Chapter 1

Seed Biology

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Introduction

Seeds are the principal means of regeneration of most woody plants. They serve as the delivery system for the transfer of genetic materials from one generation to the next. The part of a tree's life cycle that involves seed formation, maturation, dissemination, and germination is a complex—yet fascinating—chain of events, many of which are still poorly understood. Yet some knowledge of these events is necessary for successful collection and utilization of seeds to produce the means for artificial regeneration. This chapter presents basic information on the biology of seeds and how this knowledge can be used in collecting, conditioning, storing, and sowing seeds.

Flowering Plants

The seed-producing organisms of the plant kingdom belong to the division Spermatophyta and are further classified into 2 sub-divisions—Gymnospermae (gymnosperms) and Angiospermae (angiosperms). Gymnosperms are further divided into orders. Only 2 are of interest here: Ginkgoales, which is represented by a single species, ginkgo (*Ginkgo biloba* L.), and Coniferales (conifers), by far the most important group of gymnosperms. The conifers contain 4 families in North America: Pinaceae, Taxodiaceae, Cupressaceae, and Taxaceae. These include economically important genera such as pine *(Pinus* L.), spruce (*Picea* A. Dietr.), sequoia (*Sequoia* Endl.), cypress (*Cupressus* L.), and yew (*Taxus* L.).

Angiosperms are divided into 2 classes—Monocotyledoneae and Dicotyledoneae. Monocotyledonous trees are not very common in North America, but they are represented in this book by the families Palmae (genera *Roystonea* O.F. Cook, *Sabal* Adans., and *Washingtonia* H. Wendl.) and Liliaceae (genus *Yucca* L.). Dicotyledonous species number over 30 families in North America and are by far the largest class of woody plants. This class includes such common genera as maple (*Acer* L.), acacia (*Acacia* Mill.), birch (*Betula* L.), ash (*Fraxinus* L.), holly (*Ilex* L.), oak (*Quercus* L.), and blueberry (*Vaccinium* L.).

Reproductive Cycles

The reproductive cycles of flowering plants begin with initiation of reproductive buds and end with maturation of the seeds. There are 3 types of reproductive cycles that have been recognized in trees of the temperate zone (Owens and Blake 1985).

The 2-year cycle is the most common type. Reproductive buds form late in the growing season of the first year; pollination occurs in the next spring, closely followed by fertilization. The embryo grows rapidly, and seeds are mature by summer or early fall of the second year. This is the cycle of most gymnosperms and angiosperms of North America. Detailed studies of individual species provide good descriptions of the cycle in birch (Macdonald and Mothersill 1987), larch (*Larix* Mill.) (Owens and Molder 1979), spruce (Owens and others 1987), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Owens and Smith 1964; Owens and others 1991a), thuja (*Thuja* L.) (Owens and Molder 1984a), and fir (*Abies* Mill.) (Owens and Molder 1977b).

The second type of reproductive cycle is the 3-year cycle that is common to most species of pines (Owens and Blake 1985). Buds form in late summer or early fall as before, followed by pollination the following spring. Pollen tube and ovule development then stop in mid- or late-summer and resume the following spring. Fertilization occurs that spring, and the seeds mature in the fall. Descriptive work on pines includes western white pine (*Pinus monticola* Dougl. ex D. Don) (Owens and Molder 1977a) and lodgepole pine (*P. contorta* Dougl. ex Loud.) (Owens and Molder 1984b). Other gymnosperms in this book that exhibit this type of reproductive cycle include araucaria (*Araucaria* Juss.) and sciadopitys (*Sciadopitys* Sieb. & Zucc.). Among angiosperms of North America, the 3-year reproductive cycle occurs only in the black oak group (Erythrobalanus) of oak (Mogensen 1965). Like that in pine, fertilization in black oak does not occur until 13 months after pollination.

The third type of reproductive cycle, found in members of the Cupressaceae family, is somewhat similar to the second type. The primary difference is that fertilization occurs within a few weeks of pollination during the second year, with embryo development going into a dormant phase in late summer or early fall (Owens and Blake 1985). This type of cycle has been described for Alaska-cedar *(Chamaecyparis nootkatensis* (D. Don) Spach) (Owens and Molder 1984a) and probably occurs in some juniper (*Juniperus* L.) species (Johnsen and Alexander 1974).

Flowering

Botanically speaking, angiosperms produce true flowers, but gymnosperms do not. Gymnosperm reproductive structures are actually strobili, but for this discussion, they will be considered flowers in the broad sense. All trees propagated from seeds pass through a period of juvenility before they acquire the capability of flowering and producing seeds of their own. The length of this juvenile period is extremely varied among species, ranging from as little as 3 years for *Pinus gieggii Engelm*. (Lopez-Upton and Donahue 1995), to 40 years for sugar pine (*P. lambertiana* Dougl.) (Krugman and Jenkinson 1974). The majority of tree species in the temperate zone, however, begin flowering at the age of 10 to 15 and produce significant seedcrops by the age of 25 to 30 (Owens and others 1991b). Woody shrubs generally flower and fruit at earlier ages. Extensive data on seed-bearing ages are presented for all species in part 2 of this book.

Among species with unisexual flowers (flowers of one sex only, either staminate or pistillate), flowers of one sex may be produced long before flowers of the other sex. For example, Scots pine (*P. sylvestris* L.) may produce female strobili at age 5 to 7, but no male strobili until age 10 to 15 (Matthews 1970). Many other pines are the same. The extent of this phenomenon in angiosperms is not known, but it does occur in some species, for example, yellow birch (*Betula alleghaniensis* Britton) (Erdmann 1990).

The length of the juvenile period can be affected by many factors other than age. Physical size of the plant seems to be important in some cases (Hackett 1985; Schmidtling 1969). Genetic differences are often obvious in even-aged plantations where spacing and tree size are equal, and there is experimental evidence to confirm the genetic effect in a few species (Sedgley and Griffin 1989). Furthermore, tree improvement programs have demonstrated that selections for early flowering within species have the potential to produce clones with precocious flowering traits (Krugman and others 1974).

Initiation

In numerous woody plants, flower initiation and development is a lengthy process extending over several months. During this period, environmental factors and the internal physiological condition of the trees interact to produce the flower crops. The effects of some environmental factors have been observed through the years, and these relationships have been used to influence flowering and seed production in some species (see below). The internal factors involved are still poorly understood, as are their interactions with the environment.

Phenology. Flower buds on most trees and shrubs of the temperate regions are initiated late in the growing season of the year preceding flowering (table 1). In species with unisexual flowers, male flowers may start earlier and differentiate more rapidly as well. Flowers may bloom from late winter to fall, depending on the species and the location. In temperate trees, flowering is primarily seasonal, that is, production only occurs in certain times of the year. Most species bloom in the spring, but there are numerous exceptions to this rule. Witch-hazel (*Hamamelis virginiana* L.) flowers from September to mid-November; California-laurel (*Umbellularia californica* (Hook & Arn.) Nutt.) from December to May; September elm (*Ulmus serotina* Sarg.*) in* September; and deodar cedar (*Cedrus deodara* (Roxb.) Loud.) in September to October. The times reported in this book for flowering are typically expressed as a range of several months to allow for the latitudinal and elevational differences throughout the range of a given species. Local variations in weather may also affect the time of flowering from year to year on the same tree.

Table 1–Chapter 1, Seed Biology: times of flower initiation in selected species as determined from microscopic examination of buds

Species	Location	Time of initiation	
		Male	**Female**
Acer pseudoplatanus L.	Indiana	June	June
Betula papyrifera Marsh.	NW Ontario	Early May	Late June–early July
Carya illinoensis (Wangenh.) K. Koch	Georgia	May	Mar
Larix occidentalis Nutt.	British Columbia	June	June
Picea glauca (Moench) Voss	Ontario	Early Aug	Early Aug
Pinus elliottii Engelm.	Florida	Late June–July	Late Aug
P. monticola Dougl. ex D. Don	British Columbia	Late June–Aug	Mid-Aug
Populus tremuloides Michx.	Connecticut	Early July	Late June
Pseudotsuga menziesii (Mirb.) Franco	Oregon	Apr	Apr
Taxodium distichum (L.) Rich.	Florida	—	Aug
Thuja plicata Donn ex D. Don	British Columbia	Early June	July
Tsuga heterophylla (Raf.) Sarg.	British Columbia	June	July

Sources: Anderson and Guard (1964), Fraser (1962), Lester (1963), Macdonald and Mothersill (1987), Mergen and Koerting (1957), Owens and Molder (1974, 1977, 1979), Owens and Pharis (1971), Owens and Smith (1964), Takaso and Tomlinson (1990), Wetzstein and Sparks (1983, 1984).

In tropical species, the time period between initiation of floral buds and anthesis is relatively short, and flowering may occur once, twice, or several times a year or even continuously throughout the year (Kramer and Kozlowski 1979; Sedgley and Griffin 1989). Some species have 2 periods of flowering per year, 1 considerably heavier than the other. The irregularity of flowering is more evident in moist tropical forests, where seasonal changes are absent (or subtle), than in dry tropical forests (Willan 1985). Flowering patterns in dry tropical forests are usually related to rainfall patterns.

Influencing factors. The natural variations in flowering that are obvious to even casual observers are evidence that flowering must be affected by many factors. These factors can be either environmental or physiological (internal) in nature, and they all interact to influence the expression of flowering in woody plants.

Temperature. High temperatures during summer enhance formation of flower buds in many species of the temperate regions (Sedgley and Griffin 1989). Most flowering studies that show this effect have correlated weather records with records of fruit and seed production (Owens and Blake 1985), but the physiological reasons for this effect have not been elucidated. Most of the examples are of conifers: Norway spruce (*Picea abies* (L.) Karst.) (Lindgren and others 1977), Douglas-fir (Lowry 1966), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) (Maguire 1956), and red pine (*P. resinosa* Ait.) (Lester 1963). Among hardwoods, European beech (*Fagus sylvatica* L.) has shown similar responses (Matthews 1955). High summer temperatures usually accompany drought conditions, however, and it is difficult to say which is the most important (see below).

There are important low temperature effects also, but they occur in the spring following bud initiation. For some species in the warmer portion of the temperate regions and for subtropical species, there is a moderate cold requirement for flowering. Examples are pecan (*Carya illinoensis* (Wangenh.) K. Koch) (Amling and Amling 1983) and olive (*Olea europaea* L.) (Hackett and Hartmann 1967). Another low temperature effect that is familiar to most people is the killing of flowers by late frosts in the spring. Citrus and other fruit crops are well-known for this, especially in the South, but native trees and shrubs suffer the same fate. Complete seedcrop failures may only occur in local stands or microsites, however, as some trees may always be protected from the cold or exposed to winds that prevent frost formation on the flowers.

Light. Unlike flowering in annuals, flowering in most woody perennials does not appear to be under strict photoperiodic control (Sedgley and Griffin 1989). Mirov (1956) and Lanner (1963) concluded that flowering in pines was not affected by day length. Other studies suggest that photoperiod may have some control on the sex of reproductive buds (Owens and Blake 1985). Experimental evidence of some type of control does exist, however, so it may be that the effect is difficult to define in woody plants. In azaleas (*Rhododendron* L.), for example, flower initiation was accelerated by short days of 8 hours light (Criley 1969), whereas flowering in some varieties of apple (*Malus* Mill.) was better under long days (14 hours) than short days (8 hours) (Tromp 1984). In western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), pollen cone buds were favored by increasing daylengths, whereas seed cone buds were favored by decreasing daylengths (Owens and Molder 1974). In coniferous species where the photoperiod effect is different for male and female flower buds, there is a natural difference between the sexes in time of bud differentiation. In species without this difference, there may be an indirect effect of photoperiod through cessation of shoot elongation, which usually coincides with reproductive bud differentiation (Owens and Blake 1985). Clearly, photoperiodic effects on flower initiation for any species cannot be understood without knowledge of the timing of the reproductive cycle in that species.

Light intensity has a more demonstrable effect on flowering in trees than photoperiod. Open-grown trees with full crowns have more flowers than trees with shaded crowns, and this is not just an effect of more sites for bud formation on open-grown trees. Any collector of tree seeds can testify that, in northern latitudes, most of the crop will be found on the southern and western portions of open-grown crowns. Increased light intensity (or at least increased sunshine) is also reported to increase flowering in tropical trees (Nanda 1962; Ng 1977).

There are conflicting reports about the effects of light intensity on sexual differentiation. Higher light intensities of open stands were found to favor female flowers in walnuts (*Juglans* L.) (Ryugo and others 1980) and male flowers in striped maple *(Acer pensylvanicum* L.) (Hibbs and Fischer 1979).

Moisture. There have been many studies that showed increased flowering in trees subjected to moisture stress in late summer (Owens and Blake 1985; Sedgley and Griffin 1989). It is extremely difficult to separate the effects of temperature and light intensity from those of moisture stress, however, as the 3 conditions typically occur together. After careful examination of published data, Owens and Blake (1985) concluded that there was little evidence that moisture stress during the period of flower bud initiation led directly to increased flower production.

There are other effects of moisture besides drought, of course. A plentiful supply of moisture during peak growth periods will indirectly benefit flowering through increased shoot growth and crown development. Excess moisture during pollination, especially for wind-pollinated species, can be a problem, but this effect will be discussed later in this chapter.

Nutrition. In general, a favorable nutrient status is required for woody plants to produce good seedcrops. Many studies have shown increased seed production after the application of fertilizers, especially nitrogen and phosphorus, but the precise roles of these elements in flowering and seed production are not known (Owens and Blake 1985). Abundant flowering in fruit trees has long been associated with a high carbon to nitrogen ratio in the shoot tissues (Kramer and Kozlowski 1979). Although this condition may be explained in term of carbon partitioning within the plant, the controlling factors are still unknown. Fertilization to increase flowering and seed production may have 2 effects. There can be a short-term effect of direct impact on flower production and fruit/seed size, and there can be a long-term effect of more buds sites just by increasing crown size.

Physiology. The physiological status of woody plants is the most important factor of all in flower initiation, yet it is the factor that is most difficult to influence. Early plant physiologists searched for a single hormone that could turn flowering on or off (Kramer and Kozlowski 1979) but were not successful. Current knowledge suggests that the balance between gibberellins, cytokinins, and other natural bioregulators controls the change from juvenile to mature stage and also the amount of flowering in the mature stage. The weak link in this reasoning is that most of the evidence comes from results of experiments in which chemicals were applied to plants externally (Sedgley and Griffin 1989). The strong point of these experiments is that flowering really can be stimulated in a host of species (primarily gymnosperms) by chemical application. A considerable amount of research remains to be done before we can understand the internal controls on the flowering process in woody plants.

Manipulation of flowering. When speaking of manipulating the flowering process in trees, we must distinguish between forcing trees to flower while they are still in the juvenile phase, or treating trees that are already in the flowering phase to produce more flowers. In the first case, the interest is usually in speeding breeding programs. In the second, increased seed production for artificial regeneration programs is usually the goal.

Juvenile phase. Precocious flowering in conifers has been produced mainly with water-based foliar sprays of gibberellins (GA). A detailed review by Owens and Blake (1985) points out that GA_3 has been most successful with members of the Cupressaceae and Taxodiaceae, whereas non-polar $GA_{4/7}$ mixtures have provided successes with the Pineaceae. In Cupressaceae and Taxodiaceae, treatment with GA_3 alone is usually successful in stimulating flower bud production; this can be seen in the following genera: “cedar” (*Chamaecyparis* Spach.), cryptomeria (*Cryptomeria* D. Don), cypress, sequoia, baldcypress (*Taxodium* Rich.), and thuja (Owens and Blake 1985). Manipulation of other cultural treatments, such as drought, fertilization, or daylength, is not really necessary unless a change in the proportion of pollen to seed cones is the goal. For example, treatment of western redcedar (*Thuja plicata* Donn ex D. Don) seedlings with GA_3 under short days favored initiation of seed cone buds, whereas treatment under long days favored initiation pollen cone buds (Pharis and Morf 1972; Pharis and others 1969).

In Pineaceae, GA treatments are often combined with cultural treatments, because there is usually a strong synergistic effect. Precocious flowering has been induced in seedlings of jack pine (*Pinus banksiana* Lamb.) with a combination of moisture stress and $GA_{4/7}$ (Cecich 1981; Riemenschneider 1985) and in Douglas-fir seedlings with a combination of girdling and the same gibberellin treatment (Pharis and others 1980). Other Pineaceae genera for which success has been reported are larch, spruce, and hemlock (Owens and Blake 1985), although these results have generally not been as successful as those for Cupressaceae and Taxodiaceae. Other factors, such as timing of treatments, developmental stage of the plants, and method of application can also have significant effects. In loblolly pine, a combination of low temperatures and short photoperiods has been used to stimulate formation of strobili on potted stock as young as 3 years (Greenwood 1978). It should also be noted that the mechanisms for these treatment effects are still unknown, and much basic research is needed to fully understand them.

Mature phase. Stimulation of flower initiation in sexually mature trees is commonly practiced in seed orchards to increase seed production. Fertilization has been the most common and most successful treatment used. Owens and Blake (1985) summarized fertilizer tests on over 20 species of trees and found, that while many were successful, others produced variable results. Interactions with other factors, such as timing, method of application, rate, formulation, and moisture conditions following treatment have significant effects (Schmidtling 1983). Most of the attention has been on nitrogen and phosphorus, but many trials used complete fertilizers. Current practice is to base fertilization levels on soil analyses of individual orchards. Typical fertilization prescriptions for seed orchards of southern pines have been annual application of about 400 kg/ha of nitrogen, 80 kg/ha of potassium, 40 kg/ha of phosphorus, and 50 kg/ha of magnesium (Zobel and Talbert 1984).

Another treatment widely used is manipulation of soil moisture levels. Irrigation of seed orchards in conjunction with fertilization is one practice, and in most cases the response is positive. Moisture stress has also been used, although this sort of treatment is difficult to apply in the field. In seed orchards, moisture stress has been created by root pruning the orchard trees to temporarily disrupt moisture uptake. The effect of moisture stress may be through its effect on carbon allocation in the tree, although other factors are sure to be involved. Ebell (1970) found that moisture stress increased the level of amino acids in Douglas-fir trees just as application of nitrate nitrogen did, and that both induced cone formation. When water was supplied to the trees, protein synthesis increased but cone formation did not.

Girdling and other wounding treatments have been popular as a means of increasing production in fruit trees. The theory behind these actions was that girdling prevented translocation of carbohydrates to the roots, thus raising the C to N ratio in the crown, which increased fruit production. Recent experimental evidence provides weak, if any, support for this theory, and a good explanation for the wounding effect is still lacking (Owens and Blake 1985). Despite the uncertainty, girdling is still used in seed orchards of Douglas-fir and other conifers.

Timing of wounding treatments seems to be important, at least in some species. Ebell (1971) girdled Douglas-fir trees at weekly intervals from April to mid-July. The optimal time of treatment was about 1 month before the vegetative buds burst. Many other studies of this nature have not controlled time of treatment as well, and timing effects cannot be determined (Owens and Blake 1985).

Thinning of seed stands is another commonly used practice to increase flowering. Thinning brings about increased light intensity to the crowns (see previous section) and less competition for moisture and nutrients. As one might expect, there is a delay before treatments are usually effective, ranging from 1 to 4 years (Allen 1953; Owens and Blake 1985). Flower and fruit production increases attributed to thinning have been documented for black walnut (*Juglans nigra* L.) (Ponder 1979), hoop-pine (*Araucaria cunninghamia* Sweet) (Florence and McWilliam 1956), loblolly pine (Bilan 1960; Allen and Trousdell 1961), longleaf pine *(Pinus palustri*s Mill.) (Allen 1953), and other conifers. Fertilization at the time of thinning enhanced cone production in Japanese larch (*Larix leptolepis* (Sieb. & Zucc.) Gord.) and Japanese red (*Pinus densiflora* Sieb. & Zucc.) (Asakawa and Fujita 1966) and ponderosa pines (Heidmann and others 1979).

Much less is known about stimulation of flowering in tropical and subtropical tree species. Many of the same treatments used on temperate species have been tested in the tropics also, and, as one would expect, results have not been consistent. Carbohydrate accumulation and an interruption of vegetative growth of the tree are the factors that have been most frequently associated with increased flower initiation (Dick 1995).

Structure and Development

Flower primordia are inconspicuous at first and rarely can be identified without careful microscopic examination of the tissues. Initially, there are no external features that serve to distinguish flower buds from vegetative buds. As flower buds grow and develop, they become distinguishable from vegetative buds by their general appearance and location. Variation among species is significant, but flower buds usually become wider and longer as they grow and may differ in color and shape from vegetative buds. In some species, such as flowering dogwood (*Cornus florida* L.), flower buds are distinctive in shape and large enough by late summer (July to August) for easy identification, thus providing a preliminary estimate of next year's flower crop.

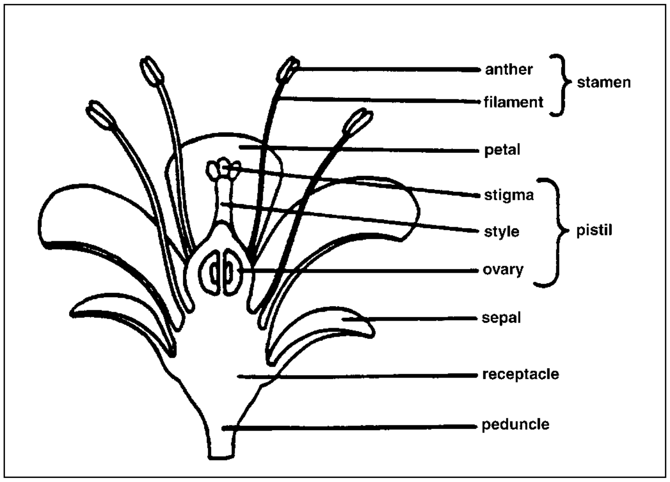
Flower buds enlarge greatly as the flowering season nears and conditions become favorable for bud growth. Individual flowers of many species open rapidly once flowering begins. This is especially true if air temperatures are unseasonably high. Conversely, colder than normal temperatures will delay flower opening. Flower opening usually does not occur simultaneously over an entire inflorescence, over an entire tree, or even among plants of the same species in a stand, but it may be in progress for many days at any one location. The evolution of flowering in this way in wild populations is a distinct advantage in perpetuation of the species, as short-term events that destroy flowers or prevent pollination cannot destroy the entire crop.

Flowers of woody plants come in many different shapes, colors, odors, and sizes. They may be minute and inconspicuous, like the flowers of thuja, or they may be large, showy, and fragrant like the 1-foot wide, white, perfect flowers of bigleaf magnolia (*Magnolia macrophylla* Michx.) (Brown and Kirkman 1990). The flowers of many species are sufficiently attractive to create a demand for their use in ornamental plantings. Well-known ornamental trees include serviceberries (*Amelanchier* Medic.), redbud (*Cercis canadensis* L.), dogwoods (*Cornus* L.), mountain-laurel (*Kalmia latifolia* L.), magnolias (*Magnolia* L.), and azaleas. Some woody vines included in this book are also used extensively for ornamental plantings because of their showy flowers: trumpet creeper (*Campsis radicans* (L.) Seem. ex Bureau), clematis *(Clematis* L.), and honeysuckle (*Lonicera* L.).

An angiosperm flower (figure 1) may have some or all of the following parts: a stalk or peduncle, a receptacle, a calyx composed of sepals, a corolla composed of petals, stamens with anthers and filaments, and 1 or more pistils, each with a stigma, style, and ovary. A flower is complete when it has a calyx, corolla, functional stamens, and 1 or more functional pistils. It may be considered incomplete when 1 or more of these parts is lacking or nonfunctional. Though lacking a calyx or corolla, a flower is perfect (or bisexual) when it has both stamens and pistil, and unisexual when only one or the other is present and functional. The calyx and corolla may be considered accessory parts, but stamens (which produce pollen) and the pistil or pistils (which contain the ovaries) are mandatory for normal seed production. The primary function of the calyx and corolla, both of which are modified leaves, is to enfold and protect the stamens and pistils while they mature. For entomophilous species, the color, odor, or nectar supply of the unfolded calyx and corolla play a role in attracting of the insects that are needed for pollination.

Many angiosperm trees and shrubs produce complete flowers, for example, cherry (*Prunus* L.), locust (*Robinia* L.), magnolia, and tuliptree (*Liriodendron tulipifera* L.). Other species bear incomplete flowers that lack a calyx as in some ashes, a corolla in silktassel (*Garrya* Dougl. ex Lindl.), or both calyx and corolla in willows (*Salix* L.) and hazels (*Corylus* L.). Some species bear separate male and female flowers on the same plant (monoecious); examples are alders (*Alnus* Mill.), birches, and oaks. Other species bear these separate flowers on different plants (dioecious); examples are maple and holly. In some species all floral parts are present but instead of being distinctly separate, some are more or less united, for example, sepals in viburnums (*Viburnum* L.), petals in catalpas (*Catalpa* Scop.), and pistils in azaleas (*Rhododendron*).

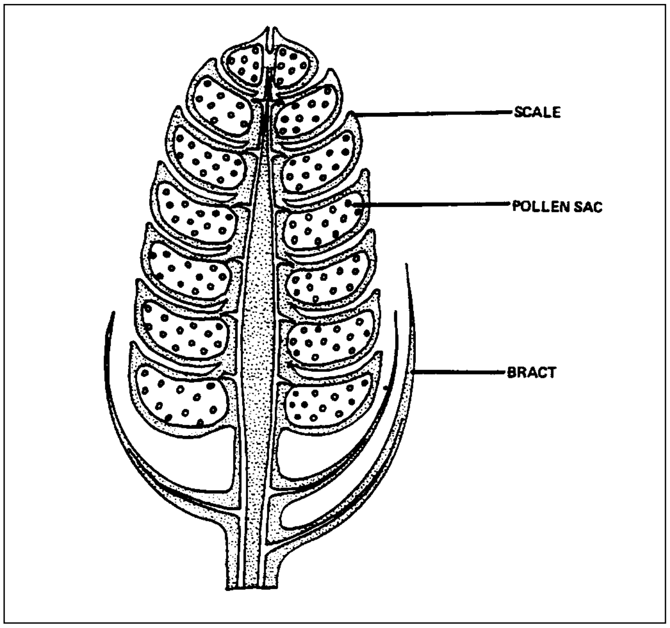
Figure 1—Chapter 1, Seed Biology: structure of a complete angiosperm flower (from Krugman and others 1974).



Some genera of angiosperms have polygamous floral habits. Bisexual as well as unisexual staminate and pistillate flowers may occur on the same tree, as in the hackberries (*Celtis* L.). This condition is defined as polygamo-monoecious, although the trees are functionally monoecious. If bisexual flowers occur with only staminate or pistillate flowers on separate trees, as in buckthorn (*Rhamnus* L.), the condition is defined as polygamo-dioecious, although the plant is functionally dioecious. In a few species, there are several flowering patterns. Silver maple (*Acer saccharinum* L.) and striped maple, for example, can be monoecious, dioecious, or sometimes polygamo-monoecious (Gabriel 1990; Hibbs and Fischer 1979).

Most coniferous gymnosperms are monoecious, but other genera—juniper and torreya (*Torreya* Arn.)—are dioecious. Coniferous gymnosperm flowers are strobili (small

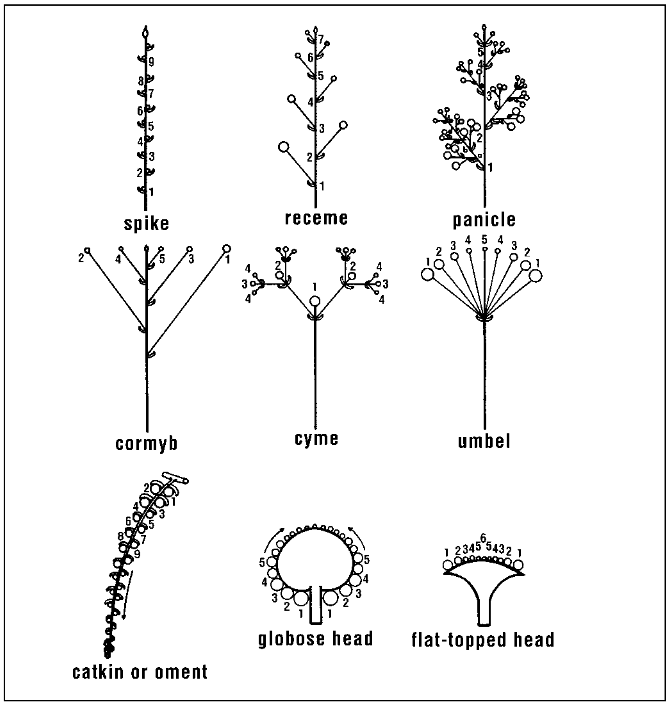
Figure 2—Chapter 1, Seed Biology: structure of a staminate flower typical of coniferous gymnosperms (Coniferales) (from Krugman and others 1974).



cones) without calyx, corolla, stamens, or pistils. These strobili characteristically have a central axis bearing a few to numerous distinctly shaped scales and bracts (figure 2). In staminate strobili, each scale (microsporophyll) bears 2 pollen sacs (microsporangia) on its lower surface. In ovulate strobili, 2 inverted ovules (megasporangia) form on the upper surface of each ovulate scale. Staminate strobili—often bright shades of yellow, red, or purple when fully developed—are numerous, short-lived, and highly productive of pollen. The less numerous, but infrequently colorful, ovulate strobili develop into woody, relatively durable structures (cones) that contain a varying number of seeds.

Coniferous strobili are similarly arranged around the central axes of cones (figure 2). Flowers of angiosperms, on the other hand, have varied and distinctive floral arrangements. Some species bear a single flower on each peduncle, for example, magnolia and tuliptree, but most others bear flowers in groups or clusters called inflorescences. The general structure of an inflorescence is a central stem, with or without branches, on which flowers, with or without pedicels, develop. Examples of the common forms of inflorescences of woody plants (figure 3) include catkin (ament), birch; raceme, serviceberry; spike, walnut (pistillate); head, sycamore (*Platanus* L.); cyme, viburnum; panicle, sumac (*Rhus* L.); and umbel, plum.

Figure 3—Chapter 1, Seed Biology: common forms of flower clusters, with individual flowers represented by circle and the order in which the flowers develop shown by numbers (#1 indicates the position of the oldest flower in the inflorescence) (from Krugman and others 1974).



On many woody plants, the flowers appear throughout the crown, but in some monoecious species, staminate or ovulate flowers tend to predominate or be restricted to certain parts of the crown. For example, in most pines, ovulate strobili are most numerous in the upper crown, whereas staminate strobili predominate in the lower crown. In true firs, ovulate strobili are found primarily on the tips of the uppermost branches, and staminate strobili are found below them, but still in the mid- to upper crown region.

In some species, flowering may occur on older branches or on the trunk itself. This phenomenon, called cauliflory, occurs frequently in tropical species, but rarely in temperate ones. Of the temperate woody plants in this book, redbud is the only genus for which cauliflory has been reported (Owens and Ewers 1991).

Pollination

Seed initiation by successful union of male and female reproductive elements is the culminating event in flowering. This union depends on 2 key steps: pollination and fertilization. Pollination is the transfer of male pollen grains from stamens in angiosperms, or staminate cones in gymnosperms, to pistils in angiosperms, or ovulate cones in gymnosperms. Fertilization occurs when subsequent pollen tube growth allows union of the sperm cell with the egg cell in the ovule. A detailed discussion of these processes is beyond the scope of this book, and the following sections will provide only brief descriptions. For additional information, readers should see the reviews by Owens and Blake (1985), Sedgley and Griffin (1989), and Marshall and Grace (1992).

Pollen grain development. Pollen grains are formed within structures called pollen sacs. In angiosperms, these sacs are found in the anthers at the tips of the stamens. Each pollen grain contains a tube cell and a generative cell, defined as the binucleate stage, and most angiosperm pollen is shed at this stage of development. The generative cell divides to form 2 male gametes, usually after shedding and germination, but before shedding in some species (Owens and Blake 1985). Pollen tube growth in most species occurs quickly after the trinucleate stage is reached. Detailed descriptions of this part of the sexual life cycle of angiosperm trees is very limited.

In gymnosperms, the pollen sacs are formed beneath each cone scale in the staminate cones. These sacs are initiated before winter in all conifers of the north temperate zone, but the rates of development after initiation vary greatly among species (Owens and Blake 1985). In the Pinaceae, the microspore division produces a large tube cell, a smaller generative cell, and 2 prothallial cells with no known function. In the Cupressaceae, Taxodiaceae, and Taxaceae, the pollen grains are binucleate, lacking prothallial cells (Owens and Blake 1985).

Pollen grains of trees are extremely varied in shape and size. Some examples of shape are spherical (hickory, *Carya* Nutt; and juniper), elongated (maple and Douglas-fir), triangular *(Eucalyptus* L'Herit.), and sac-like (pine and spruce). A few genera exhibit more than one shape: spherical or elongated (birch and mountain-ash, *Sorbus*) and triangular or tetrahedral (silk-oak, *Grevillea robusta* A. Cunn.). Pollen grains may range in size from 3 to 300 μm. Within a given genus, grain sizes are fairly uniform. Some reported ranges are 10 to 30 μm for birch and 70 to 103 μm for true firs (Sedgley and Griffin 1989). The outer walls of pollen grains (exines) are relatively thick and very resistent to degradation by external agents. The exine surfaces are furrowed and sculptured, which may play some role in pollination.

Pollen dispersal. Dispersal of tree pollen is primarily by wind (anemophily) and insects (entomophily), although birds (ornithophily) and animals (therophily) can also be dispersal agents, especially in tropical genera such as albizia, *Albizia* Durz.; bauhinia, *Bauhinia* L.; eucalyptus, and silk-oak (Sedgley and Griffin 1989). Pollen dispersal in conifers is mainly by wind, which is also the primary agent for angiosperms that lack floral parts (ash; casuarina, *Casuarina* L. ex Adans; sycamore; and elm, *Ulmus* L.), particularly if the flowers are catkins or aments (birch, hickory, walnut, oak, willow, and poplar, *Populus* L.). Species with brightly colored or scented flowers, such as dogwood, magnolia, apple, and tuliptree, often have heavy or sticky pollen grains. Their pollinating agents are almost always insects. Some species, notably maple, willow, and mulberry (*Morus* L.), are pollinated both by wind and by insects (Sedgley and Griffin 1989). Quite a few shrubs and understory plants depend on entomophilous pollination, as their positions within the stand preclude good wind movement. Some examples of this are azalea, mountain-laurel, and California-laurel.

Pollen dispersal must occur at the time of receptivity by the stigma of the pistil for pollination to be successful. This required synchronization occurs in many cases within and among perfect flowers or among monoecious flowers on a single plant. In other species, male and female organs mature at different times, creating a condition called dichogamy, in which pollen may be supplied by different perfect flowers on the same tree or by unisexual flowers from different trees. Dichogamy is strong in magnolia (Thien 1974). In southern magnolia (*Magnolia grandiflora* L.), stigmas are receptive in the morning before pollen is released (anthesis). The flowers close in the evening and reopen the following day. The stigmas are no longer receptive, but the anthers will now release pollen, which will only be "successful" in other flowers. Among dioecious species, dichogamy clearly will reduce self-pollination and encourage cross-pollination, thus promoting greater genetic diversity.

Weather conditions have a strong influence on pollination. Dry, warm weather will usually enhance pollen dispersal by wind. If winds are excessively dry, however, pollen of white oaks may be shed before maturity (Sharp and Chisman 1961). In contrast, rain or high humidity greatly hinders anemophilous pollination. Complete seedcrop failures can occur locally if heavy rains dominate the weather when anthesis is occurring. Late spring freezes can also kill staminate flowers and cones and prevent any dissemination of pollen in some species. Entomophilous pollination is not as greatly affected by the weather, but low temperatures and heavy rains will curtail the activities of insect pollinators.

Anemophilous pollen dispersal depends primarily on weather factors and stand structures. Under near-calm conditions, pollen of many pines and hardwoods can be expected to disperse only a few dozen meters (Sedgley and Griffin 1989), but in turbulent wind conditions, dispersal of pine pollen for 1 km and more is likely (Griffin 1980; Lanner 1966). Entomophilous pollen dispersal distances are not precisely known but probably are considerably less than anemophilous dispersals.

Pollen viability and flower receptivity. For pollination to be successful, the pollen grains must remain viable until they reach the stigma, and the female flowers or cones must be receptive when the pollen arrives. Not much is known about the length of viability of pollen in nature; some pollens survive for only hours and others for weeks. The pollen of many species, notably conifers, can be carefully dried to below 10% moisture content and stored below freezing for several years (Copes 1987; Wang and others 1993). Like pollen viability, flower receptivity varies greatly among species. For angiosperms, the receptive period for an individual flower may last for less than a day, as noted earlier for southern magnolia (Thien 1974), or it may continue for up to 10 days in some cherries (Stösser and Anvari 1982). Among gymnosperms, the receptive period ranges from less than a day in japanese larch, *Larix kaempferi* (Lam.) Carr. (Villar and others 1984) to 2 weeks or more in true firs, hemlocks, and pines (Owens and Blake 1985).

Pollination in angiosperms. When pollen grains reach the stigma of a receptive flower and germinate, the pollination process is set into motion. Pollen grains are captured on the stigmas due to their own sticky surface characteristics or the nature of the stigma surface. The stigma surface is naturally dry in some genera (maple; dogwood; sweetgum, *Liquidambar* L.; elderberry, *Sambucus* L.; and basswood, *Tilia* L.) and wet in others (hickory, eucalyptus, holly, plum, and serviceberry) (Sedgley and Griffin 1989), but there are no strong correlations between surface condition and other aspects of pollination and fertilization. Some have suggested that pollen germination rates are quicker on dry stigmas, but evidence for this is weak (Owens 1992). Germination is rapid, usually occurring within a few hours (Owens 1992), and is temperature-dependent. Luza and others (1987) reported that pollen of English (*Juglans regia* L.) and black walnuts would not germinate at 40 °C or below 14 °C; maximum germination occurred at 28 to 32 °C.

Many of the pollen grains that reach stigmas may not germinate, and many that do will abort in the early stages of tube growth. Germinating grains form a microscopic tube that grows between the cell walls of the stigma and style toward an ovule. Usually only 1 pollen tube will penetrate an ovule; the others abort soon after germination.

Pollination in gymnosperms. In gymnosperms, the scales of the ovulate cones spread apart when the cones are receptive, and small drops of extracellular secretion (pollination drops) are formed. Pollen grains drift between the scales and are "captured" by the drops. Entry into the ovule through the micropyle is accomplished via these drops. The process differs among the gymnosperm families; Cupressaceae, Taxodiaceae, and Taxaceae have one mechanism, and Pinaceae another. These difference have been described in detail by Owens and Blake (1985) and Sedgley and Griffin (1989).

Fertilization

Fertilization occurs when the pollen tube enters the ovule and "delivers" the 2 sperm cells (gametes). In angiosperms, a typical ovule contains within its matured embryo sac 8 separate cells: an egg cell, 2 synergid cells, 2 polar cells, and 3 antipodal cells (figure 4). In the actual process of fertilization, 1 sperm (N) unites with the egg cell (N) to form a zygote that develops into the embryo (2N) of the seed. Generally, only 1 embryo develops, but multiple embryos are not uncommon in some species. The other sperm (N) unites with the 2 polar cells located near the center of the embryo sac, forming what will become the endosperm (3N). This process is commonly described as double fertilization. Endosperm tissue is triploid (3N) and functions as a source of nutrients available to the growing embryo and, in some species, to the young seedling that develops from the embryo at germination. As embryo and endosperm develop, the synergid and antipodal cells disintegrate.

Ovule and embryo sac formation in angiosperms may precede, occur synchronously with, or follow pollination. In tuliptree, the embryo sac is ready for fertilization by the time pollen is mature (Kaeiser and Boyce 1962). In sweetgum, sac development occurs 1 to 3 weeks after pollination (Schmitt 1966). Ovule development in oaks is extremely slow. It begins about 1 month after pollination in the white oak group, and 13 months afterwards in the black oak group (Stairs 1964). In all cases, development proceeds rapidly once it is underway. These time differences are also reflected in the elapsed times from pollination to fertilization. Most angiosperms require approximately 24 hours or less (Sedgley and Griffin 1989), but others require much longer: 60 hours in English walnut (Luza and others 1987), 8 to 9 days in *Rhododendron nuttallii* T.W. Booth (Palser and others 1989), 12 days in peach (*Prunus persica* Batsch) (Herrero and Arbeloa 1989), and 12 to 14 months in some species of oak (Kramer and Kozlowski 1979).

As the pollen tubes of gymnosperms elongate into the ovule, their generative cells divide into a stalk cell and a body cell. The body cell divides again to form 2 male gametes. One gamete fuses with the egg nucleus within an archegonium, a multicellular organ within the ovule, and the other usually disintegrates. Each gymnosperm ovule consists of an integument surrounding a multicellular body, the female gametophyte. The female gametophyte tissue is often incorrectly called "endosperm," a usage that should be discouraged. During later stages of ovule development, archegonia differentiate within the female gametophyte (figure 5). The number of archegonia varies by genus and by species. Florida torreya (*Torreya taxifolia* Arn) almost invariably has 1; the Pinaceae have 1 to 10; and sequoia may have up to 60 (Willson and Burley 1983). Occasionally more than 1 archegonium is fertilized, either by the second male gamete or by gametes from other pollen tubes, but normally only 1 embryo matures. Archegonia usually complete development less than 1 week before fertilization, but this interval is longer in some conifers. The elapsed time between pollination and fertilization in gymnosperms is generally much longer than that in angiosperms. These periods range from 3 weeks for Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (Singh and Owens 1981) to 15 months for Monterey pine (*Pinus radiata* D. Don) (Lill 1976).

Reproductive Abnormalities

Occasionally the physiological processes associated with sexual reproduction break down and abnormalities result. In woody plants these abnormalities seldom have an impact on seed production or seed quality, but their general nature should be understood.

Polyembryony. Polyembryony is the occurrence of more than 1 embryo per ovule. It is unusual in angiosperms (Sedgley and Griffin 1989), but more common in gymnosperms with multiple archegonia, where pollination and fertilization produce multiple embryos, all differing in genetic composition. This type of polyembryony is found in araucaria, cypress, and all Pinaceae (Chowdhury 1962; Haines and Prakash 1980; Konar and Banerjee 1963). Another type of polyembryony can be produced through cleavage or division of a developing embryo. It has been noted in many coniferous genera of the northern temperate zone (Sedgley and Griffin 1989).

Parthenocarpy. Parthenocarpy is the formation of fruit without fertilization and is a desirable trait for selection in genetic improvement of fruit crops. Parthenocarpy is not common in forest species but has been noted in apples and pears (*Pyrus* L.) when adverse environmental conditions induce ovule abortion (Sedgley and Griffin 1989).

Agamospermy. Agamospermy, sometimes called apomixis when it occurs in trees, is the development of seeds without fertilization. Some forms of this phenomenon seem to require pollination, while others do not. Agamospermy has been reported in sugar maple (*Acer saccharum* Marsh.) (Gabriel 1967), several species of serviceberries (Campbell and others 1987), and hawthorns (Crataegus L.) (Dickinson and Phipps 1986).

Figure 4—Chapter 1, Seed Biology: longitudinal section through a typical pistil just before fertilization (from Krugman and others 1974).

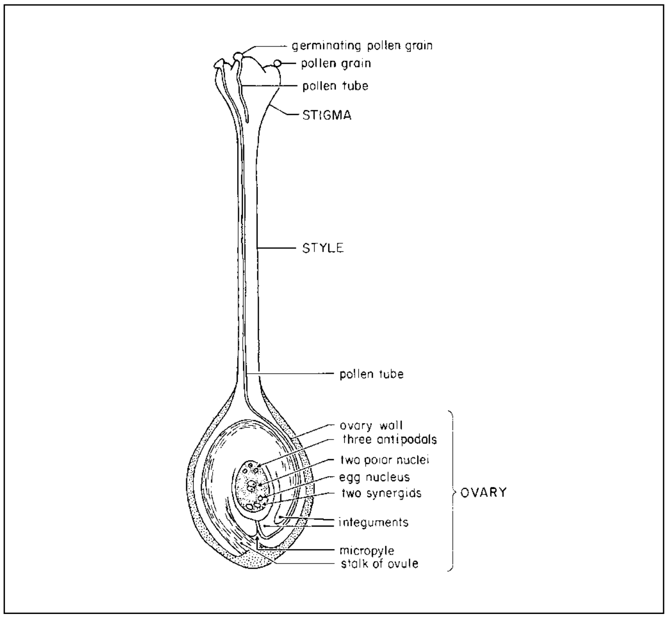
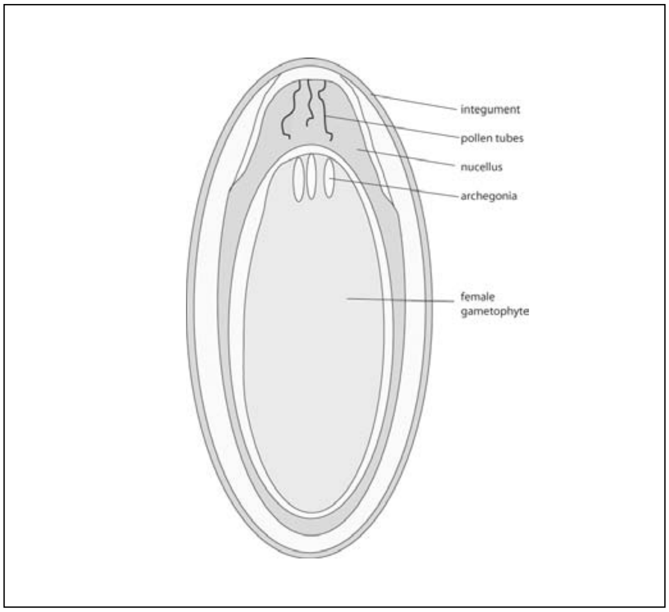


Figure 5—Chapter 1, Seed Biology: longitudinal section through an ovule of *Pinus ponderosa.* during the period of pollen tube development preceding fertilization.



Fruit and Seed Development

Morphological Development

The life history of a fruit generally includes 4 distinct phases of growth and development:

1. Pre-anthesis cell initiation and multiplication within the floral buds and enlarging flowers
2. Anthesis, pollination, pollen tube growth, and fertilization
3. Post-fertilization growth, mostly by cell enlargement in the fruit and cell multiplication in the seed
4. Maturation of the fruit through ripening and senescence (Nitsch 1965)

In most species, phase 3 does not proceed unless pollination and fertilization of some ovules has occurred. If it does proceed without fertilization, parthenocarpy or agamospermy is taking place. This section will briefly outline the events of phases 3 and 4. More complete discussions can be found in reviews on embryology, development, and maturation (Bewley and Black 1994; Chowdhury 1962; Johri 1984; Maheshwari 1950; Sedgley and Griffin 1989).

Angiosperms. Following fertilization, the first tissue to develop in the embryo sac is the endosperm, which follows 1 of 2 patterns. A nuclear endosperm, in which there is no early cell wall formation, is most common in woody plants. In the latter stages of growth, cell walls do form in this endosperm. Examples can be found in silk-oak and plum. Cellular endosperm, as found in ash and fringetree (*Chionanthus virginicus* L.), develops cell walls in the first and all subsequent divisions (Johri 1984). Endosperm tissue provides nutrition for the developing embryo, and in some genera, such as persimmon (*Diospyros* L.), magnolia, gooseberry (*Ribes* L.), and snowberry (*Symphoricarpos* Duham.), it persists as the primary food storage tissue in the mature seeds. Such seeds are described as endospermic. The monocotyledonous palms are also endospermic. In other genera, such as acacia, hickory, catalpa, and teak (*Tectona grandis* L.f.), the endosperm is consumed during embryo development and is absent or exists only as a very thin layer of tissue in mature seeds. The cotyledons of the embryo become the site of food storage, and these species are designated as nonendospermic. Still other genera have significant food storage capacity in both endosperm and cotyledons; examples are barberry (*Berberis* L.), ash, wintergreen (*Gaultheria* L.), and basswood (*Tilia* L.).

In most species, the perisperm, comprised of the maternal nucellar tissue in the ovule, fails to develop and is absorbed by the developing embryo. In a few species, the perisperm develops into a food storage tissue that is outside of the embryo sac. In these cases there is no endosperm development, and the perisperm becomes the major food storage tissue. In this book, yucca is the only genus with a fully developed perisperm.

Embryos differentiate and attain their full size in most species by the time the fruits or seeds are shed. In fact, relative length of the embryo can be a good maturity index for decisions on when to collect seeds of many species. In a few species, however—for example, American holly (*Ilex opaca* Ait.), European ash (*Fraxinus excelsior* L.), and common snowberry (*Symphoricarpos albus* (L.) Blake—embryos are still immature when seeds are shed from the trees, and full size is only attained following a period of after-ripening. This condition causes the very slow germination that is a major problem in nursery production of these species.

As endosperm and embryo grow, the surrounding maternal tissues develop into the seed-covering structures, collectively called the seedcoat. Most seedcoats are composed of a firm outer layer, the testa, and a generally thin, membranous inner coat called the tegmen. There are many variations of seedcoat structure, however, and many species do not fit the model described above. In some genera, the testa is thin and permeable, as in poplar (*Populus* L.) and willow. In others, it may be thick and bony, as in hawthorn and apple. Some hard seedcoats have special cutinized layers, as in redbud and honeylocust (*Gleditsia triacanthos* L.). In some genera both covering structures are membranous, as in elm; the outer layer partially membranous and the inner one bony, as in chastetree (*Vitex* L.); or the outer layer soft and fleshy and the inner layer hard, as in magnolia.

Many species develop extended tissues on their seedcoats that play a role in dissemination of the seeds. These extensions may be wings, as in ailanthus, *Ailanthus altissima* (Mill.) Swingle, and tuliptree; tufts of short, bristly hairs, as in baccharis, *Baccharis* L., and sycamore; long soft hairs, as in poplar and willow; wings with hairs, as in catalpa and desertwillow, *Chilopsis linearis* (Cav.) Sweet; or various other appendages, such as small points on sourwood (*Oxydendron arboreum* (L.) DC.; and long, feathery styles on cercocarpus, *Cercocarpus* H.B.K. Actually, the appendages on baccharis, sycamore, and cercocarpus are on the fruits, which are single-seeded achenes, commonly called seeds.

It is useful to define and classify fruit types, although all authorities do not completely agree on the results. The classification presented here (table 2) is based on that of Krugman and others (1974) and Sedgley and Griffin (1989), but with modifications.

Premature fruit shedding may occur late in phases 3 or 4. Premature shedding can seriously reduce the size of the potential seedcrop, especially in tropical fruit crops, where over 99% of the fruits may drop (Chaplin and Westwood 1980). Three periods of premature shedding in angiosperm fruit trees are recognized (Sedgley and Griffin 1989). The first occurs within 2 weeks of anthesis and usually involves unfertilized flowers. The second period (the most serious) occurs within 2 months of anthesis when young fertilized fruits are shed. The third shedding period is when immature, but full-sized, fruits are shed. Premature shedding can result from a number of conditions, but an imbalance of growth regulators and competition for nutrients are probably the most important (Sedgley and Griffin 1989).

Gymnosperms. Postfertilization growth of most gymnosperm cones is actually the continued enlargement of an existing structure, the ovulate cone. In most genera, for example, true fir, spruce, and hemlock, the young conelet develops into the mature woody cone in just a few months. In pine, the conelet is already more than a year old at fertilization. In other genera, such as juniper, the cone scales fuse together to form a berrylike structure around the seeds. Other fleshy gymnosperm fruits are found on yew and torreya, where the seeds develop within fleshy arils.

The food storage tissue in gymnosperms, the female gametophyte, is already present when fertilization occurs, so development from that point centers on the embryo. The embryo grows and differentiates into a miniature plant with radicle (rudimentary root), hypocotyl (stem), plumule (bud), and cotyledons. The cotyledons are usually quite small and range in number from 2 in thuja and sequoia to 18 in some pine (Chowdhury 1962).

In most gymnosperms, the embryo is both morphologically and physiologically mature at the time of seed dispersal from the cones. Exceptions to this are ginkgo and certain pines that grow at high altitudes and/or extreme northern latitudes. Examples of the latter include Swiss stone (*Pinus cembra* L.), Korean (*P. korainsis* Sieb. & Zucc.), Japanese white (*P. parviflora* Sieb. & Zucc.), and Siberian stone pines (*P. sibrica* Du Tour) (Krugman and Jenkinson 1974). Like the angiosperm seeds that are shed with immature embryos, these species require special treatments for prompt germination.

Seedcoats of gymnosperms may be relatively thin and soft, as in true fir; thin to thick and woody, as in pine; or very hard, as in juniper. Some genera have resin vesicles on

Table 2—Chapter 1, Seed Biology: classification of fruits of woody angiosperms

Fruit type	Description and examples
DERIVED FROM SINGLE FLOWERS	
Dry, dehiscent—pericarp dry and splitting open at maturity to release seeds	
Capsule	Two or more fused carpels, as in *Aesculus, Eucalyptus, Kalmia*
Legume (pod)	Splits along 2 sutures, as in *Acacia, Gleditsia, Lupinus*
Follicle	Splits along 1 suture, as in *Grevillea, Magnolia*
Dry, indehiscent—pericarp dry, but not splitting open at maturity	
Achene	Small, 1-seeded fruit with seed attached to ovary wall at only 1 point, as in *Cowania, Eriogonum*; or pericarp fused with calyx tube and embryo completely filling the ovarian cavity, as in *Artemisia, Chrysothamnus*
Nut	One-seeded fruit with woody or leathery pericarp, as in *Quercus*, or generally partially or wholly encased in an involucre (husk), as in *Carya, Corylus*
Samara	One-seeded pericarp modified with a wing-like appendage, as in *Fraxinus, Ulmus*; sometimes with 2 samaras fused together, as in *Acer*
Fleshy–part of the fruit wall comprised of fleshy or pulpy tissue with relatively high moisture content	
Berry	Pericarp has a skin that encloses a fleshy or pulpy mass that contains 1 or more seeds, as in *Berberis, Diospryros, Ribes*
Drupe	One-seeded fruit with pericarp usually in 3 distinct layers; the exocarp forms a skin, the mesocarp a fleshy layer, the endocarp a hard, stony layer, as in *Cornus, Nyssa, Prunus*; the seed, enclosed in endocarp only, is sometimes called a pyrene.
Pome	A many-sided fruit with the seeds enclosed in a papery inner wall, as in *Crataegus, Malus*
Hesperidium	Many-seeded fruit with leathery exocarp and mesocarp, and thick, fluid-filled endocarp, as in *Citrus*
DERIVED FROM INFLORESCENCES	
Dry, dehiscent—pericarp dry and splitting open at maturity to release seeds	
Strobile	A dry, conelike fruit developing from pistillate catkins, as in *Alnus, Betula*
Head	A multiple fruit that forms a compact cluster of simple fruits; the shape may be globose, as in *Liquidambar*, or conelike, as in *Casuarina;* the simple fruits can be different types, such as achenes in *Platanus* or capsules in *Liquidambar*
Fleshy—part of the fruit wall comprised of fleshy or pulpy tissue with relatively high moisture content	
Synconium	A type of pseudocarp in which achenes are actually borne on the inside of a hollow receptacle, as in *Ficus*
Sorosis	A fruit derived from the ovaries of several flowers, as in *Morus*
Coenocarp	A fruit incorporating ovaries, floral parts, and receptacles of many flowers, as in *Artocarpus*

or within their seedcoats: true fir, hemlock, and incense-cedar (*Calocedrus* Endl.). The resin makes seeds sticky and more difficult to handle in all phases of extraction and cleaning. Most gymnosperm seeds are winged, but there are exceptions: baldcypress, yew, torreya, and some pines. These pines are often called the "nut" pines: Swiss stone pine, piñyon (*Pinus edulis* Engelm.), chilgoza pine (*P. gerardiana* Wall.), etc. Wings may be loosely adhering structures that are easily separated from the seeds, as in most pines, or they may be integral parts of the seedcoat, as in Douglas-fir, longleaf pine, and incense-cedar.

Cones of gymnosperms that require more than 1 year to mature generally remain small during the first year after flowering in the interval between pollination and fertilization. In a few species, such as western juniper (*Juniperus occidentalis* Hook) and Alaska-cedar, the fruit grows before fertilization occurs and attains almost full size during the first growing season, a full year or more before the seeds are physiologically mature. Seed collectors must be aware of this condition to avoid collecting cones with immature fruits. In Alaska-cedar, there are distinct color differences between immature and mature cones (Harris 1990), and position of cones on the branches is an indicator for both species. Gymnosperm fruit classification is much simpler than that of angiosperms (table 3) (modified from Krugman and others 1974).

Table 3—Chapter 1, Seed Biology: classification of fruits of woody gymnosperms

Fruit type	Description and examples
Dry strobili	
Cone	Woody structures that generally open on the trees and release seeds at maturity, as in *Abies, Picea,* and most *Pinus*; some *Pinus* cones remain closed at maturity and open only in fires or disintegrate over time
Fleshy strobili	
Drupelike	Enclosing a single seed, as in *Ginkgo, Taxus, Torreya,* and some *Juniperus*, or multiple seeds in other *Juniperus*, that are shed from trees intact

Sources: Modified from Kregman and others (1974).

Premature cone shedding can also be important in gymnosperms. It is most common several weeks after anthesis, when pollination has not occurred, but can also result from damage from frost, hail, drought, insects, or pathogens (Owens and Blake 1985; Sedgley and Griffin 1989; Sweet 1973). There are also losses from what Bramlett (1972) described as "physiological drop," when there were no visible signs of external injury. In general, the physiology of immature cone abscission is much less understood than premature fruit shedding in angiosperms (Sedgley and Griffin 1989).

Physiological Development

The growth of fruits that starts soon after fertilization (or prior to fertilization in a few species) involves a complex array of physiological processes and conditions. These processes are generally similar for fruits of most temperate trees, and they produce comparable trends in size, weight, and moisture content. A typical pattern of development for dry fruits is provided by the single-seeded samaras of green ash (*Fraxinus pennsylvanica* Marsh.) (figure 6). Fresh weight, dry weight, and moisture content increase slowly through early summer. By the end of August, the embryo is 2 to 3 mm long. Over the next 6 weeks there are sharp increases in dry weight and significant decreases in moisture as embryo length increases 5-fold (Bonner 1973). In drupes of the temperate zone, weight trends are similar, but moisture changes are somewhat different. In black cherry (*Prunus serotina* Ehrh.), for example, moisture contents decrease during spring to early summer, then increase again as maturity approaches (figure 7). In temperate recalcitrant seeds, such as acorns, the patterns are more like those of dry fruits (figure 8). Similar trends occur in the maturation of most tropical tree fruits also, but the changes are not always correlated with the seasons as they are in temperate species.

Moisture content. Any discussion of seed moisture must be based upon the 2 physiological classes of seeds in respect to moisture: orthodox and recalcitrant. Orthodox seeds are seeds that can be dried to low moisture levels (below 10% of fresh weight) without losing viability. Recalcitrant seeds cannot be dried below rather high levels (25 to 50%, depending on the species) without losing viability. This sensitivity to desiccation has important implications in the storage of seeds, and chapter 4 contains a broader discussion of this subject.

Among orthodox seeds, the dry types (tables 2 and 3) are generally shed from the trees at rather low moisture contents. Exact measurements of the moisture levels at which shedding occurs are hard to find, but some preliminary data suggest a range of about 10 to 15% for sweetgum, green ash, and boxelder (*Acer negundo* L.) (Bonner 1996). The fleshy fruits (tables 2 and 3) also contain orthodox seeds, but because they are still enclosed in the fleshy tissues of the fruits, they are shed at higher moisture contents. Black cherry fruits, for example, are shed at fruit moisture contents of 70 to 75% (Bonner 1975). Seed moisture contents are not quite as high, but they are much higher than those that are found in species with dry fruits. Some examples of seed moisture contents from fleshy fruits at shedding are 34% for flowering dogwood, a drupe, and 50% for persimmon (*Diospyros virginiana* L.), a berry (Bonner 1996).

Moisture contents of recalcitrant fruits are also high at the time of shedding. Some representative values for temperate species are 40% for acorns of black oaks, 50% for those of white oaks (Bonner and Vozzo 1987; Finch-Savage and others 1992), 50% for horsechestnut (*Aesculus hippocastanum* L.) (Tompsett and Pritchard 1993), and 58% for planetree maple (*Acer pseudoplatanus* L.) (Hong and Ellis 1990). Similar values have also been reported for tropical recalcitrant species (Tamari and Jacalne 1984).

In orthodox species with dry fruits, the maturation drying that occurs on the plants prior to shedding is the final stage of development as the seeds enter their quiescent period. This stage is apparently necessary for the synthesis of

Figure 6—Chapter 1, Seed Biology: seasonal changes in fresh weight, dry weight, and moisture content during maturation of a dry fruit, green ash (*Fraxinus pennsylvanica* Marsh.) (from Bonner and others 1994).

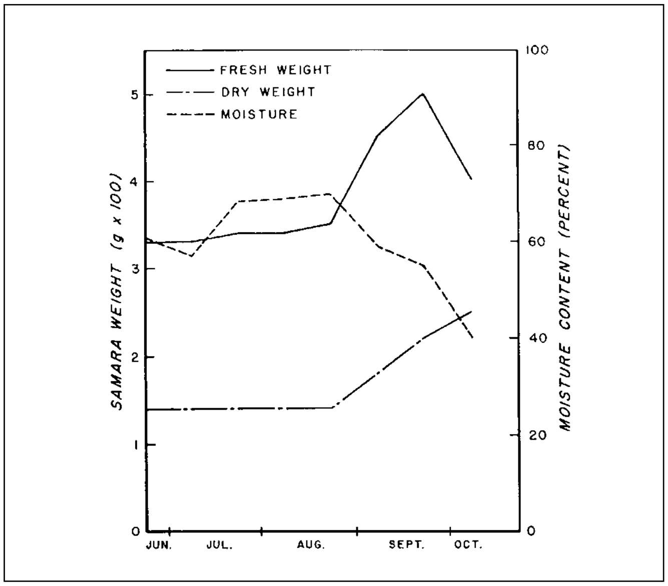


Figure 7—Chapter 1, Seed Biology: seasonal changes in fresh weight, dry weight, and moisture content during maturation of a fleshy drupe, black cherry (*Prunus serotina* Ehrh.) (adapted from Bonner and others 1994).

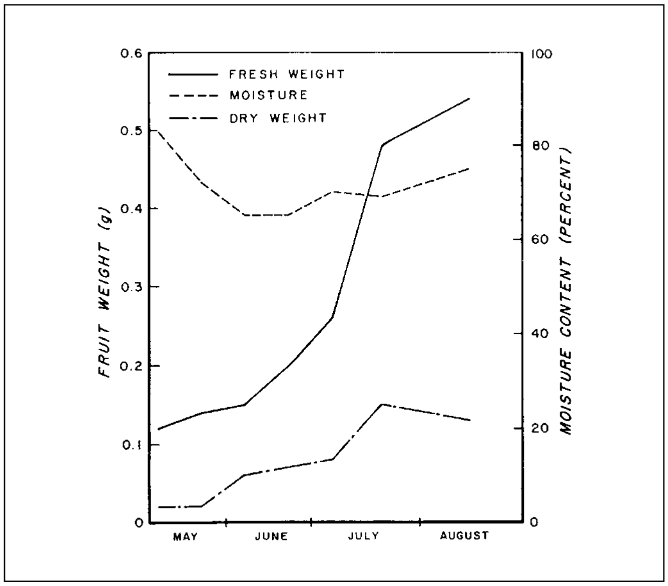
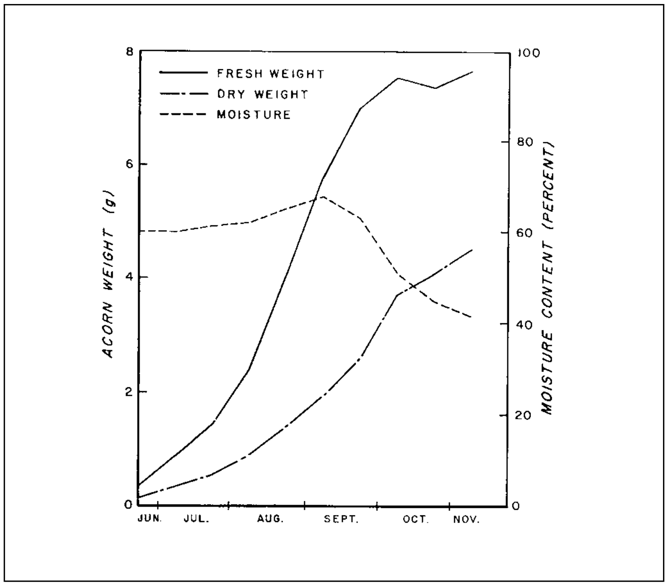


Figure 8—Chapter 1, Seed Biology: seasonal changes in fresh weight, dry weight, and moisture content during maturation of a recalcitrant fruit, Shumard oak (*Quercus shumardii* Buckl.) (from Bonner and others 1994).



many enzyme systems, including those required for desiccation tolerance and germination when rehydration occurs (Bewley and Black 1994). There are some data for tree seeds (Finch-Savage and others 1994), but most of the work in this area has been done on castor bean (*Ricinis communis* L.) (Kermode and Bewley 1985) and cereal grains (Bewley and Black 1994). There is no reason to doubt, however, that the same physiological processes take place during maturation of orthodox seeds of woody plants. Conditions are different in orthodox seeds from fleshy fruits, however, as they are shed before complete desiccation. Desiccation occurs later after the fleshy covering has dried or been removed (eaten in many cases). Many of these species have complex dormancy periods, and it can be hypothesized that there are interactions between the dormancy and the delay in maturation drying of the seeds.

In recalcitrant seeds, there is no pronounced maturation drying stage, because development never stops completely. There are slight decreases in moisture content that are apparently associated with shedding of fruits (figure 8), but there is no true quiescent period with recalcitrant seeds. Most species, especially tropical recalcitrant species, germinate soon after shedding, and some, including several *Quercus* species, will germinate while still on the tree, an event defined as vivipary.

Stored food reserves. As postfertilization growth proceeds, carbon fixed by photosynthesis is transferred to the seeds in the form of sucrose. In the seeds the sucrose is converted into many components, but most of it goes into stored food reserves of carbohydrate, lipid, or protein (Bewley and Black 1994). Many seeds have more than one type of food reserve, but one is usually predominant (table 4). The type of food reserve has implications for seed storage (see chapter 4), and it has been suggested that there are other important relationships. Korstian (1927), for example, suggested that dormancy in the black oak group was related to the high lipid content of these seeds, and that stratifica-

Table 4—Chapter 1, Seed Biology: some characteristic stored food reserves in tree seeds (expressed as % of dry weight)

Species	Tissue	Carbohydrate	Lipid	Protein*
Abies balsamea (L.) P. Mill.	Seed	—	37.6	13.9
Acer saccharinum L.	Samara	41.2	1.5	17.0
Aesculus pavia L.	Seed	42.9	1.9	8.2
Carya ovata (P. Mill.) K.Koch	Husked fruit	13.0	37.4	5.9
Cornus florida L.	Fruit	18.3	20.5	4.0
Euonymus americana L.	Seed	10.6	36.2	12.6
Juniperus virginiana L.	Cone	79.8	6.8	5.6
Liquidambar styraciflua L.	Seed	11.6	26.2	25.3
Picea glauca (Moench) Voss	Seed	—	44.2	23.8
Pinus palustris P. Mill.	Seed	3.1†	28.1	24.4‡
P. sylvestris L.	Seed	2.3	20.5	21.9
P. taeda L.	Seed	2.9†	18.5	13.8‡
Prunus serotina Ehrh.	Fruit	20.8	4.9	7.8
Pseudotsuga menziesii (Mirbel) Franco	Seed	5.1	37.2	—
Quercus alba L.	Acorn	46.6	2.9	4.6
Q. nigra L.	Acorn	25.8	20.3	3.8
Q. rubra L.	Acorn	67.1	20.8	6.6
Robinia pseudoacacia L.	Seed	12.3	9.0	38.7
Sassafras albidum (Nutt.) Nees	Fruit	13.6	46.6	17.1
Ulmus alata Michx.	Seed	8.9	15.3	27.4

Sources: Barnett (1976a), Bennett (1966), Bonner (1971, 1974a), Ching (1963), Pulliainen and Lajunen (1984), Waino and Forbes (1941).
* Most values obtained by multiplying total N by 6.25.
† Total sugars only.
‡ Insoluble N only multiplied by 6.25.

tion was needed to convert the lipid to soluble carbohydrates for germination. This conversion does take place during stratification of black oaks (Vozzo and Young 1975), but no direct connection to dormancy has been made. Also, some species with large lipid components, such as southern catalpa (*Catalpa bignonioides* Walt.) and winged elm (*Ulmus alata* Michx.), exhibit no dormancy, whereas some with high carbohydrate levels, such as sugarberry (*Celtis laevigata* Willd.) and eastern redcedar (*Juniperus virginiana* L.) are usually dormant.

Accumulation of food reserves follows similar patterns in most seeds. First there are slow increments of accumulation, then much more rapid accumulation as maturity and shedding are approached (figure 9). Soluble carbohydrates are converted to insoluble fractions in starchy seeds (figure 10), and the protein- nitrogen fraction increases at the expense of soluble forms (figure 11). During this period of development, seeds are strong sinks for current photosynthate, and vegetative growth is somewhat reduced (Bazzaz and Ackerly 1992; Owens and Blake 1985). The extent of growth lost in this trade-off in heavy seed years has not been accurately measured in woody plants, but estimates range from 30% in Norway spruce, *Picea abies* (L.) Karst, in Europe (Buyak 1975) to less than 5% in flowering dogwood in Mississippi (Bonner 1996). Rohmeder (1967) estimated that between the start of seed-bearing and the typical harvest age of forest trees, 10 to 30% of the potential volume yield may be used in seed production.

Some data on elemental concentrations in mature seeds are available (table 5). Such information is of great value to wildlife biologists in studies of the nutritive value of browse to wildlife.

Hormones. At the same time that the growing seeds are accumulating food reserves, there are certain hormonal changes that are taking place within the seeds. The major hormones in seeds are auxins, gibberellins, cytokinins, and abscisic acid (ABA) (Bewley and Black 1994). These hormones appear to play important roles in the growth and development of both fruits and seeds, but it is not always clear what these roles are. The major auxin in seeds, indoleacetic acid (IAA), is found in both free and bound forms. It has been extracted and identified from a number of tree seeds, for example, pecan (Lipe and others 1969), water oak (*Quercus nigra* L.) (Hopper and Vozzo 1982), English

Figure 9—Chapter 1, Seed Biology: changes in insoluble carbohydrate and crude lipid fractions in maturing acorns of white oak (*Quercus alba* L.) and water oak (*Q. nigra* L.) (from Bonner and others 1994).

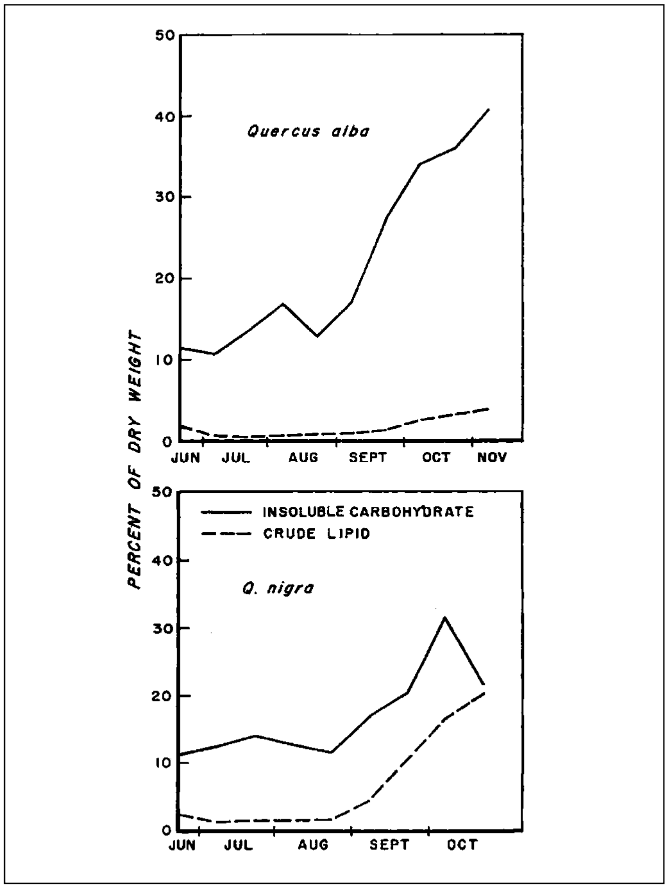


Figure 10—Chapter 1, Seed Biology: changes in soluble **(solid circles)** and insoluble **(open triangles)** carbohydrate contents of maturing acorns of whtie oak (*Quercus alba* L.) (adapted from Bonner 1976).

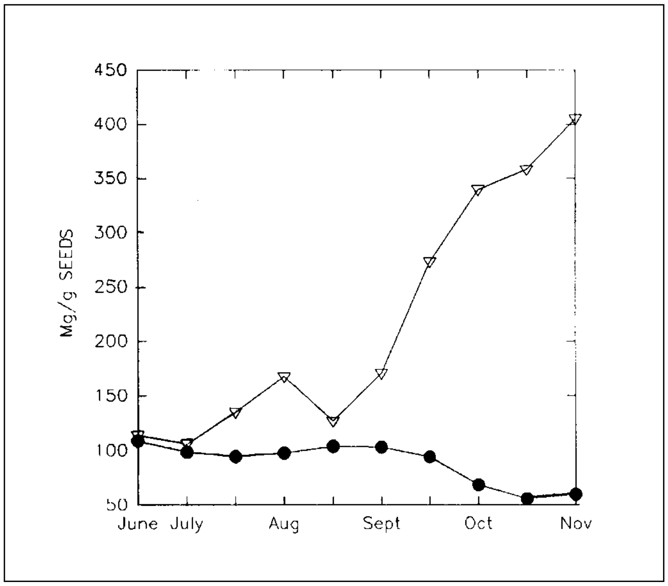
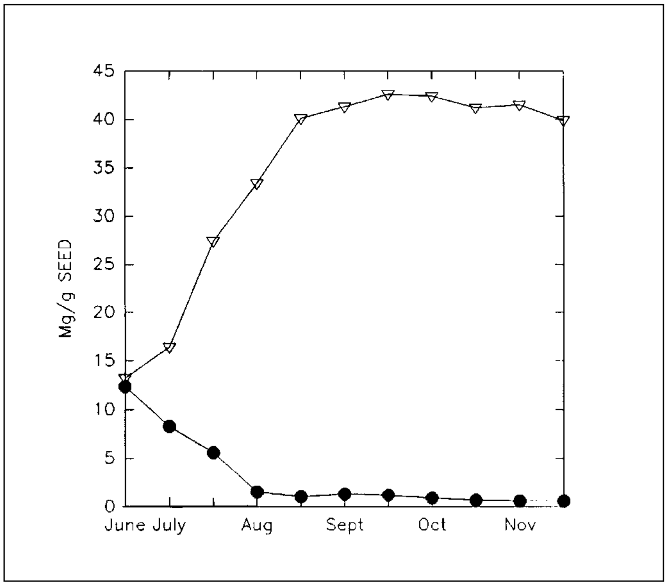


Figure 11—Chapter 1, Seed Biology: changes in soluble-nitrogen **(solid circles)** and protein-nitrogen **(open triangles)** contents of maturing seeds of sweetgum (*Liquidambar styraciflua* L.) (adapted from Bonner 1972).



oak (*Q. robur* L.) (Michalski 1969), apple, and plum (*Prunus cerasus* L.) (Bewley and Black 1994). Over 80 gibberellins are now known, and more than half of them have been identified in seeds (Bewley and Black 1994). Gibberellins or gibberellin-like substances have been identified in seeds of Jeffrey (*Pinus jefferyi* Grev. & Balf.), sugar, and ponderosa (Krugman 1967); and Monterey pine and Douglas-fir (Pharis and Kuo 1977); pear (*Pyrus communis* L.) (Martin and others 1977), water oak (Hopper and Vozzo 1982), and English oak (Michalski 1968).

Cytokinins have not been studied as much in seeds of woody plants, but they (or cytokinin-like compounds) have been found in English oak (Michalski 1974), apple, and sour cherry (Bewley and Black 1994). ABA has received much attention in seeds of woody plants, first for its possible role in dormancy, then for its possible role in tolerance of desiccation. ABA has been identified in developing seeds of English oak (Finch-Savage and others 1992), pear (Martin and others 1977), and peach (Piaggesi and others 1991).

The highest concentrations of gibberellins and cytokinins have been found in immature seeds during their most rapid phase of development, and both decline later as they apparently become bound up with other compounds. Immature seeds are also rich in auxins, and they are thought to be the source of this group of hormones needed for normal fruit growth. Removal of developing seeds will inhibit growth of the fruit (Bewley and Black 1994). In contrast to

Table 5—Chapter 1, Seed Biology: some characteristic seed elemental compositions (expressed as % of dry weight)

Species	Tissue	Ca	K	Mg	P
Acer rubrum L.	Samara	0.34	—	0.23	0.34
Callicarpa americana L.	Fruit	.26	1.34	—	.13
Corylus avellana L.	Seed	.10	.73	.19	.40
Ilex vomitoria Ait.	Fruit	.24	1.25	—	.11
Juglans regia L.	Nut	.08	.45	.17	.41
Picea abies (L.) Karst	Seed	.02	.79	.31	.66
Pinus sylvestris L.	Seed	.04	.63	.30	.73
Prunus serotina Ehrh.	Fruit	.14	—	.09	.14
Quercus pagoda Raf.	Acorn	.27	—	.06	.06
Q. stellata Wangenh.	Acorn	.25	—	.06	.08
Sassafras albidum (Nutt.) Nees	Fruit	.06	—	.11	.23
Ulmus alata Michx.	Seed	.51	—	.20	.52
Vaccinium arboreum Marsh.	Fruit	.33	—	.07	.06

Sources: Bonner (1971, 1974a), Hastings (1966), Lott and Buttrose (19780, Pulliainen and Lajunen (1984).

the other hormones, ABA concentration is low in developing seeds and highest at maturity. In conjunction with maturation drying, ABA may prevent embryos from germinating while still on the tree (Bewley and Black 1994). These correlations do not prove a causal relationship between seed maturity and dormancy, however, and much research remains to be done.

Factors That Influence Seed Production

There are many factors that can reduce the size of a seed crop on woody plants no matter how abundant flower production may be. Flower abortion and premature fruit drop have been discussed earlier. This section will briefly review factors that reduce seedcrops well after fertilization and early development of fruits or cones has occurred.

Physiological factors. Most of the fruit and cone losses that can be attributed to physiological factors occur early in the fruiting season. On some occasions, however, fruits or cones will abscise late in the growing season. The exact mechanisms are not understood, but they may be related to competition for a shrinking supply of nutrients late in the season between reproductive structures and vegetative shoots. Early abscision of acorns as maturation is completed may appear to be physiological in nature, but the primary cause is often insect damage that triggers a physiological reaction.

Weather. Weather can influence seedcrops in a variety of ways. Interference with flowering and pollination through late freezes, rain during pollination, etc., have been discussed previously. Severe drought can have a noticeable effect on the size of many angiosperm seeds. This effect is particularly noticeable for large single-seeded fruits such as oak acorns (Bonner 1996). Other damaging effects of weather can be more direct. Strong winds and hail can destroy flowers and fruits, sometimes to the point that most of the crop is lost. Hurricanes along the coastal areas of the Southeast are infrequent but very serious, and they can create problems locally for longleaf pine, a species with large, heavy cones that are fairly easy to knock to the ground.

Biotic factors. Flowers, fruits, and seeds are susceptible to damage by many insects, pathogens, and animals. Flower damage, particularly by insects, often goes unnoticed in branch terminals and in the tops of trees. Much more is known about damage to fruits and seeds, because they are handled and observed closely when collected.

Insects. Little is known about insects that destroy flowers, as the damage is often not seen. Both larvae and young adults of treehoppers (Membracidae) destroy pistillate flowers of oaks (Cecich 1993). Thrips, both Phlaeothripidae and Thripidae, destroy young strobili on several pines, true firs, and Douglas-fir (Hedlin and others 1980). The most serious economic damage is done by *Gnophothrips fuscus* (Morgan) on slash pine (*Pinus elliottii* Engelm.). Other insects that damage pine strobili in the Southeast include Nantucket pine tip moth, *Rhyacionia frustrana (*Comstock); pine conelet looper, *Nepytia semiclusaria* (Walker); the Virginia pine sawfly, *Neodiprion pratti pratti* (Dyar) and other sawflies, *Xyela* spp.; leaffooted pine seedbug, *Leptoglossus corculus* (Say); cone midges, *Cecidomyiidae*; and several coneworms, *Dioryctria* spp. (Ebel and others 1975). Strobili damage in other conifers has been reported for *Xyela* spp. on lodgepole, Coulter (*Pinus coulteri*

D. Don), ponderosa, digger (*P. sabiniana* Dougl.), and Monterey pine; western conifer seed bug (*Leptoglossus occidentalis* Heidemann) on Douglas-fir, grand fir, incense-cedar, and several pine species; and the European pine shoot moth (*Rhyacionia buoliana* (Schiffermuller)) on red, Scots, eastern white (*Pinus* strobus L.), pitch (*P. rigida* Mill.) and other pines (Hedlin and others 1980).

Insect damage to fruits and seeds is much more common than damage to flowers and strobili. Most damage is caused by larvae that hatch from eggs deposited in young, developing fruits and devour the embryo tissues. In angiosperms, major damage is caused by *Curculio* spp., *Conotrachelus* spp., and *Melissopus* spp. in oaks (Gibson 1972, 1982; Vozzo 1984); *Thysanocnemis* spp. in ash (Solomon and others 1993); several species of seed beetles (Bruchidae) in acacias (Southgate 1983); and the fruit borers *Pagyda salvalis* Walk. and *Dichocrosis punctiferalis* Guenee in teak (Neelay and others 1983). There are numerous insects that cause minor damage to fruit- and seed-crops of other angiosperms, but they do not seriously threaten to decimate seed supplies.

Because most major commercial forest species are conifers, insect damage to their cones and seeds is more economically important than damage to fruits and seeds of angiosperms. Cones of many species can be heavily damaged by cone worms (*Dioryctria* spp.) and cone beetles (*Conophthorus* spp.). Lesser damage to cones is also caused by the cone borers *(Eucosma* spp.) and cone midges (Cecidomyiidae) (Hedlin and others 1980). The southern pine coneworm, *D. amatella* (Hulst), is a major pest in seed orchards of the southern pines and many control programs are designed to reduce its impact (Ebel and others 1975). Significant damage to other conifers has been recorded for red pine cone beetle (*Conophthorus resinosae* Hopk.) (Hard 1964), sugar pine cone beetle (*C. lambertianae* Hopk.) (Bedard 1968), and *C. monticolae* on western white pine (Graham 1990). The major seed damage in conifers has been attributed to seedworms, *Laspeyresia* spp.; seed chalcids, *Metastigmu*s spp.; seedbugs, *Leptoglossus* spp.; and *Tetyra bipunctata* Herrich-Schaeffer (Ebel and others 1975; Hedlin and others 1980; Kinzer and others 1972; Krugman and Koerber 1969; Scurlock and others 1982).

Control of seed insects in natural stands is normally not economical. In seed orchards, where considerable resources have been invested to produce seedcrops and many other cultural practices are being carried out, control programs are feasible. In recent years, however, environmental concerns are forcing stringent limitations on chemical application programs in seed orchards. Insect populations can be reduced with light and chemical attractant traps, but these methods have a limited impact.

Pathogens. Flowers, fruits, and seeds of woody plants are exposed to great numbers of microorganisms in their natural environments; some of these are pathogenic and some are beneficial. Of the 3 types of pathogenic microorganisms causing damage to woody plants—viruses, bacteria, and fungi—only fungi have serious effects on seed production.

The most important group of fungi is the cone rusts. These fungi attack first- and second-year cones on a wide range of conifers throughout North America (table 6). Degree of infection varies, but losses are often significant. Losses from southern pine cone rust and inland spruce cone rust have been sufficient to warrant spraying orchards with fungicides (Sutherland and others 1987). Other fungi that can reduce seed production in conifers include sirococcus blight (*Sirococcus strobilinus* Preuss) and pitch canker (*Fusarium moniliforme* Sheld. var. *subglutinans* Wollenw. & Reink.). Sirococcus blight is primarily a problem in nurseries and young stands, but it can kill branches in older trees

Table 6—Chapter 1, Seed Biology: major cone rust diseases of conifers

Disease	**Fungal pathogen**	**Species infected**
inland spruce cone rust	*Chrysomyxa pirolata* Wint.	*Picea engelmannii, P. glauca, P. mariana, P. rubens, P. pungens, P. sitchensis, P. abies*
coastal spruce cone rust	*Chrysomyxa monesis* Ziller	*Picea sitchensis*
southern pine cone rust	*Cronartium strobilinum* (Arth.) Hedgc. & Hahn	*Pinus elliottii, P. elliottii* var. *densa, P. palustris*
southwestern pine cone rust	*Cronartium conigenum* Hedgc. & Hunt	Many *Pinus* species from S Arizona, S into Central America
western gall rust	*Endocronartium harknessii* (J.P. Moore) Y. Hirat.	*Pinus banksiana, P. contorta, P. ponderosa,* and to a lesser. degree, many others in W US, Canada, & NE US

Source: Sutherland and others (1987).

as well. It can be found on larch, spruce, pine, and Douglas-fir (Sutherland and others 1987). Pitch canker damages shoots, cones, and seeds of pines in the South and East. In a few short years, pitch canker has become a major disease problem in seed orchards of all southern pines (Barrows-Broaddus and Dwinell 1985; Blakeslee and others 1980).

With the exception of species that attack trees with edible nuts, such as scab disease—*Cladosporium caryigenum* (Ell. & Lang.) Gottwald—on pecan (Graves and others 1989), reduction of seedcrops in angiosperms by fungi is generally not serious. There are, however, numerous fungi that infect flowers and fruits and cause only incidental or local damage to the seedcrop (table 7). For additional information on seed pathogens and other microorganisms and the species on which they are found, readers are referred to Mittal and others (1990).

Birds. Birds feed on flowers, fruits, and seeds, especially the latter. Many small birds—such as finches, grosbeaks, and sparrows (Fringillidae), doves (Columbidae), and quail (Phasianidae)—feed on small seeds after they are shed, but these losses are incidental to the total seedcrop. Larger birds that feed on maturing fruits and seeds still on the trees can have serious, though usually local, impacts on seed yield. Acorns are a favorite of grackles (*Quiscalus* spp.), jays (Corvidae), and woodpeckers (Picidae). The California woodpecker (*Balanosphyra formicivora*) can devour enough acorns, its favorite food, to severely reduce the crop within its foraging range (Bent 1939). Pine seeds are a favorite of Clark's nutcracker (*Nucifraga columbiana*) and piñyon jays (*Cyanocephalus cyanocephalus*), which specialize in piñyon seeds and even young cones (Bent 1946). Berries of various juniper species are eaten in large numbers by jays, Clark's nutcracker, and robins (*Turdus migratorius*). Robins also are heavy feeders in the winter on Pacific madrone (*Arbutus menziesii* Pursh.) on the west coast (Bent 1949).

Losses of seeds are most serious when the birds feed in flocks. Heavy feeding of grackles on acorns has been mentioned previously in connection with seed dispersal. Flock depredation also occurs when robins or cedar waxwings (*Bombycilla cedrorum*) feast on cherries, eastern redcedar, hollies, and elms.

Not as many quantitative data or observational data have been collected for tropical and subtropical species, but it is certain that birds play a large role in the depredation and dispersal of tropical fruits and seeds (Terborgh 1990). A study of *Virola surinamensis* (Rol.) Warb. (Myristicaceae) in a moist, tropical forest in Panama by Howe (1990) found that more than 80% of the fruits were eaten or removed by birds.

Although less damaging to the total seedcrop, birds' feeding on flowers can have a local impact. Grouse (*Bonasa umbillas,* and *Dendragapus* spp.) are known to feed heavily on buds and flowers of alder and poplars and strobili of pines, spruces, firs, and larches (Bent 1932).

Mammals. Significant amounts of fruits and seeds are lost to mammal predation by many species. Squirrels (*Citellus* and *Sciurus* spp.) are heavy feeders on acorns of almost all species of oak throughout North America. Not only are many acorns eaten, but also many more are buried in the ground for winter retrieval. Squirrels are also heavy feeders on pines, usually dissecting or removing the green cones. Several western squirrel species cache the cones for winter retrieval, and these caches were once heavily utilized by cone collectors. Cone losses to squirrels can be very

Table 7—Chapter 1, Seed Biology: fungi that cause minor or locally severe decreases to fruit crops of angiosperms

Fungus	Tissue attacked	Species infected
Botrytis spp	Flowers	*Ilex opaca*
Ciboria acerina Whetz. & Buchew.	Flowers	*Acer rubrum, A. saccharinum*
Coniothyrium spp.	Seeds	*Betula alleghaniensis*
Cytospora spp.	Fruits	*Prunus serotina*
Gymnosporangium clavipes (Cooke & Peck) Cooke.& Peck	Fruits	*Amelanchier, Cotoneaster, Crataegus, Malus, Pyrus*
G. clavariiforme (Pers.) DC	Fruits	*Amelanchier, Cotoneaster, Crataegus, Malus, Pyrus*
Taphrina johansonii Sadeb.	Catkins	*Populus* spp.
T. occidentalis W.W. Ray	Catkins	*Alnus* spp.
T. amentorum (Sadeb.) Rostr.	Catkins	*Alnus* spp.

Sources: Hepting (1971), Ziller (1974).

significant. Fowells and Schubert (1956) reported that in 1 year in an area in California, the Douglas pine squirrel (*Tamiasciurus douglasii*) destroyed over 50% of the sugar pine and ponderosa pine cones. Squirrels may remove over 90% of the cone crops of white spruce (*Picea glauca* (Moench) Voss) in Alaska (Nienstaedt and Zasada 1990). Losses of cones of southern pines to squirrels in the Southeast are normally not nearly so severe.

Squirrels also reduce seedcrops by cutting and feeding on cambial tissues in branches in the spring, thus destroying buds, flowers, and strobili. There is evidence of this type of damage on ponderosa pine (Adams 1955), red pine (Roe 1948), sugar maple (Godman and others 1990), and American elm (*Ulmus americana* L.) (Bey 1990).

Minor fruit depredation also occurs from other animals, such as bears (*Ursus* spp.), raccoons *(Procyon lotor*), deer (*Odocoileus* spp.), and opossums (*Didelphis virginiana*). In tropical and subtropical forests, many more animals are fruit and seed predators than in temperate forests.

Maturity and Dispersal

As a general rule, fruits should be collected only after the seeds have reached full maturity. One problem with this rule is that full maturity is not easily defined. To some, dispersal from the tree of seeds with the ability to germinate and grow is a sign of full maturity, yet serotinous cones with germinable seeds remain on the some pine species for several years after others have dispersed and germinated. Other seeds are shed naturally but require an after-ripening period before they can germinate. These are examples of dispersal strategies that have been favorable for regeneration of these species but also seem to contradict the simple definition of maturity. Others propose that physical or chemical attributes of the seeds define maturity: minimum moisture content, maximum dry weight, maximum level of stored food reserves, or maximum germination performance. As in the previous definition, there are numerous apparent exceptions to all of the proposed criteria. Another problem with the general rule about collection at maturity is that, in actual practice, fruits and seeds must often be collected before full maturity, whatever that is, because of possible losses to predators, difficulties in collecting small wind-dispersed seeds, or time constraints in commercial collection operations. The solution to both of these problems is to develop practical indices of maturity for fruits and seeds so that collectors can tell when they can proceed without danger of gathering immature seeds that will not germinate properly and produce healthy seedlings.

Indices of maturity. In order to collect seeds at the optimum stage of their development, collectors need some sort of index of seed maturity to guide them in their choice of collection time. Indices of seed maturity should ideally be simple procedures that require little or no equipment and that can be administered in the field.

Physical. The most commonly used indices of fruit or seed maturity are those that are based on physical characteristics. Change of fruit color is widely used on both dry and fleshy fruits. The most common color changes are from a "vegetative green" to a shade of brown in dry fruits or to a bright or blue-black color in fleshy fruits. Common patterns are changes from green to yellow to brown (ash, maple, and white oak, *Quercus alba* L.); from green to red to purple or black (cherries and tupelos, *Nyssa* L.); from green to yellow to purple (for example, honeylocust); and from green to brown (conifers).

Embryo size is a simple maturity index. When embryo length reaches 75% of the length of the embryonic cavity, seeds of many species are considered mature enough to collect (Edwards 1979). The relative size of embryos can be easily seen on radiographs or determined from cross-sections of seeds.

Moisture content also is a simple indicator of maturity in some species, but overnight or 24 hours of drying of samples in ovens is required for accurate measurement. "Critical" samara moisture levels (percentage of fresh weight) were reported to be 16% for green ash (Cram and Lindquist 1982) and 59% for sugar maple (Carl and Snow 1971). Moisture content of cones is also a very good maturity index for many conifers, but instead of actually measuring it, most collectors estimate cone moisture content by measuring specific gravity of the cones. This can be accomplished easily in the field with a graduated cylinder of water

Table 8—Chapter 1, Seed Biology: cone specific-gravity values that indicate seed maturity in some conifers

Species	Specific gravity
Abies grandis (Dougl. ex D. Don) Lindl.	0.90
Cunninghamia lanceolata (Lamb.) Hook.	0.95
Pinus elliottii Engelm.	0.95
P. merkusii Junghuhn & Vriese ex Vriese	1.00
P. palustris P. Mill.	0.90
P. strobus (L.)	0.90
P. taeda (L.)	0.90
P. virginiana P. Mill.	1.00

Sources: Barnett (1976a), Bonner (1986), Daryano and others (1979), Fenton and Sucoff (1965), Jian and Peipei (1988), Pfister (1967).

(Barnett 1979). Cone weight is estimated by water displacement of the floating cone, and volume is estimated by water displacement of the submerged cone. Specific gravity is equal to weight divided by volume (examples of cone specific gravities used to judge maturity are listed in table 8).

Other physical indices of seed maturity are easy cup release from acorns of oak; a white, brittle embryo of some ash species that breaks when bent at a sharp angle; and white pine cone scales that flex open when cones are bent double. For details on maturity indices of individual genera or species, see part 2 of this book.

Chemical. Although chemical indices of maturity are biologically sound, they are seldom practical to use in collection. Most potential chemical indicators are based on the level of stored food reserves (table 9), but elemental phosphorus and IAA concentrations have been suggested as indices for green ash (Bonner 1973) and English oak (Michalski 1969), respectively.

Shedding and dispersal. The majority of temperate genera shed their fruits and seeds in the fall or winter, although many—for example, birch and poplar—shed theirs in the spring. In some genera—for example, maple, eucalyptus, willow, and elm—there are both spring-shedding and fall-shedding species. Other species have seeds that mature and are shed in mid-summer—for example, ceanothus (*Ceanothus* L.).

The seeds of many species are shed or dispersed quickly (within a few days) after they mature, and collectors must be alert to the phenological characteristics of the species in order to collect what they need. Some species that shed fruits quickly when they mature are maples and elms. In others, the fruits are persistent on the tree but open to disperse the seeds quickly after maturity; examples include sweetgum, poplars, and willows. In still other species, fruit opening and seed dispersal are very dependent on the weather. Cones of loblolly pine, for example, open readily in warm, dry conditions and disperse their seeds. At night, they close back up again when humidity rises. If a weather front brings rain, the cones may close up completely and not reopen for dispersal for several days. The primary seed dispersal agent of all of the above species is wind.

Drupes, berries, and other fleshy fruits are not usually shed quickly, but they can be removed from the trees rapidly by birds and animals. This can be a major problem for seed collectors wishing to harvest the seeds of species such as pawpaws (*Asimina* Adans.), hollies, plums, and prickly-ash (*Zanthoxylum* L.). Seeds will usually have to be collected exactly at the time of maturity on the trees, or the entire crop may be lost. The same problem occurs for some fruits that are not fleshy, for example, hickories, walnuts, and oaks. These fruits are favorite foods of rodents, deer, and other animals, and they must be collected from the ground as soon as they are shed. Birds will also take many of these fruits before shedding; for example, a flock of grackles can completely strip a large willow oak (*Q. phellos* L.) of its acorn crop in several hours.

The cones of most conifers disperse their seeds soon after maturity. In true firs, dispersal occurs as the cone disintegrates on the trees, leaving the spike-like cone axis still upright on the branches. In some pines, cedars, and hemlocks, the cones are slow to give up their seeds, and dispersal may take 3 to 12 months. Serotinous cones of several species—such as jack (*Pinus banksiana* Lamb.), sand (*P. clausa* (Chapm. ex Engelm.) Vasey ex Sarg.), pitch (*P. rigida* Mill.), and lodgepole pines—do not normally open on the trees but open on the ground following fires that melt the resin seals on the cone scales. Other pines—Swiss stone and Siberian stone pines, etc.—shed their cones while still

Table 9—Chapter 1, Seed Biology: chemical levels that indicate seed maturity

Species	Chemical	Percent of dry weight fraction
Abies procera Rehd.	Crude fat	25
Fraxinus pennsylvanica Marsh.	Crude fat	10
Liquidambar styraciflua L.	Crude fat	25
Quercus (black oaks)	Crude fat	15–25
	Insoluble CHO	25
Quercus (white oaks)	Insoluble CHO	40
Pseudotsuga menziesii (Mirbel) Franco	Crude fat	*23*
	Reducing sugars	1.3

Sources: Bonner (1972, 1973, 1974b, 1976, Rediske (1961), Rediske and Nickolson (1965).
CHO=carbohydrates.

closed or only partly open, and seed dispersal occurs only as the cones disintegrate on the ground over several months (Krugman and others 1974).

The major dispersal agents for seeds of woody plants are wind, animals, and water. Wind-dispersed species are mostly small, and many have hairs or other appendages that help to prolong their flight. Other seeds, such as those of ailanthus, catalpas, or ashes, are somewhat larger but have wings that are large in relation to the size of the embryos. Food value and color aid in dispersal by animals, which is very local if by rodents or widespread if by birds. Dispersal by water is usually by flotation and can be very important for wetland species such as tupelos, willows, and the 1 oak species that has floating acorns–the overcup oak (*Quercus lyrata* Walt.). At least 2 genera in this book—ceanothus and witch-hazel disperse seeds with an explosive force when drying fruits split suddenly and expel the seeds. For more detailed treatments of seed dispersal, readers should see Bawa and Hadley (1990) and Fenner (1992).

Dormancy

Once seeds have matured and been dispersed, survival of the species requires that they germinate at a time and place favorable for growth and survival of the seedlings. Plants have evolved many mechanisms and processes that ensure survival. Some species produce prodigious numbers of seeds, so that even if only a tiny proportion germinate and grow, some seedlings will survive. In others, germination at unfavorable times is prevented by a mechanism that is commonly described as dormancy. Dormancy is defined as a physiological state in which a seed disposed to germinate does not, even in the presence of favorable environmental conditions (Bonner 1984). Seeds are able to overcome dormancy and germinate when "triggered" by certain internal processes that are usually induced by environmental changes. There is a tremendous range in the degree of dormancy among woody species. Some seeds lie in the soil for years before germinating, whereas other are delayed for only a few weeks. The latter condition is sometimes described as "delayed germination" to indicate something less than true dormancy. In fact, the distinction between dormancy and delayed germination is not at all clear, and among the majority of species, the interval between maturity and germination (in natural conditions) is a continuum with no distinct gradation.

Types of Dormancy

Many different classifications of dormancy have been devised by seed scientists and there is no universal agreement on the subject. Most tree seed workers accept the definitions of the Seed Problems Working Party of the IUFRO—International Union of Forest Research Organizations (Bonner 1984)—and these definitions will be used in this discussion.

Seedcoat (or external) dormancy. Seedcoat dormancy has 3 primary modes of action. In the most common mode, the seedcoats (or other covering structures) are impermeable to the entry of moisture or gases. Members of the Leguminoseae—for example, acacia, albizia (*Albizia* Durazz.), honeylocust, mesquite (*Prosopis* L.), black-locust, sophora (*Sophora* L.)—usually display this characteristic, which is commonly called hardseededness by those who work with seeds. Members of other families also have seedcoats that impose a similar dormancy, but seedcoat structures are different; some examples include American beautyberry (*Callicarpa americana* L.), hollies, sumacs, and basswood.

The second mode of dormancy action attributed to seedcoats is the mechanical resistance to swelling of the embryo as it absorbs moisture. This resistance delays full imbibition and emergence of the radicle from within the seed. Mechanical resistance frequently contributes to dormancy and has been documented in big sagebrush (*Artemesia tridentata* Nutt.) (McDonough and Harniss 1974), pecan (Van Staden and Dimalla 1976), loblolly pine (Barnett 1976b), Korean pine (Hatano and Asakawa 1964), and water oak (Peterson 1983). It does not appear to be the primary factor in tree seed dormancy, however.

A third possible mode of seedcoat dormancy is the presence of germination inhibitors in the seedcoats (Bewley and Black 1994; Nord and Van Atta 1960; Peterson 1983) that may or may not play a significant role in dormancy. Some of the phenolic substances in seedcoats that could possibly be germination inhibitors could actually be beneficial by inhibiting the growth of pathogenic microorganisms (Mohamed-Yasseen and others 1994). In some herbaceous species, there are inhibitors that must leach from the embryo before germination can take place, and seedcoats prevent this leaching (Bewley and Black 1994). There is no conclusive evidence of this condition in seeds of woody plants, but success in stratifying seeds by placing them in porous sacks in running water suggests that it may occur.

Embryo (or internal) dormancy. Embryo dormancy arises from a condition within the embryo itself. The most likely cause of embryo dormancy is the presence of germination inhibitors in the embryonic axis or in the food storage tissues of the seed. For germination to occur, these inhibitors must be metabolically inactivated, or their effect must be overcome by germination-promoting substances. Germination inhibitors have been isolated and identified in a number of woody plant seeds, with ABA the most common inhibitor. Species with ABA functioning as an internal inhibitor include sugar (Enu-Kwesi and Dumbroff 1978), Norway (*Acer platanoides* L.) (Tilberg and Pinfield 1982), and planetree maples (Webb and Wareing 1972); European hazel (*Corylus avellana* L.) (Williams and others 1973); white ash (*Fraxinus americana* L.) (Sondheimer and others 1968); apple (*Malus pumila* Mill.) (Singh and Browning 1991); and northern red (*Quercus rubra* L.) and English oaks (Szczotka 1977). Correlations of changing ABA levels with degree of dormancy in mature seeds is not evidence of cause and effect, however, and more detailed research is needed in this field. ABA also seems to play a role in preventing precocious germination in English oak (Finch-Savage and others 1992) and shedding of silver maple samaras (Tomaszewska 1973). Other germination inhibitors have also been found in dormant seeds of woody plants, but there is no good evidence for their modes of action in the seed.

In another type of embryo dormancy, called physiological immaturity, a critical enzyme system or other biochemical factor is not in place at shedding and afterripening is required for complete physiological maturation. Evidence for the existence of this type of dormancy is weak, so it probably is the same as morphological dormancy.

Morphological dormancy. Morphological dormancy results from the embryo not being completely morphologically developed when seeds are shed. Additional growth of the embryo is required in an afterripening period. Morphological dormancy has been documented in black (*Fraxinus nigra* Marsh.) and European ashes (Vanstone and LaCroix 1975; Walle 1987), American holly (Ives 1923), and several pines that grow at high altitudes or latitudes (Krugman and Jenkinson 1974).

Combined dormancy. Combined dormancy is a condition in which 2 or more primary factors, such as seedcoat dormancy and embryo dormancy, are present to the extent that each requires treatment to overcome. Some examples of combined dormancy in North American species are seeds of Mexican redbud (*Cercis canadensis* var. *mexicana* (Rose) Hopkins) (Tipton 1992), skunkbush (*Rhus trilobata* Nutt.) (Heit 1967b), and American basswood (Barton 1934). For basswood, seedcoat scarification with acid for 10 to 40 minutes, followed by moist stratification for 90 days is the recommended treatment to overcome dormancy (Heit 1967b).

Double dormancy. Double dormancy is a condition in which there is dormancy in both the radicle and the epicotyl of the embryo, but each require different conditions to overcome it. This type of dormancy is difficult to demonstrate, but it has been reported for viburnums (Giersbach 1937). A similar condition is found in some oaks, in which radicles are not dormant, but epicotyls are.

Secondary dormancy. Secondary dormancy results from some action, treatment, or injury to seeds during collection, handling, or sowing. Pine seeds can incur secondary dormancy if exposed to high temperatures and moisture at crucial times (McLemore and Barnett 1966). When stratified seeds are redried to storage levels (below 10%), they are often said to have incurred secondary dormancy. Germination can certainly be delayed under these conditions, but this is not a true secondary dormancy.

Overcoming Dormancy

Dormancy is a great advantage when one wants to store seeds, but a disadvantage when prompt germination in desired. With the exception of hardseeded species, years of research have revealed little about how seed dormancy really functions and how it can be overcome. Applied research and practical experience, however, have combined to provide ways to hasten the germination of dormant seeds.

Seedcoat dormancy. Treatments are designed to breach the seedcoat, or other covering structures, and remove barriers to moisture uptake, gas exchange, swelling of the embryo, and radicle emergence. Methods used to overcome seedcoat dormancy are collectively known as scarification treatments, and there are risks to seed viability inherent in all of them. In selecting a scarification treatment, the most gentle method should be tested first; then increasingly severe treatments until the desired effect is obtained. The methods below are listed in order of increasing severity. Complete details on how to apply them can be found in chapter 5 for small samples, as in seed testing, and in chapter 7 for large quantities. Suggested methods for individual species may be found in part 2 of this book.

Cold water soak. In some hardseeded species, the seedcoats are not completely impermeable to water. Soaking such seeds in water at room temperature for 24 to 48 hours may be sufficient for full imbibition and subsequent germination.

Hot water soak. Similar to the cold water soak, except that seeds are put into very hot or boiling water and left there as the water cools. The hot water softens the seedcoats or causes them to crack, and imbibition occurs as the water cools. Numerous leguminous species can be treated in this manner—for example, acacia, albizia, and prosopis.

Hot wire. This technique requires a heated needle or an electric woodburning tool to burn small holes through seedcoats (Sandif 1988; Stubsgaard 1986). A belt-driven burner that scarifies seeds electrically shows promise for treatment of larger lots (Danida Forest Seed Centre 1993). "Burned" seeds can be shipped or returned to storage after treatment (Lauridsen and Stubsgaard 1987), something that other scarification methods normally do not allow.

Acid treatment. Treatment with concentrated sulfuric acid (or other mineral acids such as hydrochloric or nitric acids) is the method of choice for many species. Seeds should be in contact with the acid for 15 to 60 minutes, depending on species or individual seedlot, and washed thoroughly in running water afterward to remove any acid that remains on the seedcoats. Acid has been used in North America to treat honeylocust and Kentucky coffeetree (*Gymnocladus dioicus* (L.) K. Koch) (Liu and others 1981), black locust (Heit 1967a), and snowbrush ceanothus (*Ceanothus velutinus* Dougl.) (Heit 1967b).

Mechanical treatments. Mechanical scarification is used extensively for large lots of seeds. There are various scarifiers in use, from small cement mixers filled with rough rocks or pieces of broken concrete, to the impact seed gun developed in Denmark (Stubsgaard 1986). A mechanical device has also been developed to crack peach seedcoats (Reid and others 1979). For small samples, seedcoats can be scarified by hand with knives, files, clippers, sandpaper, etc.

Internal dormancy. Treatments to overcome internal dormancy are expected to bring about physiological changes within the embryo that will enhance rapid germination. The most successful treatments have been those that simulate natural conditions in a crucial time period in the reproductive life cycle of the plant. For temperate species, this is usually a moist, chilling period, commonly called stratification, because it was formerly done by alternating layers of seeds and sand or peat in a pit in the ground. Stratification in pits is seldom used anymore, but the principles are the same.

Stratification (chilling). The usual procedure for stratification is to refrigerate fully imbibed seeds at 1 to 5 °C for 1 to 6 months. This procedure simulates the natural winter conditions of temperate seeds that are lying on the forest floor. During stratification (1) enzyme systems are activated (Eichholtz and others 1983; Li and Ross 1990a&b; Michalski 1982; Slater and Bryant 1987); (2) stored foods are changed to soluble forms (Dumbroff and De Silva 1972; Kao and Rowan 1970; Pukacka 1986; Tylkowski 1986; Vozzo and Young 1975); and (3) the inhibitor/promoter balances change (Enu-Kwesi and Dumbroff 1978; Tillberg and Pinfield 1982; Webb and others 1973; Williams and others 1973). For a more detailed review of the biochemical changes during this period, see Bewley and Black 1994.

The optimum length of the stratification period varies greatly among species and among different seedlots of the same species. There may be differences even within the same lot if some portions are handled differently. In southern pines, dormancy often appears to increase during storage, and stored seeds require longer stratification than the same lots when fresh (Bonner 1991). Details on stratification procedures can be found in chapters 5 and 7. Recommendations for particular genera or individual species are provided in part 2 of this book.

One tremendous benefit of stratification for nurseries is an increased uniformity of emergence. The low temperatures used in stratification inhibit germination of the seeds that are no longer dormant while the remaining seeds are undergoing the needed internal changes. When the seeds are finally sown in favorable temperatures, there is a flush of uniform germination and emergence, which is crucial to even seedling development. This condition also explains why some non-dormant species appear to respond favorably to short periods (1 to 2 weeks) of stratification with faster and more complete germination.

There is a growing body of evidence that suggests that full imbibition is not the optimum moisture content for stratification. Careful regulation of seed moisture content at levels below full imbibition has produced improved seed performance and sowing options for both conifers (Edwards 1986; Poulsen 1996) and hardwoods (Muller 1993).

Incubation and stratification. A number of species that exhibit complex embryo dormancy or morphological dormancy will germinate quicker if given a warm, moist incubation period prior to cold stratification. The incubation period promotes embryo growth and other internal processes and is usually shorter than the stratification period. Species for which this treatment has been effective include cherry plum (*Prunus cerasifera* Ehrh.) (Tylkowski 1986), black ash (Vanstone and LaCroix 1975), and several species of juniper (Rietveld 1989; Van Haverbeke and Comer 1985).

Chemical treatment. Various studies have shown that some species will germinate quicker following treatment with exogenous chemical agents, such as hydrogen peroxide, citric acid, and gibberellins. Although these benefits can be demonstrated in the laboratory with small samples, they are rarely, if ever, used in production nurseries.

Combined treatments. Some species—such as American basswood—have seeds with combined dormancy charateristics that seem to require 2 types of treatment for good germination. Impermeable seedcoats must first be scarified before seeds are stratified (Brinkman 1974).

Variation in Dormancy

As noted earlier, there is widespread variation in the degree of dormancy, both among species, and within a species. For some species, there are patterns of dormancy that have been documented and that can have practical application. For example, degree of dormancy appears to increase with increasing elevation of seed source for black cherry and red maple (*Acer rubrum* L.) in Tennessee (Farmer and Barnett 1972; Farmer and Cunningham 1981). Seeds from more northern sources generally require longer stratification periods than seeds from southern sources. This relationship has been reported for sugar maple (Kriebel and Gabriel 1969), red maple (Farmer and Goelz 1984; Tremblay and others 1996), sweetgum (Wilcox 1968), and sycamore (Webb and Farmer 1968). In contrast, eastern white pine showed just the reverse in a range-wide study (Fowler and Dwight 1964): seeds from the southern sources are more dormant, but this phenomenon may be related to the higher altitudes of the natural stands of white pine at the southern extremities of its range. Warmer climates during seed maturation typically produce heavier and larger embryos in seeds (Durzan and Chalupa 1968), presumably because the growing seasons are longer. This conditions suggests that degree of dormancy (or delayed germination) is related to degree of physiological maturity in temperate seeds, but the evidence for this is lacking.

Variation in dormancy among individual trees at the same site has been documented for loblolly pine (McLemore and Barnett 1966) and sweetgum (Rink and others 1979), and can probably be assumed to occur in all woody plants. Partial genetic control of dormancy is also obvious, because most seed dormancy is related in some way to seedcoats or other covering structures, all maternal tissues. The best way to understand dormancy is to quantify it in mathematical terms. A number of studies have attempted this for temperate trees (Bonner and Harrington 1993; Donald 1987; Richter and Switzer 1982; Rink and others 1979; Sorensen 1983) and all of the proposed methods have application under certain conditions.

Germination

Germination is defined as "the resumption of active growth in an embryo which results in its emergence from the seed and development of those structures essential to plant development" (Bonner 1984). In another sense, it is the culminating event of seed maturation, the establishment of the seedling. It is useful to think of germination as occurring in overlapping events (Kramer and Kozlowski 1979):

1. Absorption of water
2. Increased respiration, enzymatic activity, and assimilation of stored foods
3. Increased adenosine phosphate and nucleic acids
4. Cell growth and division
5. Differentiation of tissues

All of these events are influenced by environmental conditions and events within the seeds themselves.

Environmental Factors

The most important environmental factors that influence germination are moisture, temperature, light, and aeration.

Moisture. The typical pattern of moisture uptake by seeds has 3 phases (Vertucci 1989): a rapid initial uptake, a short lag period of extremely slow uptake, and another rapid period of uptake just before germination. The first phase is primarily imbibitional in nature and occurs in dead seeds as well as live ones. It is a physical process of moisture moving from a substance with high water potential (soil) to one with a low water potential (dry seed). This uptake displaces gases from dry seeds (Simon 1984) and is visually evident in the bubbles that slowly escape from dry seeds when they are submerged in water. The length of the second phase is related to the degree of dormancy or delayed germination in the seeds. It can be practically absent in the rapidly germinating seeds of oak (Bonner 1968) or extended in the case of very dormant seeds. The third phase occurs when metabolism becomes very active, and the seedcoats split, leading to greater oxygen uptake.

There are minimum amounts of moisture required for germination to proceed, and several studies have sought to measure the moisture stresses that will retard or halt germination (table 10). Significant decreases in germination occurred, in general, from – 0.8 MPa and below, and germination was effectively stopped at stresses of – 0.3 to – 2.0 MPa. All of these studies used osmotic solutions to impose stress, and there are concerns that this method may hinder germination by inhibiting gas exchange. McDonough (1979) used thermocouple psychrometer chambers to impose moisture stress on seeds of quaking aspen (*Populus tremuloides* Michx.), however, and his results agree quite well with those reported with osmotic solutions. Comparisons among species should be made with caution, as methodology and equipment varied widely in these studies. There were also significant interactions with seed source, seed treatment, and temperature for some species (Bonner and Farmer 1966; Farmer and Bonner 1967; Moore and Kidd 1982).

Table 10—Chapter 1, Seed Biology: critical levels of water potential (MPa) for germination within a 20 to 30 °C range of temperatures as determined with osmotic solutions*

Species	Water potential (MPa) Strongly decreased germination	Effectively stopped germination
Artemisia tridentata Nutt.	–0.1	–1.6
Acacia tortillis (Forsskal) Hayne	–0.29	–0.51
Cercocarpus montanus (Raf.)	–0.4	–1.3
Chrysothamnus nauseosus (Pallas ex Pursh) Britt.	–0.4	–1.6
Liquidambar styraciflua L.	–0.5	–1.52
Pinus contorta Dougl. ex Loud	–0.8	—
P. eldarica Medw.	–0.6	–1.2
P. elliottii Engelm.	–0.81	–1.82
P. palustris P. Mill.	–0.81	–1.82
P. ponderosa P. & C. Lawson	–0.4	–0.8
Picea engelmannii Parry ex Royle	–0.8	—
Populus ciliata Wall. ex Royle	–0.1	–0.3
P. deltoides Bartr. ex Marsh.	–1.01	–1.52
Quercus palustris Muenchh.	–0.5	–2.0

Sources: Barnett (1969), Bonner (1968), Bonner & Farmer (1966), Choinski and Tuohy (1991), Djavanshir and Reid (1975), Farmer and Bonner (1967), Kaufman and Eckard (1977), Moore and Kidd (1982), Sabo and others (1979), Singh and Singh 1983

* Some data were converted from atmospheres and bars to MPa as follows: 1 bar = 0.1 MPa; 1 atm = 0.1013 MPa.

Temperature. Seeds of temperate woody plants can germinate over a wide range of temperatures, from a minimum of 2 or 3 °C, to a maximum of about 45 °C (Bonner and others 1994). Radicle emergence will occur in most species at 45 °C, but few will produce normal seedlings at this temperature. Low temperatures, on the other hand, are favored by some species. Northern red oak from Wisconsin, for example, germinated best at 1 °C in a trial reported by Godman and Mattson (1980). Some true firs and mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) will germinate in snowbanks in Oregon and Washington (Franklin and Krueger 1968). Many dormant temperate species will sometimes germinate in stratification bags at 3 to 5 °C if left for long periods. The major effect of temperature on germination, however, is on rate rather than total germination.

Natural seedbeds do not remain at constant temperatures, but experience diurnal fluctuations from lows at night to highs in the daytime. Most temperate woody plants have adapted to these conditions and germinate most rapidly at alternating temperatures of approximately 20 °C at night and 30 °C in the daytime. Other species germinate faster at lower temperatures regimes, for example, 15 to 25 °C or 10 to 20 °C, or at constant temperatures of 5 to 22 °C (Sabo and others 1979; Wang and Pitel 1991). Official seed testing prescriptions are based on the known optimum temperatures for each genus or species (ISTA 1993). Experiments with 2-way thermogradient plates suggest that germination of many temperate species will occur at a wide range of temperature regimes, and that an amplitude of change between day and night of 10 to 12 °C may be more important than the cardinal points (Bonner 1983; Mayer and Poljakoff-Mayber 1963; Sabo and others 1979).

In the tropics, pioneer species that invade forest gaps also respond to alternating temperatures with increased germination (Vázquez-Yanes and Orozco-Segovia 1982). Temperatures are more constant underneath canopies, and light becomes more of an important factor in germination in these conditions (Clark 1990; Vázquez-Yanes and others 1990.).

Light. Light plays a complex role in the germination of woody plants, in that it stimulates the germination of most species but is absolutely necessary for only a few. It is often difficult to separate the effects of light and the effects of temperature. Dry, dormant seeds normally do not germinate in the dark, but stratification at low temperatures or treatment with high temperatures can overcome the dark inhibition in some species.

The key to seed response to light is thought to be the phytochrome system. Phytochrome is a pigment that exists in 2 forms within the embryonic axes of seeds (Bewley and Black 1994). One form (Pr) has a maximum absorption at 660 nm, whereas the other form (Pfr) has a maximum absorption at 730 nm. Red light converts Pr to Pfr in imbibed seeds, which is associated with overcoming dormancy. Far-red light drives the process in the other direction, accompanied by a partial return of dormancy. The red/far-red reaction has been demonstrated in seeds of numerous temperate species: Virginia (*Pinus virginiana* Mill.) (Toole and others 1961), longleaf (McLemore and Hansbrough 1970), and Scots pines (Nyman 1963); red alder (*Alnus rubra* Bong.) (Bormann 1983); paper (*Betula papyrifera* Marsh.) (Bevington and Hoyle 1981), hairy (*B. pubescens* Ehrh.), and European white birches (*B. verrucosa* Ehrh.) (Junttila 1976); and northern catalpa (*Catalpa speciosa* Warder ex Engelm.) (Fosket and Briggs 1970). There is also evidence that the red/far-red system is operative in seeds of many tropical rainforest species (Vázquez-Yanes and Orozco-Segovia 1990). For a detailed discussion of phytochrome and its reactions, readers should see Bewley and Black (1994).

Phytochrome reactions require only a short exposure to the proper wavelength to take effect (Bewley and Black 1994). Other light responses that are related to daylength have been noted in seeds of woody plants. In terms of germination, eastern hemlock appears to have long-day light requirements of 16 hours at 27 °C, but shorter requirements of 8 to 12 hours at 17 °C (Stearns and Olson 1958). In many temperate species—for example, Fraser fir (*Abies fraseri* (Pursh.) Poir). (Adkins and others 1984); sweetgum (Bonner 1967), and ponderosa pine (Harrington 1977)—stratification decreases the light requirement for prompt germination. These responses may or may not be related in some way to phytochrome, but they demonstrate the complex nature of the relationship of light to seeds.

Aeration. Respiration supplies energy to germinating seeds, and oxygen is a primary electron acceptor in the process (Kramer and Kozlowski 1979). Insufficient oxygen is not usually a major barrier to germination, except when seeds are buried too deeply in the soil or are submerged in water. A few small seeds can germinate as they float on the surface of water—for example, willows, cottonwood (*Populus deltoides* Bartr. ex Marsh.), and sycamore—but oxygen is usually too limiting for germination when seeds are submerged. Poor oxygen supply is often a problem in seed testing when blotters are kept too moist. Moisture will actually form a film around seeds and inhibit the entry of oxygen (Gordon and Edwards 1991).

As seeds begin to germinate, the pattern of oxygen uptake is practically identical to that of water uptake (Kozlowski and Gentile 1959): (1) a short period of rapid uptake; (2) a period of very slow uptake; and (3) a second period of rapid uptake. Measurements of seedcoat permeability to oxygen in some herbaceous species suggest that the coats are much more permeable to water than to oxygen. Part of this may be due to the consumption of oxygen by the seedcoat itself in oxidative reactions (Bewley and Black 1994). There are lots of phenolic compounds in seedcoats, for example, and their oxidation could consume a considerable amount of oxygen.

Biochemical Changes

When non-dormant seeds are placed in environments that are conducive to germination, internal processes that drive the growth of the embryo start to take place. These processes are dominated by the conversion of storage foods into soluble forms and their translocation into the embryonic axis. In stratified seeds, these processes have already been initiated during the treatment period. In the past 25 years, there has been an enormous amount of research that has greatly advanced our knowledge of the biochemical mechanisms of seed germination. Although most of this research has been centered on seeds of agricultural crops, the basic processes are similar in most seeds and the conclusions drawn from this research can be readily extrapolated to include the seeds of woody plants. A detailed discussion of biochemical changes in seed germination is beyond the scope of this book. For additional information, readers should see Bewley and Black (1994), Murray (1984), and Pehap (1983).

Most recent work on seeds of woody plants has been on oily seeds. In these seeds, lipid reserves are converted to starch, which is then hydrolyzed into soluble carbohydrates (mainly glucose) for embryo growth. Much of this change takes place within the storage tissues (endosperm, cotyledon, female gametophyte, or haustoria) before axis elongation signals the start of germination, so it is difficult to say if this change is part of dormancy removal or part of the germination process (Arce and others 1983; Li and Ross 1990a&b; Murphy and Hammer 1993;). Recent studies on gene expression and enzyme formation in several pine species should help in this regard (Gifford and others 1991; Murphy and Hammer 1993; Pitel and Cheliak 1988; Pitel and others 1984; Salmia 1981).

Other changes within germinating embryos include the hydrolysis of storage proteins to form amino acids and other soluble nitrogenous compounds for enzyme synthesis

(Bouvier-Durand and others 1984; Salmia 1981) and a large increase in soluble phosphorus compounds (Ching 1966).

The transfer of reserve foods from storage tissue to the axis is usually direct. In endospermic Leguminosae (which include honeylocust), however, the reserves are transferred from the endosperm to the cotyledons, then to the growing axis (Bewley and Black 1994). A similar transfer process may exist in other species that have both endosperm and cotyledons, but there is no evidence for it. In oil palm (*Elaeis guineensis* Jacq.), a slow-germinating monocot, the haustoria form at one end of the embryo and absorb the food reserves from the endosperm as they are broken down and pass the nutrients on to the developing plumule and radicle (Oo and Stumpf 1983).

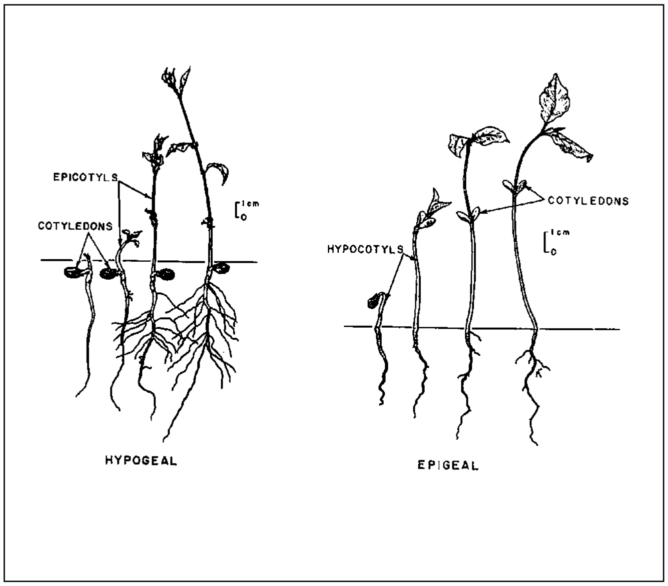


Figure 12—Chapter 1, Seed Biology: the common forms of seed germination in temperate trees. These are hypogeal germination **(left)**, here that of American plum (*Prunus americana* Marsh.), with seedlings at 1, 3, 5, and 9 days after germination, and epigeal germination **(right)**, here that of common chokecherry (*P. virginiana* L.) seedlings at 1, 3, 7, and 11 days after.

Physical Development

Physical changes in germinating seeds are practically the same for all species. The first sign is usually swelling of the seed from water uptake. Embryo elongation occurs second, but unseen within the seed's covering structures. Then the seedcoat splits, and the emerging radicle elongates. At this point, germination in temperate species takes one of two forms. One form is epigeal germination, in which the hypocotyl elongates, arches upward, then straightens, pushing the cotyledons upward through the soil (figure 12). In many species the seedcoats are still attached to the cotyledons after emergence and are not shed until the cotyledons start growing. Genera that exhibit epigeal germination include pine, cedar, eucalyptus, juniper, magnolia, and mountain-ash.

In the second form, hypogeal germination, it is the epicotyl that elongates, pushing the young plumule through the soil while the cotyledons remain below ground (figure 12). There they remain attached to the seedling and supply reserve foods for weeks or more. Genera that exhibit hypogeal germination include buckeye, oak, walnut, chestnut (*Castanea* Mill.), and torreya.

Germination form is normally the same for all species in a genus, but like most things in seed biology of woody plants, there is an exception. In cherries and plums, both forms occur; common chokecherry (*P. virginiana* L.) is epigeal, but the remaining species of the genus are hypogeal (figure 12).

Some authorities recognize other forms of germination in tropical species. Bunya-pine (*Araucaria bidwillii* Hooker) and Parana-pine (*A. angustifolia* (Bert.) O. Kuntze) seeds germinate on the surface of the soil, then the cotyledonary stalks elongate and push the hypocotyl, plumule, and radicle into the soil. The hypocotyl subsequently develops into a tuber that serves to transfer the food reserves from the female megagametophyte to the growing seedling. This type of germination has been defined as cryptogeal (Burrows and Stockey 1994), and these araucarias are the only species in this book that exhibit this form of germination. Ng (1991) also has defined durian germination in which the hypocotyl elongates but the cotyledons remain within the seed. This form of germination occurs in common durian (*Durio zibethinus* Murr.), a popular, edible fruit of Southeast Asia that is cauliferous.

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