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Physiological Function of Phenolic Compounds in Plant Defense System

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Abstract

Plants respond to various abiotic and biotic stress conditions through accumulation of phenolic compounds. The specificity of these phenolic compounds accumulation depends on the type of stress condition and the response of plant species. Light stress induces biosynthesis of phenolic acids and flavonoids in plants. Temperature stress initially induces biosynthesis of osmoprotective compounds and then later stimulates synthesis of antioxidant enzymes and antioxidant compounds such as flavonoids, tannins and phenolic acids in plant cells. Salinity causes oxidative stress in plants by inducing production of reactive oxygen species. To resist against oxidative stress plants produce polyphenols, flavonoids, anthocyanins, phenolic acids and phenolic terpenes. Plants biosynthesize phenols and flavonoids during heavy metal stress to scavenge the harmful reactive oxygen species and to detoxify the hydrogen peroxide. Plants accumulate phenols at the infection sites to slow down the growth of microbial pathogens and restrict them at infected site. Plants also accumulate salicylic acid and H_2O_2 at the infection site to induce the systemic acquired resistance (SAR) against microbial pathogens. Plants accumulate phenolic compounds which act as inhibitor or toxicant to harmful nematodes, insects and herbivores. Hence, phenols regulate crucial physiological functions in plants to resist against different stress conditions.

Keywords: plant defense, salinity, drought, microbial pathogens, insects, herbivores, phenols, flavonoids, tannins, terpenes

1. Introduction

Plants have developed various metabolic pathways which respond to different abiotic and biotic stress conditions specifically through biosynthesis of secondary metabolites. These metabolic pathways are linked with the primary metabolic pathways which are the integral part of growth regulating programmes in plants. During stress, plants reduce their growth and divert the primary metabolism towards biosynthesis of secondary metabolites. It specifically controls the expression level of genes through ontogeny and circadian clock phenomenon which are transcription factors responsible for regulation of growth and accumulation of various secondary metabolites in plants [1–6]. The

transportation and accumulation of secondary metabolites regulates defense and development processes in plants based on the developmental stage, type of tissue or organ, and specific stress condition. Among various plant metabolites, phenolic compounds are the natural secondary metabolites that are biosynthesized in plants through metabolic pathways such as pentose phosphate, shikimate, and phenylpropanoid pathway [7–9]. These pathways are used by plants to produce either monomeric phenolic compounds such as flavanoids, phenolic acids and phenylpropanoids or polymeric phenolic compounds like tannins, lignins, lignans, and melanins. Phenolic compounds possess structural diversity due to their specific function in plant growth and defense mechanism. Some phenolic compounds are widely available in many plant species while others are specifically available only in certain plants species [10]. These phenolic compounds not only help in regulating various types of physiological functions in plants during growth and development but are also involved in plant defense mechanisms. They are known to have defensive function against abiotic and biotic stress conditions. Abiotic stress includes stress generated due to environmental changes such as high or low light and temperature, ultraviolet (UV) radiation, deficiency of nutrients, drought or flood like conditions. Biotic stress includes infection from microbial pathogen, attack by herbivorous organisms, increased production of oxidative species and free radicals in cells. The capability to synthesize specific phenolic compounds in response to biotic or abiotic stress is developed in plants through adaptive evolutionary phenomenon. Due to different environmental challenges plants have developed diversity in synthesizing various phenolic compounds [11].

For example, there are remarkable accumulation of flavanoids and isoflavones when plants experience low temperature stress, nutrients deficiency, exposure to UV radiation, microbial infection or injured through herbivores attack [12–14]. Anthocyanins accumulation was observed in flowers and fruits to attract pollinators for pollination. Anthocyanins also accumulate in young leaves to protect them from herbivorous insects and photodamage to regulate normal growth of plants [15]. Flavanoids are observed in guard cells of plants to protect tissue from UV radiation. They also accumulate to reduce the reactive oxidative stress generated through UV-B radiation [16]. Accumulation of phenols is observed in plants when plant experiences toxic metal stress from soil [17, 18]. Phenolic compounds help plant to develop resistance against microbial pathogens by inducing position explicit oversensitive response to protect spread of infection [8]. Proanthocyanidins, gallotannins and ellagitannins accumulation was observed in plants when infected with viruses, fungi or herbivores during early development stages of plant [8]. Secretion of t-cinnamic acid was observed from barley roots when it was infected by fungal pathogen fusarium [19]. Secretion of rosmarinic acid was observed in roots of *Ocimum basilicum* when it was infected with fungal pathogen *Pythium ultimum* [20]. Nematicide iridoid glycosides accumulation was observed in roots of plant *Plantago lanceolata* when it was infected with nematodes [21].

2. Plant defense against light stress

Plants accumulate phenolic acids and flavonoids in the vacuoles of mesophyll and epidermal cells during the light stress through photosynthetic apparatus and metabolism [22–24]. Falcone Ferreyra et al. [25] observed that when maize plants are exposed to UV-B radiation expression of genes P1, B and PL1 increases which induces biosynthesis of transcription regulators anthocyanin and 3-deoxy-flavanoid which in turn regulates the activity of protein ZmFLS1 for converting the dihydroflavonols, dihydroquercetin and dihydrokaempferol to flavonols, quercetin and kaempferol respectively. Radyukina et al.

[26] observed the accumulation of flavonoids, and anthocyanins in plants exposed to light and salinity stress. They suggested that flavonoids protect plants from UV-B radiation and anthocyanins protect from salinity stress. Manukyan [27] observed high accumulation of total phenol in *Melissa officinalis*, *Nepeta cataria* and *Salvia officinalis* plants after exposure to low UV-B radiation. Ma et al. [28] observed in *Salvia miltiorrhiza*, that UV radiation increases concentration of rosmarinic acid and lithospermic acid in plant. They suggested that methyl jasmonate induces transcripts of genes accountable for biosynthesis of enzymes tyrosine aminotransferase, cinnamic acid 4-hydroxylase, 4-hydroxyphenylpyruvate reductase and phenylalanine ammonia lyase (PAL) which in turn regulates the biosynthesis of rosmarinic acid and lithospermic acid. Ghasemzadeh et al. [29] observed that the accumulation of specific phenolic compounds in sweet basil leaves was dependent on the intensity of UV-B radiation. They suggested that phenolic compounds are synthesized in plants as a response towards the generated reactive oxygen species due to UV light damage. They observed that phenolic acids such as cinnamic acid, gallic acid, quercetin, ferulic acid, catechin, rutin, luteolin and kaempferol which are precursors for biosynthetic pathway of flavonoids are synthesized earlier in leaves through phenylpropanoid metabolism using PAL and chalcone synthase enzymes. Jang et al. [30] observed in plant *Salvia plebeian* that under sunlight the level of rosmarinic acid reduces whereas level of homoplantagin and luteolin-7-glucoside increases. Csepregi et al. [31] observed that the accumulation of flavonols, quercetin and kaempferol derivatives increases in leaves of *Arabidopsis thaliana* when it is exposed to low UV-B light. León-Chan et al. [32] observed that the low temperature and UV-B radiation causes degradation of chlorophyll and accumulation of carotenoids, chlorogenic acid, flavonoids apigenin-7-O-glucoside and luteolin-7-O-glucoside in bell pepper plant leaves. They specifically observed that UV-B radiation increases flavonoids concentration in leaves whereas combination of low temperature and UV-B radiation increases chlorogenic acid concentration in leaves. They also observed that the luteolin-7-O-glucoside is involved in quenching of the reactive oxygen species developed due to low temperature and UV-B radiation stress. Peng et al. [33] observed that flavone O-glycosides are modulated by flavone 7-Oglucosyltransferase and flavone 5-O-glucosyltransferase during light stress. They suggested that allelic variation provides UV-B tolerance to plants in nature. Zhou et al. [34] also observed that flavonol accumulation is upregulated by UV-B irradiation in rice plants. Lobiuc et al. [35] suggested that the phytochemical content of basil green cultivar was high in red light whereas phytochemical content of basil red cultivar was high in blue light when exposed to different proportions of blue and red light. They observed that accumulation of rosmarinic acid, caffeic acid and anthocyanin increased when exposed to blue light as compared to white light. Chen et al. [36] suggested that the downregulation of genes *SmDXR*, *SmDXS2*, *SmGGPPS*, *SmCPS*, *SmHMGR* and *CYP76AH1* decreases tanshinone IIA content in *Salvia miltiorrhiza*. They also suggested that rosmarinic acid content increases when *Salvia miltiorrhiza* is exposed to UV light or combination of red and blue light. Taulavuori et al. [37] observed accumulation of phenolic compounds (chicoric acid and chlorogenic acid derivatives) in leaves of *Ocimum basilicum* and flavonoids (luteolin-glycoside derivatives, isorhamnetin diglycoside, apigenin derivatives) in plants of *Rumex sanguineus* after exposure to blue and blue-violet light. Stagnari et al. [38] observed that exposure of basil plants to colored light reduces the level of rosmarinic acid and caftaric acid in leaves whereas increased caffeic acid level in leaves. Nadeem et al. [39] observed that yellow light increases rosmarinic acid and chicoric acid in callus of basil whereas green light increases rosmarinic acid, eugenol and chicoric acid in callus of basil. They suggested that change in phytochemical content of callus of basil was due to the accumulation of reactive oxygen species by the metabolic action of CYP450 enzyme.

3. Plant defense against temperature stress

During high and low temperature stress, photosynthesis metabolism is inhibited and production of reactive oxygen species is stimulated which in turn damages the cells [40, 41]. To combat with this stress plants accumulate osmoprotective compounds such as soluble sugars, proline and glycine betaine which provides protection from oxidative damage [42]. Plants also biosynthesize antioxidant enzymes and substances to defense against oxidative stress [43]. Plants accumulate antioxidant metabolites such as phenolics, terpenes or alkaloids during temperature stress and develop stress resistance ability [44–47]. During temperature stress activity of enzyme phenylalanine ammonia lyase increases which results in accumulation of phenolic compounds in plant cells. Rivero et al. [48] has suggested that during heat and cold stress there is remarkable accumulation of soluble phenolics in watermelon and tomato. Kasuga et al. [49] suggested that cold induced phenols accumulation in plant cells decreases the freezing point, maintains water potential and protects from cell disruption. Weidner et al. [50] observed increased content of tannins and soluble phenols in roots of grapevine after cold treatment. Amarowicz et al. [51] observed increased concentration of gallic acid, ferulic acid and caffeic acid in grapevines during cold stress. Isshiki et al. [52] observed accumulation of farinose flavonoids on aerial part of primula during the freezing cold stress. Rana and Bhushan [53] have suggested that temperature stress induces biosynthesis of phenolic compounds in plants and provides tolerance against cold stress. Commisso et al. [54] suggested that phenolic compounds protect cytoskeleton of microfilaments from reactive oxygen species. Chalker-Scott and Fuchigami [55] suggested that cellular injury and stress tolerance capacity in plants is increased by accumulation of phenolic compounds and then its incorporation in to the cell wall of cells in the form of either suberin or lignin.

4. Plant defense against drought stress

During drought stress plants produce reactive oxygen species (hydrogen peroxide H_2O_2 , singlet oxygen O , superoxide anion O^{2-} , and hydroxyl radical OH) which may cause protein degradation, cell mortality, membrane damage, lipid peroxidation and deoxy ribose nucleic acid (DNA) damage [56, 57]. In order, to prevent this damage, plants have detoxification system to neutralize the deleterious effect of reactive oxygen species which is regulated either by enzymes (superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), peroxidase (POD)) or by antioxidant molecules (phenols, vitamin C, carotenoids, tocopherol and glutathione) [58]. In plants over-production of reactive oxygen species during stress is balanced through production of phenolic compounds and flavonoids using phenylpropanoid pathway [59]. Akula and Ravishankar [60] observed accumulation of flavonoids in leaves of willow plant during drought stress. Similarly, Nakabayashi et al. [61] observed increase in accumulation of anthocyanin and flavonoids in leaves of *Arabidopsis* in response to drought stress.

The biosynthesis and accumulation of phenolic compounds during drought stress is regulated by enzymes of phenylpropanoid pathway. Initially, phenylalanine ammonia lyase (PAL) diverts the central carbon flux of primary metabolism towards synthesis of phenolic compounds. Increase in PAL activity indicates beginning of plant antioxidant defense mechanism and is regulated by feedback inhibition process through increase in accumulation of its own product cinnamic acid [62]. The variations in the transcription level of genes encoding for phenylalanine ammonia lyase (PAL) regulates

the activity of the enzyme and in turn specific phenolic compounds are synthesized in response to biotic or abiotic stress. Chalcone synthase is an enzyme which shows high activity during drought stress. It is a key enzyme in flavonoid synthesis pathway which acts on the CoA-ester of cinnamic acid to form chalcone. The chalcone is converted to flavanone by chalcone flavanone isomerase (CHI) enzyme through isomerization which is a precursor for synthesis of numerous flavonoid compounds [59]. Hura et al. [63] observed accumulation of ferrulic acid and high activity of PAL enzyme in leaves of maize under water stress conditions. Even Phimchan et al. [64] observed high PAL activity and ferrulic acid accumulation in fruits of capsicum during drought stress. Nakabayashi et al. [61] observed high activity of another enzyme chalcone synthase in response to drought stress in *Arabidopsis*. Gharibi et al. and Siracusa et al. [65, 66] have observed high accumulation of phenolic compounds in vegetables, fruits and cereals under drought stress. Sarker and Oba [67] observed high accumulation of flavonoids in leaves of *Amaranthus tricolor* during drought stress. Brunetti et al. [68] suggested that the high metabolic plasticity and accumulation of flavonoids in leaves of *Moringa oleifera* has provided ability to the plant to survive in water deficit conditions.

5. Plant defense against salinity stress

Salinity stress induces production of reactive oxygen species in plants which in turn causes oxidative stress. To resist against oxidative stress plants produce antioxidative metabolites such as polyphenols, flavonoids, anthocyanins, proanthocyanidins, phenolic acids and phenolic terpenes which quench the singlet oxygen, neutralize or absorb free radicals, decompose peroxides [45–47]. Yang et al. [69] suggested that accumulation of specific phenolic compounds in plants during salinity stress also depends on the type of plant species. Parida et al. [70] suggested that there was significant increase in polyphenols content in plants of *Aegiceras corniculatum* after 250 mM NaCl treatment. Ksouri et al. [71] suggested that there was significant increase in polyphenols in *jerba* plants after treatment with 100 mM and 400 mM NaCl. Hanen et al. [72] suggested that the phenol content in leaf of plant *Cynara cardunculus* increases in response to 50 mM NaCl treatment. Lim et al. [73] suggested that the accumulation of phenolic compounds in response to salinity stress in *Fagopyrum esculentum* (*Fagopyrum esculentum*) plants is due to the increased content of compounds such as vitexin, isoorientin, rutin, and orientin. Petridis et al. [74] suggested that the salinity stress stimulated the biosynthesis of phenols and oleuropein in leaves of olive plants. Borgognone et al. [75] observed that salinity stress increases the concentration of total phenols and flavonoids in leaves of artichoke and cardoon plants.

Another mechanism acquired by plants to resist against salinity stress is through salicylic acid which is an endogenous growth regulator and signaling molecule. It is a phenolic phytohormone which controls stress by decreasing H_2O_2 level and reducing oxidative damage in plants [76]. It enhances growth, development and productivity in plants during stress conditions [77]. Many research studies have suggested the function of salicylic acid in increasing salinity tolerance in plants. Jini and Joseph and Khan et al. [78, 79] had suggested that salicylic acid strengthens the salinity tolerance in plants such as *Medicago sativa*, *Vicia faba*, *Brassica juncea* and *Vigna radiate* (*Vigna radiate*). Jayakannan et al. [80] observed that exogenous salicylic treatment increased water content and growth of shoots in *Arabidopsis* plants growing under saline conditions. Various studies of mutant plants have suggested the function of salicylic acid in providing salinity tolerance to plants [81–85]. Various studies on exogenous application of

salicylic acid to salinity stressed plants have also confirmed that salicylic acid alleviates the toxic effect of salt and increases the resistance of plants against salinity [86–91].

6. Plant defense against heavy metals

Ciriakova [92] has suggested that plants take up heavy metals through their roots which get accumulated inside the cell wall by apoplastic system. These heavy metals cause harm to plants by hindering the biochemical metabolisms such as cell division and elongation, photosynthesis, nitrogen metabolism, respiration, mineral nutrient utilization and water transportation [92, 93]. They inactivate essential enzymes by binding to their active sites, induce biosynthesis of reactive oxygen species, and exchange metal ions from biomolecules [94]. Plants biosynthesize phenols and flavonoids to scavenge the harmful reactive oxygen species which donates their electron to peroxidase enzymes to detoxify hydrogen peroxide produced under heavy metal stress conditions [95]. Shemet and Fedenko [96] observed accumulation of phenolic compounds in roots of maize under cadmium stress. Ali et al. [97] observed high activity of enzymes responsible for biosynthesis of phenols and flavonoids in roots of *Panax ginseng* exposed to copper sulphate. Kováčik et al. [98] observed in *Matricaria chamomilla* plants that when plants were exposed to nickel activity of polyphenol oxidase enzyme decrease and there was increase in total phenol content of leaf rosettes. There was remarkable increase in activity of phenylalanine ammonia lyase (PAL) and shikimate dehydrogenase enzymes with accumulation of chlorogenic acid, protocatechuic acid and caffeic acid. Pawlak-Sprada et al. [99] suggested from transcriptional analysis of lupine and soyabean roots exposed to cadmium and lead that heavy metal stress induces phenylpropanoid pathway in plants. Márquez-García et al. [100] observed in *Erica andevalensis* plants that when plants are exposed to cadmium, the concentration of rutin, cinnamic acid derivatives and epigallocatechin increases. He suggested that excess cadmium exposure decreases the concentration of phenolic in plants to reduce the deleterious effect of produced phenoxyl radicals. Malčovská et al. [101] suggested that the production of phenolic compounds increases in plant cells when plants are under heavy metal stress as phenols are reactive oxygen species scavengers and metal chelators. Kisa et al. [102] observed in *Zea mays* leaves that when plants are exposed to cadmium and lead, the phenolic compounds increased in leaves were chlorogenic acid and rutin whereas there was decrease of caffeic acid and ferulic acid.

7. Plant defense against microbial pathogens

The plant defense mechanism occurs in two stages, in first response there is rapid accumulation of phenols at the infection site which slows down the growth of pathogen. In second response it biosynthesizes specific stress related substances (simple phenols, phenolic phytoalexins, hydroxycinnamic acids etc.) which restrict the pathogen at the infected site. The step by step process of plant defense mechanism includes host cell death, necrosis, accumulation of phenolic compounds, modification of cell wall through phenolic compounds deposition or development of barriers, and at last synthesis of specific toxic compounds to eliminate the pathogens [103]. Pathogenic microbes are recognized by plant cell membrane proteins which are known as pattern recognition receptors (PRRs). They recognize conserved pathogen associated molecular patterns (PAMP) of microorganisms and gives signal to synthesize specific phenolic compounds, through defense mechanism known as PAMP induced immunity [104–110].

Plants induce multicomponent defense response after pathogen attack which includes reprogramming of genetic resources, expression of large number of defense related genes, and encoding of enzymes that catalyze defense metabolites (phytoalexins). This physiological process is regulated by transcriptional factors responsible for accumulation of specific phytoalexins in plants. On the other hand, salicylic acid also plays crucial role in resisting pathogen attack in plants. During pathogenic infection there is remarkable accumulation of pathogenesis related (PR) protein at the location distant from the infection site. Simultaneously, there is accumulation of salicylic acid and H_2O_2 at the infection site to regulate the systemic acquired resistance (SAR) in plant. It is being observed that exogenous application of salicylic acid induces systemic acquired resistance (SAR) in plants and provides resistance against pathogens [10].

Plants possess innate immunity against pathogenic bacterial species. They have developed metabolic mechanism to resist against pathogenic bacterial through accumulation of phenolic compounds. Postel and Kemmerling [111] suggested that plants recognize the bacterial pathogens through pathogen associated molecular patterns (PAMPs). Mikulic Petkovsek et al. [112] observed accumulation of hydroxycinnamic acid, gallic acid, quercetins and catechin in walnut husk plant infected by *Xanthomonas arboricola* bacteria. Cho and Lee [113] observed accumulation of sakuranetin in rice plants infected by *Xanthomonas oryzae* and *Burkholderia glumae*. Wang et al. [114] suggested that polyphenols inhibit bacterial species such as *Escherichia coli*, *Klebsiella pneumonia*, *Staphylococcus aureus*, *Salmonella choleraesuis*, *Bacillus subtilis*, *Serratia marcescens* and *Pseudomonas aeruginosa* by altering the properties and permeability of plasma membrane of cell and generation of reactive oxygen species.

Previous studies by various scientists have suggested that phenolic compounds eliminate fungal pathogens by altering the permeability of cell membrane, altering the integrity of cell wall, suppression of enzymes activity, formation of free radicals, inhibition of certain protein biosynthesis, damage of DNA and suppressing the expression of virulence genes [115–118]. The mode of action of flavonoids against fungal pathogens include damage of cytoplasmic membrane, distraction of cell wall, induction of cell death process, inhibition of enzyme activities, chelating of metal ions, binding with extracellular or soluble proteins, inhibition of efflux pump activity [12]. Gallego-Giraldo et al. [119, 120] suggested that the suppression of lignin biosynthesis genes (HCT) leads to the accumulation of salicylic acid which in turn increases transcription level of some pathogenesis related genes to improve immunity of plants. Widodo et al. [121] suggested that coumarins inhibit growth of fungi by altering the thickness of mitochondrial matrix, inducing apoptosis or inducing cell wall perforation which leads to release of cytoplasm from cell. Rahman [122] observed accumulation of furanocoumarin in celery and parsnip roots after *Sclerotinia sclerotiorum* infection. Al-Barwani and Eltayeb [123] observed antifungal activity of psoralen and furanocoumarin against fungi *Alternaria brassicicola*, *Sclerotinia sclerotiorum* and *Cercospora carotae*. Al-Amiery et al. [124] observed antifungal activity of coumarins against *Aspergillus niger* and *Candida albicans*. Serpa et al. [125] suggested that the flavone compound baicalein inhibits the infection caused by *Candida albicans* by inhibiting the activity of efflux pump and inducing apoptosis process. Zuzarte et al. [126] suggested that the chalcone carvacrol disrupts the cytoplasmic membrane of cell and induces apoptosis process in various *Candida* species. Belofsky et al. [127] suggested that the isoflavone sedonan A isolated from plant *Dalea formosa* prevents from infection caused by *Candida albicans* and *Candida glabrata* by inhibiting the activity of intracellular transcription targets and efflux pumps. Sherwood and Bonello [128] suggested that lignin has potent antifungal activity against fungi *Diplodia pinea* under *in vitro* conditions. Anttila et al. [129] suggested that the tannins extract isolated from

cone and bark of conifer plants has toxic effect on four soft rot fungi, three white rot fungi and eight brown rot fungi. Dos Santos et al. [130] observed antifungal activity of *Accacia mearnsii* tannin extract against *Aspergillus niger* and *Candida* sp. Wang et al. [114] observed that the ester derivatives of monoterpenes carvacrol and thymol were toxic against the phytopathogenic fungi in *in vitro* conditions. Rashed et al. [131] observed the toxic effect of *Ammi visnaga* seed extract against fungi *Rhizoctonia solani* was due to the presence of coumarins. Marques et al. [132] observed accumulation of phenolic compounds and lignin at the infected site during early stage to prevent the penetration of *Sporisorium scitamineum* fungi in other parts of sugarcane plant. Ogawa and Yazaki [133] suggested that the inhibitory mode of action of tannins is the inhibition of the activity of extracellular enzymes, inhibition of oxidative phosphorylation, or prevention of nutrient availability from substrate by protein insolubilization or metal complex formation.

Kumar and Pandey [134] suggested that Phenolic compounds suppress the viral infection in plants and represses the replication of viruses through mode of actions such as damage of protein, DNA or ribose nucleic acid (RNA), inhibition of viral enzyme activities. Zakaryan et al. [135] suggested that flavonoids suppresses the viral infection by distraction of viral RNA translation, inhibition of viral DNA replication, inhibition of viral protein synthesis, inhibition of transcription factors responsible for viral enzymes and genome synthesis and interfering with viral structural protein. Shokoohinia et al. [136] suggested that coumarins inhibit viral replication in cells by inhibition of enzymes such as protease, integrase and reverse transcriptase. Dunkić et al. [137] observed that the monoterpenes carvacrol and thymol present in essential oil of *Satureja montana* L. ssp. Variegata has antiviral activity against cucumber mosaic virus and tobacco mosaic virus. Hu et al. [138] observed antiviral activity of different phenolic compounds isolated from *Arundina graminifolia* against tobacco mosaic virus. Zhao et al. [139] suggested that the two flavonoids (fistula flavonoid B and C) isolated from bark and stem of plant *Cassia fistula* has antiviral activity against tobacco mosaic virus. Li et al. [140] identified phenolic compound gramniph-enol which exhibited antiviral activity against tobacco mosaic virus. Liu et al. [141] observed antiviral potential of two coumarins (6-hydroxy-5-methoxy-7-methyl-3-(40-methoxyphenyl)-coumarin and 6-hydroxy-7-methyl-3-(40-methoxyphenyl)-coumarin) isolated from leaves of *Nicotiana tabacum* against tobacco mosaic virus.

8. Plant defense against insects, nematodes and herbivorous organisms

Plants have to face various pathogenic attacks in natural environment. To resist against these pathogens plants have adjusted their physiological metabolism and developed metabolic pathways which synthesize wide range of phenolic compounds. These phenolic compounds are used either to attract or repel different organism as per plants benefit. They protect plants by acting as inhibitors and toxicants against insects, nematodes and herbivorous animals which feeds on them [142–145]. Maxwell et al. [146] suggested that phenolic pigment (gossypol) found in cotton plants has toxic effect on *Heliothis zea*, *Heliothis virescens* and various other insect pests. Feeny [147] suggested that the tannins have inhibitory effect on the growth of *Opheropthera brumata* larvae. Levin [148] suggested that the phenolic quinone hypericin secreted by glans on leaves, sepals or petals of *Lypericum* spp. is toxic foe insects and mammals. He also suggested that the presence of gossypol in leaves and flowers of plants can inhibit grazing by mammals and infection by tobacco budworm or bollworm. Hedin et al. [149] suggested that some flavonoids present in cotton plants are feeding inhibitors for boll weevil, *Anthonomus*

grandis. Luczynski et al. [150] suggested that the concentration of catechol increases in leaves of strawberry when infected by spotted spider mites. Byers [151] suggested that the bark beetle *Scolytus multistriatus* does not consume *Carya ovate* due to the presence of phenolic compound juglone which is not palatable to them. Accumulation of anthocyanins provides red, blue or purple color to leaves, flowers or fruits which protects plant from the herbivorous animals and insect pathogens. These pigments developed in leaves are either not palatable for animals to eat or they are not visible to animals due to lack of red visualization receptor. Insect pathogens avoid red leaves and they always colonize in green leaves. Better chemical defense, worst nutritional value and induced adverse effect in insects is observed in plants having red leaves. Hence autumn colors of leaves is an adaptive mechanism of plants to reduce the pathogen attacks [152–157]. Rehman et al. [158] suggested that catechol binds to the digestive system of mites and inactivates its digestive enzymes. Fürstenberg-Hägg et al. [159] suggested that wheat cultivars rich in phenolic content are not consumed by cereal aphids *Rhopalosiphum padi*.

9. Conclusions

Phenolic compounds regulate crucial physiological functions in plants to provide resistance against various biotic and abiotic stress conditions. To protect against UV radiation plants synthesize phenolic acids and flavonoids to scavenge the reactive oxygen species generated due to light stress. During temperature stress activity of phenylalanine ammonia lyase enzyme increases which results in accumulation of phenols in plants. The accumulation of phenols during drought stress is regulated by the activity of either phenylalanine ammonia lyase (PAL) or chalcone synthase. Phenylalanine ammonia lyase (PAL) activity accumulates phenolic acids which are used as precursors for biosynthesis of specific phenolic compounds. Chalcone synthase activity accumulates numerous flavonoid compounds in plants during water deficiency. During salinity stress plants accumulate polyphenols, flavonoids, anthocyanins, phenolic acids and terpenes to resist against the oxidative stress. Plants also accumulate salicylic acid during salinity stress to decrease the level of H_2O_2 and reduce the oxidative damage. Plants synthesize phenols and flavonoids to scavenge the reactive oxygen species produced during heavy metal stress. Plants accumulate phenolic compounds at infection site to reduce growth and penetration of microbial pathogens in other tissues and organs. It recognizes microbial pathogens and induces defense response at genetic level to biosynthesize defense metabolites. Plants also accumulate salicylic acid and H_2O_2 at infection site to regulate systemic acquired resistance. Plants accumulate phenolic compounds in organs which acts as inhibitors or toxicants for nematodes, insects and herbivores.

10. Future prospectives

The biosynthesis of phenolic compounds in plants during abiotic and biotic stress increases adaptation of plants in harsh environment. Hence, it is necessary to understand the molecular mechanism regulating biosynthesis and accumulation of specific phenolic compounds during particular stress condition. There should be genetic level studies on regulation of transcription factors responsible for biosynthesis of specific phenolic compounds during each stress. There should be progressive studies on interactive biology between phenolic compounds and salicylic acid to understand the crosstalk between them during salinity stress, oxidative damage and microbial pathogen attack.

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Conflict of interest

Authors declare that there is no conflict of interest.

Abbreviations

UV	ultra violet
H ₂ O ₂	hydrogen peroxide
ROS	reactive oxygen species
SOD	superoxide dismutase
APX	ascorbate peroxidase
CAT	catalase
POD	peroxidase
PAL	phenylalanine ammonia lyase
CHI	chalcone flavanone isomerase
SA	salicylic acid
PRRs	pattern recognition receptors
PAMP	pathogen associated molecular patterns
PR	pathogenesis related
SAR	systemic acquired resistance
DNA	deoxy ribose nucleic acid
RNA	ribose nucleic acid

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