# Biology

# I. Flowering, Pollination, and Seed Maturation

A. Introduction

Knowledge of the seed biology of a tree species is essential to successful seed production and handling. The sexual life cycle must be known to plan for genetic improvement, production, collection, conditioning, storage, and planting of the seeds.

B. Objectives

1. Define common terms used to describe life cycles of plants.
2. Describe the general sexual cycle, flower structure, seed structure, and origin of the fruit of gymnosperms.
3. Describe the general sexual cycle, flower structure, seed structure, and origin of the fruit of angiosperms.
4. Identify primary differences between angiosperm and gymnosperm sexual cycles.
5. Describe the general development of fruits and seeds.

C. Key Points

The following points are essential for understanding flowering, pollination, and seed maturation:

1. A plant's life cycle is the time required to grow from zygote to seed production; there are two developmental cycles — a sexual cycle and an asexual cycle.
2. Knowledge of the sexual cycle is required for:
   a. tree-breeding programs
   b. seed orchard management
   c. seed collection
   d. seed conditioning and storage
   e. nursery management
3. The gymnosperm life cycle follows this order:
   a. naked seed
   b. seedling
   c. mature sporophyte
   d. strobili (cones)
   e. microspore and megaspore mother cells
   f. meiosis
   g. microspores and megaspores
   h. male and female gametophytes
   i. pollination
   j. single fertilization
   k. zygote and gametophytic tissue
   l. embryo
   m. naked seed on ovulate cone scale
4. The angiosperm life cycle differs from the gymnosperm life cycle in having:
   a. seeds enclosed in fruit (ripened ovary)
   b. true flowers rather than strobili
   c. double fertilization
   d. triploid endosperm tissue rather than haploid female gametophytic tissue in the seed

D. Definition of Terms

1. **Life cycle—the** time required to progress from zygote to seed production. There are two possible developmental cycles — the sexual cycle involving seeds (used in regeneration of "high forest" systems) and the asexual cycle involving vegetative propagules of coppice forestry (used in regeneration of "low forest" systems).
2. **Genotype — the** genetic makeup of a cell nucleus or an individual.
3. **Phenotype — the** external appearance of an organism; it is an expression of the genotype interacting with the environment.
4. **Mitosis —** nuclear (and usually cellular) cell division in which the chromosomes duplicate and divide to produce two nuclei that are identical to the original nucleus.
5. **Meiosis—** two successive nuclear divisions in which the chromosome number is halved and genetic segregation occurs; it occurs in reproductive cells during sexual reproduction.
6. **Pollination—transfer** of pollen grains from the anther or microsporophyll to the stigma or ovule.
7. **Fertilization—fusion** of sperm and egg (and also sperm with two polar nuclei to form endosperm in angiosperms).
8. **Diploid** (2N) — two sets of chromosomes in a cell nucleus. Somatic cells have two sets and are diploid (except for polyploid plants).
9. **Haploid (1N)—** one set of chromosomes in a cell nucleus. Germ cells (egg and sperm cells) from a diploid plant are haploid.
10. **Fruit** —a ripened ovary, sometimes including accessory flower parts, that surrounds the seed in angiosperms. The term "fruit" is used to refer to any seed-bearing structure; thus, it can include the ovulate cone of fleshy aril of the conifers.
11. **Seed—a** ripened ovule that consists of an embryo, its stored food supply, and protective coverings. The term "seed" is also often used to include the fruit wall of one-seeded, dry, indehiscent fruits, such as achenes and nuts. The "seed of commerce" is the reproductive structure as bought and sold. It may be multiseeded in some species. Examples include *Tectona* and *Liriodendron.*

12. **Mature seed—** a seed that can be removed from the tree without impairing the seed's germination.

**E.** Life Cycles

An understanding of life cycles is needed because:

1. Sexual and asexual systems reproduce genetically different populations.
2. Knowledge of the asexual cycle is needed before vegetative propagation can be used for coppice systems, cloning of selected genotpes, conservation of germplasm, direct planting of propagules, or enhancement of flowering in clonal seed orchards.
3. Knowledge of the sexual cycle is needed for success in:
   a. tree breeding
   b. seed production
   c. seed orchard management
   d. seed harvesting and conditioning
   e. nursery management
   f. planting and subsequent management of forest stands

**F.** Angiosperm and Gymnosperm Sexual Cycles

1. **All tree species** are seed-producing plants (division, Spermatophyta) and belong to either the class Gymnospermae or Angiospermae.
   a. The true flowering plants of angiosperms have seeds enclosed in carpels.
   b. The coniferous gymnosperms have seeds borne naked on scales arranged spirally on a central axis to form a cone.
   c. Seeds of nonconiferous gymnosperms are borne singly, each enclosed in a fleshy, arillike covering.
2. **Gymnosperm life cycle** (fig. 2) [figure 1 in Student Outline]

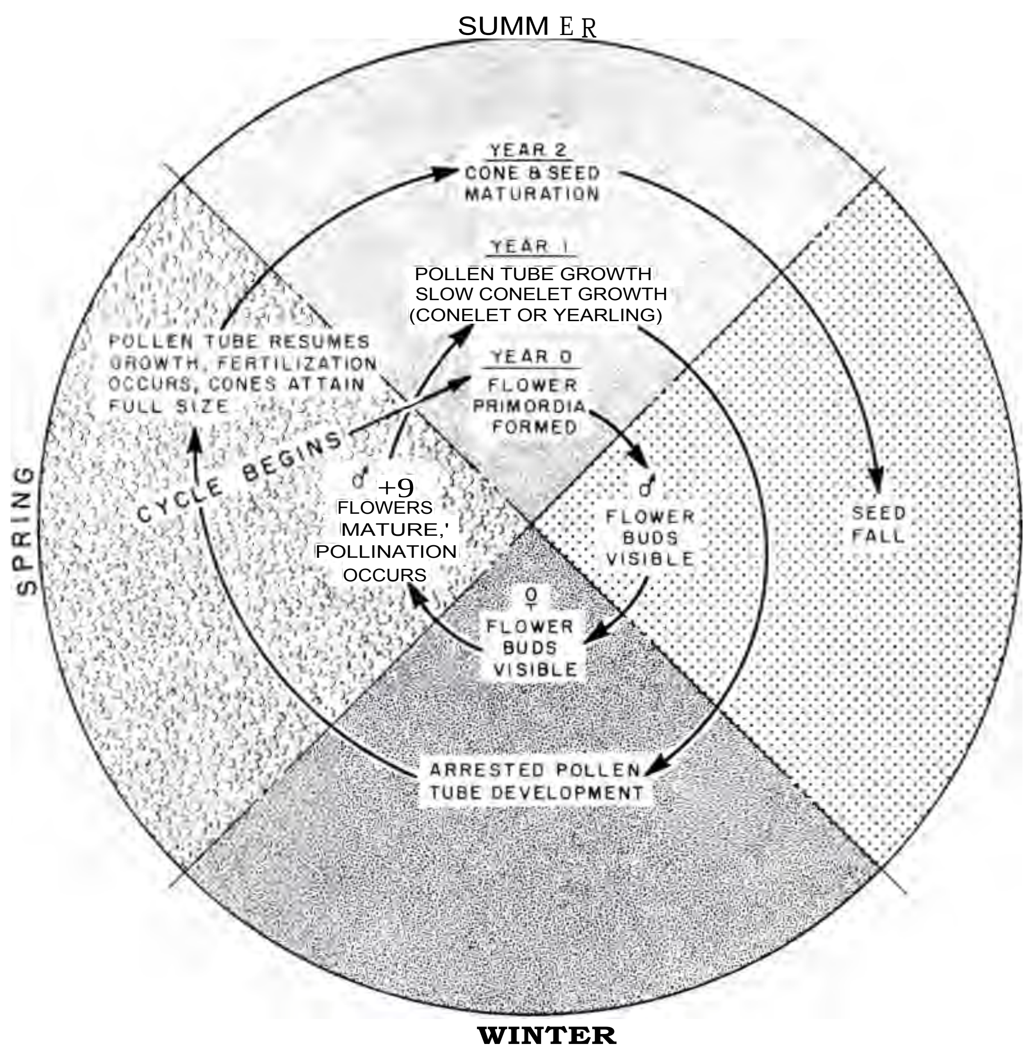


Figure 2. —*Life cycle of a gymnosperm* (Pinus *spp.) (Bonner 1991b) [figure 1 in Student Outline].*

a. Sporophyte — The diploid plant (tree) that arises from the zygote.
b. Strobilus or cone — Using a pine from the Coniferales as an example:
   (1) Reproductive short shoot (not a "flower" — a term that should be limited to angiosperms).
   (2) Staminate cone (male) — axis with spirally arranged microsporophylls and two microsporangia on the bottom side of each sporophyll.
   (3) Ovulate cone (female) — axis with spirally arranged bracts and ovuliferous scales. Two ovules are located on the upper side near the base of each scale.
   (4) Gymnosperms may be either monoecious (female and male strobili on same tree) or dioecious (tree has only one sex).
c. Meiosis and gametophytes
   (1) Diploid microspore mother cell in microsporangium undergoes meiosis to produce four haploid microspores (pollen grains). After pollination, the pollen grain germinates to produce a six-nucleate male gametophyte, two sperm nuclei, two generative nuclei, tube nucleus, and stalk nucleus).
   (2) Diploid megaspore mother cell in the megasporangia of the ovule undergoes meiosis to produce four haploid megaspores, of which three deteriorate. The remaining megaspore undergoes many mitotic nuclear divisions, has a free nuclei stage, and finally forms cell walls to produce a haploid female gametophyte (archegonia with egg and gametophytic tissue).
d. Fertilization — A sperm cell from the male gametophyte unites with the egg cell to form the diploid zygote (single fertilization).
e. Seed (fig. 3) [figure 2 in Student Outline]
   (1) Develops from the fertilized ovule.
   (2) Contains an embryo (cotyledons, hypocotyl, radicle) (2N from sexual recombination), a seedcoat (2N of mother plant, from integuments), storage tissue (1N from female gametophyte), and sometimes a seed wing (2N from mother plant, from upper surface of ovuliferous scale).

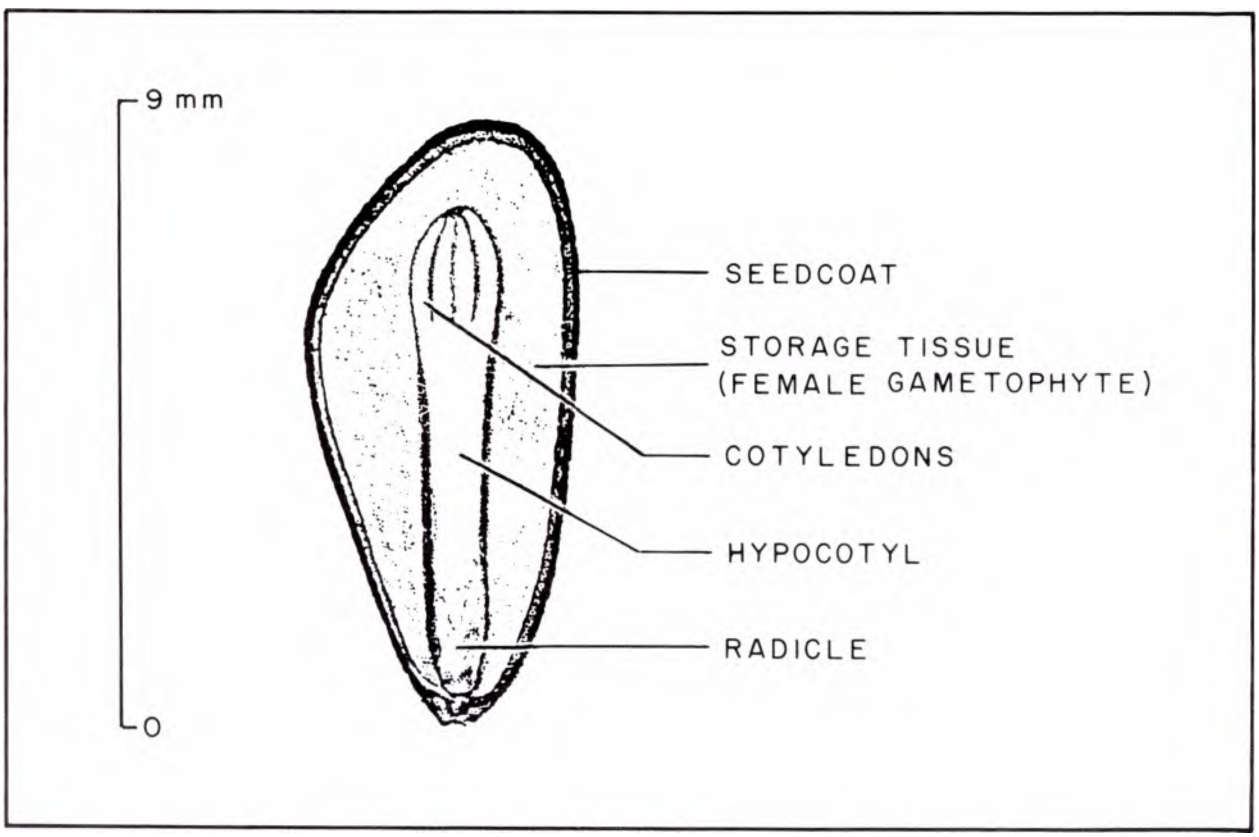


Figure 3.—*Cross section of a typical mature gymnosperm seed* (Pinus ponderosa) *(adapted from Krugnzan and Jenkinson 1974) [figure 2 in Student Outline].*

f. Fruit
   (1) Gymnosperms do not have true "fruits" (matured ovaries).
   (2) The types of structures that enclose gymnosperm seeds are:
      (a) dry ovulate cones (e.g., *Abies, Araucaria, Cupressus, Pinus,* and *Tsuga)*
      (b) fleshy, arillike structures enclosing single seeds (e.g., *Ginkgo, Taxus,* and *Torreya)*
      (c) berrylike ovulate cones (e.g., *Juniperus* — one to two seeds per cone)

3. **Angiosperm life cycle**
   a. Sporophyte — the diploid plant (tree) that arises from the zygote (same as gymnosperm).
   b. Flower — a short shoot with sterile and reproductive leaves and a receptacle.
      (1) Sterile leaves include:
         (a) sepals (outer whorl), collectively, corolla
         (b) petals (inner whorl), collectively, corolla
         (c) perianth, a collective term for sepals and petals
      (2) Reproductive leaves (sporophylls) include:
         (a) stamen (male), composed of anther (a pollen sac containing microsporogenous tissue) and filament
         (b) carpel (female), composed of stigma, style, and ovary. The ovary is the basal portion of a pistil that bears the ovules and its surrounding carpel wall. The ovule is composed of megasporogenous tissue surrounded by the nucellus, two integuments, and the micropyle.
         (c) pistil, a collective term that describes visible female structures, whether a single carpel or a fusion of many carpels.
      (3) Receptacle, a stem axis of the flower.
      (4) Flowers may have one or both sexes.
         (a) Perfect flowers contain both stamens and pistils.
         (b) Imperfect flowers contain only one sex, and the tree may be either monoecious or dioecious.
         (c) Polygamous includes some perfect and imperfect flowers on the same tree.
   c. Meiosis and gametophytes
      (1) Diploid microspore mother cell in microsporogenous tissue of anthers undergoes meiosis to produce four haploid microspores (pollen grains). After pollination, the pollen grain germinates to produce a six-nucleate male gametophyte (same as for gymnosperms).
      (2) Diploid megaspore mother cell in megasporogenous tissue of ovule undergoes meiosis to produce four haploid megaspores, of which three deteriorate. The remaining megaspore undergoes three mitotic divisions and forms cell walls to produce a haploid female gametophyte (eight-nucleate, seven-celled embryo sac containing three antipodal cells, two polar nuclei, two synergid cells, and the egg).
   d. Fertilization
      (1) A sperm cell unites with the egg cell to form the diploid zygote (one fertilization).
      (2) The second sperm cell unites with the two polar nuclei (triple fusion) to form a triploid (3N) endosperm nucleus (second fertilization).
   e. Seeds (figs. 4, 5) [no equivalent figures in Student Outline]
      (1) Seeds develop from the double-fertilized ovule.
      (2) They contain an embryo (2N from sexual recombination), seed coat, storage tissue (may be 2N cotyledons, hypocotyl from embryo, 3N endosperm from triple fusion, or 2N perisperm from nucellus of mother tree), and sometimes other seed coverings (2N of mother tree from remains of nucellus, 3N from remains of endosperm, or 2N of mother tree from attached parts of fruit).
      (3) They may be classified as endospermic (embryo is reduced in size compared with the rest of the seed) or nonendospermic (embryo is dominant).
   f. Fruits
      (1) Fruits develop from the matured ovary (and sometimes from the receptacle or perianth); thus, the ovary has the mother tree's diploid genotype.
      (2) They enclose the seed (matured ovule).

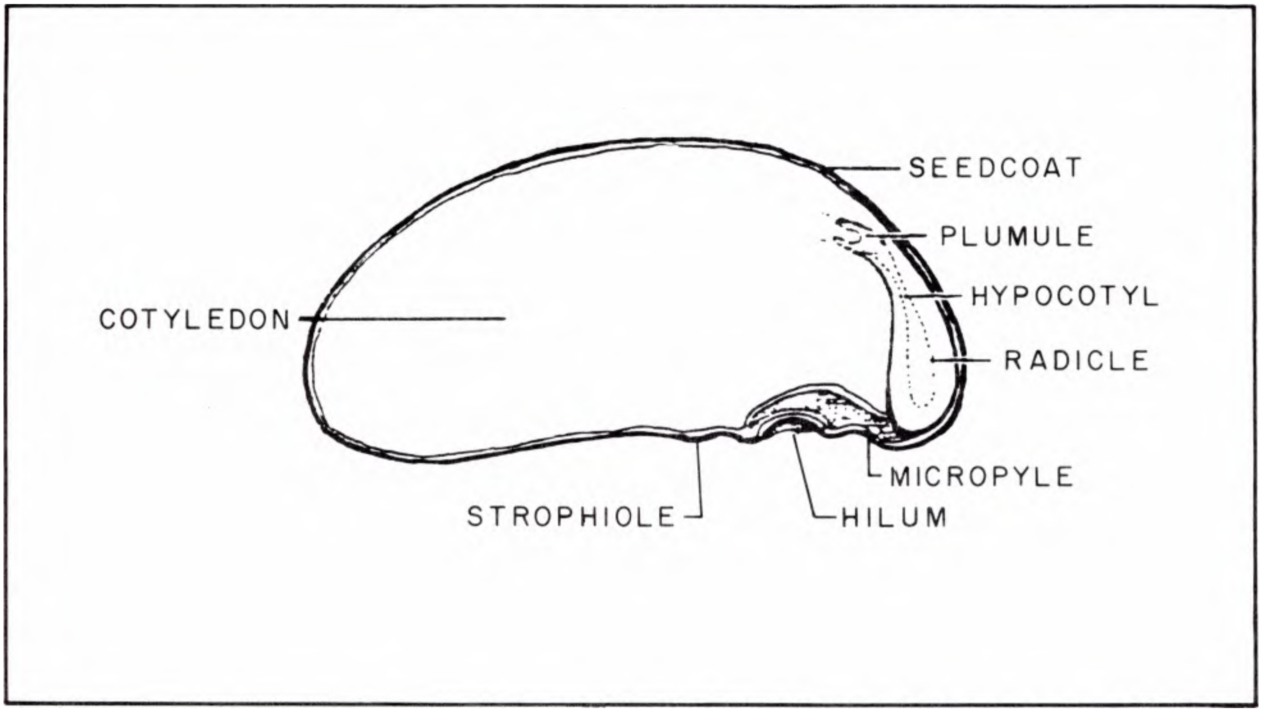


Figure 4. — *Cross section of a mature seed of* Centrolobium paraense *(adapted from Triviiio and others 1990) [no equivalent figure in Student Outline].*

(3) It is not always possible to separate the fruit and the seed when the seedcoat and fruit are joined as a single unit. In this case, the fruit itself is referred to as the "seed."

4. **Sexual cycles—** The gymnosperm and angiosperm sexual cycles differ in four ways:
   a. In gymnosperms, seeds are not enclosed in the ovary, and flowers are unisexual; in angiosperms, seeds are borne in a closed ovary, and flowers are perfect or imperfect.
   b. Flowers are true flowers in angiosperms but are strobili (cones) in gymnosperms.
   c. Double fertilization takes place in angiosperms; single fertilization takes place in gymnosperms.
   d. In gymnosperms, the developing embryo is nourished by the haploid female gametophyte; in angiosperms, it is nourished from either diploid cotyledons, hypocotyl of the embryo, triploid endosperm, or diploid nucellar material.

G. Seed and Fruit Development

1. **Physical development**

a. Angiosperms

(1) Pollination and fertilization trigger:

(a) Formation of embryo and endosperm within ovules.

(b) Cell divisions and enlargements in ovary and peripheral tissues leading to production of fruit. Most angiosperms flower and ripen in one growing season (except for the red oak subgenus of *Quercus).*

(2) Legumes have:

(a) simple pistil (one) with a superior ovary having one cavity (locule). When the pistil matures, a fruit (pod) is produced — a single, dry, dehiscent fruit. Seeds develop along the side of the pod where the carpel margins join. The other side is the midrib, where the pod splits open. A typical seed is dicotyledonous and lacks endosperm. Each seed is attached to the pod by the seedstalk (funiculus). As the seeds leave the pod, the seedstalk breaks off, leaving a scar (hilum). Above the hilum is the raphe; below is the micropyle (fig. 6) [figure 3 in Student Outline].

(b) Seedcoats are composed of a histologically dense cuticle, radial columnar cells, sclerenchy-

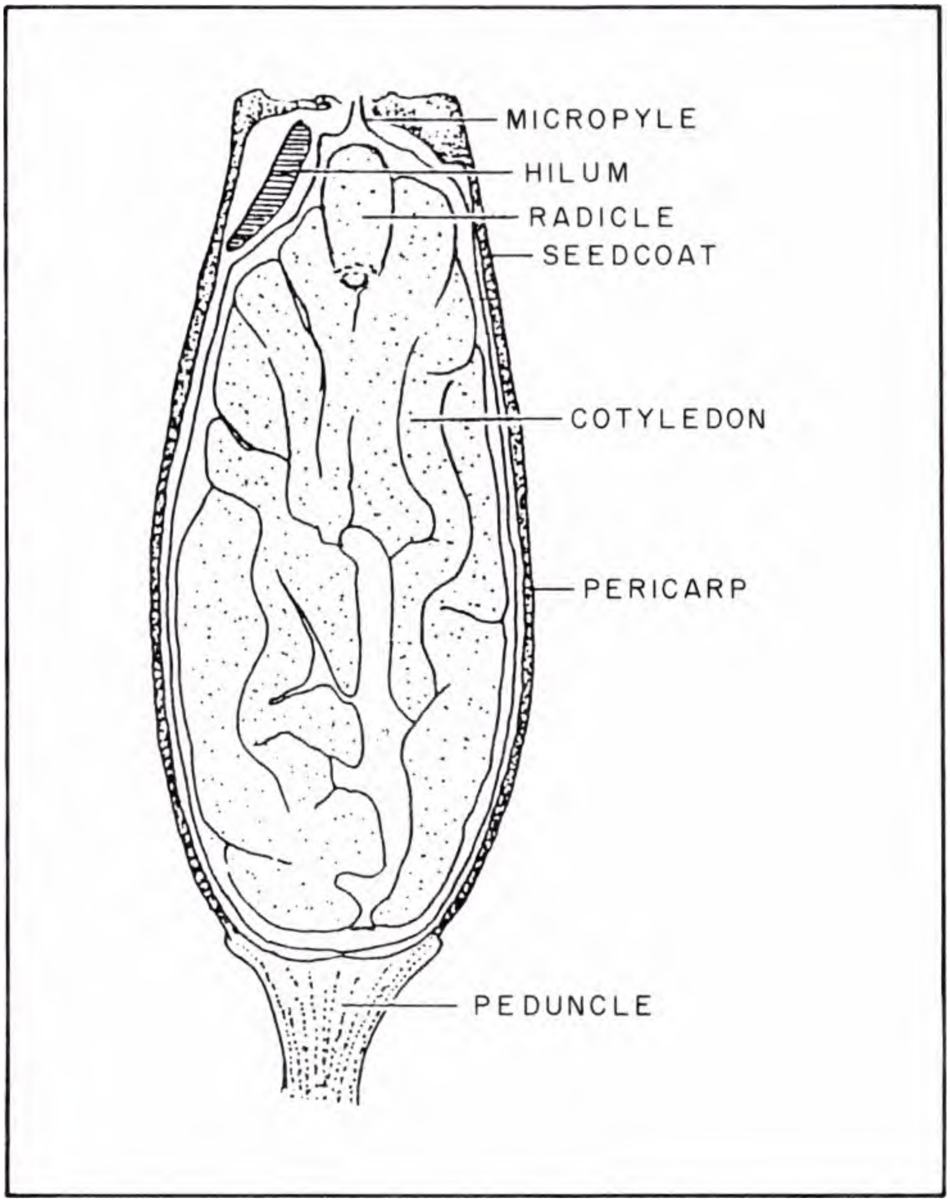


Figure 5. — *Cross section of a mature seed of* Cordia alliodora *(adapted from 7}-Mino and others 1990) [no equivalent figure in Student Outline].*

matous cells, lignin, and osteosclereid cells. These seedcoats are highly impervious to water and gases. Malpighian cells internal to the palisade layer are characterized as sclerenchyma without intercellular spaces— very dense cells, protecting the seed and denying water uptake. The "light line" in the palisade cells is caused by wax globules, also a water barrier (See fig. 7) [figure 4 in Student Outline].

(3) Definition of Terms

- **(a)** **cuticle—waxy** layer on outer walls of epidermal cells
- **(b)** **lignin —** organic component of cells associated with cellulose
- **(c)** **light line—continuous** thin layer of wax globules
- **(d)** **osteosclereid — bone-shaped** sclerenchyma
- **(e)** **palisade cells — elongated** cells perpendicular to the coat surface
- **(f)** **parenchyma—** undifferentiated, live cells

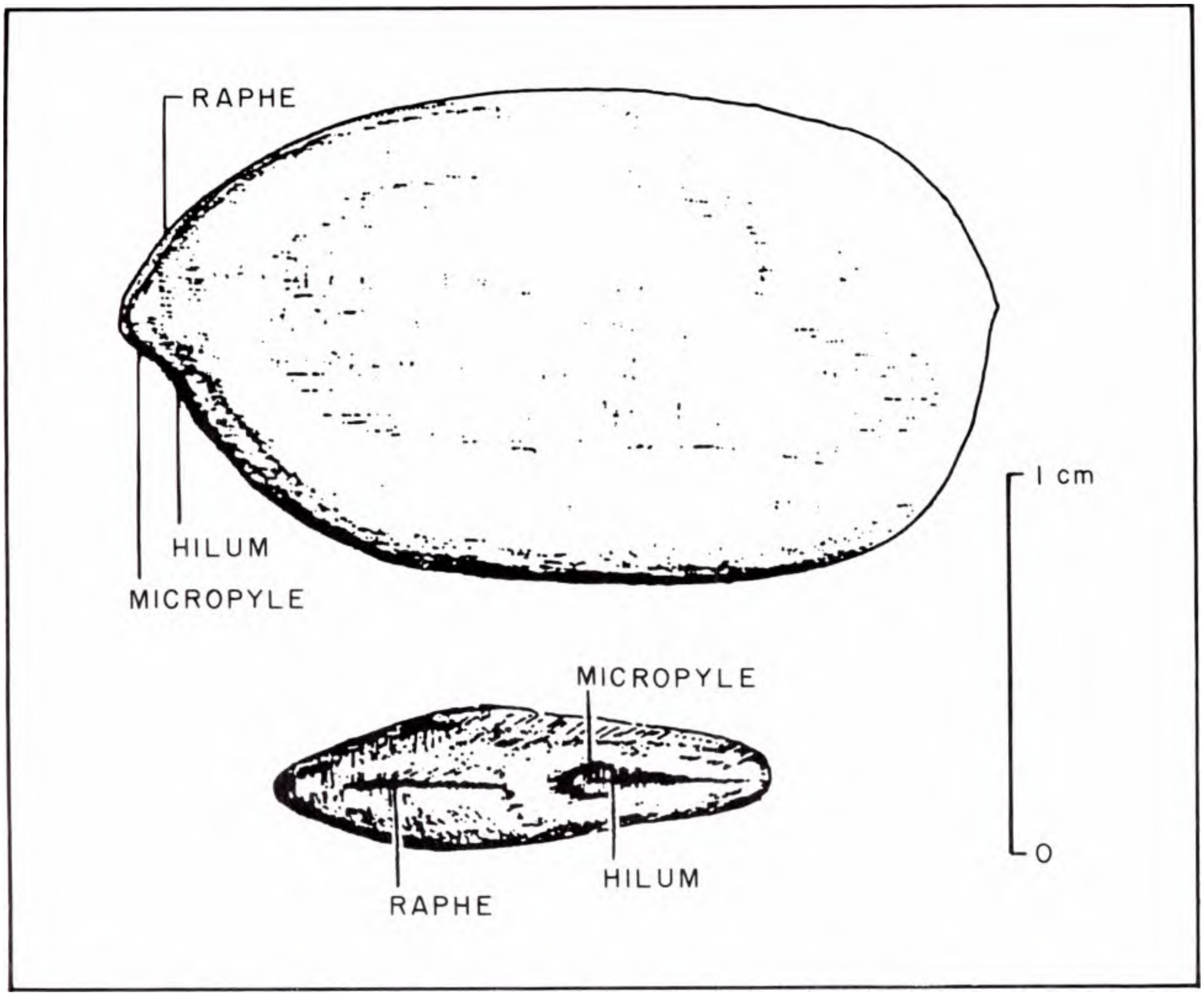


Figure 6. —*External morphology of a typical legume seed of* Schizolobium parahybium *(adapted from Trivirio and others 1990) [figure 3 in Student Outline].*

(g) **sclerenchyma** —thick, lignified cells

b. Gymnosperms — Fertilization stimulates growth of conelets and development of the embryo; female gametophytic tissue is already present when fertilization occurs. Many conifers flower and ripen seeds in one growing season, but some require two seasons, and a few require three seasons (pines require 2.25 years from formation of flower primordia to seed dispersal) (fig. 2) [figure 1 in Student Outline'.

2. **Physiological development**

a. Moisture content increases rapidly after fertilization and decreases at maturity. There is evidence that a desiccation period is required before all germination and growth enzymes can be synthesized in orthodox seeds (fig. 8) [no equivalent figure in Student Outline]. In recalcitrant seeds there is only slight desiccation before maturity (fig. 9) [no equivalent figure in Student Outline].

b. Hormone contents are higher where meristematic activity is greater, that is in immature (maturing) seeds.

c. Metabolic changes are many; simple sugars, fatty acids, and amino acids are converted to proteins, oils, and lipids (fig. 10) [no equivalent figure in Student Outline 1.

3. **Classification of mature fruits** (see table 1) [table 1 in Student Outline]

H. Sources

For additional information, see Dogra 1983; Hardin 1960; Hartmann and others 1983, chap. 3, p. 59-65; Krugman and others 1974; Willan 1985, p. 7-10, 13-15.

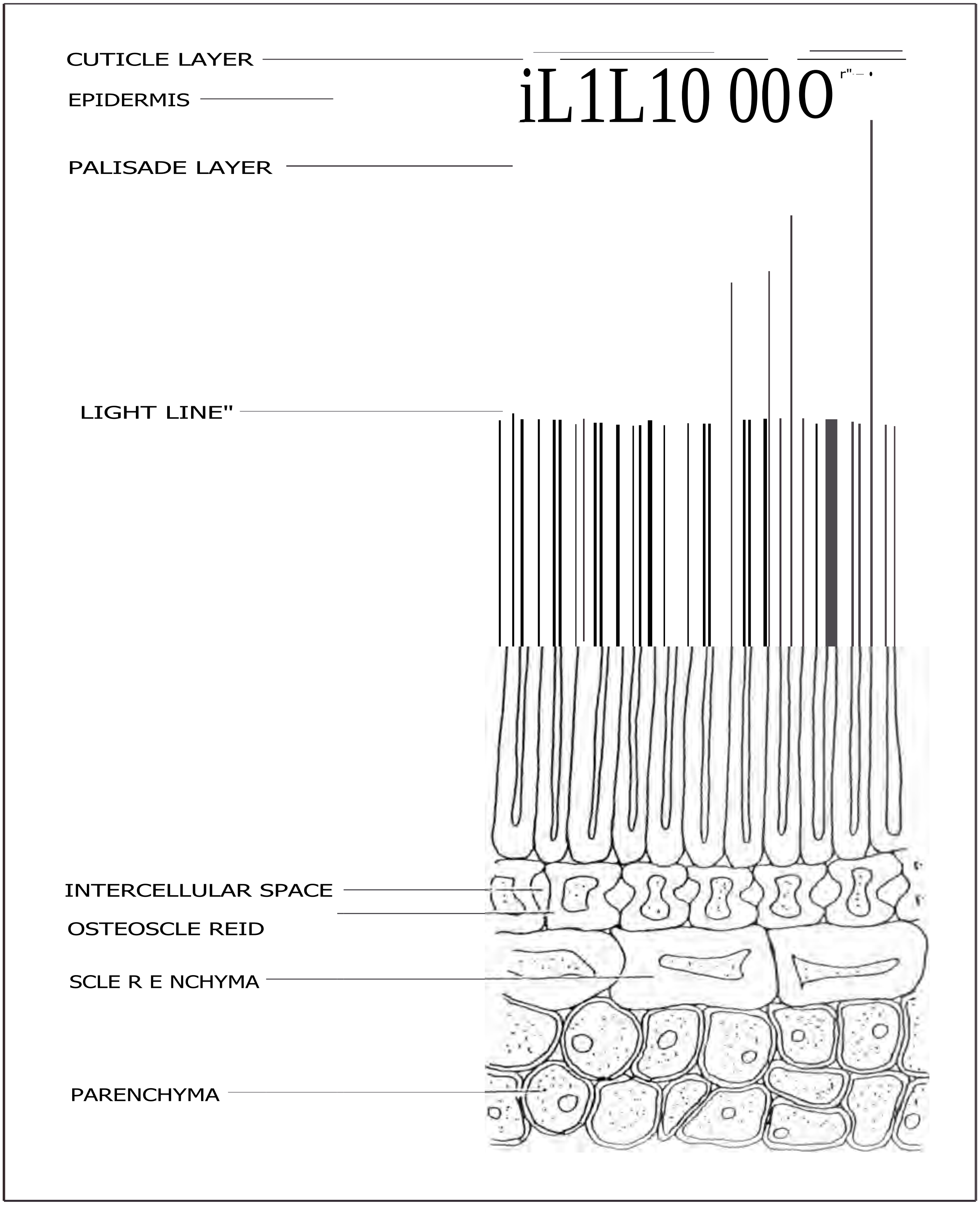


Figure *7. —Partial section through the seedcoat of a hard seed (legume) [figure 4 in Student Outline].*

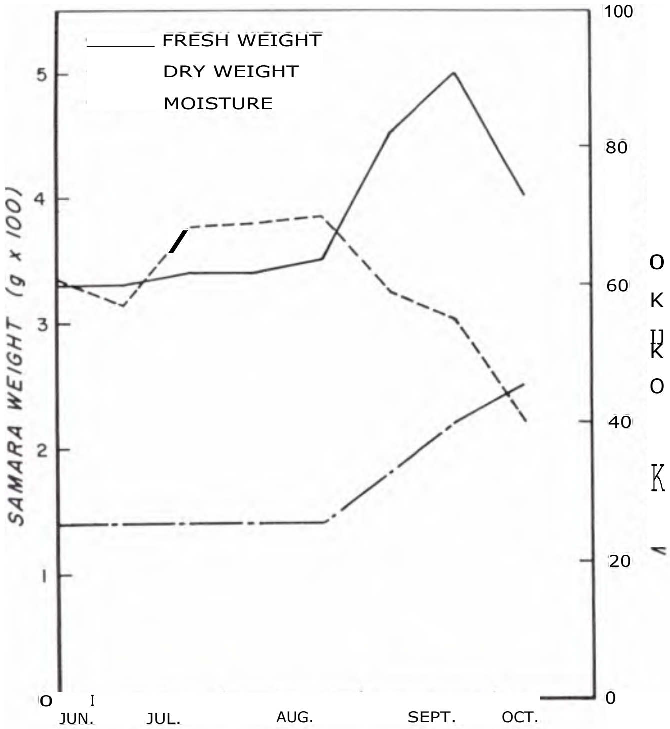


Figure 8.— *Seasonal changes in fresh weight, dry weight, and moisture content during maturation of samaras of* Fraxinus pennsylvanica *(adapted from Bonner 1973) [no equivalent figure in Student Outline].*

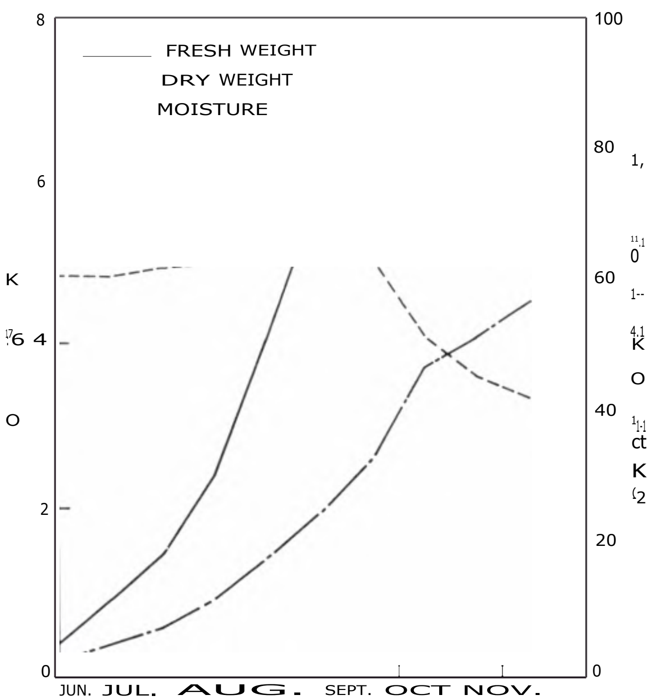


Figure 9. — *Seasonal changes in fresh weight, dry weight, and moisture content during maturation of* Quercus shumardii *acorns (adapted from Bonner 1976) [no equivalent figure in Student Outline].*

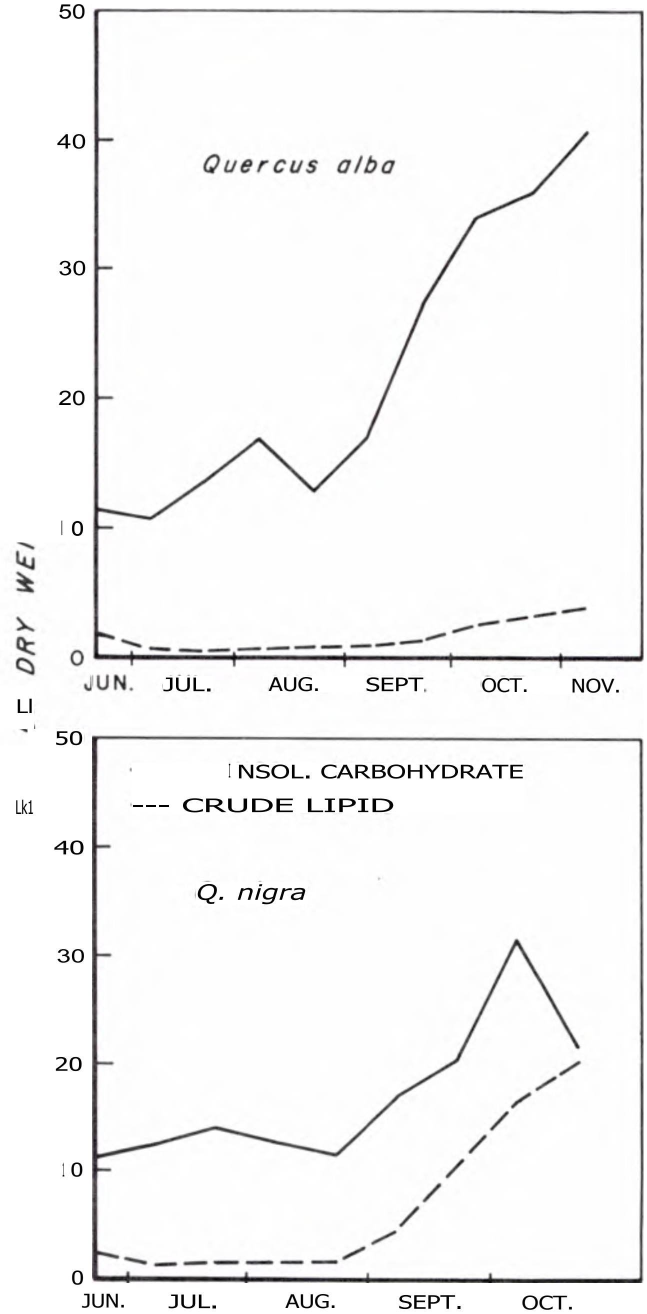


Figure 10. — *Changes in insoluble carbohydrate and crude lipid fractions in maturing acorns of* Quercus alba *and* Q. nigra *(adapted from Bonner 1974b, 1976) [no equivalent figure in Student Outline].*

Table 1.— *Common fruit types for woody trees (adapted from Hardin 1960) [table 1 in Student Outline]*

| Description | Type | Example |
|---|---|---|
| **Simple Fruit** (product of single pistil) | | |
| Dehiscent walls (splitting naturally) | | |
| Product of one carpel | | |
| Dehiscing by one suture | Follicle | *Zanthoxylum* |
| Dehiscing by two sutures | Legume | *Acacia, Prosopis, Robinia* |
| Product of two or more carpels | Capsule | *Eucalyptus, Populus* |
| Walls indehiscent (not splitting naturally) | | |
| Exocarp fleshy or leathery | | |
| Pericarp fleshy throughout | Berry | *Vaccinium, Diospyros* |
| Pericarp heterogeneous | | |
| Exocarp leathery rind | Hesperidium | *Citrus* |
| Exocarp fleshy | | |
| Endocarp a "stone" | Drupe | *Prunus, Vitex, Tectona* |
| Endocarp cartilaginous | Pome | *Malus, Crataegus* |
| Exocarp dry (papery, woody, or fibrous) | | |
| Fruit winged | Samara | *Triplochiton, Terminalia, Acer* |
| Fruit without wings | | |
| One-loculed ovary; thin wall; small seed | Achene | *Platanus, Cordia* |
| Several-loculed ovary; thick wall; large seed | Nut | *Quercus* |
| **Compound Fruit** (product of multiple pistils) | | |
| Pistils of a single flower | Aggregate | *Magnolia* |
| Pistils from different flowers (inflorescence) | Multiple | *Platanus* |

## II. Seed Dormancy

A. Introduction

Once seeds have matured, survival of the species requires that they germinate at a time and place favorable for growth and survival of the seedlings. The mechanism that prevents germination at undesirable times is called dormancy. The mechanics of seed dormancy must be known before nursery practices for overcoming dormancy can be developed to ensure timely germination and uniform growth of the seedlings.

B. Objectives

1. Describe the different types of seed dormancy.
2. Discuss methods for overcoming seed dormancy, both for germination testing and for nursery operations.

C. Key Points

The following points are essential to understanding seed dormancy:

1. To a large degree, dormancy is under genetic control.
2. Environmental conditions during seed maturation can influence the degree of dormancy.
3. Seeds can have more than one type of dormancy mechanism.
4. Postharvest environment can create secondary dormancy.
5. The distinction between "dormancy" and "delayed germination" is not always clear.
6. The least severe treatment to overcome dormancy should be tested first to avoid damage to the seeds; then increasingly severe treatments can be tested as needed.

D. Definition of Terms (Bonner 1984a)

1. Afterripening — physiological process in seeds after harvest or abscission that occurs before, and is often necessary for, germination or resumption of growth under favorable environmental conditions.
2. **Dormancy** — a physiological state in which a seed disposed to germinate does not, even in the presence of favorable environmental conditions.
3. **Chilling** — subjection of seeds to cold and moisture to induce afterripening.
4. **Prechilling** —cold, moist treatment applied to seeds to hasten afterripening or to overcome dormancy before sowing in soil or germinating in the laboratory.
5. **Pretreatment** — any kind of treatment applied to seeds to overcome dormancy and hasten germination.
6. **Scarification** — weakening of seedcoats, usually by mechanical abrasion or by brief

soaks in strong acids, to increase their permeability to water and gases or to lower their mechanical resistance to swelling embryos.

7. **Stratification—placing** seeds in a moist medium, often in alternate layers, to hasten afterripening or to overcome dormancy. Commonly applied to any technique that keeps seeds in a cold, moist environment, it is sometimes used to describe warm stratification (warm incubation).
8. **Delayed germination—** a general term applied to seeds that do not germinate immediately but are not slow enough to be described as dormant.

E. Types of Dormancy

Many different classifications of dormancy have been used by seed scientists. Because there is no universal agreement on the subject, anyone can devise a system. However, most workers accept the following classifications:

1. **Seedcoat (or external) dormancy**
   a. Impermeability to moisture or gases; e.g., *Acacia, Prosopis, Robinia,* and other legumes
   b. Mechanical resistance to swelling embryo; e.g., *Pinus* and *Quercus.* (Mechanical resistance frequently contributes to seedcoat dormancy but is seldom the primary factor.)
2. **Embryo (or internal) dormancy**
   a. Inhibiting substances usually within the embryo or surrounding tissues; e.g., *Fraxinus, Ilex,* and *Magnolia.*
   b. Physiological immaturity—Some enzyme system or crucial metabolite may not be "in place"; e.g., *Juniperus uirginiana.* (Supporting data are weak for this type of dormancy.)
3. **Morphological dormancy** results from the embryo not being completely developed when the seeds are disseminated; additional growth is required; e.g., *Ilex opaca* and some *Fraxinus* spp. and *Pinus* spp. in northern latitudes or high elevations. Morphological dormancy is similar to physiological immaturity.
4. **Secondary dormancy** results from some action, treatment, or injury to seeds during collecting, handling, or sowing; e.g.; *Pinus taeda* being exposed to high temperatures and moisture during storage.
5. **Combined dormancy** results from two or more primary factors, such as seedcoat dormancy and embryo dormancy; e.g., *Tilia,* which has a very hard seedcoat, plus embryo dormancy that requires stratification.
6. **Double dormancy** results from embryo dormancy in both the radicle and epicotyl. Double dormancy is difficult to demonstrate but apparently common in *Prunus.* In some *Quercus* species, radicles are nondormant, while epicotyls have a dormancy.

F. Overcoming Dormancy

1. **Seedcoat dormancy—** Treatment must increase moisture uptake and gas exchange and ease radicle emergence. Try the gentlest method first; then increase the severity of the method until success is achieved.
   a. Cold water soak— Soak seeds in water at room temperature for 24 to 48 hours. This method softens seedcoats and may remove inhibiting substances in the outer coverings. Change the soak water every 12 to 24 hours if inhibitors are present.
   b. Hot water soak—Bring water to a boil, put seeds in, remove from heat, and allow to stand until water cools. Hot water softens the seedcoat, and imbibition occurs as the water cools. Some workers prescribe a specific period for the hot water soak, but seed variation prohibits such specific recommendations for most species.
   c. Hot wire —Use a heated needle or electric woodburner to burn a small hole through the seedcoats. Hot wire is a promising new method. Once "burned," seeds can be shipped or even stored without damage; the length of storage is still being tested, but at least several months are possible. The method works on all hard-seeded species, not just legumes.
   d. Acid treatment —Pour a strong mineral acid over the seeds and mix. (Sulfuric acid is preferred.) Remove the seeds after a time determined by trials with samples, usually 15 to 60 minutes, and wash thoroughly to remove acid from the surface. Seeds scarified by water soaks or acid cannot be returned to storage. Acid treatment has three disadvantages:
      (1) Excessive treatment can harm seeds.
      (2) Acid is expensive.
      (3) Unskilled workers may be injured.
   e. Physical scarification — Crack or break the hard seedcoats.
      (1) Use hand methods (nicking) with

files, knives, clippers, sandpaper, etc.

(2) Use mechanical methods for large quantities including motor-driven scarifiers, cement mixers with rocks, or the impact machine recently developed by DANIDA (Stubsgaard 1986) for *Prosopis* and *Acacia.*

2. **Embryo dormancy —** Treatment must overcome physiological barriers within the seeds.

a. Stratification (chilling and prechilling) — Refrigerate fully imbibed seeds at 1 to 5 °C for 1 to 6 months. Primarily for Temperate Zone species, this treatment simulates natural winter conditions after seeds fall. Many nondormant seeds respond to short stratification periods (1 to 2 weeks) with faster and often more complete germination. One benefit that nurseries often overlook is the delay of early germination by low temperature, which produces a big flush of germination when high temperature is encountered (table 2) [table 2 in Student Outline]. During stratification:

(1) Imbibition is completed.

(2) Enzyme systems are activated.

(3) Storage foods change to soluble forms.

(4) Inhibitor/promoter balances change.

b. Incubation/stratification — Some species respond to a short, warm incubation (15 to 20 °C), followed by cold stratification.

c. Chemical treatment — Some species respond to chemical stimuli well enough to justify treatment.

(1) Hydrogen peroxide—Soak for 48 hours in a 1-percent hydrogen peroxide solution *(Pseudotsuga menziesii).*

(2) Citric acid—Soak for 48 hours in 1-percent citric acid solution, followed by 90-day stratification *(Juniperus, Taxodium distichum).*

(3) Gibberellins — Many species respond in the laboratory, but field results are lacking or rare.

(4) Ethylene—Treat seeds for 48 hours with 0.021 M Ethrel solution (reported to help germination for *Ricinodendron rautentenii* in South Africa).

d. Light — Provide light treatments (red/far-red mechanism) *(Betula).*

G. Significance

1. **Survival strategy—Dormancy** allows germination during favorable environmental conditions. It also permits seed survival in litter or soil for several years, even in the Tropics.

Table 2. —*Recommended prechill periods for nursery sowing of some pines of the Southern United States (Bonner 19916) [Table 2 in Student Outline]*

| Pine species | Normal sowing* | | Early sowings | Seed conditions | |
|---|---|---|---|---|---|
| | Fresh seed | Stored seed | | Deep dormancy | Low vigor |
| | | | Prechil I *(Days)* | - - - - - - - - - - - - - - - - - - | |
| *Pinus strobus* | 30-60 | 60 | 60-90 | 60-90 | 30 |
| *P. taeda* | 30-60 | 30-60 | 60 | 60-90 | 20-30 |
| *P. palustris* | 0 | 0 | ... | 0-15 | 0 |
| P *rigida* | 0 | 0-30 | | | ... |
| *P serotina* | *0* | 0-30 | | | |
| *R clausa* | | | | | |
| var. *immuginata* | 0-15 | 0-21 | | | |
| var. *clausa* | *0* | *0* | | | |
| *P echinata* | 0-15 | 0-30 | 15-30 | 30-60 | 0 |
| *P elliottii* | | | | | |
| var. *elliottii* | 0 | 0-30 | | 15-30 | 0 |
| var. *densa* | 30 | 0-30 | | | |
| *P glabra* | 30 | 30 | | | |
| *P virginiana* | 0-30 | 30 | 30 | | |

*Spring sowing when mean minimum soil temperature at seed depth is at least 10 °C.
tEarly sowing when soil temperatures at seed depth may be below 10 °C.
Wormancy demonstrated by paired tests or past performance of the seedlot.
§Conditions not encountered with this species.

2. **Genetic factor —** Dormancy in many seeds is under genetic control, particularly those with seedcoat dormancy because seedcoats are maternal tissue. Dormancy has been "bred out" of most agricultural crops.
3. **Multiple causes—Many** species have probably evolved with more than one dormancy mechanism; that is, if one fails, another is in place. *Quercus nigra is* a good example, with probably three separate mechanisms.
4. **Environmental influence—Hot,** dry weather during maturation may increase dormancy, particularly that associated with seedcoats. Research is just beginning to show this effect in trees.

**H.** Sources

For additional information, see Khan 1984; Krugman and others 1974; Murray 1984b; Nikolaeva 1967; Willan 1985, p. 17-19, chap. 8.

## III. Germination

A. Introduction

The goals of seed technology are successful germination and seedling establishment. The two major considerations are the physiology of the seed and the condition of the environment. In the two preceding sections, seed maturation and dormancy were considered. **In** this section, environmental factors and how they control germination through their interactions with seed biology will be examined.

B. Objectives

1. Describe the two types of germination and their importance in woody plants.
2. Review environmental requirements for germination.
3. Review physiological changes within seeds that lead to germination.
4. Discuss how seed physiology and environmental factors interact in germination.

C. Key Points

The following points are essential to understanding germination:

1. The two types of germination are epigeous and hypogeous.
2. Moisture availability is the primary factor controlling germination.
3. The effects of temperature and light on germination are strongly related.
4. Constant and alternating temperature regimes may lead to similar total germination, but germination is usually faster under alternating regimes.
5. As germination begins, the key to internal processes is the change from insoluble to soluble metabolites. Details of such metabolism are beyond the scope of this course.

D. Types of Germination

1. **Epigeous (epigeal)** germination occurs when cotyledons are forced above the ground by elongation of the hypocotyl (fig. 11) [figure 5 in Student Outline]; e.g., *Pinus, Acacia, Fraxinus,* and *Populus.*
2. **Hypogeous (hypogeal)** germination occurs when the cotyledons remain below ground while the epicotyl elongates (fig. 12) [figure 6 in Student Outline]; e.g., *Juglans, Quercus,* and *Shorea.*
3. In *Prunus,* both types of germination may be found (fig. 13) [no equivalent figure in Student Outline].

E. Environmental Requirements for Germination

The four primary environmental requirements for germination are moisture, temperature, light, and gases.

1. **Moisture**
   a. Imbibition is usually considered the first step in germination; thus, availability of moisture is the first requirement for germination.
   b. Uptake typically occurs in the following three phases:
      (1) A rapid, mainly physical, initial phase that occurs in dead seeds as well as live ones.
      (2) An extremely slow second phase, the "flat" portion of the uptake curve. The greater the dormancy, the longer this phase takes.
      (3) A rapid third phase that occurs as metabolism becomes very active. Some evidence suggests that splitting of seedcoats by emerging radicles is required for the most rapid examples of this phase.
   c. The first phase is imbibitional; it releases energy in the form of heat, displaces gases, and creates great imbibitional pressure via colloidal swelling (proteins).
   d. A minimum state of hydration is needed within a seed for mobilization of food reserves and activation of enzyme systems.
   e. Minimal requirements for germination are frequently studied with osmotic solutions of mannitol or polyethylene glycol.
      (1) The best germination may occur at slight moisture stress (0.005 to

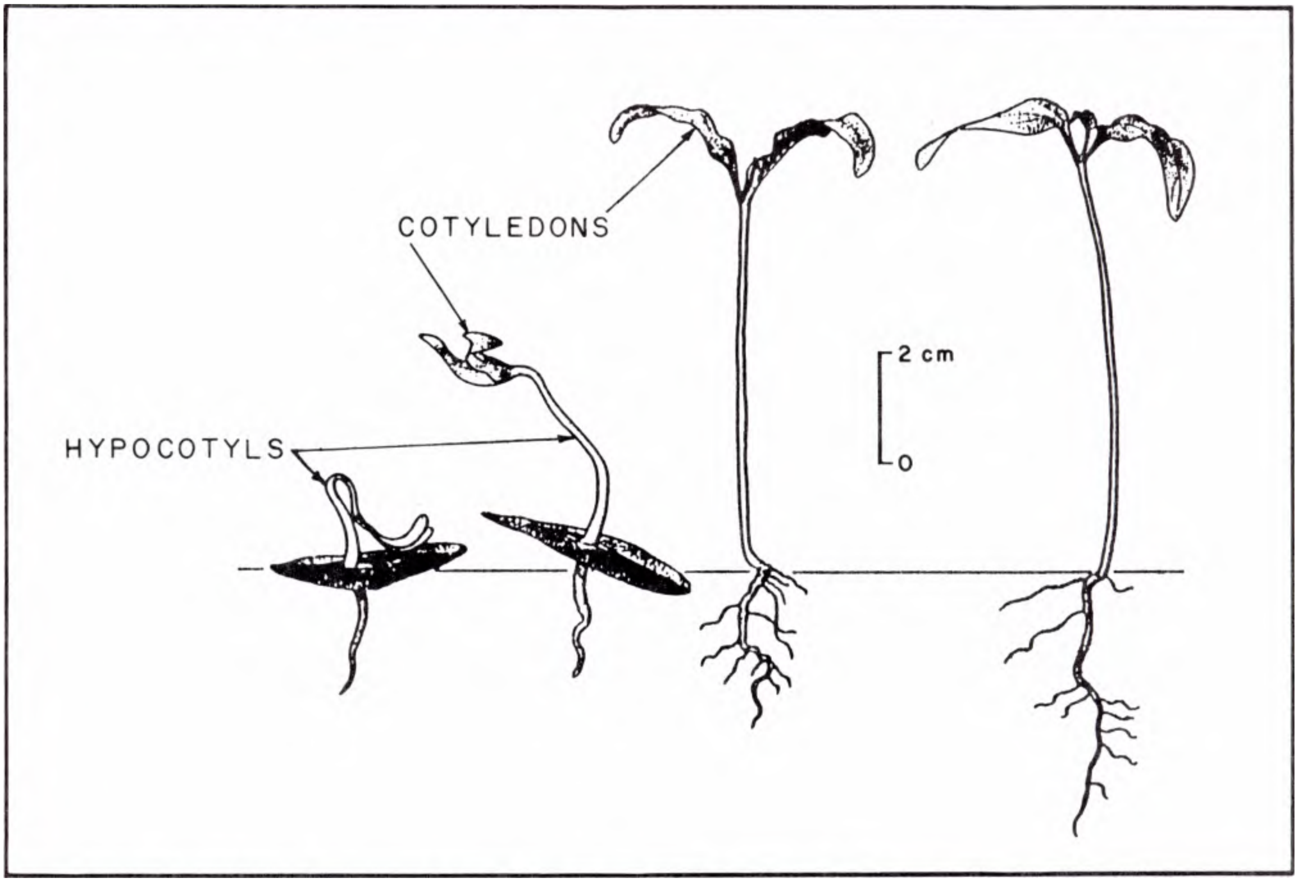


Figure 11 . —*Epigeal germination sequence of* Fraxinus *spp. (adapted from Bonner 1974a) [figure 5 in Student Outline).*

0.500 bars); zero stress may form a film of water around the seed, inhibiting oxygen uptake.

(2) Even slightly lowered water potentials will slow, but not stop, germination.

(3) Critical levels of water potential vary by species (table 3) [no equivalent table in Student Outline]. Germination stops in 12 European conifers at — 8 to — 12 bars.

2. **Temperature**

a. It is difficult to separate the effects of temperature from those of light and moisture.

b. Woody species usually germinate over a wide range of temperatures; the germination rate is strongly temperature dependent. Some Temperate Zone species will eventually germinate in stratification.

c. The upper limit of temperature is around 45 °C. Many species begin germinating above 40 °C, but seedlings are abnormal.

d. The lower limit is around 3 to 5 °C because germination processes will occur near freezing with emergence of radicle and plumule; however, few species can produce normal seedlings under these conditions. *Picea mariana* (black spruce) is one that can.

e. Optimum temperatures are as follows:

(1) For Temperate Zone species, alternating regimes of 20 °C (night) and 30 °C (day) have proved best for many species; similar results can be obtained at constant temperatures of about 25 °C, but germination rates are almost always greater with alternating regimes. Amplitude (10 to 12 °C), not cardinal points, seems to be most important (within limits).

(2) For tropical species, although few critical studies are available, constant temperatures may be best, although optimums are not necessarily higher than those of temperate species. Examples include: *Azadirachta indica,* 25 °C; *Bombax ceiba,* 25 °C; *Eucalyptus camaldulensis,* 30 °C; *Leucaena leucocephala,* 30 °C; *Prosopis cineraria,*

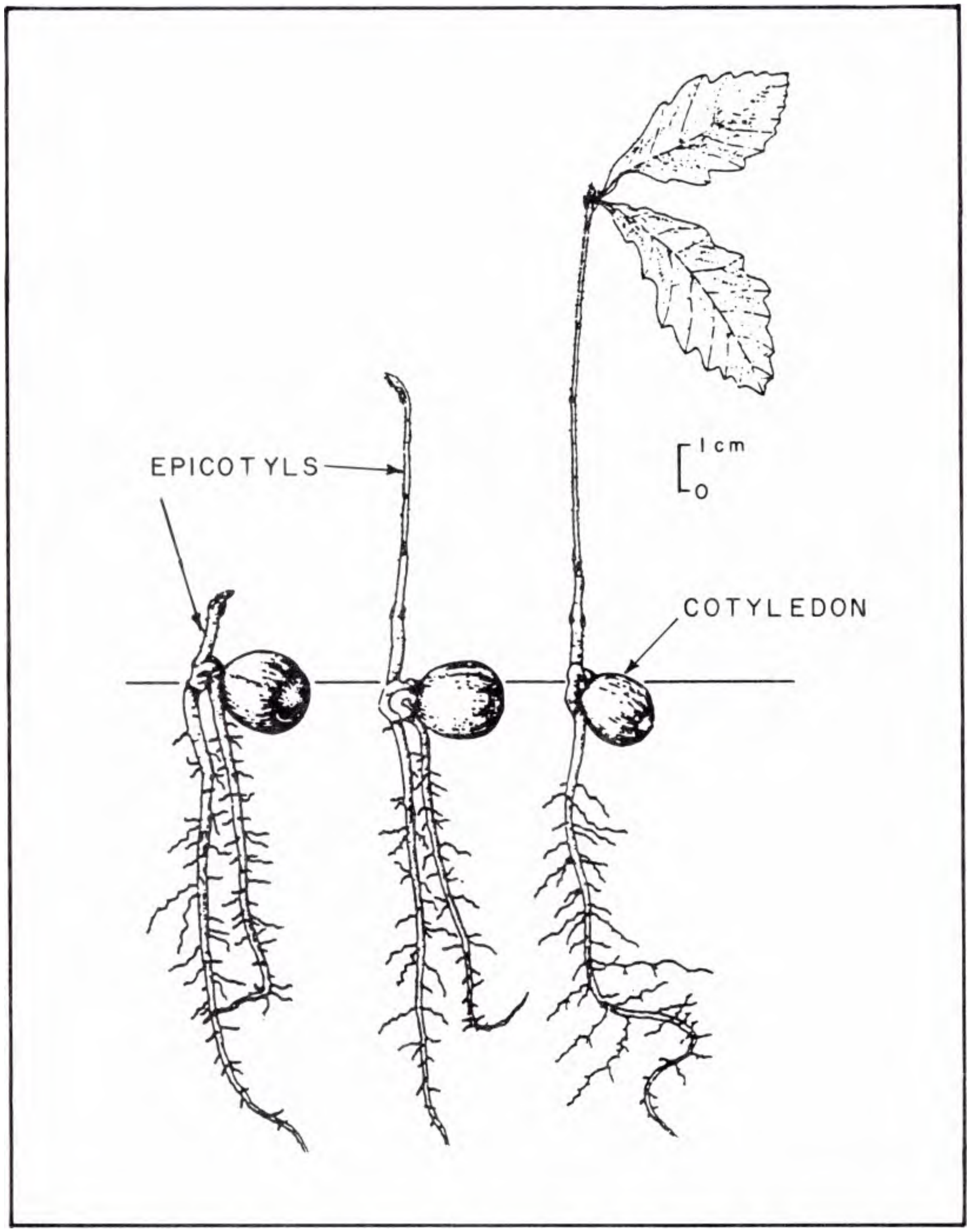


Figure 12. —*Hypogeal germination sequence of* Quercus *spp. (adapted from Olson 1974) [figure 6 in Student Outline].*

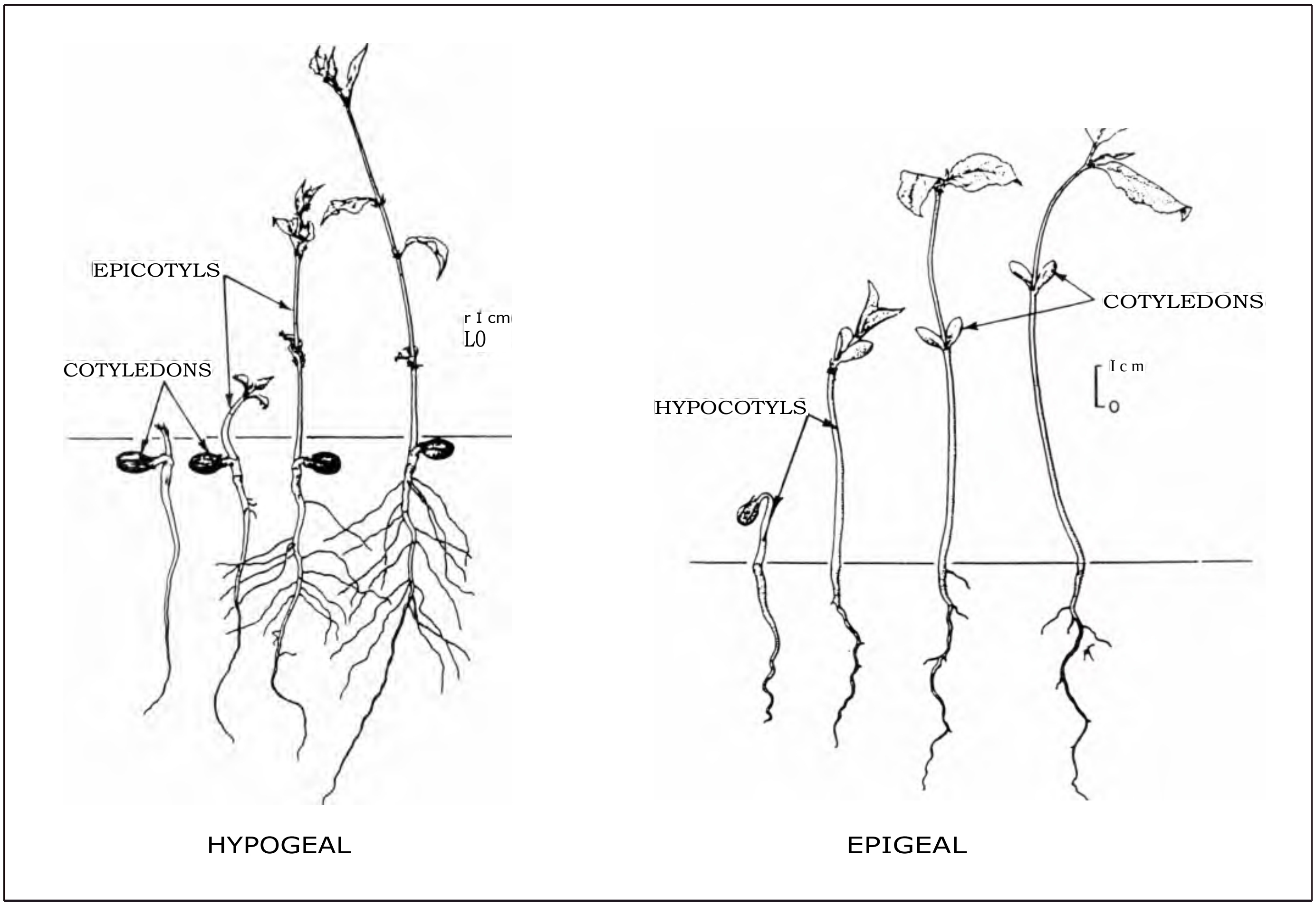


Figure 13.—*Both epigeal and hypogeal germination as they occur in* Prunus *spp. (adapted from Grisez 1974) [no equivalent figure in Student Outline].*

Table 3. — *Critical levels of water potential for germination [no equivalent table in Student Outline]*

| Species | Germination: Significantly decreased | Germination: Effectively stopped | Reference |
|---|---|---|---|
| | Bars* -------- | | |
| *Pinus ponderosa* | −4 | −8 | Djavanshir and Reid 1975 |
| *R eldarica* | −6 | −12 | Djavanshir and Reid 1975 |
| *Populus ciliata* | −1 | −3 | Singh and Singh 1983 |
| *Quercus palustris* | −5 | −20 | Bonner 1968 |

'1 bar equals 0.1 MPa.

30 °C; and *Tectona grandis,* 30 °C. Other species do as well or even better under alternating temperatures; e.g., *Acacia* spp., *Cedrela* spp., and tropical *Pinus* species.

3. **Light**
   a. Light stimulates germination of many tree seeds but is necessary for few, if any. Stratification or high temperature can sometimes overcome dark inhibition, probably through the phytochrome system.
   b. Phytochrome is a pigment involved in the photocontrol of germination. It exists in two reversible forms. One form, Pr, has a maximum absorption at 6,600 Å, while the other, Pfr, has a maximum absorption at 7,300 Å. Less than a second of exposure to red light can supply the stimulation, which increases as seed moisture increases. Among trees, it has been shown to occur in *P. taeda* and *Betula pubescens.* The exact mechanisms of this action are still unknown. The general reaction is as follows:

$$\mathrm{Pr} \underset{\text{far red light}}{\overset{\text{red light}}{\rightleftharpoons}} \mathrm{Pfr} \rightarrow \text{dormancy removal}$$

   c. In germination testing, minimal light levels should be 75 to 125 fc (750 to 1,250 lux). Light is usually supplied during testing of all species, even to those that do not require it or to those that have been stratified.
4. Gases
   a. Respiration requires a certain supply of oxygen, and the carbon dioxide produced must be removed. High levels of carbon dioxide can inhibit germination of most species, while lowering oxygen can do the same. Excessive moisture on germination test blotters will retard germination of many species.
   b. Some species germinate well in anaerobic conditions, even under water.
   c. Oxygen uptake patterns in seeds are similar to those of moisture.
   d. Many aspects of the influences of gases on germination need to be studied.

F. Internal Physiological Changes

1. **Structural changes — Imbibition** is a precursor to necessary metabolism through its role in restoring structural integrity in membranes and organelles.
2. **Enzymes—Some** systems are present in dry seeds; others are synthesized as imbibition proceeds. In some species, a desiccation period at the end of maturity is necessary before rehydration to produce all the needed enzymes. No research on this subject has been done on tree seeds, but this finding can probably be assumed for orthodox species.
3. **Reserve food mobilization—Generally,** insoluble forms are converted to soluble forms (in some ways a reverse of maturation trends).
   a. Carbohydrates. Amylases are the primary enzyme systems to change starch to soluble sugars.
   b. Lipids. Lipase enzymes are important for these compounds; they separate fats into fatty acids and glycerol. Fatty acids then undergo beta-oxidation to acetyl coenzyme A, which enters the glyoxylate cycle, eventually showing up as carbohydrates.
   c. Proteins. Some proteins are important storage foods, but most tree seeds depend on carbohydrates and lipids.
4. **Nucleic acids —** These compounds are closely allied to the new enzymes formed during germination.
5. **Translocation—** The movement of materials within the embryo is crucial. In some plants, a stimulus originates from the radicle tip, which controls amylase activity. There are also other stimuli (possibly hormones) in cotyledons that are necessary for translocation in some species. These stimuli have been studied very little in tree seeds.

G. Sources

For additional information, see Bonner 1972, Mayer and Poljakoff-Mayber 1975, Murray 1984b, Stanwood and McDonald 1989, Willan 1985.