

Review

An Overview of Plant Phenolics and Their Involvement in Abiotic Stress Tolerance

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Abstract: Secondary metabolites, such as phenols and salicylic, play a crucial role in the regulation of development and tolerance mechanisms against a wide range of stresses. During adverse conditions such as biotic and abiotic stresses, plants induce the biosynthesis of phenolic compounds to provide tolerance. Phenolics are secondary aromatic metabolites synthesized through the shikimate/phenylpropanoid pathway or polyketide acetate/malonate pathway, which produce monomeric and polymeric phenolics. Phenolic compounds in plants not only take part in preventing stresses but also in regulating physiological activities. These compounds significantly regulate both below- and above-ground defense mechanisms. Plants synthesize thousands of phenolic compounds throughout their evolution to survive in changing environments. Environmental factors, such as high light, cold, drought, heavy metals, etc., increase the accumulation of phenolics to neutralize any toxic effects. This review focuses on the biosynthesis of phenolic compounds and their updated studies against abiotic stresses.

Keywords: phenylpropanoids; flavonoids; drought; heavy metals; UV radiation; ROS



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1. Introduction

Phenolic compounds are ubiquitously present in the plant kingdom. Phenolics are very rarely present in bacteria, fungi, and algae. Vascular plants are the primary source of a wide range of polyphenols, while lower plants such as bryophytes are the leading producers of flavonoids [1,2]. Plant phenolics can be defined by ‘phenol’, a chemical term describing a phenyl ring bearing one or more hydroxyl substituents. Several classes of phenolics have been categorized based on their basic skeleton [3]. Phenolic compounds range from simple to low molecular weight, single aromatic-ringed to large and complex tannins and their derived polyphenols. Phenolic compounds are broadly classified into two major groups: flavonoids and non-flavonoids [3]. Secondary metabolites, such as phenolic compounds, do not directly affect plant growth and development. They regulate other associated pathways for their function via signal transduction. These compounds protect plants from disease/damage and also contribute to the plant’s color, aroma and flavor [4]. During the last four decades, several researchers have shown keen interest in investigating their regulatory mechanism, which involves tolerance mechanisms, against several biotic and abiotic factors such as microbial infections, pollinators, seed-dispersing animals, UV, temperature, drought, etc. Phenolic compounds function as signal molecules and are also involved in forming root nodules in legume plants for the nitrogen fixation [5]. They exhibit diverse structures, from single aromatic rings (caffeic acid and ferulic acid) to more complex polymeric structures such as lignins/lignans, coumarins, quinones, tannins, and flavonoids (Figure 1). This review highlights the importance of plant phenol compounds in plant abiotic stress response.

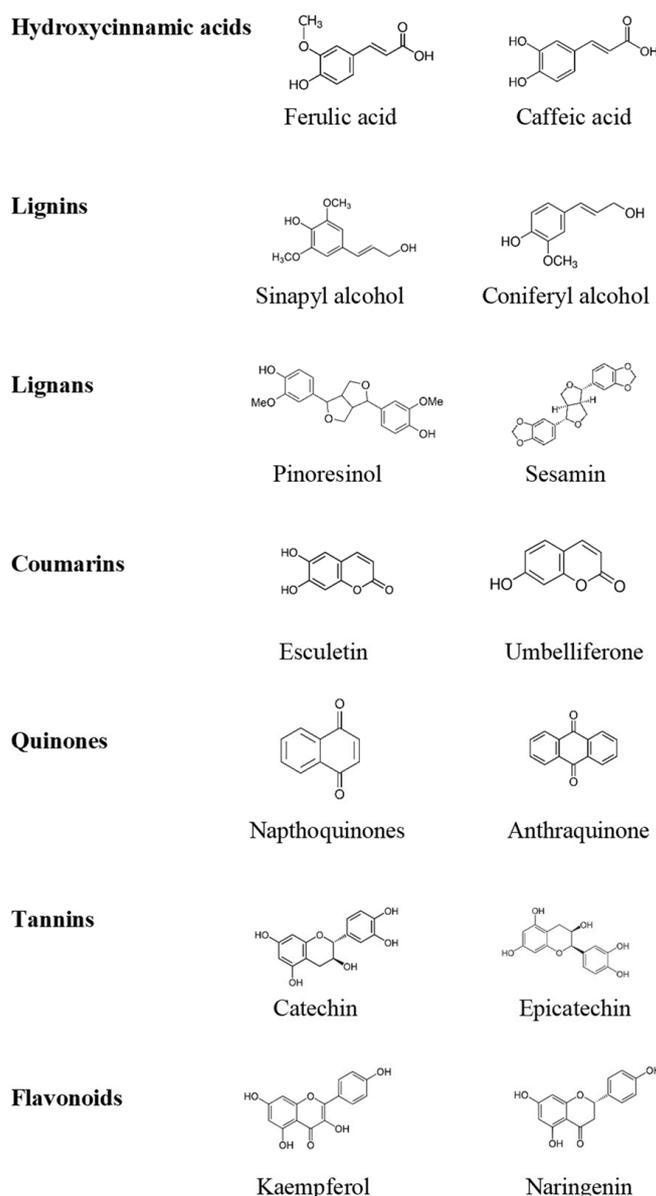


Figure 1. Structural representation of the phenolic compounds.

2. Different Types of Phenolic Compounds and Their Biosynthesis

Plants produce an exceptionally diverse array of low molecular mass compounds, often called secondary metabolites, and they are essential for anticipating and responding to biotic and abiotic stress. [6]. These metabolites are generally derived from different biosynthetic routes such as isoprenoid, phenylpropanoid, alkaloid, or fatty acid pathways. The phenolic compound is derived either from the shikimic acid pathway or pentose phosphate through phenylpropanoid metabolism [7]. The phenolic compound contains benzene rings with one or more hydroxyl substituents, which are synthesized from simple phenolic molecules to highly polymerized compounds according to their demand function. The primary metabolisms, such as glycolysis and pentose phosphate pathways, provide compounds such as phosphoenolpyruvate and erythrose-4-phosphate to initiate the biosynthesis of phenolic compounds. Together, phosphoenolpyruvate and erythrose-4-phosphate produce shikimic acid via the shikimate pathway. Further, this pathway provides L-phenylalanine, which takes part in the phenylpropanoid pathway to produce *p*-coumaroyl CoA. This compound initiates the synthesis of phenylpropanoids and monolignols to produce more complex phenolic compounds such as stilbenes or flavonoids

after reacting with three malonic acid molecules [8] (Figure 2). An overview of these participating pathways has been summarized below.

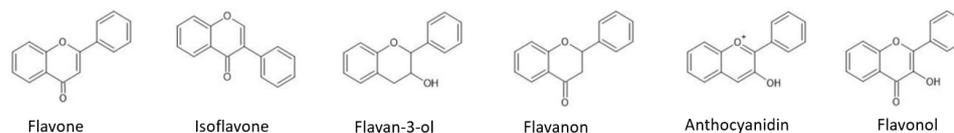


Figure 2. Structural representation of the major flavonoid classes.

2.1. Flavonoids

Flavonoids are polyphenolic molecules containing 15 carbon atoms with two aromatic rings. Flavonoids are the most diverse class of phenolic compounds and are present in all types of plants within the plant kingdom [9]. They mostly accumulate in very high concentrations in the leaf's epidermis and fruits' skins. The flavonoid biosynthesis is mainly initiated through the phenylpropanoid pathway. During normal conditions, flavonoids act as a signaling molecule and UV protectant and regulate plant hormones such as auxin and cytokinin [10]. However, during stress conditions, they protect from oxidative damage [11]. Stress-induced dihydroxy B-ring-substituted flavonoids actively scavenge ROS [12]. Flavonoids are classified into many groups, and the main subclasses are flavonols, flavan-3-ols, isoflavones, flavones, anthocyanidins, and flavanones (Figure 2). Minor flavonoid groups are dihydroflavonols, flavan-3,4-diols, coumarins, chalcones, dihydrochalcones, and aurones. Flavonoids contain various substituents such as hydroxyl groups, present at the skeleton's 4th, 5th, and 7th positions.

2.1.1. Flavonoid Biosynthetic Pathway

Plants produce an exceptionally diverse array of low molecular mass compounds, often called secondary metabolites, which are essential for anticipating and responding to biotic and abiotic stress. These metabolites are generally derived from different biosynthetic routes such as isoprenoid, phenylpropanoid, alkaloid, or fatty acid pathways. The phenolic compound is derived either from the shikimic acid pathway, phenylpropanoid, or both [13]. The shikimic acid pathway is a major route for the biosynthesis of aromatic compounds in plants and microorganisms. Phenylalanine, tyrosine, and tryptophan are the primary metabolites that provide the precursor for most of the secondary metabolite compounds. Flavonoids are synthesized from phenylalanine which is derived from the shikimate pathway [7,14] (Figure 3). The shikimate pathway initiates with the molecule as phosphoenol pyruvate (PEP) and D-erythrose-p-phosphate and forms the intermediate precursor-shikimic acid following several steps (Figure 3). This shikimic acid gets converted to chorismic acid, which leads to the synthesis of phenylpropanoid pathway, starts with aromatic amino acid, phenylalanine, and tyrosine. The derived phenylalanine gets converted to coumaric, caffeic, and ferulic acids through the activity of phenylalanine ammonia-lyase (PAL), cinnamic acid 4-hydroxylase (C4H), and 4-coumarate: CoA ligase (4CL), which ultimately opens the lignin biosynthesis route in the plant systems. The coumaric acid also leads towards the biosynthesis of hydroxycinnamic acids such as caffeic, ferulic, and chlorogenic acids. On the other hand, the shikimic acid from the shikimate pathway also contributes towards the synthesis of gallic acid by the action of shikimate dehydrogenase (SDH). Synthesized gallic acid is then converted to glucogallin by UDP-3-glucosyltransferase (UGT), which then produces two important tannins-gallotannins and ellagitannins of the hydrolysable tannin pathway (Figure 3).

In general, the flavonoid biosynthesis pathway (Figure 3) also includes several intermediates such as flavanones (naringenin, hesperitin, dihydrokaempferol and eriodictyol), flavanols (kaempferol, myricetin, quercetin) and flavanone glycosides (delphinidin 3-O-glucoside, quercetin 3-O-glucoside). Flavanones are an important phenolic class that mostly occurs in citrus fruits such as lemons and oranges. The formation of naringenin chalcone from the condensation of p-coumaroyl-CoA with three malonyl CoA residues, catalyzed

by chalcone synthase (CHS), is described in Figure 3. The product naringenin chalcone is then converted to naringenin by the action of chalcone isomerase (CHI) and finally to dihydrokaempferol. This dihydrokaempferol further diverges for the production of different classes of flavonoids, including isoflavones, flavanones, flavones, flavanols, flavan-3-ols and anthocyanins (Figure 3).

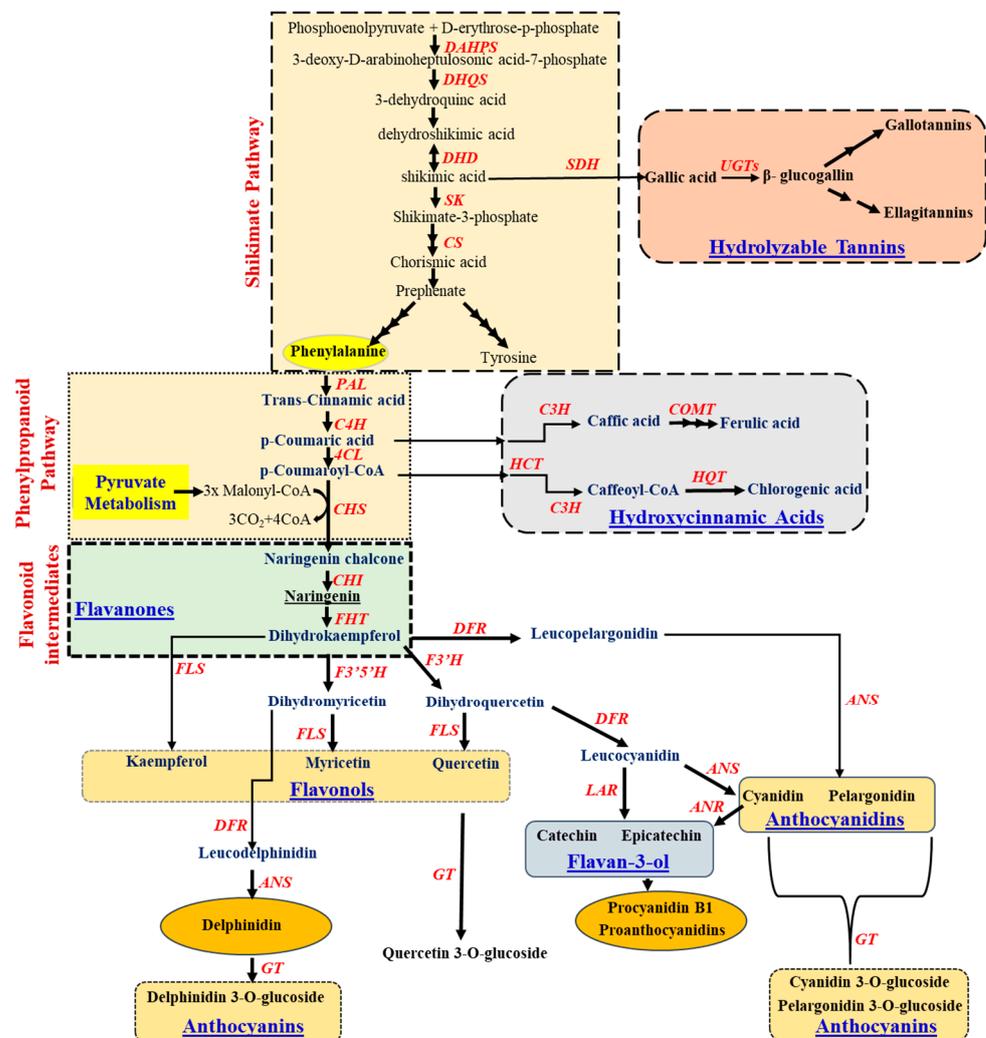


Figure 3. Schematic representation of the flavonoids and their intermediates (shikimate, phenylpropanoid, flavanones, flavanols, flavan-3-ol, flavanol glycosides, anthocyanidins and anthocyanin biosynthetic pathway). The respective enzymes catalyzing the reaction in each pathway have been denoted in red colour. Abbreviation: 3-deoxy-D-arabinoheptulosonic acid-7-phosphate synthase (DAHPS); 3-dehydroquinate synthase (DHQS); 3-dehydroquinate dehydratase (DHD); Shikimate kinase (SK); chorismate synthase (CS); shikimate dehydrogenase (SDH), UDP-3-glucosyltransferase (UGT); Phenylalanine ammonia lyase (PAL); cinnamate-4-hydroxylase (C4H); 4-coumarate-CoA ligase (4CL); coumaroyl-3-hydroxylase (C3H); Caffeoyl-O-methyltransferase (COMT); Chalcone synthase (CHS); Hydroxycinnamoyl-CoA: shikimate/ quinate hydroxycinnamoyltransferase (HCT); hydroxycinnamoyl (CoA); quinate hydroxycinnamoyl transferase (HQT); chalcone-flavanone isomerase (CHI); fatty alcohol hydroxycinnamoyl transferase (FHT); flavonoid 3',5'-hydroxylase (F3'5'H); flavonol 3' hydroxylase (F3'H); dihydroflavonol 4-reductase (DFR); flavonol synthase (FLS); anthocyanidin synthase (ANS); anthocyanidin reductase (ANR); leucocyanidin reductase (LAR); flavonoid-3-O-glucosyltransferase (GT).

2.1.2. Flavone and Flavanone Biosynthesis

The dehydrogenation of flavanones results in the formation of flavones (2-aryl-4H-chromen-4-ones) by the action of enzyme flavone synthase via the conversion of flavanones to flavones, for example as leteolin, apigenin, and galangin. Such conversion requires NADPH and oxygen to introduce a double bond between the C-2 and C-3 residues in flavanones (Figure 3).

2.1.3. Isoflavonoid Biosynthesis

A leguminous plant predominantly accumulates the isoflavonoids and the responsible enzymes for their biosynthesis, as have been identified and characterized earlier [15]. During these pathways, microsomal cytochrome P450 isoflavone synthase catalyzes and converts naringenin and isouiritigenin into the isoflavones genistein and daidzein, respectively [16].

2.1.4. Anthocyanin Biosynthesis

Cyanidin, pelargonidin, and delphinidin are the most commonly explored anthocyanidins; they are present in flowers and fruits and are also responsible for their distinct colour variations [13]. The regulatory mechanism of anthocyanin biosynthesis has been explored broadly, starting with the hydroxylation of flavanones to produce dihydroflavonols by flavanone 3-hydroxylase (F3H) (Figure 3). Then, dihydroflavonols were reduced to flavan-3,4-diols (leucoanthocyanins) by the enzyme dihydroflavonol reductase (DFR). Anthocyanidin synthase (ANS) catalyzes the last step in the biosynthesis of anthocyanins. Finally, Flavonoid-3-O-glucosyltransferase (FGT) transfers the glucosyl moiety from UDP glucose to the 3-hydroxyl group of anthocyanidins and forms anthocyanins (Figure 3).

2.2. Non-Flavonoids

Non-flavonoids are classified as phenolics acid, tannins, stilbenes and lignans [17]. Most of the non-flavonoids present in fruits and vegetables have dietary significance. Phenolic acids such as gallic acid, acts as a precursor of hydrolysable tannins. Similarly, C6-C3 hydroxycinnamates (p-Coumaroyl) and their derivatives are polyphenolic C6-C2-C6 stilbenes. However, lignans derived from phenylpropanoid E-coniferyl alcohol.

Stilbene Biosynthesis

The stilbene is also synthesized by the condensation of p-coumaroyl CoA with three units of malonyl CoA, catalyzed by the enzyme stilbene synthase. Stilbene synthase and chalcone synthase (CHS) are structurally very similar enzymes. Stilbene synthase is induced by a wide range of stresses such as UV radiation and bacterial and fungal infections [17].

3. Responses of Phenolic Compound to Abiotic Stress

Plants regularly synthesize secondary metabolites in response to environmental changes, which leads to the ability to adapt and survive in response to environmental cues and various kinds of stresses. Accumulations of phenolic compounds in plants are associated with the growth conditions and factors related to metabolic pathways, which can be associated with stress conditions or signaling (Figure 4) [18]. Plants are exposed to a diverse range of abiotic stresses (temperature, drought, salinity, alkalinity, UV) and pathogens/herbivores, which cause severe damage to the plants [15]. These biotic and abiotic factors increase reactive oxygen species (ROS), causing oxidative damage in plants. ROS such as superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), singlet oxygen (1O_2), and the hydroxyl radical (HO^\cdot) are highly reactive compounds which react with different biomolecules, leading to an alteration in biochemical and physiological activities. ROS generally generates in lower amounts during the cellular metabolic process, where it works as a signal molecule. However, several external factors highly enhance the level of ROS, which starts to cause oxidative damage. Oxidative stress elevates several stress mechanisms in plants, such as different enzymatic antioxidants (superoxide dismutase, SOD; catalase,

CAT; ascorbate peroxidase, APX; glutathione reductase, GR; monodehydroascorbate reductase, MDHAR; dehydroascorbate reductase, DHAR; glutathione peroxidase, GPX; guaiacol peroxidase, GOPX; glutathione S-transferase, GST; nicotinamide adenine dinucleotide phosphate (NADPH) oxidase-like alternative oxidase, AOX; thioredoxins, TRXs; glutaredoxin, GRX; etc.) and nonenzymatic antioxidants (ascorbic acid, AsA; glutathione, GSH; phenolic acids; alkaloids; flavonoids; carotenoids; α -tocopherol; nonprotein amino acids; etc.) [16]. In nonenzymatic antioxidants, the elevated level of phenolic compounds during oxidative stress, potentially protects plants from oxidative damage [16]. Phenols directly or indirectly other defence mechanisms, which protect plants from massive damage, caused by oxidative stress. Oxidative bursts damage several biomolecules, such as nucleic acids, proteins and lipids. When ROS reacts with the membrane lipids, it converts into lipid peroxides (LOOH), producing different carbonyl compounds such as aldehydes and ketones. Some of these compounds contain carbonyl-conjugated C-C bonds, known as reactive carbonyl species (RCS). RCS contains one or more carbonyl groups, generally known for their toxic effects on organisms [19].

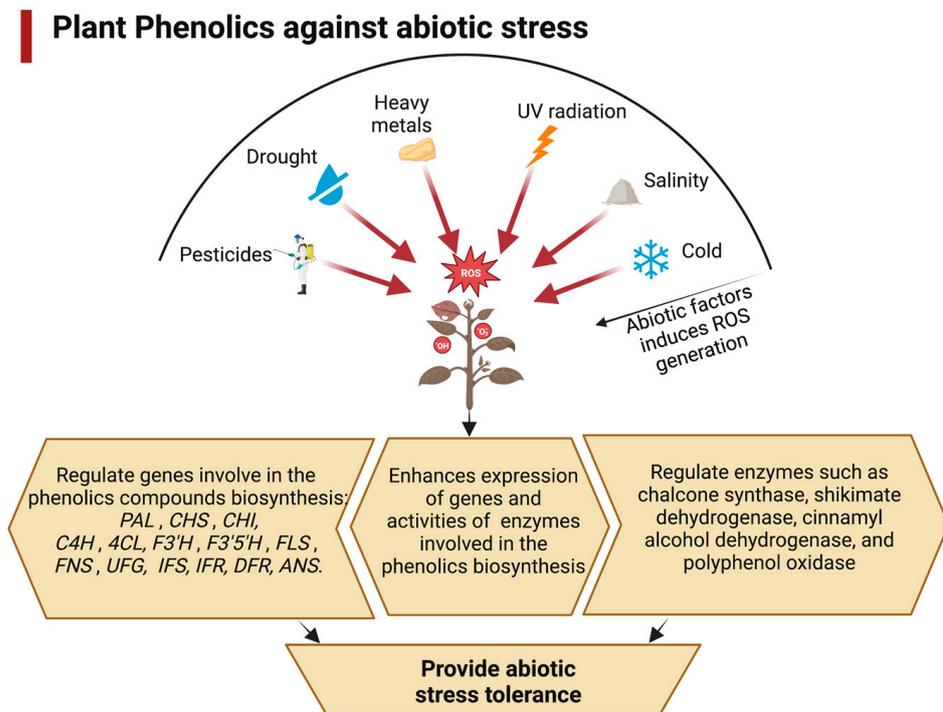


Figure 4. Schematic diagram of the regulation of gene expressions and enzymatic activities involved in the phenolic compound's biosynthesis against abiotic stress tolerance in plants. Abbreviation: phenylalanine ammonia lyase (PAL); chalcone synthase (CHS); chalcone-flavanone isomerase (CHI); cinnamate-4-hydroxylase (C4H); 4-coumarate-CoA ligase (4CL); 4-coumarate-CoA ligase (4CL); flavonol 3' hydroxylase (F3'H); flavonoid 3',5'-hydroxylase (F3'5'H); flavonol synthase (FLS); flavone synthase (FNS); UDP flavonoid glycosyltransferase (UFG); isoflavone synthase (IFS); isoflavone reductase (IFR); dihydroflavonol 4-reductase (DFR); anthocyanidin synthase (ANS).

On the other hand, during antioxidative activities, phenols oxidized into univalent form by enzymatic or nonenzymatic activities with respect to phenoxyl radicals. Phytophenols, such as polyphenols, support ascorbate-dependent antioxidative defence mechanisms to protect plants against oxidative damage [20]. In another defence mechanism against ROS, flavonoids and other polyphenols such as quercetin, rutin, and catechin react with some of the biometal ions (Fe(II) and Cu(I)) as a chelating agent to reduce lipid alkoxy radicals (a strong oxidant, participating in lipid-peroxidation) [21]. Simultaneously, polyphenols provide rapid chemical scavenging for free radical damage on biomolecules through H-atom donation or electron transfer. Similarly, the number of hydroxy groups in the aromatic

B-ring of flavonoids directly participates in ROS scavenging activity. However, few studies indicate that phenolic compounds, such as phoretin (which synthesizes in tea and apple) [22] and pelargonidin (which synthesizes in brown rice) [23], act as RCS scavengers. Besides these, several multi-omics technologies are used to understand the mechanism of different phenolic compounds against abiotic stresses. This review discusses the recent updates in the responses of phenolic compounds to different abiotic stresses.

3.1. Drought

The integral approach to stabilizing the negative impacts of drought stress on plants is enhancing their inherent accumulation of phenolic compounds [24]. Studies of many plant species revealed an improved accumulation of flavonoids under drought conditions that provide resistance to these plants [25]. The distinct antioxidant properties of phenolic acids and flavonoids prevent plants from the adverse effects of water deficit conditions. Drought stress induces the biosynthesis of phenolic and flavonoids, ultimately leading to enhanced plant production [26,27]. The enhanced accumulation of kaempferol and quercetin in tomatoes helps them to cope with the improved drought conditions via detoxification of H₂O₂. The accumulation of phenolic compounds results from modulation in the phenylpropanoids pathway. Many of the important protein-encoding genes of these pathways are regulated by the drought, which leads to the stimulation of phenolic compounds. A study reported that drought stress enhances potato tubers' polyphenol biosynthesis genes (PAL, HCT, C3H, CHS, CHI, F3H, DFR, and AN1) [28]. Similarly, a recent study indicated that drought stress upregulates the biosynthesis of flavonoids by regulating the heat shock factors. In this study, under drought conditions, MdHSP90-MdHSA8a (*Malus domestica* heat shock factor A8a) was released from MdHSP90-MdHSA8a (*Malus domestica* heat shock factor 90) complexes and interacted with an AP2/ERF family transcriptional factor MdRAP2.12 to activate the genes involved in the flavonoid biosynthesis in *Malus domestica* [29]. In another study, different types of anthocyanins, such as A11, A9, A8, and A5 were found to be induced by short-term drought stress in *Arabidopsis*, in which A11 was the major anthocyanin [30]. The impact of drought stress on the accumulation of phenolic and related processes is also described in Table 1.

Table 1. The positive impact of drought stress on the endogenous levels of phenolic compounds in different plant species.

Plant Species	Increased Endogenous Level of Phenolic Compounds	References
<i>Brassica napus</i>	Total phenols, flavonoid and flavonols	[26]
<i>Cucumis sativus</i>	Vanillic acid, 4-hydroxycinnamic acid	[27]
<i>Nicotiana tabacum</i>	Lignin	[31]
<i>Ocimum</i> spp.	Total phenols	[32]
<i>Vitis vinifera</i>	Polyphenols (4-coumaric acid, caffeic acid, ferulic acid, <i>cis</i> -resveratrol-3- <i>O</i> -glucoside, caftaric acid, epicatechin gallate, kaempferol-3- <i>O</i> -glucoside, cyanidin-3- <i>O</i> -glucoside)	[33]
<i>Lactuca sativa</i>	Caftaric acid, rutin	[34]
<i>Thymus vulgaris</i>	Total flavonoids, polyphenols	[35]
<i>Lotus japonicus</i>	Kaempferol, quercetin	[36]
<i>Chrysanthemum morifolium</i>	Total phenolics, anthocyanins, chlorogenic acid, luteolin, rutin, ferulic acid, apigenin and quercetin	[37]
<i>Zea mays</i>	p-coumaric acid and caffeic acid increased	[38]
<i>Zea mays</i>	Total phenols	[39]
<i>Oryza sativa</i>	Flavonoids	[25]
<i>Oryza sativa</i>	Vanillic acid and p-hydroxybenzoic acid	[40]

3.2. Salt Stress

Salt stress causes osmotic disturbance in plants, which reduces the volume of vacuoles and cytoplasm cells, ultimately leading to cellular dehydration. Additionally, higher salt concentration also induces oxidative stress via the generation of ROS such as superoxide

anions, hydrogen peroxide, and hydroxyl ions. To counter this type of adverse effect, a differential accumulation of specific secondary metabolites occurs in plants [41,42]. Phenolic compounds are well known for their potential antioxidant properties, which help to scavenge ROS under salt stress [43–45]. Salt stress induces the phenylpropanoid biosynthetic pathway, which consequently elevates various kinds of phenolic compound biosynthesis [44,46,47]. The polyphenols content increases in different plant tissue with an increase in salinity level [48]. A report demonstrated that total phenolic content increased in red pepper under a moderate increase in salinity level [49]. In tobacco plants, NtCHS1 (*Nicotiana tabacum* chalcone synthase 1) enhanced the accumulation of flavonoids upon the salinity stress, which lead to the scavenging of ROS [43]. In *Vitis vinifera*, the induction of a transcriptional factor, such as VvbHLH (*Vitis vinifera* basic helix–loop–helix), enhances flavonoid biosynthesis and protects from salt stress damage [50,51]. In *Glycine max*, an upregulation of the flavone synthase gene was observed against salt stress, which indicates that the flavones play a crucial role under salinity stress [52]. Other phenolic compounds, such as anthocyanin and phenolic acid, are also induced by salinity stress [44,53]. An overview of the positive effect of salt stress on the endogenous levels of phenolic compounds in different plant species is given in Table 2.

Table 2. Overview of the positive effect of salt stress on the endogenous levels of phenolic compounds in different plant species.

Plant Species	Increased Phenolic Compounds	References
<i>Carthamus tinctorius</i>	Total phenols and flavonoids	[47]
<i>Cynara cardunculus</i>	Luteolin-O-glucoside, apigenin 6-c-glucoside 8-c-arabinoside, galocatechin, leucocyanidin, quercitrin	[54]
<i>Ocimum basilicum</i>	Caffeic acid, caftaric acid, cinnamyl malic acid, feruloyl tartaric acid, quercetin-rutinoside, rosmarinic acid	[55]
<i>Triticum aestivum</i>	Total phenols	[56]
<i>Hordeum vulgare</i>	Total phenols	[57]
<i>Carthamus tinctorius</i>	Total phenols and flavonoids	[50]
<i>Mentha piperita</i>	Total phenols	[58]
<i>Solanum lycopersicon</i>	Total caffeoylquinic acid	[59]
<i>Asparagus aethiopicus</i>	Phenolics (apigenin, chlorogenic acid, caffeic acid)	[52]
Red pepper	Total phenolic compound	[48]
<i>Zea mays</i>	Anthocyanin	[60]
<i>Oryza sativa</i>	Hydroxycinnamic acid and ferulic acid	[61]
<i>Oryza sativa</i>	Ferulic and p-coumaric acid	[62]

3.3. Heavy Metal

Heavy metals are a potential abiotic stress factor, which reduces growth and physiology by generating oxidative stress [24]. These metals lead to changes in the metabolic as well as the photosynthetic activity of plants. Metal/metalloid ions, mainly lead, nickel, silver, cadmium, arsenic, etc., enhance the production of secondary metabolites, which helps plants to cope with stresses [26]. The accumulation of heavy metals triggers oxidative bursts by generating ROS such as O_2^- , H_2O_2 , and HO^\cdot , which cause several biomolecular damages, leading to toxicity in the plant and ultimately a retard its growth and productivity [63–66]. Heavy metals contain several donating electrons in their outer shell, which are in a cellular condition gained by native O_2 , leading to highly reactive ROS. To cope with this adverse effect, plants enhance the biosynthesis of secondary metabolite production, especially phenolic compounds. Under metal toxicity, flavonoids play a crucial role, which enhances the metal chelation and reduces the hydroxyl radicals from the plant's tissue [67,68].

Metal toxicity mainly induces the accumulation of flavonoids such as anthocyanins and flavones [69,70]. During metal stress, the upregulation of some of the key enzymes, such as chalcone synthase, shikimate dehydrogenase, cinnamyl alcohol dehydrogenase, and polyphenol oxidase, induces phenylpropanoid biosynthesis in plants [70]. The key

enzymes, such as SKDH (Shikimate dehydrogenase) and G6PDH (glucose-6-phosphate dehydrogenase), catalyze several biological actions needed for the synthesis of the starting precursors for the phenylpropanoid biosynthesis, during metal stress [71]. A recent study demonstrated that an elevated accumulation of Pb and Cu induces the activities of PAL (Phenylalanine ammonia-lyase) and TAL (tyrosine ammonia-lyase) in winter wheat plants, which are the key enzymes of phenylpropanoid biosynthesis [72]. Generally, activating the phenylpropanoid pathway synthesizes nonenzymatic compounds such as flavonoids, coumarins, and lignans, which protect plants from oxidative stress [73]. Similarly, in another study, chlorogenic acid was found to be enhanced against Pb stress in *Zea mays* [69]. Polyphenols such as tannins contain unique structures, facilitating electrostatic, hydrogen bonding, and hydrophobic interactions with metal ions. Simultaneously, the catechol or galloyl groups of tannin compounds provide chelating sites for metals, which protect them from metal toxicity [74].

3.4. UV Radiation

Light quality and UV radiation also influence the synthesis of secondary metabolites in plants [75,76]. UV radiation damages the protein structure and causes a mutation in the genome, which is harmful in nature and leads to ROS generation in plants. To overcome the detrimental effects of UV radiation, plants elevate the biosynthesis of secondary metabolites production. The higher accumulation of secondary metabolites such as alkaloids [60], terpenoids [59], and phenolic compounds protect from UV radiation [43]. A higher level of phenolic compound underneath epidermal cells provides a protective layer, which further prevents thymine dimerization and ultimately reduces DNA damage [24]. Many reports suggest that plants accumulate more flavonoids under high light and UV radiations [59,77], which can screen the UV and visible lights by absorbing capacity and protecting the plant from damage [78,79].

There is a higher accumulation of phenolic compounds as a result of the induction of flavonoid biosynthesis pathway genes under high light and UV radiation [80,81]. Flavonoids are potential scavengers of ROS, specifically, those flavonoids which contain a catechol group in the B-ring of the flavonoid skeleton (e.g., quercetin derivatives). An excess of light or UV-B radiation induces the biosynthesis of dihydroxy B-ring-substituted flavonoids (e.g., luteolin derivatives) at the cost of other less effective flavonoids (e.g., kaempferol derivatives) [82]. The essential biosynthesis pathway genes of flavonoids such as CHS, CHI, FLS, DFR, FHT, FGT, and PAL are induced with UV radiation [83,84]. Simultaneously, acylated anthocyanins absorb UV radiation and provide tolerance against UV stress in plants [85]. A few reports indicate that the higher accumulation of phenolic compounds is also caused by the jasmonic acid and ABA-mediated modulation of phenylpropanoid pathways under UV radiation [86,87]. Table 3 briefly summarizes the effect of UV exposure on the endogenous phenolic composition of plants.

Table 3. Outline of the affirmative impact of UV light exposure on phenolic compounds in different plant species.

Plant Species	Increased Endogenous Level of Phenolic Compounds	References
<i>Brassica oleracea</i>	Gallic acid, sinapic acid	[88]
<i>Cuminum cyminum</i>	Total phenolics, anthocyanins	[81]
<i>Solanum lycopersicum</i>	Total phenolics	[89]
<i>Vigna radiata</i>	Total flavonoids and phenols	[83]
<i>Vitis vinifera</i>	Stilbenes, quercetin, kaempferol	[90]
<i>Triticum aestivum</i>	Total phenolics, ferulic acid, p-coumaric acid, vanillic acid	[91,92]
<i>Ribes nigrum</i>	Flavonols, anthocyanins, hydroxycinnamic hydroxybenzoic acids	[93]
<i>Kalanchoe pinnata</i>	Total flavonoids, quercitrin	[94]
<i>Triticum aestivum</i>	Total phenolics	[89]

Table 3. Cont.

Plant Species	Increased Endogenous Level of Phenolic Compounds	References
<i>Caryopteris mongolica</i>	Flavonoids, anthocyanidins	[95]
<i>Zea mays</i>	Anthocyanin	[96]
<i>Oryza sativa</i>	Anthocyanin	[97]
<i>Oryza sativa</i>	Kaempferol and quercetin	[98]

3.5. Some Other Abiotic Factors

Abiotic factors such as nanoparticles, aerosol, temperature and pesticides also stimulate the production of phenolic compounds in plants. Phenolic compounds prevent plants from the phytotoxic effects of these abiotic stresses [99]. Plants also produce and accumulate more anthocyanins, flavonoids, flavanols, and phenolic acids upon temperature stress, and these metabolites protect plant cells from any damage caused by these types of stress [100–103]. Under pesticide stress, plants enhance phenolic compounds to avoid any toxic effects. The accumulation of phenolic compounds results from upregulating key biosynthetic genes and activating the key enzymes of phenylpropanoid-branched chain reactions such as PAL and CHS [103,104]. It was also reported that the plant *Festuca trachyphylla* under heat stress conditions increased biosynthesis and the accumulation of phenolic compounds such as 4-hydroxybenzoic acid, benzoic acid, caffeic acid, coumaric acid, cinnamic acid, gallic acid, homo-vanillic acid, ferulic acid, and salicylic acid [105]. The accumulation of these compounds enhanced plant resistance via detoxifying ROS, which is generated under heat-stress conditions [106]. The plant produces more phenolic compounds, such as suberin or lignin, which strengthen the plant cell wall and help the plant to avoid chilling injuries [24].

4. Effect of Biostimulants on Polyphenols Accumulation

Plant biostimulants are substances or microorganisms that, when applied to plants, aim to enhance their nutrient uptake, physiological processes, and stress tolerance, ultimately promoting plant growth and development [107]. Biostimulants can be treated as an additive to fertilizers, and they support the uptake of nutrients, promote plant growth, and increase their tolerance to abiotic stress. Biostimulants can stimulate the synthesis of secondary metabolites, including polyphenols, in plants. These compounds act as signaling molecules that trigger the plant's defense responses against stress factors such as pests, pathogens, and abiotic stresses such as drought and heat [107]. Polyphenols, on the other hand, are a diverse group of secondary metabolites found in plants that have various biological activities and are of interest for their potential health benefits for both plants and humans. The effects of plant biostimulants on polyphenols can vary depending on the specific biostimulant used, the plant species involved, and the environmental conditions. A study reported that the biostimulants Kelpak and Asahi SL significantly enhance polyphenols in potato leaves and tubers [108]. Similarly, a biostimulant (VIVEMA TWIN) made from a combination of condensed and hydrolysable tannins was used against salt stress in *Solanum lycopersicum* L. This study indicated that the application of biostimulant VIVEMA TWIN upregulated several of the genes (285 genes) involved in root development and salt stress tolerance. Another biostimulant (BALOX[®]) based on polyphenols at 1.4% (*w/w*) and glycine betaine at 3.0% (*w/w*) was reported to enhance the salt stress tolerance and polyphenols content in tomato plants. This biostimulant enhanced plant growth, especially at the root level and in saline soil conditions [109]. Similarly, *A. nodosum* seaweed extract was reported to significantly enhance the phenolic compound content of grapes [110]. In a study, protein hydrolysate was used as a biostimulant to enhance phenolic compounds in tomato plants. In this study, protein hydrolysate not only enhanced phenolic compounds but also significantly increased the level of ascorbic acid and lycopene, which indicates its potential role in the enhancement of antioxidants and stress-responsive compounds [111].

Biostimulant application is a non-toxic and feasible option for agriculture to boost the phenolic compounds in plants to aid against abiotic stresses.

5. Conclusions

Plants are sessile in nature and adapt to various protective mechanisms for their better survival with respect to diverse environmental cues. Secondary metabolites such as flavonoids, phenolics, stilbenes, hydroxycinnamic acids, etc., are produced in extremely lower concentrations within plants under normal environmental conditions for signaling and metabolism. However, external abiotic factors such as drought, light, temperature, etc., retards overall plant growth/development. Furthermore, it leads to the induction of biosynthesis of specific types of secondary metabolites to combat the wide range of adverse effects. In addition, other abiotic factors, such as pesticides, can also accelerate the endogenous phenolic biosynthesis and facilitate resistance against the phytotoxic consequences of these abiotic stresses. In recent years, integrating multiple omics methods such as transcriptome, proteome, and metabolome has become essential to understanding and identifying the crucial stress-responsive genes in plants during abiotic stresses. Amongst the secondary metabolism in plants, the phenylpropanoid pathway is likely the most studied pathway in terms of abiotic stresses. The change in the environmental condition acts as a stimulus which activates the phenylpropanoid pathways via induction of the signaling process and transcriptional upregulation of the key pathway genes. These compounds provide resistance to the plant and regulate multiple of its functions. Some polyphenolic compounds serve as a scavenger that removes the ROS molecules generated during oxidative bursts, and some of them function as protective in nature, such as flavonoids and anthocyanins. Although there are several reports available in which induction of the phenylpropanoid pathway leads to a change in phenylpropanoid metabolite composition irrespective of the kinds of stimuli, few studies have indicated whether these responses share a similar type of mechanism, and which specific conditions are responsible for the shift from primary metabolites to phenylpropanoid pathways. In addition, the application of biostimulant is a sustainable approach to inducing phenolic compounds in plants to aid against abiotic stresses. However, their mechanisms of action are, in some cases, still a challenge and need to be recognized because the nature of their beneficial influence is not fully understood. Biostimulants are, therefore, a hot topic in agriculture and still require in-depth research.

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