Recently Discovered Plant Growth Regulators

22

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22.1 Salicylic Acid

Salicylic acid is a phenolic plant growth regulator known to regulate various aspects of plant growth and development. It also functions in various ways in modulating biotic and abiotic stress responses. Plants, such as willow tree (*Salix* sp.) and poplar (*Populus* sp.), have been used since the fourth century BC to relieve pain in the human body. But it was only in the nineteenth century that salicylic acid (SA) and related compounds such as methyl salicylate, saligenin, and their glycosides were isolated from the bark of willow tree and were found to be analgesic. Oil of wintergreen, extracted from the American plant *Gaultheria procumbens*, which was widely used as analgesic during the mid-nineteenth century, is also rich in methyl salicylate. SA was chemically synthesized in 1858 in Germany, and it replaced wintergreen oil as an analgesic. The sharp bitter taste and gastric irritation caused by SA, however, did not make it popular for its application as an analgesic. Subsequently, Bayer and Co. (a German pharmaceutical company) produced acetyl derivative of SA, i.e., acetyl salicylic acid, with the trade name Aspirin which became popular as an analgesic since then (Fig. 22.1). In the recent past, action of this phenolic compound, i.e., SA (chemical name: 2-hydroxybenzenecarboxylic acid), has also been discovered in various aspects of plant growth and development and acquisition of disease/wound resistance.

22.1.1 Biosynthesis

Biosynthesis of salicylic acid in plants occurs via two routes (Fig. 22.2):

1. **The *trans*-cinnamic acid** (tCA) pathway whereby tCA is synthesized from phenylalanine in a reaction catalyzed by phenylalanine ammonium lyase (PAL). tCA is then converted to benzoic acid which gets converted to salicylic

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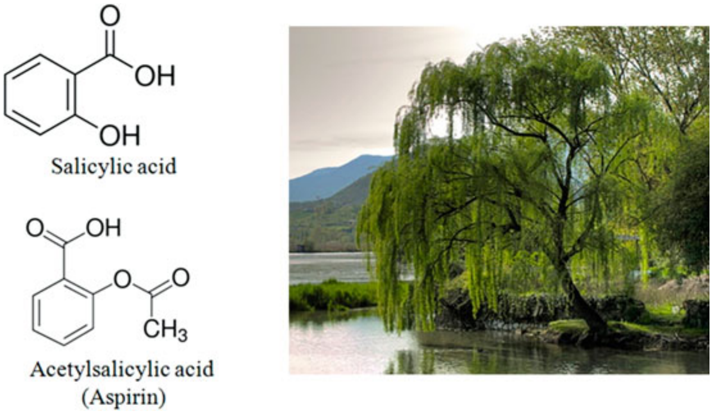


Fig. 22.1 Chemical structures of salicylic acid and acetyl salicylic acid (aspirin) and picture of a weeping willow (*Salix babylonica*) tree whose bark is known to contain salicylic acid and its derivatives

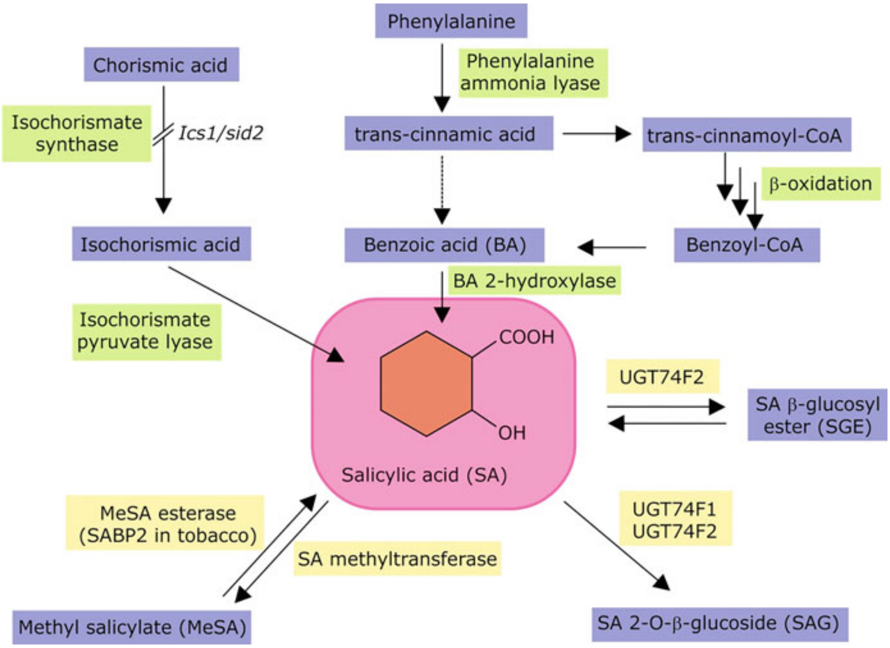


Fig. 22.2 Proposed pathway for salicylic acid (SA) biosynthesis and metabolism in plants

acid through hydroxylation catalyzed by benzoic acid 2-hydroxylase. In support of this pathway of SA synthesis, it has been observed that when tobacco plants are inoculated with tobacco mosaic virus (TMV), PAL activity is suppressed, and this coincides with low levels of SA.

2. **The chorismate pathway** of SA biosynthesis occurs in two steps. The first step is catalyzed by isochorismate synthase (encoded by ICS1/SID2) leading to conversion of chorismic acid into isochorismic acid which subsequently gets converted to salicylic acid by the activity of isochorismate pyruvate lyase. The ICS1/SID2 mutant of *Arabidopsis* fails to accumulate SA under otherwise inductive conditions suggesting the operation of chorismate pathway of SA biosynthesis in this species. The information available so far suggests the operation of both the pathways of SA biosynthesis in plants though species specificity and treatment specificity may be evident for the operation of one or the other of the two pathways. SA has been reported to get converted to methyl salicylate (MeSA). Methylation of SA is catalyzed by a carboxyl methyl transferase. It can also be converted into a glucoside derivative called SA-2-*O*-β glucoside, SAG, or an ester (SA β-glucosyl ester, SGE).

22.1.2 Physiological Functions

22.1.2.1 Senescence

Addition of aspirin (acetyl salicylic acid) to a flower vase containing cut flowers is known to retard senescence of petals and thus enhance their longevity. This is due to the conversion of acetyl salicylic acid into SA in water and consequent lowering of the rate of ethylene biosynthesis in cut flowers. SA positively regulates leaf senescence. In *Arabidopsis* leaves SA content increases as the chlorophyll concentration begins to decline with the onset of senescence. Senescing leaves also exhibit an upregulation of many genes involved in SA biosynthesis. These observations suggest that SA plays a significant role not only in the onset of senescence but also in its progression.

22.1.2.2 Regulation of Thermogenesis

During thermogenesis, most of the electron flow in mitochondria gets diverted from cytochrome respiration pathway to cyanide-insensitive non-phosphorylating electron transport pathway which is unique to plant mitochondria. The energy released by electron flow through this alternative respiratory pathway is not conserved as chemical energy but is released as heat. Some plants are known to generate large amount of heat as a result of the above-stated alternative respiratory pathway. Thus, in voodoo lily (*Sauromatum* sp.), the part of the inflorescence becomes much warmer than the surrounding air causing the release of amines and other chemicals as vapors which serve as chemical attractants for pollinators. The cyanide-resistant oxygen uptake is catalyzed by the **alternative oxidase**. When electrons pass to the alternative pathway, there is no energy conservation site between ubiquinone and oxygen. Thus, the free energy which is normally conserved as ATP is lost as heat when electrons are shunted through this pathway. The functional usefulness of the activity of alternative oxidase in thermogenic flowers is evident with a rise in temperature of the upper appendix in voodoo lily to as much as 25 degrees over and above the ambient temperature. It has been observed that salicylic acid acts as a signal which initiates this thermogenic event in voodoo lily. The thermogenic-inducing principle was initially called **calorigen** and was identified as SA in the 1980s. SA application to the arum spadix can bring about thermogenecity accompanying an increase in endogenous SA levels as well (an example of positive feedback) (Box 22.1). Through this mechanism the inflorescence in voodoo lily can

Box 22.1: Thermogenic Plants

Thermogenicity (heat production) in plants, first described by Lamarck in 1778 for the genus *Arum*, is now known to occur in the male reproductive structures of cycads and in the flowers or inflorescence of some angiosperm species belonging to families *Annonaceae*, *Araceae*, *Aristolochiaceae*, *Cyclanthaceae*, *Nymphaeaceae* and *Palmae*. The heating is believed to be associated with a large increase in the cyanide-insensitive non-phosphorylating electron transport pathway unique to plant mitochondria. The increase in this so called alternative respiratory pathway is so dramatic that oxygen consumption in the inflorescence of *Arum* lilies at the peak of heat production is as high as that of a humming bird in flight. In addition to the activation of the alternative oxidase, thermogenicity involves activation of the glycolytic and Krebs cycle enzymes which provide substrates for this remarkable metabolic explosion. In one of the *Arum* lilies, *Sauromatum guttatum* (voodoo lily), the inflorescence develops from a large corm, and can reach 80 cm in height. Early on the day of anthesis, a large bract (spathe) which surrounds the central column of the inflorescence (spadix) unfolds to expose the upper part of the spadix known as the appendix. Soon thereafter, the appendix starts to generate heat, which facilitates volatilization of foul-smelling amines and indoles attractive to the insect pollinators. By early afternoon the temperature of the appendix can increase by 14 °C above ambient, but it returns to ambient in the evening. The second thermogenic episode in the lower spadix starts late at night and ends the following morning after the maximum temperature increases more than 10 °C. In 1937, Van Herk suggested that the burst of metabolic activity in the appendix of the voodoo lily is triggered by "calorigen", a water-soluble substance produced in then male flower primordia located just below the appendix. Van Herk believed that calorigen begins to enter the appendix on the day preceding the day of anthesis. At that time attempts to isolate and characterize calorigen were not successful and hence his ideas met the scepticism. Mass spectroscopic analysis of the purified calorigen have indicated the presence of salicylic acid.

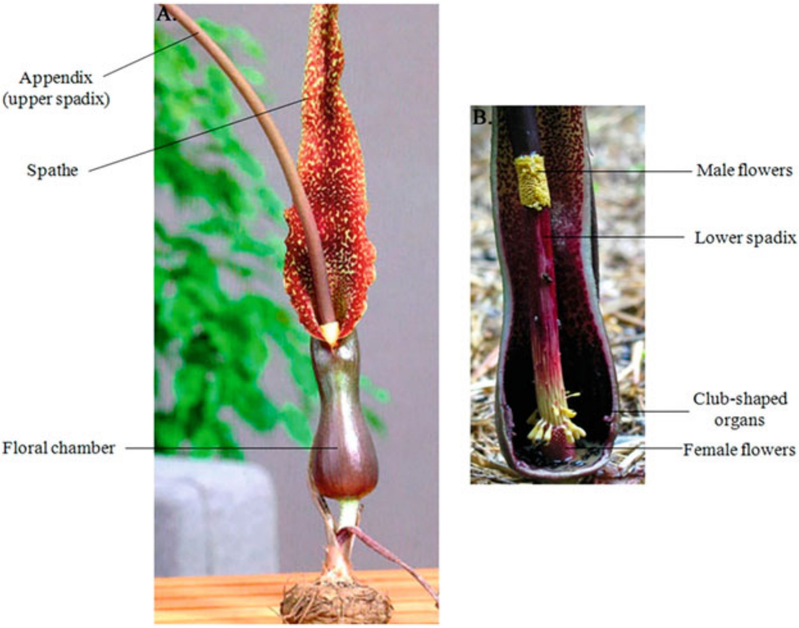


Fig. 22.3 (**a**) *Sauromatum* sp. (Voodoo lily) inflorescence. (**b**) A cut-open inflorescence

mimic the scent of rotting flesh and is used to deceive insects that lay their eggs (Fig. 22.3). Likewise, skunk cabbage (*Symplocarpus foetidus*) often begins its floral development while still covered with snow. But as a result of generation of large quantities of heat, it melts the snow cover and exposes its flowers. Thus, in this case too, thermogenic respiration appears to be a metabolic event taking place rarely to help plants survive stress conditions.

22.1.2.3 Systemic Disease Resistance

SA is an important participant in systemic acquired resistance (SAR) to pathogenic infections. Initial experiments demonstrated that treatment of tobacco leaves (susceptible to TMV) with SA induces the synthesis of pathogenesis-related (PR) proteins and resistance to TMV infection. It is now well established that SA induces SAR in a variety of pathogen-infected plants. Furthermore, an increase in the endogenous SA concentration in TMV-resistant plants accompanies an enhanced expression of genes responsible for encoding PR proteins both in inoculated and un-inoculated leaves. Tobacco plants susceptible to TMV do not show an increase in SA levels or PR protein gene expression when infected with the virus, indicating that SA plays a key role in signal transduction events leading to the development of SAR (Fig. 22.4).

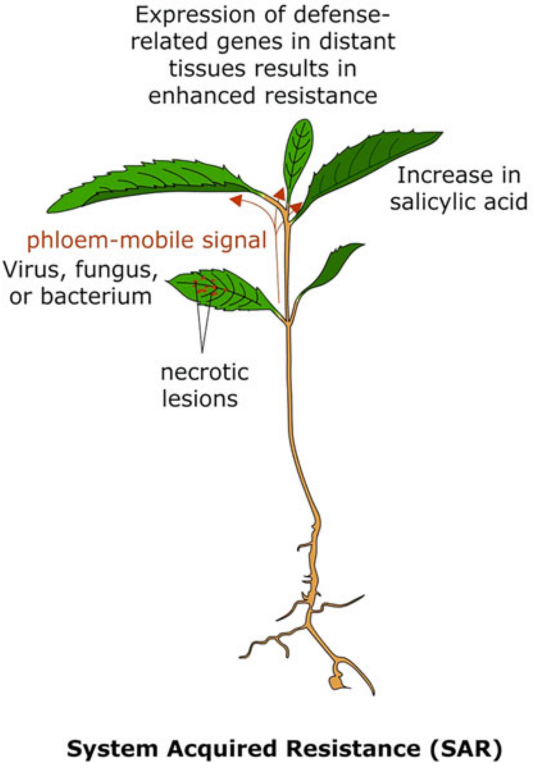


Fig. 22.4 In systemic acquired resistance (SAR), a hypersensitive response to invasion by a pathogen results in the generation of a signaling molecule that moves from the infected leaf to other parts of the plant via the phloem and triggers the expression of defense-related resistance in the remote parts of the plant. SAR requires production of the signaling molecule salicylic acid, although this is not the signal that moves in the phloem

22.1.2.4 Induction of Flowering

SA has been observed to induce flowering in duckweeds—*Lemna gibba*, *Spirodela polyrhiza*, and *Wolffia microscopica*—when these long-day plants are grown under noninductive short-day photoperiods.

22.2 Nitric Oxide

Nitric oxide (NO) is an established bioactive signaling molecule which was first described in mammals and was shown to be involved in several physiological processes, such as relaxation of smooth muscles, apoptosis, immune regulation, and neural communication. Although NO is a noxious chemical in the atmosphere, in the human body, it brings about great benefits when available in small and controlled doses. The great significance of the physiological roles of NO in mammals was recognized in 1998 with the award of Nobel Prize for Physiology and Medicine to three US scientists for their pioneering work on its role as a signaling molecule in the relaxation of smooth muscles (Box 22.2). In plants, NO has emerged as an important signaling molecule with diverse physiological functions in growth and development, starting from seed germination to flowering,

Box 22.2: 1998 Nobel Prize for Physiology and Medicine to Three US Scientists

Prof. Murad (Univ. of Texas)

Identification of NO as a signaling molecule in cells

Prof. Ignarro (UCLA School of Medicine, California)

Role of nitrates in vasodilation through release of NO

Prof. Furchgott (State Univ. of New York)

Identified nitric oxide as a biological agent for relaxation of vascular smooth muscles

fruit ripening, and also during senescence of organs. Under environmental stress conditions caused by various biotic and abiotic stress factors, different plant species and organs exhibit enhanced NO generation. In plant cells, NO can induce both harmful and beneficial effects depending on its local concentration, translocation, rate of biosynthesis, and ability to get removed as various reactive nitrogen species (RNS).

22.2.1 Physicochemical Properties of NO

NO is a highly diffusible, gaseous free radical which is soluble both in hydrophilic and hydrophobic phases. Thus, it easily migrates both in the hydrophilic regions of the cell, such as in the cytoplasm, and can also freely diffuse across the lipid phase of the membranes. In biological systems, NO has a half-life of about 3–5 s. It is a very reactive species in the presence of atmospheric oxygen and readily reacts with superoxide anions ($O_2^{-\cdot}$) resulting in the formation of peroxynitrite ions ($ONOO^-$). Peroxynitrite ions are unstable at the physiological pH and consequently react with thiol groups of proteins and polyunsaturated radicals of fatty acids, thereby damaging the cell structure. NO radical ($NO^{\cdot}$) also readily reacts with transition metals,

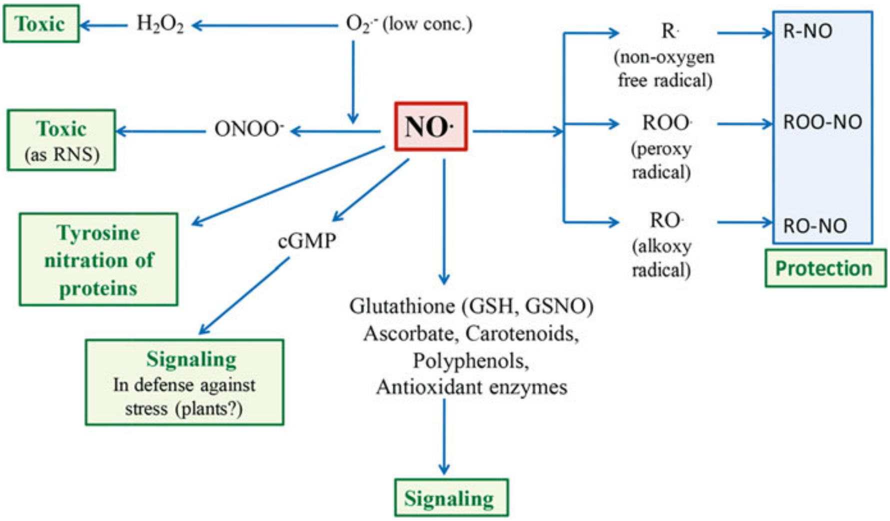


Fig. 22.5 Is nitric oxide toxic or protective for cells?

such as heme iron and iron-sulfur centers of proteins. It also leads to reversible nitrosylation of sulfhydryl groups in proteins. Thus, S-nitrosylation/denitrosylation of proteins is responsible for modulating the biological activities of these biomolecules. NO also readily complexes with Fe^{2+} and low molecular weight thiols. It is known to interact with plant hemoglobins under aerobic conditions resulting in the formation of NO_3. Thus, depending on its endogenous concentration in the cells and its ability to react with various biomolecules, NO can be toxic or protective for the cells (Fig. 22.5).

22.2.2 NO Biosynthesis in Plants

There are three probable routes of NO biosynthesis in plants: (1) L-arginine-dependent pathway, (2) nitrite-dependent pathway, and (3) nonenzymatic NO production (Fig. 22.6). Differential activity of these three probable NO biosynthesis routes is collectively responsible for NO generation in plant cells. The L-arginine-dependent pathway is prevalent in plastids and mitochondria. In terms of substrate and product formation, this pathway of NO production in plants is presumed to be catalyzed by the action of putative nitric oxide synthase (NOS) on L-arginine, resulting in the formation of L-citrulline and NO. There is, however, enough controversy about the nature of NOS activity in plants. The putative NOS in plants, though functionally similar in terms of its substrate requirement (arginine), has been found to be a structurally different protein as compared to the well-characterized NOS in animals. The AtNOS1 (putative NOS in plants) is a mitochondrial protein which bears a

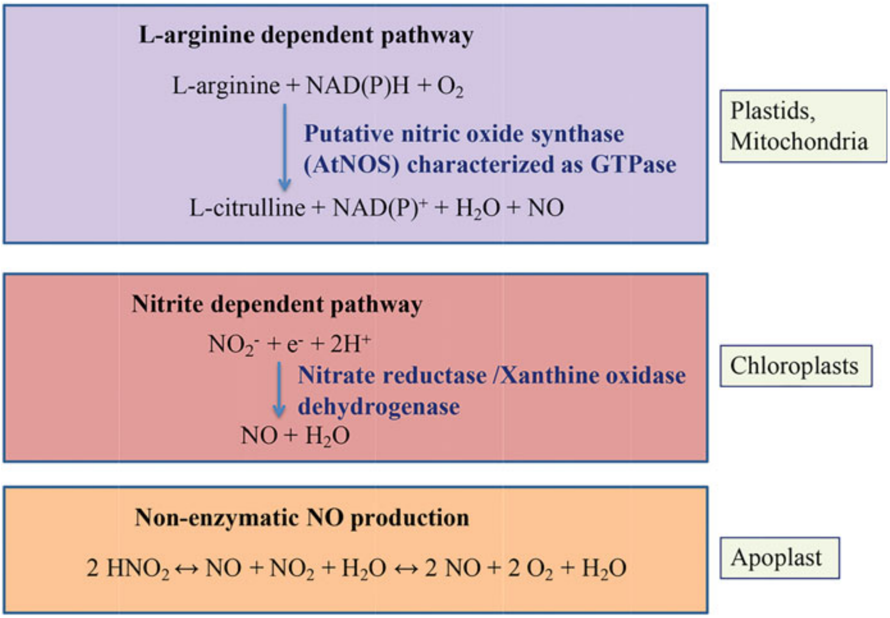


Fig. 22.6 Routes of nitric oxide production in plants

centrally positioned GTP-binding domain. NO production through nitrite-dependent pathway is evident in chloroplasts, whereas nonenzymatic NO production is evident in the apoplast. Additionally, NO is also produced in the peroxisomes and cytoplasm in plant cells (Fig. 22.6).

22.2.3 NO as a Signaling Molecule and Its Effect on Gene Expression

Like in most animals, NO exerts its signaling function through cGMP-mediated pathways leading to various post-translational modifications of proteins, such as S-nitrosylation/denitrosylation. It also brings about its effect through calcium mobilization by modulating the activity of intracellular calcium channels leading to elevation of free cytosolic calcium levels in plants. NO treatment activates protein kinases. Thus, it brings about its cascade of signaling roles through more than one biochemical routes. In plant cells exposed to varied biotic or abiotic stress conditions, NO modulates the activity of various ROS-scavenging enzymes through their tyrosine nitration, metal nitrosylation, or S-nitrosylation thereby facilitating homeostatic regulation of enhanced ROS levels generated in plant cells under stress conditions (Fig. 22.7). There is enough evidence that NO affects gene expression in plants. Additionally, protein products of S-nitrosylation or products of NO activity, for example, histidine and cysteine units of various proteins, may also directly alter

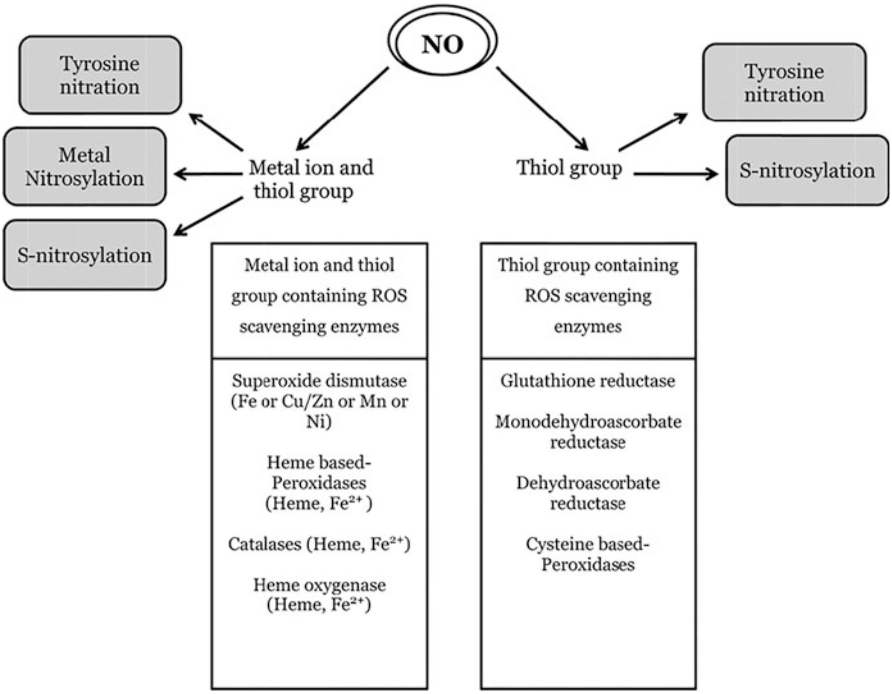


Fig. 22.7 NO modulated post-translational modifications of ROS-scavenging enzymes

their transcript profile. They may diffuse to the nucleus and modify transcription factors. Indirectly, NO may affect transcription process through the activation of signaling cascade, such as synthesis of cyclic GMP and calcium channel proteins.

22.2.4 Physiological Functions of NO in Plants

22.2.4.1 NO and Plant Growth and Development

Under normal growth conditions, plants are known to emit NO. In tomato plants, high levels of NO (40–80 pphm) have been reported to inhibit growth, whereas in lettuce low levels of NO (0–20 pphm) enhance growth. Excessive NO from the atmosphere generated through industrial pollution can have detrimental effects on photosynthesis through reversible suppression of electron transport and ATP synthesis in chloroplasts. Application of NO through NO donors inhibits hypocotyl growth, stimulates de-etiolation process, and increases chlorophyll content in potato, lettuce, and *Arabidopsis*. The positive effect of NO on chlorophyll accumulation reflects its effect on iron availability. In wild maize plants, NO treatment has in fact been shown to inhibit chlorosis induced by iron deficiency. Iron-deficient *yellow stripe* mutants of maize exhibit chlorophyll accumulation by NO application (Fig. 22.8). In pea leaves, NO donor application inhibits ethylene biosynthesis

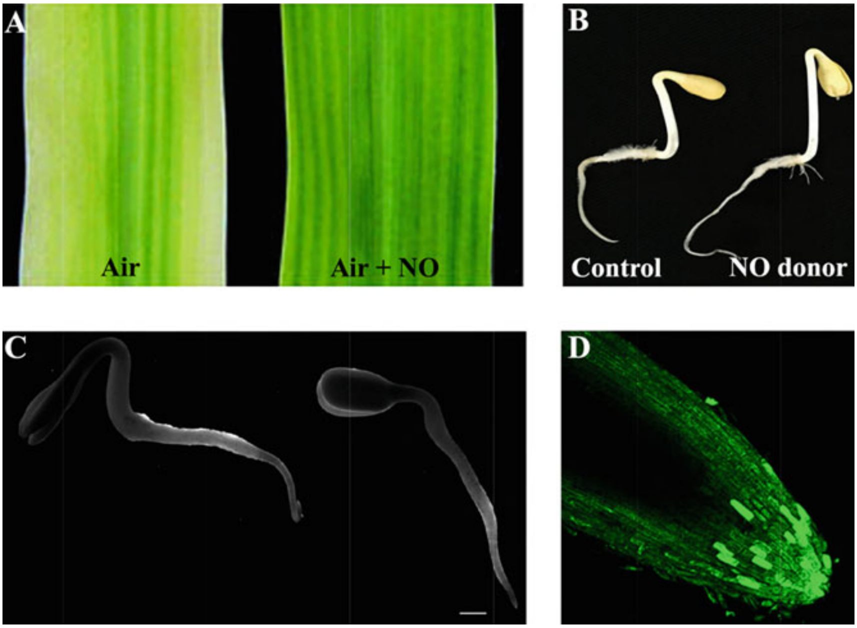


Fig. 22.8 Role of NO in plant growth and development. (**a**) Leaves of *yellow stripe* mutant of maize seedlings raised hydroponically in a nutrient solution containing 50 μM Fe(III)-EDTA and transferred to a translucent chamber with air (control) or air supplemented with 100 μL.L^{-1} gaseous NO. Note enhanced chlorophyll accumulation in the leaf in response to NO treatment. (**b**) Two-day old sunflower seedlings grown in Hoagland solution (control) or Hoagland solution containing 250 μM sodium nitroprusside (NO donor). Note enhanced extension growth of hypocotyl in response to NO application. (**c**) Endogenous NO in sunflower seedlings visualized (fluorescing sites) using MnIP-Cu (a fluorochrome to detect NO). (**d**) Root tip treated with DAF showing NO accumulation (green fluorescence) predominantly in the apical region

thereby delaying senescence. Several varieties of cut flowers exhibit enhanced longevity upon application of NO donors in solution. Thus, NO delays flower senescence as well. Application of NO also extends postharvest life of several vegetables and fruits. It can break seed dormancy and stimulate seed germination in some plants (e.g., lettuce, sunflower, tomato). Endogenous nitric oxide accumulation is also observed in the zone of elongation of primary roots indicating the role of endogenous NO in the extension growth of the roots (Fig. 22.8). Many more new roles of NO in plant growth and development are likely to be reported in the near future.

22.2.4.2 NO-Phytohormone Interaction

NO can modify phytohormone action in plants in three different ways:

1. It can chemically modify the transcription factors (TFs) and other proteins (P) which are involved in phytohormone metabolism, transport, or signaling.

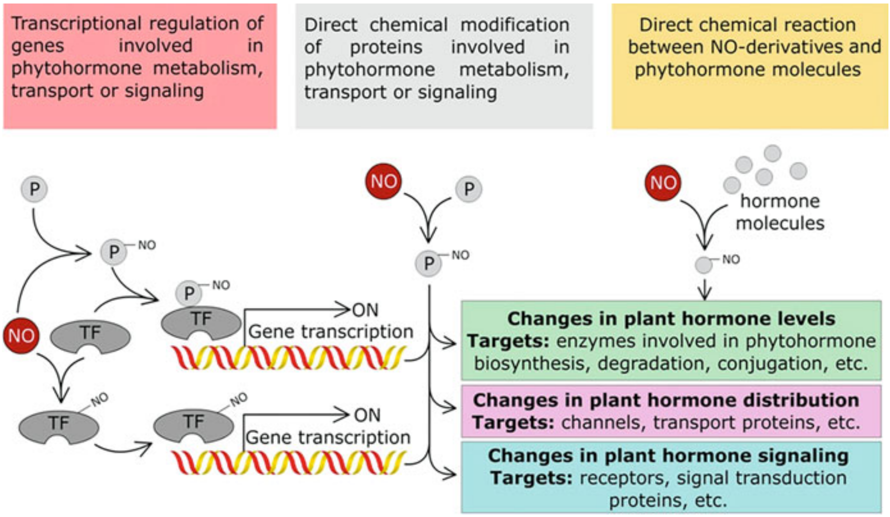


Fig. 22.9 Potential mechanisms of NO-phytohormone interaction. *TF* transcription factor, *P* protein

2. NO may modify proteins involved in the production, distribution, and signaling of plant hormones at post-translational level.
3. NO or RNS may also directly react with certain plant hormones thereby altering their biological activity (Fig. 22.9).

Synergistic action of auxin and NO has been observed during the regulation of various plant responses, such as root differentiation, gravitropic response, nodule formation, and embryogenesis. A direct influence of NO on auxin perception and signal transduction has also been suggested through S-nitrosylation of auxin receptor protein (TIR1) which is a part of E3-ubiquitin ligase complex. Both synergistic and antagonistic actions between NO and cytokinins have been reported depending on the physiological response, plant species, and experimental approach. One of the initial reports of NO-cytokinin interaction pertains to accumulation of red pigment betalain in *Amaranthus cordatus* seedlings which is positively affected both by cytokinins and NO donors. In *Arabidopsis* seedlings, zeatin treatment triggers a rapid increase in NO production in the tissue. Synergistic interaction between cytokinins and NO has also been reported to regulate leaf senescence, programmed cell death (PCD), and plant's adaptability to drought stress in terms of photosynthesis. NO and abscisic acid (ABA) have been reported to interact during water deficit and UV-B radiation stress. Thus, under such stress conditions, their interaction regulates stomatal closure and antioxidant defense responses. NO may act as a downstream element in ABA-signaling pathway since removal of NO from the tissue usually decreases or eliminates ABA-triggered responses, while the inhibition of ABA production does not affect the induction of these responses by exogenous

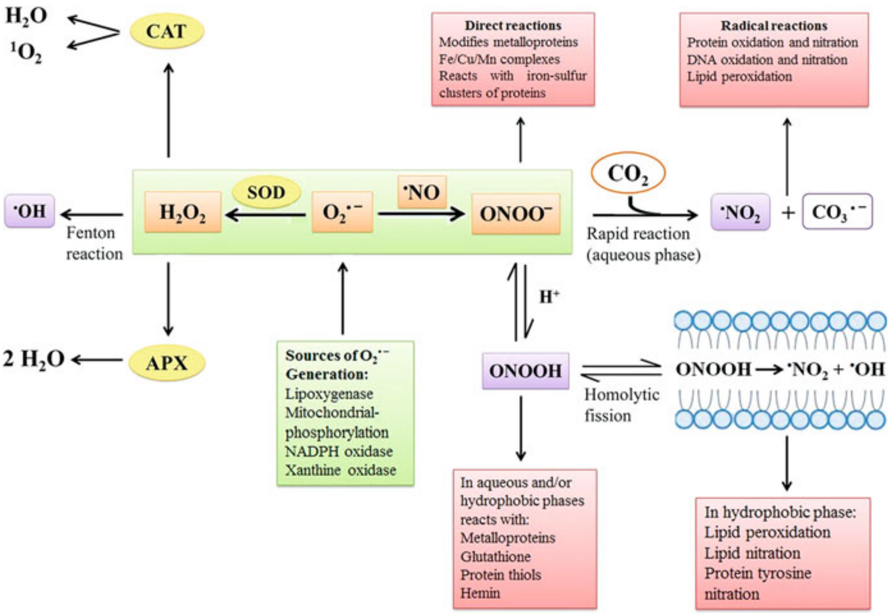
NO application. NO has also been reported to directly modulate calcium-independent outward rectifying potassium channels through post-translational modifications of these channel proteins or their regulatory moieties. NO affects ABA catabolism by regulating the activity of ABA 8′ hydroxylase, a key enzyme in ABA catabolism. It may also affect the sensitivity of plants to ABA. NO has been reported to influence several GA-modulated developmental events in plants. These include seed germination, hypocotyl elongation, primary root growth, pollen tube growth, and acquisition of photomorphogenic traits. In quite a few instances, NO and GA antagonize each other's effects on the physiological processes. It is further evident that DELLA proteins represent a key crosstalk component in GA and NO signaling interaction. DELLA proteins are a relatively small family of transcriptional regulators which play important role in diverse hormonal signals, such as those of GA, ethylene, jasmonate, and ABA. NO enhances the cellular concentration of DELLA proteins thereby bringing about its negative impact on GA signal transduction. Thus, NO-driven DELLA accumulation alters the tissue sensitivity to GA. Additionally, NO and GA may also control each other's endogenous levels. In wheat roots, exogenously supplied NO induces apical growth which is also accompanied with increase in GA_3 levels. NO may stimulate germination not only by breaking seed dormancy but also be alleviating the influence of inhibitory environmental factors on the process of germination. NO and ethylene exhibit an antagonistic relationship with each other in a number of ethylene-mediated developmental processes. Exogenously supplied NO has been reported to delay senescence of both vegetative and reproductive organs by negatively regulating a number of elements involved in ethylene production. In many climacteric fruits, NO can modulate both the transcription and activity of ACS and ACO, the key enzymes in ethylene biosynthesis. Besides interacting with "classical phytohormones," NO has also been reported to crosstalk with other plant hormones such as jasmonic acid, salicylic acid, polyamines, and brassinosteroids. During the induction of plant defense responses against biotic challenges, NO positively affects the production of both SA and JA. A rapid NO production has also been observed in plant tissues exposed to millimolar concentrations of polyamines.

22.2.4.3 NO and Abiotic Stress

Abiotic stresses, such as low and high temperature, salinity, and drought, generally lead to enhanced generation of ROS which oxidatively destroy/disturb several metabolic and signaling pathways. NO interacts with ROS in various ways, and it might serve an antioxidant function during various stresses (Fig. 22.10). Modulation of superoxide formation and inhibition of lipid peroxidation by NO demonstrate some of its potential antioxidant roles. NO can also result in nitrosative stress; thus a favorable balance of ROS/NO is important.

22.2.4.4 NO and Biotic Interactions

NO plays a key signaling role during the induction of hypersensitive response (HR). HR is a defense process activated in plants in response to pathogen attack. HR is also associated with enhanced ROS generation, PCD, and induction of signaling



Abbreviations : $O_2^{\bullet -}$ - Superoxide radical, $^\bullet NO$ - Nitric oxide, $^\bullet NO_2$ - Nitrogen dioxide, $^\bullet OH$ - Hydroxyl radical, $^1O_2$ - Singlet oxygen, $CO_3^{\bullet -}$ - Carbonate radical, $ONOO^-$ - Peroxynitrite, ONOOH - Peroxynitrous acid, H_2O_2 - Hydrogen peroxide, APX - Ascorbate peroxidase, SOD - Superoxide dismutase, CAT - Catalase

Fig. 22.10 Interactions between NO and ROS and their possible roles

pathways leading to expression of various defense-related genes. NO donors have been reported to induce cell death indicating an interaction between NO and ROS accumulation. NO treatment of soybean cotyledons triggers biosynthesis of phytoalexins which are normally produced as a response to pathogen attack. NO has also been implicated during bacteria-legume interaction accompanying nodule formation. There are reports that NO acts as a negative regulator of nitrogen fixation due to its interaction with leghemoglobin.

22.2.4.5 NO and Programmed Cell Death (PCD)

PCD is a genetically determined and metabolically directed cellular process during which cells die because of activation of intrinsic signaling processes rather than due to necrosis. In soybean cell culture NO, superoxide ratio determines the extent of PCD. If superoxide levels are greater than NO, then it results in peroxynitrite formation which slows down PCD, but if NO levels are higher, then it reacts with H_2O_2 to induce cell death. In barley aleurone layer, GA-induced PCD is delayed in presence of NO due to a loss of activity of antioxidant enzymes, namely, catalase and superoxide dismutase. PCD is correlated with altered mitochondrial function, and it seems that NO has an emerging role in this process.

22.2.5 NO Metabolism

Nitric oxide can be endogenously removed through the activity of an enzyme called GSNO reductase (GSNOR) which degrades S-nitrosoglutathione (GSNO). GSNOR thus prevents excessive formation of S-nitrosylated proteins to damaging levels by transnitrosation reactions with GSNO. Other NO-metabolizing mechanisms have also been characterized during plant-pathogen interactions. Bacterial flavohemoglobin serves a protective role in bacteria such as *Salmonella typhimurium* and *Escherichia coli* against nitrosative stress imposed within the host environment. These proteins possess NO dioxygenase activity thereby converting NO to nitrite and nitrate.

22.2.6 NO Transport

Although NO is a diffusible gas, it is possible that NO precursors or NO adducts could serve as NO reservoirs or transport forms operative over short or long distances in plant system. In animals, S-nitrosohemoglobin circulates in the blood as a source of NO for varying distances. Since nitrite is a precursor of NO in plant cells, it is possible that nitrite can serve as a mobile source of NO across the xylem stream. Additionally, GSNO can serve as another mobile source of NO in plants through its migration across phloem or xylem elements. Plants also contain hemoglobin genes, thereby indicating the possibility of hemoglobin-NO complexes as transport molecules for NO.

22.3 Indoleamines (Serotonin and Melatonin)

Two major indoleamines, serotonin (5-hydroxytryptamine) and melatonin (*N*-acetyl-5-methoxytryptamine), known to function as neurotransmitters in animals, have also been reported to play major roles in the regulation of growth and development in plants. These compounds perform varied biological functions in plants which include flowering, shoot-root morphogenesis, apoptosis, and defense mechanisms associated with stress induction. They have been detected in various plant parts (leaf, root, fruit, seed, etc.) at different concentrations, ranging from picogram to microgram. **Melatonin** (N-acetyl-5-methoxytryptamine) is a pleiotropic molecule with numerous physiological and cellular actions. It was first discovered in bovine pineal gland in 1958. It is a hormone which is secreted into the cerebrospinal fluid and blood stream by the pineal gland. It regulates various physiological processes, including sleep, body temperature, circadian rhythm, appetite, retina function, immunological system, sexual behavior, and mood. It is involved as an antioxidant in various cellular actions and possesses strong antioxidative properties. Plant tissues, in general, contain higher melatonin levels as compared to that in vertebrate blood or tissues. **Serotonin** (5-hydroxytrytamine) is produced from the same biochemical route prior to melatonin biosynthesis. Both these compounds have great antioxidant potential. **Serotonin** was first identified in mammalian systems in the 1930s and was initially called as "enteramine" since it was reported from enterochromaffin cells of the gut and was found to cause contraction of smooth muscles. Serotonin has also been established as an essential neurotransmitter in the central nervous system and is known to play significant roles in various diseases, particularly in neurological disorders, such as Parkinson's, Alzheimer's, and depression. It has been detected in a number of plant species and was first reported from the fruits of cowhage plant (*Mucuna pruriens*).

Since the 1950s, serotonin has been identified in over 90 species from 37 families. Its endogenous concentration varies significantly depending on plant species, cultivar, tissue types, and stage of maturity (Table 22.1). Like melatonin, serotonin is also a multifunctional indoleamine. Edible tissues of cranberry, corn, banana, walnut, coffee bean, and ginger are also known to have moderately high levels of serotonin. Immunolocalization analysis has shown the abundance of serotonin in the vascular parenchyma cells (xylem and companion cells) of rice plants. It helps in the maintenance of the cellular integrity during senescence which facilitates efficient

Table 22.1 Plants known to contain high concentration of serotonin and melatonin

Plant	Common name	Serotonin		Melatonin	
		Tissue	Concentration (ng.g^{-1})	Tissue	Concentration (ng.g^{-1})
Brassica rapa L.	Chinese cabbage	Edible tissue	110,900	Edible tissue	0.113 FW
Cucumis sativus L.	Cucumber	Edible tissue	23,700	Seeds	11 FW
Helianthus annuus L.	Sunflower	Vegetative tissue	9100–27,800	Seeds	29 DW
Hordeum vulgare L.	Barley	Edible tissue	44,900	Seeds	0.58 FW
Juglans regia L.	Walnut	Edible tissue	87,000	Edible tissue (nuts)	3.5 DW
Oryza sativa L.	Rice	Edible tissue	77,300	Edible tissue	1.006 FW
Solanum lycopersicum L.	Tomato	Edible tissue	221,900	Fruit	4.1–114.5 FW
Vitis vinifera L.	Grapevine	Fruit	9000–10,000	Fruit	3–18 FW
Zea mays L.	Sweet corn	Edible tissue	108,200	Edible tissue	1.37 FW

DW Dry weight, *FW* Fresh weight

recycling of nutrients from senescing to sink tissues. In banana, it has been detected in the vascular bundles of fruit wall. Protein bodies of cotyledons also show serotonin accumulation in the developing embryos of *Juglans regia*.

22.3.1 Biosynthesis of Serotonin and Melatonin

Tryptophan is the common precursor for the biosynthesis of IAA and serotonin and melatonin (Fig. 22.11). Biosynthesis of serotonin is a two-step enzymatic process. Tryptophan decarboxylase (TDC; EC 4.1.1.28) catalyzes the conversion of tryptophan to tryptamine which is followed by serotonin formation by the action of tryptamine hydroxylase (T5H). *N*-acetylserotonin, the precursor for melatonin,

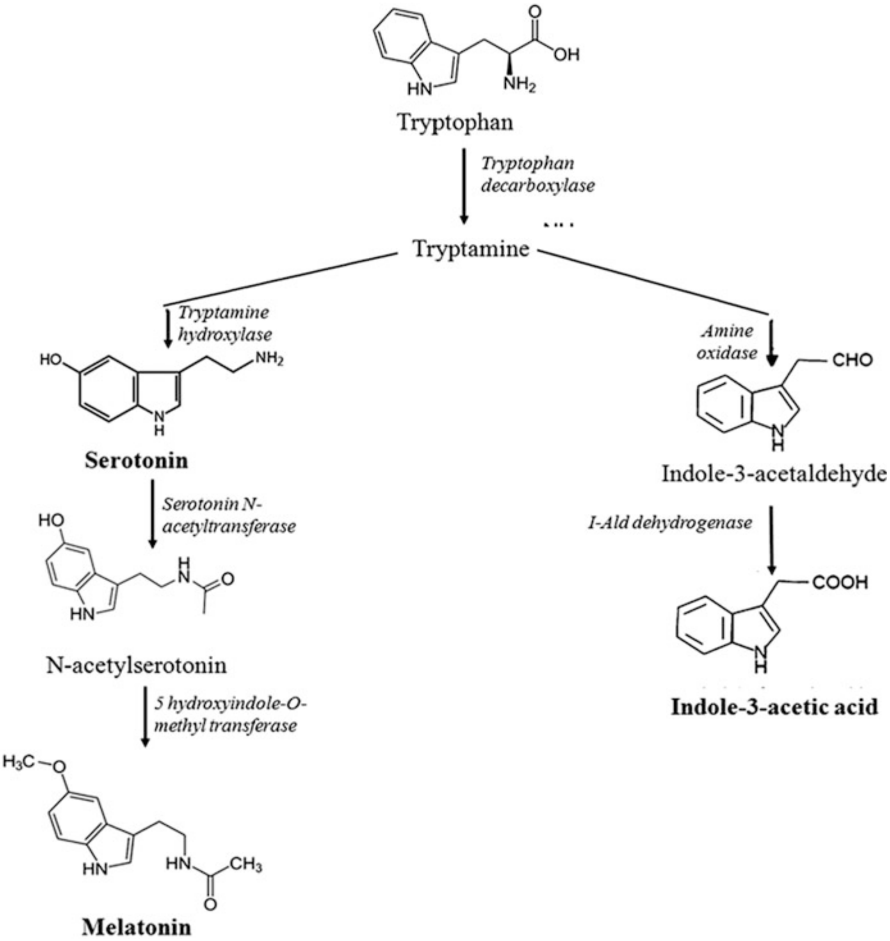


Fig. 22.11 Biosynthetic pathway for the synthesis of melatonin and serotonin from tryptophan

leads to the formation of melatonin by the conversion of serotonin further downstream in this pathway. Tryptophan decarboxylase (TDC), with a high K_m (690 μM) for tryptophan (its substrate), is the rate-limiting key regulatory enzyme of this pathway. The major sites for serotonin and auxin biosynthesis, i.e., root tips and stele, exhibit tissue-specific differential expression of tryptophan biosynthesis genes in rice.

22.3.2 Melatonin: Structure and Activity Relationship

An electron-rich indole moiety together with two side chains, a 5-methoxy group and a 3-amide group, constitutes the melatonin molecule (Fig. 22.12). The high resonance stability, electroreactivity, and low activation energy barriers make melatonin a potent free radical scavenger. The side chains also have a significant contribution in the antioxidative properties of the molecule. Carbonyl moiety present in the C3 amide side chain (in the functional group (N–C=O)) plays a major role in scavenging a number of reactive oxygen species. One molecule of melatonin can scavenge up to four or more ROS. Various mechanisms are involved in the interaction of melatonin with free radicals, such as addition reaction, nitrosation, substitution, hydrogen donation from nitrogen atom, and melatoninyl cation radical formation due to electron donation. Melatonin can also repair oxidized molecules

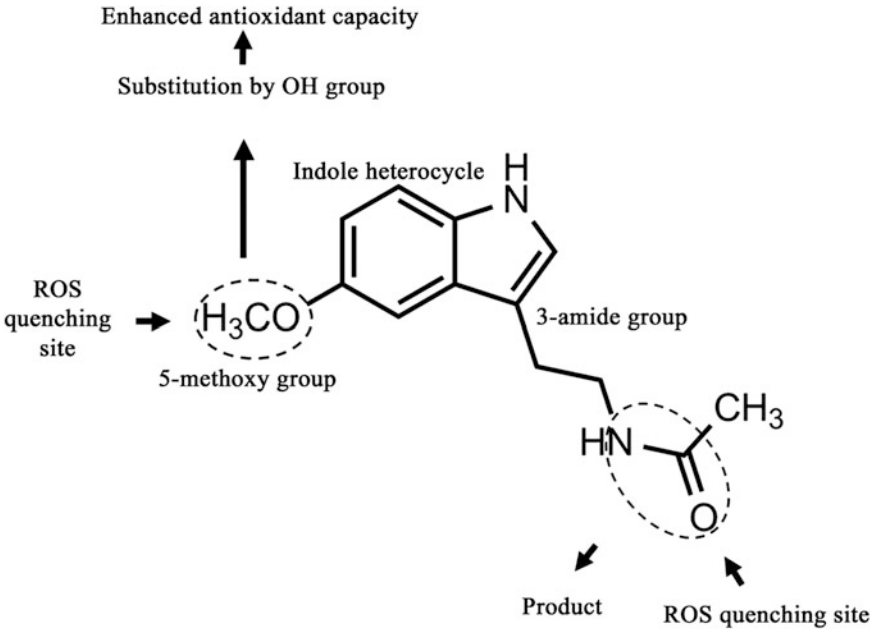


Fig. 22.12 Structure of melatonin showing the reactive groups on the indole heterocycle and two side chains

and thus shows damage repairing abilities. Melatonin exhibits several functional similarities to serotonin and auxin. It is a potential antioxidant and acts as a photoregulatory molecule in plants. Melatonin possesses high affinity for calcium-dependent protein kinase and calmodulin and thus plays a role in the regulation of microtubule polymerization and auxin activity in plants.

22.3.3 Roles of Serotonin and Melatonin

22.3.3.1 Morphogenesis

Serotonin plays a crucial role in root development and shoot morphogenesis. It modulates auxin-induced primary root growth and lateral root branching. It is involved in stimulation of pollen germination, growth regulation, plant morphogenesis, flowering, and ion permeability, and it has been detected in the exudates of root xylem sap. It also stimulates germination of radish seeds and acts as a growth regulator. In *Arabidopsis thaliana*, exogenously applied serotonin (10–160 μM) promotes lateral root development. The endogenous levels of serotonin and melatonin may also play a crucial role in in vitro plant morphogenesis. Indoleamines also regulate secondary metabolite levels in plants. Exogenous application of both these indoleamines also augments caffeine and polyamine levels in in vitro callus cultures of *Coffea canephora*. The influence of serotonin and melatonin has also been reported on somatic embryogenesis in *C. canephora*. SER stimulates the turnover of phosphoinositide (PI) which mimics the effect of red light and enhances the transcript levels of nitrate reductase and releases second messengers in maize.

22.3.3.2 Plant Defense Responses

Serotonin is known to accumulate in the sting nettle (*Urtica dioica*) and in trichomes in the pods of *Mucuna pruriens*. Pathogenic infection also leads to synthesis of serotonin in rice leaves which then accumulates in the cell walls, thereby strengthening it. Rice plants accumulate tryptamine, serotonin and their phenolic acid coupled amides in response to fungal pathogen infection. All these compounds prevent pathogen invasion by forming a physical barrier. Serotonin plays an important role as a potential antioxidant by quenching ROS, and it exhibits in vitro antioxidative properties (Fig. 22.13). Serotonin has the highest antioxidant activity among tryptamine, tryptophan, and related derivatives. It helps in maintaining the reducing potential of cells due to its antioxidative properties by detoxifying the cells (relieves the accumulated toxic tryptamine). It delays senescence by efficient scavenging of ROS and protects young reproductive tissues from different environmental stresses in *Datura metel*. Increased level of serotonin has been reported in flowers of *Datura* undergoing cold stress. Some foods, such as pineapple, nuts, banana, milk, and plum, are rich in this indoleamine, and tryptophan may elevate mood by increasing serotonin levels in the brain.

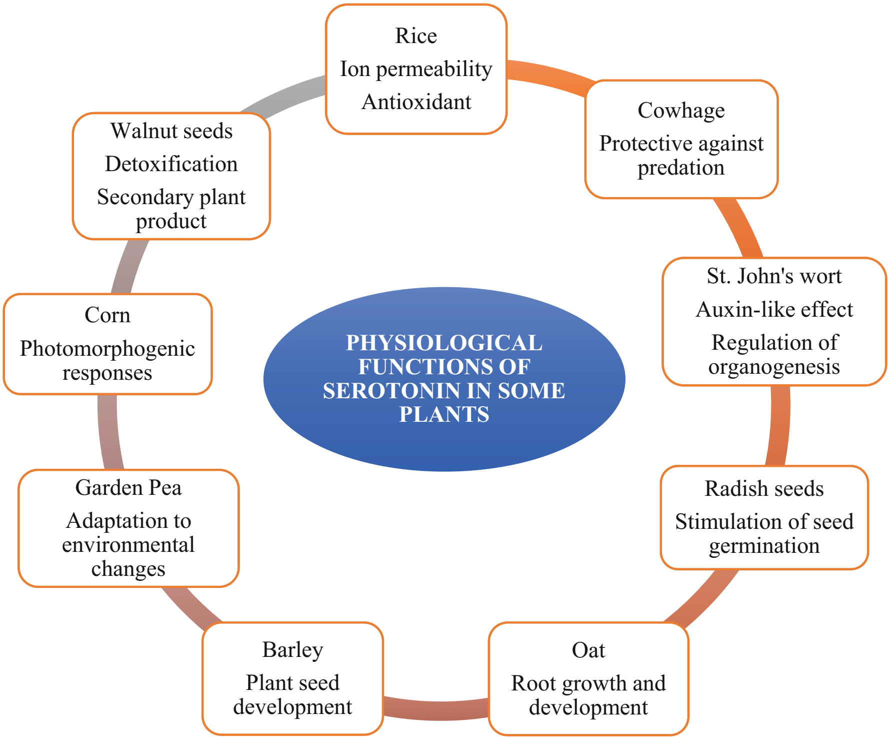


Fig. 22.13 Physiological functions of serotonin in some plants

22.3.3.3 Gene Expression of Auxin Responsive Genes

Serotonin regulates gene expression associated with auxin response pathways. In plant tissues, polarity, growth, and gravitropism are regulated by auxin transport and its spatiotemporal distribution. Serotonin accumulation is likely to increase due to the abiotic stress-induced inhibition of auxin biosynthesis in plant tissues. NaCl stress leads to enhanced distribution of serotonin in the vascular cells of primary root and sunflower seedlings. At the sites of primary roots, adventitious roots, and lateral root primordia, serotonin has been reported to elicit tissue-specific inhibitory effects on various auxin responsive genes, and, therefore, it modulates root growth partially independent of auxin activity. Inhibition of lateral root primordia development and primary root length has been reported under salt stress due to inhibition of auxin accumulation in the emerging lateral root primordial in *Arabidopsis*. Under normal conditions, plant tissues have lower serotonin levels, but stress signals can lead to enhanced serotonin accumulation and, therefore, inhibit synthesis of auxin and impair its functions. These two indoleamines have been proposed to show auxin-like action and thus affect shoot and root growth in in vitro conditions. Exogenously applied melatonin and serotonin also alter root development in seedlings. Enhanced primary root elongation and lateral root branching have also been reported in sunflower seedlings due to supplementation of melatonin. In *Brassica juncea* and *Lupinus albus*, role of exogenously provided melatonin in the regeneration of lateral root has been suggested.

22.3.3.4 Modulation of Responses Due to Abiotic and Biotic Stress

Serotonin and melatonin prevent oxidative damage by regulating cellular ROS levels and serve as line of defense against stress. Involvement of serotonin has been reported in the senescence of leaves in rice due to overexpression of enzyme tryptophan decarboxylase (TDC). Significantly high melatonin content has been reported in mature seeds which act as a free radical scavenger during seedling growth and seed germination in sunflower and in various other edible seeds. Variable ozone sensitivity, depending on the melatonin content, has been reported in the leaves of *Nicotiana tabaccum* and *Lycopersicon esculentum*. Enhanced melatonin formation in the dark is associated with the protection of photosynthetic pigments from ROS (by quenching) produced during photosynthesis. Melatonin has a protective role against leaf senescence. It helps in increasing the photosynthetic efficiency in plants. Under light and dark conditions, melatonin increases the efficiency of photosystem II in apple trees by mitigating the inhibitory effect of drought stress on photosynthesis and, therefore, allows plant leaves to maintain a higher capacity for stomatal conductance and CO_2 assimilation. Exogenously applied melatonin increases photosynthetic rate and activities of various ROS-scavenging enzymes and reduces chlorophyll degradation. Melatonin reduces oxidative damage by decreasing the ROS burst. It leads to increase in the activity of antioxidants such as SOD, peroxidase, catalase, and glutathione reductase under different stresses (Fig. 22.14).

22.3.4 NO-Melatonin CrossTalk

It has been established through investigations on animal systems that under nitrosative stress melatonin acts as a mediator of RNS and ROS crosstalk. It interacts with nitrogen-centered radicals to form nitrosated products, such as N-nitrosomelatonin (formed due to the reaction between NO and melatonin). It also maintains NO levels by the inhibition of activity of nitric oxide synthase. Melatonin can scavenge peroxynitrite anions ($ONOO^-$) which are formed due to interaction of $O_2^{\cdot -}$ and NO or peroxynitrous acid by interacting with the indole moiety present in melatonin. This, however, needs to be verified in plant cells.

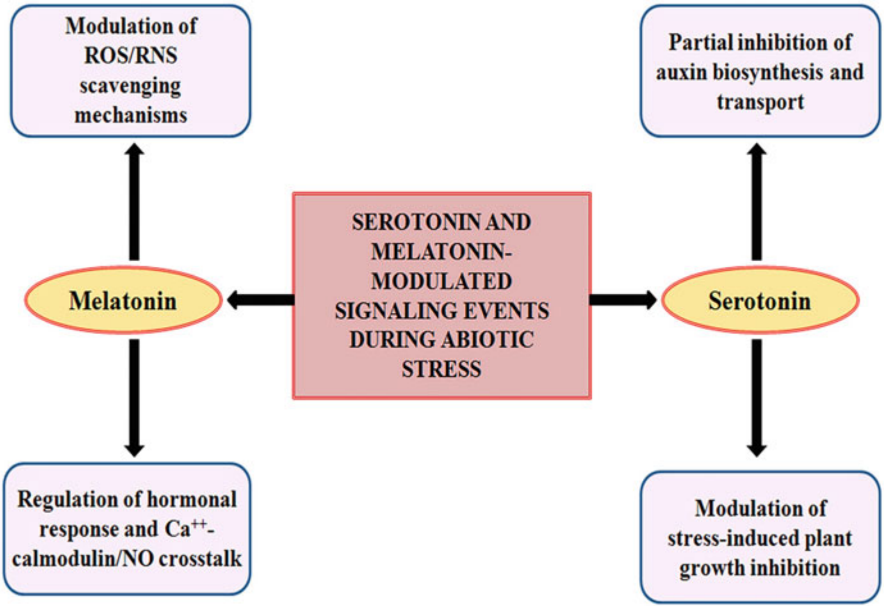


Fig. 22.14 Scheme depicting the signaling events during serotonin and melatonin-modulated abiotic stress

22.4 Strigolactones

Strigolactones (SLs) are carotenoid derivatives which were first identified as germination stimulants for the seeds of root parasitic weeds such as *Striga*, *Orobanche*, and *Phelipanche* spp. A variety of SLs differing in the side group associations on the four-ringed basic structure have been identified from a number of plants.

To date, more than 15 SLs have been characterized from various plant spp. (Fig. 22.15). Some of the common naturally occurring SLs are strigol, orobanchol, and sorgomol. GR24 is an extensively used synthetic SL. SL biosynthesis occurs in plastids, starting from β-carotene and using three sequentially acting enzymes, D27, β-carotene isomerase, and CCD7 and CCD8, which are carotenoid cleavage dioxygenases (Fig. 22.16). The reaction product is an apocarotenoid (carlactone) which can move between cells and undergo two oxygenation steps to produce **5-deoxystrigol**. These oxygenation steps are catalyzed by a cytosolic enzyme—P450. The common precursor for the major natural SLs is 5-deoxystrigol. Through the process of hydroxylation, decarboxylation, oxidation and dehydration, various SLs are finally synthesized in the cytosol. The ABC ring of 5-deoxystrigol (basic moiety) is derived from a C15-carotenoid cleavage product. The enzyme D27 isomerizes trans-β-carotene into cis-β-carotene (C40). Then CCD7 (carotenoid cleavage dioxygenase 7) cleaves all cis-β-carotene into cis-β-apo-10-carotenal

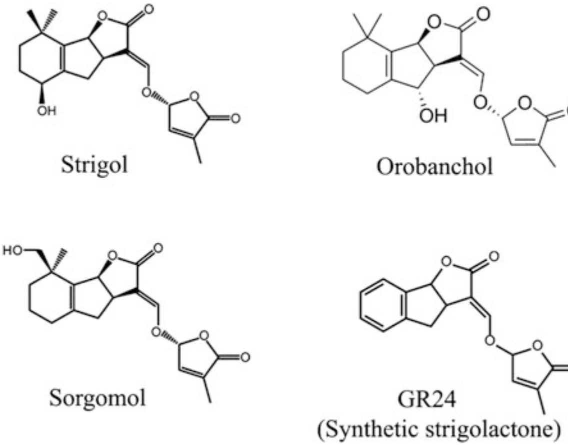


Fig. 22.15 Commonly known natural and synthetic strigolactones

(C27) and β-ionone (C13). Subsequently, CCD8 cleaves C27 molecule to the C18 ketone (carlactone), which moves into the cytosol and cyclizes to form various strigolactones.

22.4.1 Physiological Roles of Strigolactones

22.4.1.1 Shoot Architecture

SLs appear to act in coordination with auxin to modulate apical dominance. Mutants of *Arabidopsis*, which are either defective in SL biosynthesis [*max1* (*more axillary growth1*), *max3*, or *max4*] or signaling (*max2*), exhibit enhanced branching without decapitation. Grafting the shoots of SL biosynthetic mutants (*max1*, *max3*, *and max4*) to wild-type roots restores apical dominance, indicating the movement of SLs from root to the shoot. Bud growth repressing SL normally comes from the shoot itself. SLs promote the development of interfascicular cambium. Under low phosphate conditions, SLs repress shoot branching. They, however, inhibit shoot branching in the presence of auxin source. It is now evident that SLs promote or inhibit shoot branching, depending on the auxin status of plants. SL signaling is believed to trigger PIN1 depletion from the xylem parenchyma cells. Accordingly, a reduction in auxin level enables the growth of lateral buds.

22.4.1.2 Root Growth

The expression of SLs biosynthetic genes is primarily evident in the vascular parenchyma cells of the root. In general, SL concentrations are higher in roots compared to other plant parts. The activity of CCD8 is upregulated in the primary root and cortical tissue of root apex upon treatment with 1-naphthaleneacetic acid (NPA) an auxin efflux blocker. SL-deficient or SL-insensitive mutant of *Arabidopsis* exhibits shorter **primary root** than those of wild-type plant. The root length is normalized in SL-deficient mutants by exogenous GR24 treatment but not in

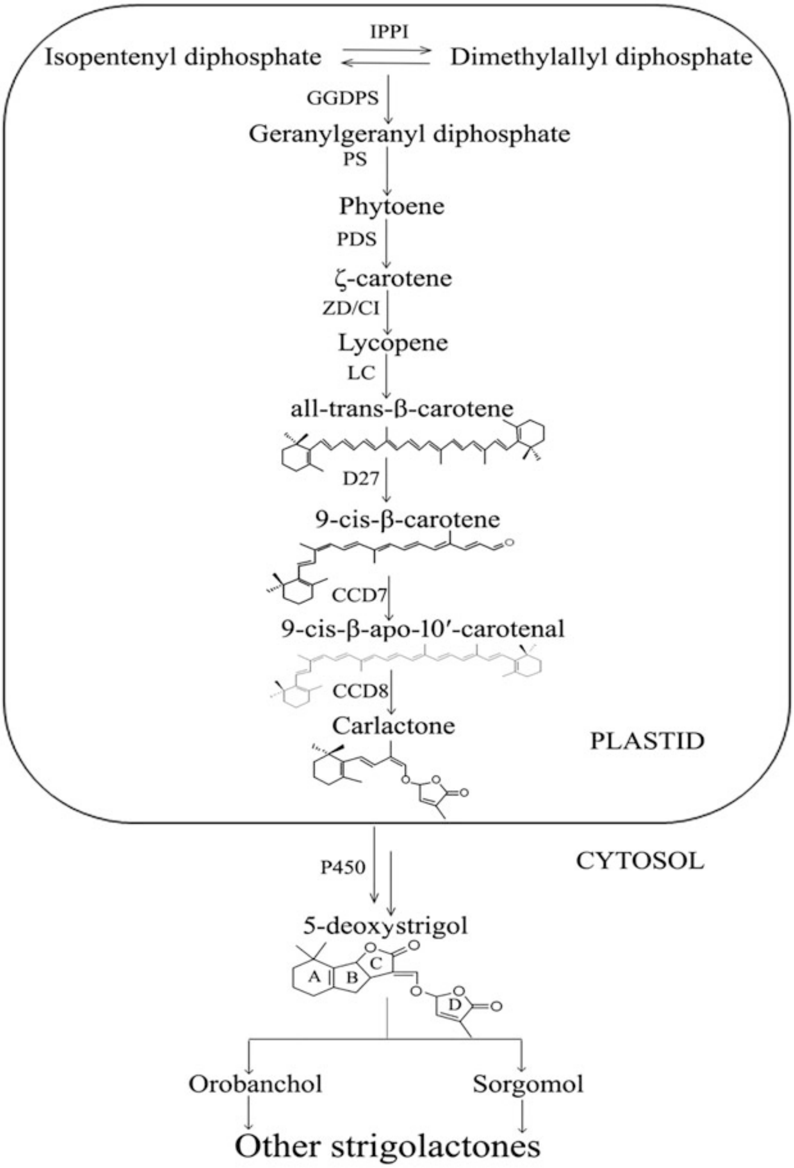


Fig. 22.16 Biosynthesis of strigolactone

SL-insensitive mutant. Furthermore, auxin-induced inhibition of primary root elongation in tomato plants can be reversed by GR24 application. Availability of phosphate in soil modulates the development of lateral roots (LRs) in response to SLs. Thus, high phosphate conditions negatively control **lateral root formation**.

Under low phosphate availability, a treatment with GR24 enhances LR formation. Thus, it has been further observed that GR24 affects LR formation but not its elongation. SLs have also been reported to suppress **adventitious root** (AR) formation in *Arabidopsis* and pea. Thus, SL-deficient and response mutants of both these plants exhibit enhanced adventitious rooting response. It has been demonstrated that SLs negatively regulate auxin accumulation in the pericycle, thereby reducing AR initiation. Treatment with GR24 has been observed to increase root hair length in both wild-type and SL-deficient mutant in *Arabidopsis*. The impact of SL on this response varies according to phosphate availability in the external environment, thereby, indicating the influence of SLs on root development.

22.4.2 SL Crosstalk with Auxin, Ethylene, and Cytokinins

Strigolactones play a significant role in shaping root architecture, whereby auxin-SL crosstalk has been observed in SL-mediated responses of primary root elongation, lateral root formation, and adventitious root (AR) initiation. Whereas GR24 (a synthetic strigolactone) inhibits LR and AR formation, the effect of SL biosynthesis inhibitor (fluridone) is just the opposite (root proliferation). Naphthylphthalamic acid (NPA) leads to LR proliferation but completely inhibits AR development. The diffusive distribution of PIN1 in the provascular cells in the differentiating zone of the roots in response to GR24, fluridone, or NPA treatments further indicates the involvement of localized auxin accumulation in LR development responses. Inhibition of LR formation by GR24 treatment coincides with inhibition of ACC synthase activity. Differences in the spatial distribution of NO in the primary and lateral roots further highlight the involvement of NO in SL-modulated root morphogenesis in sunflower seedlings. Thus, a negative modulation of SL biosynthesis through modulation of CCD activity by endogenous nitric oxide during SL-modulated LR development is evident (Fig. 22.17). SLs are synthesized primarily in the root, and they can be transported acropetally to the shoot in the xylem. SLs have been reported to get transported from the sites of their synthesis using plasma membrane-associated ABC transporters, and they move in the xylem from the root to shoot. SLs and auxins primarily interact in the shoot. In the root tissue system, auxins have been shown to induce SL synthesis. It is, thus, apparent that SLs are modulators of auxin flux and reduce auxin import to the root leading to inhibition of LR formation. This is further evident from the distorted expression of PIN-auxin efflux carrier in tomato and *Arabidopsis* upon GR24 treatment.

SLs can induce ethylene biosynthesis in the seeds of parasitic plant—*Striga*—leading to seed germination. Ethylene biosynthesis inhibitor 2-aminoethoxyvinylglycine (AVG) abolishes the effect of SL on root hair elongation. GR24 elevates the transcription of *At-ACS2*, which encodes one of the rate-limiting enzymes in ethylene biosynthesis. It is evident from the investigations undertaken so far that SLs induce ethylene biosynthesis, both SL and ethylene regulate root hair elongation through the same pathway, and ethylene may be epistatic to SLs in this hormonal pathway. According to a simplified model, antagonistic interaction exists between cytokinins and SLs.

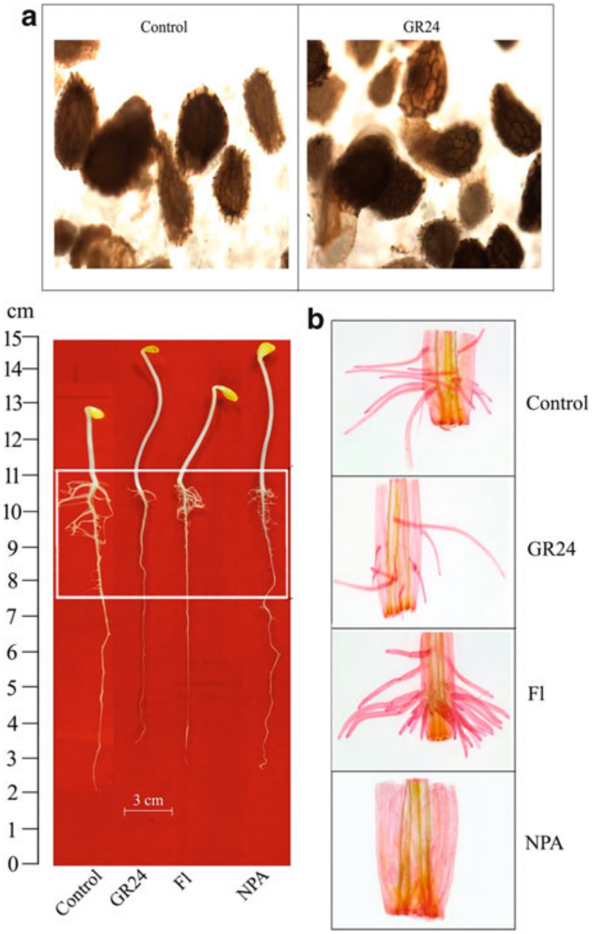


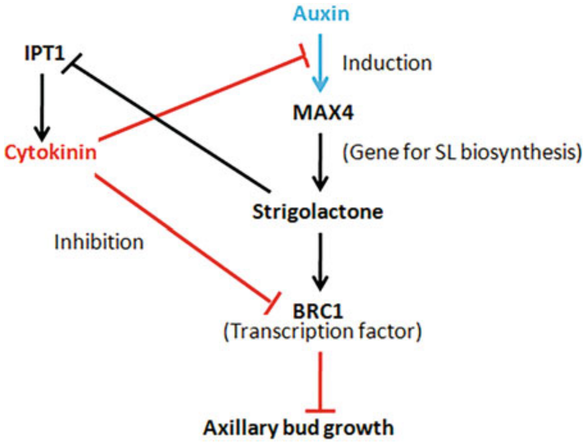
Fig. 22.17 (**a**) Seed germination in *Orobanche* induced by application of a commercial strigolactone (GR24). (**b**) Strigolactone (GR24) inhibits lateral root extension, fluoridone (Fl), an inhibitor of SL biosynthesis does the opposite, i.e., LR proliferation, and NPA (auxin efflux blocker) completely suppresses LR induction in sunflower seedlings

Auxins maintain apical dominance by stimulating SL synthesis via the *MAX4* gene. SLs then activate *BRC1*, a transcription factor known to suppress axillary bud growth. Additionally, SLs also inhibit cytokinin biosynthesis by negatively regulating the expression of *IPT* genes which otherwise would prevent BRC1 production (Fig. 22.18).

22.4.3 Signaling Mechanism for Strigolactone Action

The probable signaling mechanism for SL actions involves targeting of proteins by degradation through ubiquitination (Fig. 22.19). SLs are perceived by a protein complex which contains an α-/β-hydrolase protein and F-box protein D14 and MAX2, respectively. D14 binds and reacts with SL, thereby changing its (D14) confirmation to the active form—D14*. D14* interacts with the F-box protein

Fig. 22.18 Probable crosstalk among auxin, cytokinin, and strigolactone and their influence on axillary bud growth



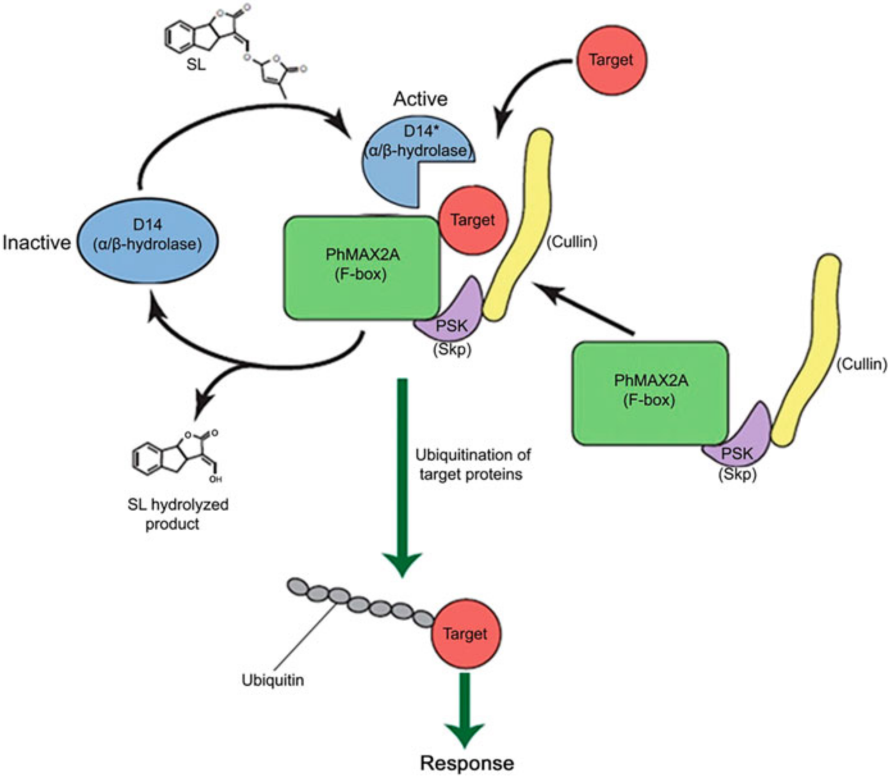


Fig. 22.19 A model for the reception and the signal transduction of strigolactone

MAX2 and other partners of the SCF^{MAX2} ubiquitin ligase complex. Target protein (s) are subsequently recognized by the D14*-SCF^{MAX2} complex and are then ubiquitinated. D14* hydrolyzes strigolactones and releases the products of hydrolysis. D14 separates from the SCF^{MAX2} complex and returns to its original confirmation, allowing it to respond to fresh SL signal.

22.5 Polyamines

Polyamines collectively comprise one of the most efficient class of compatible solutes found ubiquitously among all organisms, both prokaryotes and eukaryotes, and are also finding essential roles in various growth and developmental processes. These are low molecular weight nitrogenous compounds which exist in positively charged state at physiological pH, a property that allows them to bind to all biological molecules bearing negative charge. So, polyamines have the ability to bind to and stabilize the anionic macro- and micromolecules within the cell, such as phospholipids in membranes, nucleic acids, proteins, and phenolic acids. The first account of polyamines dates back to 1678, when the presence of a crystalline substance in human semen was reported by Anton van Leeuwenhoek, and was named “spermine.” It was found to be phosphate derivative of an organic compound. Chemical characterization of spermine further revealed that it is an amine and subsequently, isolation of other polyamines, like spermidine and putrescine, was also reported. Polyamines are believed to be involved in diverse fundamental cellular processes, such as cell division and elongation, chromatin organization, DNA replication and transcription, protein synthesis, signaling, and regulation of ion channels. They are also involved in modulating various growth- and development-related processes, including regulation of organogenesis, embryogenesis, development of flowers and fruits, and senescence. They have also been implicated to play roles in governing defense responses against abiotic and biotic stresses.

22.5.1 Most Common Polyamines in Plants and Their Distribution

A diverse array of polyamines occurs in plants which can be categorized into aliphatic and aromatic types depending on the basic chemical structure they possess. However, the most commonly occurring polyamines are the aliphatic diamine putrescine, the triamine spermidine, and the tetramine spermine, with cadaverine being present in considerable levels in some plant species. Besides these, several uncommon polyamines with a very limited distribution have also been reported in plants (Table 22.2). These include norspermidine, norspermine, thermospermine, and longer penta- and hexaamines. Polyamines are localized in almost all compartments of the cell where they perform their regulatory roles in diverse cellular events. The relative abundance of polyamines may vary between micro- to millimolar range, majorly depending upon the species and the stage of development.

Table 22.2 Some common and uncommon polyamines existing in plants

Types of polyamines	Structure
Common polyamines	
Putrescine	$NH_2(CH_2)_4NH_2$
Cadaverine	$NH_2(CH_2)_5NH_2$
Spermidine	$NH_2(CH_2)_3NH(CH_2)_4NH_2$
Spermine	$NH_2(CH_2)_3NH(CH_2)_4NH(CH_2)_3NH_2$
Uncommon polyamines	
1,3-Diaminopropane	$NH_2(CH_2)_3NH_2$
Homospermidine	$NH_2(CH_2)_4NH(CH_2)_4NH_2$
Norspermidine	$NH_2(CH_2)_3NH(CH_2)_3NH_2$
Homospermine	$NH_2(CH_2)_3NH(CH_2)_4NH(CH_2)_4NH_2$
Norspermine	$NH_2(CH_2)_3NH(CH_2)_3NH(CH_2)_3NH_2$
Thermospermine	$NH_2(CH_2)_3NH(CH_2)_3NH(CH_2)_4NH_2$
Caldopentamine	$NH_2(CH_2)_3NH(CH_2)_3NH(CH_2)_3NH(CH_2)_3NH_2$
Caldohexamine	$NH_2(CH_2)_3NH(CH_2)_3NH(CH_2)_3NH(CH_2)_3NH(CH_2)_3NH_2$

However, they are known to exert their biological effects in millimolar range. Additionally, they can occur in soluble fractions in free (cytoplasmic) and/or conjugated (attached to organic acids like hydroxycinnamic acids) forms as well as insoluble fractions bound to the macromolecules, like phospholipids in the plasma membrane, nucleic acids, proteins, and cell wall polysaccharides.

Putrescine and cadaverine are both diamines and chemically very similar, having a primary amine group on either end of a short hydrocarbon chain. The difference in their structure is due to their different precursors—putrescine is produced from arginine by removal of carboxylic acid group, whereas cadaverine is derived from lysine. Both of these diamines are foul-smelling and are responsible for the foul odor associated with the process of putrefaction (decaying of dead tissue). They also contribute to the distinctive odor of semen and urine. Spermidine and spermine belong to higher amines which are synthesized from putrescine by addition of extra chains of three carbons, each ending with another amine group, to one and both ends of putrescine, respectively.

22.5.2 Polyamine Homeostasis

The endogenous levels of polyamines are very closely regulated to maintain homeostasis and achieve desired requirements and functions during various stages of growth. This homeostasis is extremely crucial since both the depletion and excess of polyamines may be deleterious to cells. Several processes together help in maintenance of appropriate levels of polyamines including their synthesis, uptake, degradation, compartmentalization, conjugation, and transport.

22.5.3 Biosynthesis of Polyamines

Putrescine is synthesized from arginine via two different biosynthetic pathways (Fig. 22.20). In one pathway, arginine is converted in three subsequent reactions into first agmatine, followed by *N*-carbamoylputrescine, and finally into putrescine via the action of arginine decarboxylase (ADC), agmatine iminohydrolase (AIH), and *N*-carbamoylputrescine aminohydrolase (CPA), respectively. In the alternate pathway, arginine is first converted into ornithine, which in turn is converted into putrescine in a reaction catalyzed by ornithine decarboxylase (ODC). Both the pathways of putrescine synthesis exist in plants, while in animals, putrescine is synthesized exclusively via the ODC pathway. Spermidine and spermine synthesis requires putrescine as well as decarboxylated *S*-adenosylmethionine as precursor molecules. Decarboxylated *S*-adenosylmethionine serves as the aminopropyl group donor for higher polyamine synthesis and is synthesized by decarboxylation of *S*-adenosylmethionine by the action of *S*-adenosylmethionine decarboxylase. Spermidine and spermine are synthesized from putrescine in reactions catalyzed by two different aminopropyltransferases, i.e., spermidine synthase (SPDS) and spermine synthase (SPMS). Spermidine synthase uses putrescine as the basic moiety and transfers the aminopropyl group from a decarboxylated *S*-adenosylmethionine molecule to it to produce spermidine. Spermidine is subsequently converted to spermine by spermine synthase by utilizing another decarboxylated *S*-adenosylmethionine molecule.

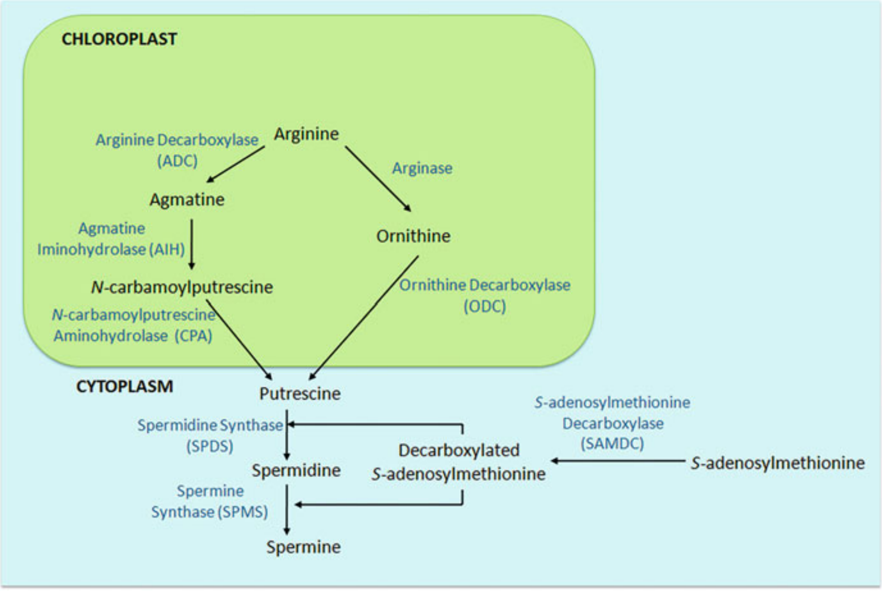


Fig. 22.20 Biosynthetic pathways for polyamines

22.5.4 Catabolism of Polyamines

Degradation of polyamines is mediated by diamine and polyamine oxidases (Fig. 22.21). The diamine oxidases preferentially work on diamines, such as putrescine and cadaverine, but can also act on spermidine and spermine, though with low affinity. Putrescine is oxidized to produce pyrroline, along with H_2O_2 and ammonia as side products. Polyamine oxidases carry out the oxidation of higher amines, such as spermidine and spermine, producing pyrroline, 1,3-diaminopropane and H_2O_2 from spermidine and 1-(3-aminopropyl)-pyrroline, 1,3-diaminopropane, and H_2O_2 from spermine. Pyrroline and 1,3-diaminopropane are further converted to succinate and β-alanine, respectively. Apart from being involved in oxidation of polyamines, polyamine oxidases are also involved in back-conversion of spermine to spermidine and spermidine to putrescine, with the release of pyrroline and H_2O_2. In such back-conversions, spermidine and spermine are first transformed by spermidine/spermine *N*-acetyl transferase (SSAT), by utilizing acetyl-CoA, into their acetyl derivatives, *N*-acetylspermidine and *N*-acetylspermine, respectively, before being acted upon by polyamine oxidases. Another enzyme, spermine oxidase (SMO), also exists which is responsible for conversion of spermine to its acetyl derivative.

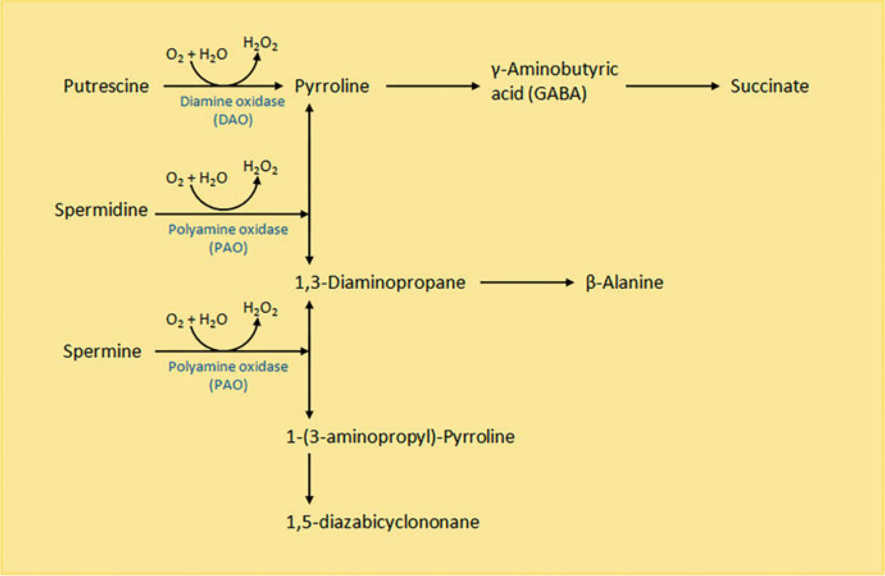


Fig. 22.21 Catabolism of polyamines

22.5.5 Functions of Polyamines

Polyamines play diverse roles throughout the life span of plants regulating various processes such as germination organogenesis, embryogenesis, flower initiation, fruit development and ripening, and senescence (Fig. 22.22). They have also been shown to play crucial roles in acclimation to both abiotic and biotic stresses. Accumulation of polyamines during various stresses has been reported to serve as an important adaptive measure to improve resistance.

22.5.6 Ionic Interactions

The growth promoting activities of polyamines are majorly accounted for by their roles in regulation of basic cellular events, like nucleic acid synthesis and protein synthesis. They bind to and modulate conformation of DNA and RNA, thereby facilitating the processes of replication, transcription, and RNA processing. They stabilize the negative charge associated with phosphate groups in nucleic acids and help in condensation of chromatin. They also interact with proteins via ionic interactions or through covalent conjugation at specific glutamyl residues (via the activity of enzyme transglutaminase). Binding of polyamines regulates the 3D

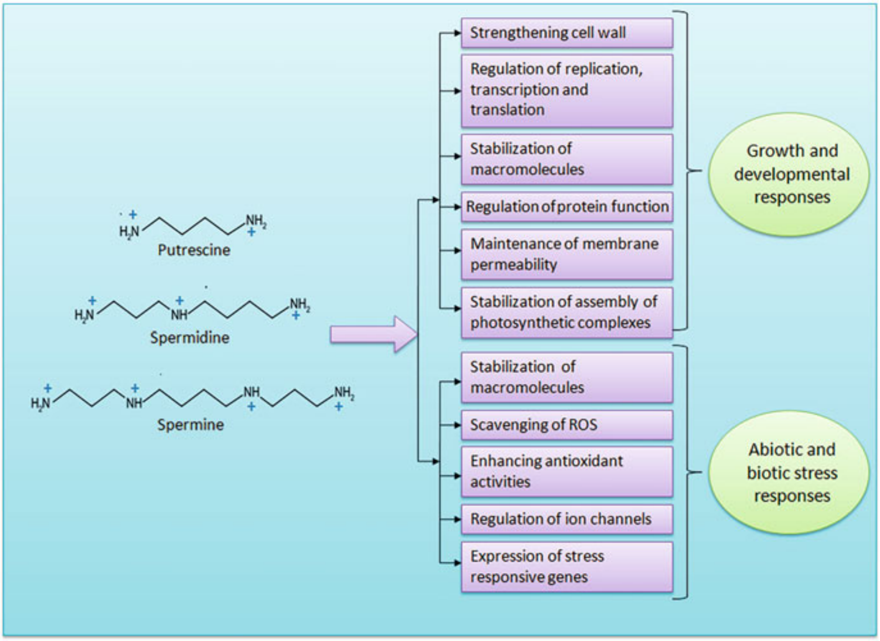


Fig. 22.22 Some regulatory roles of polyamines in plant growth and development and under abiotic and biotic stresses

conformation of proteins and also their functions. They interact with negatively charged membrane lipids and strengthen their binding with other lipids and membrane-associated proteins and, therefore, increase the stability of the membrane. In the cell wall, they bind to polysaccharides, pectin, and phenolic acids in lignin to enhance the strength of primary cell wall as well as deposition of secondary cell wall and lignification. Thus, they play important role in cell wall extension and development of vasculature. All of these roles played by polyamines help in regulating cell growth and wall extension as well as cell division and therefore help in overall growth of plant. Other important roles played by polyamines in plant life cycle include induction of root initiation and growth, pollen development and pollen-pistil interaction, and promoting flower and fruit development.

22.5.7 Crosstalk with Hormones

Because of their involvement in numerous growth- and development-related processes, polyamines have since long been argued to be “hormones” in their action. One contradictory argument to this belief is that polyamines are active at millimolar concentrations, while the hormones elicit their effects in much smaller amounts. However, they have been well-documented to interact with different phytohormones in synergistic or antagonistic manner to regulate many processes, including the stress responses. For instance, polyamines act antagonistically to ethylene to control leaf senescence and fruit ripening. They are thus considered “anti-senescent” molecules as they prevent loss of chlorophyll and retard fruit ripening. On the other hand, they have been reported to have a synergistic interaction with abscisic acid in reducing stress-induced damage to plants. A remarkable example of such an interaction is in facilitating stomatal closure under water-deficit conditions. Polyamines are also known to interact with hormones associated with plant defense against biotic stress, like jasmonic acid and salicylic acid. Both of these hormones have been demonstrated to induce polyamine biosynthesis and enhance accumulation of conjugated form of polyamines in response to pathogen attack, thereby increasing the tolerance to infection. Accumulation of conjugated polyamines, or polyamines in general, contributes to reduction of the symptoms associated with diseases. Jasmonates are also known to induce polyamine oxidation which plays essential role during pathogen attack. Polyamine oxidation generates H_2O_2 which is associated with defense responses, like induction of the hypersensitive (HR) response to elicit host cell death and improve tolerance against pathogens. The other reaction products of polyamine oxidation give rise to intermediaries which have substantial role in acclimation during pathogen invasion. For example, pyrroline and 1,3-diaminopropane are metabolized to γ-aminobutyric acid (GABA) and β-alanine, respectively, both of which are involved in improving plant resistance.

22.5.8 Polyamines as Signaling Molecules and in Modulating Stress

Recently polyamines have also been implicated to serve as signaling molecules in many cellular signaling routes, particularly via their interaction with other such signaling molecules, like nitric oxide, Ca^{2+}, and H_2O_2. They have been suggested to induce nitric oxide biosynthesis, a molecule which has been known to mediate several stress responses in plants, especially under stressful conditions. One of the best examples of the interaction of these signaling molecules is seen under salinity and drought stress, where polyamines regulate cytoplasmic Ca^{2+} levels and induce nitric oxide, which work in concert with each other to trigger ABA-induced stomatal closure. Polyamine oxidation product H_2O_2 has also been reported to play a crucial role in stress-induced stomatal closure. Other responses to stresses include enhanced production and accumulation of compatible solutes, modification of cell wall, and maintenance of cellular redox and ionic homeostasis. Polyamines have a role in all of the abovementioned responses which collectively help in overcoming detrimental effects of stress. The major roles of polyamines during stress can be summarized as follows:

1. Preserving cell membrane integrity by reducing lipid peroxidation and stabilizing lipids
2. Reinforcement of cell wall during pathogen attack and wound healing
3. Preserving thylakoid membrane, assembly of photosystems, and increasing abundance of photoprotective molecules like zeaxanthin and carotenoids, therefore, increasing photosynthetic efficiency and improving dissipation of excess energy
4. Modulating the activities of ion channels and maintaining ionic balance
5. Scavenging of reactive oxygen species (ROS) and increasing antioxidant activities, therefore maintaining redox homeostasis
6. Regulating stress responses, such as HR, accumulation of GABA, and other compatible solutes, and inducing expression of pathogen-related (PR) proteins

22.5.9 Role in Plant-Microbe Interactions

Besides providing tolerance to pathogens, polyamine metabolism also influences the establishment and development of beneficial plant-microbe associations, such as those with nitrogen-fixing bacteria (rhizobia), mycorrhizal fungi, and growth-promoting rhizobacteria. Both accumulation of polyamines and their oxidation seem to be important for initiation of nodulation and maintenance of nodules. H_2O_2 formed as a result of polyamine oxidation promotes cross-linking of plant matrix glycoproteins in the lumen of infection threads during initial stages of rhizobia colonization. Polyamine accumulation enhances nodule tolerance to osmotic stress caused by establishment of the symbiotic association with rhizobia in plant roots. Similarly, they also facilitate establishment of mutualistic associations with mycorrhizal fungi by stimulating the colonization of roots by the fungus and hence contribute significantly to increased absorption of minerals by the host. Therefore, polyamines not only provide important measure against pathogens (and abiotic stresses) to control plant diseases, but also have important roles during establishment of beneficial plant-microbe interactions.

22.6 Peptide Signaling Molecules

A number of plants are routinely wounded by treading and grazing. The cells so damaged are prone to easy colonization by microbes than the healthy cells of unwounded regions of the plants. Wounded and exposed cells thus provide a point of microbe entry into plant body since it is no longer protected by any thick epidermal cell wall and cuticle. Wounding of plant tissue leads to enhanced ROS production which, in turn, induces certain defense responses including gene expression for the lignin and polyphenol biosynthesis. Lignin and similar other hydrophobic polymers seal the wound against pathogen invasion, whereas polyphenols provide further protection to the wounded tissue which is exposed to an oxidizing environment. Polyphenols are also the cause of browning of the cut surface (such as in potatoes and apples) due to accumulation of cross-linked phenolic compounds synthesized by the action of polyphenol oxidases. In addition to these localized defenses, host plants also exhibit activation of several genes in the unwounded cells near the wounding tissue, leading to synthesis of defense-related proteins. Such an activation of genes in the intact zones of a wounded plant is referred as a **systemic response** which is triggered in the uninfected parts of the plant by a broad spectrum of pathogens, and it leads to plant immunization, thereby limiting pathogen growth. Plants achieve this systemic resistance through long distance transport of certain peptides known as **signal peptides** (Fig. 22.23).

22.6.1 Systemins

Small polypeptide signaling molecules play important roles in short-range intercellular communications. First plant signaling peptide was discovered by Clarence E. Ryan in 1970 from tomato and was named **systemin** (TomSys). When healthy young plants were irrigated with water containing wounded tomato leaves, it induced the production of proteinase inhibitor (TomSys) in healthy plants. TomSys or systemin was characterized as an 18-amino-acid signaling peptide and was shown to be involved in the production of jasmonic acid, the main wound response signaling molecule. Systemin is capable of imitating defense responses at very low concentrations in the range of few femtomoles per plant. Systemin is synthesized at the wounding site by cleavage from the C-terminus of a 200 residue precursor protein called **prosystemin**. It then moves rapidly (within 1–2 h) through phloem to the unwounded parts of the plant (Fig. 22.24). Transgenic tomato plants which

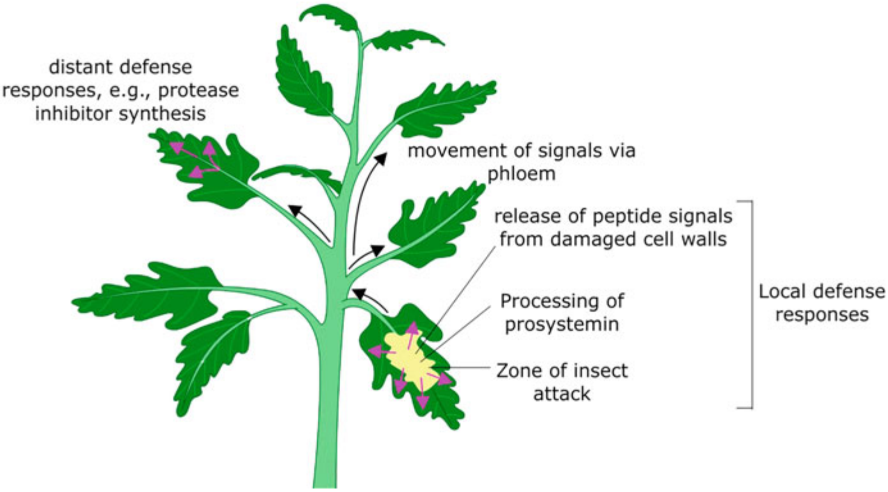


Fig. 22.23 The process of induction of defense response in unwounded plant parts by peptide signal transport from the zone of damage by wounding/insect attack

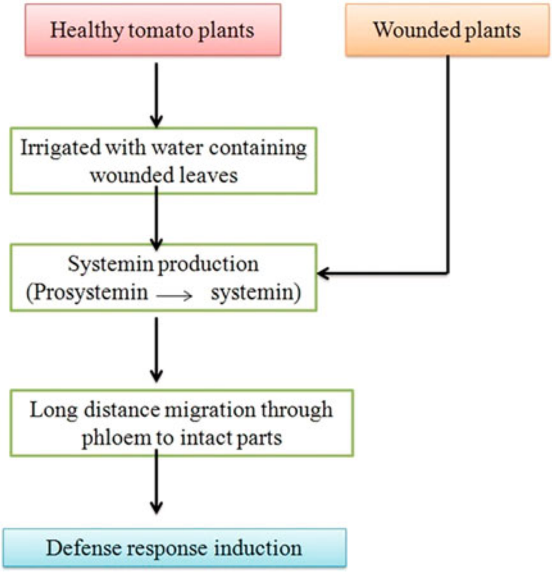


Fig. 22.24 Events leading to induction of defense response in plants through systemin formation and transport

produce lower than normal levels of systemin exhibit severely reduced systemic induction of defense mechanisms and have reduced resistance to herbivory by the larvae of tobacco hornworm (*Manduca sexta*). Transgenic plants producing high levels of systemin production, constitutively express defense mechanisms even if they are not wounded.

22.6.2 Types of Signaling Peptides

About 13 families of signaling peptides have been identified so far. They can be grouped into two categories:

1. **Small post-translationally modified peptides:** They are composed of 5–20 amino acids, e.g., CLE, IDA, and RGF (ROOT GROWTH FACTOR) peptides.
2. **Cysteine-rich polypeptides:** They have a length of approx. 50 amino acids and are synthesized as precursor proteins, e.g.: RALF (RAPID ALKALINIZATION FACTOR) and PDF (PLANT DEFENSIN) peptides.

Most of the signal peptides are derived from the proteolysis of precursor proteins. Some of them are produced by non-ribosomal synthesis, e.g., glutathione and phytochelatins. Processing of the precursor molecules can take place both in the cytosol and apoplast since proteases are a part of the plant secretome as well.

22.6.3 Perception of Signal Peptides by the Cells

The perception of signal peptides occurs via plasma membrane localized receptor-like kinases (RLKs). RLKs exhibit an extracellular domain, a transmembrane domain, and intracellular kinase domain. RLK gets activated by the binding of signal peptide to the extracellular domain, leading subsequently to induction of different pathways monitoring cell growth, differentiation, or defense response (Fig. 22.25). Thus, some peptides regulate meristematic activity in shoot or root meristem (e.g., CLV3 and CLV40) or promotion of abscission (IDA). STOMAGEN is a cysteine-rich signal peptide and is involved in stomata development. Overexpression of STOMAGEN enhances the number of stomata on the leaves (Fig. 22.26). Signal peptides are also important in stress responses and in symbiotic interactions. Thus, FLS 2 (FAGELLIN SENSING 2) is a signal peptide that senses pathogens by binding to bacterial flagellin. This binding triggers intracellular calcium signaling and further activation of downstream responses.

22.6.4 Signal Peptides and Their Potential Benefits in Agriculture

Our understanding of the roles of signal peptides in plant development can benefit agriculture. A knowledge about novel signal peptides which influence the size of meristem, is likely to help in finding mutants which can result in enhanced yield. Identification and characterization of mutations carrying genes for signal peptides or their receptors hold promise for benefits. in agriculture. For example, mutations in the maize orthologs of CLV1 thick tassel dwarf 1 (td1) influence male and female inflorescence ear and have been found to modulate seed production. The male inflorescence shows increased density of spikelets and female inflorescence exhibits more kernels. So far, information is available for only very few signal peptide-

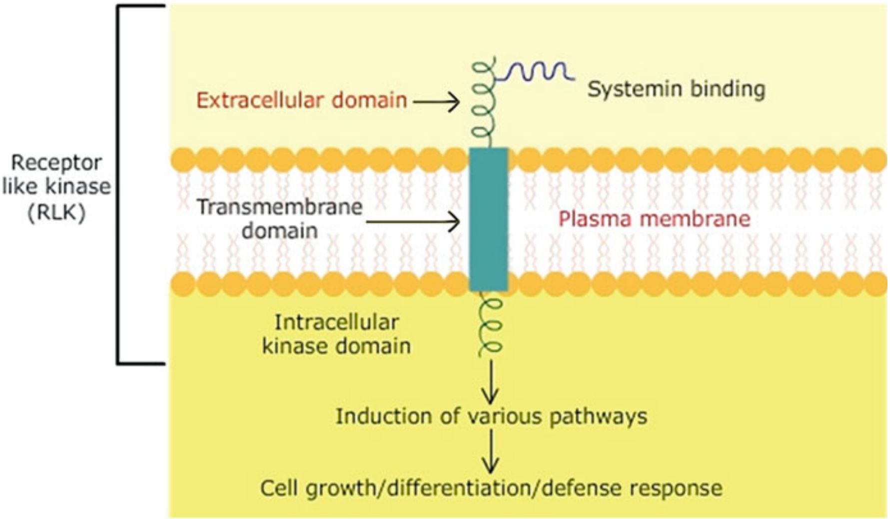


Fig. 22.25 Perception of signal peptides by the cells

triggered pathways in plants. A deeper understanding of more of such pathways is likely to provide us information about the biochemical/metabolic routes to modify plant architecture and development for crop improvement.

22.7 Karrikins: A New Class of Plant Growth Regulators in Smoke

Karrikins are a class of butanolide compounds derived from burnt plant material which can stimulate seed germination in a number of plants. The term “karrikin” is derived from the aboriginal word “karrik” for smoke used by Western Australian Noongar people. It is a common observation that some plants grow immediately after wildfires or bushfires and their seeds remain dormant in soil until a fire generates karrikins which get bound to soil particles as a result of subsequent rainfall following fire. Such plants which remain dormant until a fire generates fresh karrikins in soil to stimulate their germination are referred as “fire followers” or “fire ephemerals.” Fires release plant-bound nutrients and create an open habitat where seedlings establish themselves before other competing plants colonize the land. Such seeds can remain viable in soil for decades between fires and undergo many cycles of wetting (imbibition) and drying (dehydration). Smoke water is sometimes used to promote germination of horticultural seeds. The smoke from cigarettes also stimulates seed germination, probably due to the presence of karrikins.

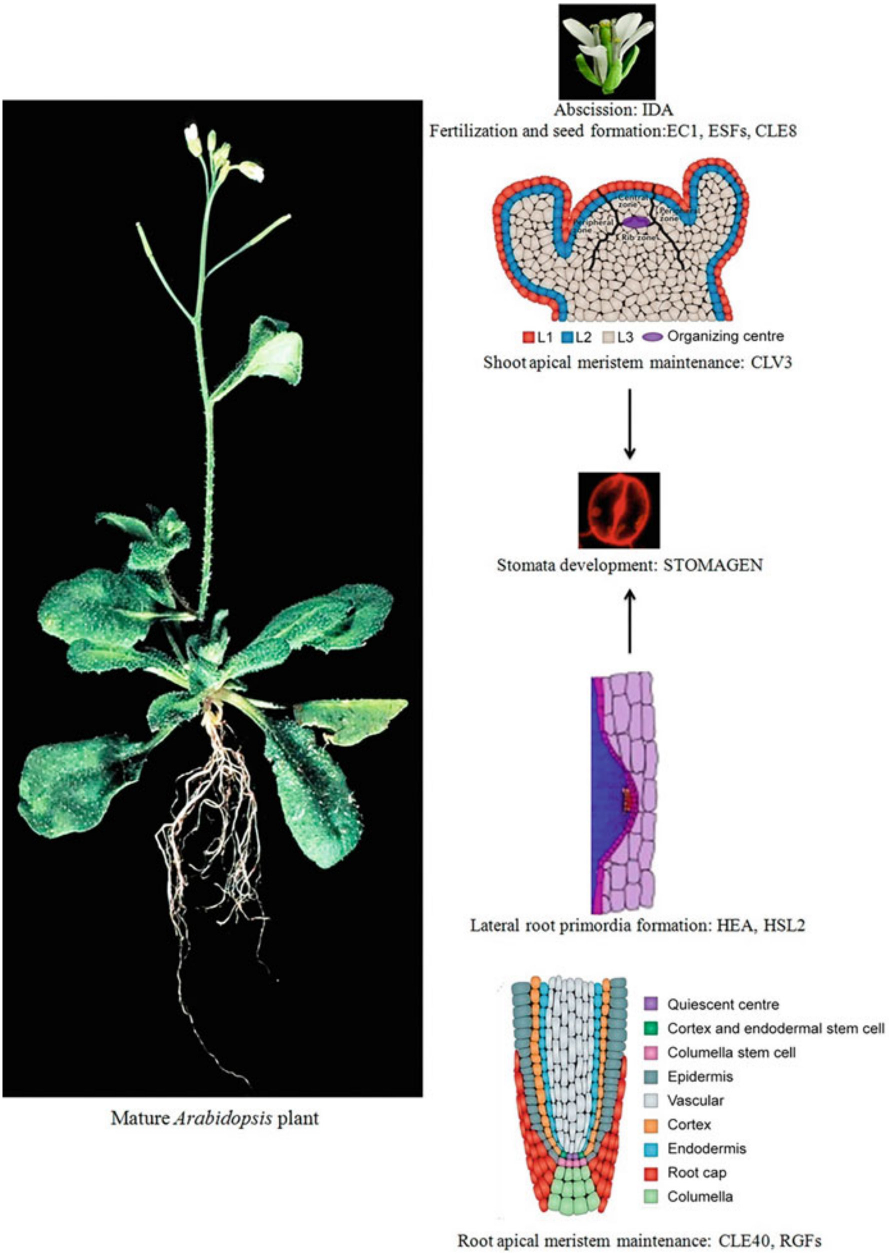


Fig. 22.26 Signaling peptides involved in some of the developmental processes in *Arabidopsis*

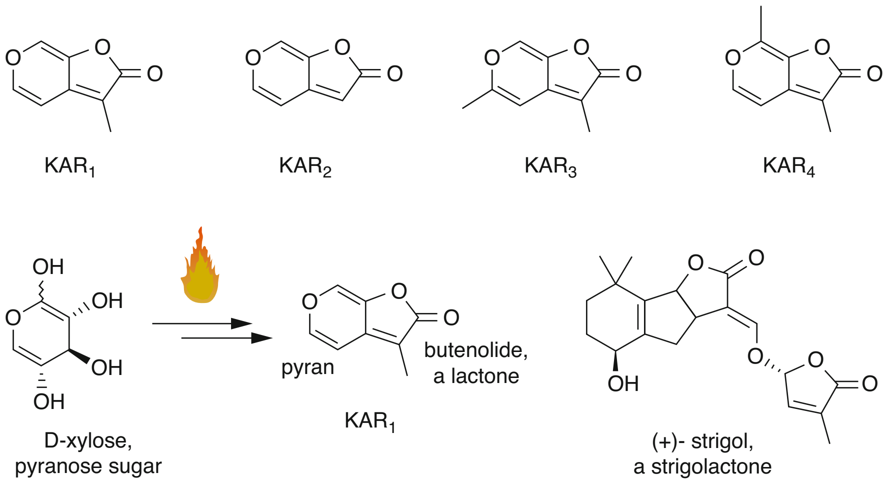


Fig. 22.27 The karrikin family. The first karrikin discovered was KAR1, also known as karrikinolide

22.7.1 Chemical Nature

Liquid chromatographic analysis of "smoke water" lead to identification of a specific type of lactone, known as a butanolide fused to a pyran ring, with the systemic name: 3-methyl-2*H*-furo[2,3-c]pyran-2-one. This was the first karrikin discovered. Subsequently, several closely related compounds were discovered in smoke and collectively referred as "karrikins" and abbreviated as KAR (Fig. 22.27). Karrikins comprise of C, H, and O only and contain two ring structures—a pyran and a lactone (a fine-membered ring known as butanolide). Since karrikins can be produced by burning sugars such as xylose, the pyran ring of karrikins is probably derived from such pyranose sugars. Both karrikins and strigolactone hormones such as strigol have a butenolide ring. The original compound identified is often referred to as "karrikinolide": the "-olide" suffix indicates that it is a lactone. The karrikins are abbreviated to KAR and numbered in order of their identification in smoke (Fig. 22.27). The first of the karrikins identified from smoke is referred as KAR1. It can stimulate seed germination at concentrations as low as 10^{-10} M, which is similar in effectiveness as many hormones.

22.7.2 Karrikin-Sensitive Plants

Karrikin response is widespread, and seeds from different flowering plants and conifers respond to karrikins by exhibiting seed germination. Plants with smoke-responsive seeds are found in both fire-prone and non-fire-prone environment. Many weeds from agricultural land and seeds of horticultural plants, such as lettuce and

Table 22.3 Some plants known to exhibit enhanced seed germination response due to karrikin

Aristolochia debilis (birthwort)
Arabidopsis thaliana (*Arabidopsis*)
Brassica tournefortii (Asian mustard)
Lactuca sativa (lettuce)
Apium graveolens (celery)

tomato, also exhibit improved germination in response to karrikins. Karrikins have also been reported to bring about vigorous growth of maize and *Arabidopsis* seedlings (Table 22.3).

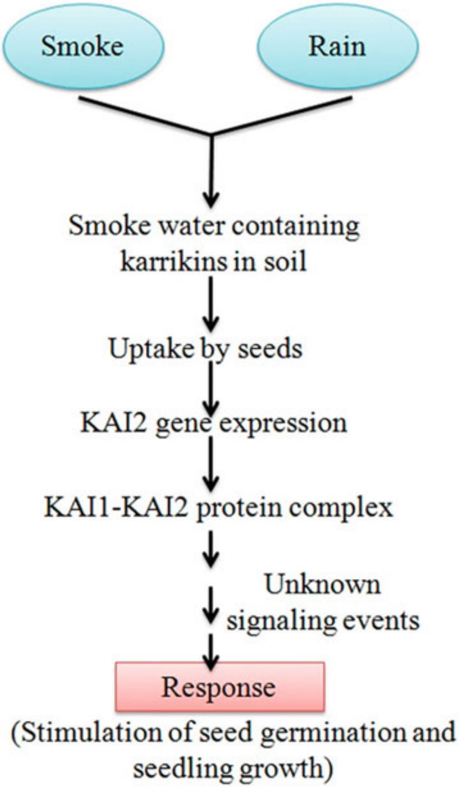
22.7.3 Mode of Karrikin Action in Plants

The genes for karrikin response are conserved in all seed plants. Two genes are essential for karrikin action. They are MAX2 (MORE AXILLARY GROWTH) and KAI2 (KARRIKIN INSENSITIVE 2). MAX2 is already known for its role in response to strigolactone hormone. Karrikins and strigolactones are perceived by plant cells separately and plants respond differently to the two classes of compounds. But the two classes of compounds are structurally closely related. All plants apparently contain KAI2 gene, but there is no evidence so far that plants produce karrikins. KAI2 gene encodes karrikin receptor—KARRIKIN INSENSITIVE 2 (KAI 2). KAI 2 is an α/β serine hydrolase involved in seed germination and seedling development. This protein has a key function in plant development, and it also responds to an endogenous signaling compound similar to karrikins (Fig. 22.28). This unidentified signaling compound is also likely to be similar to strigolactones since KAI2 is very similar to strigolactone receptor DWARF14. It is believed that plants take up karrikins and convert them to some active compounds which interact with KAI2 protein to cause subsequent seed germination response.

Summary

- Biosynthesis of salicylic acid in plants is occurs via two routes the *trans*-cinnamic acid (tCA) pathway and the chorismate pathway. The information available so far suggests the operation of both the pathways of SA biosynthesis in plants though species specificity and treatment specificity may be evident for the operation of one or the other of the two pathways. SA plays a significant role not only in the onset of senescence but also in its progression. During thermogenesis, most of the electron flow in mitochondria gets diverted from cytochrome respiration pathway to cyanide-insensitive non-phosphorylating electron transport pathway which is unique to plant mitochondria. The thermogenic inducing principle was initially called **calorigen** and was identified as SA in the 1980s. Thus, thermogenic respiration appears to be a metabolic event taking place rarely to help plants survive stress conditions. SA is an important participant in systemic acquired

Fig. 22.28 Scheme of events leading to karrikin-induced seed germination



resistance (SAR) to pathogenic infections. SA induces SAR in a variety of pathogen-infected plants. SA has been observed to induce flowering in duckweeds, when these long-day plants are grown under noninductive short-day photoperiods.

- NO has emerged as an important signaling molecule with diverse physiological functions in growth and development, starting from seed germination, flowering, fruit ripening, and also during senescence of organs. Under environmental stress conditions caused by various biotic and abiotic stress factors, different plant species and organs exhibit enhanced NO generation. In plant cells, NO can induce both harmful and beneficial effects depending on its local concentration, translocation, rate of biosynthesis, and ability to get removed as various reactive nitrogen species (RNS). There are three probable routes of NO biosynthesis in plants: (1) L-arginine-dependent pathway, (2) nitrite-dependent pathway, and (3) nonenzymatic NO production. There is, however, enough controversy about the nature of NOS activity in plants. The AtNOS1 (putative NOS in plants) is a mitochondrial protein which bears a centrally positioned GTP-binding domain. In plant cells exposed to varied biotic or abiotic stress conditions, NO modulates the activity of various ROS-scavenging enzymes through their tyrosine nitration, metal nitrosylation, or S-nitrosylation thereby facilitating homeostatic regulation of enhanced ROS levels generated in plant cells under stress conditions. NO can modify phytohormone action in plants in three different ways. It can chemically modify the transcription factors (TFs) and other proteins (P) which are involved in phytohormone metabolism, transport, or signaling, 2. NO may modify proteins involved in the production, distribution, and signaling of plant hormones at post-translational level, 3. NO or RNS may also directly react with certain plant hormones thereby altering their biological activity.

- NO plays a key signaling role during the induction of hypersensitive response (HR). NO has also been implicated during bacteria-legume interaction accompanying nodule formation. There are reports that NO acts as a negative regulator of nitrogen fixation due to its interaction with leghemoglobin. Nitric oxide can be endogenously removed through the activity of an enzyme called GSNO reductase (GSNOR) which degrades S-nitrosoglutathione (GSNO). Since nitrite is a precursor of NO in plant cells, it is possible that nitrite can serve as a mobile source of NO across the xylem stream. Plants also contain hemoglobin genes, thereby indicating the possibility of hemoglobin-NO complexes as transport molecules for NO.
- Melatonin (N-acetyl-5-methoxytryptamine) is a pleiotropic molecule with numerous physiological and cellular actions. Like melatonin, serotonin is also a multifunctional indoleamine. Tryptophan is the common precursor for the biosynthesis of IAA and serotonin and melatonin. Tryptophan decarboxylase (TDC), with a high K_m (690 μM) for tryptophan (its substrate), is the rate-limiting key regulatory enzyme of this pathway. One molecule of melatonin can scavenge up to four or more ROS. Serotonin plays a crucial role in root development and shoot morphogenesis. Serotonin has the highest antioxidant activity among tryptamine, tryptophan, and related derivatives. It helps in maintaining the reducing potential of cells due to its antioxidative properties by detoxifying the cells (relieves the accumulated toxic tryptamine). It delays senescence by efficient scavenging of ROS and protects young reproductive tissues from different environmental stresses. Serotonin regulates gene expression associated with auxin response pathways. Serotonin accumulation is likely to increase due to the abiotic stress-induced inhibition of auxin biosynthesis in plant tissues. Serotonin and melatonin prevent oxidative damage by regulating cellular ROS levels and serve as line of defense against stress. Melatonin has a protective role against leaf senescence.
- Strigolactones (SLs) are carotenoid-derivatives which were first identified as germination stimulants for the seeds of root parasitic weeds such as *Striga*, *Orobanche*, *Phelipanche* spp. Some of the common naturally occurring SLs are strigol, orobanchol, and sorgomol. GR24 is an extensively used synthetic SL. The common precursor for the major natural SLs is 5-deoxystrigol. SLs appear to act in coordination with auxin to modulate apical dominance. SLs promote the development of interfascicular cambium. SL signaling is believed to trigger PIN1 depletion from the xylem parenchyma cells. Accordingly, a reduction in auxin level enables the growth of lateral buds. SLs have also been reported to suppress **adventitious root** (AR) formation in *Arabidopsis* and pea. SLs

negatively regulate auxin accumulation in the pericycle, thereby reducing AR initiation. SLs are synthesized primarily in the root and they can be transported acropetally to the shoot in the xylem. SLs have been reported to get transported from the sites of their synthesis using plasma membrane-associated ABC transporters, and they move in the xylem from the root to shoot. SLs can induce ethylene biosynthesis in the seeds of parasitic plant—*Striga*—leading to seed germination. Auxins maintain apical dominance by stimulating SL synthesis via the *MAX4* gene. SLs then activate *BRC1*, a transcription factor known to suppress axillary bud growth. Additionally, SLs also inhibit cytokinin biosynthesis by negatively regulating the expression of *IPT* genes which otherwise would prevent BRC1 production. SLs are perceived by a protein complex which contains an α-/β-hydrolase protein and F-box protein D14 and MAX2, respectively.

- Polyamines are low molecular weight nitrogenous compounds which exist in positively charged state at physiological pH, a property that allows them to bind to all biological molecules bearing negative charge. So, polyamines have the ability to bind to and stabilize the anionic macro- and micromolecules within the cell, such as phospholipids in membranes, nucleic acids, proteins, and phenolic acids. The most commonly occurring polyamines are the aliphatic diamine putrescine, the triamine spermidine, and the tetramine spermine, with cadaverine being present in considerable levels in some plant species. Polyamines are localized in almost all compartments of the cell where they perform their regulatory roles in diverse cellular events. Putrescine is synthesized from arginine via two different biosynthetic pathways. Both the pathways of putrescine synthesis exist in plants. Spermidine and spermine synthesis requires putrescine as well as decarboxylated *S*-adenosylmethionine as precursor molecules. The growth promoting activities of polyamines are majorly accounted for by their roles in regulation of basic cellular events, like nucleic acid synthesis and protein synthesis. They bind to and modulate conformation of DNA and RNA, thereby facilitating the processes of replication, transcription, and RNA processing. Binding of polyamines regulates the 3D conformation of proteins and also their functions. In the cell wall, they bind to polysaccharides, pectins, and phenolic acids in lignin to enhance the strength of primary cell wall as well as deposition of secondary cell wall and lignification. Polyamines act antagonistically to ethylene to control leaf senescence and fruit ripening. They are thus considered "anti-senescent" molecules as they prevent loss of chlorophyll and retard fruit ripening. Besides providing tolerance to pathogens, polyamine metabolism also influences the establishment and development of beneficial plant-microbe associations, such as those with nitrogen-fixing bacteria (rhizobia), mycorrhizal fungi, and growth-promoting rhizobacteria.
- An activation of genes in the intact zones of a wounded plant is referred as a **systemic response** which is triggered in the uninfected parts of the plant by a broad spectrum of pathogens, and it leads to plant immunization, thereby limiting pathogen growth. Plants achieve this systemic resistance through long distance transport of certain peptides known as **signal peptides.** Systemins are small polypeptide signaling molecules that play important roles in short-range

intercellular communications. The first plant signaling peptide was discovered by Clarence E. Ryan in 1970 from tomato and was named systemin (TomSys). TomSys or systemin was characterized as an 18-amino-acid signaling peptide and was shown to be involved in the production of jasmonic acid, the main wound response signaling molecule. Systemin is capable of imitating defense responses at very low concentrations in the range of few femtomoles per plant. Systemin is synthesized at the wounding site by cleavage from the C-terminus of a 200 residue precursor protein called **prosystemin**. It then moves rapidly (within 1–2 h) through phloem to the unwounded parts of the plant. About 13 families of signaling peptides have been identified so far.

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Multiple-Choice Questions

1. Perception of signal peptides by cells occur via:
   (a) RLKs
   (b) MAPKs
   (c) CDPKs
   (d) PKC
2. First plant signaling peptide was named as:
   (a) Systemin
   (b) Prosystemin
   (c) Defensin
   (d) None of the above
3. Signaling peptide involved in the development of stomata in *Arabidopsis* is:
   (a) IDA
   (b) STOMAGEN
   (c) CLV3
   (d) HEA

4. SA has the following physiological functions:
   (a) To retard senescence
   (b) To induce flowering
   (c) To regulate thermogenesis
   (d) All of the above
5. Plants like *Sauromatum* sp. are known to generate large amount of heat as a result of:
   (a) Cytochrome respiration pathway
   (b) Alternative respiratory pathway
   (c) Release of amines
   (d) Photophosphorylation
6. Sequentially acting enzymes for synthesizing strigolactones in plastids are:
   (a) P-450, D27, CCD8
   (b) CCD7, D27, P-450
   (c) D27, β-carotene isomers, CCD7, CCD8
   (d) CCD7, CCD8, D27
7. Which other hormones functions in coordination with auxin to modulate apical dominance?
   (a) Jasmonic acid
   (b) Brassinosteroids
   (c) Salicylic acid
   (d) Strigolactones
8. Two indoleamines known to function as neurotransmitters in animals and growth and development in plants are:
   (a) Brassinosteroids and jasmonic acid
   (b) Serotonin and melatonin
   (c) Tryptophan and brassinosteroids
   (d) Salicylic acid and tryptophan
9. Two enzymes leading to the formation of serotonin are:
   (a) Tryptophan decarboxylase (TDC) and tryptamine hydroxylase
   (b) Tryptophan decarboxylase and tryptophan synthase
   (c) Tryptophan decarboxylase and anthranilate synthase
   (d) Tryptophan synthase and anthranilate synthase
10. Rate-limiting step in the synthesis of serotonin, melatonin and IAA is the one catalyzed by:
    (a) TDC
    (b) Tryptamine hydroxylase
    (c) Amine oxidase
    (d) 5-hydroxyindole-o-methyl transferase
11. The first polyamine reported by Anton von Leuwenhoek was:
    (a) Spermidine
    (b) Putrescine
    (c) Spermine
    (d) Cadaverine

12. Compounds responsible for distinctive odor of sperm and urine are:
    (a) Spermidine
    (b) Putrescine
    (c) Non-spermines
    (d) Thermospermine
13. Compounds helping in condensation of chromatin by stabilizing negative charges associated with phosphate groups in NAs:
    (a) Polyamines
    (b) Arginine
    (c) Methionine
    (d) S-adenosylmethionine
14. Anti-senescent molecules to control leaf senescence and fruit ripening are:
    (a) Ethylene
    (b) Polyamines
    (c) Abscisic acid
    (d) Jasmonic acid
15. A compound important for initiation of modulation and maintenance of nodules is:
    (a) NO
    (b) Polyamines
    (c) Salicylic acid
    (d) Strigolactones
16. NO is synthesized in plants through:
    (a) L-arginine-dependent pathway
    (b) Nitrite-dependent pathway
    (c) Nonenzymatic NO production
    (d) All of the above
17. NO can be endogenously removed through activity of enzyme:
    (a) Nitrate reductase
    (b) Nitrite reductase
    (c) S-nitrosoglutathione reductase (GSNO)
    (d) Oxidoreductase xanthine
18. Putative NOS (At NOS) is known to be present in:
    (a) Plastids and mitochondria
    (b) Apoplast
    (c) Chloroplasts
    (d) Cytosol
19. Compounds derived from burnt plant material, responsible for stimulating seed germination in plants are:
    (a) Strigolactones
    (b) Polyamines
    (c) Jasmonic acid
    (d) Karrikins

Answers

1. a 2. a 3. b 4. d 5. b 6. c 7. d
8. b 9. a 10. a 11. c 12. b 13. a 14. b
15. b 16. d 17. c 18. a 19. d

Suggested Further Readings

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