Seed Development

Chapter 4

Hartmann and Kester's Plant Propagation Principles and Practices 8e
Hudson Hartman, Dale Kester, Fred Davies and Robert Geneve

INTRODUCTION

- Propagation by seeds is the major method by which plants reproduce in nature, and one of the most efficient and widely used propagation methods for cultivated crops.
  - Plants produced from seeds are referred to as **seedlings.**
  - Sowing seeds is the physical beginning of seedling propagation.
- The seed itself, however, is the end product of a process of growth and development within the parent plant.

REPRODUCTIVE LIFE CYCLES OF VASCULAR PLANTS

- Seedless Vascular Plants
- Seed Plants

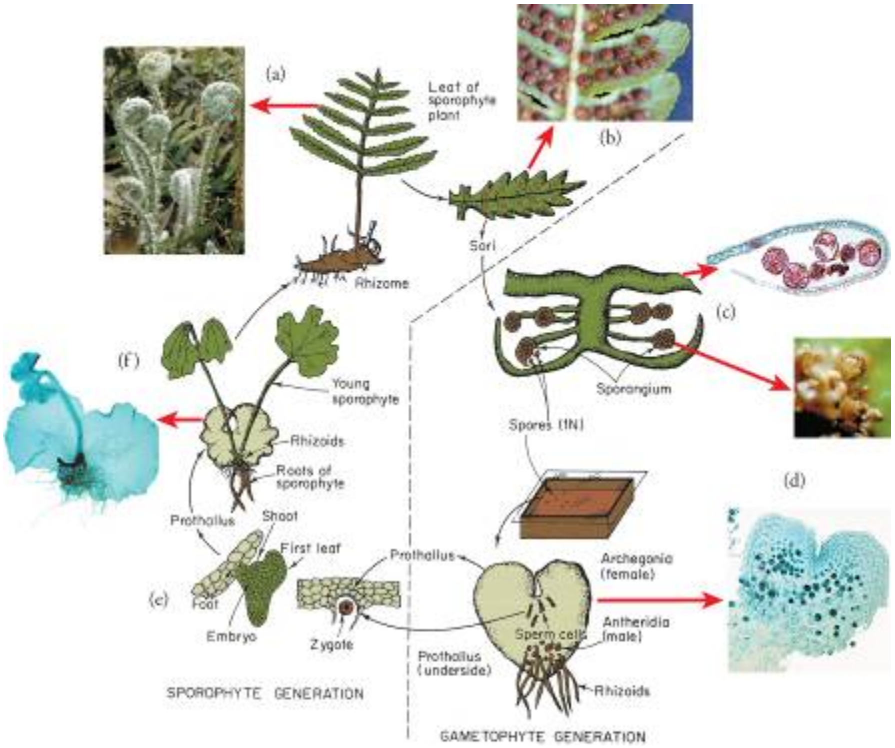


Figure 4–1 A representative fern life cycle includes alternate sporophytic and gametophytic generations. (a) A mature fern sporophyte produces fronds that typically produce (b) sori (spore producing structures) on the underside of the leaf-like frond. (c) Within the sori are sporangia that contain the spores that initiate the gametophytic gerneration. (d) When the spore germinates it produces a leaf-like gametophyte called the prothallus. On the prothallus, several female archegonia and many male antheridia are formed. (e) Fertilization occurs when the male sperm unites with the female egg within the archegonium. (f) The resultant young sporophyte becomes the long-lived fern. Adapted from Linda R. Berg. 1997. Introductory Botany. Saunders College Publishing.

REPRODUCTIVE LIFE CYCLES OF VASCULAR PLANTS

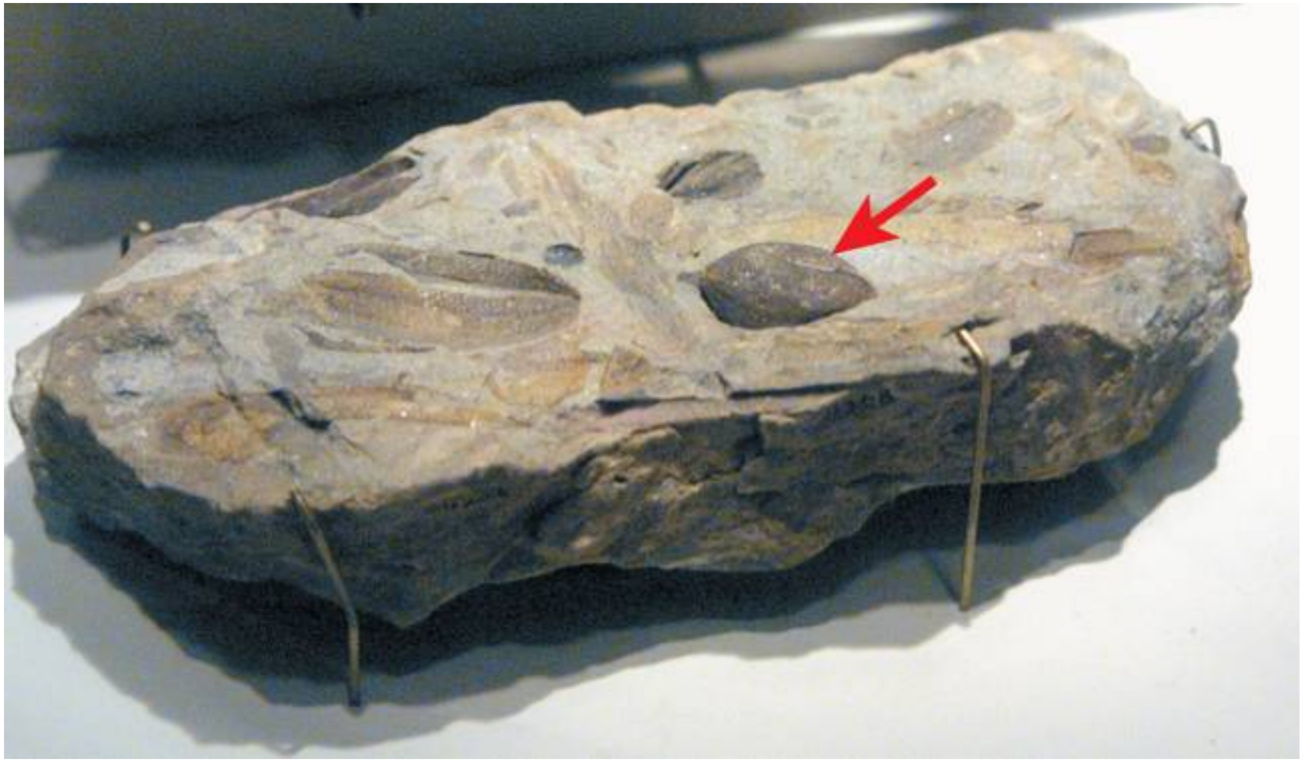


Figure 4–2 Seed-producing plants evolved approximately 360 million years ago, but most were not successful and became extinct. Progymnosperms developed seeds enclosed within a cupule (arrow) and are thought to be the progenitors of the gymnosperms.

REPRODUCTIVE LIFE CYCLES OF VASCULAR PLANTS

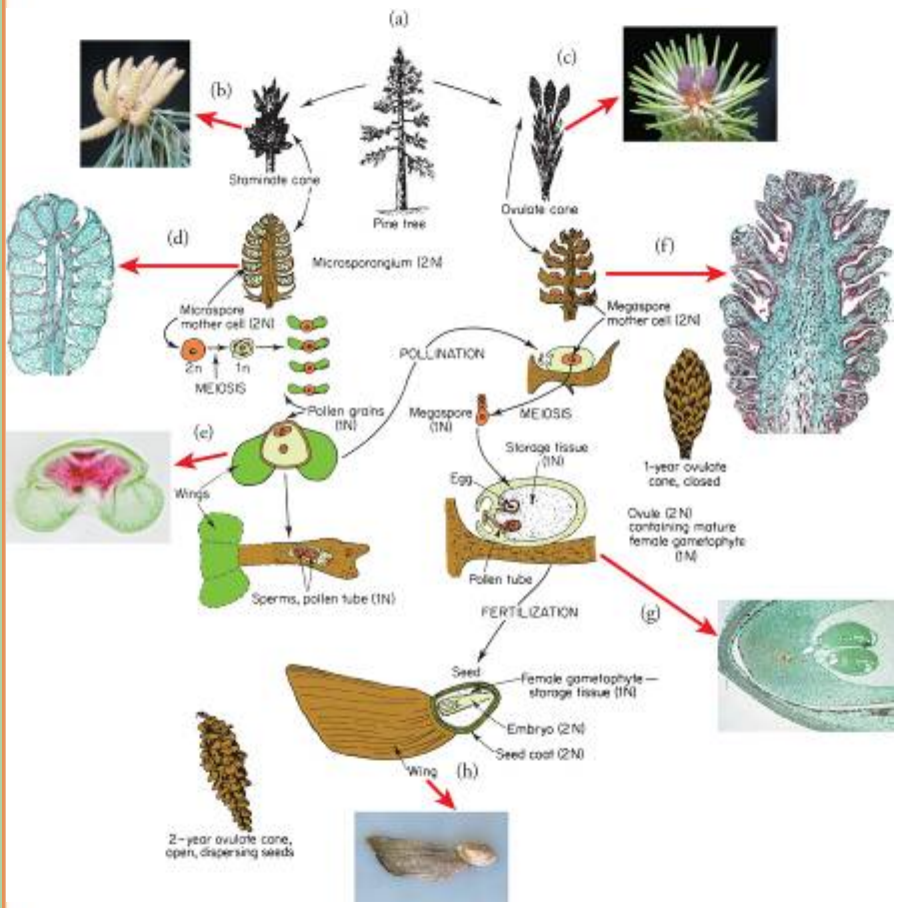


Figure 4–3 A representative gymnosperm life cycle. (a) A pine tree is a mature sporophyte. It produces separate male (b) and female (c) reproductive structures. The male gametophytes are produced in a (d) staminate cone as winged pollen grains (e) spread by the wind. The female gametophyte is produced within the female ovulate cone (f). The female egg cell (g) is fertilized by the male sperm to produce a seed (h)—the next sporophytic generation.

REPRODUCTIVE LIFE CYCLES OF VASCULAR PLANTS

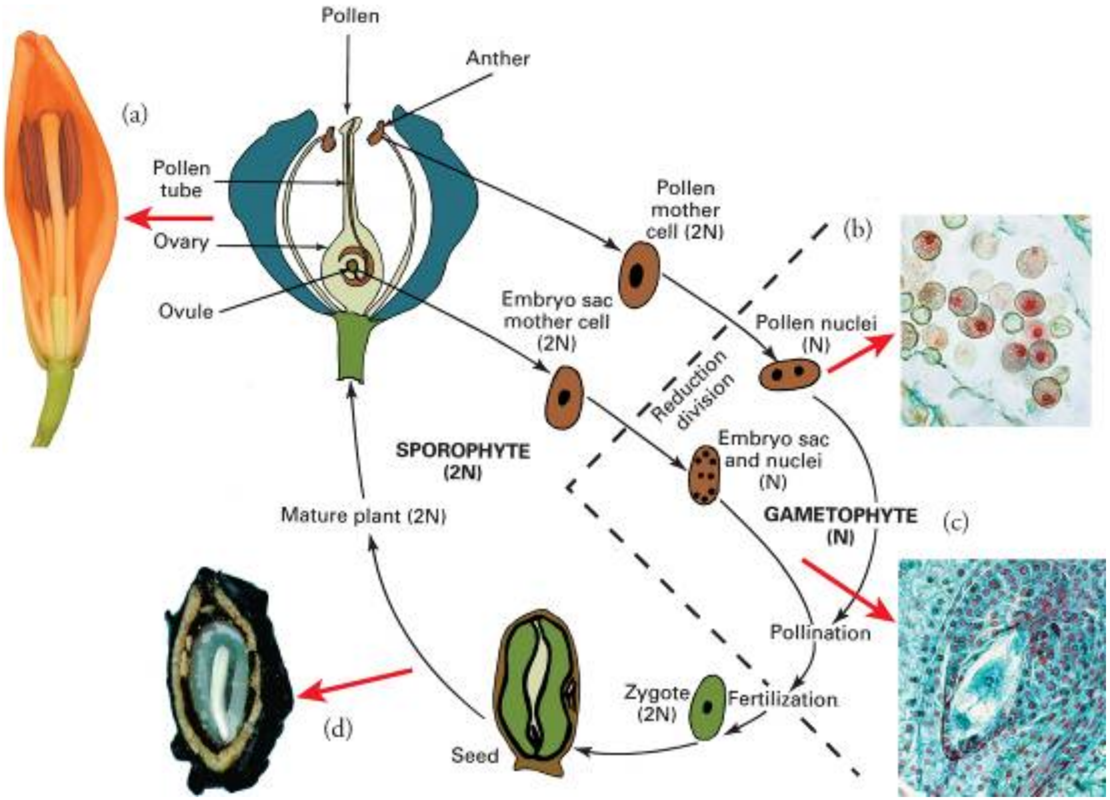


Figure 4–4 A representative angiosperm life cycle. (a) Flowers are formed during the sporophytic generation. In the gametophytic generation, (b) male gametophytes are produced within the anther as pollen grains and (c) the female gametophyte is produced in the ovule within the ovary. (d) The seed is formed following male and female gamete fusion (fertilization), which reinitiates the sporophytic generation.

CHARACTERISTICS OF A SEED

- A **seed** (20, 21) is a matured ovule containing an embryo, storage reserve tissue, and a protective outer covering (Figs. 4–5, 4–6, page 115).
  - Seeds are the sexual reproductive unit in a plant.

CHARACTERISTICS OF A SEED

- Embryo
- Storage Reserves
- Protective Seed Coverings

CHARACTERISTICS OF A SEED

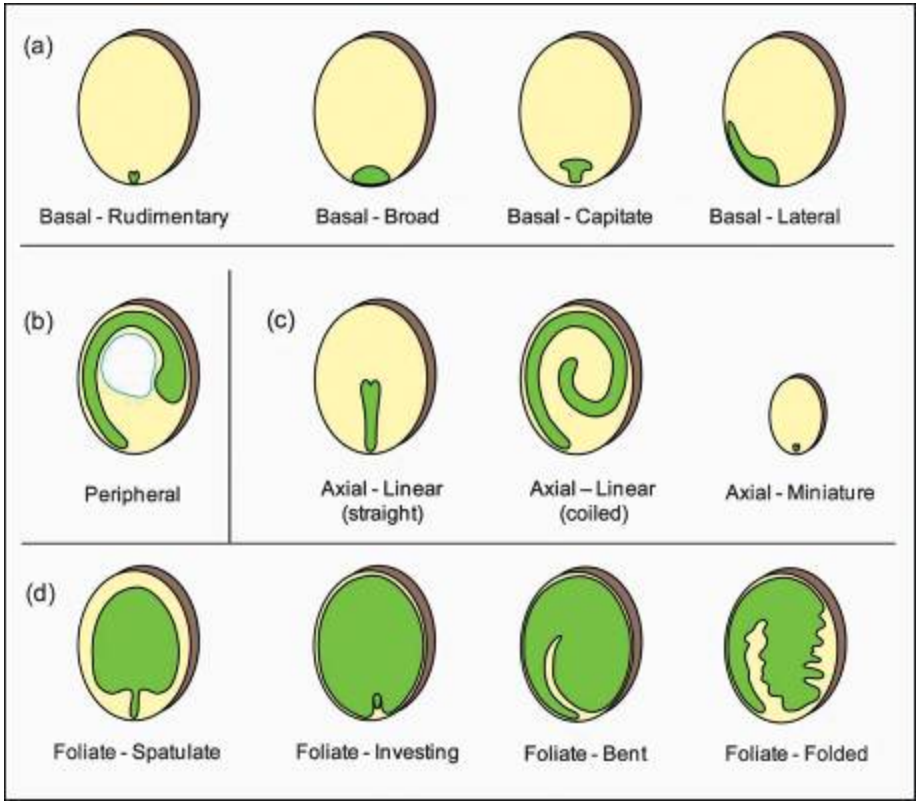


Figure 4–5 The basic embryo types found in seeds. Major forms include: (a) Basal embryos that have a high endosperm to embryo ratio. This is considered a more primitive evolutionary condition; (b) Peripheral embryos surround and inner mass of perisperm storage tissue; (c) Axial embryos occupy the center of the seed and contain a significant amount of endosperm; and (d) Foliate embryos where the cotyledons develop to occupy most of the seed and function as storage reserve tissue. Color codes for these images have the embryo in green, endosperm in yellow, perisperm in white, and seed coverings are brown. Adapted from Martin, A. C. 1946.

CHARACTERISTICS OF A SEED

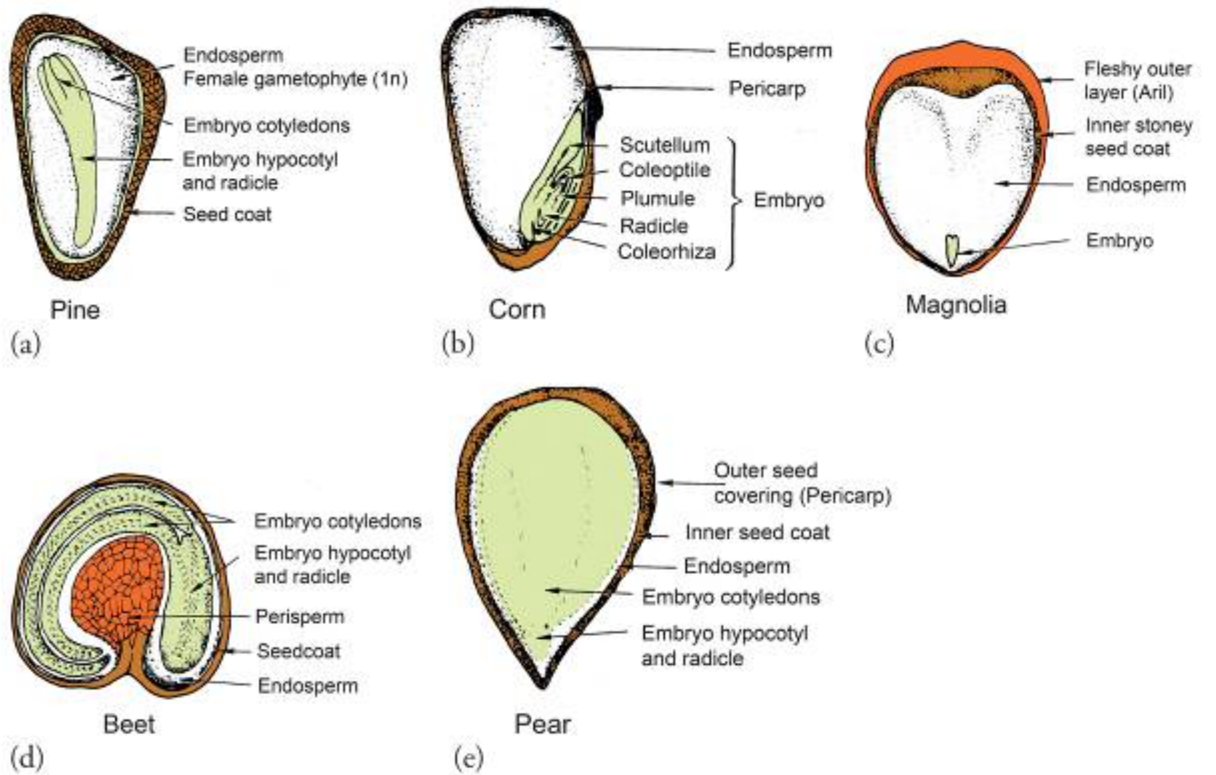


Figure 4–6 Representative seed morphologies. (a) Gymnosperm (conifer) seeds have embryos with multiple cotyledons and use the female gametophyte as reserve material. (b) Corn is an example of a monocot in the grass family. It has a peripheral embryo and a large endosperm reserve. The outer protective layer is fruit tissue—pericarp. (c, d, and e) Each of the representative dicots has embryos with two cotyledons. Magnolia has a small embryo and a large endosperm reserve. The fleshy outer covering is an aril derived from the funiculus. Beet seeds have a curved embryo and utilize perisperm derived from nucellar tissue. In pear, the cotyledons fill the seed and are used for storage reserve. The nutritive reserves in the endosperm have been transferred to the cotyledons, so there is only a small remnant endosperm between the embryo and seed coat. The outer layer is fruit (pericarp) tissue.

CHARACTERISTICS OF A SEED

Table 4–1
Classification of Seeds

The following classification is based upon morphology of embryo and seed coverings. It includes, as examples, families of herbaceous plants.

I. Seeds with dominant endosperm (or perisperm) as seed storage organs (endospermic).
   A. Rudimentary embryo. Embryo is very small and undeveloped but undergoes further increase at germination (see Fig. 4–5a, 4–6c Magnolia).
      1. Ranunculaceae (*Aquilegia, Delphinium*), Papaveraceae (*Eschscholtzia, Papaver*), Fumariaceae (*Dicentra*), Araliaceae (*Fatsia*), Magnoliaceae (*Magnolia*), Aquifoliaceae (*Ilex*).
   B. Linear embryo. Embryo is more developed than those in (A) and enlarges further at germination (Fig. 4–5c).
      1. Apiaceae (*Daucus*), Ericaceae (*Calluna, Rhododendron*), Primulaceae (*Cyclamen, Primula*), Gentianaceae (Gentiana), Solanaceae (*Datura, Solanum*), Oleaceae (*Fraxinus*).
   C. Miniature embryo. Embryo fills more than half the seed (Fig. 4–4c).
      1. Crassulaceae (*Sedum, Heuchera, Hypericum*), Begoniaceae (*Begonia*), Solanaceae (*Nicotiana, Petunia, Salpiglossis*), Scrophulariaceae (*Antirrhinum, Linaria, Mimulus, Nemesia, Penstemon*), Lobeliaceae (*Lobelia*).
   D. Peripheral embryo. Embryo encloses endosperm or perisperm tissue (Fig. 4–4b).
      1. Polygonaceae (*Eriogonum*), Chenopodiaceae (*Kochia*), Amaranthaceae (*Amaranthus, Celosia, Gomphrena*), Nyctaginaceae (*Abronia, Mirabilis*).

II. Seeds with embryo dominant (nonendospermic); classified according to the type of seed covering (Fig. 4–4d).
   A. Hard seed coats restricting water entry.
      1. Fabaceae (*Cercis, Gymnocladus, Gleditsia*), Geraniaceae (*Pelargonium*), Anacardiaceae (*Rhus*), Rhamnaceae (*Ceanothus*), Malvaceae (*Abutilon, Altea*), Convolvulaceae (*Convolvulus*).
   B. Thin seed coats with mucilaginous layer.
      1. Brassicaceae (*Arabis, Iberis, Lobularia, Mathiola*), Linaceae (*Linum*), Violaceae (*Viola*), Lamiaceae (*Lavandula*).
   C. Woody outer seed coverings with inner semipermeable layer.
      1. Rosaceae (*Geum, Potentilla*), Zygophyllaceae (*Larrea*), Balsaminaceae (*Impatiens*), Cistaceae (*Cistus, Helianthemum*), Onagraceae (*Clarkia, Oenothera*), Plumbaginaceae (*Armeria*), Apocynaceae, Polemoniaceae (*Phlox*), Hydrophyllaceae (*Nemophila, Phacelia*), Boraginaceae (*Anchusa*), Verbenaceae (*Lantana, Verbena*), Labiateae (*Coleus, Moluccela*), Dipsacaceae (*Dipsacus, Scabiosa*).
   D. Fibrous outer seed covering with more or less semipermeable membranous layer, including endosperm remnant.
      1. Asteraceae (many species).

III. Unclassified
   A. Rudimentary embryo with no food storage.
      1. Orchidaceae (orchids, in general).
   B. Modified miniature embryo located on periphery of seed (Fig. 4–6b).
      1. Poaceae (grasses).
   C. Axillary miniature embryo surrounded by gametophyte tissue (Fig. 4–6a).
      1. Gymnosperms (in particular, conifers).

Source: After Atwater (1).

CHARACTERISTICS OF A SEED

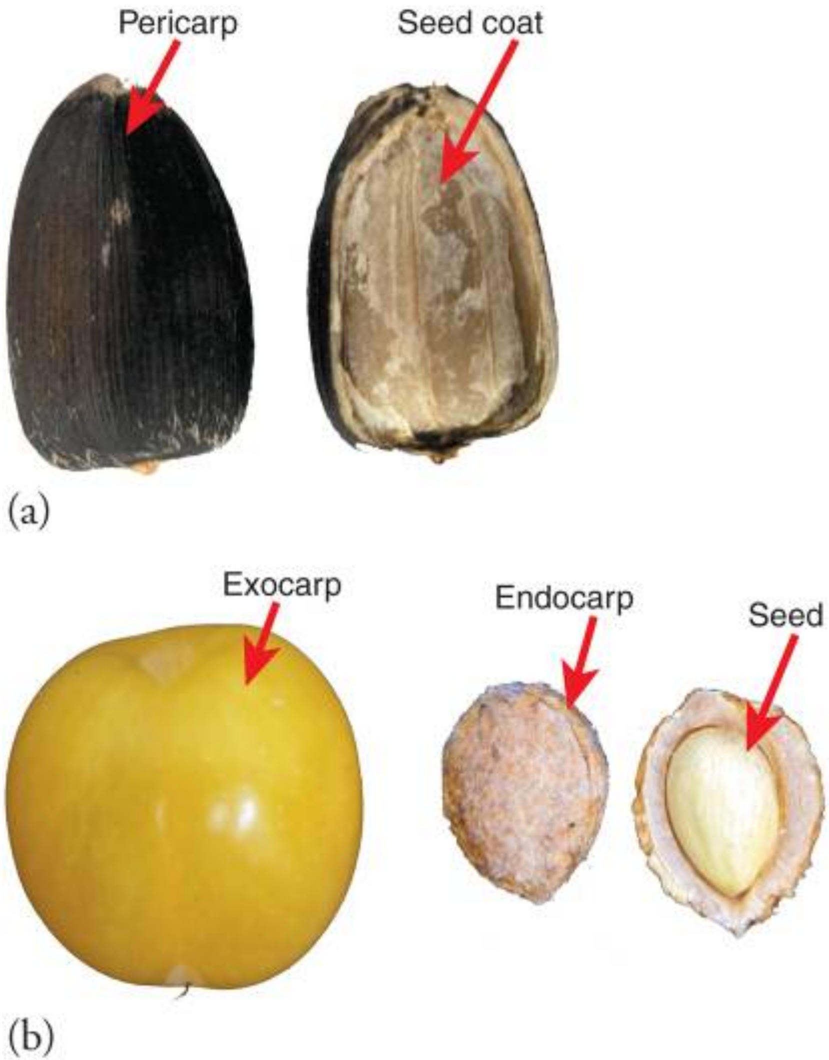


Figure 4–7 Fruit structures included as the "seed" unit. (a) Sunflower "seeds" actually include the entire fruit, called an achene. (b) Plum is an example of a pome (stone fruit) where the inner part of the fruit (endocarp) adheres to the seed and usually part of the seed unit.

CHARACTERISTICS OF A SEED

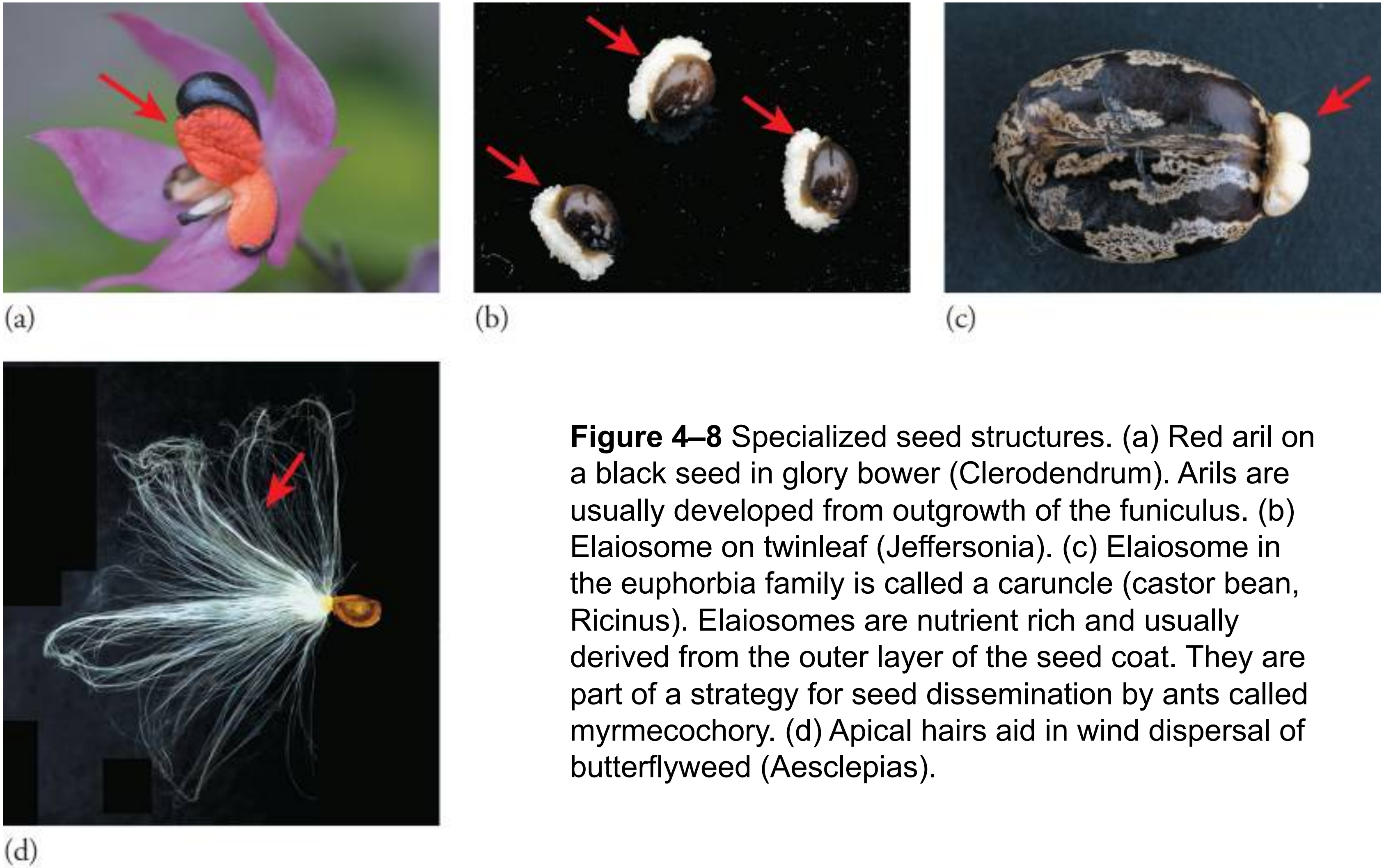


Figure 4–8 Specialized seed structures. (a) Red aril on a black seed in glory bower (Clerodendrum). Arils are usually developed from outgrowth of the funiculus. (b) Elaiosome on twinleaf (Jeffersonia). (c) Elaiosome in the euphorbia family is called a caruncle (castor bean, Ricinus). Elaiosomes are nutrient rich and usually derived from the outer layer of the seed coat. They are part of a strategy for seed dissemination by ants called myrmecochory. (d) Apical hairs aid in wind dispersal of butterflyweed (Aesclepias).

REPRODUCTIVE PARTS OF THE FLOWER

- Sexual reproduction (fusion of male and female gametes) occurs in the flower.
  - The sexual cycle of plant reproduction starts with meiotic cell divisions that halve the number of chromosomes in male pollen cells and female cells in the embryo sac.

REPRODUCTIVE PARTS OF THE FLOWER

- Pollen Development (Microsporogenesis)
- Ovule Development (Megasporogenesis)

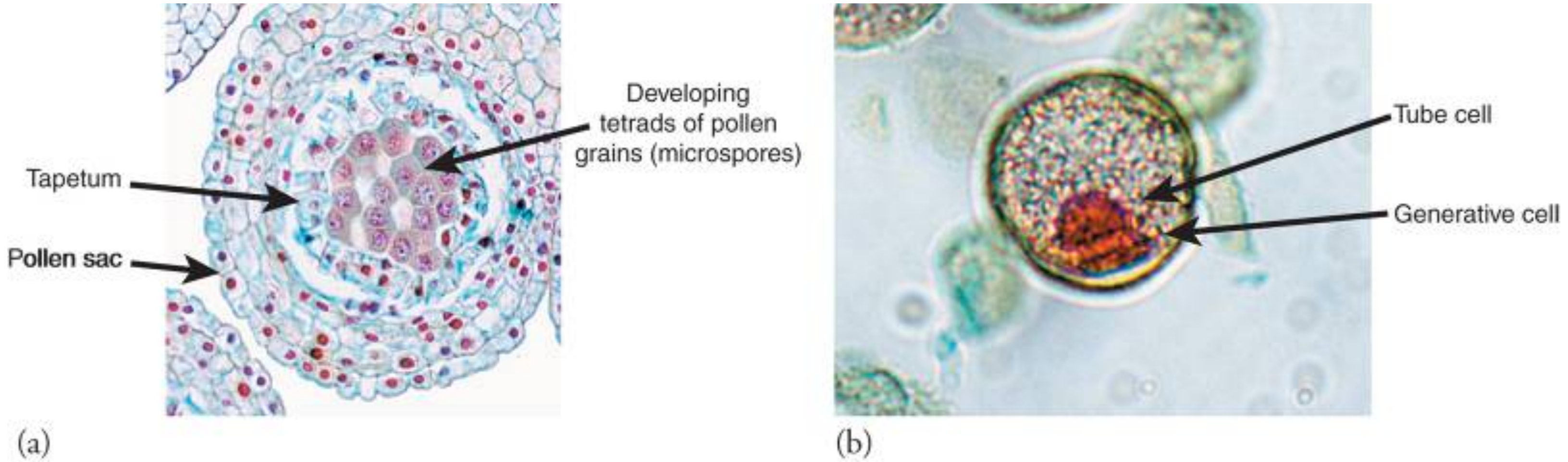
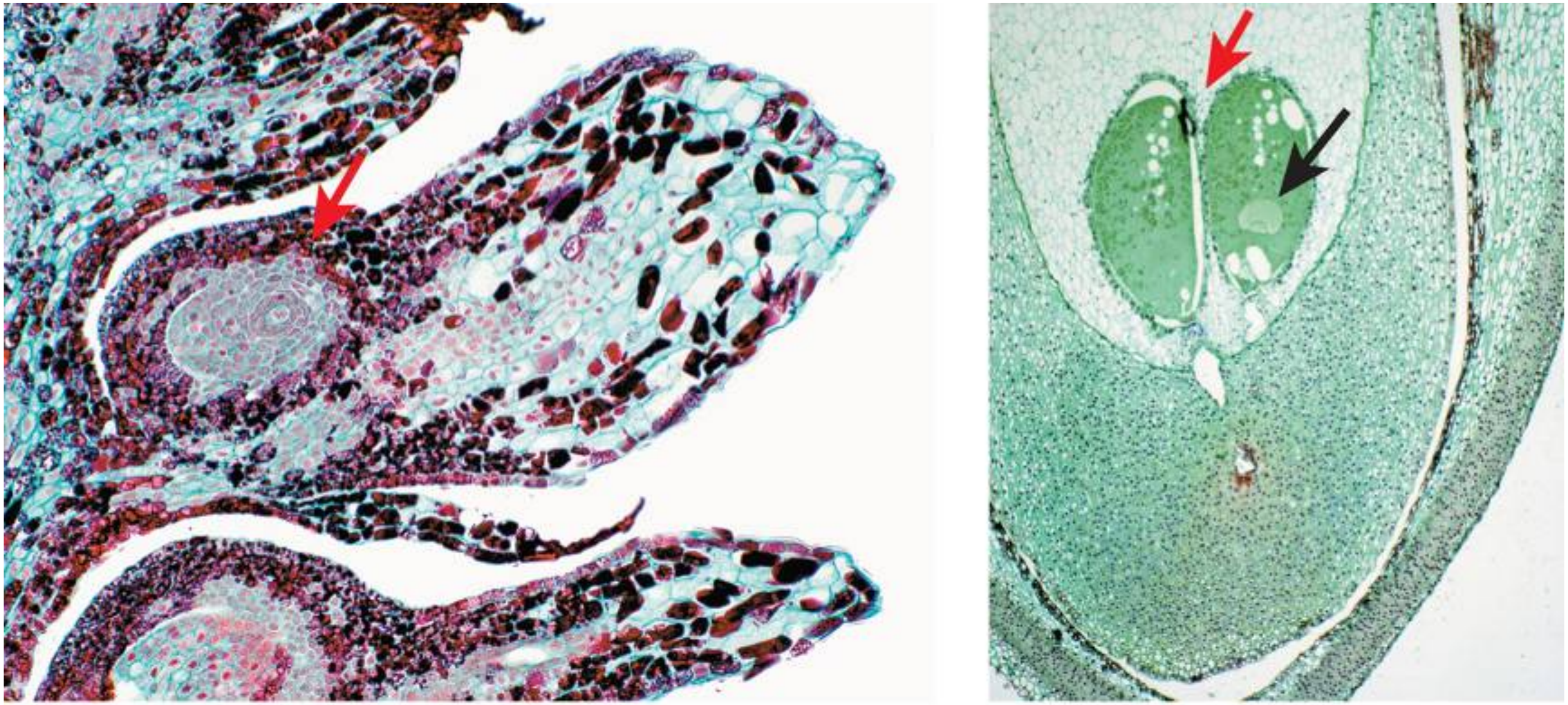


Figure 4–9 Pollen development in a typical angiosperm. (a) Within the pollen sac, meiotic divisions give rise to the male gametes contained within a pollen grain. The tapetum is a nutritive layer of cells enclosing the pollen grains. (b) Mature pollen grain containing a tube and generative cell.

REPRODUCTIVE PARTS OF THE FLOWER



(a) (b)

Figure 4–10 Development of the female gametophyte in a representative gymnosperm (pine). (a) The megaspore mother cell (arrow) develops in the female nucellar tissue. (b) Two archegonia (red arrow) form, each containing a female egg cell (black arrow).

REPRODUCTIVE PARTS OF THE FLOWER

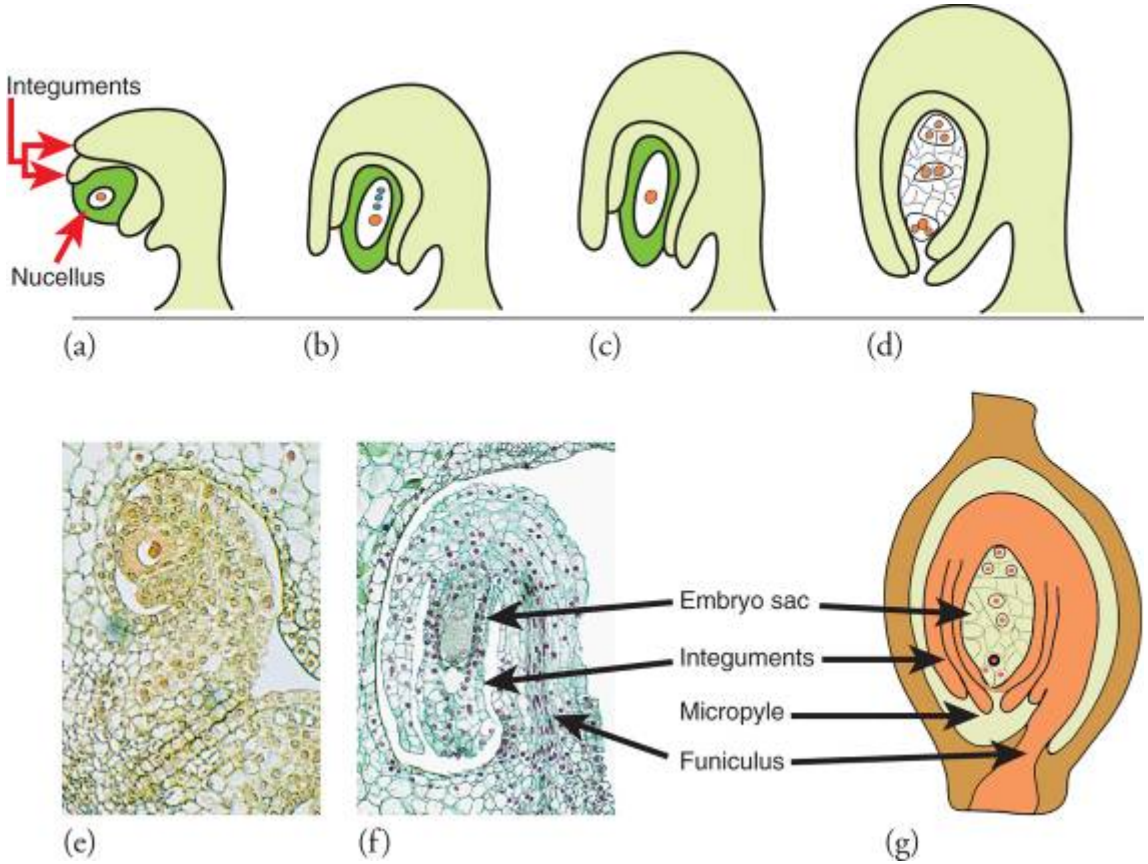


Figure 4–11 Development of the embryo sac in a representative angiosperm (lily). (a) The megaspore mother cell develops in the flower's nucellar tissue. (b) Meiosis results in one viable and three degenerative nuclei. (c and e) Progenitor nucleus for the embryo sac. (d, f, and g) Embryo sac within the ovule bounded by the integuments and attached to the ovary by the funiculus. It is common for the ovule to turn during development. The orientation illustrated is the most common form, called anatropous.

REPRODUCTIVE PARTS OF THE FLOWER

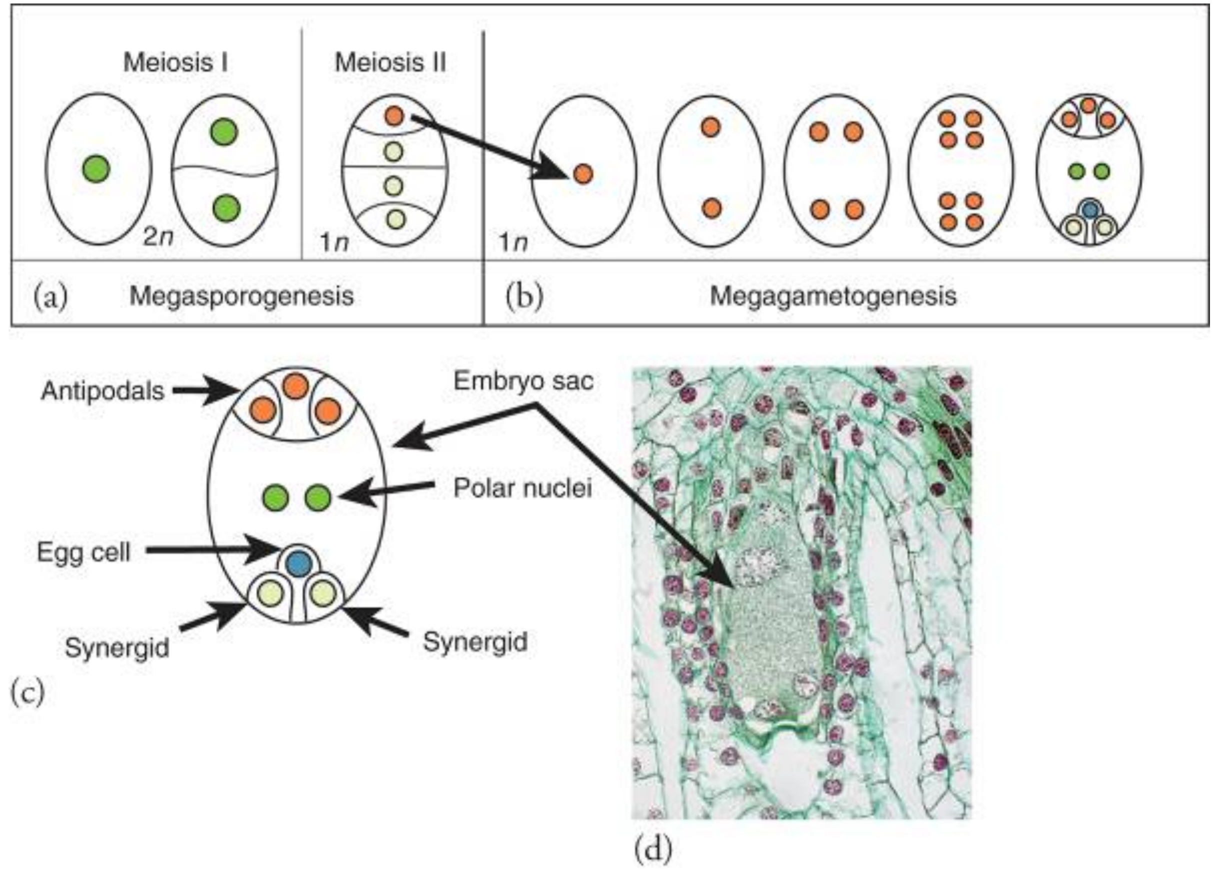
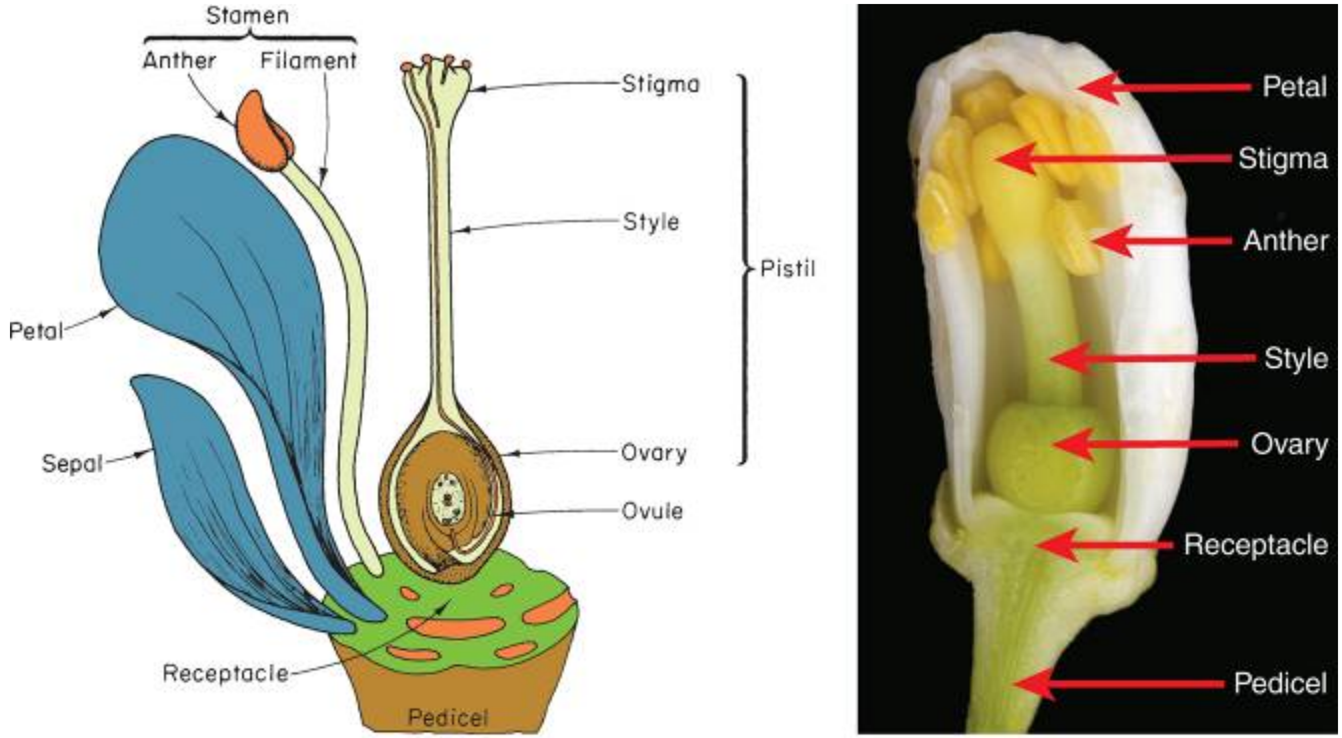


Figure 4–12 Development of the most common form of embryo sac (Polygonum type). (a) Initially a mother spore or mother cell develops in the nucellar tissue of the flower. Four haploid cells are formed during meiosis, but only one is retained. (b) It then divides to form the cell in the embryo sac. Each cell has a distinct role. (c, d) Three become antipodals, one is the central cell with two polar nuclei, two become synergids, and one becomes the egg cell.

RELATIONSHIP BETWEEN FLOWER AND SEED PARTS

- The initiation of seed formation generally requires two processes—**pollination** and **fertilization.**
  - Pollination is the transfer of pollen within a single flower (self-pollination) or from separate flowers (cross-pollination) to a receptive stigma.
  - Fertilization is the fusion of haploid (1n) male and female gametes inside the ovule.

RELATIONSHIP BETWEEN FLOWER AND SEED PARTS



(a) (b)

Figure 4–13 In a typical angiosperm flower, floral organs are produced in separate whorls. The outermost whorl are the sepals (caylx), the next are the petals (corolla), inside the petals are the male stamens, and innermost is the female pistil. Pollination occurs with the transfer of pollen from the stamens to the stigma of the pistil. The pollen grain germinates and the pollen tube grows down the style. Eventually, the pollen tube enters the ovule through the micropyle and deposits two male sperm cells. Fertilization involves the fusion of the male and female cells in the embryo sac.

RELATIONSHIP BETWEEN FLOWER AND SEED PARTS

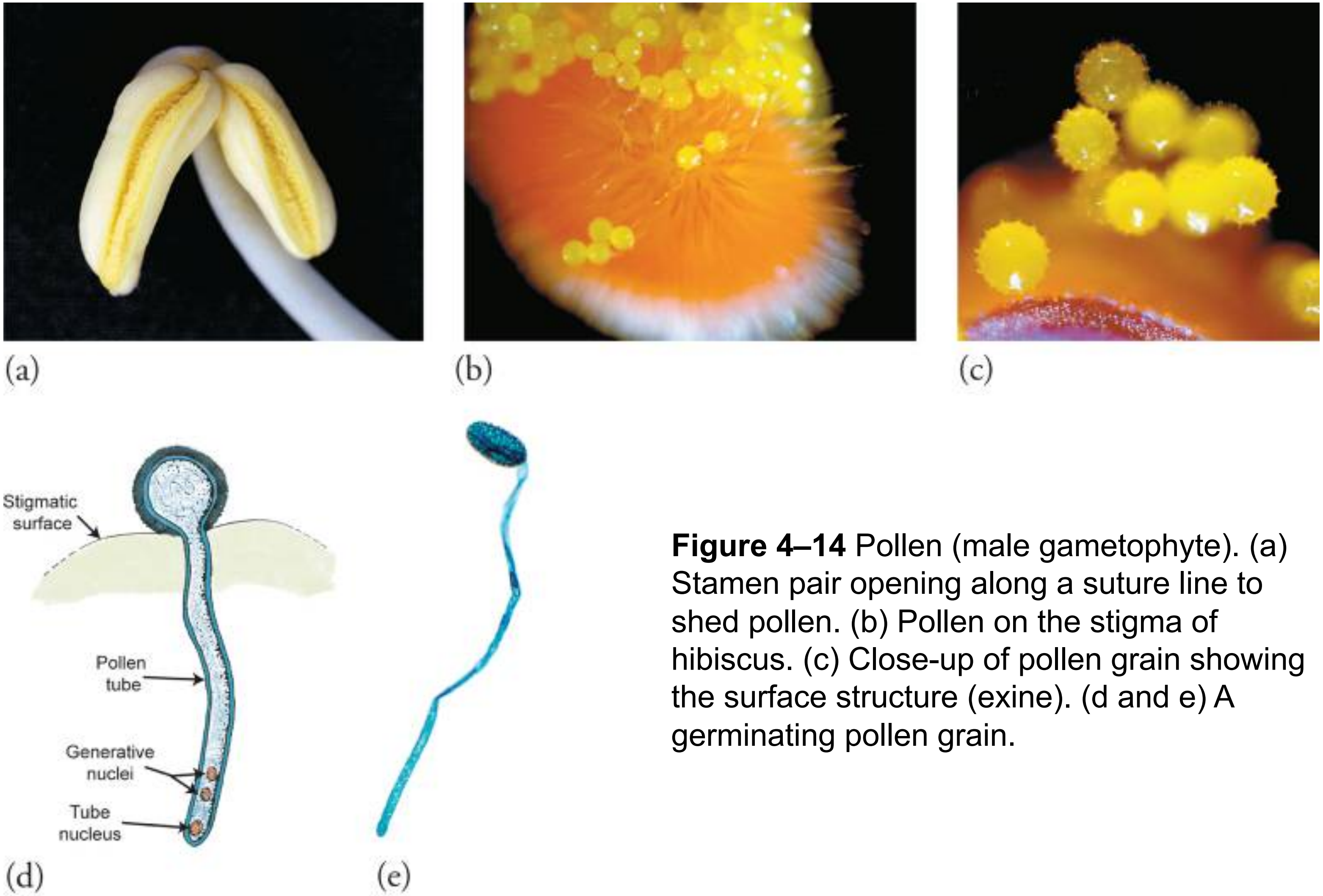


Figure 4–14 Pollen (male gametophyte). (a) Stamen pair opening along a suture line to shed pollen. (b) Pollen on the stigma of hibiscus. (c) Close-up of pollen grain showing the surface structure (exine). (d and e) A germinating pollen grain.

RELATIONSHIP BETWEEN FLOWER AND SEED PARTS

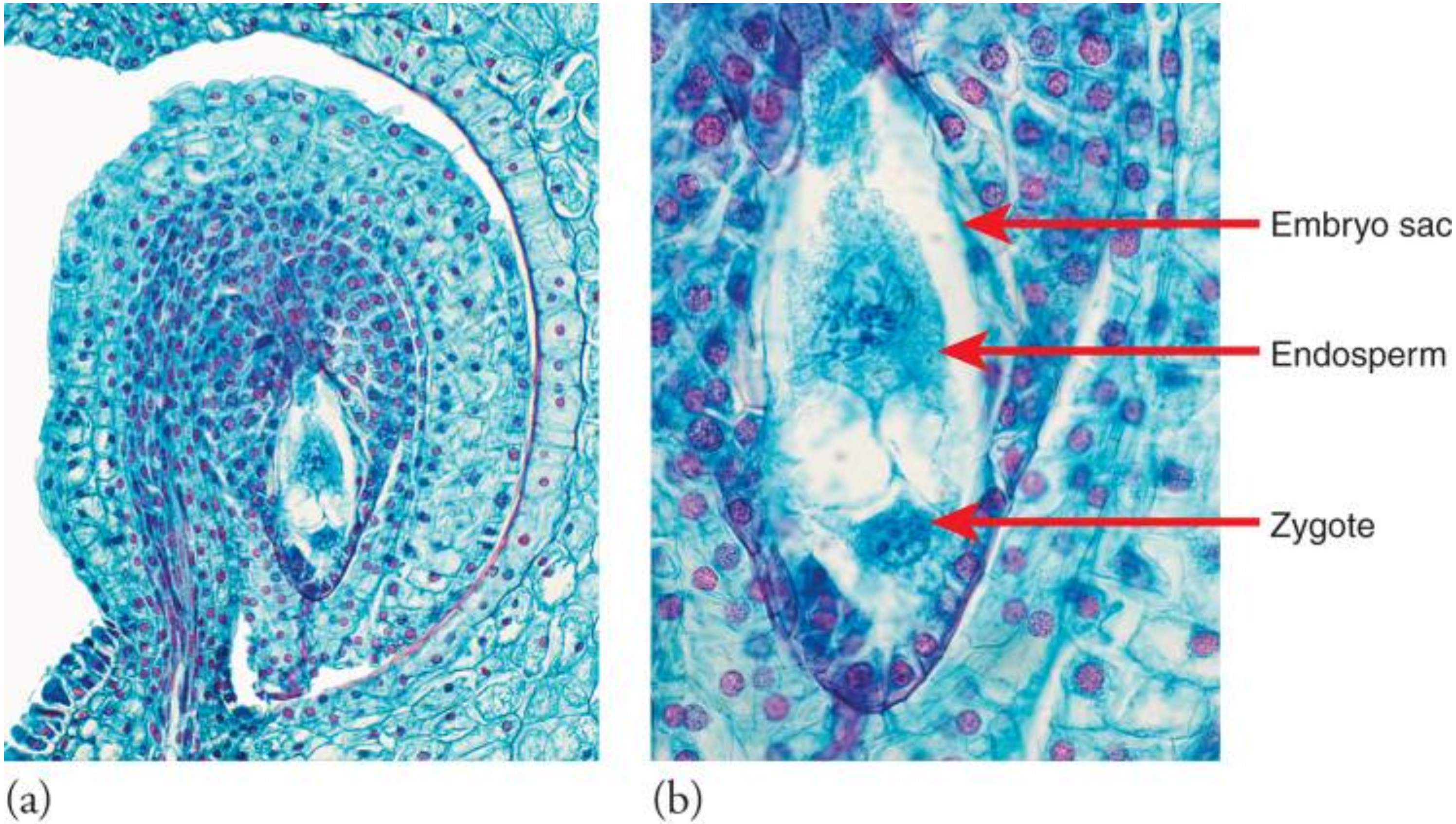


Figure 4–15 Double fertilization in lily. One sperm nucleus fuses with the egg cell to form the zygote and the other male nucleus fuses with the polar nuclei to form the triploid endosperm. (a) Shows the embryo sac within the developing ovule. (b) Is a close up of the embryo sac showing the onset of cell division following double fertilization.

STAGES OF SEED DEVELOPMENT

- Three physiological stages of development are recognized in most seeds.
- These include
  - **Histodifferentiation**
  - **Cell expansion**
  - **Maturation drying**

STAGES OF SEED DEVELOPMENT

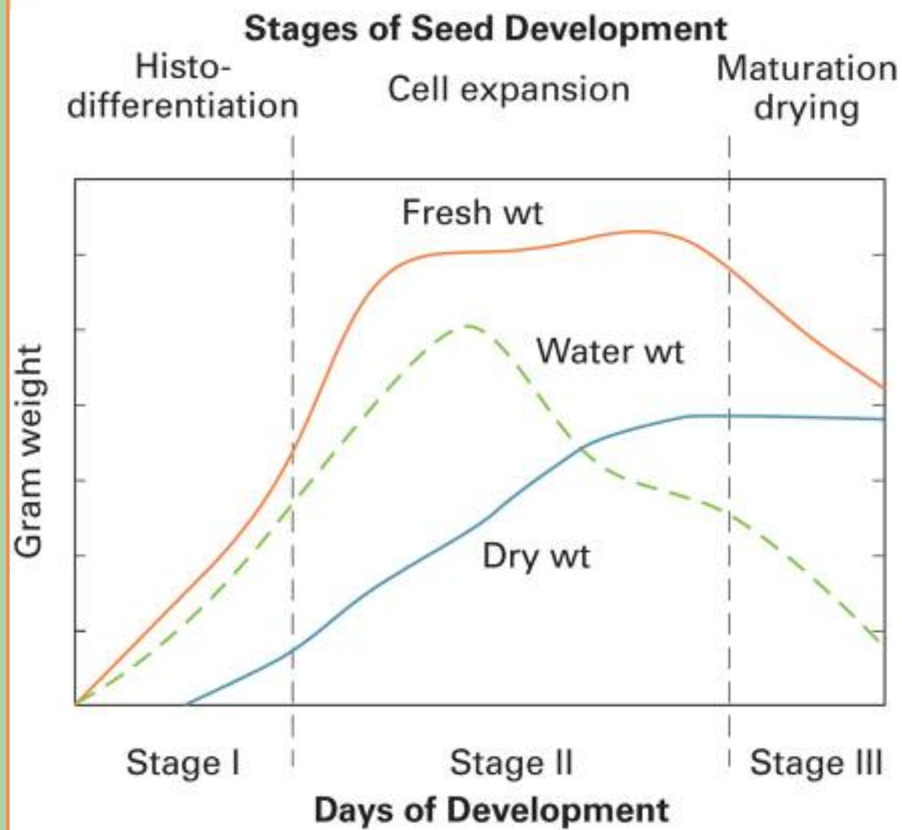


Figure 4–16 The stages of seed development. The stages include histodifferentiation (rapid increase in seed size due predominantly to cell division), cell expansion (largest increase in seed size for deposition of food reserves), and maturation drying (dramatic loss in seed fresh weight due to water loss). Redrawn from Bewley and Black, 1994.

STAGES OF SEED DEVELOPMENT

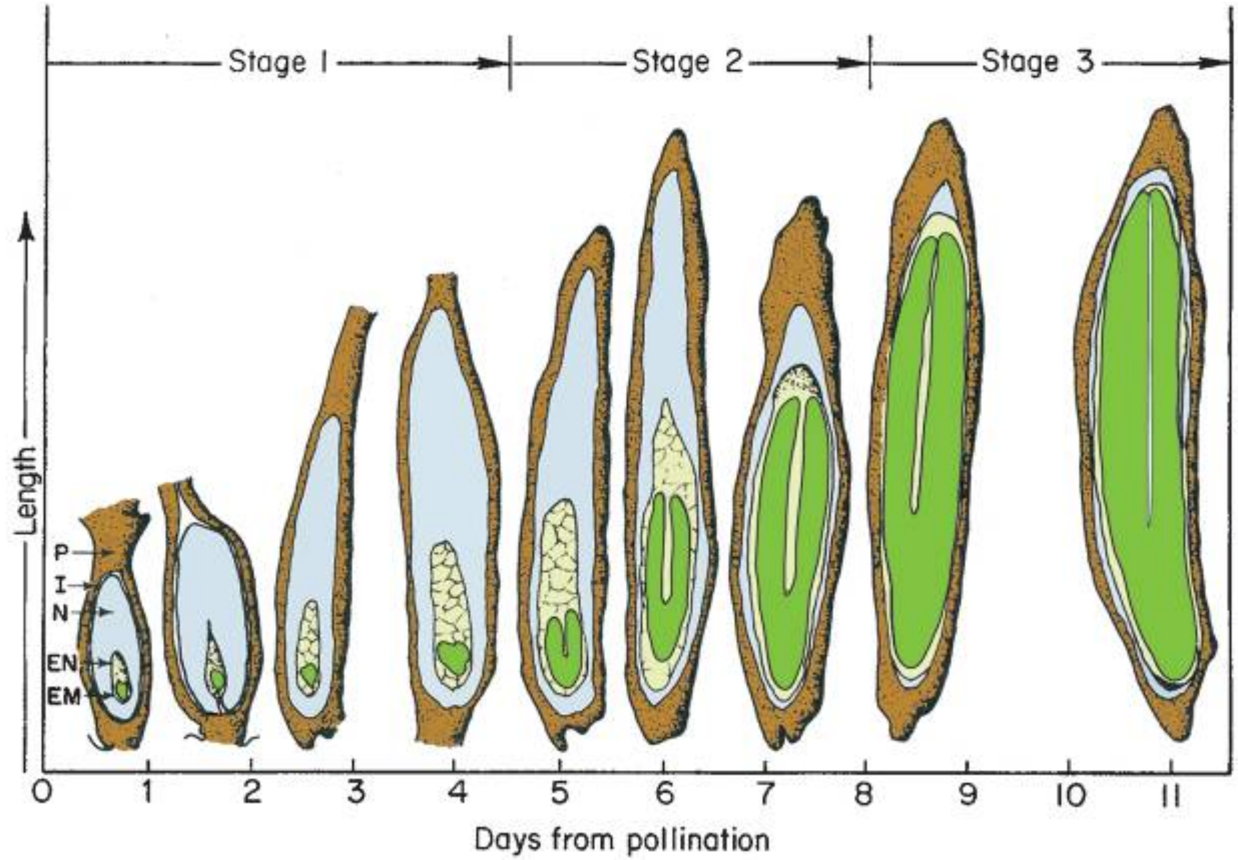


Figure 4–17 Growth and development of the fruit and seed in lettuce showing the relative changes in seed size during the three stages of seed development. P, pericarp; I, integuments; N, nucellus; EN, endosperm; EM, embryo. Redrawn from Jones 1927.

STAGES OF SEED DEVELOPMENT

- Stage I Histodifferentiation (Embryo Differentiation)
  - Embryo Differentiation in Dicots
  - Embryo Differentiation in Monocots
  - Embryo Differentiation in Gymnosperms
- Stage II Cell Expansion
- Stage III Maturation Drying

STAGES OF SEED DEVELOPMENT

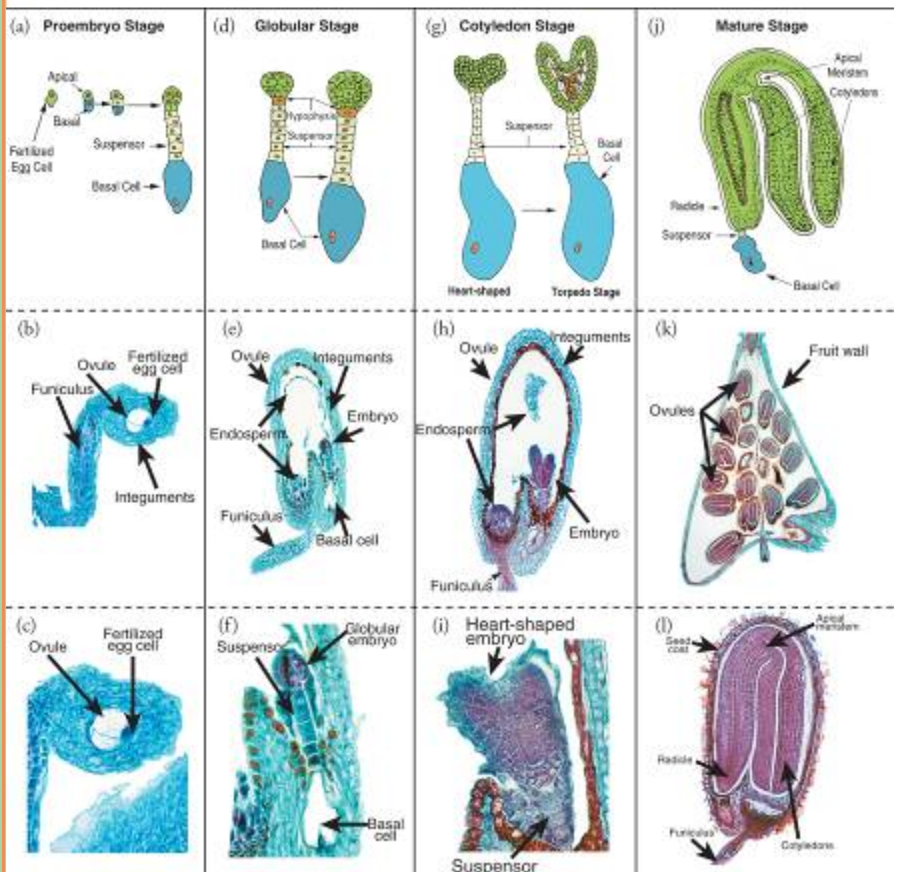


Figure 4–18 Embryo development in a typical dicot (shepherd's purse) showing the proembryo (a–c), globular (d–f), cotyledon (g–i), and mature (j–l) stages. See text for detailed description of each stage.

STAGES OF SEED DEVELOPMENT

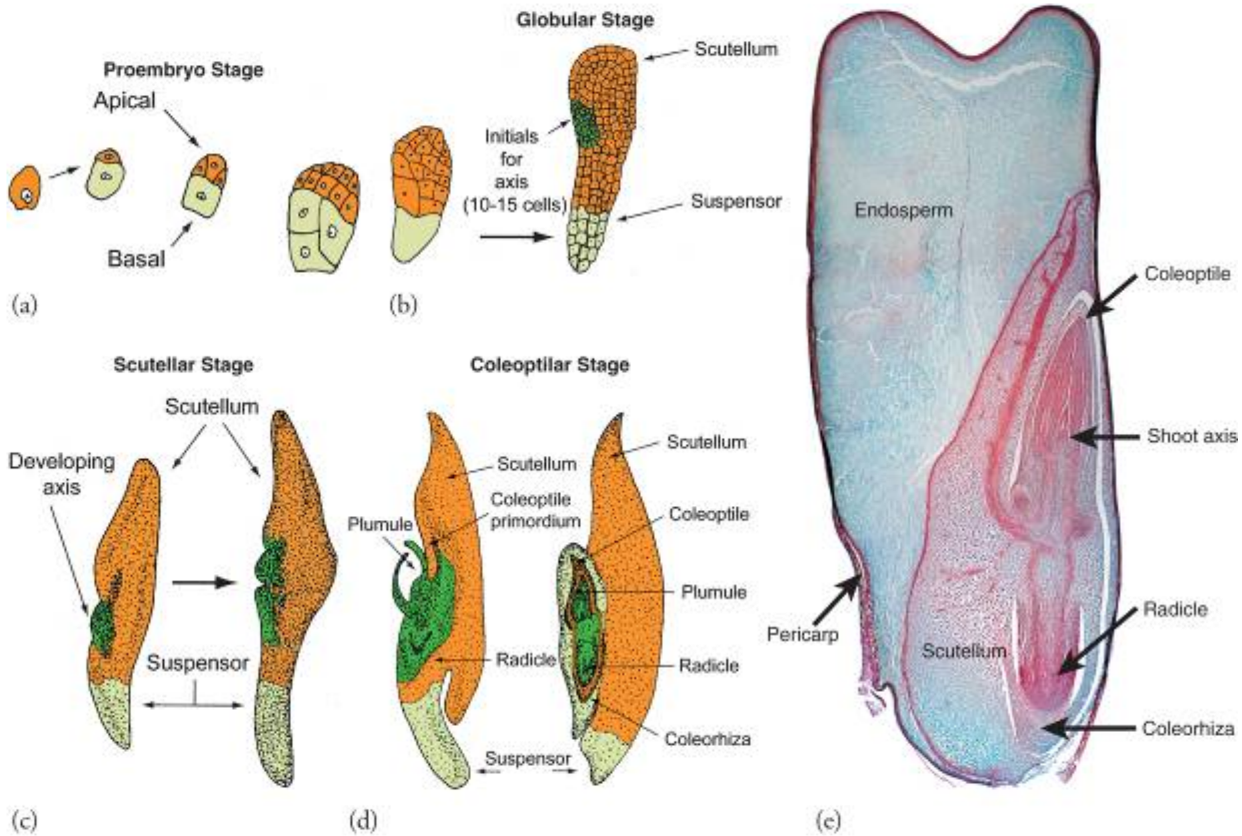


Figure 4–19 Embryo development in a typical monocot (corn). See text for description of figure. (e) Cross section of a mature seed of corn showing basic anatomical features.

STAGES OF SEED DEVELOPMENT

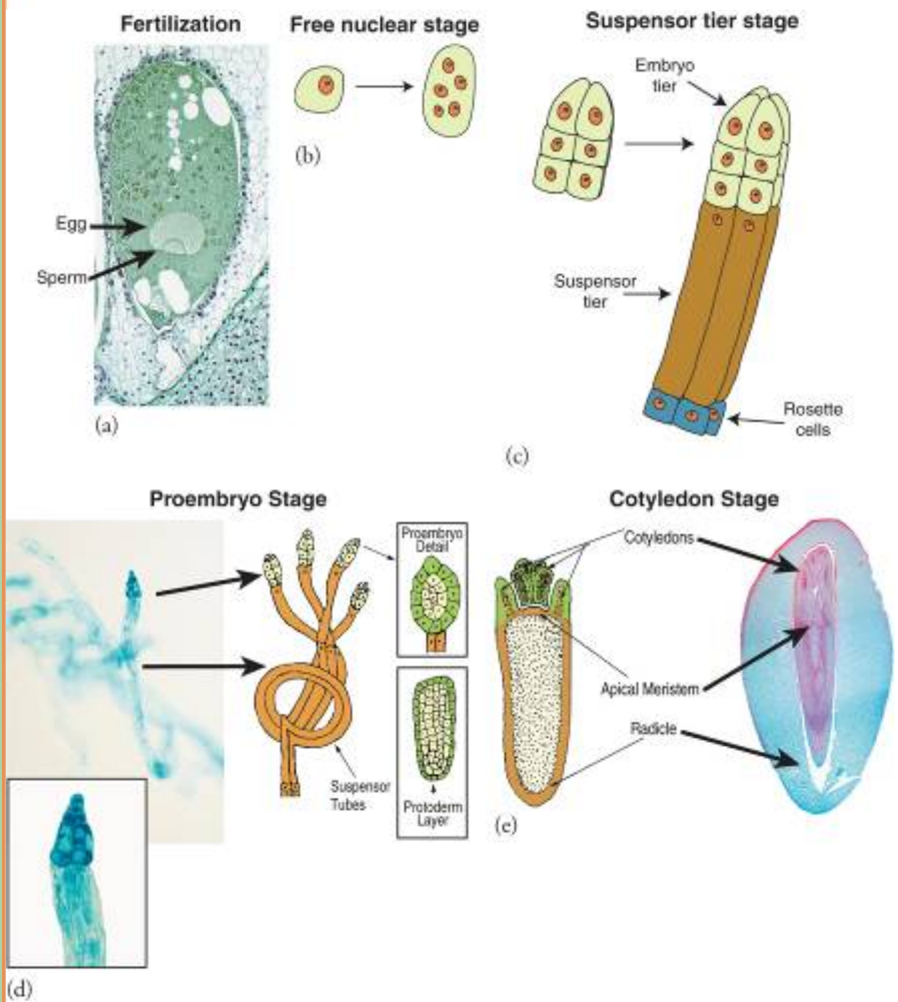


Figure 4–20 Embryo development in a typical gymnosperm (pine). See text for description of figure.

STAGES OF SEED DEVELOPMENT

Table 4–2
FOOD RESERVES FOUND IN VARIOUS PLANT SPECIES

	Average percent composition			
Species	Protein	Oils	Starch	Major storage organ
Cereals	10–13%	2–8%	66–80%	Endosperm
Oil palm	9%	49%	28%	Endosperm
Legumes	23–37%	1–48%	12–56%	Cotyledons
Rape seed	21%	48%	19%	Cotyledons
Pine	35%	48%	6%	Female gametophyte

Source: From (7, 18, 62).

STAGES OF SEED DEVELOPMENT

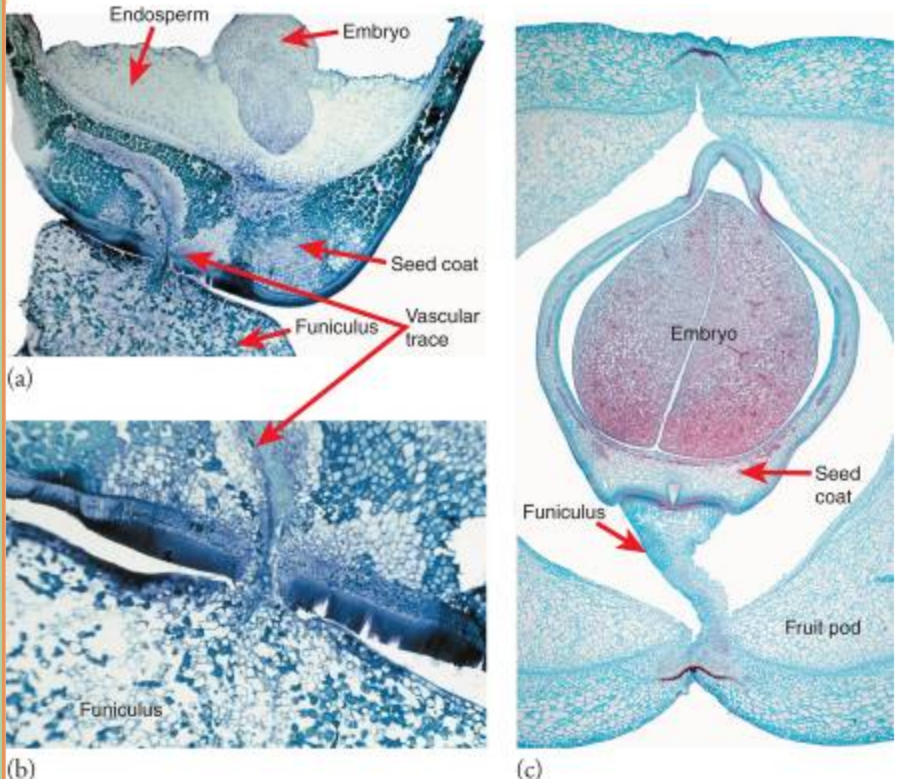


Figure 4–21 (a) Longitudinal section through a developing ovule of eastern redbud (Cercis canadensis) about 57 days post-anthesis (pollen shedding) showing the vascular connection between the funiculus and the ovule. (b) Close-up of the vascular trace. Note typical xylem cells in the vascular trace. (c) Bean seed with funiculus attached to the pod. From Jones and Geneve (36).

STAGES OF SEED DEVELOPMENT

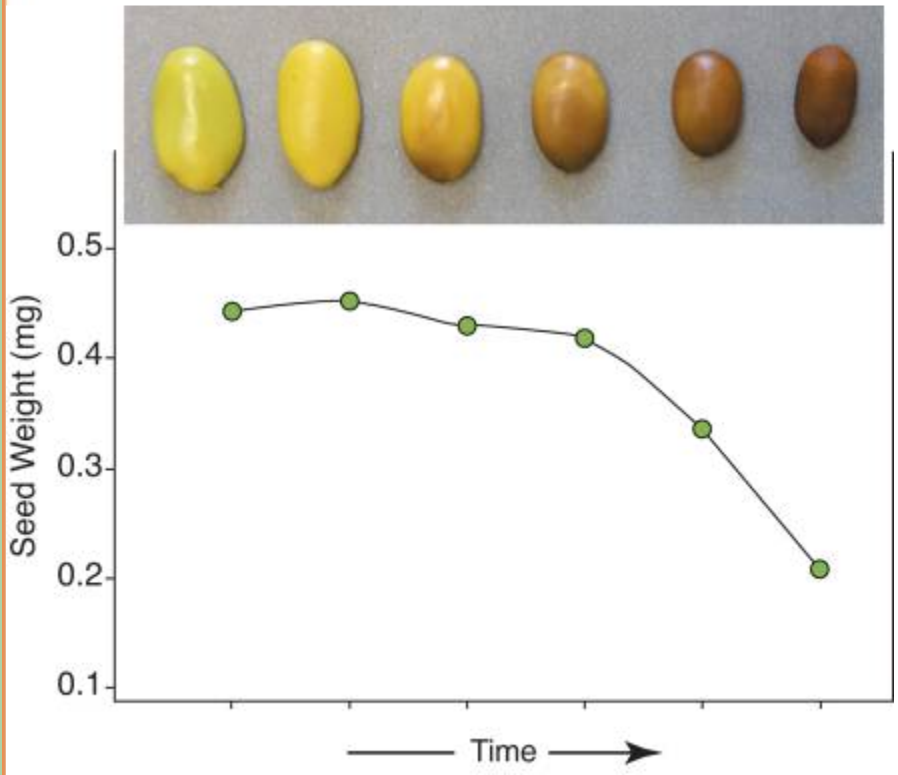


Figure 4–23 Water loss in honeylocust (Gleditsia triacanthos) seeds during development. Note the typical loss of chlorophyll during maturation drying and the overall reduction in seed size.

STAGES OF SEED DEVELOPMENT

Figure 4–24 Precocious or viviparous germination occurs when the seed prematurely germinates in the fruit. This is the result of the developing seed not completing the third stage of development—maturation drying. The cause of precocious germination is usually the inability of the embryo to produce or perceive abscisic acid (ABA). ABA is a potent germination inhibitor and one of its roles during seed development is to prevent precocious germination. The tomato illustrated here is most likely an ABA production mutant.

UNUSUAL TYPES OF SEED DEVELOPMENT

- Apomixis and polyembryony represent variations from the normal pattern of zygote formation and embryogenesis.
- Although related, they are not necessarily the same phenomenon.
- **Apomixis** is the asexual development of seeds that represent clonal duplicates of the mother plant.

UNUSUAL TYPES OF SEED DEVELOPMENT

- Apomixis
  - Nonrecurrent Apomixis
- Polyembryony
- Vegetative Apomixis

UNUSUAL TYPES OF SEED DEVELOPMENT

Figure 4–26 Polyembryony in trifoliate orange (Poncirus trifoliata) seeds as shown by the several seedlings arising from each seed. One seedling, usually the weakest, may be sexual; the others arise apomictically from cells in the nucellus and are diploid copies of the mother plant.

UNUSUAL TYPES OF SEED DEVELOPMENT

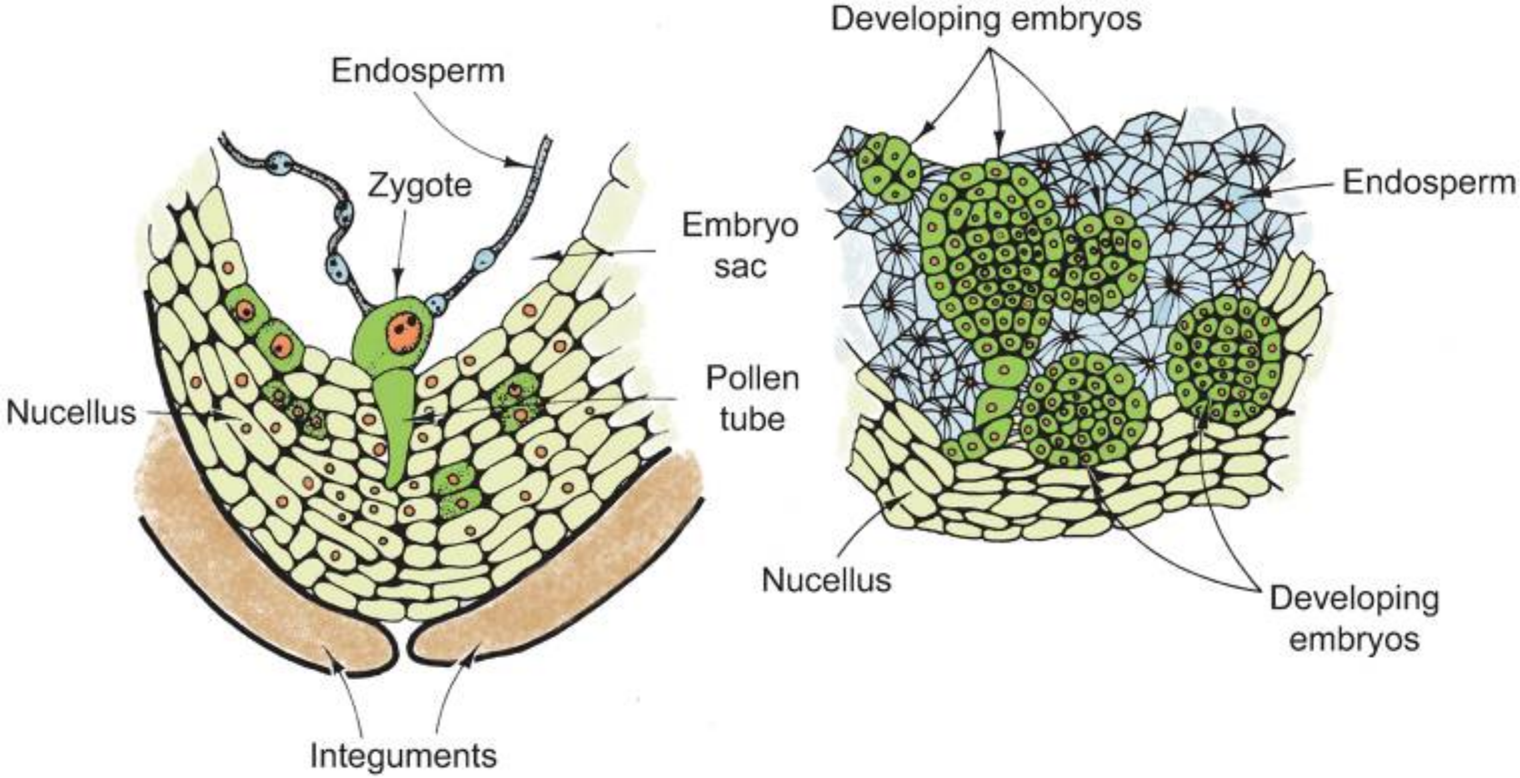


Figure 4–27 Development of nucellar embryos in Citrus. Left: Stage of development just after fertilization showing zygote and remains of pollen tube. Note individual active cells (shaded) of the nucellus, which are in the initial stages of nucellar embryony. Right: A later stage showing developing nucellar embryos. The large one may be the sexual embryo. Redrawn from Gustafsson, 1946.

PLANT HORMONES AND SEED DEVELOPMENT

- Plant hormones are involved in seed development in several ways:
  - 1. growth and differentiation of the embryo
  - 2. accumulation of food reserves
  - 3. storage for use during germination and early seedling growth, and
  - 4. growth and development of fruit tissue

PLANT HORMONES AND SEED DEVELOPMENT

- Auxin
- Gibberellins
- Cytokinins
- Abscisic Acid (ABA)
- Ethylene

PLANT HORMONES AND SEED DEVELOPMENT

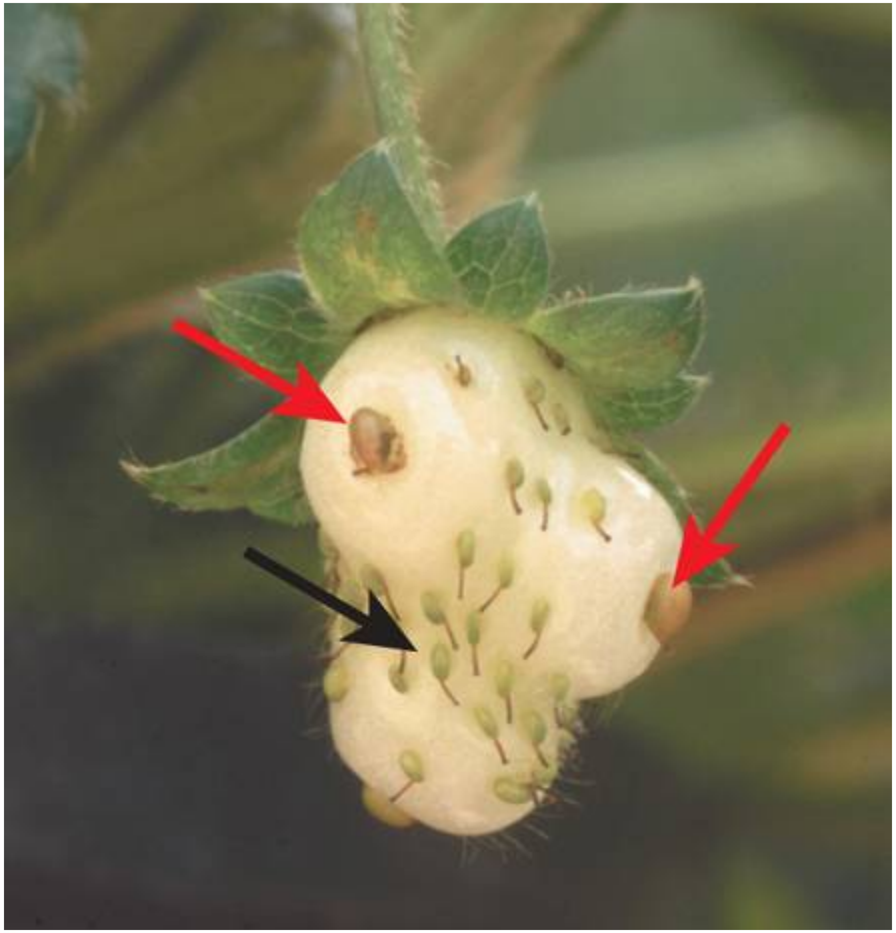


Figure 4–28 Strawberry "fruit" (receptacle) enlargement requires auxin from the developing seed (actually the fruit-achene). Notice how the only swelling in the receptacle tissue is around the developing achenes (red arrow). The black arrow shows a non-fertilized seed where you can still see the style and stigma attached. There is no swelling in this area because there is no developing seed to provide the auxin.

RIPENING AND DISSEMINATION

Table 4–3
DIFFERENT TYPES OF FRUITS

Type of fruit		Description	Example
Dry Fruits	Indehiscent Fruits		
	1. Caryopsis	Pericarp and seed coat are fused forming a single seed.	Most often in monocots like corn and wheat
	2. Samara	A one-seeded fruit with a specialized wing for wind dissemination.	Maple, ash, and elm
	3. Achene	A one-seeded fruit.	Strawberry, sunflower, and clematis
	4. Nut	Fruit develops from an ovary with multiple carpels, but only one survives.	Walnut and hazelnut
	5. Utricle	Single-seeded fruit with inflated pericarp.	Chenopodium
	Dehiscent Fruits		
	1. Follicle	Pod-like fruit from a single carpel that splits on one side.	Delphinium and columbine
	2. Legume	Pod that opens on both sides.	Bean, locust, and pea
	3. Capsule	There are numerous types of dry capsules that open along different suture lines near top of fruit.	Poppy, iris, and lily
	4. Silique	Develops from two carpels and opens along two suture lines.	Cabbage and arabidopsis
Fleshy Fruits	1. Berry	A fleshy fruit with many seeds with an endocarp, mesocarp, and exocarp that are soft.	Tomato and grape
	2. Drupe	Has a hard endocarp.	Peach, cherry, and fringe tree
	3. Pome	Has a papery endocarp.	Apple and pear
	4. Pepo	Outer endocarp forming hard rind.	Squash and pumpkin
	5. Hesperidium	Similar to a pepo but endocarp is not hard.	Orange and lemon
	6. Multiple fruits	Several fruits aggregated into a single structure.	Blackberry (multiple drupes), pineapple, and mulberry
Schizocarpic Fruits	Schizocarp	Fruits develop so that locules in an ovary separate into separate single-seeded units.	Sycamore, carrot, and parsley

DISCUSSION ITEMS

- Knowledge of seed development is most important for understanding various aspects of seed quality discussed in Chapter 6. The environment during seed development and the conditions during seed harvest are critical to producing quality seeds. To evaluate problems related to seed quality, a fundamental understanding of seed development, especially seed filling (deposition of food reserves) and seed desiccation (maturation drying), are most important.

DISCUSSION ITEMS

1. What are the three differences between pollination and fertilization?
2. How does the seed storage tissue differ among a monocot, dicot, and gymnosperm?
3. Compare zygotic and apomictic seed development.
4. How are the stages of embryogenesis similar and different in shepherd's purse vs. corn?
5. What might be the ecological advantages of vivipary as demonstrated by mangrove plants?
6. How is the scutellum of a monocot similar to and/or different from the cotyledons in a dicot?