TWELFTH EDITION

CAMPBELL BIOLOGY URRY · CAIN · WASSERMAN MINORSKY · ORR



## Chapter 38

# Angiosperm Reproduction and Biotechnology

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## How do angiosperms reproduce sexually?

- Angiosperms have adapted mechanisms to attract animal pollinators that help them reproduce sexually by transferring their pollen
  - For example, the flowers of the Ophrys speculum orchid resemble female Dasyscolia ciliata wasps
  - Male wasps are attracted to the flowers and attempt to mate with them, transferring pollen in the process





#### How do angiosperms reproduce sexually?

#### Pollen grain is transferred.



## How do angiosperms reproduce sexually?

- Angiosperms are the most important group of plants in most terrestrial ecosystems
- The cultivation of angiosperms forms the basis for much of agriculture
- Humans have used artificial selection and genetic engineering to modify wild angiosperms into modern crop species

## CONCEPT 38.1: Flowers, double fertilization, and fruits are key features of the angiosperm life cycle

- Plant life cycles are characterized by the alternation between multicellular sporophyte and gametophyte generations
- Sporophytes are diploid (2n) plants that produce haploid spores by meiosis
- Spores divide by mitosis and form gametophytes, which are haploid (n) plants that produce gametes (sperm and eggs) by mitosis

- In angiosperms, the sporophyte is the dominant generation; they are larger, more conspicuous, and longer-lived than gametophytes
- The angiosperm life cycle is characterized by "three Fs": flowers, double fertilization, and fruits

## **Flower Structure and Function**

- Flowers are the reproductive shoots of the angiosperm sporophyte; they attach to a part of the stem called the receptacle
- Flowers consist of four floral organs: carpels, stamens, petals, and sepals
- Stamens and carpels are sporophylls (leaves specialized for reproduction); sepals and petals are sterile modified leaves



## Video: Flower Blooming (Time Lapse)



- A carpel (megasporophyll) has a long style with a sticky stigma on top that captures pollen
- At the base of the style is an ovary containing one or more ovules
- Fertilized ovules produce seeds
- A single carpel or group of fused carpels is called a pistil



- A stamen (microsporophyll) consists of a filament topped by an **anther**
- The anther contains microsporangia (pollen sacs) that produce pollen

- Sepals are structures that resemble leaves; they enclose and protect unopened floral buds
- Petals are typically brightly colored to attract pollinators

- Complete flowers contain all four floral organs
- Incomplete flowers lack one or more floral organs, for example, petals or stamens
- Sterile flowers lack both stamens and carpels; unisexual flowers lack one or the other
- Clusters of flowers are called inflorescences

## **Methods of Pollination**

- In angiosperms, pollination is the transfer of pollen from anthers to stigma
- Pollination can occur by wind, water, or animals
- Wind-pollinated species (e.g., grasses and many trees) release large amounts of smaller-sized pollen
- Most angiosperm species depend on animal pollinators to transfer pollen directly between flowers

## Figure 38.4 Exploring Flower Pollination

## **Abiotic Pollination by Wind**

- About 20% of angiosperm species are windpollinated
  - For example, grasses and many trees are windpollinated
- Wind-pollinated angiosperms tend to produce small, inconspicuous flowers that lack nectar or scent and release large amounts of pollen

#### Abiotic Pollination by Wind



Hazel staminate flowers (stamens only) releasing clouds of pollen

## **Pollination by Bees**

- About 65% of all angiosperms require insects for pollination
- Bees are the most important insect pollinators, and there is concern that their populations are declining
- Bee-pollinated flowers are typically brightly colored, primarily yellow or blue, and have a sweet fragrance
- "Nectar guides" are markings that direct insects to the nectar-producing glands

#### **Pollination by Bees**



Common dandelion under normal light



Common dandelion under ultraviolet light

## **Video: Bee Pollination**



## Video: Bee Colony Decline



## Pollination by Moths and Butterflies

- Flowers pollinated by moths and butterflies produce sweet fragrances
- Butterfly-pollinated flowers are brightly colored; moth-pollinated flowers are usually white or yellow



### Moth on yucca flower

## **Pollination by Flies**

- Many fly-pollinated flowers look and smell like rotten meat
- Flies mistake the flower for a rotting corpse and lay their eggs on it
- Pollen is transferred in the process, but the fly larvae will have no carrion to eat when they hatch



# Blowfly on carrion flower

## **Pollination by Bats**

 Bat-pollinated flowers are light-colored and aromatic



## Long-nosed bat feeding on agave flowers at night

## Video: Bat Pollinating Agave Plant



## **Pollination by Birds**

- Bird-pollinated flowers are usually large and bright red or yellow, have little odor, and produce large quantities of nectar
- The petals of bird-pollinated flowers are often fused into a floral tube that fits the curved beak of the bird



#### Hummingbird drinking nectar of columbine flower

- Coevolution is the joint evolution of two or more interacting species in response to selection imposed by each other
- The shapes and sizes of flowers often correspond to the pollen-transporting parts of their animal pollinators
  - For example, Darwin correctly predicted a moth with a 28-cm-long tongue based on the morphology of a particular flower



- Climate change may be affecting long-standing relationships between plants and animal pollinators
  - For example, flowers requiring long-tongued pollinators have declined under warmer conditions in the Rocky Mountains
  - Selective pressure has consequently favored bees with shorter tongues

## The Angiosperm Life Cycle: An Overview

- The angiosperm life cycle includes
  - Gametophyte development
  - Sperm delivery by pollen tubes
  - Double fertilization
  - Seed development
- Gametophytes have evolved to become reduced in size and wholly dependent on the sporophyte for nutrients
- Angiosperm gametophytes are microscopic, and their development is obscured by protective tissues



# Video: Flowering Plant Life Cycle (Time Lapse)





### **Animation: Angiosperm Life Cycle**



Angiosperm Life Cycle



# Animation: Sexual Reproduction in Angiosperms



# Development of Female Gametophytes (Embryo Sacs)

- The embryo sac, or female gametophyte, develops within the ovule
- Within an ovule, two integuments surround a megasporangium, except at a gap called the micropyle

- One cell in the megasporangium enlarges and undergoes meiosis, producing four megaspores, only one of which survives
- The megaspore divides without cytokinesis, producing one large cell with eight haploid nuclei
- This cell is partitioned into a multicellular female gametophyte, the embryo sac

- Near the micropyle, two synergid cells flank the egg and help guide the pollen tube
- Three antipodal cells of unknown function are found at the opposite end of the embryo sac
- The other two nuclei, the polar nuclei, share the cytoplasm of the central cell
- The complete ovule consists of the embryo sac, enclosed by the megasporangium and surrounded by two integuments

# Development of Male Gametophytes in Pollen Grains

- Pollen develops within the microsporangia, or pollen sacs, of anthers
- Diploid microsporocytes undergo meiosis to produce four haploid microspores
- Each microspore undergoes mitosis to produce two haploid cells: the generative cell and the tube cell
- A pollen grain consists of this two-celled male gametophyte and the spore wall
- The generative cell will pass into the tube cell

# Sperm Delivery by Pollen Tubes

- After landing on a receptive stigma, a pollen grain absorbs water and germinates by producing a pollen tube
- The pollen tube grows down into the ovary, and discharges two sperm cells near the embryo sac

### **Double Fertilization**

- Fertilization, the fusion of gametes, occurs after the two sperm reach the female gametophyte
- One sperm fertilizes the egg, forming the zygote
- The other sperm combines with the two polar nuclei, giving rise to the triploid (3n), food-storing endosperm
- This double fertilization ensures that endosperm only develops in ovules containing fertilized eggs

#### **Animation: Plant Fertilization**



### Seed Development

- After double fertilization, each ovule develops into a seed
- The ovary develops into a fruit, which encloses the seed and aid in dispersal by wind or animals
- When a seed germinates, the embryo develops into a new sporophyte

#### **Seed Development and Structure**

- After pollination and double fertilization, both the endosperm and the embryo develop within the forming seed
- A mature seed consists of a dormant embryo surrounded by stored food and protective layers

#### Endosperm Development

- Endosperm development usually precedes embryo development
- In most monocots and many eudicots, endosperm stores nutrients that can be used by the seedling
- In other eudicots, the food reserves of the endosperm are exported to the cotyledons (seed leaves)

### Embryo Development

- The first mitotic division of the zygote is asymmetrical, splitting it into a large basal cell and a small terminal cell
- The basal cell produces a suspensor, which anchors the embryo to the parent plant
- The suspensor also helps transfer nutrients from the parent plant to the embryo

- The terminal cell divides to form a proembryo (early embryo) that is attached to the suspensor
- The cotyledons form as bumps on the proembryo, forming a heart-shape
- The embryo elongates after cotyledon appearance
- The embryonic shoot apex forms between the cotyledons; the embryonic root apex forms near the suspensor attachment



# Animation: Embryo and Endosperm Development



#### Structure of the Mature Seed

- The embryo and its food supply are enclosed by a hard, protective seed coat
- The seed dehydrates and enters a state of dormancy
- A mature seed is only about 5–15% water

- In some eudicots, such as the garden bean, the embryo consists of the embryonic axis attached to two fleshy cotyledons
- Below the cotyledons, the embryonic axis is called the hypocotyl and terminates in the radicle (embryonic root)

- Above the cotyledons and below the first pair of leaves, the embryonic axis is called the epicotyl
- The *plumule* comprises the epicotyl, young leaves, and shoot apical meristem





(b) Maize, a monocot

- The cotyledons of garden beans absorb the carbohydrates from the endosperm during seed development
- The seeds of other eudicots, such as castor beans, retain food resources in the endosperm and have thin cotyledons

- Monocot embryos have only one cotyledon
- Grasses, such as maize and wheat, have a specialized cotyledon called a scutellum
- The scutellum absorbs nutrients from the endosperm during germination

- Two sheathes enclose the embryo of a grass seed: a coleoptile covering the young shoot and a coleorhiza covering the young root
- Both structures aid in soil penetration after germination



(b) Maize, a monocot

# Seed Dormancy: An Adaptation for Tough Times

- The breaking of seed dormancy often requires a specific environmental cue
  - For example, the seeds of desert plants only germinate after rainfall
  - In areas where fires are common, intense heat or smoke may be required
  - Where winters are harsh, a period of cold may be required prior to germination
  - Some must pass through the digestive system of an animal before breaking dormancy

- Seed dormancy increases the chances that germination will occur at a time and place most advantageous to the seedling
- Most seeds remain viable for one or two years after dormancy, but some last days while others are viable for centuries

# Sporophyte Development from Seed to Mature Plant

- Seed dormancy breaks when environmental conditions are conducive for growth
- Germination is followed by growth of stems, leaves, and roots and eventually by flowering

# Seed Germination

- Germination depends on **imbibition**, the uptake of water due to the low water potential of the dry seed
- The radicle (embryonic root) emerges first; the developing root system anchors the plant and provides water for cell expansion
- Next, the shoot tip breaks through the soil surface

- In many eudicots, a hook forms in the hypocotyl, and growth pushes the hook above ground
- Light causes the hook to straighten and pull the cotyledons and shoot tip up



(a) Common garden bean

 In some monocots, the coleoptile pushes up through the soil, creating a tunnel for the shoot tip to grow through



#### **Animation: Seed Germination**


#### **Growth and Flowering**

- Flowers are typically synchronized to appear at a specific time of the year
- This promotes outbreeding—reproduction between two genetically distinct individuals
- Flowering is triggered by a combination of environmental cues and internal signals
- A developmental switch from vegetative to reproductive growth occurs in the apical meristem

#### **Fruit Structure and Function**

- A fruit is the mature ovary of a flower
- Fruit protects the enclosed seeds and aids in seed dispersal by wind or animals
- Fruit only develops in response to hormonal changes triggered by fertilization
- In some fruits, the ovary wall dries out at maturity; in others the ovary wall remains fleshy



- Fruits are classified based on their developmental origin
  - Simple fruits develop from a single or several fused carpels
  - Aggregate fruits result from a single flower with multiple separate carpels
  - Multiple fruits develop from a group of flowers called an inflorescence
  - Accessory fruits contain other floral parts in addition to ovaries



- A fruit usually ripens at the same time that the seeds complete development
- In dry fruits, ripening involves aging and drying of tissues
- Fleshy fruits change from green to another contrasting color, and sugar is produced to attract animal dispersers

#### **Animation: Fruit Development**



 Fruit dispersal by wind, water, or animals ensures that seeds germinate away from the competitive influence of the parent plant

#### **Dispersal by Water**

Coconut seed embryo, endosperm, and endocarp inside buoyant husk



**Dispersal by Wind** 





Dandelion "seeds" (actually one-seeded fruits)



Winged fruit of a maple



Tumbleweed

# Figure 38.12 Exploring Fruit and Seed Dispersal Dispersal by Water

 Some buoyant seeds and fruits can survive months or years at sea



Coconut seed embryo, endosperm, and endocarp inside buoyant husk

#### **Dispersal by Wind**

- Winged fruits glide or spin through the air
- Tumbleweeds break off at the ground and tumble across the terrain, scattering their seeds
- Some fruits float through the air attached to umbrella like "parachutes" made of branched hairs



#### Giant seed of the tropical Asian climbing gourd Alsomitra macrocarpa



#### Winged fruit of a maple



### Tumbleweed



#### Dandelion "seeds" (actually one-seeded fruits)

#### **Dispersal by Animals**

- Some dry fruits are adapted to attach to the skin or fur of passing animals
- Others, are collected and buried in the underground caches of animals, such as squirrels
- Edible fruits are broken down in the digestive system of animals and the seeds are dispersed in their feces
- Some seeds have "food bodies" rich in fatty acids, amino acids, and sugars that are collected by ants



## Fruit of the puncture vine (Tribulus terrestris)



#### Seeds dispersed in black bear feces



### Squirrel hoarding seeds or fruits underground



### Ant carrying seed with attached "food body"

### CONCEPT 38.2: Flowering plants reproduce sexually, asexually, or both

- Asexual reproduction produces offspring from a single parent without the fusion of egg and sperm
- The offspring is a clone, genetically identical to the parent
- Asexual reproduction is common in angiosperms and other plants

#### **Mechanisms of Asexual Reproduction**

- Many species reproduce asexually through fragmentation, separation of a parent plant into parts that develop into whole plants
- In other species, a parent plant's root system gives rise to adventitious shoots that become separate shoot systems

Figure 38.13



- Apomixis, the asexual production of seeds from a diploid cell, has evolved in dandelions and some other plants
- These plants produce asexual clones but also have the advantage of seed dispersal

### Advantages and Disadvantages of Asexual and Sexual Reproduction

- Asexually reproducing plants do not require pollinators or nearby individuals of the same species to produce offspring
- All progeny are genetically identical to the parent, whereas sexually produced offspring only share half their DNA with each parent
- This can be beneficial to a successful plant in a stable environment

- When asexual progeny arise from mature vegetative fragments, it is called vegetative reproduction
- These progeny are more resilient than the fragile seedlings that germinate from seeds
- Production of enormous numbers of seeds compensates for odds against individual survival

- The lack of genetic variation among asexually producing plants makes them vulnerable to local extinction if there is an environmental change
- Sexual reproduction generates genetic variation that makes evolutionary adaptation possible
- Seed production also facilitates long distance dispersal to escape catastrophic environmental change

- Some plants can self-fertilize to ensure that every ovule will develop into a seed
- However, this process of "selfing" reduces genetic diversity among offspring
- Many species have evolved mechanisms to prevent selfing

#### **Mechanisms That Prevent Self-Fertilization**

- Many angiosperms have mechanisms that make it difficult or impossible for a flower to self-fertilize
- Some species have staminate flowers (lacking carpels) and carpellate flowers (lacking stamens) on different individuals to prevent self-fertilization



(a) Staminate flowers (left) and carpellate flowers (right) of a dioecious species

- Some species prevent self-fertilization by having stamens and carpels that mature at different times
- Others spatially arrange the stamens are carpels to prevent contact between the stamens and the stigma



#### Thrum flower (b) Thrum and pin flowers

**Pin flower** 

- Self-incompatibility, a plant's ability to reject its own pollen or the pollen of close relatives, is the most common mechanism to avoid selfing
- Analogous to the animal immune response, cells of "self" can be distinguished from those of "nonself"
- In contrast, self-incompatibility in plants is rejection of self, whereas the animal immune response rejects nonself

- Recognition of "self" pollen is based on S-genes, which can have dozens of alleles in a population
- Some plants reject pollen that have the same Sgene allele that is present in their own stigma cells
- There are two types of self-incompatibility: gametophytic and sporophytic

- In gametophytic self-incompatibility, the S-allele in the pollen genome governs blocking of fertilization
- By this mechanism, a pollen grain cannot fertilize eggs from a flower with the same S-allele as itself
  - For example, an  $S_1$  pollen grain from an  $S_1S_2$  flower cannot fertilize the eggs of an  $S_1S_2$  flower, but it can fertilize the eggs of an  $S_2S_3$  flower
- In sporophytic self-incompatibility, fertilization is blocked by incompatibility between S-gene products of the sporophyte tissue
- A pollen grain cannot fertilize a flower that shares either of the S-alleles present in the parental sporophyte that produced the pollen grain
  - For example, an  $S_1$  pollen grain from an  $S_1S_2$  flower cannot fertilize the eggs of either an  $S_1S_2$  flower or an  $S_2S_3$  flower

- Research on self-incompatibility has agricultural applications
- Hybridization of different genetic strains can help counter the loss of vigor resulting from inbreeding
- This process is hindered by the labor involved in mechanically removing anthers to prevent selfing
- Genetically engineering self-incompatibility into crop plants could help overcome this limitation

## Totipotency, Vegetative Reproduction, and Tissue Culture

- Totipotent cells, those that can divide and asexually generate a clone of the original organism, are common in plants
- Humans have devised methods to clone plants using totipotent cells

#### Vegetative Propagation and Grafting

- Vegetative reproduction that is facilitated or induced by humans is called vegetative propagation
- Many domesticated plants are asexually reproduced from plant fragments called cuttings
- A callus, a mass of dividing, undifferentiated totipotent cells, forms where a stem is cut and produces adventitious roots

- The shoot of one plant can be grafted onto the stem of another plant to combine the best qualities of different species or varieties in one plant
- The stock provides the root system; the scion is the twig that is grafted onto the stock
  - For example, a scion from a vine that produces superior wine grapes can be grafted onto the stock of a variety more resistant to soil pathogens

#### **Test-Tube Cloning and Related Techniques**

- Plant biologists have adopted *in vitro* methods to create and clone novel plant varieties
- A callus of undifferentiated totipotent cells can sprout shoots and roots in response to plant hormones



- Some pathogenic viruses can be eliminated by excising virus-free apical meristems for tissue culture
- Plant tissue culture also facilitates the production of genetically modified (GM) plants

# CONCEPT 38.3: People modify crops by breeding and genetic engineering

- Domestication of most crops occurred over a short period about 10,000 years ago through artificial selection by humans for favorable traits
  - For example, maize has been artificially selected to have kernels permanently attached to the "cob," which is protected by the leaves of the "husk"
  - It would quickly go extinct in the wild because it cannot spread its seeds



### **Plant Breeding**

- Plant breeders search the world for wild or domesticated plants with desirable traits
- New, desirable traits can arise spontaneously through mutation, but natural mutation rates are slow
- Breeders can induce mutations for research rapidly by treating seeds or seedlings with radiation or chemicals

- In traditional plant breeding, wild plants with beneficial traits are crossed with a domesticated variety
- Progeny are repeatedly selected for the favorable trait and crossed back to the domesticated variety to remove any traits undesirable for agriculture

- Some breeding methods rely on hybridization between distant species of the same genus
- Often, the embryos are not viable, but can be rescued by removing them from the ovule and culturing them *in vitro*

- Natural genetic modification of plants occurred long before humans began using artificial selection to modify crops
  - For example, wheat evolved by natural hybridization between different species of grasses

- The introduction of a transgene, a gene transferred from one organism to another, can also occur in nature
  - For example, an early ancestor of modern sweet potato (*Ipomea batatas*) received a horizontal gene transfer from the soil bacterium *Agrobacterium*

#### **Plant Biotechnology and Genetic Engineering**

- Plant biotechnology has two meanings
  - In a general sense, it refers to innovations in the use of plants to make useful products
  - In a specific sense, it refers to use of genetically modified (GM) organisms in agriculture and industry
- CRISPR-Cas9 gene-editing technology is rapidly changing plant biology

- Modern plant biotechnologists are not limited to the transfer of genes between closely related species
- With genetic engineering, genes can be directly transferred between species as distantly related as daffodils and rice, without the need for intermediates

#### **Reducing World Hunger and Malnutrition**

- Global hunger currently affects nearly a billion people; food production will have to increase by 40% per hectare by 2030 to feed our growing population
- Plant biotechnology can help address this problem by increasing crop yields and the quality of food without expanding agricultural lands

- One approach to increasing yields is to genetically modify crops to resist feeding by pests
- Some transgenic crops have been developed to produce the *Bt* toxin, which is toxic to insect pests but not vertebrates



Non-Bt maize

#### Bt maize

- Biofortification, improving the nutritional quality of plants, is another strategy to combat world hunger
  - For example, "Golden Rice" is a transgenic variety being developed to address vitamin A deficiencies among the world's poor
  - In 2018, Golden Rice received positive food safety evaluations from the governments of Canada, New Zealand, and the United States

- Cassava, a starchy root crop, is a major source of carbohydrates for 800 million of the world's poor
- Transgenic, biofortified cassava has been developed with increased levels of iron and betacarotene and reduced cyanide-producing chemicals



- Engineering plants with enhanced resistance to disease is another strategy for increasing crop yields
  - For example, transgenic papaya was developed to be resistant to a ringspot virus, thereby saving the papaya industry

- Some transgenic crops are resistant to the herbicide glyphosate
- Overuse has resulted in the evolution of glyphosate resistance in many weed species
- Glyphosate may also have negative effects on the health of humans and livestock by interfering with beneficial gut bacteria

#### Reducing Fossil Fuel Dependency

- Burning fossil fuels contributes to global warming by releasing the greenhouse gas CO<sub>2</sub>
- Biofuels—fuels derived from living biomass—could meet much of the world's energy needs in the future
- **Biomass** is the total mass of organic matter in a group of organisms in a particular habitat

- Biofuels can be produced by rapidly growing crops, such as switchgrass and poplar
- These crops take up CO<sub>2</sub> during photosynthesis to balance out that which is released when they are burned, creating a carbon neutral cycle

- Plant biomass is not burned directly in biofuels; polymers in the cell walls, such as cellulose, are broken down into sugars by enzymatic reactions
- The sugars are fermented into alcohol and distilled to yield biofuels
- Genetically engineering plant cell walls could increase the efficiency of this process

- Some biologists are concerned about risks of releasing GM organisms (GMOs) into the environment
- One concern is that the introduction of novel organisms into the biosphere is an unstoppable "experiment"

#### Issues of Human Health

- Some biologists are concerned about risks of releasing GM organisms (GMOs) into the environment
- One concern is that the introduction of novel organisms into the biosphere is an unstoppable "experiment"

- Some GMOs have health benefits
  - For example, maize that produces the *Bt* toxin has reduced infection by *Fusarium*, a fungus that produces a cancer-causing toxin
  - Bt maize contains 90% less of the cancer-causing toxin than non-Bt corn

 Widespread adoption of *Bt* cotton in India has led to a 41% decrease in insecticide use and an 80% reduction in acute poisoning cases in farmers

#### **Possible Effects on Nontarget Organisms**

- Many ecologists are concerned that GM crops may have unforeseen effects on nontarget organisms
  - A study showing that pollen from *Bt* maize had negative effects on monarch butterfly larvae has been discredited
  - In fact, spraying chemicals on non-*Bt* maize is much more harmful to monarch butterflies than *Bt* maize production

#### Addressing the Problem of Transgene Escape

- Perhaps the most serious concern is the possibility of introduced genes escaping into related weeds through crop-to-weed hybridization
- This could result in "superweeds" that would be resistant to many herbicides

- Efforts are underway to prevent this by introducing
  - Male sterility
  - Apomixis
  - Transgenes into chloroplast DNA (not transferred by pollen)
  - Genetic modification to prevent flowers from opening, forcing strict self-pollination


## Data from the Experiment

Species	Nectar Volume (µL)	Nectar Concentration (% weight of sucrose/ total weight)	Seeds per Flower	Visits per Flower	Rooted Branches per Gram Shoot Weight
M. rupestris	4.93	16.6	2.2	0.22	0.673
M. eastwoodiae	4.94	19.8	25	0.74	0.488
M. nelsonii	20.25	17.1	102.5	1.08	0.139
M. verbenaceus	38.96	16.9	155.1	1.26	0.091
M. cardinalis	50.00	19.9	283.7	1.75	0.069

Data from S. Sutherland and R. K. Vickery, Jr., Trade-offs between sexual and asexual reproduction in the genus Mimulus, Oecologia 76:330-335 (1998).



One sperm cell will fuse with the two polar nuclei, forming an endosperm nucleus (3*n*).

