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Chapter

Role of Secondary Metabolites to Attenuate Stress Damages in Plants

Masuma Zahan Akhi, Md. Manjurul Haque and Md. Sanaullah Biswas

Abstract

Plants are constantly facing various threats posed by the biotic and abiotic stressors. To survive in these challenged environment, plants evolve a variety of defense mechanism. Among the various phytochemicals, secondary metabolites (SMs) accumulate higher amount under stressful conditions and initiate signaling functions to up-regulation of defense responsive genes. SMs ensures the survival, persistence and competitiveness of the plant against the threat generated under stressful conditions. Therefore, the signaling functions of SMs to protect the plant from biotic and abiotic stressors are getting importance in the recent times. In this chapter the contribution of SMs to protect the plant from specific environmental stresses has been discussed.

Keywords: reactive oxygen species, environmental stress, biotic and abiotic stress, plant tolerance and adaptation, programmed cell death

1. Introduction

A hundred years ago it is reported that primary metabolites (carbohydrates, proteins, amino acids, vitamins, acetone, ethanol, etc.), are involved in various life functions in plants such as cell division, growth and development, photosynthesis, respiration, and reproduction [1]. However, Kossel was the first to define the secondary metabolites (SMs) as opposed to the primary ones and then concept of SMs has been introduced in plant biology [2]. The term metabolite is usually confined to tiny molecules and products of metabolism. Plants produce unlimited and manifold assortment of organic compounds, the great majority of which do not take part in growth and development immediately. These substances commonly referred to as SMs, often are differentially distributed among limited taxonomic groups within the plant kingdom [3]. In the last decade SMs, low molecular compounds occurring in all living organisms while mostly distributed in plants, became a subject of dramatically increasing interest relevant to their outstanding practical implication for medicinal, nutritive and cosmetic purposes, as well as to their undebatable importance in plant stress physiology [4].

Recent advances of SMs research on plant stress physiology suggesting its involvement to the mitigating detrimental effects of various stressors [5, 6]. In addition to the protective functions of SMs, they also act as defending molecules of primary metabolites such as proteins and nucleic acids from stress-induced damages [7, 8]. Therefore, physiological modifications such as secondary metabolism

adjustment, ion and water balance, minimization of oxidative damage etc. occurred in plant body which can provide the phenotypic response of stress tolerance directly or indirectly. The stress response could also be a growth inhibition or cell death [9–11], which will depend upon how many and which kind of genes are up- or down-regulated [12]. However, most of the cases secondary metabolism adjustment play an important role in defense mechanism either increasing or decreasing their production in plant body. In this chapter the role and involvement of SMs in regulation of various biotic and abiotic stresses in plants has been discussed.

2. Plant responses to stress factors

Plants throughout their life cycle are subjected to various forms of biotic and abiotic stresses, as a sessile organism plants lack the ability to escape from that danger areas. Plants express responses to stress conditions in three ways. Some plants avoid the stress altogether (e.g. ephemeral, short-lived, desert plants), some show susceptibility to stress which may ultimately lead to plant death and some show resistant capacity [13]. To defend themselves against diverse stresses, plants have evolved complicated and highly regulated systems. To cope with these challenging environment plants evolve some efficient mechanism such as adjustment in photosynthetic rates, stomatal conductance, transpiration, cell wall architecture, remodeling of membrane structure, alterations in cell cycle and division rates with overall effect on general growth to fine-tune physiology and metabolism of bioactive compounds [14]. Initiation of stress and defense responses are mediated by signaling processes and pathways which trigger the primary metabolism that provides biosynthetic intermediates for secondary metabolism in plant body. These include the stress responsive system and the inducible defense system which depends on inducible activation of massive defense-related genes, suit of molecular and cellular process as well as inducible production of diverse defense-related SMs [15]. Plant accumulate a large number of SMs from primary metabolites in cells, and the production of that metabolites are regarded as an adaptive capacity in coping with stressful constraints during challenging environment [16–18].

3. Mechanism of stress adaptation in plant

Generally, a stress signal transduction pathway comprises the following key steps: (i) signal perception; (ii) signal transduction; and (iii) stress response. The first step in the activation of signaling cascade for any given stress is the recognition of stress signals via receptors located on the membrane of plant cell. Recently a few research works indicated that various plasma membrane proteins like COLD1 (Chilling Tolerance Divergence-1) [19], CNGCs (cyclic nucleotide nucleotide-gated channel), GLR (glutamate-receptor like) channel, histidine kinases, calcium channel are the main sensors for stress signaling. After recognition, the receptors transmit the signal into downstream through phytohormones and second messengers such as Ca^{2+} and ROS [20]. The second messengers, like ROS, trigger the activation of another set of ROS-modulated protein kinases (PKs) and protein phosphatases (PPs), including MAPK (mitogen-activated protein kinase) cascades, CDPKs (calcium-dependent protein kinases), CBLs (calcineurin-B-like proteins), CIPK (CBL-interacting protein kinase), and many other PKs as well as PPs such as some PP2Cs (protein phosphatase 2Cs). Subsequently, these PKs and PPs deliver the information downstream and trigger a series of phosphorylation or dephosphorylation of transcription factors (TFs), that finally culminates either directly in the

expression of functional genes involved in cellular protection, or indirectly in the expression of regulatory genes participating in signaling cascades and transcriptional regulation of gene expression.

In addition of the enzymatic (such as superoxide dismutase, catalase, ascorbate peroxidase) and non-enzymatic antioxidants (such as ascorbic acid, reduced glutathione, α-tocopherol, carotenoids, flavonoids), primary metabolites including sugars, amino acids contribute to cellular homeostasis to adapt under stressful conditions [21]. Recently, the research advances supporting that products of secondary metabolism are important to alleviate toxic effects of stresses [5] through expression of stress responsive genes. Therefore, in presence of stress signals accumulated various species of SMs are critically important for adaptation and tolerance to the altering environment.

4. Generation and diversity of secondary metabolites in plants

Plant SMs are classified into four major categories. These four categories include (i) terpenes (such as carotenoids, sterols, cardiac glycosides and plant volatiles), (ii) phenolics (such as lignans, phenolic acid, tannins, coumarins, lignins, stilbenes and flavonoids), (iii) nitrogen containing compounds (such as cyanogenic glycosides, alkaloids, and glucosinolates) and (iv) sulfur containing compounds (such as glutathione, phytoalexins, thionins, defensins and lectins) [22, 23]. But on the basis of biosynthesis pathways plant SMs are usually classified into three chemically distinct groups [24]. The diverse chemical structures of the SMs determine their functions to the medicine and stress adaptation. Three major categories are (i) terpenes derived from mevalonic acid pathway [25] and methyl erythritol phosphate pathway [26], (ii) phenolics derived from malonic acid pathway or a few case shikimic acid pathway [27], (iii) N (Nitrogen) and S (Sulfur) containing compounds via tricarboxylic acid cycle or sometimes via shikimic acid pathway. Among the pathways of SMs accumulation, shikimic acid, mevalonic acid, phenylpropanoic acid and methyl erythritol phosphate pathways are highly regulated under stress stimuli.

5. Terpenes for stress responses in plant

Plants produce various types of SMs, many of which have been subsequently exploited by humans for their beneficial roles in a diverse array of biological functions [28]. Terpenes are one of the diverse species of SMs contribute to the various biological process in plants. Terpenoids are terpenes with an oxygen moiety and additional structural rearrangements. Therefore, these two terms of terpenes and terpenoids are used interchangeably. Terpenoids have their roles in plant defense against biotic and abiotic stresses or they are treated as signal molecules to attract the insects for pollination. The first step of terpenoid biosynthesis is generation of C5 unit like as isopentenyl diphosphate (IPP) or dimethylallyl diphosphate (DMAPP). On the basis of C5 units, we can classify the terpenoids as C5 (hemiterpenes), C10 (monoterpenes), C15 (sesquiterpenes), C20 (diterpenes), C25 (sesterpenes), C30 (triterpenes), C40 (tetraterpenes), C40 (polyterpenes) [29–31].

5.1 Terpenes for biotic stress responses

The rate of terpene emission in *Pinus sylvestris subsp. nevadensis* is increased due to attack of the caterpillar of Pine Processionary Moth (PPM). PPM is the main

defoliator of pine tree in the mediterranean region. The emission rates of terpenes are higher in attacked branches of trees than non-attacked trees. That indicates, terpenes are toxic volatile compounds accumulate in plant to provide sufficient defense mechanism [32]. Terpenoids can serve as repellents and reduce larval feeding and oviposition by herbivores [33, 34]. Isoprene is volatile organic compound and belongs to the terpenoids group. *Manduca sexta* caterpillars were released to the transgenic tobacco plants containing isoprene synthase gene and the wild type of which does not emit isoprene. This study showed that isoprene-emitting transgenic tobacco plants deters *Manduca sexta* from feeding [35].

In attack of root feeding herbivore, plant produce various types of metabolites such as sesquiterpene lactone taraxinic acid β-D glucopyranosyl ester (TA-G) [36]. The main function of these compounds is to protect the plant against below ground herbivore attack. Dandelion (*Taraxacum officinale*) is known to release secondary metabolite-rich latex from wounded roots which help to protect this plant from its native root feeding enemy, larvae of the common cockchafer beetle (*Melolontha melolontha*). A study showed that TA-G-deficient lines lost more main and side root mass than control lines after 10 d of feeding by *M. melolontha* relative to undamaged control plants [37].

5.2 Terpenes for abiotic stress responses

Under abiotic stress conditions volatile terpenes alleviate the effects of oxidative stress either through direct reactions with oxidant intercellularly, and alteration of ROS signaling. The amphipathic nature of isoprene enhances hydrophobic interactions between membrane proteins and lipids [38] which prevents membrane disintegration and protein disintegration. In response to oxidative stimuli, membrane bound SMs such as such as tocopherol and carotenoids (zeaxanthin, neoxanthin, and lutein) acts as antioxidants and may directly scavenge ROS in response to photoinhibition [39–43]. Singlet oxygen generated under oxidative stress considered is one of the strong oxidants also removed by the isoprenoids [44]. Oleuropein, a member of terpene family SMs, found higher amount of accumulation in leaves and roots of olive tree in response to salinity stress. The increase accumulation of oleuropein under salinity stress protect the olive tree from the oxidative stress [45]. The reason behind this relationship is that oleuropein acts as a glucose-reservoir for osmoregulation or high energy-consuming processes required for plant adaptation to salinity. Furthermore, oleuropein may act as an additional constituent of the antioxidant defense system of olive trees. Although most studies showed plant tolerant mechanism largely depends on the functions of non-volatiles antioxidant compounds. However, various volatiles organic compounds of the terpenes family have been connected in the protection to abiotic stresses, in particular photooxidative stress, heat stress and ozone stress. In response to ozone and heat stress, plant emitting isoprene alleviate ROS accumulation and protected plant from oxidative damages. Grapevines are not isoprene emitting plants but other volatiles isoprenoids such as monoterpenes emitter grapevine clone showed tolerance to heat stress [46].

Among the terpenes, isoprene (C5) and monoterpene hydrocarbons ameliorate abiotic stress in a number of plant species via membrane stabilization and direct antioxidant effects. Besides antioxidants properties of isoprene and monoterpene hydrocarbons they also rapid react with ozone to reduce its toxicity. A transgenic tobacco (*Nicotiana attenuata*) overexpressing a maize terpene synthase gene (ZmTPS10) might protected plants from intermitted heat stress by the accumulation of sesquiterpene hydrocarbons (C15) (E)-ß-farnesene and (E)-α-bergamotene [47–49]. Rice seedlings exposed to UV-B radiation and hydrogen peroxide accumulated higher amount of dozens of monoterpenes such as limonene, sabinene and myrcene to adapt in the altering environment [50].

Zealexins and kauralexins are two acidic terpenoid phytoalexins mediate biotic damages caused by insect and pathogen in aboveground part of maize plants. Recently it is showed that terpenoid phytoalexins also protect root damages under abiotic stress factors such as drought and salinity stress. Wild type maize plant accumulated terpenoid phytoalexins are positively correlated with the biomass accumulation of the plants. On the other side, mutant maize deficient with kauralexin synthesis are sensitive to water deficit condition [51]. Carnosic acid (CA), a diterpene protect Labiatae species from water stress-induced oxidative damages in combination with that of other low-molecular weight antioxidants (α-tocopherol and ascorbate) in chloroplasts [52]. These findings suggest that terpenes protect plants from biotic and abiotic stress damages due to their antioxidant properties or direct quenching of oxidants.

6. Phenolics for stress responses in plant

Phenolics are one of the most ubiquitous groups of SMs which are synthesize in plants and possess biological properties like antifeedant [53], antioxidant, anti-apoptosis, anti-aging, anticarcinogenic, anti-inflammation, and cell proliferation activity. Phenolics consist of an aromatic ring with one or more hydroxyl groups. Coumarin, furano-coumarins, lignin, flavonoids, isoflavonoids and tanins are the available forms of phenolics. Phenolics are often produced and accumulated in the sub-epidermal layers of plant tissues exposed to stress and pathogen attack [54]. The concentration of a particular phenolic compound within a plant tissue is dependent on season and may also vary at different stages of growth and development [55]. Several internal and external factors, including trauma, wounding, drought and pathogen attack, affect the synthesis and accumulation of phenolics [56, 57].

6.1 Phenolics for biotic stress responses

Phenolics are ubiquitous SMs in plants serves as a protective agent, inhibitors, natural animal toxicants and pesticides against invading herbivores, nematodes, phytophagous insects, and fungal and bacterial pathogens [58, 59]. Among the phenolic compounds coumarins are simple phenolic widespread in vascular plants and appear to function in different capacities in various plant defense mechanisms against insect herbivores and fungi. Several studies in many different plant species have shown that coumarins can accumulate in response to infection by a diversity of pathogens, including viruses, bacteria, fungi and oomycetes. The extent and timing of coumarin accumulation in plant parts have been associated with the level of disease resistance [60, 61]. The phenolic compounds ferulic acid and protocatecuic acid are accumulated increasingly in rice by the fungal attack to reduce mycotoxin. The accumulation of these two phenolics are positively correlated with *p*-coumaric acid and 4-hydroxybenzoic acid to protect plant from mycotoxin [62].

6.2 Phenolics for abiotic stress responses

The accumulation of phenolics in plant tissues is considered as an adaptive response of plants to adverse environmental conditions. In response to various external stimuli plant cell increases accumulation of phenolic substances. Therefore, the degree of interactions between plants and their changing environments has been a major driving force behind the emergence of specific natural products. For example, cold stress increases phenolic production into the cell wall in winter rye (*Secale cereale*) either as suberin or lignin. Lignification and suberin

deposition increase resistance to cold stress. These cell wall thickenings protect the plant from freezing stress. An increase in cell wall thickening could reduce cell collapse during freezing-induced dehydration and mechanical stress, thus providing freezing resistance to the plant [63]. Inhibition of root growth was recorded due to the accumulation of soluble phenolics and higher lignification in cucumber. Soluble phenolic compounds increased with time at chilling temperature but after rewarming these were decreased slightly. The decreased level in both organs (hypocotyl and root) after rewarming may suggest their important role in protection of both soybean organs against chilling injury. These compounds may participate in auxin metabolism, change membrane permeability, influence respiration and oxidative phosphorylation or protein synthesis [64].

Metabolic name of phenol	Nature of response	Abiotic stress	Plant species	Reference
Coniferyl alcohol, ferulic acid and p-coumaric	Increase accumulation and tolerance level	Nutrient deficiency	Reviewed in various plant species	Ahagnar et al. [72]
Chlorogenic acid, apigenin and luteolin	Increase accumulation and tolerance level	Drought stress	*Capsicum annuum L.*	Rodríguez-Calzada et al. [73]
Chlorogenic acid, rutin, hyperoside, isoquercetine, quercitrine and quercetine	Increased accumulation and tolerance level	Salinity	*Hypericum pruinatum*	Caliskan et al. [74]
Protocatecuic acid	Increased tolerance level	Salinity *S. macrosiphon*	Valifard et al. [67]	
Flavonols and hydroxycinnamic acids	Increase accumulation and tolerance level	Heat stress, salinity stress	*Solanum lycopersicon cv. Boludo*	Martinez et al. [75]
Chlorogenic acid	Increased accumulation	Full sunlight	*V. myrtillus*	Alqahtani et al. [68]
Caffeic acid, p-coumaric acid and ferulic acid	Decreased accumulation and tolerance level	Drought	*Vitis vinifera* L.	Kro'l et al. [76]
Flavonoids, isoflavonoids	Increased accumulation, become drought resistant	Drought *Arabidopsis thaliana*	Nakabayashi et al. [66]	
Quercetin	Increased level of deposition provide protection from damaging light	UV	*F. esculentum*	Regvar *et al*. [65]
Catechin and quercetin	Increased accumulation and become resistant against heavy metal	Heavy metal	*Zea mays L*	Michalak [69]
Lignin or suberin	Increased deposition and become freezing resistant	Cold stress/free zing	*Secale cereal*	Griffith and Yaish [63]

Table 1.
Nature of responses of phenolic compounds to abiotic stress in some plant species.

Exposure of ambient solar UV-B radiation to plants in open fields adversely affects macromolecules through the generation of ROS. At the same time, plants synthesize phenolic compounds, which act as a screen inside the epidermal cell layer to defend themselves from this damaging radiation and by adjusting the antioxidant systems at both the cell and whole organism level. A comparative accumulation of phenolics were measured after UV irradiation in buckwheat genotypes (*Fagopyrum esculentum and F. tataricum*) and found a specific increase of quercetin concentration in *F. esculentum* [65]. Drought is the major abiotic stress that affects plant growth and development and causes losses in agricultural production. As has been reported by several studies, phenolics content increased in plants under water scarcity to improve drought tolerance in *Arabidopsis thaliana* [66]. Tolerant and sensitive rice cultivars to salinity showed variable amount of phenolic compounds. A large increase of total phenolics and the content of protocatechuic acid was found in tolerant varieties, whereas in contrast, a markedly reduce was found in the susceptible cultivar [67]. In addition, the content of flavonoids and chlorogenic acid are positively correlated to the growth-lighting condition in Australian *Centella asiatica* (L.) *Urb* [68].

Certain flavonoids exhibit the ability to provide heavy metal stress protection by transition metals chelation (e.g., Fe, Cu, Ni, Zn), which generates hydroxyl radical via Fenton's reaction revealed that the chelation of these metals in the soil may be an effective form of defense against the effects of high metals concentration toxicity. The biosynthesis of phenolic compounds that are precursors of lignin intensifies under stress conditions [69]. Research on corn plants (*Zea mays* L.) confirmed this phenomenon when grown on soil contaminated with aluminum ions and root exudates were found with high levels of catechin and quercetin. Phenolic compounds also contribute to reduce heavy metal toxicity in plants. Cadmium metal-stressed *Brassica juncea* plants accumulated higher amount of rutin polyphenol than untreated plants to prevent oxidative damages [70]. Phenolic compounds were related to the antioxidant activity, and they play a major role in stabilizing lipid peroxidation. Actually during stress condition plants become potentially active and by releasing phenolic substance, modulating the activities of antioxidants, enzyme activities, and radicals scavenging activities demonstrated their active participation in oxidative stress management [71]. Some other evidences of nature of responses of phenolic compounds to abiotic stress in some plant species are summarized in **Table 1**.

7. N and S containing SMs for stress responses in plant

A large family of N and S containing SMs found in approximately 20% of the species of vascular plants, most frequently in the herbaceous dicot and relatively a few in monocots and gymnosperms. They include alkaloids, cyanogenic glucosides, non-protein amino acids phytoalexins, thionine, defensins and allinin. Most of them are biosynthesized from common amino acids.

7.1 N and S containing SMs for biotic stress responses

Alkaloids are nitrogenous organic SMs that have been shown to have antimicrobial activity (such as quinolones, metronidazole, or others) through inhibiting enzyme activity or other mechanisms. Squalamine, a polyamine alkaloid, acts through a detergent-like mechanism of action against gram-negative bacteria, leading to the disruption of their outer membranes, and it depolarizes gram-positive bacterial membranes [77].

Phytoalexins are S containing SMs, in response to fungal and bacterial pathogen, other forms of stress such as mechanical damages accumulate in the infection sites. The accumulation of phytoalexins limit the spreading of pathogen by inducing cell death known as hypersensitive response (HR) in a diverse group of plants. Defensins, thionins and lectins S-rich SMs accumulate in pathogen attack and external injury. These compounds also showed broad range of inhibition of microbial pathogen such as fungi and bacteria [78]. Glucosinolates are sulfur-rich SMs, widely synthesized in all vegetable and oilseed species of the order Brassicales (*Brassica oleracea*). The enzyme myrosinase (thioglucosidase) are stored in special myrosinase cells. When the tissue damage is commenced due to insect feeding, this enzyme comes into contact with glucosinolates and hydrolyses indole glucosinolates to produce nitriles and unstable isothiocyanates and aliphatic glucosinolates to produce volatile and pungent isothiocyanates. These products have toxic properties that inhibits growth (antibiosis) and act as feeding deterrents (antixenosis) against a range of insects; from leaf chewing lepidopteran larvae to phloem-feeding aphids [79]. Glucosinolate accumulation by the attack of diamondback moth insect on cabbage protect the plant by creating toxicity [80].

7.2 N and S containing SMs for abiotic stress responses

Alkaloids are N containing SMs also trigger adaption mechanism of plants. The concentration of four kind of alkaloids such as vindoline, catharanthine, vinblastine and vincristine significantly increased with the increasing saline concentration but the total dry weight to some extent were decreased. The reduction in plant growth may be an adaptive response to salt stress which allows the conservation of energy, thereby launching the appropriate defense response and also reducing the risk of heritable damage [81]. To adapt in the water scarcity stress *Senecio jacobaea*, *Senecio aquaticus*, and their hybrids increased the accumulation of pyrrolizidine alkaloids (PAs) [82]. The influence of drought stress changes the contents of alkaloids such as narkotine, morphine, codeine in *Papaver somniferum.* The comparison to the control group demonstrated that alkaloids narkotine and morphine trigger tolerance mechanism of plants [83]. The contents of alkaloids such as vindoline, catharanthine and vinblastine were significantly increased in the seedling leaves of *Catharanthus roseus* under short exposure of heat stress. Therefore, accumulation of alkaloids species under stressful conditions are critically important to adapt in the altering environments.

8. Conclusion

Plant tolerance to stresses is jointly controlled by the plants' anatomy, physiology, biochemistry, genetics, development and evolution. In addition to the primary metabolites, in response to various stresses either biotic and abiotic plants start to synthesize SMs in their cell. As a result, some physiological modification such as metabolic adjustment, ion and water balance, regulation of stomatal conductance, activation of different types of antioxidant and enzyme occurs which help the plant to increase tolerance level. Plant tolerance and adaptation mechanism to stressful conditions are mainly adjusted by the modifying primary metabolism pathway. According to the aforementioned data, SMs functions on stress adaptation are established in the recent year. Therefore, manipulating the generation and action of SMs and the activity of genes responsible for the accumulation of SMs are critically important to enhance the tolerance level and adaptability of plants under stressful conditions.

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