H1 Physiology of floral initiation and development

Key Notes

Floral meristems

Flowers originate from the shoot meristem. The change in the vegetative meristem to develop a flower is termed induction. This is followed by evocation, the development of the floral meristem. The flower then forms and becomes functional when the reproductive structures are mature. Flowers are formed in concentric whorls of sepals, petals, stamens and carpels.

Floral evocation

Floral evocation usually requires an external stimulus such as cold (vernalization) sensed by the meristem, or appropriate daylength sensed by phytochrome, species being long-day, short-day or day-neutral. Hormones are important in the control of flowering.

Floral development genes

Heterochrony (flowering-time) genes regulate the conversion of the vegetative meristem to a floral meristem. Floral meristem identity genes then regulate the formation of a flower. When flowering has been initiated, cadastral genes govern the formation of the whorls. Finally, homeotic genes control the structure of the flower, influenced by the cadastral genes. The ABC model of flower development predicts that the four whorls of the flower are controlled by three homeotic genes A, B and C. Mutations of these genes form flowers in which the organs are misplaced.

Related topics

- Methods in experimental plant science (E2)
- Features of growth and development (F1)
- Ecology of flowering plants and pollination (K1)
- Self incompatibility (H3)

Floral meristems

Flowers originate from the shoot meristem (Topic C1) which normally generates leaves and shoots. The meristem stops vegetative growth when flowering commences and either produces a single flower (**determinate** or **closed inflorescence**) or a succession of floral meristems, each of which will become a flower (**indeterminate** or **open inflorescence**). Like a shoot meristem, a floral meristem is divided into layers: the **tunica** producing the outer cell layers, and the **corpus** the inner cell layers (Topic C3). The first stage of the flowering process is termed **induction**, the change in form and function of the vegetative meristem to develop a flower. This is followed by **evocation**, the development of the floral meristem. The flower itself is then formed and becomes functional when the reproductive structures are mature. The basic structure of an arabidopsis flower is shown in Topic D1.

Floral evocation

Forming a flower requires the differentiation (Topic F1) of the vegetative shoot meristem into a floral meristem when it has reached an appropriate stage of development. Flowering usually requires one of a range of external stimuli that bring about floral evocation. In temperate plants, this may be **vernalization**, a chilling period preceding flowering, possibly by weeks or months, or daylength, species being classified as long-day, short-day or day-neutral species (Topic G1). Vernalization appears to be sensed by the meristem itself, as chilling the plant while the meristem is warmed does not induce flowering. Day length is sensed by **phytochrome** (Topic G1) in the young leaves, suggesting that a **hormone** is involved in transmitting the signal to the meristem. This flowering hormone was originally named florigen, but its existence has never been proven.

Floral development genes

Genes for many aspects of the process of floral development have been described in two species, **arabidopsis** and ***Antirrhinum majus***. It will be helpful to have read Topic E2 before studying this section. The arabidopsis flower is actinomorphic (Topic R5) and mainly self-pollinated, while the *Antirrhinum* flower is zygomorphic (Topic R5) and insect-pollinated.

The earliest stages of flower formation involve the activity of genes known as **heterochrony** or **flowering-time** genes which regulate the conversion of the vegetative meristem to a floral meristem. Once this has happened, **flower meristem identity genes** regulate the formation of the flower. The arabidopsis mutant known as leafy (*lfy*), for instance, that has a mutation in a flower meristem identity gene, forms shoots where flowers should be. Once flowering has been initiated, a third group of genes known as **cadastral genes** are initiated which govern the formation of the whorls of the flower. Finally, the structure of the flower is governed by **homeotic genes**, which cause the right structure to appear in the right place. The function of homeotic genes is influenced by the cadastral genes expressed before them. The **ABC model** of flower development predicts that the four whorls of the flower are controlled by the action of three genes A, B and C. By studying floral mutants affecting each of these genes (*Table 1*), the way in which they control development has been established.

Each whorl is specified by the activity of one or two of the three homeotic genes, A, B and C, where: A alone → sepals; A and B → petals; B and C → stamens; C alone → carpels. This will occur regardless of where A, B and C are active in the flower; so a mutant, where B is inactive, makes two whorls of sepals and no petals (*Table 1*). A and C inhibit each other: if A is inactive, C becomes more active and *vice versa*, so a plant without C will form petals in whorls 2 and 3 and sepals in whorls 1 and 4. Sepals form in whorl 4, because the action of the A gene in this whorl was being inhibited by the activity of the C gene.

Table 1. Mutants of arabidopsis and Antirrhinum *and the ABC model for formation of the structures of the flower*

Genotype	Gene function	Whorl 1	Whorl 2	Whorl 3	Whorl 4
Wildtype		Sepals	Petals	Stamens	Carpels
apetala 2	A	Carpels	Stamens	Stamens	Carpels
squamosa					
apetala 3,	B	Sepals	Sepals	Carpels	Carpels
pistillata deficiens					
agamous plena	C	Sepals	Petals	Petals	Sepals

The arabidopsis mutants described are: *ap2* (*apetala 2*), *ap3* (*apetala 3*); *pi* (*pistillata*) and *ag* (*agamous*); the *Antirrhinum* mutants are *squa* (*squamosa*), *def* (*deficiens*) and *ple* (*plena*).

H2 Breeding systems

Key Notes

Range of breeding systems

Most plants are hermaphrodite and they may cross or self-fertilize. Others have unisexual flowers either on the same plant (monoecious), or separate plants (dioecious), and others are intermediate or variable. A few are asexual.

Cross- and self-fertility

Many plants have a self-incompatibility system stopping self fertilization, but others are self-fertile. Early maturation of flowers can lead to self-fertility. Some species are partially self-incompatible.

Separation of floral organs

Cross-pollination is favored by a separation of fertile organs in the flower. Stamens may mature before carpels, known as protandry, or after, protogyny. Protandry is common in specialized insect-pollinated flowers in inflorescences and protogyny is associated with wind pollination and unspecialized flowers. Stamens and carpels may be separated spatially.

Asexual reproduction

A few plants have bulbils in place of some or all flowers and others produce seeds without any fertilization. These are often polyploids derived from hybridization between sexual species and many of these clones have spread.

Control of sex expression

Floral development genes and hormones affect sex expression in all plants, but in dioecious species there is a chromosomal XX/XY system too, sometimes overridden in polyploids. There is an interaction with environmental conditions and sex expression can vary in plants with unisexual flowers.

Related topics

The flower (D1)
Self incompatibility (H3)
Ecology of flowering plants and pollination (K1)
Evolution of flowers (R5)

Range of breeding systems

Most flowering plant species bear **hermaphrodite** flowers with functional stamens and carpels (Topic D1). Some of these are almost entirely cross-fertilized, some mainly self-fertilized (see below). Other plants bear **unisexual** flowers, with only stamens or carpels functional, and others reproduce **asexually**. These have different implications as breeding systems (*Table 1*; see also Topic R5). Breeding systems are flexible in plants, e.g. in populations of many hermaphrodite species occasional individuals produce no viable pollen; individuals of dioecious species sometimes produce flowers of the opposite sex. A few species have a mixture of hermaphrodite, male and female plants.

Cross- and self-fertility

In hermaphrodite and monoecious species, there is the potential for **self-pollination** leading to **self-fertilization** (**selfing**) unless there is a mechanism to avoid it. The commonest form of inhibition of selfing is some form of

Table 1. Types of flowers and breeding systems in flowering plants

Type	Description	Comments
Hermaphrodite	Both sexes in each flower	Widespread: 80% of all flowering plants
Monoecious	Flowers unisexual; male and female on same plant	Particularly wind-pollinated trees and certain families, e.g. arum lilies; 5% of plant species
Dioecious	Flowers unisexual; male and female on separate plants (*Fig. 1*)	Widespread in many families; common in tropics and on islands; 10% of plant species
Other mixed types	Some flowers hermaphrodite, others unisexual on same or different plants	Some members of certain families, e.g. male and hermaphrodite flowers on each plant in carrot family; female and hermaphrodite plants in thyme family
Asexual	Clonally produced bulbils in place of flowers, or seeds without fertilization	A few genera; mainly polyploids with odd numbers of chromosomes
Sterile	Flowers without fertile parts	Flowers for attraction only; always associated with fertile flowers in inflorescences

physiological **self-incompatibility** (**SI**) system (Topic H3). In most plants with an SI system that have been extensively studied, a few individual plants have been shown to be **self-compatible**, showing that there is always the potential for self-compatible individuals to spread if cross-pollination fails in the long term. SI systems do not work if the stigma is pollinated experimentally when the flower is still in bud (allowing easy study of the system). Situations favoring a quick life cycle, such as agricultural land, have probably led to the evolution of selfing many times, since rapid development and early maturation of the stamens or early opening of the flower (*Fig. 2*) may allow self-fertilization before the SI system becomes operational. These plants will have smaller flowers than self-incompatible relatives.

Some plants are partially self-incompatible, with a plant's own pollen growing more slowly than that from another individual, allowing for self-fertilization if there is no cross-pollination. In general it seems that many hermaphrodite species are flexible in their degree of outbreeding and, among flowering plants, there is a whole range from nearly 100% outbreeding to nearly 100%

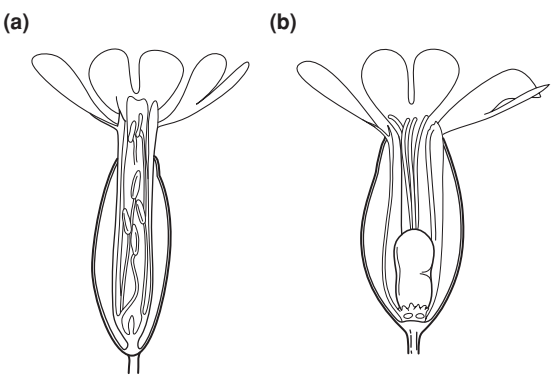


Fig. 1. Dioecious flowers of the campion, Silene dioica *(a) male, (b) female, each showing rudimentary organs of the opposite sex. (Redrawn from M. Proctor, P. Yeo and A. Lack (1996),* A Natural History of Pollination, *Harper Collins Publishers.)*

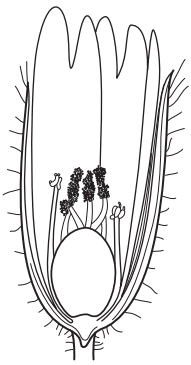


Fig. 2. Self-fertilizing flower of the mouse-ear, Cerastium glomeratum. *(Redrawn from M. Proctor and P. Yeo (1973)*, The Pollination of Flowers, *Harper Collins Publishers.)*

inbreeding. In a few plants self-fertilized seeds have slightly different properties from cross-fertilized seeds (e.g. larger and with a softer testa).

Separation of floral organs

Many species with an SI system, and some without one, separate stamens from stigmas either temporally, one maturing before the other, or spatially. This will favor the dispersal of pollen to other flowers, important in self-incompatible species because the stigma can otherwise become clogged with a plant's own incompatible pollen. Cross-fertilization will be more likely in self-compatible species. If the stamens mature before the carpels the plant is known as **protandrous**; if the carpels mature first, **protogynous**. Protogyny is common among some unspecialized insect-pollinated flowers and in wind-pollinated plants, whereas protandry is a common feature of the more specialized insect-pollinated flowers. Protandry is a feature of plants that bear their flowers in inflorescences in which the insects visit the older flowers first, e.g. spikes of flowers that mature from the base upwards, or composite inflorescences maturing from the outside inwards. In protogyny and protandry there may be overlap in function between the sexes allowing for self-pollination if cross-pollination fails.

The floral organs may be separated spatially within the flower. Some flowers have their parts separated, often by a small distance, and rely on visitors crawling around the flower for pollen to reach the stigmas. Some others have parts that move as they mature or in response to insect visits; in these a spatial separation can be combined with a temporal separation. After a flower has been open for a time the anthers and stigmas may come together allowing selfing if there has been no cross-pollination.

Asexual reproduction

Many plants can spread by vegetative means, with rhizomes, root or stem fragments, etc., not involving floral structures (Topic C3). These reproduce sexually with flowers as well. A few plants have **bulbils** in place of some or all of their flowers. These resemble tiny bulbs (*Fig. 3*) or plants and are clones of the parent plant. A few plant groups produce seeds that are formed without any fertilization of the embryo, so again they are clones of the parent plant. This is particularly associated with members of the rose family (Rosaceae) such as the brambles (*Rubus*) and composites (Asteraceae) such as the dandelions (*Taraxacum*). These **agamospermous** plants are nearly all high **polyploids**, often with odd numbers of chromosomes, derived by hybridization from sexual diploids in the center of

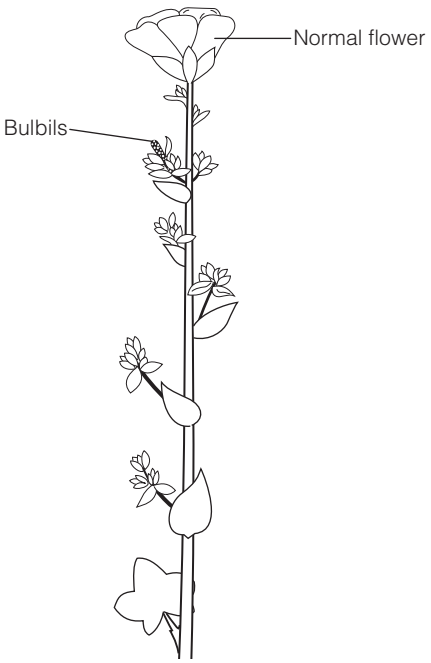


Fig. 3. One normal flower and bulbils in place of others in the saxifrage, Saxifraga cernua*. (Redrawn from P.R. Bell and A.R. Hemsley (2000),* Green Plants*, 2nd edn, Cambridge University Press.)*

the range of the genus. Numerous different agamospermous clones, differing in minor ways, have appeared and these present a problem of classification, each clone sometimes being described as a separate species.

Control of sex expression

In hermaphrodite flowers sex expression is controlled by floral development genes (Topic H1). In unisexual flowers some of the same genes are likely to be present and their expression is subject to hormonal and genetic control. Dioecious plants normally have identifiable sex chromosomes with an XX/XY system, XX normally but not always being the female. In some dioecious plants the Y chromosome is visually distinct from the X. This works for diploid plants, but numerous plant species are polyploid and must therefore have multiple sex chromosomes. Many of these polyploids are hermaphrodite even if the diploid is dioecious, although this is not always so. In some, the Y genes seem to override expression of X genes even if there is only one Y and several X chromosomes, and the polyploids remain dioecious.

In some dioecious species, such as willows, sex expression never varies, but in others production of male and female flowers can be influenced by environmental conditions, and hormonal expression within the plant interacts with the genetic makeup. This can make genetically male plants produce female flowers and *vice versa*. Auxin levels (Topic F3) differ along a shoot and affect which flowers grow, the auxin levels themselves being affected by day length, temperature and quantity and quality of light. In monoecious species, male flowers are usually produced nearer the tip of a shoot than female flowers, this being related to the levels of auxins and other hormones.

H3 Self incompatibility

Key Notes

Types of self-incompatibility

In many hermaphrodite and monoecious plants there is a physiological self-incompatibility (SI) in which a plant's own pollen is rejected. There are several systems involving differences in the sites of recognition and in genetics. The carpel recognizes either the growing pollen tube (gametophytic recognition) or the pollen surface (sporophytic recognition).

Gametophytic systems

In the commonest system, incompatible pollen tubes burst in the style. The recognition is controlled by one locus with many 'S' alleles. In the grasses the pollen tube is blocked at the stigma surface with pectins and callose. Alleles at both loci need to be the same for an incompatible reaction.

Sporophytic systems

One sporophytic system has a single locus with many S alleles, but the genetics may be complex involving dominance hierarchies. The pollen is inhibited from germinating or the tube is blocked before penetration. Heteromorphic systems involve two or three different forms of flower with differences in pollen and stigma structure and usually differences in style and stamen length. Pollen–stigma interaction may differ but each form can cross only with other forms. The system involves one or two loci each with two alleles.

Late-acting systems

This is a little known group of SI systems in which the pollen tube reaches the ovule but the ovule aborts. It may involve sporophytic or gametophytic recognition or a combination of both.

Molecular basis of self-incompatibility

In gametophytic SI, glycoproteins with ribonuclease activity are produced by the S gene, perhaps disabling RNA at the pollen tube tip. In the grass system, wall formation is inhibited by glycoproteins. In sporophytic SI, two linked loci produce glycoprotein and a kinase that disable each other.

Related topics Pollen and ovules (D2) Breeding systems (H2)

Types of self-incompatibility

Many hermaphrodite and monoecious plants have a physiological self-incompatibility (SI) system involving an interaction between the pollen and the carpel which prevents seeds forming or maturing as a result of self-fertilization (Topic H2). These interactions all involve the ability of the carpel to recognize and reject its own pollen and accept pollen from a different plant. The site of recognition and the mechanisms vary widely within plants (*Table 1*) but the main interaction is known as either gametophytic or sporophytic (*Fig. 1*). In a **gametophytic** interaction, the pollen germinates and the growing pollen tube is recognized by the female plant, normally in the style. Since a pollen grain is the result

Table 1. Types of self-incompatibility (SI) in flowering plants

Name	Site of recognition	Genetic basis	Features	Distribution
Gametophytic (normal type)	Pollen tube in the style	One locus, many alleles	Stigma with wet surface and cuticle with gaps	Widespread
Gametophytic (grass type)	Pollen tube on stigma surface	Two loci, several alleles	Stigma dry with continuous cuticle	Grasses (others?)
Sporophytic	Surface of pollen grain on stigma	One locus, many alleles	Stigma dry with continuous cuticle	Mainly cabbage and daisy families
Heteromorphic (two forms)	Surface of pollen grain on stigma or style	One locus, two alleles	Stigma normally dry with continuous cuticle	25 mainly unrelated families
Heteromorphic (three forms)	Surface of pollen grain on stigma or style	Two loci each with two alleles	Stigma normally dry with continuous cuticle	Four unrelated families
Late-acting	Mainly pollen tube at ovule	Unknown	Variable	Probably widespread

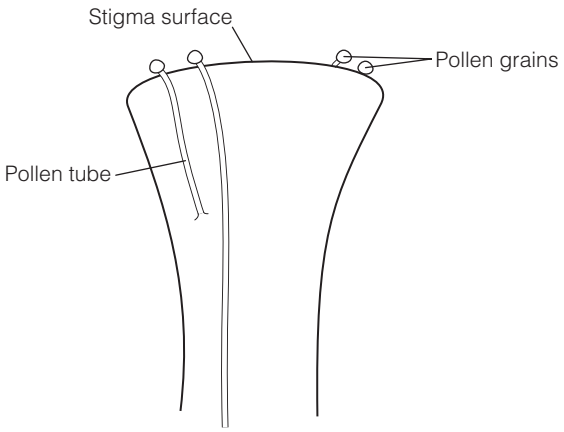


Fig. 1. Stigma showing incompatible and compatible pollen from a typical gametophytic interaction (left) and incompatible pollen from a sporophytic interaction (right).

of meiosis, it has a single set of chromosomes and it is this that is recognized. In a **sporophytic** interaction, the surface of the pollen grain is recognized, normally by the stigma. The pollen surface is impregnated with the anther tapetum before being shed (Topic D2) and it is this coating, derived from the parent plant and with both sets of parental chromosomes, that is recognized. The terms 'gametophytic' and 'sporophytic' are used to indicate the origins of the structures (Topic R4). In all SI systems the controlling genes are known as S genes.

Gametophytic systems

In the most widespread SI system in flowering plants, both compatible and incompatible pollen tubes grow down the style. Compatible pollen tubes reach the ovule where they burst and release the sperm cells. Incompatible pollen tubes grow more slowly and, at least in some, the pollen tube bursts before it reaches the ovule and the polysaccharide callose is deposited around the tube. This system involves one gene locus with many alleles (i.e. different forms of

the one gene), probably 20–50 in most species. If the S allele of the pollen tube is the same as either one of those in the style the tube will be stopped, thereby stopping all a plant's own pollen and other pollen with one of the same S alleles.

In the grasses (and possibly some members of the nightshade family, Solanaceae) the germinating pollen tube is blocked before it penetrates the stigma or just as it starts. Incompatible pollen is blocked initially by pectins followed by callose deposition. Two gene loci are involved and only if the alleles at both loci in the pollen are the same as two of the alleles in the female parent is the incompatibility reaction triggered. The number of alleles at each locus is probably 6–20, smaller than in the single-locus system, but the two independent loci allow for more compatible pollinations.

There are other rather ill-defined gametophytic systems with two or more loci, often giving partial self-incompatibility.

Sporophytic systems

Two large unrelated families, the cabbage family and the daisy family, Brassicaceae and Asteraceae, respectively, and a few other unrelated plants in at least three more families show a sporophytic interaction (*Table 1*) with a mode of action similar to that of the grasses. One gene locus is involved but genetic control is more complex than in gametophytic systems and there is some variation in the response, although a plant's own pollen is always stopped. The number of S alleles is similar to that in gametophytic systems but some have a dominance hierarchy.

Heteromorphic systems (*Table 1*) mainly have sporophytic recognition and the system occurs in widely scattered plant families. In this SI system, the flowers of different plants usually take one of two or three different forms and the site of recognition can differ between the forms of one species. The dimorphic type has one form with a short style and long stamens and the other with a long style and short stamens (*Fig. 2*). In trimorphic plants there are three different style lengths with stamens occupying the other two sizes in each plant. In most heteromorphic plants the stigmas of the different morphs have different surface textures and the pollen may be of different size or sculpturing or both. In dimorphic systems each plant can cross only with a plant with the other type of flower, or either of the other types in trimorphic systems.

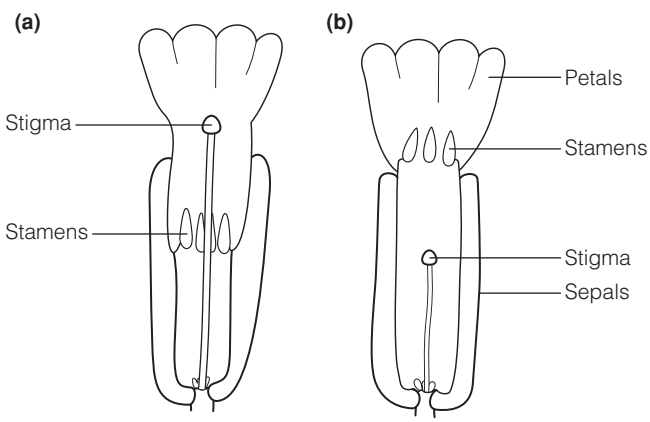


Fig. 2. Heteromorphic flowers of the cowslip, Primula veris*. (a) Long-styled; (b) short-styled.*

Late-acting systems

In some self-incompatible plants the pollen tube reaches the ovule but the ovule aborts, either because fertilization fails or because the ovule aborts at an early stage after fertilization. The recognition, the mechanisms and the genetics are not well understood. Both gametophytic and sporophytic recognition probably occur in different groups and there may be both types within one species. The production of weak offspring as a result of selfing, **inbreeding depression**, may be hard to distinguish from late-acting SI systems. Some form of late-acting system is known from 16 families.

Molecular basis of self-incompatibility

The S gene of arabidopsis (Topic E1) and other plants have been cloned and been shown to produce a glycoprotein with ribonuclease (RNase) activity. In gametophytic recognition, ribosomal RNA at the tip of the pollen tube is probably recognized by this protein in the style and disabled. As the pollen tube grows, enzymes from the tube digest the stylar tissue providing a path and this may activate the RNase. The mechanism is still not clear but some form of nucleic acid–enzyme recognition seems likely. In the grass system it is likely that the S allele glycoprotein interacts with carbohydrates at the pollen tube tip. This interferes with the extension of microfibrils of carbohydrate that would normally occur to make the pollen tube wall. The precursors of these wall molecules, microfibrillar pectins, then accumulate and block the tube.

In the sporophytic SI system of the cabbage family, the S gene is actually two linked loci, one producing a glycoprotein and the other a receptor kinase. These are structurally similar and are expressed on both the stigma surface and the surface of the pollen grain. If the kinase is disabled there is no incompatibility reaction so it must involve some interaction between the two proteins. Pollen grains in sporophytic SI hydrate by enzymic breakdown of cells on the stigma surface and this stage may be inhibited, so that pollen germination is stopped through insufficient hydration. In wet or very humid conditions more incompatible pollen germinates, but this is stopped from penetrating, so the interaction is clearly not confined to germination.

H4 Seed development, dormancy and germination

Key Notes

Seed development

Stage I of seed development produces the radicle, which gives rise to the root, and the plumule, giving the shoot and cotyledons. Stage II involves maturation, post-abscission and desiccation.

Seed dormancy

Dormancy may be due to the barrier to water and oxygen presented by the seed coat or to abscisic acid produced by the embryo. Breaking dormancy may require low temperature (vernalization), light or darkness.

Gene expression in germination

Germination begins with water absorption (imbibition). Next, the seed food reserves are mobilized. In grasses, the starch in the endosperm is broken down by enzymes synthesized in the aleurone layer in response to gibberellic acid from the embryo. Production of a photosynthetic apparatus involves: Phase I, cell division and division of etioplasts; Phase II, plastids go on dividing, plastid and nuclear genes for the photosynthetic apparatus and Calvin cycle are active; Phase III, maintenance of the photosynthetic apparatus.

Related topics

The seed (D3)
Biochemistry of growth regulation (F2)
Molecular action of growth regulators (F3)

Seed development

The first stage of seed development generates the major organs of the embryo: a radicle that gives rise to the root, and the plumule that gives rise to the shoot and cotyledons. Once these are formed, cell division stops and the second stage of seed development begins. This results in the formation of a seed capable of protecting the embryo and supplying its food until germination has taken place and a viable seedling has been established.

The next stage of seed development involves three phases: **maturation**, **post-abscission** and **desiccation** (*Table 1*). Genetic analysis of mutants of seed development in arabidopsis indicates that regulation of the events in the different phases is complex, with a number of genes being involved. One, ***abi3***, is involved in sensitivity to abscisic acid (ABA) as, when mutated, the plant is ABA-insensitive. It is only expressed in the seed and it controls expression of some of the genes of the maturation and post-abscission stages. *abi3* mutants germinate on the mother plant and do not undergo desiccation. Other mutants are also known that result in this type of early (precocious) germination. These include *fus3* mutants of arabidopsis which have cotyledons which develop to be

Table 1. Stages of phase 2 of seed development

Maturation	Embryo completes growth; dehydration of embryo begins; ABA levels reach maximum in dicots. High levels of storage reserve synthesis (protein, lipid, carbohydrate, depending on species)
Post-abscission	Seed separated from connection with mother plant; ABA levels peak in monocots. Browning of seed coat (testa). mRNAs for storage proteins decline and disappear. Late embryogenesis abundant (LEA) mRNAs for highly hydrophilic proteins increase which protect during dehydration
Desiccation	Seed metabolically inactive. Very little DNA turnover or mRNA synthesis; embryo inactive until germination initiated

mRNA, messenger RNA.

like the primordia of true leaves and which do not synthesize seed storage proteins.

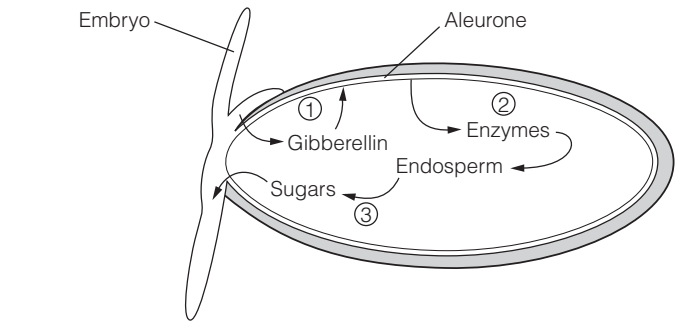
Seed dormancy

For a seed to be successful, the embryo must be inactive until after it has separated from its parent. For many species, it must also remain inactive (**dormant**) until after a period of harsh conditions such as cold or drought has passed. As the embryo is complete well before the seed is shed it will germinate if removed from the seed. Dormancy mechanisms ensure it remains inactive until an appropriate time. Species vary in the length of this embryo inactivity. In some species, removal of the seed coat permits germination, and dormancy is due to lack of oxygen and water for the embryo. In others, dormancy remains even if the coat is removed. In these, the dormancy regulator is **ABA**, produced by the embryo during the late stages of seed maturation (Topic F2). Dormancy may be broken by a variety of means, depending on the type of seed dormancy present. Coat-imposed dormancy may be ended by removal of external layers by microbes or even passage through an animal's gut. In other seeds, breaking dormancy may require a period of low temperature (vernalization), light or darkness.

Gene expression in germination

The first stage of germination is **imbibition**, in which the seed takes up water. Next, **seed storage reserves** are mobilized and the embryo grows. Mobilization of food reserves varies depending on the nature of the major reserves of the seed. The process has been studied in detail in barley.

Cereal seeds (**grains**) contain a large reserve of **starch** that is broken down to sugars that supply the developing embryo. A barley seed is made up of three components: an **embryo**, an **endosperm** containing storage reserves, and a layer surrounding the endosperm called the **aleurone** (*Fig. 1*). When a dormant seed imbibes water, **gibberellic acid** (Topic F2) is produced by the embryo and diffuses to the aleurone layer, resulting in the synthesis of new proteins, including hydrolytic enzymes such as **α-amylase** that break down the starch of the endosperm. Gibberellic acid greatly enhances the rate of transcription of the α-amylase gene. A small number of **gibberellic acid-response elements** (**GAREs**) have been identified, 200–300 bp from the transcription start site of the gene, which form a **gibberellic acid response complex** (**GARC**). The GARC is activated by the binding of **transcription factors**, proteins produced in response to gibberellic acid that bind to DNA. One such factor, **GAMYB**, is one of a



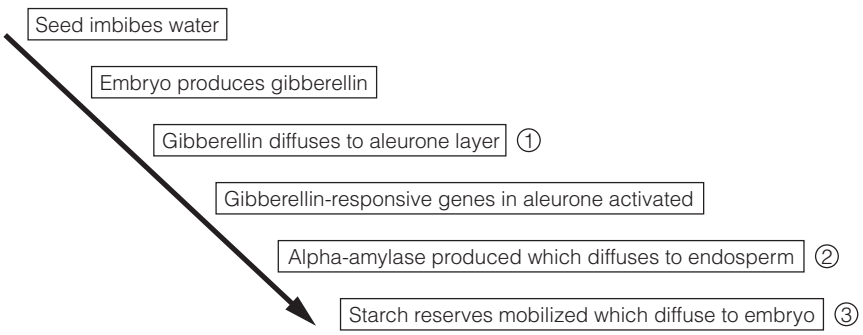


Fig. 1. The mobilization of storage reserves in barley seeds. After imbibition, the embryo produces gibberellic acid (1) which initiates gene expression in the aleurone (2) including the starch degrading enzyme α-amylase. This breaks starch down to yield sugars that are transported to feed the growing embryo (3).

family of transcription factors (**MYBs**) known to be involved in development and is up-regulated by gibberellic acid well before α-amylase gene expression begins.

After emergence of the seedling, the shoot can photosynthesize and supply the nutrients required for growth. Production of a fully functional photosynthetic apparatus (described for a grass) occurs in three phases.

Phase I. The coleoptile (Topic C3) and primary leaf (plumule) contain etioplast**s** (precursors of chloroplasts which cannot photosynthesize; Topic B3). In phase I, the meristematic cells of the leaf divide together with the etioplasts within them. In phase II, cell division ceases, but plastids go on dividing and increase in abundance. Genes are activated which generate the photosynthetic apparatus (Topic J1) and enzymes of the Calvin cycle (Topic J2). This involves activity of genes of both the plastid genome (plastome) and nuclear genome and the efficiency of the photosynthetic system increases as more components are added. In phase III, the activity of the photosynthetic apparatus is maintained, and damage repaired. Finally, the apparatus begins to senesce and efficiency is lost.