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.
2. **Genotype —** the genetic makeup of a cell nucleus or an individual.
3. **Phenotype** —the external appearance of an organism.
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.
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.
9. **Haploid** (1N)—one set of chromosomes in a cell nucleus.
10. **Fruit** —a ripened ovary, sometimes including accessory flower parts, that surrounds the seed in angiosperms.
11. **Seed—a** ripened ovule that consists of an embryo, its stored food supply, and protective coverings.
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.
3. Knowledge of the sexual cycle is needed for successful tree breeding and seed production.

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. Angiosperm seeds are enclosed in carpels.
   b. Gymnosperm seeds are borne naked on scales.

c. Seeds of nonconiferous gymnosperms are borne singly.

2. **Gymnosperm life cycle** (fig. 1)
   a. Sporophyte
   b. Strobilus or cone, including:
      (1) reproductive short shoot
      (2) staminate cone (male)
      (3) ovulate cone (female)
      (4) gymnosperms may be either monoecious (female and male strobili on same tree) or dioecious (tree has only one sex).
   c. Meiosis and gametophytes
   d. Fertilization
   e. Seed (fig. 2)
      (1) Develops from the fertilized ovule.
      (2) Contains an embryo (cotyledons, hypocotyl, radicle), a seedcoat, storage tissue, and sometimes a seed wing.
   f. Fruit
      (1) Gymnosperms do not have true "fruits."
      (2) Gymnosperm seeds are enclosed by the following structures:
         (a) dry ovulate cones (e.g., *Abies,*

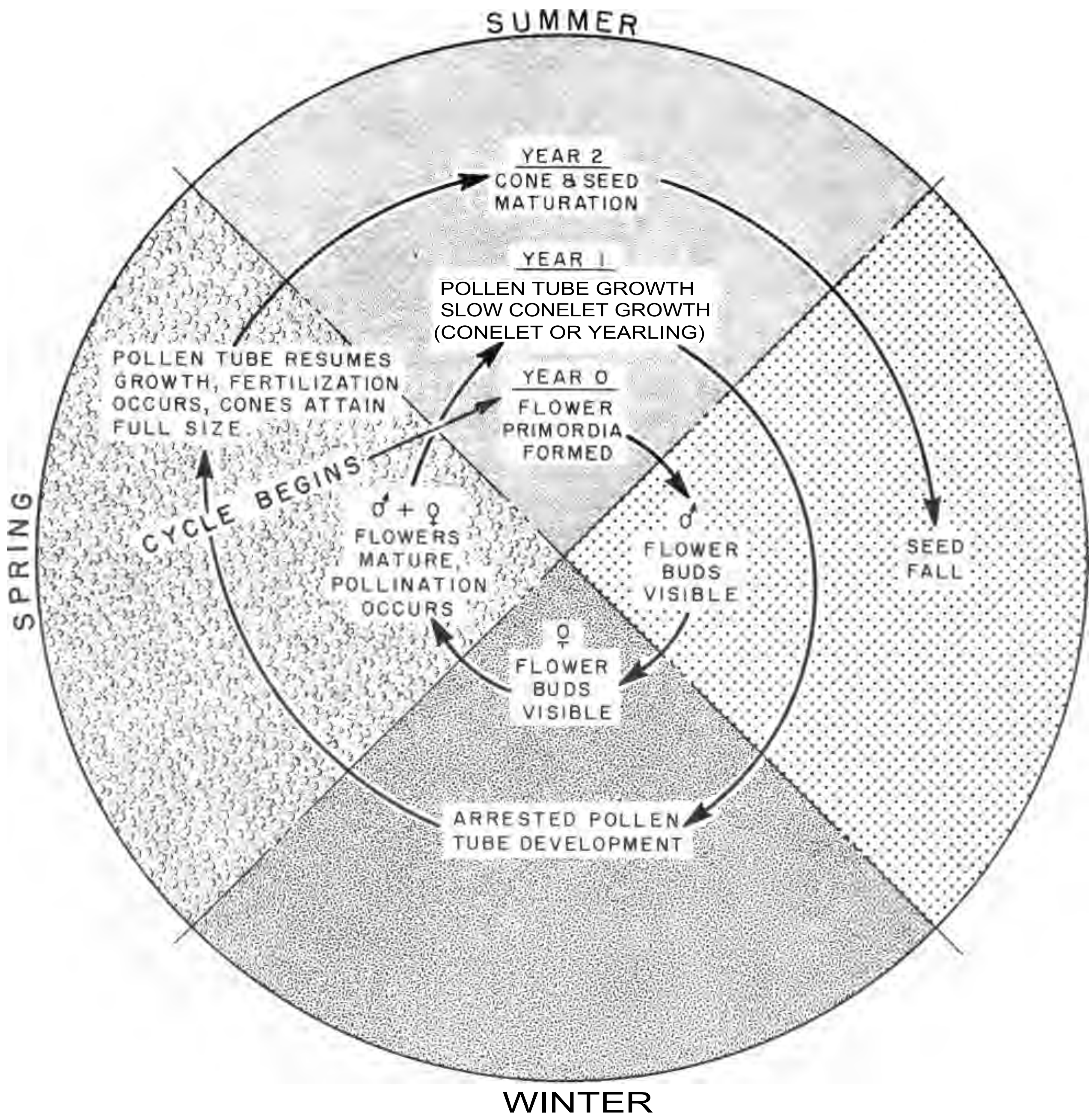

Figure 1. —*Life cycle of a gymnosperm* (Pinus *spp.) (Bonner 1991b).*

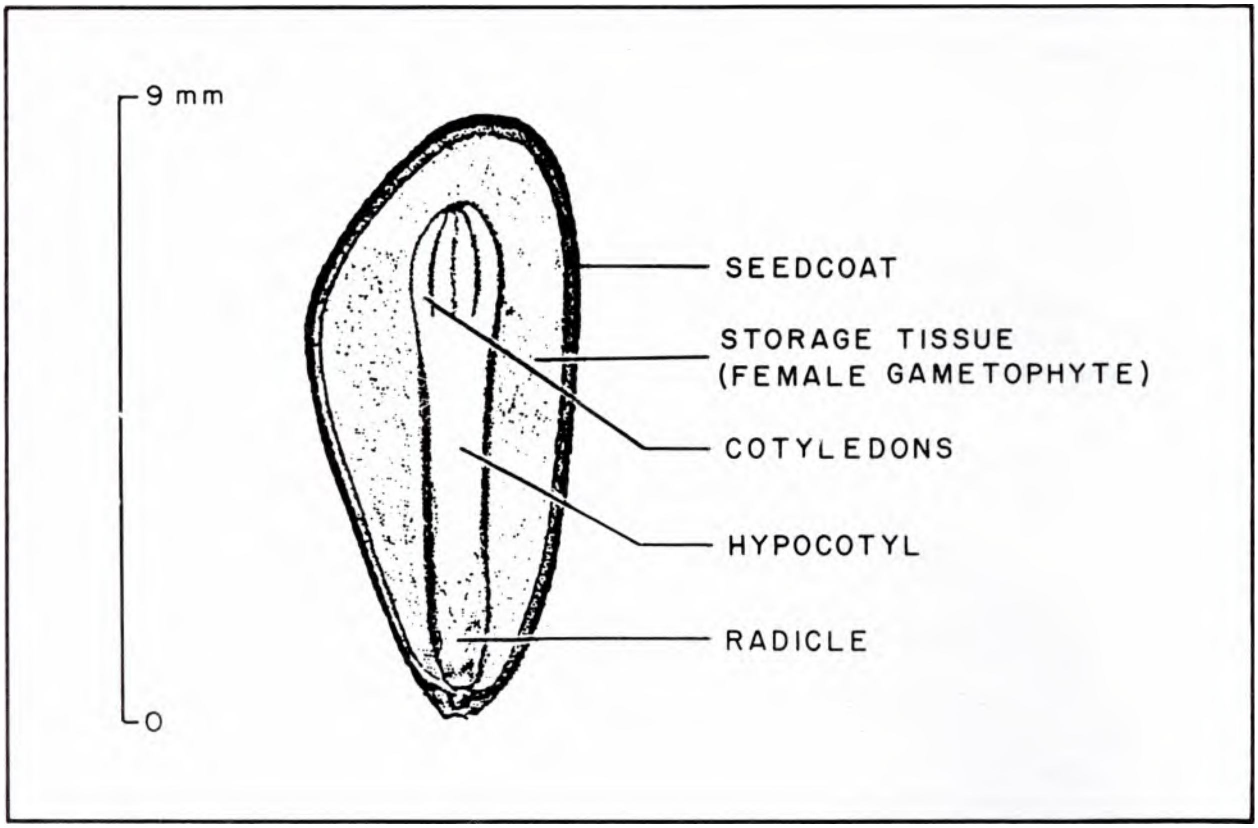

Figure 2. —*Cross section of a typical mature gymnosperm seed* (Pinus ponderosa) *(adapted from Krugman and Jenkinson 1974).*

Araucaria, Cupressus, Pinus, and *Tsuga)*
- (b) fleshy, arillike structures (e.g., *Ginkgo, Taxus,* and *Torreya)*
- (c) berrylike ovulate cones (e.g., *Juniperus)*

3. **Angiosperm life cycle**
   - a. Sporophyte
   - b. Flower—a short shoot with sterile and reproductive leaves.
     - (1) Sterile leaves include:
       - (a) sepals
       - (b) petals
       - (c) perianth
     - (2) Reproductive leaves include:
       - (a) stamen (male)
       - (b) carpel (female)
       - (c) pistil, a collective term that describes visible female structures
     - (3) Receptacle
     - (4) There are perfect flowers, imperfect flowers, and polygamous flowers
   - c. Meiosis and gametophytes
   - d. Fertilization
   - e. Seeds
     - (1) Develop from the double-fertilized ovules
     - (2) Contain an embryo (cotyledons, hypocotyl, radicle), storage tissue, seed coat, and sometimes other seed coverings
     - (3) May be endospermic or nonendospermic
   - f. Fruits
     - (1) Develop from the matured ovary
     - (2) Enclose the seed (matured ovule)
     - (3) Are difficult to separate from the seeds

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. Angiosperms have true flowers, but gymnosperms have strobili (cones).
   - c. Double fertilization takes place in angiosperms; single fertilization takes place in gymnosperms.
   - d. In gymnosperms, the developing embryo

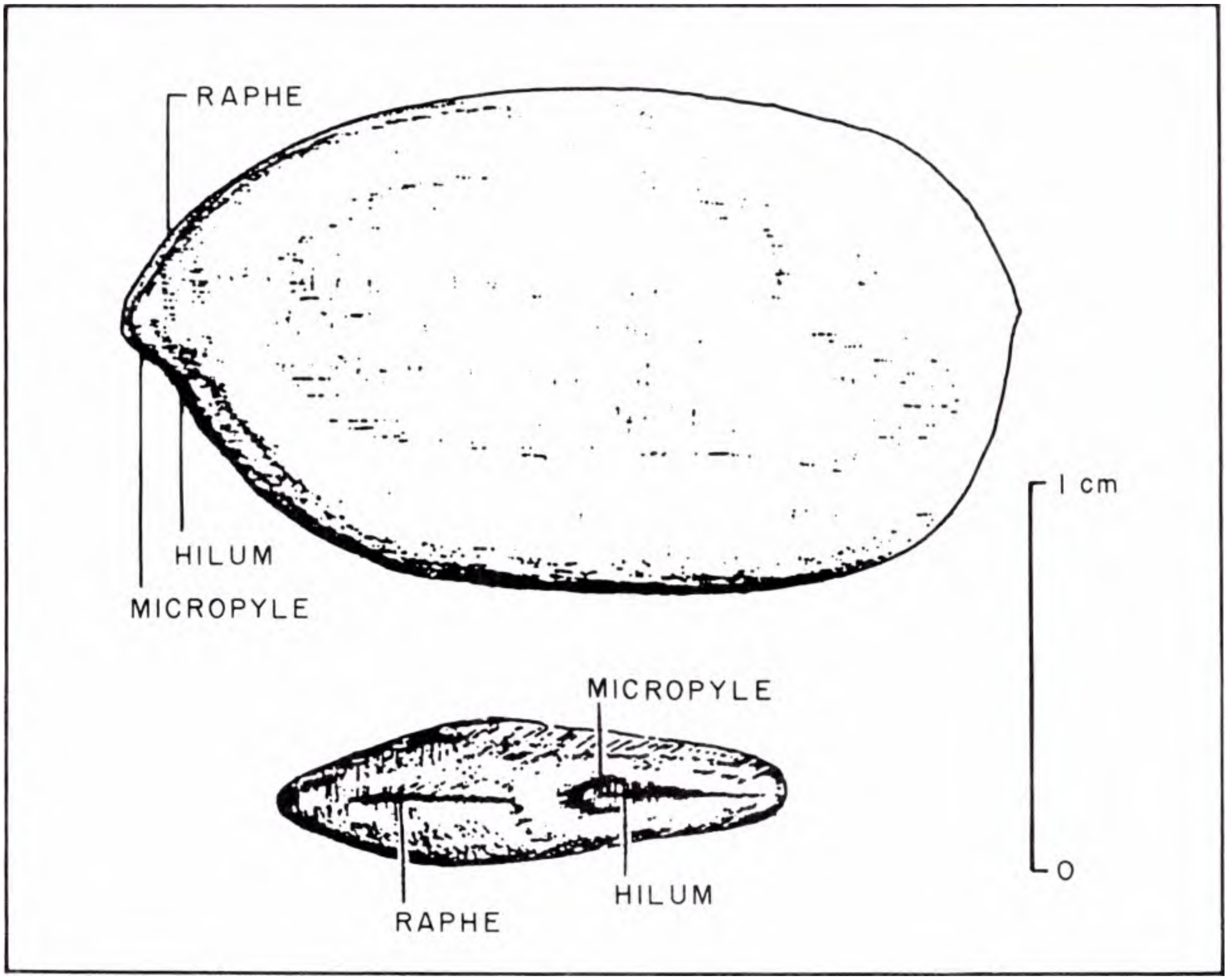

Figure 3. —*External morphology of a typical legume seed of* Schizolobium parahybium *(adapted from Trivino and others 1990).*

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

(b) cell divisions and enlargements

(2) Legumes have:

(a) a simple pistil with a superior ovary having one cavity (locule) (fig. 3)

(b) seedcoats composed of histologically dense cuticle, radial columnar cells, sclerenchymatous cells, lignin, and osteosclereid cells

(3) Structural terms relating to the seedcoat are defined as follows (fig. 4):

(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

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

b. Gymnosperms—Many conifers flower and ripen seeds in one growing season, some require two seasons, and a few require three seasons.

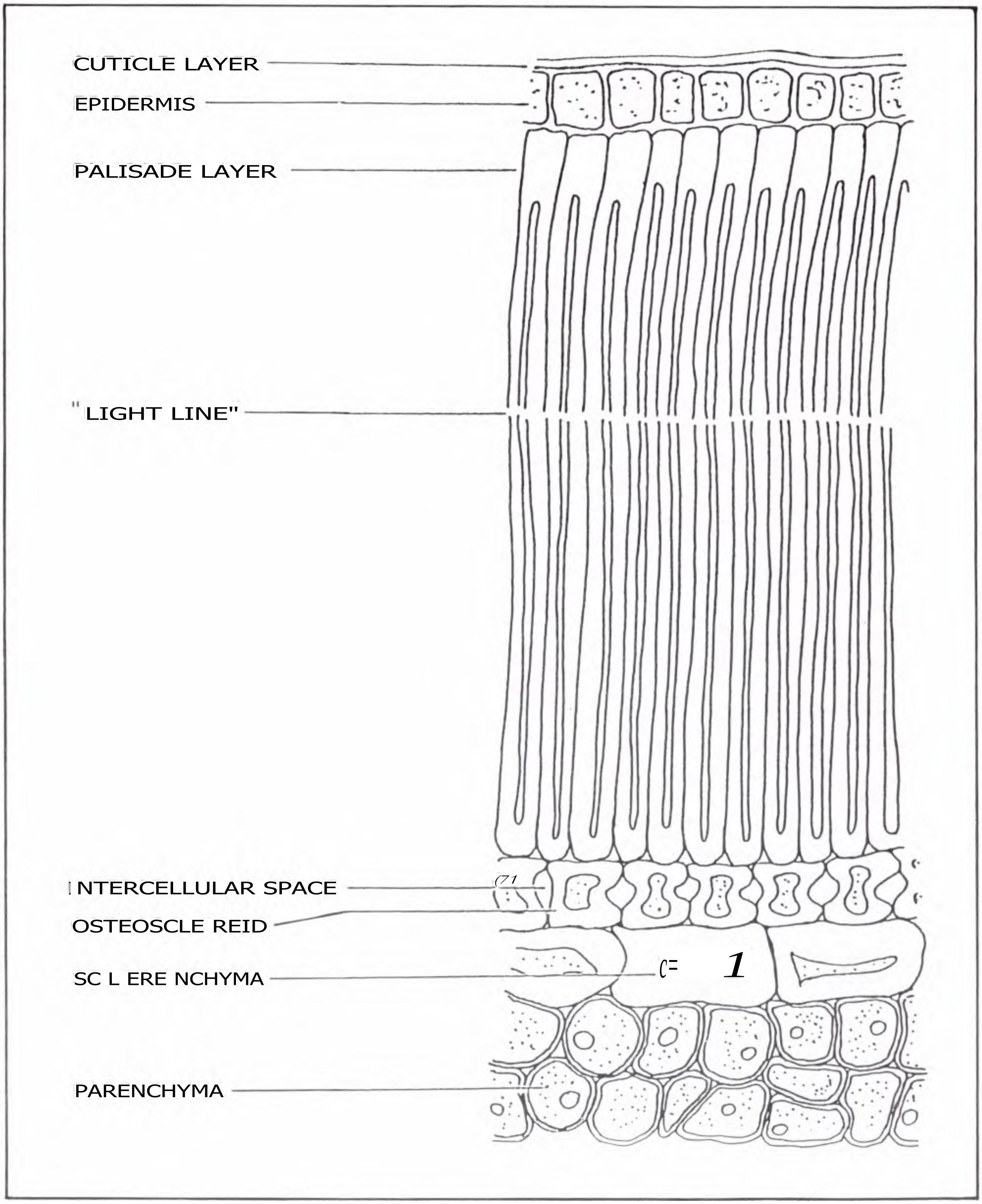

Figure 4. —*Partial section through the seedcoat of a hard seed (legume).*

2. **Physiological development**
   a. Moisture content increases rapidly after fertilization and decreases at maturity.
   b. Hormone contents are higher where meristematic activity is greater.
   c. Metabolic changes are many; simple sugars, fatty acids, and amino acids are converted to proteins, oils, and lipids.
3. **Classification of mature fruits** (table 1)

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.

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.

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.

Table 1. —*Common fruit types for woody trees (adapted from Hardin 1960)*

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*

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.
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

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.*
2. **Embryo (or internal) dormancy**
   a. Inhibiting substances; e.g., *Fraxinus, Ilex,* and *Magnolia*
   b. Physiological immaturity; e.g., *Juniperus virginiana*
3. **Morphological dormancy** results from the embryo not being completely developed; e,g., *Ilex opaca,* some *Fraxinus* spp., and *Pinus* spp.
4. **Secondary dormancy** results from some action, treatment, or injury to seeds; 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.*
6. **Double dormancy** results from embryo dormancy in both the radicle and epicotyl; e.g., *Prunus.*

F. Overcoming Dormancy

1. **Seedcoat dormancy—** Treatment must increase moisture uptake and gas exchange and ease radicle emergence.
   a. Cold water soak—Soak seeds in water at room temperature for 24 to 48 hours.
   b. Hot water soak—Bring water to a boil, put seeds in, remove from heat, and allow to stand until water cools.
   c. Hot wire—Use a heated needle or electric woodburner to burn a small hole through the seedcoats.
   d. Acid treatment — Pour a strong mineral acid over the seeds and mix. (Sulfuric acid is preferred.) Remove seeds after a time determined by trials with samples, usually 15 to 60 minutes, and wash thoroughly to remove acid.
   e. Physical scarification — Crack or break the hard seedcoats.
      (1) Use hand methods (nicking).
      (2) Use mechanical methods for large-scale operations.
2. **Embryo dormancy—** Treatment must overcome physiological barriers within the seeds.
   a. Stratification (chilling, prechilling) — Refrigerate fully imbibed seeds at 1 to 5 °C for 1 to 6 months (table 2).
      (1) Imbibition is completed.
      (2) Enzyme systems are activated.
      (3) Storage foods change to soluble forms.
      (4) Inhibitor/promoter balances change.
   b. Incubation/stratification — For some species, provide short, warm incubation (15 to 20 °C), followed by cold stratification.
   c. Chemical treatment
      (1) Hydrogen peroxide—Soak for 48 hours in 1-percent solution (e.g., *Pseudotsuga menziesii).*
      (2) Citric acid—Soak for 48 hours in 1-percent solution, followed by 90-day stratification (e.g., *Juniperus, Taxodium distichum).*
      (3) Gibberellins
      (4) Ethylene
   d. Light — Dormancy is overcome by the red/far-red mechanism.

G. Significance

1. **Survival strategy—Dormancy** allows germination during favorable environmental conditions.
2. **Genetic factor — Dormancy** in many seeds is under genetic control.
3. **Multiple causes—Many** species have probably evolved with more than one dormancy mechanism.

Table *2.—Recommended prechill periods for nursery sowing of some pines of the Southern United States (Bonner 1991b)*

Pine species	Normal sowing*		Early sowings	Seed conditions	
	Fresh seed	Stored seed		Deep dormancy	Low vigor
			Prechill *(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
R rigida	0	0-30			...
P. serotina	0	0-30			
P clausa					
var. *immuginata*	0-15	0-21			
var. *clausa*	0	0			
P. echinata	0-15	0-30	15-30	30-60	0
R 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.
' Early 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.

4. **Environmental influence — Weather** conditions during maturation may increase the degree of dormancy.

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. 5); e.g., *Pinus, Acacia, Fraxinus,* and *Populus.*
2. **Hypogeous (hypogeal)** germination occurs when the cotyledons remain below ground while the epicotyl elongates (fig. 6); e.g., *Juglans, Quercus,* and *Shorea.*
3. In *Prunus,* both types of germination may be found.

E. Environmental Requirements for Germination
The four environmental requirements for germination are moisture, temperature, light, and gases.
1. **Moisture**
a. Imbibition is usually considered the first step in germination; thus, avail-

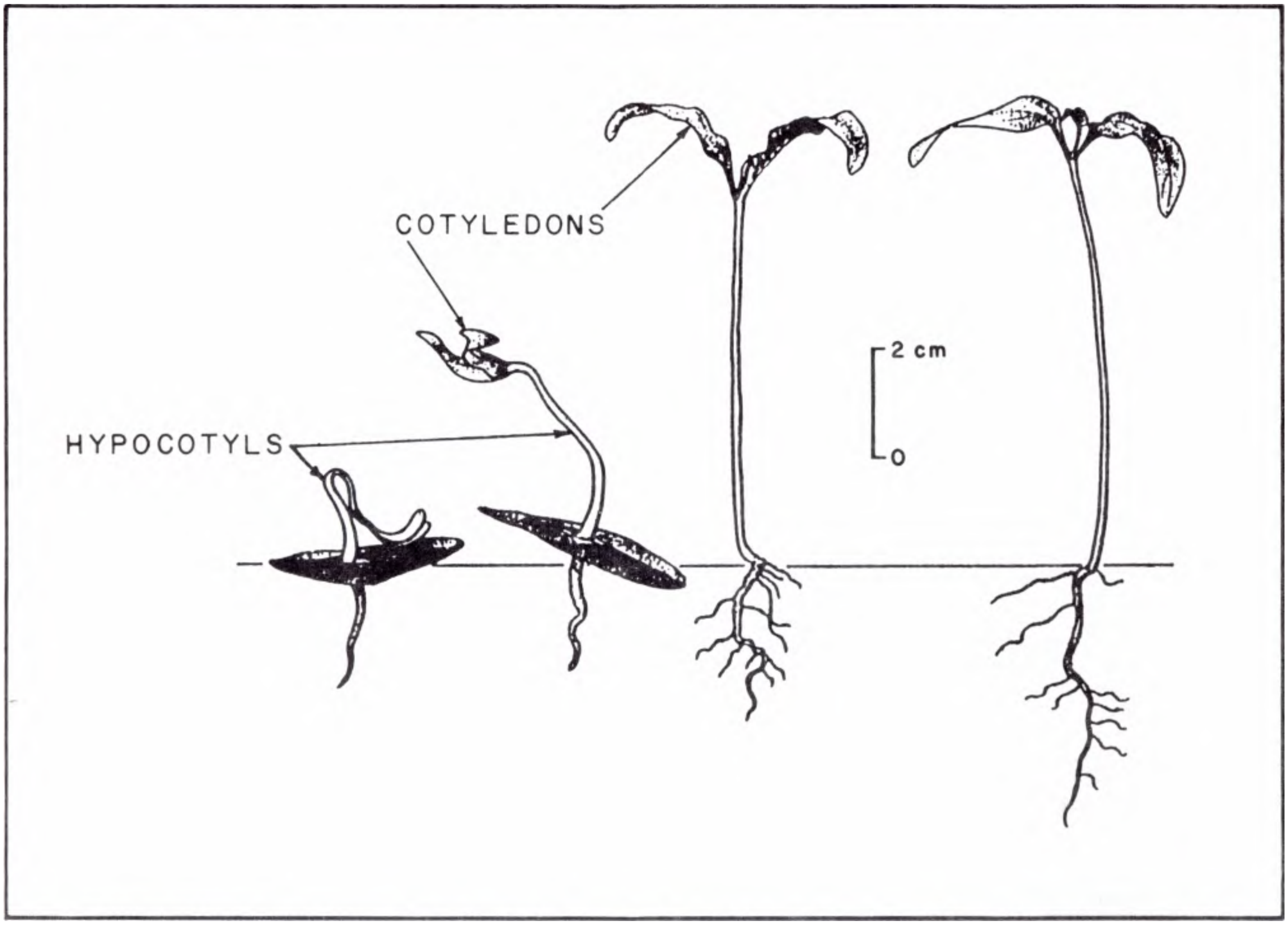

Figure 5 . —*Epigeal germination sequence of* Fraxinus *spp. (adapted from Bonner 1974).*

ability of moisture is the first requirement for germination.

b. Uptake typically occurs in the following three phases:
   (1) Rapid initial phase, mainly physical
   (2) Extremely slow second phase
   (3) Rapid third phase that occurs as metabolism becomes very active

c. The first phase is imbibitional.

d. A minimum state of hydration is needed.

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 0.500 bars).
   (2) Even slightly lowered water potentials will slow, but not stop, germination.
   (3) Critical levels of water potential vary by species.

2. **Temperature**

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

b. For woody plants, germination usually occurs over a wide range of temperatures.

c. The upper temperature limit is around 45 °C.

d. The lower limit is around 3 to 5 °C because germination processes will occur near freezing.

e. Optimum temperatures vary little:
   (1) For Temperate Zone species, alternating regimes of 20 °C (night) and 30 °C (day) have proved best for many species.
   (2) For tropical species, although few critical studies are available, constant temperatures may be best for some; e.g., *Azadirachta indica,* 25 °C; *Bombax ceiba,* 25 °C; *Eucalyptus camaldulensis,* 30 °C; *Leucaena*

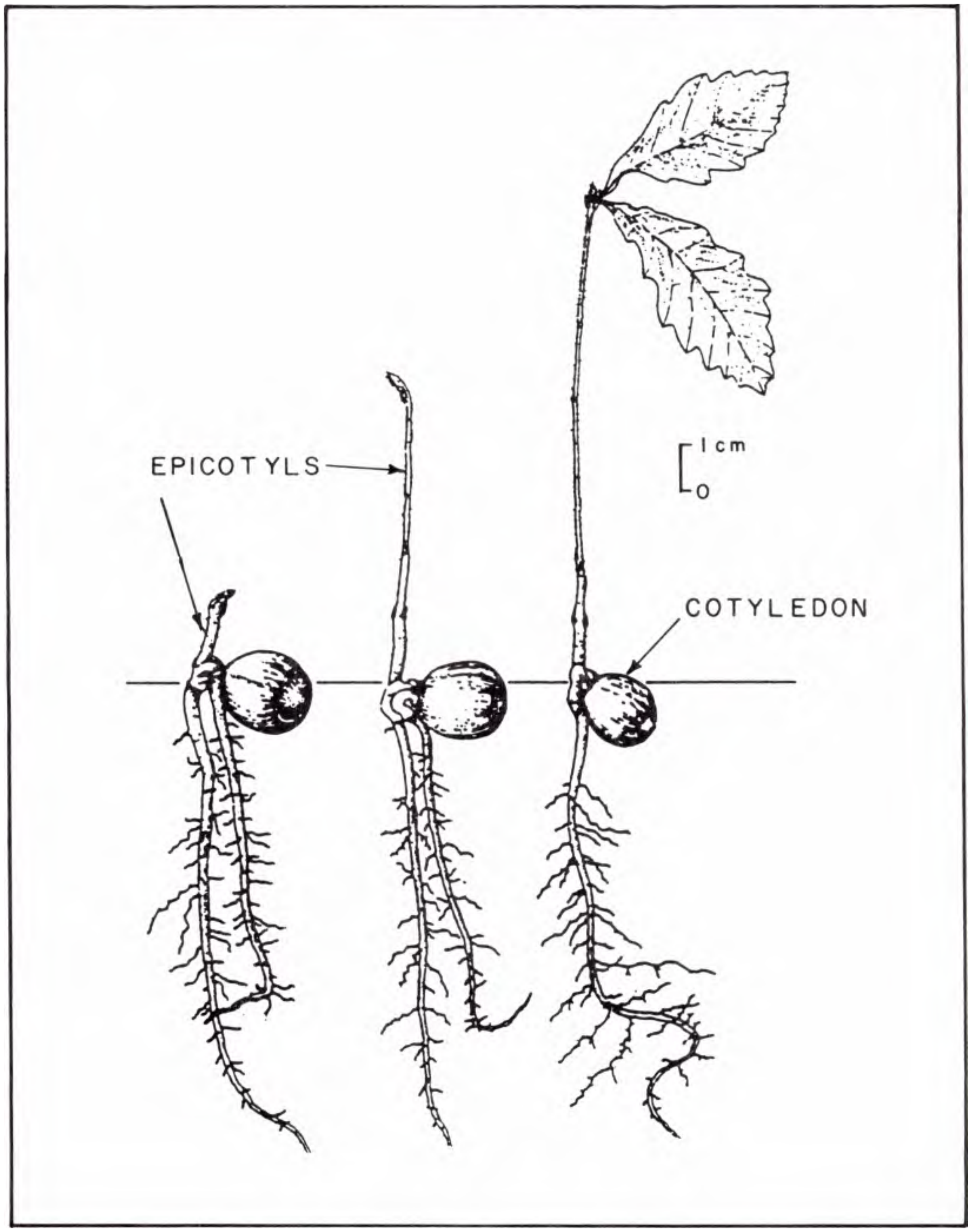

Figure 6. —*Hypogeal germination sequence of* Quercus *spp. (adapted from Olson 1974).*

leucocephala, 30 °C; *Prosopis cineraria,* 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 pines.

3. **Light**
   a. Light stimulates germination of many tree seeds but is necessary for few.
   b. Phytochrome is a pigment involved in the photocontrol of germination.
   c. Minimal light levels in germination testing should be 750 to 1,250 lux.
4. **Gases**
   a. Respiration requires a certain supply of oxygen, and the carbon dioxide produced must be removed.
   b. Some species germinate well in anaerobic conditions.
   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.
2. **Enzymes—Some** systems are present in dry seeds; others are synthesized as imbibition proceeds.
3. **Reserve food mobilization —** Generally, insoluble forms (carbohydrates, lipids, and proteins) are converted to soluble forms (in some ways a reverse of maturation trends).
4. **Nucleic acids—These** compounds are essential for the formation of new enzymes.
5. **Translocation —** The movement of materials within the embryo is crucial.

G. Sources

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