

Review

Response of Phenylpropanoid Pathway and the Role of Polyphenols in Plants under Abiotic Stress

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Abstract: Phenolic compounds are an important class of plant secondary metabolites which play crucial physiological roles throughout the plant life cycle. Phenolics are produced under optimal and suboptimal conditions in plants and play key roles in developmental processes like cell division, hormonal regulation, photosynthetic activity, nutrient mineralization, and reproduction. Plants exhibit increased synthesis of polyphenols such as phenolic acids and flavonoids under abiotic stress conditions, which help the plant to cope with environmental constraints. Phenylpropanoid biosynthetic pathway is activated under abiotic stress conditions (drought, heavy metal, salinity, high/low temperature, and ultraviolet radiations) resulting in accumulation of various phenolic compounds which, among other roles, have the potential to scavenge harmful reactive oxygen species. Deepening the research focuses on the phenolic responses to abiotic stress is of great interest for the scientific community. In the present article, we discuss the biochemical and molecular mechanisms related to the activation of phenylpropanoid metabolism and we describe phenolic-mediated stress tolerance in plants. An attempt has been made to provide updated and brand-new information about the response of phenolics under a challenging environment.

Keywords: abiotic stress; anthocyanin; antioxidant; flavonoid; phenolic acid; polyphenol

1. Introduction

Plants face a plethora of biotic and abiotic stresses during their entire life which have negative impact on their growth, development, and productivity [1–3]. Biotic factors include insect pests, fungi, and weeds whereas abiotic stresses include salinity, drought, heavy metals, pesticides, ultraviolet (UV) radiation, as well as heat and cold stress [3–18]. The amplitude of these abiotic stresses has increased severely in recent years principally due to anthropogenic activities [7,19]. Plants, being sessile, are persistently exposed to these factors and require a set of effective mechanisms which can be activated under unfavorable circumstances to sustain their life cycle [20]. According to some reports, the projection of these stresses contributes significantly and affects the growth and productivity by reducing crop yield and overall crop production by 70% and 50%, respectively [21,22]. Thus, it is imperative to reduce the crop productivity losses by improving crop performance through various approaches, including application of plant bio-stimulant products as well as stimulation

of plant secondary metabolism [11,23,24]. Plants need to endure different abiotic stresses and polyphenols accumulate in response to these stresses helping plants to acclimatize to unfavorable environments [25,26]. Hence, the concentration of phenols in plant tissue is a good indicator to predict the extent of abiotic stress tolerance in plants which varies greatly in different plant species under an array of external factors.

Phenolic compounds influence the plant growth and development, including seed germination, biomass accumulation, and improved plant metabolism [27–30]. In this regard, we summarized different studies showing a broad spectrum of different effects of abiotic stresses and discussed how endogenous phenol levels can help in mitigating abiotic stress in plants. Moreover, physiological and molecular mechanisms connected to the phenylpropanoid pathway underlying abiotic stress tolerance have extensively discussed. At the end, we explained phenol-mediated stress tolerance and suggestions have been made to further escalate the extent of deep mechanistic studies.

2. Biosynthetic Pathway of Polyphenols in Plants

Phenolics are known to be the largest groups of secondary metabolites in plants varying from simpler aromatic rings to more complex ones, such as lignins. These compounds originated from phenylalanine therefore are also called as phenylpropanoids. Polyphenols are characterized by the presence of large multiples of phenol structural units. The number and characteristics of these phenol structures underlie the unique physical, chemical, and biological properties of particular members of each class. Phenols are indeed divided into several groups such as phenolic acids, flavonoids, stilbenes, and lignans with peculiar properties. Plant phenolics are synthesized biogenetically through a shikimate/phenylpropanoid pathway, whereas a mevalonate pathway generates terpenoids. Both these secondary pathways produce a wide array of monomeric and polymeric structures encompassing a comprehensive array of physiological and biochemical roles in plants. The term “secondary metabolites” refers to the metabolites or phytochemicals synthesized through secondary metabolism. During the biosynthesis of phenolic compounds, erythrose 4-phosphate is combined with phosphoenolpyruvate (PEP) to form phenylalanine. Then phenylalanine ammonia lyase (PAL) catalyzes the conversion of phenylalanine to *trans*-cinnamic acid. Several other phenolic compound such as flavonoids, coumarins, hydrolysable tannins, monolignols, lignans, and lignins are formed through this pathway, formally known as the phenylpropanoid pathway (see complete details in [26,31–33]).

3. Physiological Roles of Phenolics in Plants

Phenolics are widely distributed and are involved in key metabolic and physiological process in plants [34,35]. Phenolics influence different physiological processes related to growth and development in plants including seed germination, cell division, and synthesis of photosynthetic pigments [36]. Phenolic compounds have been exploited for several application including bioremediation, allelochemical, promotion of plant growth, and antioxidants as food additives [37]. In plants, phenolic accumulation is usually a consistent feature of plants under stress, which represents a defensive mechanism to cope with multiple abiotic stresses [31]. Plant phenolics play an important role in several physiological processes to improve the tolerance and adaptability of plants under suboptimal conditions [38–40]. In particular, a large number of secondary metabolites having antioxidant properties belong to this group [41] which can ameliorate plant performance under stress conditions.

Plants interact with their living environment through secondary metabolites. Polyphenols are, for example, involved in signal transduction from the root to the shoot and also help in nutrient mobilization. The roots exudates contain phenolic compounds which alter the physiochemical properties of the rhizosphere. Soil microbes transform phenolics into compounds which help in N mineralization and humus formation [42]. Furthermore, phenolics improve nutrient uptake through chelation of metallic ions, enhanced active absorption sites, and soil porosity with accelerated mobilization of elements like calcium (Ca), magnesium (Mg), potassium (K), zinc (Zn), iron (Fe), and manganese (Mn) [43]. Recently, Rehman, et al. [44] found that Zn application and plant growth

promoting rhizobacteria (PGPRs) treatment enhanced the contents of phenolics and organic acids (pyruvic acid, tartaric acid, citric acid, malonic acid, malic acid, succinic acid, oxaloacetic acid, oxalic acid, and methyl malonic acid) in root exudates of wheat, which helped in nutrient mobilization of Zn, N, and Ca and their uptake [44,45]. Phenolic compounds also help in N fixation in legumes. Legumes release several secondary metabolites from roots, principally flavonoid compounds (flavanols and iso-flavonoids) which play crucial role in Nod factors synthesis and in the production of infection tube during nodulation, given that they inhibit auxin transport and facilitate cell division [46].

Plant phenolics, as physiological regulator or chemical messenger, inhibit the IAA catabolism (dihydroxy B-ring flavonoids) or limit the IAA synthesis (monohydroxy B-ring flavonoids) [47]. Flavonoids play a key role in the development of functional pollen. For instance, addition of a very small dose of flavonol aglycones kaempferol or quercetin restored the fertility in mature pollen during pollination [48,49]. Some phenolic compounds (*trans*-cinnamic acid, coumarin, *p*-hydroxybenzoic acid, and benzoic acid) might be potentially phytotoxic if accumulated in high quantity and can inhibit germination and seedling growth [50] due to the disruption of cellular enzyme functioning and impairment of cell division. For instance, some phenolic compounds inhibit the prolyl aminopeptidase and phosphatase enzyme involved in seed germination in legumes [51]. Conversely, high phenolic acid contents have been reported to exert positive effects in seed germinating. In a recent study, Chen et al. [52] found a substantial increase in free (1042%), bound (120%), and total phenolic acid content (741%) in canary grass during germination. The spruce bark extract containing polyphenols stimulated the germination rate in *Lycopersicon esculentum* while inhibited root elongation [53]. Phenolics reduced the thickness and increased the seed tegument porosity which help in water imbibition and boost the germination rate [54]. Polyphenolic extracts of spruce bark intensified the photosynthetic activity and biosynthesis of assimilatory pigment (chlorophyll *a* and *b*) in maize and sunflower [55,56]. Phenolics reduced the energy required for ion transfer by modifying the structure of thylakoids and mitochondrial membranes [57]. As antioxidants, phenolic compounds participate in the scavenging of reactive oxygen species (ROS), catalyzing oxygenation reactions through formation of metallic complexes, and inhibiting the activities of oxidizing enzymes [58].

In conclusion, polyphenols are produced under optimal and (with higher levels) in suboptimal conditions in plants and play crucial role in the development encompassing signal transduction, cell division, hormonal regulation, photosynthetic activity regulation, germination, and reproduction rate. Plants exhibiting increased synthesis of polyphenols under abiotic stresses usually show a better adaptability to limiting environments.

4. Abiotic Stresses and Their Toxic Effects on Plants

In recent times, producing more food and preventing crop losses to meet the demands of ever-increasing human populations has gained unprecedented importance. Nevertheless, a large proportion of arable land face abiotic stresses (drought, salinity, cold, heat, heavy metal toxicity, UV radiation, etc.) which are expected to increase due to climate change and the incidence of these environmental stresses are further fueled by anthropogenic activities. These abiotic stresses cause alteration in physiological and biochemical processes of plants which results in diminished plant growth and poor yield [59]. These stresses bring rapid changes in cellular redox homeostasis with excessive reactive oxygen species (ROS) generation which eventually damage cell organelles and interfere in ROS-promoted signaling pathways [60]. Contrary to over production of ROS, a physiological redox state hampers normal cell functions and affects the plant immune system, suggesting that a threshold level of ROS is necessary for normal plant functioning (Figure 1; Farooq, et al. [61]). Increased ROS generation under abiotic stresses enhanced itself exponentially the production of ROS [62], which result in peroxidation and destabilization of cellular membranes. Recently Rehman, et al. [63] observed that heat stress and Zn deficiency cause reductions in growth (shoot and root biomass, and root length), and consequently impeded nutrient uptake, enhanced lipid peroxidation and impaired photosynthetic performance. In plants, ROS is produced from 1–2% of total O₂ consumed in high active cell organelles

like chloroplasts, mitochondria, and peroxisomes (Figure 1; [64]). The most common ROS are singlet oxygen ($^1\text{O}_2$), superoxide radicle ($\text{O}_2^{\bullet-}$), hydrogen peroxide (H_2O_2), and hydroxyl radicle ($\bullet\text{OH}$) [65].

Abiotic stresses disturb the balance between ROS generation and scavenge and accelerate ROS propagation which damages vital macromolecules (nucleic acids, proteins, carbohydrates, and lipids) and eventually leads to cell death. ROS-induced protein damage is caused by oxidation of amino acid residues (e.g., cysteine) for disulphide bond formation, oxidation of arginine, lysine, and threonine residues resulting in irreversible carbonylation in side chains and oxidation of methionine residue to form methionine sulphoxide [66]. ROS production also limits CO_2 fixation in chloroplasts which are the main site for ROS generation in green plants [67]. ROS reacts with chlorophyll during photosynthesis and forms the chlorophyll triplet state which can rapidly generate ($^1\text{O}_2$), thus causing damage to photosynthetic complexes (principally PSII) and perturbing the molecular reaction of the photosynthetic pathway [68]. Apart from the chloroplast, the mitochondria also increase ROS production under abiotic stress which influences plant cellular processes [24]. In mitochondria, ~1–5% of O_2 consumed leads to H_2O_2 formation which is subsequently transformed in $\bullet\text{OH}$ during the Fenton reaction [69]. Furthermore, intensive respiratory/photorespiratory metabolism demands high electron input leading to escalated ROS production which results in protein oxidation [61]. Peroxisomes are also major sites for ROS production, particularly H_2O_2 , and have two- and 50-fold higher concentration of H_2O_2 than chloroplasts and mitochondria, respectively [70]. This H_2O_2 is involved in stress induced oxidative damage given that it can freely pass lipid membranes. Under the physiological level, different antioxidant defense mechanism detoxify ROS. However, over production of ROS can overwhelm the defense system, resulting in oxidative stress, cell damage, and cell death (Figure 1) [71].

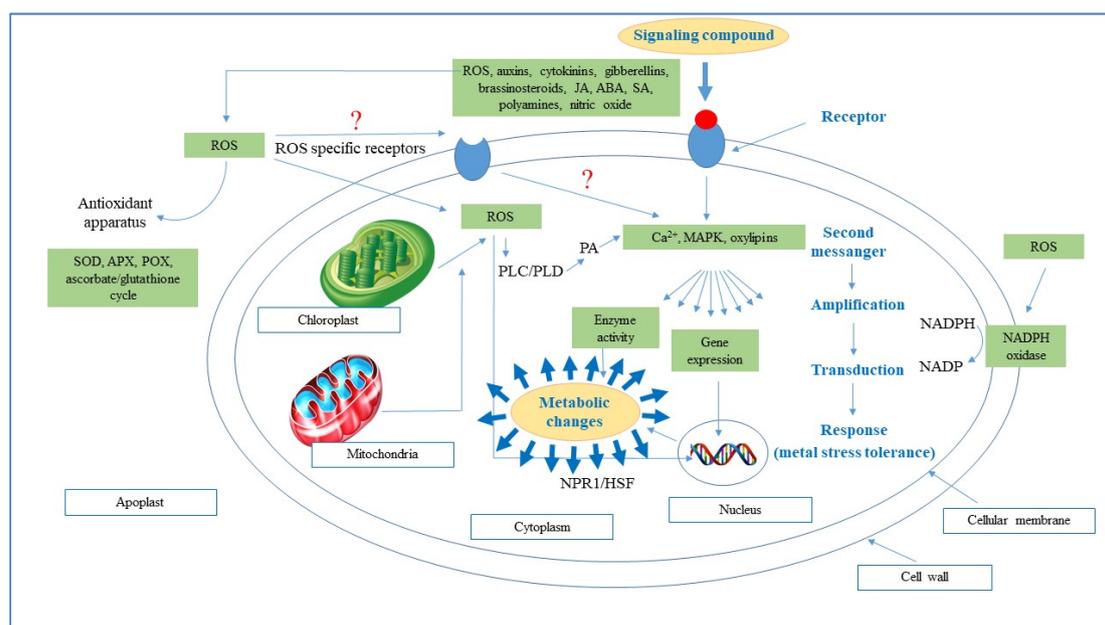


Figure 1. Schematization of signal transmission and transduction in plant cells. Abbreviation: ABA, abscisic acid; APX, ascorbate peroxidase; HSF, redox-sensitive transcription factor; JA, jasmonic acid; MAPK, mitogen-activated protein kinase; NADP, oxidized nicotinamide adenine dinucleotide; NADPH, reduced nicotinamide adenine dinucleotide; NPR1, redox-sensitive transcription factor; OXI1, serine/threonine kinase; PA, phosphatidic acid; PLC/PLD, phospholipases class C and D; POX, peroxidase; ROS, reactive oxygen species; SA, salicylic acid; SOD, superoxide dismutase.

5. Response and Role of Endogenous Phenolics in Plants against Abiotic Stress

In response to abiotic stresses, biosynthesis of secondary metabolites, including polyphenols, is usually increased in plants. Phenolics confer indeed higher tolerance to plants against various stress conditions like heavy metals, salinity, drought, temperature, pesticides, and UV radiations [33,72–77].

Plants growing under stressful environments have the ability to biosynthesize more phenolic compounds in comparison to plants growing under normal conditions [78]. These compounds have antioxidative properties and are capable of scavenging free radicals, resulting in reduction of cell membrane peroxidation [79], hence protecting plant cells from ill effects of oxidative stress. Biosynthesis of phenolics under stressful environments is regulated by the altered activities of various key enzymes of phenolic biosynthetic pathways like PAL and CHS (chalcone synthase). Enhanced performance of enzymes is also accompanied by the up-regulation of the transcript levels of genes encoding key biosynthetic enzymes like *PAL*, *C4H* (cinnamate 4-hydroxylase), *4CL* (4-coumarate: CoA ligase), *CHS*, *CHI* (chalcone isomerase), *F3H* (flavanone 3-hydroxylase), *F3'H* (flavonoid 3'-hydroxylase), *F3'5'H* (flavonoid 3'5'-hydroxylase), *DFR* (dihydroflavonol 4-reductase), *FLS* (flavonol synthase), *IFS* (isoflavone synthase), *IFR* (isoflavone reductase), and *UFGT* (UDP flavonoid glycosyltransferase) [74,80–86]. The responses of phenolic compounds under different abiotic stresses have been discussed in individual sections mentioned below.

5.1. Heavy Metal

Metal stress causes oxidative stress to plants by triggering the generation of harmful ROSs and ultimately cause toxicity and retarded growth [11,87,88]. However, enhanced biosynthesis of phenolics in plants under metal stress helps in protecting plants from oxidative stress [72,89,90]. Flavonoids can enhance the metal chelation process which helps in reducing the levels of harmful hydroxyl radical in plant cells [91,92] and this fits well with the observation that the levels of flavonoids in plants have found to be enhanced by metal excess [90,93]. Under metal toxicity, accumulation of specific flavonoids which are involved in aiding to the plant's defense mechanism is also enhanced including anthocyanins and flavonols [72,94–96]. Accumulation of phenolic compounds is due to the up-regulation of the biosynthesis of phenylpropanoid enzymes including phenylalanine ammonia-lyase, chalcone synthase, shikimate dehydrogenase, cinnamyl alcohol dehydrogenase, and polyphenol oxidase [95,97], which in turn, is dependent on the modulation of transcript levels of genes encoding biosynthetic enzymes under metal stress [72,85]. Flavonoids are also known for their scavenging capability of H₂O₂ and are considered to play a crucial role in the phenolic/ascorbate-peroxidase cycle [98,99].

Shikimate dehydrogenase (SKDH) and glucose-6-phosphate dehydrogenase (G6PDH) are two important enzymes which catalyze the biological reaction required for the production of important precursors of phenylpropanoid pathways [100]. Another enzyme cinnamyl alcohol dehydrogenase (CADH) catalyzes biochemical reactions which produce precursors required for synthesis of lignin [101]. Heavy metals stimulate phenylpropanoid the biosynthetic pathway in plants by up-regulating the activities of key biosynthetic enzymes like PAL, SKDH, G6PDH, and CADH [101]. Additionally, polyphenol oxidase (PPO) helps during the process of ROS scavenging, and enhancing a plant's resistance to abiotic stress conditions like heavy metals [100–102]. Table 1 summarizes the impact of metal stress on phenolic composition of plants.

Table 1. Summary table describing the impact of heavy metal stress on the endogenous levels of various phenolic compounds in plants.

Plant Species	Heavy Metal	Response of Endogenous Phenolics and Related Parameters	Reference
	Cu	Increase in contents of total phenols, anthocyanins and other phenolic compounds like catechin, caffeic acid, coumaric acid, kaempferol.	[103]
<i>Brassica juncea</i>	Cr	Increase in total contents of phenols, flavonoids and anthocyanins, accompanied by enhanced expressions of <i>PAL</i> and <i>CHS</i> .	[72]
	Cr	Increase in anthocyanins accompanied by up-regulation of <i>CHS</i> gene.	[93]

Table 1. Cont.

	Cd	Increase in the contents of total flavonoids and anthocyanins.	[90]
	Cd	Increase in total contents of flavonoids and anthocyanins, accompanied by enhanced expressions of <i>PAL</i> and <i>CHS</i> .	[104]
	Cd	Increase in total contents of phenols, polyphenols, flavonoids and anthocyanins.	[105]
	Pb	Increase in total contents of phenols, flavonoids and anthocyanins, accompanied by enhanced expressions of <i>PAL</i> and <i>CHS</i> .	[106]
	Pb	Increase in total contents of phenols, polyphenols, flavonoids and anthocyanins.	[89]
<i>Fagopyrum esculentum</i>	Al	Increase in total phenolic, flavonoid and anthocyanin contents. Increase in the activity of <i>PAL</i> enzyme.	[77]
<i>Kandelia obovata</i>	Cd and Zn	Enhanced levels of total phenolics accompanied by increased activities of phenol metabolic enzymes like shikimate dehydrogenase, cinnamyl alcohol dehydrogenase and polyphenol oxidase.	[97]
<i>Prosopis farcta</i>	Pb	Increase in total contents of phenols accompanied by enhanced activity of <i>PAL</i> enzyme. Contents of other phenolic compounds were also increased including ferulic acid, cinnamic acid, caffeic acid, daidzein, vitexin, resveratrol, myricetin, quercetin, kaempferol, naringinine, luteolin and diosmin.	[95]
<i>Vitis vinifera</i>	Cu	Enhanced transcript levels of various genes encoding enzymes involved in biosynthesis of phenolics (<i>PAL</i> , <i>C4H</i> , <i>CHS</i> , <i>F3H</i> , <i>DFR</i>) and down-regulation of <i>UFGT</i> and <i>ANR</i> .	[85]
<i>Withania somnifera</i>	Cd	Increase in total contents of flavonoids and phenolics	[101]
<i>Zea mays</i>	Cu, Pb, Cd	Increase in the contents of total phenols and some polyphenols like chlorogenic and vanillic acid.	[96]

PAL (phenylalanine ammonia lyase); *CHS* (chalcone synthase); *CHI* (chalcone isomerase); *C4H* (cinnamate 4-hydroxylase); *4CL* (4-coumarate: CoA ligase); *F3H* (flavanone 3-hydroxylase); *UFGT* (UDP flavonoid glycosyltransferase); *IFS* (isoflavone synthase); *DFR* (dihydroflavonol 4-reductase).

5.2. Drought

Phenolic accumulation is very crucial to counteract the negative impacts of drought stress in plants [33]. Transcriptomic and metabolomic studies carried out on *Arabidopsis* plants confirmed that enhanced flavonoid accumulation under drought stress is very helpful to provide resistance [107]. Biosynthesis and accumulation of flavonols were also stimulated in plants under water deficit conditions accompanied by enhanced resistance against drought stress [108,109]. Drought stress also regulated the biosynthetic pathways of phenolic acids and flavonoids, leading to enhanced accumulation of these compounds [82,110,111] which acted as antioxidants and prevented plants from adverse effects of water deficit conditions [112]. For example, contents of flavonoids like kaempferol and quercetin were enhanced in tomato plants accompanied by enhanced drought tolerance [113]. Flavonoid accumulation in cytoplasm can efficiently detoxify harmful H₂O₂ molecules generated as a result of drought stress and, at the end oxidation of flavonoids is followed by ascorbic acid mediated re-conversion of flavonoids into primary metabolites [114]. The main reason for this drought-induced accumulation of phenolic compounds is the modulation of phenylpropanoid biosynthetic pathway. Drought regulates many key genes encoding main enzymes of phenylpropanoid pathway, which results in stimulated biosynthesis of phenolic compounds. The impact of drought stress on accumulation of phenolics and related processes has been summarized in Table 2.

Table 2. Summary table describing the impact of drought stress on the endogenous levels of various phenolic compounds in plants.

Plant Species	Response of Endogenous Phenolics and Related Parameters	Reference
<i>Achillea</i> spp.	Increase in the contents of chlorogenic acid, caffeic acid, rutin, luteolin-7-O-glycoside, 1,3-dicaffeoylquinic acid, luteolin, apigenin and kaempferol under 21 days exposure of drought. Enhanced transcript levels of <i>PAL</i> , <i>CHS</i> , <i>CHI</i> , <i>F3H</i> , <i>F3'H</i> , <i>F3'5'H</i> and <i>FLS</i> .	[82]
	Increase in contents of total phenols and flavonoids.	[115]
<i>Brassica napus</i>	Increase in contents of total phenols, flavonoid and flavonol. Increase in PAL enzyme activity accompanied by enhanced expression of <i>PAL</i> .	[110]
<i>Chrysanthemum morifolium</i>	Increase in contents of total phenolics, anthocyanins, chlorogenic acid, luteolin, rutin, ferulic acid, apigenin and quercetin. Enhanced expression of <i>PAL</i> , <i>CHI</i> , and <i>F3H</i> , particularly in cultivar Taraneh.	[116]
<i>Cucumis sativus</i>	Up-regulation of phenolic metabolites including vanillic acid and 4-hydroxycinnamic acid.	[111]
<i>Fragaria ananassa</i>	Enhanced transcript levels of <i>PAL</i> , <i>C4H</i> , <i>4CL</i> , <i>DFR</i> , <i>ANS</i> , <i>FLS</i> and <i>UFGT</i> .	[81]
<i>Lactuca sativa</i>	Increase in the contents of phenolic compounds such as caftaric acid and rutin.	[117]
<i>Larrea</i> spp.	Increase in the contents of polyphenols including flavonoids, proanthocyanidins and flavonols.	[118]
<i>Lotus japonicus</i>	Increase in the contents of kaempferol and quercetine. Up-regulation of the expression of <i>PAL</i> , <i>C4H</i> , <i>4CL</i> , <i>CHS</i> , <i>CHI</i> , <i>DFR</i> , <i>IFS</i> and <i>IFR</i>	[119]
<i>Nicotiana tabacum</i>	Increase in PAL enzyme activity and lignin content.	[120]
<i>Ocimum</i> spp.	Increase in content of total phenols	[121]
<i>Thymus vulgaris</i>	Increase in the contents of total flavonoids and polyphenols.	[122]
	Increase in content of total phenols	[123]
<i>Triticum aestivum</i>	Increase in the total contents of phenolics, flavonoids and anthocyanins. Enhanced expression of genes like <i>CHS</i> , <i>CHI</i> , <i>F3H</i> , <i>FNS</i> , <i>FLS</i> , <i>DFR</i> and <i>ANS</i> .	[84]
<i>Vitis vinifera</i>	Increase in the contents of polyphenols including 4-coumaric acid, caffeic acid, ferulic acid, <i>cis</i> -resveratrol-3-O-glucoside, <i>trans</i> -resveratrol-3-O-glucoside, catechin, epicatechin, caftaric acid, epicatechin gallate, kaempferol-3-O-glucoside, cyanidin-3-O-glucoside, quercetin-3-O-glucoside and quercetin-3-O glucuronide.	[124]
	Increase in anthocyanin content accompanied by up-regulation of associated biosynthetic genes like <i>UFGT</i> , <i>CHS</i> and <i>F3H</i> .	[125]

PAL (phenylalanine ammonia lyase); CHS (chalcone synthase); CHI (chalcone isomerase); C4H (cinnamate 4-hydroxylase); 4CL (4-coumarate: CoA ligase); F3H (flavanone 3-hydroxylase); F3'H (flavonoid 3'-hydroxylase); F3'5'H (flavonoid 3'5'-hydroxylase); FLS (flavonol synthase); FNS (flavone synthase) UFGT (UDP flavonoid glycosyltransferase); IFS (isoflavone synthase); IFR (isoflavone reductase); DFR (dihydroflavonol 4-reductase); ANS (anthocyanidin synthase).

5.3. Salinity

Salt stress results in generation of ROS like superoxide anions, hydrogen peroxide, and hydroxyl ions [126,127] and require activation of well-orchestrated and finely-tuned plants antioxidant system to contrast ROS propagation [128,129]. Phenolic compounds have powerful antioxidant properties and help in scavenging of harmful ROS in plants under salt stress [130–132]. Moreover, in response to salt stress, phenylpropanoid biosynthetic pathway gets stimulated and results in production of various phenolic compounds which have strong antioxidative potential [131,133,134].

Some genes like *VvbHLH1* are involved in the enhanced production of flavonoids by regulating the genes of the biosynthetic pathways and confer salt tolerance to plants [135,136]. In tobacco plants, *NtCHS1* plays a crucial role in the biosynthesis of flavonoids under salt stress, where accumulation

directly favors the scavenging of ROS [130]. Flavone biosynthesis also was enhanced under saline conditions and in *Glycine max*, it was observed that salinity up-regulates the expression of flavone synthase genes, *GmFNSII-1* and *GmFNSII-2* [137]. Some phenolic acids also accumulate in plants under saline conditions including caffeic acid, caftaric acid, cinnamylmalic acid, gallic acid, ferulic acid, and vanillic acid [131,138–140]. Biosynthesis of anthocyanins also was promoted in plants growing under saline conditions [141,142]. A detailed explanation about the effect of salt stress on phenolic composition has been provided in Table 3.

Table 3. Summary table describing the impact of salt stress on the endogenous levels of various phenolic compounds in plants.

Plant Species	Response of Endogenous Phenolics and Related Parameters	Reference
<i>Amaranthus tricolor</i>	Increase in contents of total phenolics, hydroxybenzoic acids (gallic acid, vanilic acid, syringic acid, <i>p</i> -hydroxybenzoic acid, ellagic acid), hydroxycinnamic acids (caffeic acid, chlorogenic acid, <i>p</i> -coumaric acid, <i>m</i> -coumaric acid, ferulic acid, sinapic acid, <i>trans</i> -cinnamic acid) and flavonoids (iso-quercetin, hyperoside, rutin)	[140]
<i>Asparagus aethiopicus</i>	Increase in the levels of phenolics like robinin, rutin, apigenin, chlorogenic acid and caffeic acid.	[134]
<i>Carthamus tinctorius</i>	Increase in contents of total phenols and flavonoids.	[136]
<i>Chenopodium quinoa</i>	Increase in total polyphenol and flavonoid contents.	[143]
<i>Cynara cardunculus</i>	Increase in contents of phenolic compounds like luteolin- <i>O</i> -glucoside, apigenin 6- <i>c</i> -glucoside 8- <i>c</i> -arabinoside, gallo catechin, leucocyanidin and quercitrin. Decrease in contents of compounds like apigenin, chrysin, genistein, daidzein and ferulic acid	[144]
<i>Fragaria ananassa</i>	Enhanced transcript levels of <i>PAL</i> , <i>C4H</i> , <i>F3H</i> , <i>DFR</i> and <i>FLS</i> .	[81]
<i>Hordeum vulgare</i>	Increase of total phenolic contents.	[145]
<i>Mentha piperita</i>	Increase of total phenolic contents.	[146]
<i>Ocimum basilicum</i>	Increase in the contents of various phenolic compounds like caffeic acid, caftaric acid, cinnamyl malic acid, feruloyl tartaric acid, quercetin-rutinoside and rosmarinic acid.	[139]
<i>Olea europaea</i>	Increase in contents of total phenolics, kaempferol and quercetin. Regulation of transcript levels of <i>PAL</i> , <i>C4H</i> , <i>4CL</i> , <i>CHS</i> and <i>CHI</i> .	[133]
<i>Salvia mirzayanii</i>	Increase of total phenolic contents.	[132]
<i>Salvia mirzayanii</i> and <i>Salvia acrosiphon</i>	Increase in total phenolic content and <i>PAL</i> activity accompanied by enhanced expression of <i>PAL</i> .	[147]
<i>Solanum lycopersicon</i>	Increase in total caffeoylquinic acid content	[129]
<i>Solanum villosum</i>	Increase in total phenolic, caffeic acid, and quercetin 3- β -D-glucoside contents. Up-regulation of the expression of <i>PAL</i> and <i>FLS</i>	[138]
<i>Thymus</i> spp.	Increase in the contents of various phenolic compounds like caffeic acid, gallic acid, <i>trans</i> -2-hydroxycinnamic acid, cinnamic acid, rosmarinic acid, rutin, syringic acid, vanillic acid, apigenin, quercitrin, naringenin and luteolin.	[131]
<i>Triticum aestivum</i>	Increase in contents of total phenols	[123]

PAL (phenylalanine ammonia lyase); *CHS* (chalcone synthase); *CHI* (chalcone isomerase); *C4H* (cinnamate 4-hydroxylase); *4CL* (4-coumarate: CoA ligase); *F3H* (flavanone 3-hydroxylase); *FLS* (flavonol synthase); *DFR* (dihydroflavonol 4-reductase).

5.4. UV Light

Exposure of UV-B radiations to plants causes damage to their protein structure, causes harmful mutations to DNA and generates harmful ROS. To counteract the negative effects of UV-B exposure, endogenous phenolics accumulated in plant cells and protect cell components by making a shield under epidermal layer. They further reduce DNA damage by preventing dimerization of thymine along with reducing photo-damage of important enzymes like NAD/NADP [33,148]. Moreover, flavonoids also act as light screens due to their capability of absorbing both visible (anthocyanins) and UV radiations (anthocyanins and colorless flavonoids), hence protecting plants from these harmful radiations [26,149]. This fact was supported by various researchers who observed enhanced biosynthesis of flavonoids in plants under UV radiations, accompanied by enhanced UV absorption and plant tolerance to these radiations [98,150] and powerful antioxidant capacity [151]. Moreover, it is also well known that plants growing at high altitude accumulate more phenolics like flavonoids than plants of a temperate region. This enhanced flavonoid accumulation under high light/UV exposure is because of stimulated flavonoid biosynthetic pathways and their corresponding gene transcript levels [33,83,152,153]. The key genes which are up-regulated in plants upon UV exposure include: *CHS* (chalcone synthase); *CHI* (chalcone isomerase); *FLS* (flavonol synthase); *DFR* (dihydroflavonol 4-reductase); *FHT* (flavanone 3 β -hydroxylase), *FGT* (flavonoid glycosyltransferases); and *PAL* (phenylalanine ammonia lyase) [154,155]. It is also believed that UV light also utilizes jasmonate dependent/independent pathways to stimulate the biosynthesis of phenols in plants [156]. Additionally, abscisic acid (ABA) is also known to modulate the phenolic biosynthetic pathway in presence of UV light [157]. Table 4 provides a brief summary about impact of UV exposure on the endogenous phenolic composition of plants.

Table 4. Summary table describing the impact of UV light exposure on the endogenous levels of various phenolic compounds in plants.

Plant Species	Response of Endogenous Phenolics and Related Parameters	Reference
<i>Arbutus unedo</i>	Increase in contents of phenolic compounds like theogallin, avicularin and juglanin.	[158]
<i>Brassica oleracea</i>	Increase in contents of gallic acid and sinapic acid.	[159]
<i>Caryopteris mongolica</i>	Increase in contents of flavonoids and anthocyanidins, accompanied by PAL and CHI activity.	[160]
<i>Cuminum cyminum</i>	Increase in contents of total phenolics and anthocyanins, accompanied by enhanced gene expression of <i>DAHP</i> and <i>PAL</i> .	[153]
<i>Fragaria x ananassa</i>	Increase in contents of kaempferol, ellagic acid and, glucoside derivative of cyaniding, pelargonidin and quercetin. Up-regulation of key genes involved in flavonoid pathway including <i>CHS</i> , <i>CHI</i> , <i>FHT</i> , <i>DFR</i> , <i>FLS</i> and <i>FGT</i> .	[155]
<i>Kalanchoe pinnata</i>	Increase in contents of total flavonoids and quercitrin.	[161]
<i>Lactuca sativa</i>	Increase in contents of total phenolics, flavonoids and anthocyanins. Contents of phenolic acids were also increased including rosmarinic acid, vanillic acid, <i>p</i> -anisic acid, methoxycinnamic acid and chlorogenic acid.	[162]
	Increase in total anthocyanin and phenolic contents. This is accompanied by enhanced activity of PAL enzyme and up-regulation of <i>PAL</i> expression.	[163]
<i>Ribes nigrum</i>	Increase in contents of flavonols, anthocyanins, hydroxycinnamic and hydroxybenzoic acids.	[164]
<i>Solanum lycopersicum</i>	Increase in total phenolic content	[165]

Table 4. Cont.

<i>Triticum aestivum</i>	After 3 days of UV exposure, increase in contents of total phenolics, ferulic acid, <i>p</i> -coumaric acid and vanillic acid, whereas no change in the contents of <i>p</i> -hydroxybenzoic acid, syringic acid and sinapic acid. Alterations in the transcript levels of <i>PAL</i> , <i>C4H</i> , <i>4CL</i> , and <i>COMT</i>	[83]
<i>Triticum aestivum</i>	Increase in contents of free, bound and total phenolics accompanied by enhanced <i>PAL</i> activity.	[166]
<i>Vigna radiata</i>	Increase in total flavonoid and phenol content, accompanied by enhanced activities of <i>PAL</i> and <i>CHI</i> enzymes.	[154]
<i>Vitis vinifera</i>	Increase in contents of astilbin, quercetin and kaempferol.	[167]
	Increase in contents of phenolic compounds like cyaniding, petunidin, peonidin, malvidin, quercetin, myricetin, kaempferol, procyanidin, gallic acid, protocatechuic acid and vanillic acid.	[157]

CHS (chalcone synthase); CHI (chalcone isomerase); FLS (flavonol synthase); DFR (dihydroflavonol 4-reductase); FHT (flavanone 3 β hydroxylase), FGT (flavonoid glycosyltransferases) *PAL* (phenylalanine ammonia lyase); *C4H* (cinnamate 4-hydroxylase); *4CL* (4-coumarate: CoA ligase); cinnamylalcohol dehydrogenase (*CAD*); *COMT* (caffeic acid O-methyltransferase); *DAPIH* (deoxyribonino heptulosinate 7-phosphate synthase).

5.5. Other Abiotic Factors

Other abiotic factors like temperature, nanoparticles, and pesticides also stimulate the endogenous phenolic biosynthesis in plants and help in providing resistance against phytotoxic effects of these abiotic stresses [74,80,153,168–171]. Phenolic biosynthetic pathways also get activated in plants growing under pesticide stress conditions. This leads to more accumulation of phenolic compounds in plants, which confer resistance to survive against pesticide toxicity [73,170]. This stimulated phenolic biosynthesis is due to the activation of key biosynthetic enzymes and up-regulation of key genes of phenylpropanoid branch, including *PAL* and *CHS* [74,80]. Increased accumulation of anthocyanins in plant leaves promote by application of insecticides also helps in recovery of plant photosynthetic efficiency [172]. Similarly, under temperature stress (both heat and chilling), plants synthesize more phenolic compounds such as anthocyanins, flavonoids, flavonols, and phenolic acids, which ultimately protect plant cells [75,129,168,169,173]. In *Festuca trachyphylla* plants growing under heat stress, enhancement in the phenolic compounds was noticed including 4-hydroxybenzoic acid, benzoic acid, caffeic acid, coumaric acid, cinnamic acid, gallic acid, homovanillic acid, ferulic acid, salicylic acid, and vanillic acid [76]. The increased accumulation of these phenolic compounds is accompanied by enhanced tolerance of *F. trachyphylla* plants against high temperature [76]. In carrot, phenolics like coumaric acid, caffeic acid, and anthocyanins are suggested to prevent heat induced oxidative damage by enhancing their accumulation [174]. Some phenolics like salicylic acid also act as stimulant for phenol biosynthesis in plants under high temperature stress. This leads to enhanced accumulation of phenolic compounds which further help in detoxification of ROS and providing heat resistance to plants [175]. Under chilling stress, phenolic compounds like suberin or lignin start accumulating in plant cell walls which helps in enhancing resistance against chilling stress [176]. This enhanced thickness of cell wall due to phenolic accumulation is beneficial for prevention of chilling injury and cell collapse under cold stress [33]. Stimulated phenolic biosynthesis under low temperature stress is due to the enhanced expression of *PAL*, *CAD* (cinnamylalcohol dehydrogenase), and *HCT* (hydroxycinnamoyl transferase), and increased phenolic levels play crucial role in protection plants against chilling stress [86]. This fact is further supported by the research carried out on peach under chilling stress by Gao et al. [177]. These researchers suggested that 24-epibrassinolide stimulated biosynthesis of phenolics is involved in reduction of heat generated oxidative stress by helping to scavenge of ROS. Table 5 provides a detailed overview about how different abiotic factors affect phenolic metabolism in plants.

Table 5. Summary table describing the impact of various abiotic factors on the endogenous levels of various phenolic compounds in plants.

Plant Species	Abiotic Factor	Response of Endogenous Phenolics and Related Parameters	Reference
<i>Brassica juncea</i>	Insecticide	Increase in total phenol and polyphenol contents.	[73]
	Insecticide	Increase in total phenol, polyphenol and anthocyanin contents accompanied by enhanced expression of <i>PAL</i> and <i>CHS</i> .	[74]
	Insecticide	Increase in total phenol and anthocyanin contents.	[178]
	Insecticide	Increase in total phenol and anthocyanin contents accompanied by enhanced expression of <i>PAL</i> and <i>CHS</i> .	[80]
<i>Dracocephalum kotschyi</i>	Silicon dioxide NP	Increase in total phenol, total flavonoid, rosmarinic acid and xanthomicrol contents, accompanied by up-regulation of the gene expression of <i>PAL</i> and <i>RAS</i> .	[179]
<i>Festuca trachyphylla</i>	Heat	Increase in the contents of phenolic compounds like 4-hydroxybenzoic acid, benzoic acid, caffeic acid, coumaric acid, cinnamic acid, gallic acid, homovanillic acid, ferulic acid, salicylic acid and vanillic acid.	[76]
<i>Lens culinaris</i>	Heat	Enhanced levels of total phenolics and flavonoids. Increase in the contents of gallic acid, salicylic acid, chlorogenic acid, ferulic acid and naringenin,	[168]
<i>Nicotiana tabacum</i>	Chilling	Alteration in the contents of various metabolites of phenylalanine metabolic pathway. Enhanced expression of <i>PAL</i> , <i>HCT</i> and <i>CAD</i> .	[86]
<i>Nicotiana langsdorffii</i>	Heat	Increase in the contents of total polyphenols and individual contents of <i>p</i> -coumaric acid, chlorogenic acid, cryptochlorogenic acid, neochlorogenic acid and ferulic acid.	[75]
<i>Oryza sativa</i>	Insecticide	Increase in the contents of phenylalanine, <i>p</i> -hydroxybenzoic acid and ferulic acid	[170]
<i>Prunus persica</i>		Increase in the activities of enzymes like <i>PAL</i> , <i>C4H</i> , <i>4CL</i> and <i>CHI</i> .	
	Chilling	Increase in the contents of phenolic compounds like protocatechuic acid, catechin, chlorogenic acid, neochlorogenic acid, quercetin-3- rutinoside, quercetin-3-glucoside, kaempferol-3- rutinoside	[169]
<i>Solanum lycopersicon</i>	Heat	Increase in total flavonol content	[129]
	Silver NP	Increase in total phenolic content.	[180]
<i>Solanum tuberosum</i>	Zinc NP	Increase in contents of total phenolics and anthocyanins.	[181]
<i>Vigna angularis</i>	Heat	Increase in the contents of anthocyanins and flavonoids.	[173]
<i>Vitis vinifera</i>	Titanium NP	Increase in contents of total phenolics, caftaric acid, quercetin derivatives and kaempferol derivatives.	[171]
<i>Withania somnifera</i>	Copper NP	Increase in contents of total phenolics and flavonoids.	[182]

PAL (phenylalanine ammonia lyase); *CHS* (chalcone synthase); *CHI* (chalcone isomerase); *C4H* (cinnamate 4-hydroxylase); *4CL* (4-coumarate: CoA ligase); cinnamylalcohol dehydrogenase (*CAD*); *HCT* (hydroxycinnamoyl transferase); *COMT* (caffeic acid O-methyltransferase); *DAPH* (deoxyribonino heptulosinate 7-phosphate synthase), *RAS* (rosmarinic acid synthase); NP (nanoparticles).

6. Conclusions

Phenylpropanoid pathway is likely the most studied pathway of secondary metabolism in plants. In plants growing under challenging environments, accumulation of phenolic compounds usually parallels enhanced plant tolerance as summarized in Figure 2. Abiotic stresses also activate the cell signaling process, resulting in transcriptional up-regulation of phenylpropanoid pathway. The increase in plant's resistance is correlated with the multiple function of polyphenols in plants, principally consisting in their ROS scavenging ability and/or the capacity of some polyphenol classes to protect the plant from excessive light such as UV (flavonoids) and visible light (anthocyanins). In addition, polyphenols might play other key ecological roles under abiotic stress, acting for example as infochemicals for other plants. Aside from the huge body of papers on the matter, further research is needed to deepen, for example, the role of specialized polyphenols as a response to certain abiotic stresses and to describe the intimate mechanisms which shift from primary metabolism to the up-regulation of phenylpropanoid pathway, which is as a cross response to several environmental stressors.

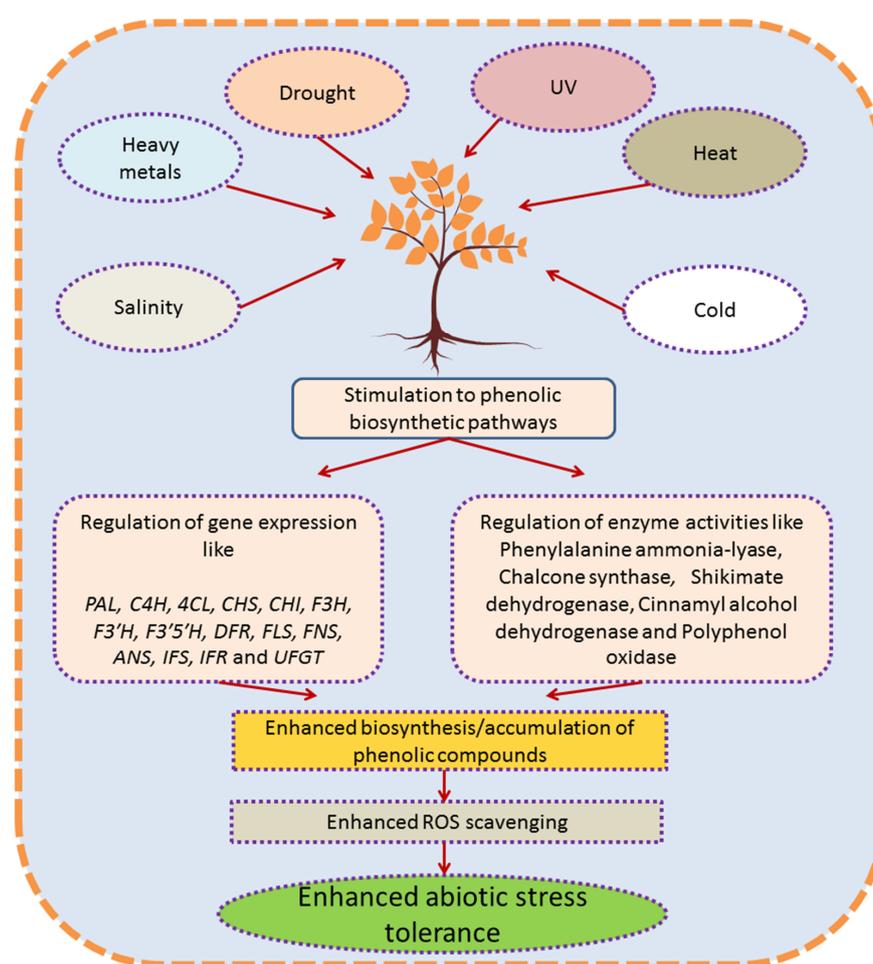


Figure 2. Diagrammatic explanation for response and role of phenolic compounds in plants growing under abiotic stress conditions. ROS (reactive oxygen species); PAL (phenylalanine ammonia lyase); CHS (chalcone synthase); CHI (chalcone isomerase); C4H (cinnamate 4-hydroxylase); 4CL (4-coumarate: CoA ligase); F3H (flavanone 3-hydroxylase); F3'H (flavonoid 3'-hydroxylase); F3'5'H (flavonoid 3'5'-hydroxylase); FLS (flavonol synthase); FNS (flavone synthase) UFGT (UDP flavonoid glycosyltransferase); IFS (isoflavone synthase); IFR (isoflavone reductase); DFR (dihydroflavonol 4-reductase); ANS (anthocyanidin synthase).

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