**SEED DEVELOPMENT AND MATURATION**

 A seed is a marvelous adaptation for survival of the embryo for long periods of time, often under adverse environmental conditions. Such survival allows opportunities for dispersal, both in time and in space. During this period, attack by bacteria and fungi is discouraged by the desiccated state of the seed as well as by the hardened seed coat; also, in many seeds, the presence of phenolics, lectins, toxic glycosides, and enzyme inhibitors discourages predation by insects, rodents, and herbivores. A seed usually comes with everything it needs for germination and early seedling growth, including reserve food and minerals, and at that time requires only the right temperature, H2O, and O2 from the environment. (Seeds of a few species are known to germinate under anoxia, but their numbers are very small.) Moreover, in many cases, the seed, more properly the embryo, exercises its own control on germination - it determines when the environmental conditions are right for germination.

 As in fruit development, seed development also occurs in defined although continuous steps. Seed development is often described on the basis of stages of embryo development, i.e., early, mid-, and late embryogenesis. These stages are not sharply defined, they partly overlap, and should be visualized as part of a continuum with shifting major activities.

**Early Embryogenesis**

 Early embryogenesis is characterized by the laying down of the body plan of the embryo, i.e., the definition of the cotyledons (a single cotyledon in monocots), the root-shoot axis, the root and shoot apices, and the demarcation of the primary tissues: protoderm, ground meristem, and provascular tissues or procambium. It is also characterized by nuclear divisions and wall formation, in what was the central cell of the embryo sac, leading to cellularization of the endosperm. In conifers, embryo development follows a slightly different course, but the laying down of the body parts and the patterning of tissue layers probably occur in a similar manner. In conifers, there is no endosperm; instead the embryo develops within the female gametophyte, which is a maternal tissue.

**Mid Embryogenesis**

 After the body pattern of the embryo has been set and differentiation of primary tissues has occurred, cell divisions decrease in frequency and eventually stop, but the embryo continues to grow by cell enlargement until it reaches its full size and then growth is arrested and the seed enters a period of rest or quiescence. Growth does not resume until after seed germination. In many dicots, such as lettuce, pea, bean, and sunflower, reserves in the endosperm are resorbed by the developing embryo, and at seed maturity that tissue is represented by a thin papery layer a few cells in thickness. In many other plants, including castor bean, all cereal crops, and coconut, the endosperm continues to grow by cell division and enlargement and eventually becomes much larger than the embryo. The endosperm consists mainly of living cells, but in some families, it consists of both living and dead cells at maturity. In cereals (Gramineae) for instance, the outer cell layer(s) becomes distinguished as the aleurone tissue (or layer), distinct from the central cell mass, which becomes the starchy endosperm. At maturity, while cells in the aleurone tissue continue to live, those in the starchy endosperm are dead. Seeds in which endosperm persists are referred to as **albuminous** (or **endospermic)** seeds vs **exalbuminous** (or **nonendospermic)** seeds where it does not.

 This period is also characterized by an accumulation of food reserves. The types of seed food reserves and their accumulation are topics of extreme importance for human and animal food supply.



Figure: A generalized scheme illustrating embryo (and seed) development and maturation in flowering plants. Relative values indicate roughly when the maximum water content, embryo growth, and so on are reached. Approximate times when amounts of free hormones are high are indicated by bars. Deposition of food reserves begins with the expansion phase of the embryo and is completed about the time desiccation begins. The approximate time for synthesis of desiccation-and stress-related proteins is indicated by shading. The scheme shows an endospermic seed, where the endosperm persists and is the chief food storage tissue.

**Late Embryogenesis**

 During the late stages of embryogenesis, the seeds lose water, desiccate, and "mature". The seed coat hardens (in some seeds, the walls of epidermal cells become lignified), and the outer walls get coated with cutin, which in some cases may be impregnated with waxy deposits. Cells raay also accumulate phenolics and, in some cases, toxic materials against pathogens and herbivores.

 Near the end of reserve food accumulation (seed filling), vascular connections *via* the funiculus between the mother plant and the seed become non-functional or are broken. As a result, the maturing seeds lose water and desiccate while still on the mother plant, although desiccation may continue after the seeds are shed. The dry weight stays constant, but the fresh weight drops. The moisture content of mature seeds, at the time of seed shed, in many species is reduced to 10-15%, although lower values are known. In this dry state, most of the metabolic processes, including respiration, are reduced to very low or undetectable levels-a state of suspended animation known as **quiescence.**

 This dry state not only allows seeds longer viability under extreme environmental conditions, but also protection against attack by bacteria and fungi. The process of desiccation, however, creates many stresses, the principal ones being increased salt concentration in the cell, crystallization of molecules, creation of toxic oxygen radicals, and attendant danger of damage to cell macromolecules and membranes. Plants have evolved several mechanisms to deal with dehydration, and some of these are utilized in seed development.

 Seeds that desiccate and become quiescent are known as "orthodox'' seeds. In contrast, seeds of many species do not mature in the above sense; they remain hydrated at the time of seed shed (moisture content 50-60%) and are unable to withstand desiccation. These seeds are referred to as ''unorthodox" or "recalcitrant" seeds because they are intolerant of desiccation and are damaged easily or killed on drying.

 Seeds of orthodox species mature and become quiescent, but will germinate given water, oxygen, and suitable temperature conditions. In some orthodox species, in addition to becoming quiescent, seeds also become dormant, i.e., they do not germinate under favorable conditions of water, temperature, and air. Dormant seeds require some other signal, usually an environmental cue such as temperature or light, before they will germinate. Thus, there is a clear distinction between seed quiescence and seed dormancy.



Figure: A general scheme connecting embryo development, maturation, and germination. The maturation "loop" is entered in the presence of ABA or high osmoticum; in the absence of ABA or osmoticum, embryos continue on the germination program.

**Desiccation Tolerance**:

 In early stages of seed development, before ABA concentrations rise, protection against desiccation damage is probably afforded by sugars and other low molecular weight solutes. The longer term capacity of seeds to withstand desiccation, however, is dependent on ABA and is gradually built up in the developing seeds. If embryos are excised from seeds at early stages of development and dried by being placed in either warm air or a solution of high osmolarity, they are not able to cope with desiccation—they die, but as they mature, especially after reserve food deposition is more or less complete, they are able to withstand desiccation to much lower moisture contents. Clearly, some changes occur in the developing embryos that prepare them for withstanding the dry state.

 The chief factor in desiccation tolerance appears to be the synthesis of late embryogenesis-abundant (or LEA) proteins. LEA proteins are not storage proteins nor do they have any specific role in seed dormancy. Rather, they are proteins that have a role in the protection of macromolecules and membranes both from crystallization due to loss of water and from high salt concentration, although precisely how they do so is still unclear. This role is supported by the activation pattern of *LEA* genes during seed imbibition and germination. *LEA* transcripts are preserved in the dry seed and are degraded soon after germination is completed.

 There is considerable evidence that ABA induces the synthesis of LEA proteins during seed development. This synthesis occurs over a considerable time— some being synthesized as early as the beginning of the expansion phase and others later, but the highest LEA concentrations occur at the start of desiccation. This period coincides roughly with the rise and peak in ABA content. Isolated embryos in culture synthesize LEA transcripts and proteins on being supplied with ABA. A specific subset of LEA proteins is induced in desiccation-intolerant barley embryos cultured for 5 days in ABA, during which time the embryos acquire desiccation tolerance. Many *LEA* genes, e.g., the *Em* gene in wheat, contain nucleotide sequences in their promoters, which specifically respond to ABA.