10 Plant Growth and Development Under Suboptimal Light Conditions

Ravinderjit Kaur, Gaganpreet Kaur, Kashmir Singh, and Baljinder Singh

Abstract

Light regulates various processes throughout the plant life from seed germination to flowering. Photoreceptors (phytochromes and cryptochromes) sense the changes in light conditions that trigger various signaling mechanisms resulting in upregulation and downregulation of several genes and transcription factors. Therefore, genetic and physiological responses, i.e., seedling growth and development, skotomorphogenesis, photomorphogenesis, shade avoidance, and flowering, are regulated by the changes in gene expression mediated by light. Phytohormones are also involved in controlling these developmental changes. Light also plays an important role in plant defense against various pathogens by inducing the jasmonic acid and salicylic acid pathways that trigger SAR (systemic acquired response). Once the plant becomes reproductively competent, light regulates the complex process of floral initiation by activation of floral genes and flowering hormones.

Keywords

Photoreceptors · Cryptochromes · Skotomorphogenesis · Jasmonic acid

10.1 Introduction

Plants being immobile have acquired intrinsic properties to adapt themselves according to the changing environmental conditions for their survival. Various abiotic factors like wind, water, temperature, and light influence the growth and development of

Ravinderjit Kaur and Gaganpreet Kaur contributed equally to this work.

R. Kaur · G. Kaur · K. Singh · B. Singh (✉)
Department of Biotechnology, Panjab University, Chandigarh, India
e-mail: sbaljinder@pu.ac.in

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plants. Light being a major environmental factor plays a vital role in overall growth and development of plants. It is responsible for induction of massive reprogramming of gene expression in plants (Petrillo et al. 2014). The change in the quantity, quality, and duration of light leads to alteration in various basic processes in plants like seed germination, photomorphogenesis, and transition to flowering which are regulated by expression of various genes.

10.1.1 Light Quantity, Quality, and Duration

Light quantity is the intensity or concentration of sunlight which increases or decreases according to seasonal variations. Basically, light quality is the color or wavelength of light that reaches to the plant surface. Light duration is the amount of time that a plant is exposed to sunlight, i.e., photoperiodism. It mainly controls the floral development. Photoperiodic regulation is controlled by various genes which are either activated or inhibited depending upon the duration of exposure to light (Thomas 2006).

10.1.2 Phytohormones

Plant hormones like auxins, cytokinins, gibberellins, abscisic acid, ethylene, and brassinosteroids regulate the developmental translations and are crucial for growth regulations. In plants, various light responses control the changes in hormonal metabolism and distribution. Phytohormones like abscisic acid, gibberellic acid, and ethylene respond to varying light duration and thus regulate the process of seed germination (de Wit et al. 2016).

Global gene expression is altered in response to changes in light conditions. Light is perceived by photoreceptors triggering many of the biological processes in plants by affecting gene expression (Rossel et al. 2002). Cryptochromes and phytochromes are the main photoreceptors that can localize in the nucleus and control light-regulated nuclear gene expression by transducing these signals to chromatin, influencing the process of transcription, post-transcription, alternative splicing, and translation that ultimately leads to adaptive changes at the cellular and organismic levels (Petrillo et al. 2014). One of the important organelle in plants, chloroplast, can also act as a light sensor and is involved primarily in the process of photosynthesis (Godoy Herz et al. 2014).

10.2 Seed Germination

The sprouting of a seedling from a seed is the beginning of a plant life which is regulated by two major environmental factors, i.e., water and light. During unfavorable conditions, seeds are present in a dormant state where metabolic activity is very low. When ample amount of water is present in the surroundings, the seed uptakes water by the process of imbibition and gets filled with water, which plays a vital role in the activation of various proteins and enzymes that are involved in the process of plant growth.

The seedling establishment and its further growth are regulated by phytochromes (photochromic proteins) which are light-sensitive proteins called photoreceptors. Various photoreceptor proteins of different families perceive the light spectrum ranging from near UV-B (280–315 nm) to far-red (750 nm) light (de Wit et al. 2016).

10.2.1 Phytochromes and Their Role in Seed Germination

Phytochromes are cytoplasmic serine/threonine kinases which sense both red and far-red light. It is a homodimer (MW 250 kDa) consisting of a polypeptide chain called apoprotein (MW 124 kDa) with a covalently attached linear tetrapyrrole light-absorbing pigment molecule called chromophore also called phytochromobilin via a thioether linkage to an invariant cysteine residue (Rockwell et al. 2006).

The five members of phytochrome gene family are PHYA, PHYB, PHYC, PHYD, and PHYE (Devlin and Kay 2000). These phytochromes are divided into two categories: TYPE I which is light labile and TYPE II which is light stable. TYPE I includes PHYA, which encodes for the protein phytochromeA (phyA) which mainly perceives far-red light, whereas TYPE 2 includes the PHYB, PHYC, PHYD, and PHYE, and this family of phytochromes perceive red light (Neff et al. 2000). The blue light and UV-A wavelength of the spectrum is sensed by another group of photoreceptors called cryptochromes and phototropins, whereas UVR8 photoreceptor receives UV-B light (Petrillo et al. 2014).

10.2.2 Photoreversibility

In etiolated seedlings, phytochromes are present in a red-light-absorbing form, Pr (λ_{max} = 660 nm) which upon exposure to red light gets photoconverted into far-red-light-absorbing form, Pfr (λ_{max} = 730 nm). When Pfr is exposed to far-red light, it is photoconverted to Pr. This process is known as photoreversibility. During the conversion of Pr to Pfr, both chromophore and protein moieties undergo conformational changes. The Pr chromophore undergoes a cis-trans isomerization of the double bond between C15 and C16 and rotation of C14–C15 single bond (Fig. 10.1).

Plant hormones like gibberellic acid and abscisic acid play an important role in seed germination. During seed germination and seedling establishment, gibberellins stimulate the production of α-amylase and other hydrolytic enzymes in the aleurone layer surrounding the endosperms of grains which help in the breakdown of complex food resources. It also plays a major role in stem elongation. Abscisic acid acts as an antagonist to gibberellins during seed germination thus inhibiting this process. This phytohormone also plays an important role during stress conditions and promotes the process of seed dormancy.

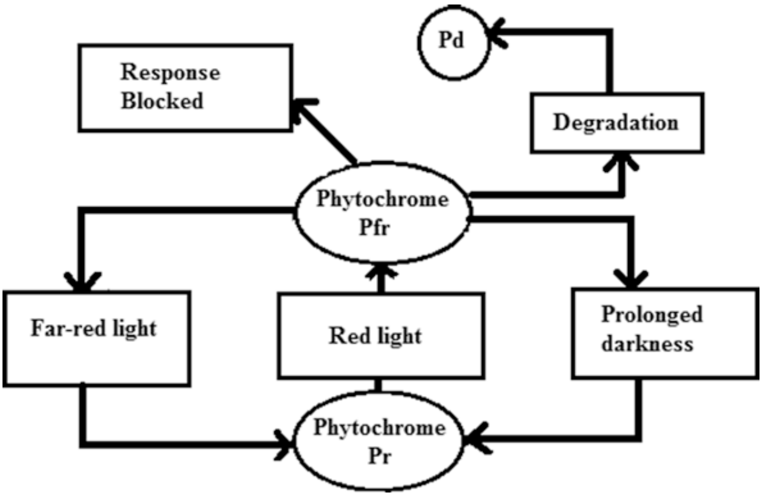

Fig. 10.1 Photoreversibility. Pr (inactive) changes to Pfr (active) upon exposure to red light, and Pfr reverts back to Pr form when exposed to far-red light. Prolonged darkness can also convert Pfr to Pr or mediate its degradation. The degraded product is referred as Pd

10.2.3 Gene Signaling Mechanism During Seed Germination

In model plant *Arabidopsis thaliana*, light-regulated germination signaling process is well understood. This process is regulated by abscisic acid that inhibits germination, whereas gibberellins promote the process of seed germination. In dark conditions, phyB resides in the cytosol in an inactivated form; thus PIF1 (phytochrome-interacting factor 1) which is a transcription factor gets accumulated in the nucleus and regulates transcription of various genes that leads to accumulation of abscisic acid, whereas the biosynthesis of gibberellic acid is inhibited.

In contrast, red light activates phyB, stabilizing its Pfr form which migrates into the nucleus. PIF1 a transcription factor interacts with phytochrome in the nucleus where its phosphorylation and degradation occur via ubiquitin ligase. Further its activity is inhibited by the heterodimer formation along with long hypocotyl in far-red 1 (HFR1). Hence, the genes involved in the process of gibberellic acid biosynthesis are activated (GA3 oxidase1 and GA3 oxidase2). Also the *CYP707A2* gene involved in abscisic acid catabolism is activated. Thus, all the events during light conditions lead to the accumulation of gibberellic acid and inhibition of abscisic acid which triggers the process of seed germination (de Wit et al. 2016) (Fig. 10.2 and Table 10.1).

Therefore, it is the light quality (red and far-red light) that regulates seed germination. We conclude that the phenomenon of seed germination is affected by varying light conditions. It is a highly complex process which is governed by the plant pigment phytochrome within the seed. Red light sensed by phytochrome induces seed germination, whereas far-red and blue light inhibits the growth and its germination. So, the amount of light either continuous or brief exposure effects the process of seed germination.

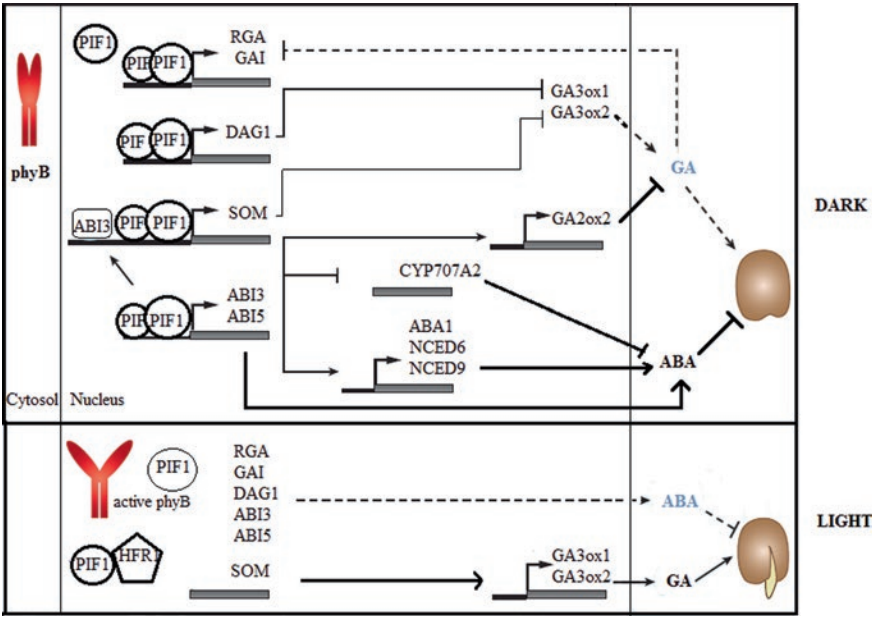

Fig. 10.2 In dark conditions, inactive phyB resides in the cytosol, due to which PIF1 is accumulated in the nucleus. Thus, genes RGA, GAI, DAG1, SOM, ABI3, and ABI5 are transcribed, as a result of which ABA is accumulated and GA biosynthesis is inhibited. Hence, the seed does not germinate in dark. In contrast, red light activates phyB and translocated into the nucleus and mediates the degradation PIF1. HFR1 forms a heterodimer with PIF1, which lowers down its activity further lowering the levels of ABA concentration and accumulation of GA concentrations. Hence, seed germination takes place in light

10.3 Seedling Growth and Development

The growth and development of the seedling start with the process of skotomorphogenesis followed by photomorphogenesis. During these developmental changes, seedling emerges from the seed and reaches the soil surface.

10.3.1 Skotomorphogenesis

After the process of seed germination has occurred, the process of etiolated growth of the seedling, i.e., skotomorphogenesis (growth in the dark), begins from the buried seed towards the soil surface in the upward direction (Toledo-Ortiz et al. 2010). In this process, hypocotyl elongation occurs in the dark at a very fast rate, such that its tip reaches the soil surface where it is exposed to light before the seed resources are exhausted. The cotyledons in the dark are tightly closed and are underdeveloped. The energy is derived from the reserve food material present in the seed as the photosynthetic machinery is inactive in this stage. The etioplasts are undifferentiated in

Table 10.1 Genes involved in seed germination in *Arabidopsis thaliana* induced by light via phytochrome B (phyB)

Genes involved in seed germination in *Arabidopsis*	Hormone effected	Gene function
RGA (Repressor of GAI-3)	Gibberellic acid (GA)	Inhibition of GA biosynthesis
GAI (Gibberellic acid insensitive)	Gibberellic acid (GA)	Inhibition of GA biosynthesis
DAG (DOF affected germination)	Gibberellic acid (GA)	Inhibition of GA3ox1 and GAox2
SOM (Somnus)	Gibberellic acid (GA)	Inhibition of GA3ox1 and GAox2
GA3ox1 (Gibberellin3-oxidase 1)	Gibberellic acid (GA)	Activation of GA biosynthesis
GA3ox2 (Gibberellin3-oxidase 2)	Gibberellic acid (GA)	Activation of GA biosynthesis
GA2ox2 (Gibberellin2-oxidase 2)	Gibberellic acid (GA)	Inhibition of GA biosynthesis
ABI3 (Abscisic acid insensitive 3)	Abscisic acid (ABA)	Activation of ABA biosynthesis
ABI5 (Abscisic acid insensitive 5)	Abscisic acid (ABA)	Activation of ABA biosynthesis
ABA1 (Abscisic acid 1)	Abscisic acid (ABA)	Activation of ABA biosynthesis
NCED6 (9-cis-epoxycarotenoid dioxygenase 6)	Abscisic acid (ABA)	Activation of ABA biosynthesis
NCED9 (9-cis-epoxycarotenoid dioxygenase 9)	Abscisic acid (ABA)	Activation of ABA biosynthesis
CYP707A2	Abscisic acid (ABA)	Inhibition of ABA synthesis (catabolism of ABA)

which the precursor of chlorophyll, protochlorophyllide, accumulates which gives it a yellowish appearance.

This type of etiolated growth, i.e., growth in the absence of light, is governed by various transcription regulators which regulate the expression of various genes. Most of them are bHLH TFs. Among these, HY5 plays an important role in hypocotyl elongation. In the absence of light, HY5 is degraded by ubiquitinylation via COP1 as HY5 is a negative regulator of hypocotyl elongation; as a result, the absence of HY5 leads to hypocotyl elongation. COP1 also degrades HFR1 (long hypocotyl in far-red 1) in the dark, which is an atypical bHLH TF and is involved in phytochrome- and cryptochrome-dependent signal transduction (Mancini et al. 2016; Toledo-Ortiz et al. 2014).

PIFs (phytochrome-interacting factors) on the other hand indirectly regulate hypocotyl elongation by degrading PhyB. Hormones involved in etiolated growth conditions are auxins, cytokinins, ethylene, gibberellins, and brassinosteroids. Gibberellins destabilize DELLA protein (growth repressing transcription regulator) and thus lead to hypocotyl elongation (Achard et al. 2004). Thus, the process of hypocotyl elongation is a characteristic of skotomorphogenesis, i.e., the growth of a seedling under the soil in the dark conditions.

10.3.2 Photomorphogenesis

Once the seedling has emerged out from the soil, further development is mediated by light which has been termed as photomorphogenesis (Godoy Herz et al. 2014; Toledo-Ortiz et al. 2010; Arsovski et al. 2012). After germination, the light-grown seedlings have a different morphology than those grown in the dark, as seedlings in the dark conditions do not express light-inducible genes. Upon exposure to light, the light-responsive genes are induced; therefore the seedling undergoes rapid light-mediated morphological changes.

In the presence of light, transcription regulators HY5 and HFR1 are accumulated in the nucleus because their degradation by COP1-mediated ubiquitin ligase is prevented, as a result of which the elongation of hypocotyls is inhibited. Upon exposure to light, the underdeveloped cotyledons start expanding; thus the light capturing surface is increased. The process of de-etiolation begins with the greening of cotyledons in which chloroplasts start accumulating the chlorophyll pigment. Hence, the green chloroplasts are photosynthetically active, and therefore now the energy is derived by the process of photosynthesis which is utilized for further growth and development.

10.4 Shade Avoidance

Once the seedling becomes a photoautotroph, both the external and the internal environments regulate the plant growth and help it to enter in the juvenile phase. Many factors like pathogens and shade due to neighboring vegetation (canopy) act as obstacles during this phase transition. Light is often a limiting factor in dense forests where canopy blocks the light from reaching the plants growing below it. These plants hence respond by the phenomenon of shade avoidance, i.e., changes which occur in response to the enrichment of far-red light under a leaf canopy (Casal 2012; Franklin and Whitelam 2004). These varying light conditions are sensed by phytochromes, and such responses include elevation of leaf angles (hyponasty), enhanced hypocotyls and petiole growth, early flowering, abundant PIF4 and PIF5 proteins, degradation of DELLA proteins, etc. collectively known as shade avoidance syndrome (Leivar et al. 2008). The R:FR ratio decreases in the shade conditions leading to alterations in the growth of the plant.

10.5 Role of Light in Plant Defense

In the initial phase of growth, the plant utilizes most of the energy fixed by the process of photosynthesis for its growth. When surplus amounts of carbohydrates are available, they are converted into secondary metabolites like terpenes, alkaloids, nitrogen-containing compounds, etc., which play an important role in plant defense.

Thus, in growing plants, these compounds are produced in a very less amount because the major proportion of carbon fixed is diverted for its growth and development. Due to the lower levels of secondary metabolites in the new emerging seedling, the growing plant is vulnerable to attack by pathogens. Thus, in this phase of growth, the plant needs to grow at a very fast rate in order to compete with its neighboring plants and also needs to defend itself from the microbial pathogens (Ballare 2014). As the plant is still growing in its juvenile phase, the intact barrier consisting of the bark or waxy cuticle is not available as a first line of defense to protect the plant against the microbial attack, as a result of which, the pathogen can easily enter inside the plant body.

Light sensed by the phytochrome B (phyB) photoreceptor induces signal transduction pathways that lead to the production of various compounds like jasmonic acid, salicylic acid, etc., which are involved in plant defense mechanism. These compounds trigger the induction of **SAR** (systemic acquired response) (Bolton 2009; Ryals et al. 1996). Hence, if the plant is growing under suboptimal conditions, i.e., shade (low R:FR), it leads to inactivation of phyB that downregulates the jasmonic acid and salicylic acid signaling.

10.6 Light-Mediated Floral Induction

With time, various developmental changes cause alterations in the plant growth due to which the plant enters from juvenile stage to a mature adult plant. In juvenile phase, vegetative meristem does not respond to internal and external signals that initiate flowering, i.e., incompetence. Under internal optimal conditions, the developmental changes allow the plant to become reproductively competent. These conditions include factors like plant size, number of vegetative nodes, and amount of sucrose, the main energy source which fuels the plant to begin the complex process of floral initiation. Along with these factors, hormones such as gibberellic acid, cytokinins, and "florigen" also known as the flowering hormone play a major role in gaining internal competence (Corbesier and Coupland 2006). Once the plant becomes internally competent to reproduce, external environmental conditions like light (photoperiod, light quality, and quantity), temperature (vernalization, i.e., exposure to long cold conditions), nutrient, and water availability determine the process of floral induction.

10.6.1 Photoperiodism

Photoperiodism plays a crucial role in regulating floral development. Different plants respond to light conditions depending upon the duration of light exposure to that respective plant. Based on this condition, these plants are divided into three basic categories, namely short-day plants, long-day plants, and day-neutral plants. The short-day plants are those in which floral initiation takes place when exposure to light is less than the critical duration, for example chrysanthemum and soybeans. These plants usually flower in late summer. The long-day plants require exposure to light for a period more than a well-defined critical duration, i.e., these plants require a long duration of light exposure, for example lettuce and spinach. These plants normally flower in spring and early summer. The third category includes day-neutral plants in which there is no relation between photoperiodism and floral induction. Initiation of flowering occurs independent of light duration. For example, *Sorghastrum nutans* commonly known as Indian grass is a day-neutral plant (Lumsden 2002; Andreas and Coupland 2012).

The shoot apical meristem (SAM) in the initial phases of plant growth leads to the formation of vegetative organs like leaves, but once the plant becomes internally competent to reproduce and all the external conditions are favorable and optimal, SAM makes transition to the reproductive development, and the production of flower is initiated (Benlloch et al. 2007). These changes are mediated by signals that turn on various genes that lead to morphological changes specifying the location of floral organs like sepals, petals, stamens, and carpels.

10.6.2 Photoreceptor Proteins Regulating Floral Formation

Various photoreceptor proteins are present in the leaf of the plant which play a vital role in the process of gene activation that leads to the initiation of flowering. In *Arabidopsis thaliana*, a facultative long-day plant, the far-red and blue light is perceived by phytochrome (phyA) and cryptochrome (cry1 and cry2) (Zuo et al. 2011) that promote floral initiation, whereas the red light perceived by phyB inhibits flowering. Florigen (flowering hormone) production takes place in leaves which is regulated by the duration of light exposure, i.e., photoperiodism, and later on this signaling hormone is translocated via phloem to SAM where the process of flower formation is induced (Tsuji and Taoka 2014).

10.6.3 Genes Involved in Floral Formation

As a result of the abovementioned events, various genes are activated that initiate the process of flowering. These genes are divided into two groups, namely floral meristem identity genes that are responsible for the transition of vegetative meristem to floral meristem, and they include *AGAMOUS-LIKE 20, LEAFY, APETALA1 (AP1),* etc. The second group is floral organ identity genes or floral homeotic genes that lead to the formation of the floral parts, and these include *APETALA2 (AP2), APETALA3 (AP3)/PISTILATA (PI),* and *AGAMOUS (AG).* These two groups of genes act in a sequential manner to initiate the process of flowering. The signaling hormone "florigen" is responsible for the activation of *CONSTANS* gene which is expressed in long days, and it encodes a transcription factor that further initiates the signaling cascade by activating *AGAMOUS-LIKE* 20, a floral meristem identity gene (Achard et al. 2007). It further activates *LEAFY* which is the most important gene for the production of flower. LEAFY in turn activates floral homeotic genes that are responsible for the formation of various floral organs (Benlloch et al. 2007; Balasubramanian et al. 2006). *AGAMOUS-LIKE* 20 is inhibited by another gene *FLOWERING LOCUS C*. Therefore, to initiate the process of floral induction, this inhibition needs to be relieved which is done upon exposure to low-temperature conditions, i.e., the process of vernalization (Figs. 10.3 and 10.4).

Along with low temperature, gibberellins also play an important role in controlling this complex process of flowering. Thus, in most of the plants, both light and temperature play a very important role in controlling the rate of flowering.

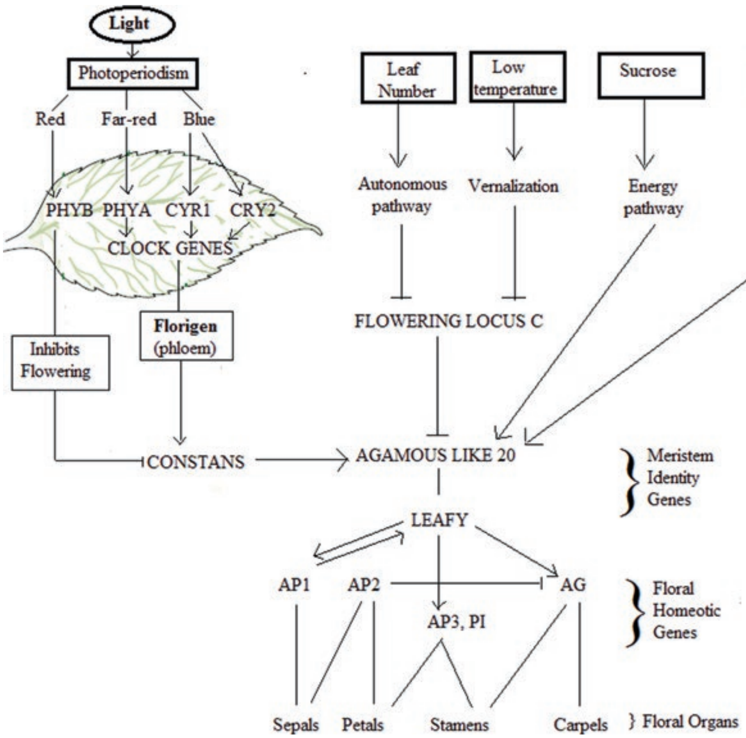

Fig. 10.3 Various genes are activated or inhibited by different floral developmental processes including photoperiodism, autonomous/vernalization pathway, energy pathway, and gibberellin pathway that eventually lead to the production of various floral organs

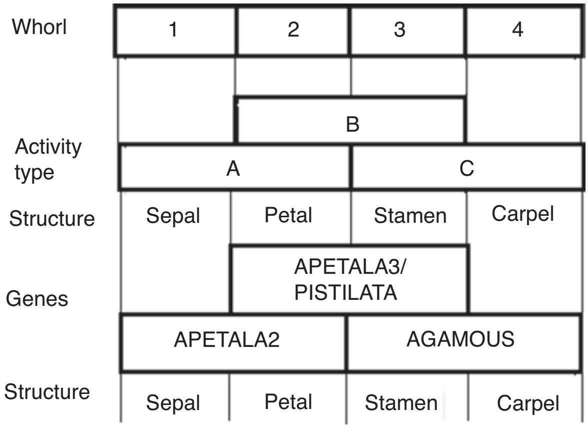

Fig. 10.4 ABC MODEL. The formation of floral organs depends upon the interaction between three floral homeotic genes AP2 (type A), AP3/PI (type B), and AG (type C). AP2 results in the formation of sepals. The interaction of AP3/PI with AP2 leads to the formation of petals, whereas the interaction of AP3/PI with AG forms stamens, and AG alone forms carpels in the last whorl

10.7 Summary

Light plays a very important role in overall growth and development of a plant starting from the seed germination till it becomes a full-fledged adult reproductive plant. Plants respond to the external light conditions via photoreceptors. Phytochromes and cryptochromes are the main photoreceptors that sense red/far-red and blue light, respectively, and trigger various signaling cascades, as a result of which, various metabolic processes are either initiated or repressed. The processes like seed germination, seedling growth and development, formation of secondary metabolites, and floral initiation are the most important events in the plant life. Light basically regulates various phytohormones like auxins, gibberellins, abscisic acid, ethylene, cytokinins, brassinosteroids, etc. which in turn regulate the overall growth and development of the plant. Photoperiodism and vernalization are the two main processes that control the process of flower formation in adult plants. Light perceived by photoreceptors upregulates and downregulates the transcription of various genes which are involved in the plant developmental process. Thus, without light, there is no life.

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