Reaction Wood

Trees can modify the structure of the walls of tracheids and fibers during their differentiation to deal with imposed stress. In gymnosperms, the tracheids formed under a compressive load on the lower side of branches and leaning stems, or the leeward side of the tree with respect to the prevailing wind, have a larger than normal microfibril angle and extra lignification. In this case the wood is known as compression wood. In angiosperms, fibers formed under tension on the upper side of branches and leaning stems and the windward side of the tree develop a special wall layer, the gelatinous layer, which comprises almost pure cellulose with a very small microfibril angle. Wood containing these fibers is known as tension wood. Collectively these two types are known as reaction wood and they are essential to the tree to maintain an upright main stem, correct branch angles, and prevent branches drooping under their own weight. However, reaction wood is a serious problem for the timber and pulp industries and has been the subject of intensive research. As with microfibril angle, however, any attempts to modify reaction wood production must also consider the consequences of doing so for the tree.

See also: **Hydrology**: Hydrological Cycle. **Tree Physiology**: A Whole Tree Perspective; Physiology and Silviculture. **Wood Formation and Properties**: Formation and Structure of Wood; Wood Quality.

Further Reading

Barnett JR (1981) *Xylem Cell Development*. Tunbridge Wells: Castle House Publications.

Barnett JR and Jeronimidis G (2003) *Wood Quality and its Biological Basis*. Oxford: Blackwell.

Braun HJ (1984) The significance of the accessory tissues of the hydrosystem for osmotic water shifting as the second principle of water ascent, with some thoughts concerning the evolution of trees. *IAWA Bulletin* 5: 275–294.

Butterfield BG (1998) *Microfibril Angle in Wood*. International Association of Wood Anatomists/International Union of Forestry Research Organizations. Canterbury, New Zealand: University of Canterbury.

Butterfield BG and Meylan BA (1980) *Three Dimensional Structure of Wood: An Ultrastructural Approach*. London: Chapman & Hall.

Carlquist S (1975) *Ecological Strategies of Xylem Evolution*. Berkeley: University of California Press.

Iqbal M (1995) *The Cambial Derivatives. Handbuch der Planzenanatomie*, Vol. 9(4). Berlin: Gebrüder Borntraeger.

Larson PR (1994) *The Vascular Cambium: Development and Structure*. Berlin: Springer-Verlag.

Savidge RA, Barnett JR, and Napier R (2000) *Cell and Molecular Biology of Wood Formation*. Oxford: BIOS Scientific.

Timell TE (1986) *Compression Wood in Gymnosperms*. Berlin: Springer-Verlag.

Wilson K and White DJB (1986) *The Anatomy of Wood, its Diversity and Variability*. London: Stobart.

Zimmermann MH (1964) *The Formation of Wood in Forest Trees*. New York: Academic Press.

Zimmermann MH (1983) *Xylem Structure and the Ascent of Sap*. Berlin: Springer-Verlag.

Tropical Tree Seed Physiology

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Introduction

Forest trees are a renewable natural resource. Understanding forest dynamics, trees, seeds, and seedlings as indisputable factors and basic units of regeneration has become important in developing effective techniques to promote conservation, management, and rational use of remaining forests. These are significant rudiments to implement successful reforestation programs.

The Angiosperm Seed

Seed Development

The fruit is the structure containing the seed. It develops from the gynoecium of the flower, which is frequently associated with other floral organs. The ovary wall forms the pericarp (fruit wall), and the fertilized ovule forms the seed. Fruit ripening is followed by senescence and, sometimes, dehiscence and abscission.

The process of seed development has three functional phases:

1. Cell divisions to produce the seedcoat, the endosperm, and the embryo (embryogenesis); this stage is characterized by an enhanced increase in fresh weight. Embryo development includes establishing a precise spatial organization of cells derived from the zygote (pattern of formation) and the generation of cell diversity inside the developing embryo (cytodifferentiation). These processes are coordinated to develop a recognizable morphological structure, regulated by the embryogenic pattern of the species (**Figure 1**).
2. Storage of reserves leading to an increase in dry weight.
3. Maturation drying leading to a stage of metabolic quiescence, interpolated between the end of seed development and the beginning of germination.

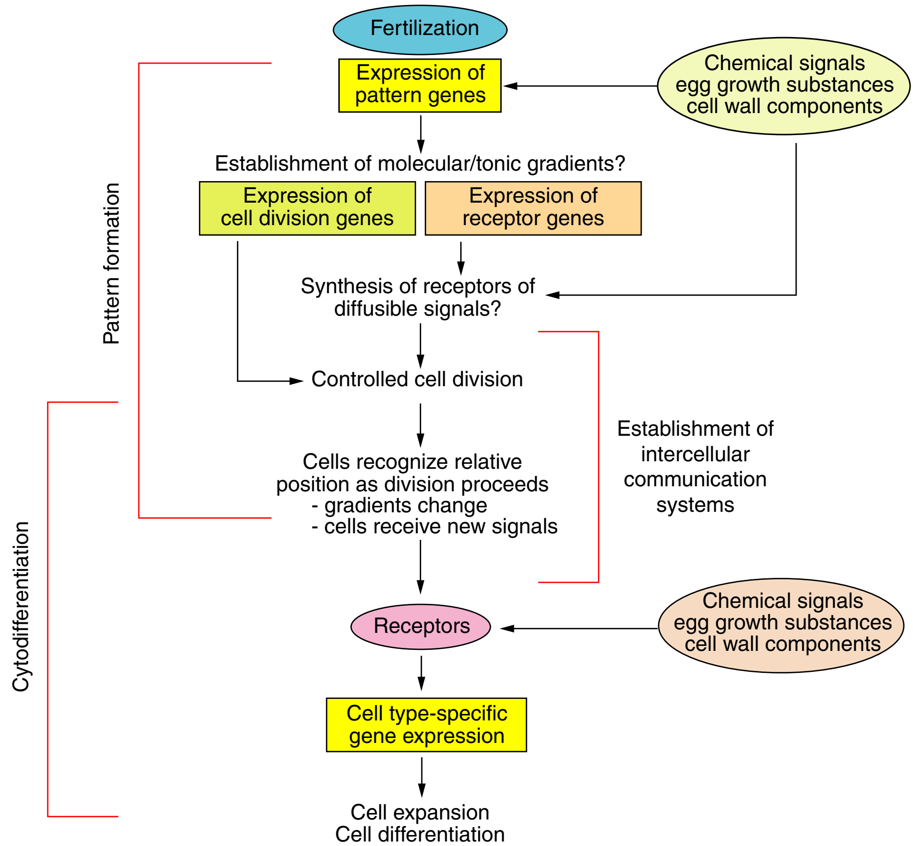

Figure 1 Gene expression during embryo development. Redrawn with permission from Lindsey K and Topping JF (1993) Embryogenesis: a question of pattern. *Journal of Experimental Botany* 44: 359–374.

> Seed inactivity is promoted by reduction of water content in the tissues, seedcoat impermeability, and inhibitors. Seed drying also reduces the synthesis of storage proteins.

Ovule, embryo, and endosperm development are coordinated and have contributions from both sporophytic and male and female gametophytic genes. Growth regulators present in the tissues of developing seeds (indol acetic acid, gibberellins, cytokinins, and abscisic acid) are active in seed development; accumulation of the storage reserves; development of the extra seminal tissues; and physiological changes of tissues and organs surrounding the developing fruit.

Many tropical and temperate seeds do not undergo drying, do not experience reduced cellular metabolism, and do not exhibit a clear end to seed development. During fruit dehiscence and dispersal, seed development is followed by germination-seed development without interruption. In some species, the seedling develops when the seed is still inside the fruit and is attached to the parent tree. These seeds are called viviparous (**Figure 2**). Mangroves growing on protected tropical coasts are the best-known examples of viviparous seeds. Overgrown seeds, which have a continuous embryo development limited by a hard and indehiscent pericarp or a late dehiscence pericarp (e.g., *Dipteryx*, *Prioria*) (**Figure 3**) may represent an intermediate type.

Figure 2 Viviparous seed of *Inga paterno*. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

Embryo development in seeds without maturation drying is similar in its early stages to that of seeds with maturation drying; however, variations

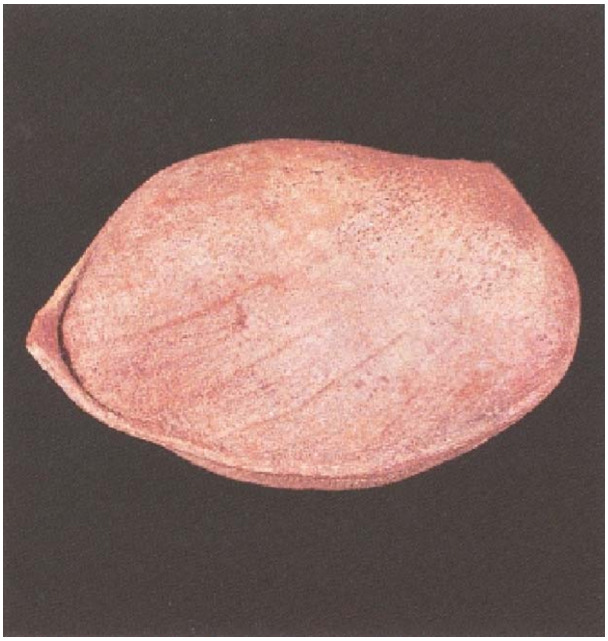

Figure 3 *Prioria copaifera* fruit (pod) enclosing an overgrown seed. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

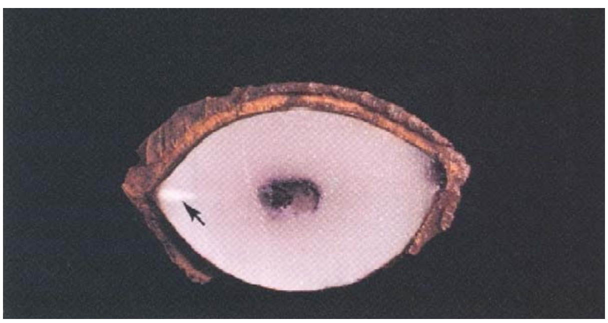

Figure 4 *Calatola costaricensis* drupe showing small, rudimentary embryo within a large seed. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

appear in late embryogenesis. Many seeds without maturation drying are large, with well-developed embryos (e.g., *Aesculus*, *Calophyllum*, *Dipterocarpus*, *Hevea*, *Quercus*, and *Sclerocarya*). Other seeds are large but have a small, rudimentary embryo (e.g., *Calatola*) (**Figure 4**). All these seeds increase in dry weight until fruit dehiscence, with insignificant loss in fresh weight. Embryo growth may continue (increasing in dry weight) after dehiscence in the absence of enough water to promote germination. However, in the tropical forest with very high rainfall the seeds or fruits (diaspores) fall down on very humid soils, sometimes inundated, and continue hydrating.

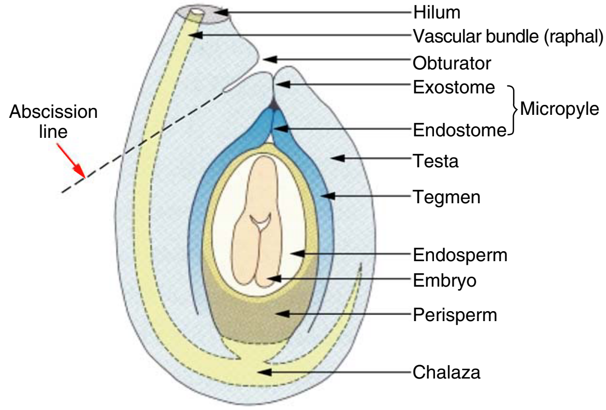

Figure 5 Diagram of typical mature seed. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

Some embryos have a suspensor. It seems to accomplish an active and dynamic role in nutrient absorption from the surrounding somatic tissues and transportation to the developing embryo as well as a source of nutrients and growth regulators for the developing embryo. The suspensor contains gibberellic acid, auxins, and cytokinins; the concentrations of these substances follow a fluctuation pattern.

The Mature Seed

The mature seed generally has a seed coat (product of one or both ovule integuments), an endosperm, and an embryo (**Figure 5**). Some mature seeds retain a remnant of nucellar tissue called a perisperm. The degree to which these structures continue their development, are reduced or reabsorbed, or disappear during the late stages of seed development leads to distinct structural patterns associated with physiological differences.

Storage of reserves Seeds store lipids, carbohydrates, and proteins to nourish the embryo (before and after germination) and to develop the early stages of seedling development. They are a source of precursors for carbon skeletons and provide energy when assembling precursors. Reserves may be stored in cell walls of different tissues, perisperm, endosperm, cotyledons, hypocotyl, and chalaza. The endosperm does not have a significant role at the proembryo stage, but it is important during embryo development and seed germination. The formation of the endosperm, its reabsorption, and the transference of reserves to the embryo are controlled genetically.

Lipids, which appear as lipidic bodies in the endosperm and the embryo, are a greater source of nourishment than the carbohydrates. The seeds without maturation drying are rich in lipids (e.g., *Virola koschnyi* ≥41%, *Calophyllum brasiliense*

38–39%). Carbohydrates are stored as starch or in thick cell walls rich in hemicelluloses.

Nearly all seeds contain proteins as reserve. They are found as aleurone grains and supply the nitrogen in early stages of plant development. In addition to the homogeneous protein matrix, aleurone grains contain crystals of proteins, minerals, and calcium oxalate. Several cations (K, Mg, Ca, Fe, Ba, Mn) are also found as globoid crystals. Seeds with maturation drying accumulate disaccharides, such as the saccharose and oligosaccharides, in the form of stachyose and raffinose. It has been suggested that these sugars are associated with tolerance to desiccation; however, some seeds sensitive to desiccation also accumulate sugars and saccharose (e.g., *Avicennia marina*) or saccharose and raffinose (e.g., *Quercus robur*).

Relationships between Seed Structure and Storage Behavior

Seeds losing water during maturation drying gradually acquire tolerance to desiccation; others maintain a high water content, do not reduce cellular metabolism, and are sensitive to desiccation and temperature decreases. The tolerance/intolerance to desiccation shown by these seeds in their natural environment is also seen in their storage.

Sensitivity to desiccation limits seed storage potential, genetic conservation, and use in trade. Two types of seeds based on sensitivity to desiccation are recognized: orthodox seeds (those that undergo maturation drying) and recalcitrant seeds (those that do not undergo maturation drying).

The ability to tolerate desiccation by orthodox seeds is associated with metabolic changes such as respiration decrease, increase of some carbohydrates or oligosaccharides, and accumulation of dehydrines (late embryogenesis abundant (LEA) proteins). During germination, seeds lose this tolerance several hours after radicle protrusion. Dehydration at this stage leads to irreversible damage, in which the peroxidation of lipids and free radicals has an important role. However, mature orthodox seeds can be dehydrated without damage to very low levels of moisture (1–5%) and in a variety of conditions. Bound water (structural) is less easily frozen than free water. Bound water seems to be a crucial component to tolerating desiccation, and in the orthodox seeds all water is bound. In storage, the longevity of seeds increases with a reduction of the water content in a predictable and quantifiable manner. These seeds may be subdivided into (1) true orthodox, which can be stored for long periods at seed moisture contents of 5–10% and subfreezing temperatures, and (2) suborthodox, which can be stored under the same conditions, but for shorter periods due to high lipid content or thin seed coats.

Recalcitrant seeds are rich in free water and neither tolerate nor survive desiccation. The dehydration of tissues provokes membrane deterioration (plasma membrane and mitochondria), protein denaturation, and reduction of both the respiratory rate and the adenosine triphosphate (ATP) level. The oxidative processes and the free radical seem to be involved in cellular and molecular deterioration. Seeds show a strong resistance to rehydration and the loss of cellular integrity leads to a loss of viability. Recalcitrant seeds are present in at least 70% of tropical trees. Their sensitivity to a low temperature is due to the high water content.

Because some seeds do not fit readily into either orthodox or recalcitrant categories, they have been clustered in a third category: the intermediate seeds. These seeds survive desiccation at intermediate moisture levels but not to the degree of orthodox seeds. This last category can be considered arbitrary, and the existence of a recalcitrance gradient throughout the different species has been suggested.

Variations in the sites of water storage and the gradual damage observed in the seed tissues when it dehydrates can be illustrated by the seeds of the following species: *Calophyllum brasiliense*, *Otoba novogranatensis*, *Minquartia guianensis*, *Caryocar costaricense*, and *Lecythis ampla* (**Figures 6–10**) (**Table 1**).

How does dehydration affect seeds? In *Calophyllum brasiliense* the hard seed coat resists desiccation; water loss is slow. Once the seed coat dehydrates, the water loss directly affects the embryo, with the exposed radicle being the most rapidly affected. The small plumule enclosed by thick cotyledons dehydrates last. *Otoba novogranatensis* and *Minquartia guianensis* have minute rudimentary embryos. The sequence of dehydration is seedcoat → peripheral endosperm and radicle → remaining embryo → inner endosperm.

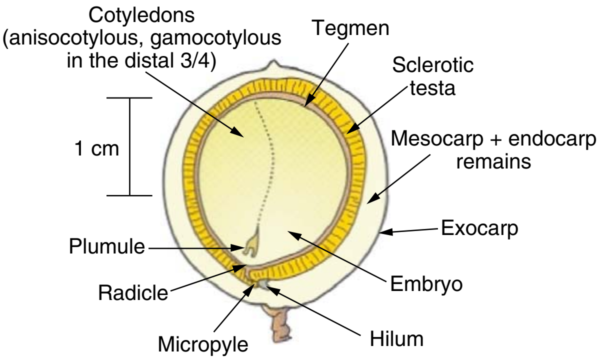

Figure 6 *Calophyllum brasiliense* berry (longitudinal section). Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

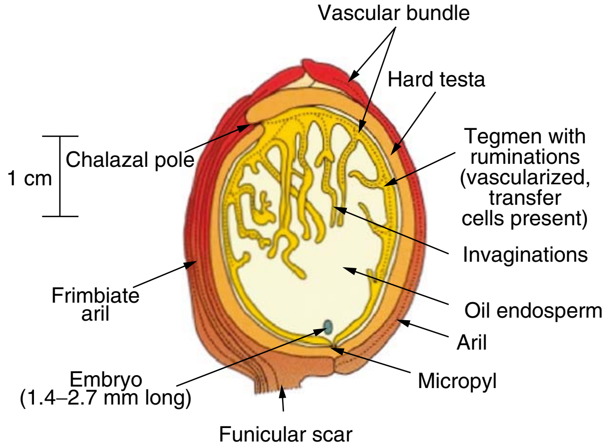

Figure 7 *Otoba novogranatensis* seed (longitudinal section). Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

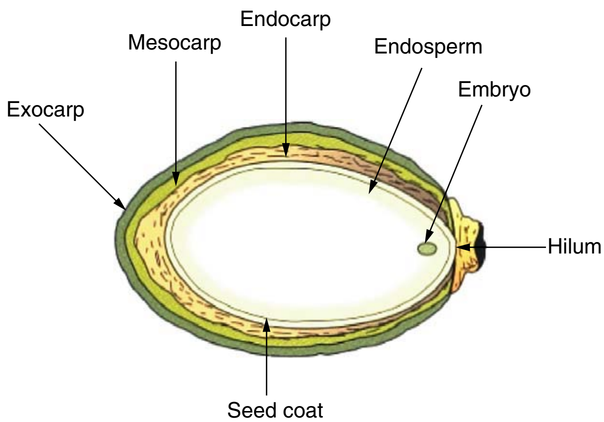

Figure 8 *Minquartia guianensis* drupe (longitudinal section). Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

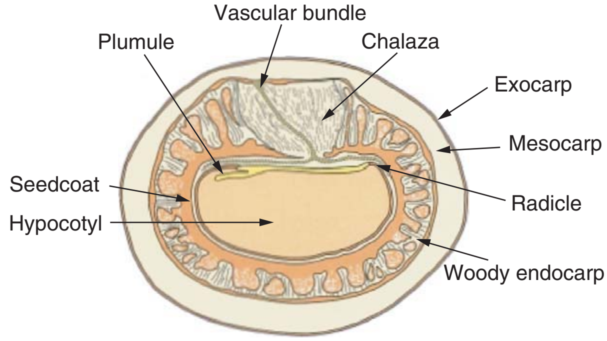

Figure 9 *Caryocar costaricense* drupe (longitudinal section). Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

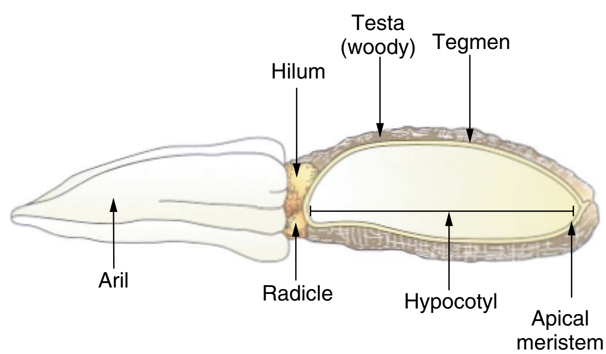

Figure 10 *Lecythis ampla* seed (longitudinal section).

Otoba novogranatensis is more sensitive to desiccation than *Minquartia guianensis,* due to endosperm rumination and tegmen vascularization. *Caryocar costaricense* has a curved, accumbent embryo and the plumule and radicle dehydrate immediately after endocarp dehydration. The dehydration of *Lecythis ampla* seeds first affects the seed coat and then the meristematic poles (radical and apical); they die instantly after seed coat dehydration.

The seeds enclosed in berries (*Calophyllum brasiliense*) or drupes (*Caryocar costaricense*, *M. guianensis*) are protected by the pericarp tissues, which help maintain seed moisture. In these cases, the functional unit is the fruit and dehydration is slower.

The moisture level below which a seed loses its viability varies from one seed to another. Variations are found among seeds collected from the same tree as well as from different trees, zones, seasons, or years. The recalcitrant behavior seems to be genetically determined and its genetic base is still not well understood. The variations found can be explained if the seed history from flower inception to seed dispersal and germination is analyzed carefully.

The difference found between temperate and tropical recalcitrant seeds must be added to the gradient found in recalcitrance manifestation. The first cannot be dried but can be stored for 3–5 years at near-freezing temperatures; the latter cannot be dried and will not survive temperatures below 10–15°C, depending on the species.

Data for tissue, cell, and biochemical alterations produced by dehydration in the recalcitrant seeds are limited, and no appropriate strategies and mechanisms to manage them under storage conditions have been found. The morphological diversity found in these seeds and the variations in the sequence and speed of seed dehydration further complicate the issue. The problem of cellular desiccation is complex; it seems to involve genetic components that lead to mechanisms of cellular protection. These mechanisms limit the cell damage produced by seed dehydration and promote cellular repair, reversing the changes induced by water loss. The accumulation of protecting substances in the tolerant tissues is

Table 1 Structural variation of recalcitrant seeds from five neotropical species during seed dispersal. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service

Structure	Calophyllum brasiliense	Otoba novogranatensis	Minquartia guianensis	Caryocar costaricense	Lecythis ampla
Fruit	Berry	Septicidal capsule	Drupe	Drupe	Pyxidium
Type of diaspores	Fruit	Seed	Fruit	Fruit	Seed
Endocarp surrounding the mature seed	Soft, thin, crushed	Absent	Drupe, hard endocarp	Drupe, hard endocarp	Absent
Seed coat	Hard	Hard	Soft	Papyraceous	Hard
Testa	Hard	Hard	Soft	Soft	Hard
Tegmen	Thin, soft	Thin, ruminate	Soft, fragmentary	Thin, soft	Remnants
Endosperm	Absent in the mature seed	Massive, nuclear–cellular	Massive, cellular	Absent in the mature seed	Absent in the mature seed
Embryo	Massive, complete	Minute, rudimentary	Minute, rudimentary	Massive, complete	Massive, undifferentiated
Cotyledons	Massive, fused	Differentiates and develops during germination	Differentiates and develops during germination	Small, scaly	Differentiates and develops during germination, small, scaly
Hypocotyl	Thick, massive	Differentiates and develops during germination	Differentiates and develops during germination	Thick, massive	Thick, massive
Epicotyl	Very small	Differentiates and develops during germination	Differentiates and develops during germination	Very small	Differentiates and develops during germination
Radicle	Thick, small	Differentiates and develops during germination	Differentiates and develops during germination	Thick, small	Rudimentary
Reserves location	Cotyledons, hypocotyl	Endosperm	Endosperm	Hypocotyl	Hypocotyl
Water storage	Whole embryo	Mainly endosperm	Mainly endosperm	Hypocotyl	Hypocotyl

quite possible. Disaccharides (saccharose) and oligosaccharides (raffinose and stachyose) may have an important role in the stabilization and maintenance of the membrane system and other sensitive systems.

The Gymnosperm Seed

Gymnosperm seeds are not enclosed within a gynoecium. They are exposed on scales or similar structures clustered in gynostrobiles (female strobiles). The zygote forms the embryo ($2n$), which remains immersed in the nutritious tissue (endosperm) of the megagametophyte (n). The integument gives rise to the seed coat ($2n$, part of the tissues of the maternal tree) (**Figure 11**).

The seed matures in two to three seasons. The content, behavior, and fluctuation of growth regulators are similar to those of the angiosperms. The lipid content in the seeds is high, although carbohydrates and proteins are also present.

Fruit and Seed Dispersal

Seed dispersal is a critical stage in the life cycle of the species. It transports physiologically independent individuals to the habitat occupied by their parents or to new suitable territories, where the seeds may

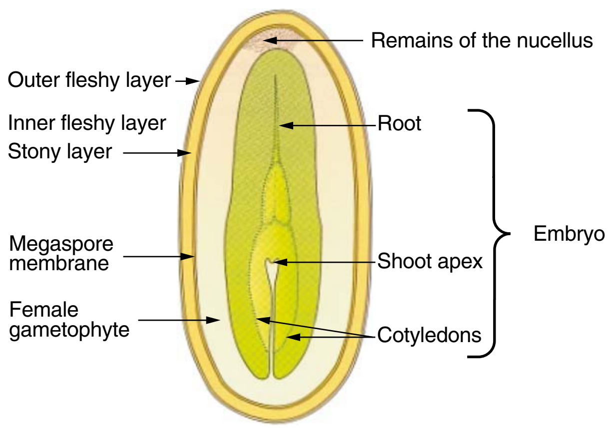

Figure 11 *Pinus* seed. From *Comparative Morphology of Vascular Plants*, 2edn. by Foster and Gifford © 1974, 1989 by WH Freeman and Company. Used with permission.

colonize if environmental conditions are favorable. The unit of dispersal (diaspore, propagule, or diseminule) is determined by the embryo, the seed, the fruit, or the fruit and associated parts of the modified perianth, the receptacle, or combinations.

Diaspores can be dispersed in space and time. Dispersal in space is the transport from one site to another, usually far from the parent tree. Dispersal in time is the quiescence or inactivity of diaspores for a variable period of time. Later, they can activate by environmental stimuli and resume the germination process.

The dispersal of diaspores can be biotic (zoochorous) or abiotic (azoochorous) and their morphology is related to the method of dispersal. In biotic dispersal the vectors are numerous: invertebrates (flies, dung insects, ants (myrmecochory), earthworms, and snails), herbivorous fish (ichthyochory), marine turtles, lizards and desert iguanas (saurochory), birds (ornithochory), and mammals including human beings (mammaliochory). Abiotic dispersal is by wind (anemochory), water (hydrochory) or the tree itself (autochory). The last is achieved by active ballistics (tension generated by the dehydration of hygroscopic tissues), passive ballistics (movements of the seeds enclosed in the fruit), creeping diaspores, and barochory (dispersal by weight).

Biotic dispersal could be epizoochorous if the transport of diaspores is passive, external, and occurs through diaspore adhesion to animal skin (hairs) or feathers. It is synzoochorous when animals, eating part of the seeds but not ingesting them, actively transport the diaspores, and it is endozoochorous if the diaspore containing the seed or the seed itself, is ingested and eventually regurgitated or defecated intact. Zoochorous dispersal requires nutritious tissues in the diaspore, chemical attractants, mimetism, or adhesive structures.

In tropical forests, most dispersal is achieved by vertebrates, which obtain food from the seeds and other edible parts of the fruit. Zoochorous dispersal ($\geq 80\%$) is dominant in the tropics. In primary forests, zoochory may increase to 87–90%. Most diaspores dispersed by water come from riparian species and are typical in marshes or mangrove vegetation, while those dispersed by wind grow at forest edges.

The specificity of disperser or dispersers is uncommon. Most fruits and seeds are used and dispersed by several or many vectors, which may include consumers, commensals, predators, commensals and dispersers, or predators and dispersers.

Germination

The process of germination involves the transition of cells from a dehydrating stage and low metabolic activity to a hydrated and metabolically active stage. Water is absorbed in a triphasic way: imbibition, germination *sensu stricto*, and embryo development. Imbibition is the rapid absorption of water leading to a regular increment in the respiratory activity. Germination *sensu stricto* is the process of embryo activation, not accompanied by any apparent morphological change. Embryo development is marked by radicle elongation and a significant change in the physiology of the embryo. This phase is crucial, because seedling development depends on it. In most cases, the seed germinates only if the respiration and production of ATP are adequate, creating an oxygen requirement.

Germination culminates with radicle protrusion into the adjacent tissues. In recalcitrant seeds with minute, rudimentary embryos or large embryos with a rudimentary radicle (reduced to a radical meristem), the development of the radicle implies cell division and elongation.

Environmental Influences

The external environmental factors regulating the activity of the maternal tree during seed maturation include temperature, light, photoperiod and thermoperiod, relative air moisture, and water potential in the soil. The internal parameters are the water potential of the maternal tree, its nutritional and hormonal state, and the position of the seed on the tree. The environmental factors involved directly in the process of germination are temperature, light, and gas.

Water

In orthodox seeds, water imbibition allows metabolic reactivation and restoration of membranes and organelles, activation of the enzymatic system, respiration, and synthesis of RNA and proteins. The water imbibing the seed is equivalent to two or three times the dry weight of the seed. The net diffusion occurs in a descendent gradient of water potential (or energetic state of the water); in other words, from pure water to water containing solutes). The potential of a cell inside a seed is determined by the osmotic potential (ψ_p), by the concentration of solutes (more solutes = less osmotic potential), the matric component (ψ_c), by the hydration of matrices (cell walls, starch, protein bodies), and the pressure potential (ψ_p), permitting water intake and putting pressure on the cell wall. In the water potential of the soil, only ψ_c has an important function. Water absorption has three phases:

1. A rapid initial imbibition that is strongly influenced by the matric forces.
2. A phase of slow water intake in which metabolic activity begins. The length of this phase is correlated with the intensity of the dormancy.
3. A rapid phase intensified by metabolism activation occurring only in nondormant seeds involved in active germination. In many cases, it coincides with seed coat breaking and radicle protrusion.

Reserve mobilization and enzymatic activation depend on hydration; the best germination occurs with a low moisture tension (0.005–0.500 bars). If the tension is zero, the water pellicle around the seed inhibits the absorption of oxygen.

Temperature

Under natural conditions, temperature determines the capacity and rate of germination, removing the primary and inducing secondary dormancy. For germination, the upper limit is about 45°C and the lower 3–5°C. Many species germinate at about 40°C, but the seedlings are abnormal; others can germinate near the lower temperature limit but they rarely produce normal seedlings. The regimes of alternating temperature (20°C at night and 30°C during the day) seem optimal for species from temperate zones, although similar results are obtained with constant temperatures of 25°C. In tropical species the best range is usually 25–30°C.

Light

Light stimulates germination, but it is not strictly necessary for most seeds; however, some pioneer tropical species (*Cecropia*, *Heliocarpus*) typical of areas in early succession, have photoblastic seeds. A pigment called phytochrome is involved in the photo control of the germination; it exists in two reversible forms (**Figure 12**).

Light sensitivity is influenced by pretreatment with temperature. With an increment of cold pretreatment, seed germination can be increased in darkness and the sensitivity to far-red light decreased. The requirement of light for germination varies with the amount of imbibed water.

Genetic Influence

The genome received by the diaspore controls germination (**Figure 13**) (**Table 2**) and a network of genes regulates ovule morphogenesis. Several parts of the diaspore differ in genotype; the tissues of the fruit, other tissues surrounding the seed, and the seed coat have the maternal genotype. The endosperm is one-third paternal and two-thirds maternal in the most common type of seed. The embryo is one-half paternal and one-half maternal. In general, the genotype of one or both parents affects the structure and composition of the various parts of the diaspore. For example, the genes expressed in the megagametophyte play a role in the induction of seed development, primarily in embryo and endosperm development. The expression of some maternal genes is required for normal endosperm development. The endogenous annual rhythm of the germinability of the seed and the internal mechanisms regulating it are not well known.

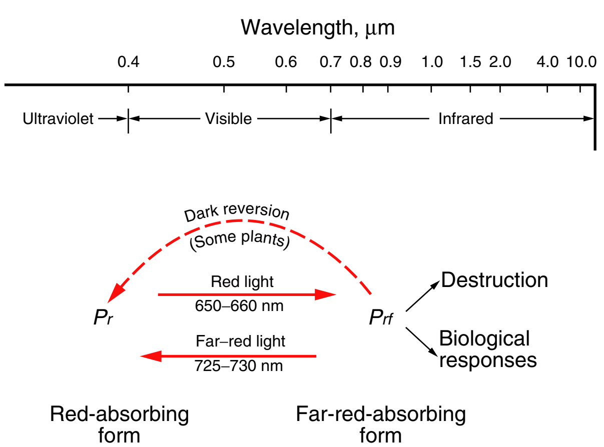

Figure 12 Diagram of reaction for spectral-driven phytochrome reversibility. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

Seed Respiration

Respiration permits the acquisition of energy. It requires oxygen and the removal of CO_2. High levels of CO_2 can inhibit germination, and a lack of oxygen has the same effect although some species can germinate in anaerobic conditions.

The inhibited seed has three active routes of respiration: glycolysis, pentose-phosphate, and the citric acid cycle (Krebs cycle). Glycolysis – catalyzed by cytoplasmic enzymes – and the Krebs cycle (inside the mitochondria) are essential for the production of ATP. The respiratory process in the orthodox seed involves three or four stages:

1. High oxygen (O_2) consumption and a linear increment in respiration during tissue hydration (hydration and activation of mitochondrial enzymes in the Krebs cycle and the electron chain).
2. Decrease in the respiration proportional to the stabilization of O_2 intake. The seed is hydrated and the enzymatic system is active. Between stages (2) and (3), the radicle protrudes (it coincides with phases (2) and (3) of the imbibition process). The seed coat (or seed coat + endocarp or pericarp) can be a physical barrier limiting O_2 intake.
3. Respiratory reactivation due to activation of the embryo axis and meristems and mobilization of stored reserves. The breaking of the seed coat may contribute to increasing the intake of O_2.
4. Respiration restricted to storage tissues whose reserves are being degraded and removed.

Longevity, Viability, and Dormancy

The period of time in which the seed remains viable in the ground is called longevity. Viability is the germinative capacity; its loss is the final stage of

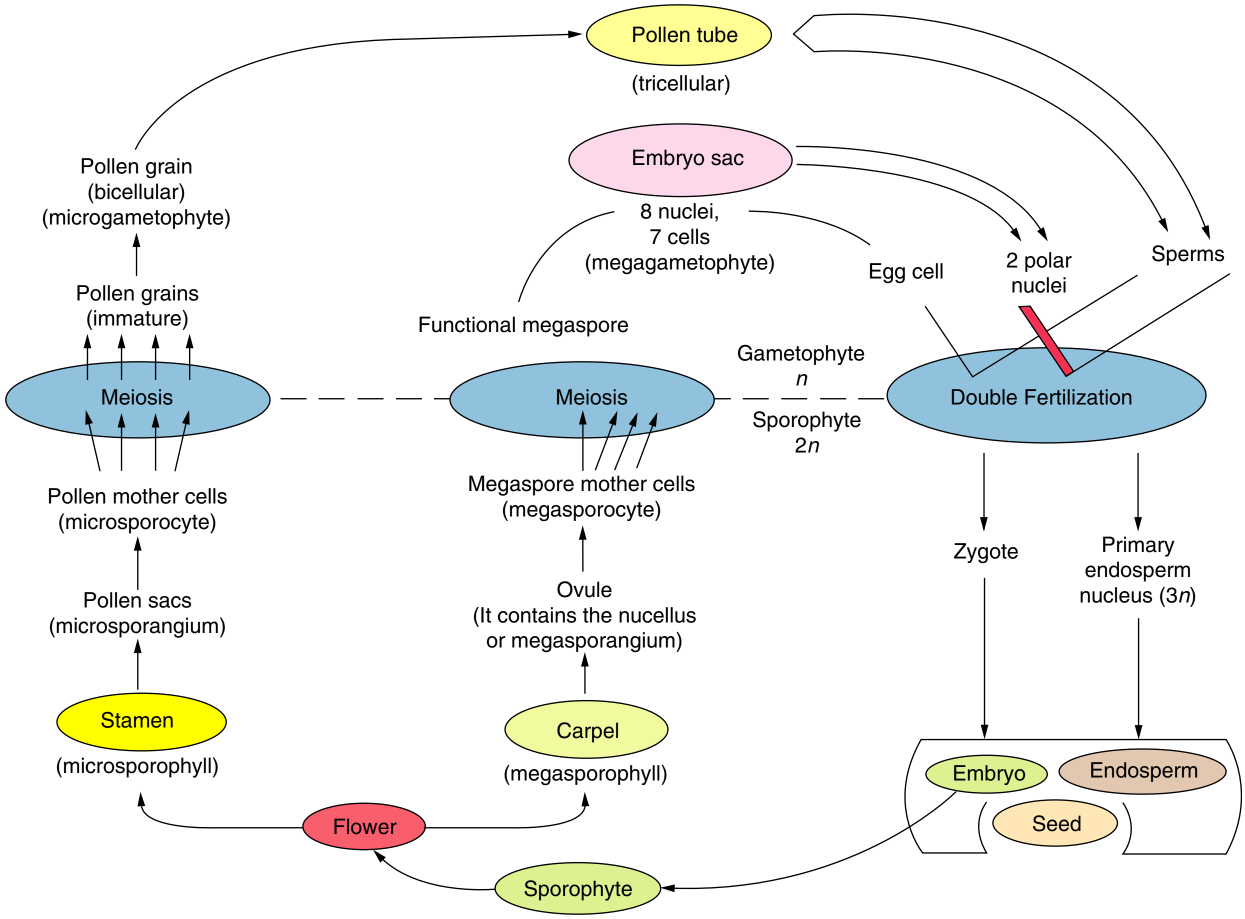

Figure 13 Angiosperm reproductive cycle. Reproduced with permission from Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

seed deterioration. Species from wet tropical forests tend to lose viability rapidly; perhaps 60% to 70% lose it in 3–6 months. Some species lose viability in days or weeks.

To survive in the ground, seeds must maintain viability during the time in which germination is inhibited by dormancy or quiescence. Dormancy is the suppression of germination under favorable environmental conditions. Approximately 10% of tropical species show dormancy. Several conditions cause dormancy: rudimentary or physiologically immature embryos, hard or impermeable seed coats, endogenous growth regulators inhibiting germination, or inadequate storage; some dormancies are the product of multifactorial interactions. Soaking in running water, hot water, hydrogen peroxide, and physical scarification are treatments used to break seed coat dormancy.

Dormancy can be innate or induced. Innate dormancy (primary) prevents the germination of seeds during their development and maturation in the maternal tree and usually some time after dispersal or collection. Dormancy is innate external (primary external) when the seed coat, the endocarp or the pericarp are hard or woody, impermeable to gases or water, or mechanically resistant (e.g., *Enterolobium*, *Samanea*). The environment can reinforce the quiescence. When the embryo contains inhibitory substances or it is physiologically immature, the dormancy is innate internal or primary internal (e.g., *Juniperus virginiana*).

The innate dormancy declines before or after dehiscence. This period is called postmaturation dormancy. The heritability of dormancy is complex because the distinct parts of the seed are genetically different.

Induced dormancy (secondary) develops after the dispersal or collection of nondormant seeds or seeds emerging with partial or total primary dormancy. Essentially, it reflects no sensitivity to germination inductors, internal or external.

Germination can be inhibited by exposing the seeds to long periods of white light, especially to densities of high radiant flows or far-red light. Dormancy can also be prevented, delayed, or reduced by intermittent light of low intensity. Innate dormancy is absent in the recalcitrant seeds of the tropics.

Table 2 Levels of genetic variation, events and facts

Levels of genetic variation		*Events and facts*
Gamete production	Microsporogenesis and microgametogenesis	• The microsporocyte or pollen mother cell (2*n*) has two chromosome sets (maternal and paternal). • Meiosis gives rise to four haploid microspores. They are not genetically equivalent. • Each microspore undergoes asymmetric division and finally produces a pollen grain with a vegetative cell and two sperm cells (frequently dimorphic).
	Megasporogenesis and Megagametogenesis	• The megasporocyte or megaspore mother cell (2*n*) has two chromosome sets (maternal and paternal). • Meiosis gives rise to four haploid megaspores. They are not genetically equivalent. • Three megaspores degenerate, one survives (chalazal) and is functional. • Megaspore divisions originate the embryo sac (megagametophyte). It contains the egg cell (*n*). • The megagametophyte is regulated by its genes and those of neighboring cells and tissues. • The megagametophyte regulates seed development after fertilization.
Gamete level		• The egg cell and the sperms have nuclear and cytoplasmic DNA (mitochondria and plastids). • Plastid DNA (plastome) interacts strongly with nuclear DNA. • In most species, plastids are inherited by maternal line (includes plastid DNA). • Plastids reproduce by binary fission. Some mutants are unable to reproduce; the mutation is lethal. • Mitochondrial DNA is usually inherited by maternal line (egg cell). • Sperm cells (two per pollen tube) are frequently dimorphic. One may have mitochondria; the other may have plastids. Probably different patterns of male cytoplasmic DNA transmission. • Is sperm behavior in double fertilization predetermined or at random?
Parent trees		• Self-sterility (homogamy) and separation of sexes in space or time to favor cross-pollination • Female parent tree: ○ The egg cell (embryo sac) in the ovule of each flower could be genetically different to that of the neighboring flowers. ○ In flowers with several ovules per gynoecium (ovary), the egg cell (embryo sac) of each ovule could be genetically different to that of the neighboring ovules. ○ Pollen received by egg cells (embryo sacs of different ovules) in an ovary with several fruits could be genetically different and provided by several sources. ○ Seeds are not genetically equivalent. • Male parent tree: ○ Pollen grains are not genetically equivalent. • Multiple parent trees: ○ Mixture of pollen grains genetically different
Incompatibility systems		• They maintain a high degree of genetic heterozygosis in the species population. • They operate at the stigma or style level. • Incompatibility could be sporophytic or gametophytic.
Gametophytic mutations		• They are lethal if the megagametophyte (embryo sac) is affected. • If the pollen is affected fertilization could fail or seed abortion takes place at different stages of development. • If both gametophytes are affected there is not fertilization, seed is empty (no embryo) or the embryo is not viable. • Endosperm: If endospermic DNA is aberrant seeds fail to develop.
Diaspore genome		• Several parts of the diaspore differ in genotype; the tissues of the fruit, other tissues surrounding the seed, and the seed coat have the maternal genotype. The endosperm is one-third paternal and two-thirds maternal in the most common type of seed. The embryo is one-half paternal and one-half maternal. In general, the genotype of one or both parents affects the structure and composition of the various parts of the diaspore.
Pollination and seed dispersal		• In cross-pollination species, the paternal genes move twice (pollination and seed dispersal) in each generation; the maternal genes move once (in autopollination or cross-pollination). Therefore, in cross-pollinated species the paternal genes move farther in each generation. • Pollination is at random. One or several donors provide pollen to the same flower or different flowers in the tree. • The pattern of dispersal contributes to structure population, to potential genetic drift, and to natural selection.

The emergence from dormancy is frequently regulated by a promoter–inhibitor system, where the principal promoter is gibberellic acid (GA_3) and the main inhibitor is abscisic acid (ABA). Low levels of inhibitor and high levels of promoter induce germination. According to some studies, it is not possible at present to determine the precise function of ABA in the induction of dormancy.

See also: **Genetics and Genetic Resources**: Cytogenetics of Forest Tree Species. **Tree Physiology**: Physiology of Sexual Reproduction in Trees.

Further Reading

Allen PS and Meyer SE (1998) Ecological aspects of seed dormancy loss. *Seed Science Research* 8: 183–191.

Bewley JD and Black M (1994) Seeds: physiology of development and germination. *Plant Cell* 9: 1055–1066.

Chaudhury AM, Koltunow A, Payne T, *et al.* (2001) Control of early seed development. *Annual Reviews of Cell and Development Biology* 17: 677–699.

Foster ANS and Gifford EM (1974) *Comparative Morphology of Vascular Plants*. San Francisco, CA: WH Freeman.

Hilhorst HWM (1998) The regulation of secondary dormancy: the membrane hypothesis revisited. *Seed Science Research* 8: 77–90.

Koornneef M, Bentsink L, and Hilhorst H (2002) Seed dormancy and germination. *Current Opinion in Plant Biology* 5(1): 33–36.

Lindsey K and Topping JF (1993) Embryogenesis: a question of pattern. *Journal of Experimental Botany* 44: 359–374.

Ray A (1997) Three's company: regulatory cross-talk during seed development. *Plant Cell* 9: 665–667.

Vozzo JA (ed.) (2002) *Tropical Tree Seed Manual*. Agricultural Handbook no. 721. Washington, DC: US Department of Agriculture Forest Service.

Welbaum GE, Bradford KJ, Yim KO, Booth DT, and Oluoch MO (1998) Biophysical, physiological and biochemical processes regulating seed germination. *Seed Science Research* 8: 161–172.

Shoot Growth and Canopy Development

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Introduction

As shoots grow and become numerous a canopy develops. The mass and surface area of the leaves in the canopy reach a maximum amount relatively early in the life of a stand. Subsequent growth of the trunk and branches serves to lift the canopy higher and higher above the ground. The form and arrangement of the branches and leaves in the canopy are an important reflection of the architectural type. Tree architecture is difficult to study and describe because trees are very large, very long-lived, and have a complex hierarchy of components. Much of tree architecture is inherited. Trees look different because they have evolved in different climates – tropical palms (e.g., *Corypha elata*) versus alpine firs (e.g., *Abies alba*), coastal mangroves (e.g., *Rhizophora mangle*) versus savanna baobabs (e.g., *Adansonia digitata*) and niches (overstory Douglas-firs (*Pseudotsuga menziesii*) versus understory Pacific yews (*Taxus brevifolia*), overstory oaks (e.g., *Quercus alba*) versus understory dogwoods (e.g., *Cornus florida*). In addition to variation in the inherited types, there is tremendous genetic variation in response to the local environmental variables of solar radiation, competition, and availability of nutrients and water. The phytochrome-mediated response to plant shade is strongly inherited. Trees appear to grow toward the light, but are really growing away from shade. The intensity of competition determines the tree size and shape. Some species can grow larger than others under extreme competition. The xylem is well suited to support the tree and conduct water, but the hydraulic limits of the xylem to transport large volumes of water from the soil to the distant transpiring leaves also sets limits to tree size and form.

Tree Growth

Plant growth is defined as the increase in size by cell production and enlargement. Apical meristems at the tips of stems are responsible for primary growth to increase stem length and for the production of initials for the lateral appendages to the stem. The lateral meristem or cambium at the periphery of the stem between the xylem and phloem provides secondary growth to maintain vascular connections and increase mechanical support through increased diameter. Stems carry the leaves responsible for photosynthesis and the flowers responsible for reproduction. Although plant growth may appear simple from this description, when the entire scope of species is considered, growth provides an enormous variety of patterns in time and space that produce a bewildering array of architectures. Extensive studies of tree architecture have shown the existence of predictable types that reflect adaptation to environmental factors and competition.

The tree phenotype is the manifestation of the genetic information in the genotype acting through