Chapter 12

Life Cycles: Meiosis and the Alternation of Generations

LIFE CYCLES TRANSFER GENETIC INFORMATION

Asexual Reproduction Transfers Unchanged Genetic Information through Mitosis
Sexual Reproduction Produces New Information through Meiosis and Fertilization

ALTERNATION BETWEEN DIPLOID AND HAPLOID GENERATIONS

Plants Vary in the Details of Their Life Cycles
Sexual Cycles Can Be Heterosporic or Homosporic
Only One Generation Is Multicellular in Zygotic or Gametic Life Cycles
The Diploid Generation Has Become Dominant over Evolutionary Time

SUMMARY

KEY CONCEPTS

1. Life perpetuates itself through reproduction, which is the transfer of genetic information from one generation to the next. This transfer is our definition of *life cycle*. Reproduction can be asexual or sexual.

2. Asexual reproduction requires a cell division know as *mitosis*. Asexual reproduction offers many advantages over sexual reproduction, one of which is that it requires only a single parent. A significant disadvantage of asexual reproduction is the loss of genetic diversity and the likelihood of extinction when the environment changes.

3. Sexual reproduction involves the union of two cells, called *gametes*, which are usually produced by two different individuals. Another kind of cell division, known as *meiosis*, ultimately is necessary to produce gametes.

4. Every species in the kingdom Plantae has both diploid and haploid phases--that is, plants whose cells are all diploid or all haploid. These phases are called generations, and they alternate with each other over time.

5. The fossil record reveals that the most recent groups to evolve have sporic life cycles, in which the gametophyte (haploid) generation is relatively small and the sporophyte (diploid) generation is dominant in terms of size, complexity, and longevity.

12.1 LIFE CYCLES TRANSFER GENETIC INFORMATION

A basic characteristic of life is that it perpetuates itself. The process can be sexual or asexual. In asexual reproduction, each generation is genetically identical to the last. Asexual reproduction occurs in unicellular and multicellular organisms. For example, a single-celled alga floating near the surface of a lake can divide asexually to produce two single-celled offspring (Fig. 12.1a). This individual cell divides to produce two new cells, then each of those cells will divide to produce others, and so on for generations of cells. Similarly, a cell within the root tip of a corn plant can reproduce asexually, first to generate two identical offspring cells and then eventually a whole tissue, layer , or region of the root, consisting of thousands of genetically identical cells (Fig. 12.1b). The succulent air plant (*Kalanchoe pinnata*) is able asexually to produce miniature plantlets along leaf edges, each of which can fall off, take root, and become a new plant identical to the parent.

Asexual reproduction requires only a single parent cell or parent organism, and all of the progeny will be genetically identical to that parent. The collection of identical individuals is called a **clone**. Many plants in nature produce clones: strawberries, aspens, and coast redwoods are only a few examples (Fig. 12.2). Strawberry plants (*Fragaria* sp.) produce horizontal aboveground stems (stolons or runners) that periodically take root at the nodes and produce new leaves, flowers, and fruits there. If the runners are severed, the plants remain alive and capable of a fully independent life. When a redwood (*Sequoia*

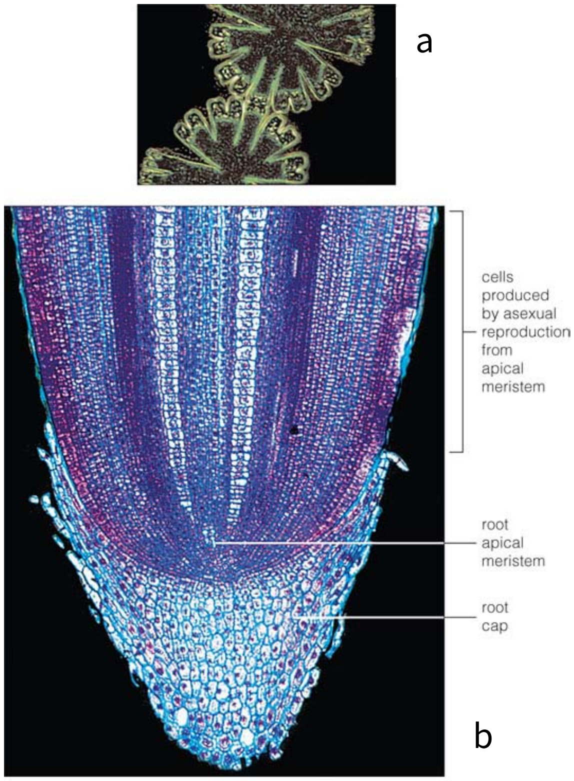

Figure 12.1. Asexual reproduction occurs in single-celled organisms and in the tissues of multicellular organisms. (a) *Micrasterias*, a single-celled freshwater alga, has just divided to produce two cells. (b) Longitudinal section of a corn plant (*Zea mays*) root tip. Cell division in the apical meristem produces many cells and several different tissue types behind (above) the tip.

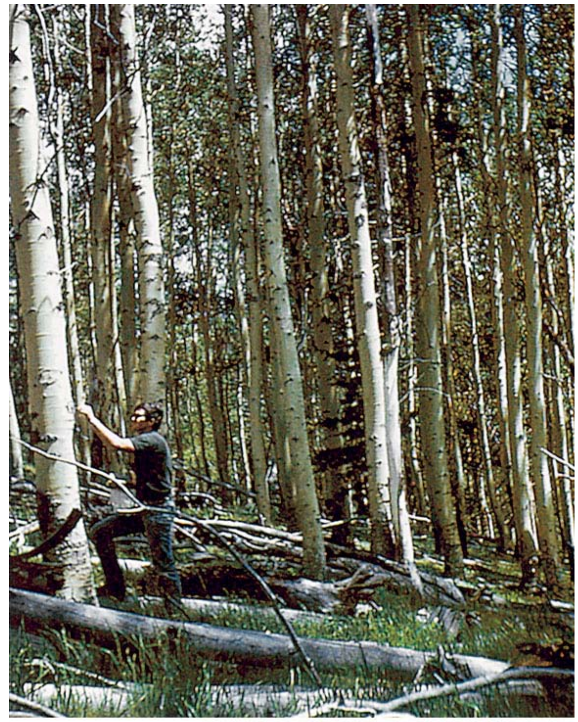

Figure 12.2. Asexual reproduction produces clones of many genetically identical plants. All these trembling aspens (*Populus tremuloides*) in the Sierra Nevada of California are probably connected underground, but if the connections are severed each tree can live independently. These individuals belong to a single clone.

sepervirens) trunk is killed by fire or removed by timber harvest, dormant buds buried under the bark at the base of the stump are stimulated to begin growth. Within decades, a cluster of young redwood trees will exist, all sharing the same root system but having separate trunks. In time, the parental stump will decompose and disappear, leaving a circular clone of equal-aged offspring. Trembling aspen (*Populus tremuloides*) trees produce special roots that grow horizontally under the soil instead of down. These roots periodically give rise to stems (which in time become mature trees) some distance from the parent tree. An entire grove of aspen, occupying several acres of ground, can be a single clone of hundreds of genetically identical trees, seemingly independent but actually all connected to each other below ground.

Sexual reproduction, in contrast, causes each generation to be genetically different. For example, when a poppy plant produces seeds, each seed produces a plant that is slightly different from the parent: perhaps taller, maybe more frost tolerant, possibly with different petal colors, or capable of flowering a few days sooner than the parent.

Both kinds of reproduction transfer genetic information from parent to offspring, which is the definition of **life cycle** as used throughout this textbook.

Asexual Reproduction Transfers Unchanged Genetic Information through Mitosis

Asexual reproduction requires a particular kind of cell division called **mitosis** (Fig. 12.3). Briefly, mitosis is preceded by a copying process in which enzymes duplicate every chromosome. The two copies of each chromosome, called *sister chromatids,* are joined together at one point. In the first part of mitosis (*prophase*), each chromosome condenses from a threadlike form to a compact rodlike form that can be moved without breaking. A *spindle apparatus* forms too, for moving chromosomes, and spindle fibers link sister chromatids of each chromosome to opposite poles of the spindle. Spindle fibers pull the chromosomes to the cell's equator. Then, in a stage called *metaphase,* the cell pauses to check whether all the chromatids are linked correctly. In *anaphase*, the spindle pulls sister chromatids to opposite poles of the cell. Next, in *telophase*, the chromosomes uncoil and new nuclear envelopes form (not shown in Fig. 12.3). Finally, in *cytokinesis*, the cell divides into two cells. Each offspring cell retains the exact same complement of chromosomes (and genes) as that of the parent cell.

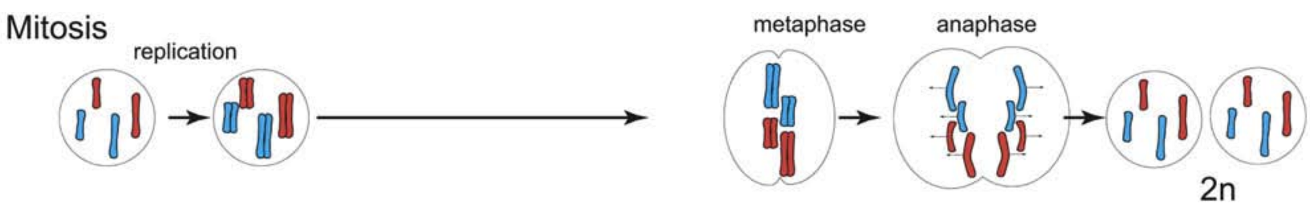

Figure 12.3. A review of mitosis. Blue and red chromosomes came from different parents that mated to produce the organism with this cell. The original cell has four chromosomes, each of which was replicated before mitosis to give two sister chromatids. Mitosis separates the sister chromatids to produce two cells, each genetically identical to the parent cell.

There are several advantages to asexual reproduction. First, only a single parent is required. Therefore, any isolated individual can produce offspring and populate a new part of the species range. Second, asexual reproduction produces offspring that may be just as successful in the habitat as the parent was, unless the parent used up too many resources. Because the parent lived to reproduce, so too should the next generation (providing the environment stays unchanged). Third, asexual reproduction generates offspring faster than sexual reproduction; therefore, an invading species can dominate the landscape quickly. Fourth, asexual reproduction costs less in terms of metabolic energy than sexual reproduction. This is because sexual reproduction requires a plant to invest in reproductive tissue (e.g. flowers) even though successful seed formation, dispersal, and germination might not occur in any given year. Asexual reproduction, in contrast, always works.

The only disadvantage to asexual reproduction is that genetic diversity remains relatively fixed, subject only to mutation, a very slow process. New plant clones are genetically identical to parents. If the environment changes, all the plants are equally susceptible to any new stress, such as a new disease, a drought, or a migratory invasion of herbivores. In contrast, sexual reproduction results in genetic diversity, thus giving the maximum probability for continued existence of a species over long periods. The geological history of the earth has consistent themes of environmental change in which species that could not adapt became extinct. Genetic diversity promotes adaptation.

Sexual Reproduction Transfers New Combinations of Information through Meiosis

Sexual reproduction requires the union of two cells called **gametes**. The gametes must find each other and join to create a single offspring cell. Sexual reproduction thus poses two problems. One problem is to find a way to bring gametes together, and the other is to reduce the number of chromosomes in gametes. If gametes with the normal number of chromosomes were to fuse, then the resulting offspring cell would have twice the normal number. A repetition of this over several generations would create cells with an unmanageable number of chromosomes.

The solution to the number problem is a type of cell division called **meiosis**, which reduces the number of chromosomes by half. To make sense of meiosis, we need the concept of a chromosome set. The information to build a body is divided between several different kinds of chromosome. A **chromosome set** consists of one chromosome of each kind. The number in a set varies among species. In humans, there are 23 chromosomes in a set. In a cotton plant (*Gossypium hirsutum*), there are 10 chromosomes in a set. Any cell with just one set of chromosomes is said to be **haploid**, symbolized as the **1*n*** state. Gametes are haploid, with one set of chromosomes. When two haploid gametes fuse, they create a cell (the **zygote**) that has two sets. A cell with two chromosome sets is **diploid**, symbolized as **2*n***. the two copies of a given chromosome in a 2n cell are said to be **homologous**. They make up a pair, each carrying the same genes. Thus, a 1*n* gamete of a cotton plant has 10 *unpaired* chromosomes, and a 2*n* zygote of a cotton plant has 10 chromosome *pairs*.

Now let us see how meiosis makes haploid cells from a diploid cell (Fig. 12.4). Before entering meiosis, the 2n cell duplicates its DNA so each chromosome has two connected copies (sister chromatids). Then meiosis carries out two rounds of cell division. The first division, *meiosis I*, opens with *prophase I*. Here each homologous pair of chromosomes comes together in a unique process call **synapsis**. Noting like it occurs in mitosis. Synapsis is important for two reasons. First, the pairing makes it easy for the cell to divide in a way that produces haploid cells. But before that happens, synapsis allows homologous chromatids to trade segments by a process called **crossing over**.

To show the consequence of crossing over, Figure 12.4 uses two colors for chromosomes from the organism's two parents. Just one crossover is shown for each homologous pair of chromosomes. Normally, several crossovers occur at random points along each homologous pair. The result is that synapsis and crossing over generate genetic diversity by giving chromosomes new combinations of parental genes. Another event in prophase I is that a spindle forms, and its fibers link one chromosome of each homologous pair to each of the cell's poles.

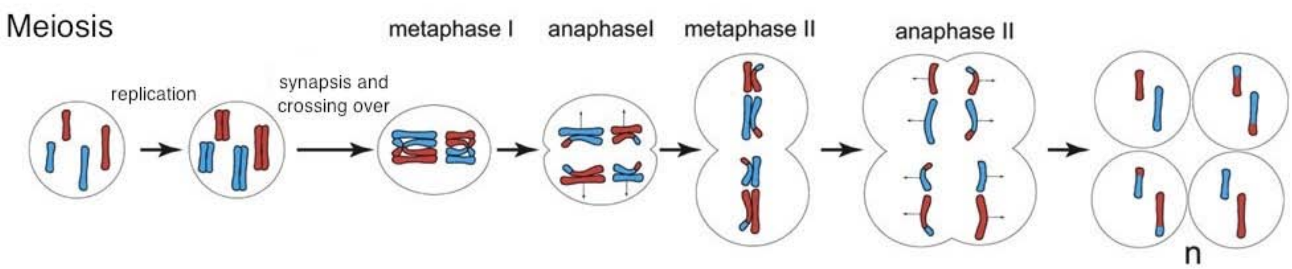

Figure 12.4. The two divisions of meiosis. Different colors are used to distinguish chromosomes from the two parents.

With prophase complete, the spindle moves chromosomes to the cell's equator. At that point the cell pauses to check whether all the chromosomes are linked properly. The pause for checking is *metaphase I*. Next, in *anaphase I*, the spindle pulls each chromosome with its two sister chromatids to one of the poles. Accurate linkage in prophase I assures that each pole will get a full set of chromosomes. Finally, *telophase I* creates new nuclear envelopes (not shown in Fig. 12.4), and **cytokinesis** divides the cell. Overall, meiosis I converts the original 2*n* cell to two 1*n* cells with different combinations of parental genes.

Meiosis II, the second round of division, is simply a mitotic division that separates the sister chromatids and converts the two haploid cells to four. There is no synapsis in prophase II, and hence, no further reduction or crossing over. But as the colors show in Figure 12.4, each of the fours haploid cells has a different combination of parent chromosome segments.

12.2 ALTERNATION BETWEEN DIPLOID AND HAPLOID GENERATIONS

As discussed in the preceding section, the sexual life cycle consists of an alternation between haploid cells and diploid cells. This is true of all sexual organisms, whether they are animal, plant, fungus, or protist. But organisms vary in the way they handle the diploid and haploid cells. In humans and other animals, haploid cells do not multiply by mitosis, but simply become gametes. In contrast, diploid animal cells--starting with the zygote--divide mitotically to make diploid bodies.

Matters are quite different in plants. They divide both haploid and diploid cells by mitosis, to make two kinds of multicellular bodies. Plant biologists refer to the creation of both diploid and haploid bodies as an **alternation of** diploid and haploid **generations**. Figure 12.5 shows how a typical flowering plant, a cherry tree, carries out the alternation of diploid and haploid generations. This diagram illustrates some fundamental ideas and terms that are essential to understanding the life of a plant.

The cherry tree, like all large plant bodies, is the diploid part of the life cycle. A diploid plant body is called a **sporophyte** because it makes reproductive units called spores. More specifically, a **spore** is a one-celled reproductive unit that can develop into a new plant without mating with another cell. The cherry tree makes two kinds of spores in different parts of the flower. One kind of spore will develop into a male haploid plant that makes gametes called *sperm* cells, whereas the other kind will develop into a female haploid plant that makes a gamete called an *egg*. Because haploid plant make gametes, they are called **gametophytes**.

As discussed earlier, meiosis produces cells with new combinations of genes. The spores made in the anther were built to disseminate those new gene combinations; therefore, they are called **meiospores** to emphasize their meiotic origin and their recombinant nature. This contrasts with **mitospores** that some organisms make to disseminate copies of the parent's own gene combination. Mitospores are made by mitotic division of the parent's cells without intervening meiosis. Within the **pollen sac**, each male meiospore divides by mitosis to become the tiniest possible gametophyte--a body with just two haploid cells. Then its outer wall hardens, making the gametophyte into a microscopic **pollen grain**. The pollen sacs split open, releasing thousands of pollen grains

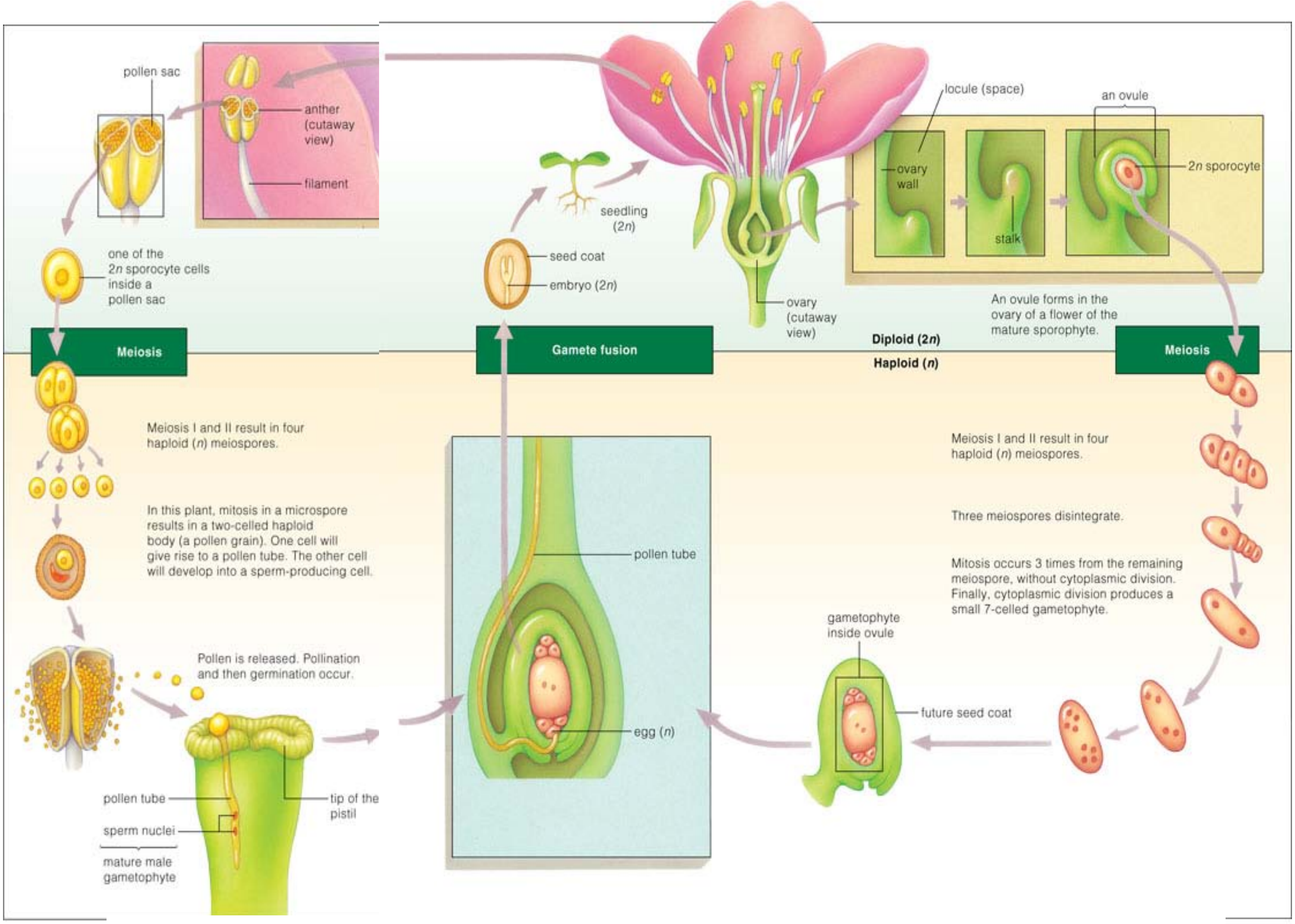

Figure 12.5. Life cycle of cherry (*Prunus*). Start with the flower, which is part of the sporophyte. Look to the flower's top left and see how meiosis in pollen sacs leads to male gametophytes. At bottom left, the pollen tube of the gametophyte has two gametes called sperm. Then at the top right, it is shown how meiosis in ovules leads to the embryo sac (female gametophyte). Inside the embryo sac is a gamete called an egg. When egg and sperm meet, they fuse to form a diploid zygote cell (not shown). Mitotic divisions and growth convert the zygote cell into an embryo sporophyte within a seed. On germination, the embryo grows into a cherry tree.

to passing air currents or animals. Later, on reaching the female part of a flower, the pollen grain grows a slender extension called a**pollen tube**, which contains two sperm nuclei (Fig. 12.5, bottom left). With the formation of the pollen tube, the male gametophyte has reached maturity.

To see how female structures are made, examine the top right of Figure 12.5. In the center of the flower is a vase-shaped **pistil** with a swollen base called an **ovary**. Chambers in the ovary are lined with microscopic bulges of tissue, each called an **ovule**. At first, all the cells of each ovule are diploid, but eventually an innermost single cell undergoes meiosis and produces four recombinant haploid cells. Three of the four cells degenerate, whereas the fourth matures into a large female spore. This, too, is a meiospore. It is not released, but remains inside the ovule where it divides by mitosis, and the resulting cells divide twice more by mitosis to make a tiny, seven-celled female gametophyte. One gametophyte cell is an **egg**.

To unite pollen with eggs, the first step is **pollination**--the transfer of pollen from the anther to the tip of a pistil. There, the pollen grain forms a pollen tube that grows down to an ovule, carrying two haploid sperm nuclei. When the pollen tube reaches an egg, one sperm fuses with the egg to make a zygote, which divides mitotically to form an **embryo** with a seed coat. The embryo is simply a small sporophyte that will grow to become a cherry tree when the seed germinates.

Plants Vary in the Details of Their Life Cycles

Not all plants reproduce like the cherry tree. Later in this textbook, Chapters 21-24 summarize how conifers, ferns, mosses, and algae carry out their life cycles. There are many life cycle similarities among flowering plants and the rest of the kingdom Plantae, but there are also differences. Fortunately, the most important differences can all be brought together in a generalized life cycle (Fig. 12.6). By mastering the vocabulary of Figure 12.6, you will be able to simplify and more easily understand the variations.

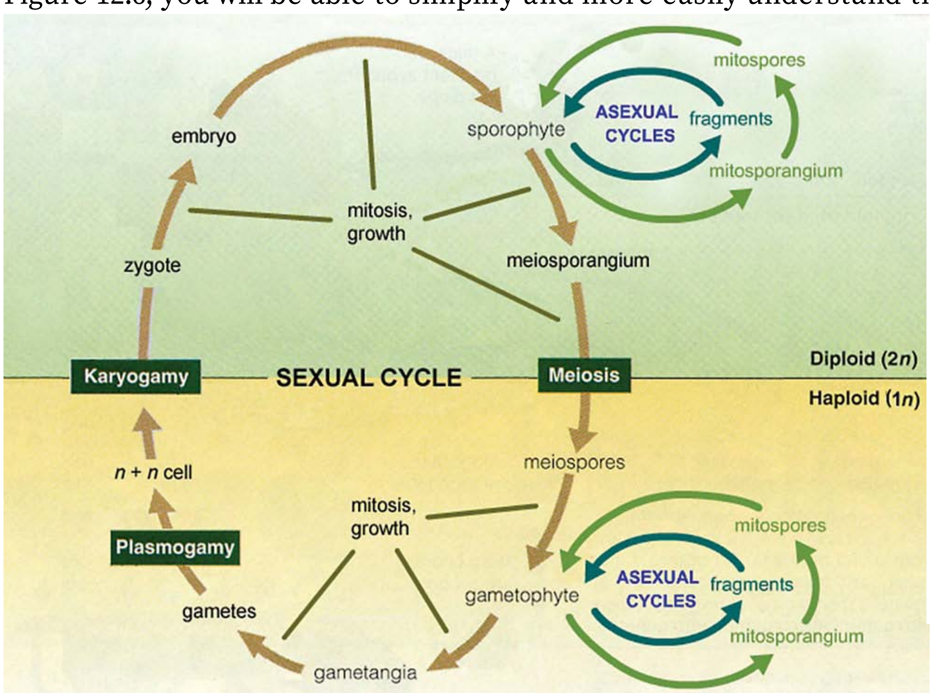

Figure 12.6. Generalized life cycle of organisms in the plant kingdom. No single species has all the steps shown here. The terms used in this diagram are basic, and many synonyms exist for variations. Mastery of these terms makes it easier to understand all plant life cycles.

Before discussing the generalized life cycle, we need to clarify the informal term *plant*. This clarification requires two more informal terms: embryophytes and green algae. **Embryophytes** are plants that shelter their sporophyte offspring as embryos within the parental gametophyte body. They include all the land plants that we know in everyday life. **Green algae**, in contrast, are simpler photosynthetic organisms that do not form embryos. They include green pond scum and the green film that grows on swimming pools and aquarium glass. Despite their many differences, green algae and embryophytes are related to each other more closely than to any other form of life (see Chapter 21). Consequently, many systematists now include both embryophytes and green algae under the informal heading *plants*. This chapter also follows that practice and uses the terms *embryophytes* and *green algae* when discussing differences between them.

To work our way through the generalized life cycle (Fig. 12.6), let us begin with the multicellular diploid plant, the sporophyte. All embryophytes produce sporophytes, ranging from giant trees down to tiny lumps that are smaller than a pinhead. Some green algae also make sporophytes, but many do not. Many sporophytes can reproduce asexually from fragments of a parental body, as when rhizomes spread horizontally and are broken up to produce many separate plants. Some green algae reproduce the sporophyte asexually by making a **mitosporangium**, a structure in which parental cells divide mitotically and then differentiate into mitospores. Each mitospore is released to grow a new sporophyte with the same genetic constitution as the parent plant.

At particular times, some cells of the sporophyte launch a sexual cycle when they differentiate to form a structure called a **meiosporangium**, in which one or more cells will divide by meiosis. In green algae, a meiosporangium is a single cell. In embryophytes, it is a multicellular structure. In the cherry tree, each pollen sac is a meiosporangium, and each ovule contains a meiosporangium. Eventually, meiospores germinate to develop into gametophytes by means of mitotic division and growth. Like sporophytes, the gametophytes may reproduce asexually from fragments of the parental body or, in the case of green algae, by producing mitosporangia and mitospores. Each fragment or mitospore has the potential to develop into a new gametophyte with the same genetic constitution as the parent gametophyte.

When environmental conditions are appropriate, gametophytes take another step in the sexual life cycle by producing structures called **gametangia** (singular, *gametangium*) in which haploid cells differentiate into gametes. In green algae, a gametangium is a single enlarged cell. Embrophytes made more complex gametangia, which contain many cells. However, even there the gametangia are microscopically small. They are particularly small in flowering plants, and they were not shown in our cherry tree life cycle. Some gametangia look like sporangia, and, in some green algae, the gametes look just like mitospores. But there is always one consistent difference between gametes and mitospores: gametes cannot produce new individuals by themselves. Gametes must fuse in pairs to produce a new organism.

The most complex life cycles have two kinds of gametes that differ in function and appearance. This is true of all flowering plants. As seen in the cherry tree, one gamete is large and immobile; the other gamete is small and mobile. In such cases, the two gametes can be given descriptive names, egg and sperm, and be called *female* and *male*. In certain algae, however, the two gametes are equally mobile and equal in size. Even though we cannot visually distinguish between such gametes, there must be profound structural and genetic differences, because only certain ones will pair. In such cases, the gametes are said to be different mating types and are labeled *plus* and *minus*. Just as two male sperm gametes do not fuse, neither will two plus or two minus gametes fuse.

When two compatible gametes meet, the cytoplasmic contents fuse (**plasmogamy**), and soon the nuclei fuse as well (**karyogamy**) to make a diploid zygote cells. In embryophytes, growth and mitotic divisions convert the zygote into a sheltered embryo and later into a mature sporophyte. In seed plants, the embryo phase is prolonged, with the embryo packaged within a protective seed coat and held in an arrested state of metabolism. Embryos of some species can remain dormant but aline within their seeds for decades or even centuries until the appropriate conditions for germination occur. By contrast, many green algae lack a sporophyte stage, and simply put the zygote through meiosis to start the next gametophyte generation.

Sexual Life Cycles Can Be Heterosporic or Homosporic

To keep the basics simple, Figure 12.6 omits one important way in which plant life cycle differ: some plants make just one kind of spore and gametophyte (they are **homosporic**), whereas others make two kinds of spores and gametophytes (they are **heterosporic**). The distinction is vital to human life, because our food supply depends on plants that, like the cherry tree, make two kinds of spores and gametophytes.

Why is heterospory important? The answer emerges when you consider the advantage that a heterosporic life cycle gives to a plant. Survival of a young plant depends on how good of a head start the parental plant gives to the offspring. To get a good start in life, two things must be done. First the offspring must avoid competition with established plants, which are so much larger; and second, offspring must carry enough stored food to survive until they can make their own food. To avoid competition, it help greatly for the offspring to differ genetically from the parents, so that some of the offspring may be able to exploit opportunities that the parental plants could not. The greatest diversity comes when eggs are fertilized by sperm from different plants--a process called **outcrossing**. Outcrossing is the opposite of **inbreeding**, where eggs and sperm come from close relatives or even from the same plant. One thing that promotes outcrossing is producing vest number of tiny reproductive units that can travel far. However, tiny offspring cannot carry much food and are likely to starve before they become established. As is thus clear, the need for much stored food conflicts with the need for travel.

Heterospory avoids the conflict in a simple way. The plant makes one kind of spore that is tiny enough to be made in huge numbers and carried far away by wind or animals and another kind of spore that is too heavy to travel far but is stuffed with food. Most of the tiny traveling male gametophytes will die of starvation, but when one of them reaches a stationary female gametophyte, the resulting diploid offspring will have a substantial food supply. Heterospory is effective, and most plant species have it. It is important for humans because the seeds that form our basic food supply come from the food-rich female structure, which could not have evolved without the simultaneous presence of tiny mobile male structures--pollen.

Thousands of plant species--most notably mosses and other seedless plants such as ferns--make only one kind of spore and one kind of gametophyte; they are homosporous. All of their spores are too tiny to travel far, and none are important in our food supply, except as emergency foods. Their continued existence does show, however, that homospory is an effective life style in some ecological situations. An example is the growth of mosses on tree trunks and rock, especially in moist cool areas; another example is the prevalence of algae in aquatic and marine environments.

Only One Generation Is Multicellular in Zygotic or Gametic Life Cycles

Plant life cycles vary in which kinds of cells, haploid or diploid, undergo many mitotic divisions to build muticellular bodies. A life cycle is said to be **sporic** if it includes alternating multicellular gametophyte (haploid) and sporophyte (diploid) stages. All embryophytes, such as flowering plants and mosses, have **sporic life cycles**. The same is true of some algae, such as sea lettuce (*Ulva*) and the brown kelps seen on beaches.

Many algae lack sporophytes and have what is called a **zygotic life cycle**. This is the case with the green alga *Chlamydomonas*. As shown in the bottom right corner of Figure 12.7, *Chlamydomonas* gametophytes are single, motile cells commonly found in freshwater habitats. Each cell has a single haploid nucleus. Cells appear to be similar, but genetically they exist as either plus or minus mating types. Occasionally, a gametophyte nucleus will undergo mitosis, producing several haploid spores. The parent cell bursts, releasing these spores, and each spore matures into a new gametophyte cell. Thus, in this case, the gametophyte cells have acted as

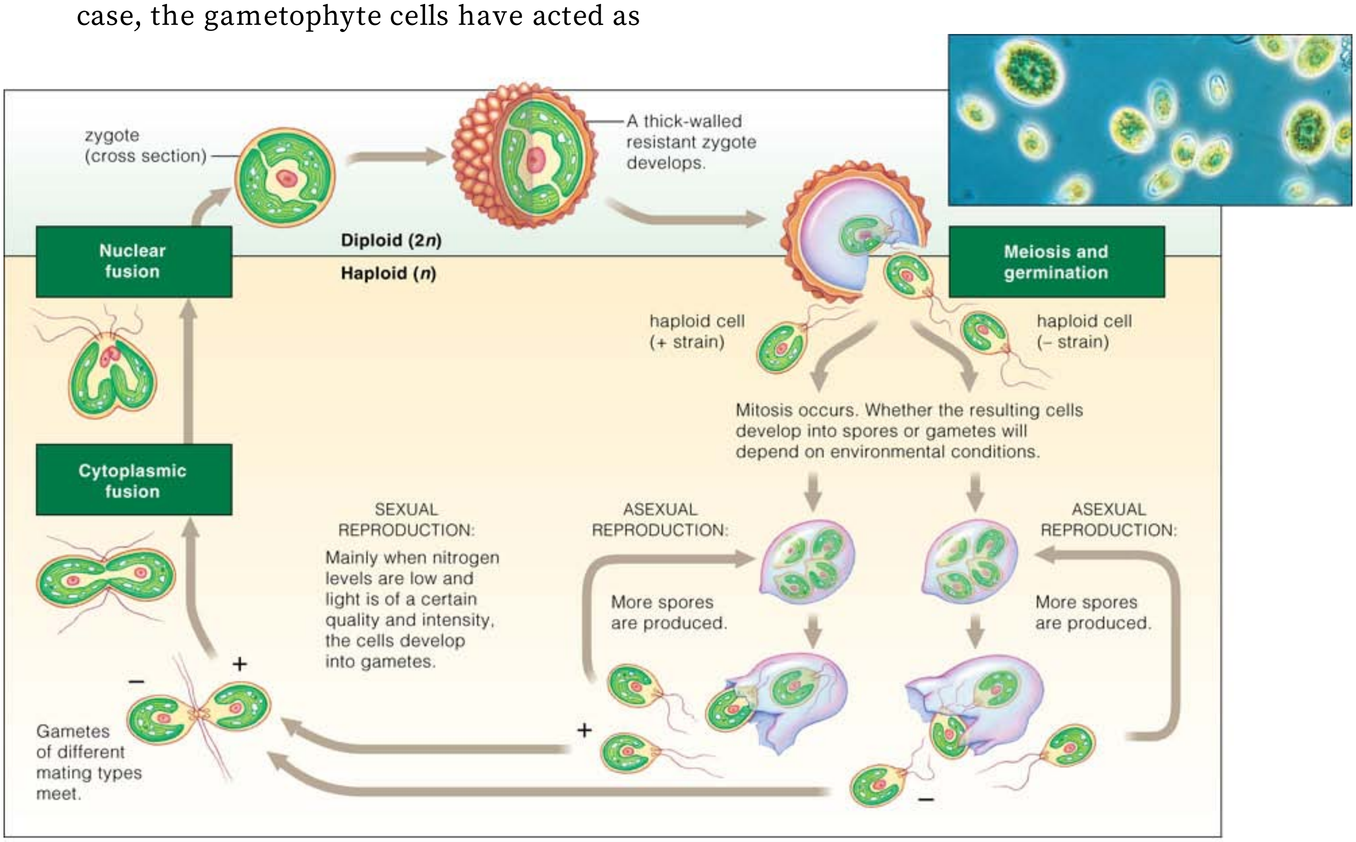

Figure 12.7. Zygotic life cycle of a single-celled species of *Chlamydomonas*, one of the most common green algae of freshwater habitats. *Chlamydomonas* reproduces asexually most of the time. It also reproduces sexually under certain environmental conditions.

mitospores in an asexual part of the life cycle. Under other conditions, one plus and one minus gametophyte cell are attracted to each other in pairs (Fig. 12.7, bottom left). Plasmogamy and karyogamy occur, resulting in a $2n$ zygote cell. In this case, the gametophyte cells have acted as gametes in a sexual part of the life cycle. The zygote may rest in a dormant stage for some time, but it does not develop further through mitotic divisions. The zygote will eventually undergo meiosis (Fig. 12.7 top right) and release haploid cells. Each cell will mature into either a plus or minus gametophyte cell. *Chlamydomonas* has a zygotic life cycle because the only diploid phase is the zygote. There is no multicellular $2n$ phase.

A **gametic life cycle**, such as that of the brown alga rockweed (*Fucus*, Fig. 12.8), begins with a multicellular sporophyte. The sporophyte is relative large and complex, with rootlike, stemlike, and leaflike regions. Within body concavities, special cells enlarge and become sporangia, and their nuclei undergo meiosis. One type of sporangium produces large meiospores, and another type produces small ones. The meiospores are not

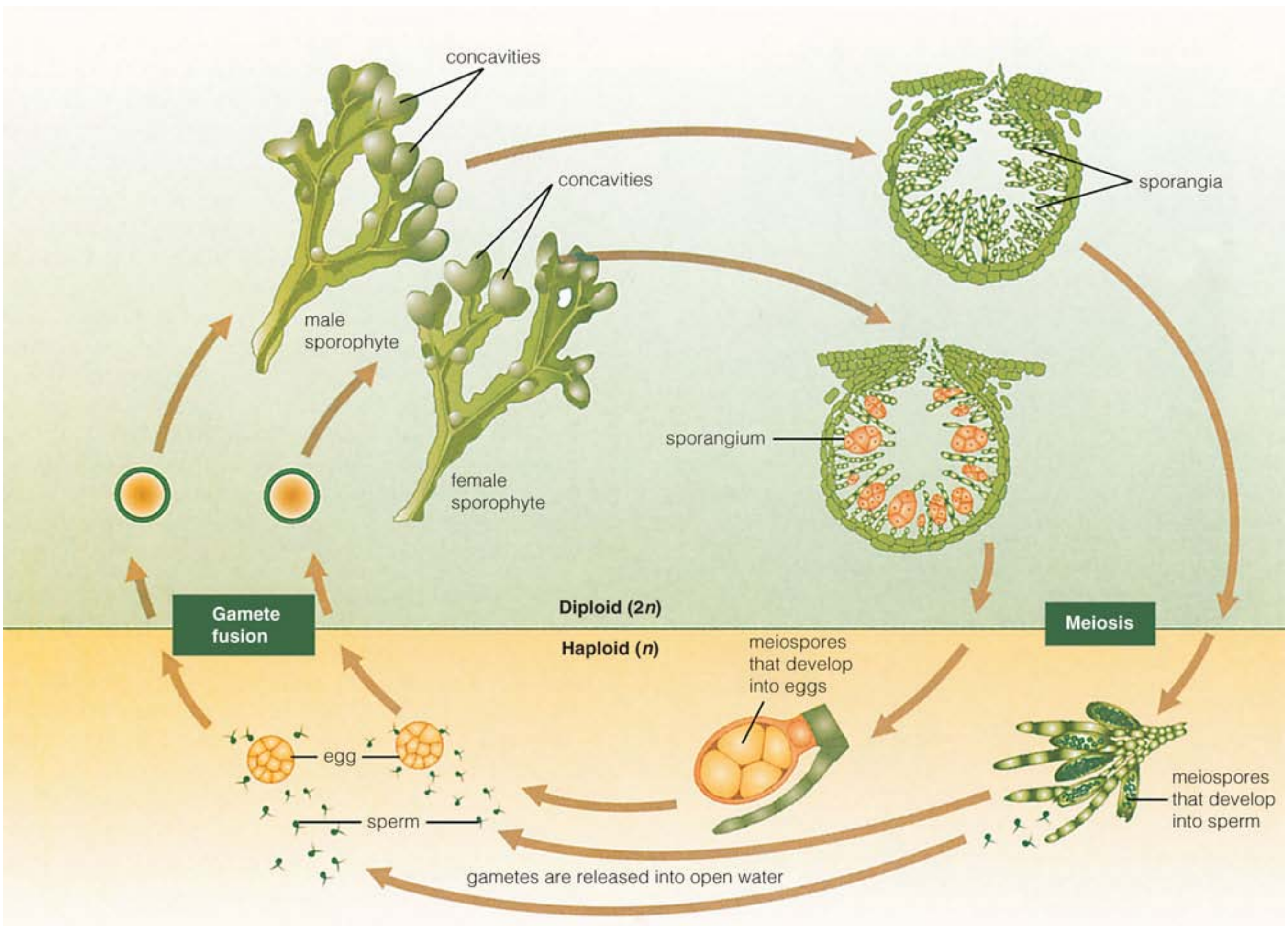

Figure 12.8. Gametic life cycle of the intertidal rockweed *Fucus*. In this life cycle, only the unicellular gametes are haploid.

released from their sporangia at this time. Each large meiospore first differentiates into a female gamete (an egg), and each small meiospore differentiates into a motile male gamete (a sperm). Then the gametes are released into the surf in such huge numbers that many eggs and sperms are brought together. Only eggs from one parent and sperm from another can fuse; eggs and sperm produced by the same plant will not be attracted to each other. Plasmogamy and karyogamy occur, and the zygote immediately begins to divide and grow into a sporophyte. As it enlarges, it sinks to the bottom of the intertidal area, becomes attached to a rock, and then grows to maturity. Fucus has a gametic life cycle because the only haploid phase is a single-celled gamete. There is no multicellular $1n$ phase.

The Diploid Generation Has Become Dominant over Evolutionary Time

The fossil record of algae, fungi, and plants is described in some detail later in this textbook. For the purposes of this chapter, it is sufficient to know that the chronologic appearance of photosynthetic organisms on earth began with algae, followed by mosses and lower vascular plants such as ferns, then by conifers, and last by flowering plants. There are parallel relationships between this evolutionary path and life cycles. Gametic and zygotic life cycles are common among algae but absent from any of the more advanced embryophytes. Sporic life cycles are the rule among the complex, more recently evolved terrestrial plants.

The generations of sporic life cycles are not the same among all terrestrial plants. There is a clear trend of increasing dominance by the sporophyte in groups that are more recent in the fossil record (Fig. 12.9). Dominance here means that the sporophyte lives longer, is larger, is more structurally complex, and is more independent than the gametophyte. There must be advantages, in our modern environment, to protecting and limiting the haploid phase of the life cycle. What could those advantages be?

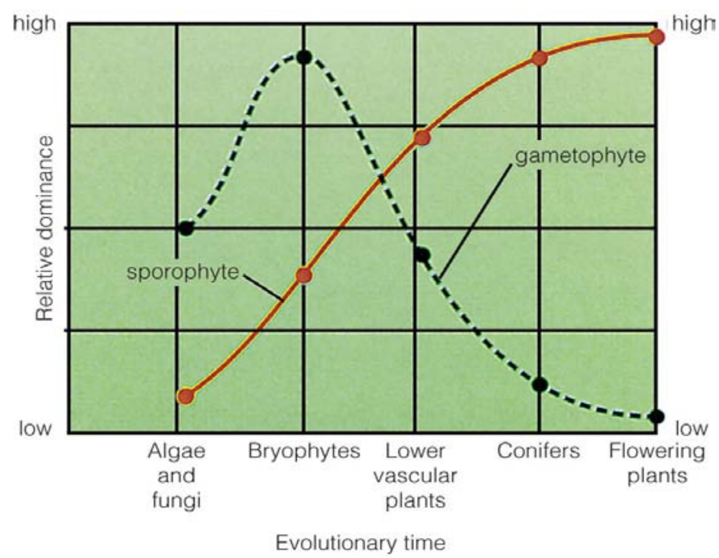

Figure 12.9. Life cycle trends, from the algae and fungi through the flowering plants. The more recently evolved the group and the more adapted it is to dry land, the more dominant is its sporophyte generation. Dominant means larger, more complex, and having a longer life span than the gametophyte generation.

The diploid condition permits many recessive genes to be carried along from generation to generation, each one masked by the dominant gene on the other homologous chromosome. Such recessive genes may have no value in the current environment (indeed, they may even be harmful), but they could be valuable in some different, future environment. The recessive genes carried now could contribute to the species' future success, especially because the genes already exist and do not have to be created (with some lag time) by future mutations. There is however, a potentially unsafe phase in the life cycle for carrying recessive genes, and that is in the gametophyte generation. In the haploid cells of gametophytes, there are no recessive genes because there is only one set of chromosomes. Therefore, every gene that is expressed can influence structure or metabolism in this phase. If, however, the gametophyte is small, simple, short-lived, and protected by the sporophyte, the presence of potentially deleterious genes might be tolerable. Perhaps the ability to be genetically diverse in the diploid chromosome condition is the explanation for the modern dominance of sporophytes on land.

KEY TERMS

1*n*
2*n*
alternation of generations
chromosome set
clone
crossing over
cytokinesis
diploid
egg
embryo
embryophytes
gametangia
gametes
gametic life cycle
gametophyte
green algae
haploid
heterosporic
homologous
homosporic
inbreeding
karyogamy
life cycle
meiosis
meiosporangium
meiospores
mitosis
mitosporangium
mitospores
outcrossing
ovary
ovule
pistil
plasmogamy
pollen grain
pollen sac
pollen tube
pollination
spore
sporic life cycle
sporophyte
synapsis
zygote
zygotic life cycle

SUMMARY

1. Life perpetuates itself through reproduction, the transfer of genetic information from one genration to the next, and this transfer is the definition of life cycle used throughout this textbook. Reproduction can be asexual or sexual.

2. Asexual reproduction produces offspring with the same genetic composition as the parent, because all cells in the offspring descend from the parent by mitosis. Asexual reproduction offers advantages of speed and economy, but the uniformity of asexual offspring can be a disadvantage when diversity is needed to survive changes in the environment.

3. Sexual reproduction involves the union of two haploid cells, called gametes, which are usually produced by two parents. The result is a diploid zygote cell, which may divide mitotically to form a diploid body. Later in the life cycle, a special type of cell division called meiosis forms new haploid cells from diploid cells.

4. Meiosis generates genetic diversity through crossovers exchanging parts of homologous chromosomes and through random division of homologous chromosomes into haploid cell products.

5. Spores are cells that grow into organisms without the need to fuse with another cell. Meiospores are formed by meiosis and contain a haploid set of chromosomes. Mitospores are formed by mitosis and can be haploid or diploid depending on the cells from which they are formed.

6. The formation of alternating diploid and haploid phases is called alternation of generations. Haploid bodies are called gametophytes because they generate gametes. Diploid bodies are called sporophytes because they form spores.

7. The informal term *embryophytes* includes all plants that shelter their diploid offspring as embryos within the parental body. They include all familiar plants of the landscape. The term *plants* also includes green algae, which do not make embryos and are not embryophytes.

8. All embryophytes have sporic life cycles, in which both diploid and haploid cells form multicellular bodies by mitotic cell divisions.

9. Some algae have sporic life cycles with complex sporophytes, but most have zygotic or gametic life cycles. A zygotic life cycle has only a single-celled zygote to represent the sporophyte phase; in the rest of the life cycle the organism is haploid. A gametic life cycle has only single-celled gametes to represent the gametophyte phase; in the rest of the life cycle the organism is haploid.

10. The fossil record reveals that the most recent groups of plants to evolve have sporic life cycles in which the gametophyte generation is smallest and the sporophyte generation is most dominant. That fact suggests that there are advantages to protecting and limiting the haploid phase of the life cycle.

Questions

1. Why do plants reproduce?

2. What are some advantages and disadvantages of asexual and sexual reproduction?

3. What is the key difference between mitosis and the reduction division step of meiosis?

4. What is meant by the expression "alternation of generations?" How could you determine whether an algal cell was a member of a gametic or zygotic generation?

5. Explain why organisms in kingdom Plantae are considered to have a sporic life cycle.

6. Summarize the life cycle of a cherry tree. Describe where meiosis occurs, what the gametophyte plants look like, how the two gametes are brought together to form a diploid zygote, and how the zygote develops back into a cherry tree.

7. Why do you think that the most recently evolved terrestrial plants have life cycles dominated by the diploid (sporophyte) generation, whereas less advanced plants (many green algae) have life cycle that are dominated by the haploid (gametophyte) generation.

Photo Credits

CO http://biology.clc.uc.edu/courses/bio1082l/mosses%20intro.htm
Fig 12.1. (a) Ronald W. Hoham, Dept. of Biology, Colgate University (b) Ripon Microslides Inc.
Fig. 12.2. Thomas L. Rost
Fig. 12.3 and 12.4. Isabelle d'Erfurth, Sylvie Jolivet, Nicole Froger, Olivier Catrice, Maria Novatchkova, Raphaël Mercier **Turning meiosis into mitosis.** PLoS Biol.: 2009, 7(6);e1000124 PMID: 19513101
Fig. 12.5. Art by Raychel Ciemma
Fig. 12.7. Art by Raychel Ciemma; inset: Photo by D.J. Patterson/Seaphot Limited: Planet Earth Pictures
Fig. 12.8. Art by Raychel Ciemma