proceeds as in the gymnosperms, but the haploid megaspore nucleus (but not the cell) divides mitotically three times, producing eight haploid nuclei enclosed within one cell. The nuclei are arranged as groups of four at the opposite ends of the cell. Two nuclei migrate to the centre of the cell to form the polar nuclei. After this rearrangement, cell walls reappear: the three nuclei near the opening of the ovary (the micropyle) form a functional egg cell and two synergids; the three nuclei of the opposite end form the antipodal cells, and the polar nuclei form a single central cell. This arrangement of the female gametophyte enables the phenomenon of double fertilization. Sperm nuclei will fuse with both the egg cell and the central cell, creating a diploid zygote and a triploid primary

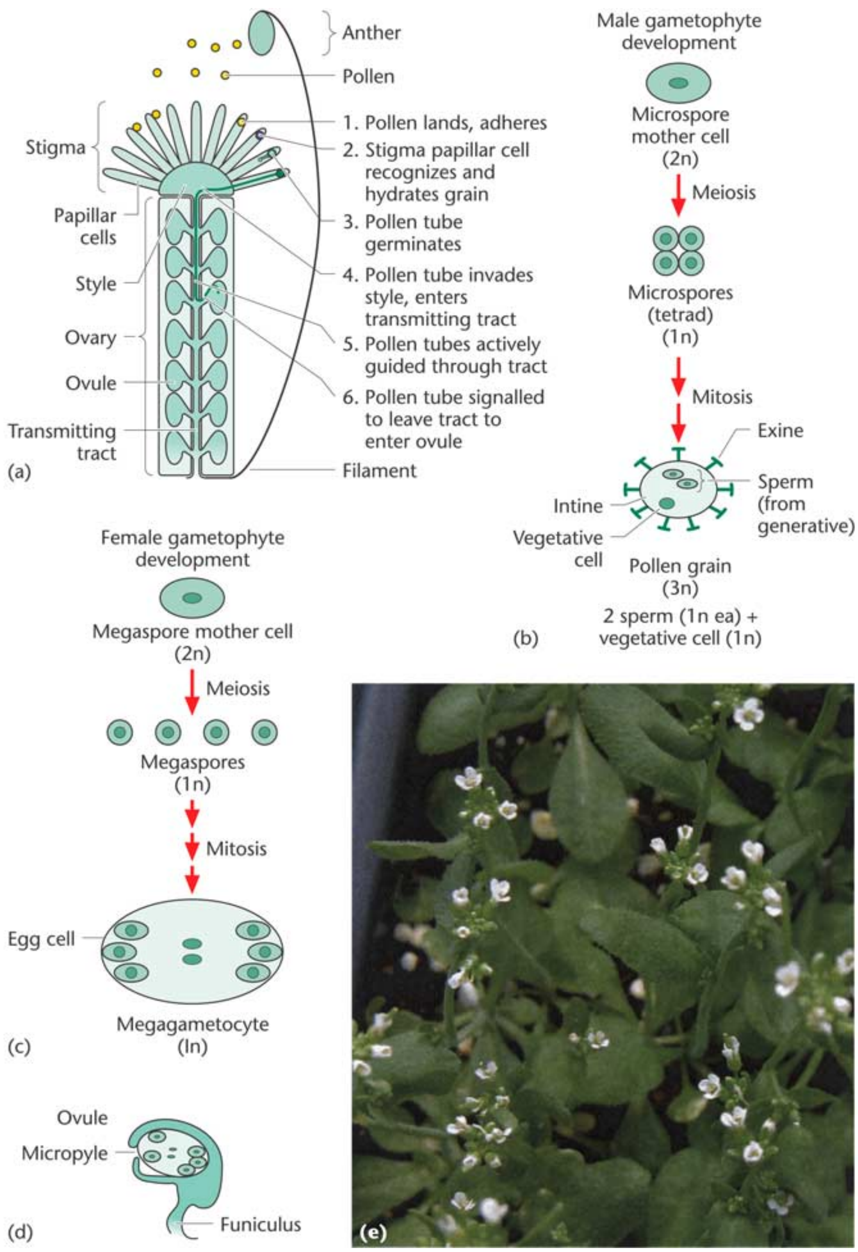

Figure 3 Sexual reproduction in *Arabidopsis thaliana*. (a) Structures of the pistil are indicated on the left-hand side, events in reproduction on the right (see text for details). (b) Schematics of male gametophyte development. (c) Schematics of female gametophyte development. (d) Structure of an ovule, housing the egg. (e) Photograph of *Arabidopsis thaliana*.

endosperm nucleus, which will give rise to the nutritive endosperm.

Sexual reproduction in *Arabidopsis thaliana*

A relative of mustard, *Arabidopsis thaliana* (**Figure 3**), has been fruitful for studies of flowering plant reproduction because of its small size, short life cycle (6 weeks from seed to seed), small amount of genetic material (recently sequenced) and small number of genes (approximately 20 000), and its amenability to many laboratory investigative techniques, including genetics, cell biology, molecular biology and biochemistry.

The process of *Arabidopsis* reproduction has begun to be elucidated (**Figure 3**). Reproduction begins when a pollen grain lands on a receptive female stigma cell. The desiccated pollen grain is hydrated by the female stigma cell, allowing a pollen tube to germinate. The pollen tube adheres to the stigma cells and then burrows into the female tissues, migrating between the cell walls of the style. From the style, the tube enters the central transmitting tract, where various female signals actively guide the tube. When the tube receives an appropriate signal, it exits the transmitting tract and approaches an ovule by adhering to the funiculus, a stalk that connects the ovule to the transmitting tract, and then enters the micropyle. The tube bursts, delivering the two sperm nuclei, which then fertilize the egg and central cell, affecting double fertilization. A remarkable aspect of *Arabidopsis* reproduction is that only one pollen tube of thousands approaches each ovule. The female gametophyte does not form archegonia as in gymnosperms, and consequently, *Arabidopsis*, like other angiosperms, does not exhibit polyembryony.

The initial interaction between pollen and flower is also the first step in which *Arabidopsis* will determine the appropriateness of the pollen. The stigma is subject to the pollen floating in the environment, and must distinguish self from non-self. While some plants, most notably *Papaver* (poppy), *Nicotiana* (tobacco), and *Petunia* have self-incompatible systems functionally analogous to human immune rejection, *Arabidopsis* mounts several different defences. First is adhesion: only *Arabidopsis* pollen adheres to the stigma cells with high fidelity. The second is related to the need for water for male gametophyte delivery. Pollen is desiccated, and must be hydrated before a pollen tube can germinate; the female actively determines, or recognizes, if the pollen is appropriate before delivering water to the grain. Some plants will hydrate pollen indiscriminately: instead of selectively giving water to pollen grains, the surface of the stigma is covered with lipid-and polysaccharide-rich secretions, which will hydrate any grain that chances to arrive there. These plants have other means of selecting appropriate pollen, usually by inactivating pollen tubes in the transmitting tract.

To illustrate the advances that *Arabidopsis* has made, some of the genes that act during reproduction have been elucidated. An important discovery was the *cer* genes that contribute to pollen coat formation. When these genes are nonfunctional, pollen without coats are produced and this pollen is sterile. However, a trick determined the role of the coat: if plants with mutant pollen are placed in an environment with high humidity providing adequate moisture to hydrate the pollen grains, then the pollen was fertile. This result suggested that the pollen coat plays a role in pollen hydration and signalling to the stigma cells.

A very exciting result was realized when a mutant plant exhibited pollen tubes that no longer 'knew' where to grow in the ovary and had aberrant interactions with the female tissues. The *pop* genes (*po*llen–*p*istil interaction) were identified that affected the ability of pollen tubes to be properly guided through the female tissues. These plants produce very few seed.

Conclusion

The field of plant reproduction is vast, encompassing unicellular photosynthetic organisms to flowering plants. While many trends are noted, many differences exist. The study of plant reproduction will continue to be fertile and fascinating.

Further Reading

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