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An Insight into the Role of Phenolics in Abiotic Stress Tolerance in Plants: Current Perspective for Sustainable Environment

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Abstract

Phenolic compounds (PCs) are a prominent class of secondary metabolites produced by plants and are essential for the natural role of the entire plant life cycle. PCs are formed in plants under both favorable and unfavorable conditions and have essential functions in signaling pathways, such as cell division, nutrient mineralization, hormone control, and reproduction. Under abiotic stress conditions, plants produce more polyphenols, which aid them in adapting to their environment. The phenylpropanoid biosynthetic pathway is activated under various environmental stress conditions, such as drought, heavy metal toxicity, salinity, and high/low temperatures, resulting in the deposition of compounds. These compounds can neutralize reactive oxygen species (ROS) produced in excessive amounts in crops under stressful conditions and adversely affect plants. It is imperative to investigate the functions of PCs in response to several abiotic stresses, as the phenylpropanoid pathway plays a crucial role in the metabolic pathway in crop plants, leading to the biosynthesis of a wide range of PCs. These compounds play various roles in plant growth, development, and response to environmental stress. Therefore, this review provides a comprehensive understanding of PCs and their exchanges with other cellular components, which is crucial for harnessing their potential to improve crop resilience to environmental stresses.

Keywords: Environment, Abiotic Stress, Phenolic, Phenylpropanoid Pathways, ROS, Plant Defense

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Abbreviation: ROS – reactive oxygen species; ABA – abscisic acid; EPS – extracellular polymeric substances; ACC – aminocyclopropane-1-carboxylic acid; JA – jasmonic acid; SA – salicylic acid; IAA – indole-3-acetic acid; BR – brassinosteroid.

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INTRODUCTION

Climate change plays a crucial role in agriculture and decreases agricultural productivity and crop quality owing to salinity, heat waves, flooding, and drought.[1-4] Based on the yearly report of Weather, Climate, and Catastrophe Insight, the economic loss due to natural calamities spiked from USD 200 billion to USD 225 billion per year between 2016 and 2018 worldwide.[1] Owing to temperature changes and atmospheric CO_2 levels triggered by unprecedented climatic events, multiple abiotic stresses are the ultimate consequences of global.[5] According to some forecast reports, agriculture is thought to be the most vulnerable industry that is negatively impacted by climate change. Currently, the two issues that worry people the most about the world are food security and ecological resilience. Before climate variations have a significant impact on global crop production, climate-smart agriculture is the only way to reduce their negative effects on crop adaptation.[4,6] Climate change has also altered the precipitation patterns, contributing to erratic drought/flood stress. The emission of greenhouse gases from various sources is one of the factors that contribute to the gradual rise in temperature. Rising temperatures, heat waves, and rainfall variations directly affect changing weather patterns. Elevated atmospheric CO_2 levels affect the quality and nutrient content of foods.[7] The loss of farmland due to sea level rise is an unintended consequence of climate change. Floods, water logging, extreme temperatures, and salinity are abiotic aspects that confine crop quality and quantity. Environmental factors significantly influence plant growth and productivity. This almost certainly results in higher food availability, disproportionately affecting poor communities disproportionately.[8] Current climate prediction models project that, as the climate deteriorates, the recurrence of heat waves, drought, and salinization will rise; therefore, agricultural output will struggle to withstand environmental challenges.

Increasing temperature and rainfall variability have affected crop yields. By 2050, it is predicted that without effective management strategies, approximately half of agricultural land will be salinized.[9] In the current scenario, soil salinity has affected one-fifth of the arable land, and each year, excessive salinity levels render 1.5 million hectares of land unfit for agricultural use. By 2050, 50% of arable land will disappear if soil salinization continues to increase.[10] Approximately 30 crops produce 90% of plant-centered human sustenance, and the bulk of these crops are salt-sensitive, if not salt-intolerant.[11] Environmental repercussions, such as salt, heat/cold, water deficit, toxic metals, and floods/waters, have grown as a result of drastic and severe climate change (Figure 1).[12] Upon the onset of abiotic stress, plants generate reactive oxygen species (ROS) owing to oxidative damage as a defense mechanism.[13] Hence, studies on plant antioxidant defence mechanisms can be a comprehensive predictor of plant damage.[14] According to previous studies, these stresses alter the overall plant growth and development and cause a 70% decrease in plant production.[15]

Phenolics are a diverse set of bioactive secondary metabolites.[16] Phenolic compounds (PCs) are present in roots, shoots, fruits, seeds, and most of the other parts of the plant.[17] In plants, phenolics are usually categorized into two types: (1) performed phenolics formed during normal plant tissue development and (2) induced phenolics produced when exposed to different environmental stress situations.[18] These compounds are often made and accrued in the subcutaneous layers of crops that are sensitive to biotic and abiotic stress. The quantity of specific PCs in tissues depends upon season as well as growth stage of the crop. Subjection to light promotes the formation of PCs in different cell organelles. Phenolics consist of variations of compounds such as stilbene, arylpyrones, flavonoids, lignans, lignins, etc.[20] The number of carbon atoms present in the molecule determines the classification of phenols.[21] Phenols are produced by three different biosynthetic pathways (i) the shikimate chorismate or succinyl benzoate pathway (ii) the acetate malonate or polyketide pathway and (iii) dehydrogenation reactions of the acetate/mevalonate pathway.[22] Understanding the contribution of phenolics to plants under abiotic stress tolerance will offer valuable insights for adopting sustainable environments and this implies an investigation into the significance of phenolics in aiding plants to withstand environmental stresses.

Biosynthesis of phenolic compounds and its effect on plants

Phenolic acid

Phenolic acids are classified into two groups based on their structure: hydroxybenzoic acids (gallic acid, vanillic acid, etc.) and hydroxycinnamic acids (ferulic acid). Lignin is an organic polymer that is important for plants to tolerate abiotic stresses. Lignin protects tobacco from the detrimental effects of cold temperatures.[23] Drought stress increases the levels of vanillic acid in *Cucumis sativus* (Table).[24] Vanillic acid has potent antioxidant properties that aid plants in dealing with a variety of stressors.[25] Application of exogenous vanillic acid to tomatoes improves salt tolerance by increasing osmolyte formation, ion regulation, and antioxidant activity of antioxidants.[26] Similarly, El-Soud *et al*.[27] found that ellagic acid alleviated salt-induced osmotic stress (Table). Salicylic acid protects plants from biotic and abiotic stressors.[28] Salicylic acid concentrations are known to change in response to various stressors.[29]

Flavanoids

Flavonoids are classified into flavones, flavonols, and isoflavones based on their structures. Water deprivation had no effect on hesperidin levels but significantly increased naringin levels in *Citrus unshiu et al.* leaves (Table).[30] Drought stress causes a significant increase in hesperidin levels in peppermint, whereas aglycone naringenin levels increase only marginally.[31] Tobacco plants with elevated CHS gene activity have higher levels of naringenin, particularly naringin, and are drought tolerant.[32] Naringenin is a powerful antioxidant and radical scavenger, making it an excellent compound for tolerating stress.[33] When chickpeas are subjected to high sodium concentrations in nodules, the naringenin concentration decreases (Table).[34] Naringenin mitigates the effects of salt and osmotic stresses on photosynthesis and the chloroplast antioxidant system in bean (*Phaseolus vulgaris*) plants.[35] Drought increases the luteolin content of chrysanthemum cultivar leaves while decreasing or maintaining unchanged apigenin levels.[36] Similarly, flooding combined with high salinity increased luteolin content in artichoke and cardoon leaves (Table).[37] Salinity promotes apigenin synthesis in black cumin.[38] Drought decreases the content of apigenin-7-O-glucosides and increases that of luteolin-7-O-glucosides

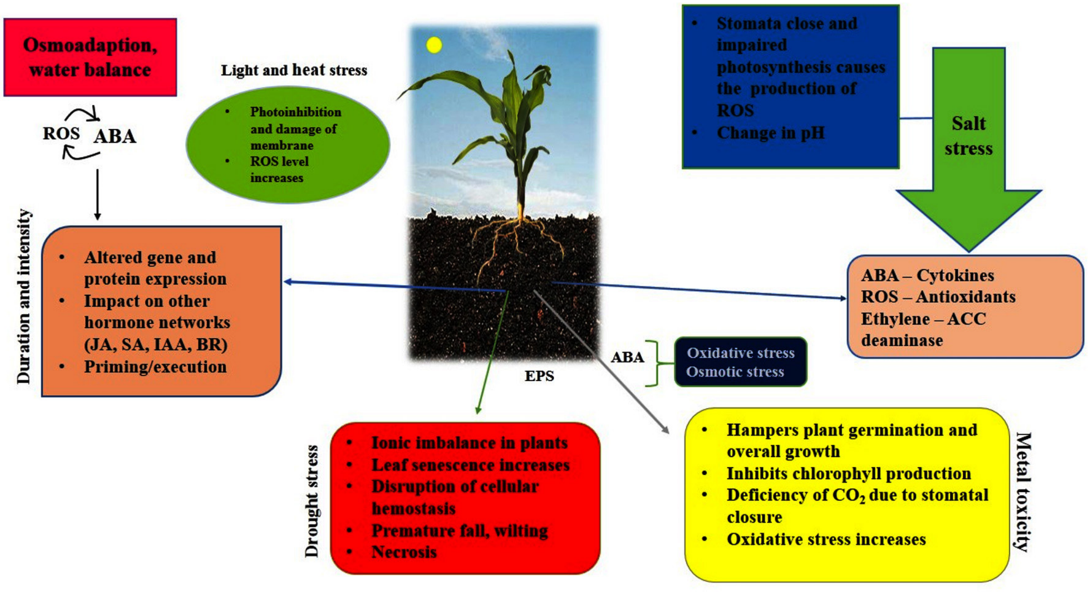

Figure 1. Schematization of various abiotic stresses and their effect on plants

Table. Synthesis and regulation of different phenolic compounds in different crops upon exposure to various abiotic stress

Abiotic stress	Phenolic acids	Crops	Reference
Cold stress	Lignin	Tobacco	23
Drought stress	vanillic acid	*Cucumis sativus*	24
Salt stress	Gallic, p-hydroxybenzoic, syringic.	*Amaranthus tricolor*	35
Salt tolerance	vanillic acid	Tomatoes	26
Salt-induced osmotic stress	Ellagic acid	Chickpea	27
Abiotic stress	Flavonoids	Crops	Citations
Drought stress	Naringin	*Citrus unshiu*	30
Drought stress	Hesperidin and aglycone naringenin	Peppermint	31
Drought stress	Naringenin, especially naringin	Tobacco	32
Salt stress	Naringenin	Chickpea	34
Water-deficit stress	Luteolin	Chrysanthemum	36
Flooding and excess salinity	Luteolin	Artichoke and cardoon	37
Salinity	Apigenin	*Nigella sativa*	38
Drought stress	Luteolin	Achillea pachycephala	39
Cold stress, osmotic stress	Isoflavones	Soybean	40
Water-deficit stress	Isoflavones	*Glycine max*	41
Salt stress	Isoflavone	Soybean	42
Cold stress	Catechin	Date palm	43
Cold stress	Catechin	Arabidopsis	44
Salt stress	Epicatechin	Wheat sprout	45
Cold stress	Flavanols	*Prunus persica*	46
Drought stress	Flavanols	*Camelia sinensis*	47
Salt stress	Quercetin-3-rutinoside	Tomatoes, Ocimum basilicum	48, 49
Salt stress	Quercetin-3-beta-glucoside	*Solanum nigrum*	50
Salt stress	Quercetin-3-beta-glucoside	*Amaranthus tricolor* and *Solanum villosum*	35, 51
Abiotic stress	Lignans	Crop	
Drought stress	Lignans	*Sesamum indicum* L.	52
Salt and drought stress	Lariciresinol	*Isatis indigotica*	19

in *Achillea pachycephala*.[39] Low temperature, osmotic stress, and combined stress all increase isoflavone levels in soybeans, according to Swigonska *et al*.[40] Long-term drought minimizes the overall isoflavone content of soybean seeds throughout seed developmental stages.[41] Flavonols play an important role in the response of plants to temperature change. The level of flavonol in *Prunus persica* increases when it is chilled.[46] Catechin build-up has been observed in date palms (Du *et al.*,[43] and Leyva *et al.*,[44]) at low temperatures (Table). Under drought conditions, flavanol accumulation is observed in *Camelia sinensis* which helps it tolerate stressful conditions.[47] The buildup of isoflavones is an indication of an increase in the salt-sensitive cultivar and a decrease in the salt-tolerant cultivator of soybeans (Table).[42] Under salt stress conditions, epicatechin levels increase in wheat is observed.[45] There has been an upsurge in quercetin-3-rutinoside levels in tomatoes and *Ocimum basilicum* under salt stress.[48,49] NaCl significantly increased quercetin-3-beta-glucoside levels in *Solanum nigrum*,[50] *Amaranthus tricolor*,[35] and *Solanum villosum* (Table).[51]

Lignans

Lignans are involved in lignin production and cell wall synthesis. Drought stress may affect lignan content in *Sesamum indicum*, depending on the genotype (Table).[52] The elevation of lariciresinol in *Isatis indigotica* has been shown to improve root development and tolerance to salt and drought stress (Table).[19,53]

Biosynthesis pathway

The general phenylpropanoid pathway, which includes numerous steps to convert phenylamine to feruloyl-CoA, and the monolignol-specific pathway, including the conversion of feruloyl-CoA to a variety of monolignols, are the two primary categories of the lignin biosynthesis pathway.[54] All species except grasses use phenylalanine (Phe) as their starting substrate.[55] The pathway includes processes such as deamination and methylation, and the 11 enzymes involved in this pathway are mentioned above (Figure 2). The major phenylpropanoid route is initiated by the ammonia lyase of Phe and conversion activity of PAL.[56] Coniferyl and sinapyl alcohols are produced by methylation of the aromatic ring, whereas hydrocyanic alcohols are produced by carboxylic acid reduction (Figure 2). This segment, referred to as the standard phenylpropanoid route, frequently uses PAL, C4H, and 4CL. In subsequent steps, p-coumaric acid, ferulic acid, and sinapic acid were stimulated to produce their respective CoA thioesters. Following reduction by CCR and CAD, these thioesters are converted into p-coumaryl alcohol, coniferyl alcohol, and sinapyl alcohol, respectively.[57] The aromatic rings of the precursors were hydroxylated and O-methylated at hydroxycinnamic acid concentrations (Figure 2). Overall, owing to their effects on caffeoyl shikimate, the enzymes HCT, CCR, C3H, and CAD produce lignin G units and caffeoyl alcohol; F5H, COMT, and CAD generate sinapyl alcohol and S units through a unique branching pathway. Most recently, the CSE enzyme has been integrated into the wet chemical process. The tyrosine route skips tyrosine catalysis, resulting in a faster monolignol synthesis. During this process, polyfunctional phenylalanine and tyrosine ammonia-lyase (PTAL) transform tyrosine into p-coumarate (Figure 2).

Regulatory genes involved in lignin and phenylpropanoid pathway for plant defense

Understanding the genes involved in lignin and phenylpropanoid pathways will improve our knowledge of plant defense mechanisms and may lead to the development of crops with increased resistance to various stressors (Figure 2). The phenylpropanoid pathway produces lignin along with other phenolic polymers, which contributes to a number of resistance mechanisms of resistance.[58] The process of producing lignin results in the synthesis of secondary compounds and phenylpropanoid chemicals, which have antibacterial properties and serve a purpose in plant defenses. It is known which genes are associated with shikimate pathways, and some studies (Bonawitz *et al.*,[56]) have shown, for the first time, how they react when given access to cell walls. Under biotic and abiotic stress conditions, many phenylpropanoid pathway genes have been reported to be strongly expressed, which increases both the production and accumulation of associated enzymes.[59] The two primary components of lignin were sinapyl alcohol and coniferyl monolignol. Lignins perform several functions under various stress conditions. The phenylpropanoid pathway also produces a variety of additional chemicals (phenolic phytoalexins, stilbenes, and coumarins) along with monolignols, which were originally linked to plant defense.[60] This disruption of flux in the system may be the cause of some resistance mechanisms. The quantity of lignin can affect its physicochemical properties, and mutations within families of genes in the lignin cascade may cause unexpected responses to disease resistance. For instance, a change in the S/G lignin element ratio has a significant effect on the transcriptional function of genes that control stress responses, although it has no effect on morphological changes. Instead, it affects how chemicals involved in protective signals are stored within the cell wall matrices.[61] According to previous research, some alterations can be effectively controlled along the path of opposition. *Arabidopsis thaliana* has been used to study illness responses by silencing or removing functional genetic variations in regulatory networks. These investigations have mainly focused on *PAL, F5H, C4H, COMT, 4CL, CAD, CSE,* and *CCoAOMT* gene families.

Control of phenylpropanoid pathways in transcription

It is well known that, in response to infection, transcriptionally active genes involved in a variety of metabolic pathways produce phenylpropanoid metabolites (Figure 3). However, it is important to emphasize that steady transcript levels are often measured to obtain this result. According to Dixon *et al.*,[60] it is impossible to distinguish between increased transcription and mRNA stability using steady-state transcript level measurements. However, several studies using nuclear transcript run-on assays have demonstrated a strong correlation between the onset of illness and higher levels of phenylpropanoid pathway gene transcription.[63] The cis-regulatory elements included in the monolignol biosynthesis pathway are used in several prediction methods to elucidate the enigmas around the phenylpropanoid pathways. The predicted and observed results for complicated transcriptional systems were validated by promoter and electrophoretic mobility shift assays (EMSA). The transcription factors *MYB, LIM, ERF,* and *KNOX* have unique binding sites in the promoters of genes implicated in pathways that create lignin.[64] It is well accepted that the main conclusions of many investigations indicate the presence of AC components in enhancers. The promoter regions of the phenylpropanoid pathway genes were subjected to detailed functional investigation that revealed their modular design and allowed the primary coordinator elements to be recognized as AC elements. It has been discovered that the majority of the genes involved, including PAL, 4CL, C3H, and CAD,have promoter regions that are

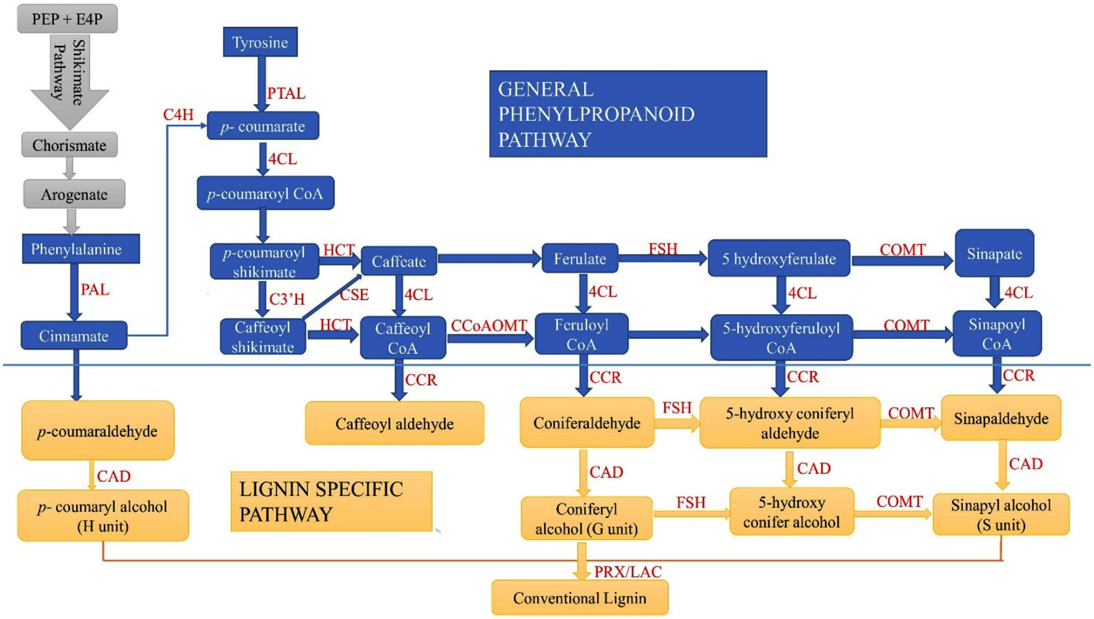

Figure 2. Genes related to the lignin and phenylpropanoid pathway in plant defence.[62] The following enzymes are involved in phenylalanine metabolism: PAL (phenylalanine ammonia-lyase), PTAL (phenylalanine tyrosine ammonia-lyase), C4H (cinnamic acid 4 hydroxylases), CAD (hydroxy) cinnamyl alcohol dehydrogenase, HCT (hydroxycinnamoyl-CoA: shikimate/quinate hydroxycin hydroxycinnamoyltransferase; C3'H, p-coumaroyl shikimate32 hydroxylase; 4CL, 4-hydroxycinnamoyl-CoA ligase; CSE, caffeoyl shikimate esterase; CCR, cinnamoyl-CoA reductase; F5H, coniferaldehyde/ferulate5 hydroxylase; COMT, caffeic acid/5-hydroxyferulic acid O-methyltransferase; CCoAOMT, caffeoyl-CoAO methyltransferase

sufficient to demonstrate the presence of these elements. However, neither the AC-rich element nor lignin-specific transcriptome factors were discovered in the S-lignin-producing genes.

Reactive oxygen species (ROS) and antioxidant defense mechanism

ROS are byproducts of the normal cellular metabolism in crops. However, their extremely active nature causes substantial harm to DNA, proteins, carbohydrates, lipids, and other essential cellular components (Figure 4). In the long run, many unfavorable effects result from oxidative stress, which is generated by an abundance of ROS, such as free radicals (hydroperoxyl radical HO_2; hydroxyl radical OH), and non-radicals, such as O_2 and H_2O_2.[65] The principal spots of ROS formation include the chloroplasts, peroxisomes, mitochondria, and cell membranes.[66,67] Chloroplasts are the primary site of ROS production. The ROS produced by chloroplast are 30-100 times higher than those produced by mitochondria.[68] Crops mainly deal with oxidative damage through defensive procedures consisting of enzymatic antioxidants, such as monodehydroascorbate reductase and ascorbate peroxidase, as well as non-enzymatic antioxidants,such as phenolic acids, flavonoids, and tocopherol.[69] These enzymes are known to be ROS-scavenging enzymes. The antioxidant defense system and the buildup of ROS in plant cells maintain a constant equilibrium, maintaining an adequate quantity of ROS inside the cell, allowing for proper redox-biological interactions, and

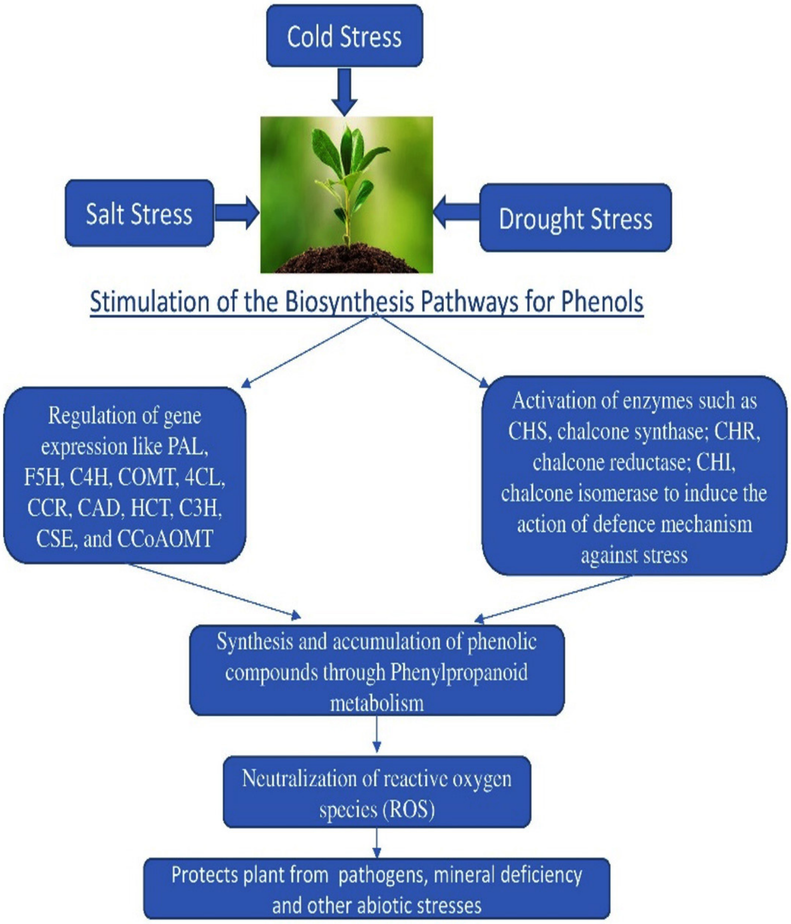

Figure 3. Expression of biosynthesis pathways involved in the formation of phenolics upon onset of various abiotic stresses.

governing various plant functions, such as growth and maturation balance between ROS formation and ROS degradation, maintain this intermediate level.[65] However, undue ROS generation breaks the equilibrium and causes oxidative stress,damaging cells and resulting in apoptosis and decreased plant yield.[70]

Oxidative stress under salinity

Salinity affects plants by creating osmotic stress, ionic toxicity, nutritional inadequacy, and genotoxicity, which causes ROS overproduction and oxidative damage.[6,71,72] Under sodium chloride (NaCl) stress, H_2O_2 production increases by three times, and the concentration of thiobarbituric acid-reactive particles (TBARS) increases by two to three times (Rehman *et al.*,[2] & Cheng *et al.*[73]) found that under salt stress, the total ROS level, electrolyte leakage (EL), and lipid peroxidation in rice root tissues were two-fold greater than those in control. Ahanger *et al.*[74] found an increase in EL and malondialdehyde (MDA) as well as an increase in O_2 and H_2O_2, indicating the oxidative impact of salinity in tomatoes. Salt stress increases MDA, EL, and O_2 in pepper by four-fold.[75] Lalarukh and Shahbaz[76] exposed two sunflower genotypes (FH-572 and FH-621) to high concentrations of saline NaCl and found that FH-572 elevated H_2O_2 whereas FH-621 reduced H_2O_2, indicating that FH-621 is more salt tolerant.

The accumulation of Na^+ ions in plant roots is associated with the overexpression of oxidative stress symptoms, such as MDA, EL, and H_2O_2 as well as lowered ASC and GSH redox status. Numerous plant cells and tissues suffer oxidative damage owing to various abiotic stresses.[77] Salt stress causes an increase in the quantity of ROS in plant tissues owing to changes in the ETS reaction in plants. This extra electrochemical energy can be released by the Mehler reaction, which leads to the generation of ROS, primarily H_2O_2, and membrane damage, as shown by greater levels of EL and MDA.[77]

Chemical elicitors improve the ability of plants to respond to salinity, which lowers the production of excess ROS (Wang *et al.*[46], Hernandez JA,[78] Yu *et al.*[79]). Furthermore, it has been demonstrated that the upregulation of a number of transgenes enhances ion homeostasis, hormone signaling, abscisic acid (ABA) synthesis, photosynthetic capacity, and antioxidant components, all of which increase stress tolerance and ROS metabolism.[78] Under high-salinity conditions, maize protects itself

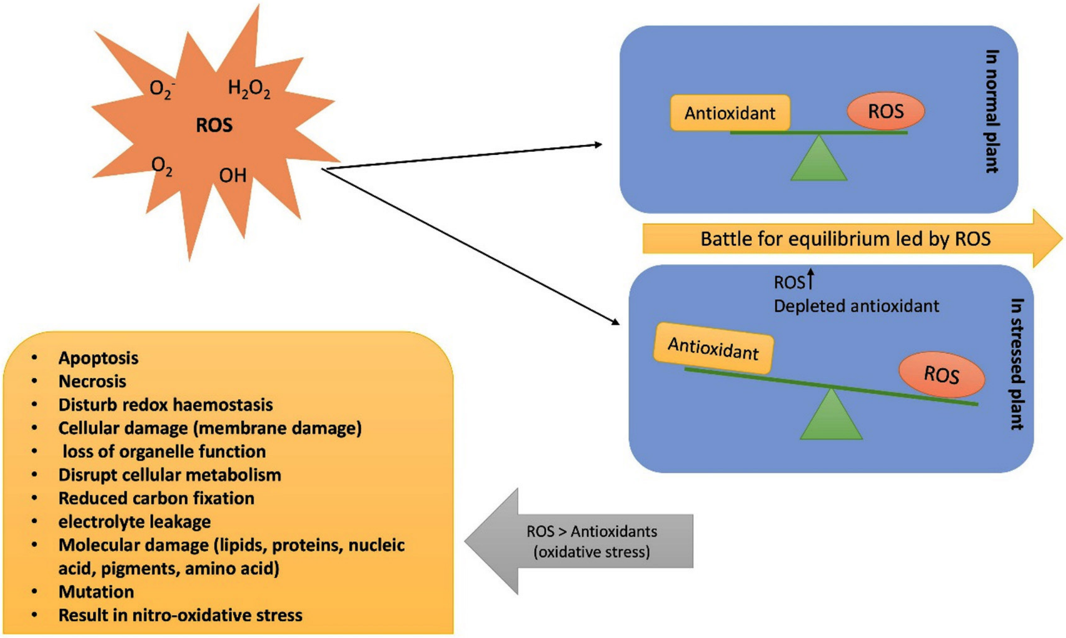

Figure 4. ROS and its effects on plants

from oxidative stress through both non-enzymatic and enzymatic processes. Although many organs respond similarly to salt stress, there are behaviors specific to each organ. An increase in polyphenol content and ASC, both of which function as non-enzymatic antioxidants, results from older leaves and roots, and this response is correlated with greater deposition of Na^+ in these tissues. Hichem *et al.*[80] found that despite newly formed leaves proliferating more than older leaves, maize plants accumulate greater amounts of polyphenols under high salinity. Tocopherol concentrations have been shown to increase to shield tomato leaves from oxidative damage.

Oxidative stress under water deficit/drought

Catalase (CAT), ascorbate peroxidase (APX), and other antioxidant defence mechanisms have been reported to be utilized by crops under water scarcity to minimize reactive oxidative stress and oxidative stress caused by drought in general.[81] Glutathione, an important signaling molecule in an array of metabolic processes, regulates the relationships between seed germination, stomatal pore closure, and drought.[82] Additionally, glutathione peroxidase (GPX) supports ROS scavenging by catalyzing the reduction of H_2O_2 and other organic hydroperoxides to protect cells from any harm caused by oxidative damage and ultimately enhance resilience to drought.[83]

Proteins that frequently appear within the ROS system, carbon metabolism, photosynthesis, signal transmission, and amino acid metabolic activity have been demonstrated to be involved in a number of stress responses in soybeans.[84,85] These proteins are thought to play genetic and molecular roles in the regulation of stress in soybean.[86] Moreover, the most sensitive reaction to water deficit is fluctuations in protein quantity.[87] Roots begin several modifications in the face of drought because they are the primary sites for collecting stress signals, and the water intake of the roots is essential for causing the strain.[87]

Drought causes stomatal closure, decreases CO_2 input, diminishes photosynthetic rate, disrupts light harvesting and use, and alters chloroplast photochemistry, all of which cause excess ROS production.[65,88] ROS overproduction is also linked to photorespiration-induced dissolution of proteins and membranes, inactivity of TCA cycle enzymes, and decreased carboxylate efficiency caused by dryness.[89] It has been found that high ROS generation in many plant species is caused by oxidative and water stress. Phragmites escape was grown under dry conditions by Abideen *et al.*,[90] who discovered a substantial increase in MDA concentrations, and Coffea arabica recorded considerably higher MDA concentrations under the same circumstances.[91] Saha *et al.*[92] removed irrigation from rice for a few days to simulate drought and observed a large increase in Oxygen, Hydrogen peroxide, and MDA due to the lack of water. Similarly, finger millets have higher H_2O_2 and EL concentrations.[93]

Oxidative stress under cold/low temperatures

ROS formation is noted in crucial biochemical processes such as photosynthesis and respiration, and is a significant biological change caused by cold stress. The function of ROS-scavenging systems in plants is linked to low temperatures. SOD converts $O_2\bullet$ into H_2O_2, a molecule with dual functions that acts in both the signaling process and in toxifying cell activities before being rummaged by APX and CAT.[94] ROS and peroxidescause severe oxidative damage in rice when exposed to low-temperature stress, and the antioxidant defense system mitigates their negative effects.[95] Proline accumulation stimulates membrane stability and subcellular structure stability, and protects cells from oxidative stress under abiotic conditions.[96] In addition to its role in reducing ROS damage, the AOX pathway also reduces ROS production in plants that can withstand abiotic stress. The electrolyte leakage index is a key measure of the permeability of the cytoplasmic membrane.[97]

Plant chloroplasts play a crucial role in sensing environmental temperature. At low temperatures, an imbalance occurs in the leaves because of their ability to collect energy from the sun and use it for metabolism. This imbalance can produce ROS, which can destroy the photosynthetic apparatus and harm healthy cells by acting as a secondary messenger. Under cold stress, there is an elevation in the concentrations of MDA and EL in rice seeds under cold stress.[98] Low-temperature stress, when applied to the cold-sensitive *S. lycopersicum* genotype, resulted in considerably greater MDA and H_2O_2 content than plants grown under normal temperature conditions.[99]

Genomic advances in abiotic stress

Plant's response to salt stress

Jasmonic acid (JA), cytokinins, gibberellic acid (GA), ethylene, and other phytohormones are crucial for plant responses to salt stress. ABI5 expression is suppressed and ABA signaling is interfered with by type-A response regulator proteins that are activated by cytokinins due to salt stress.[100] A complex is formed when GA and gibberellin-insensitive dwarf 1 (GID1) bind, causing DELLA proteolysis.[101] When combined with *XERICO*, *DELLA* proteins function as regulators of the pro-salt stress response. By inhibiting the negative salt stress regulators ETR1/ETR2/EIN4, the ethylene act as a beneficial regulator in the response of plants to salinity stress by inhibiting the negative salt stress. EIN2 is activated by ethylene receptor inactivation and positively controls salinity tolerance reactions.[102]

High salinity-induced osmotic stress promotes ABA production. The mechanism by which rice produces ABA via the terpenoid route begins with isopentenyl pyrophosphate (IPP). Within a few hours of salt exposure, *OsNCED5, OsNCED3, OsNCED4,* and *OsPSY3* are activated in rice, and their expression is closely related to ABA levels in rice roots. Both jasmonate deactivation and increased CYP94C2b expression have been linked to salinity.[103] Two MAPKs, *OsMSRMK2* and *OsMSRMK3*, are expressed in response to numerous climatic stimuli, indicating their potential association with stress-response pathways.[104,105]

The thioredoxin protein-encoding gene *MsTRX* boosts the salt tolerance capacity of transgenic tobacco by preserving the osmotic balance (*Nicotiana tabacum* L.).[106] Abscisic acid-sensitive (ABI) regulates ROS metabolism by adhering to vitamin C insufficiency 2 (VTC2) and RbohD during salt stress regulation of Arabidopsis seed germination. ABI is an essential component of ABA signaling and is associated with ROS production and scavenging.[107]

Plant's response to drought

Drought is a major concern in the study of how climate change affects agricultural productivity.[108,109] Owing to natural selection and long-term evolution, plants have developed many drought-coping strategies, including drought escape via developmental flexibility and drought resistance by stomatal adjustment, antioxidant capabilities, osmotic adaptation, and water absorption.[110] Several studies have shown that genes that affect how species adapt to dry conditions are also activated. Several interrelated molecular systems support various metabolic functions, including stress signal reception, DNA and protein expression signal transduction, and cellular metabolic processes.[111]

The *RD29A* gene and its product keep cells hydrated. The dehydration-responsive element (DRE) is required for cis-acting RD29A initiation in an ABA-independent reaction under dehydration and cold stress conditions.[112] Three *CBF/DREB1* genes found in Arabidopsis plants have a crucial function not only in water deficit conditions but also in cold stress. These genes were *DREB1B/CBF1, DREB1A/CBF3*, *DREB1C/CBF2. DREB2A* and *DREB2B* are *DREB2* proteins. *DREB2* is induced under water-deficient and cold stress.[113]

Numerous genes are induced under water deficit conditions during plant reproductive development. Examples include *OsMID1, ANAC019*, and *OsERF101*.[114,115,116] These genes improve anther (pollen) fertility and seed production by mitigating anther defects under drought conditions. ANAC019 is an early drought response regulator.[117] ANAC019 not only promotes reproductive development but also protects crops under water deficit stress conditions.[116] AtMYB37 plays a significant role in seed production regulation and drought stress response in *Arabidopsis*. *OsMID1* (Guo *et al.*,[114]) and *OsERF101* are found in rice flowers and are activated under stress conditions. Upregulation of *OsMID1* enhances pollen fertility and reduces anther defects, resulting in increased grain production.[114] Upregulation of *OsERF101* elevates peroxidase activity and proline content, which in turn enhances pollen fertility and drought tolerance.

Plant's response to cold

Plants growing atextremely low temperatures require unique systems to handle such climatic conditions. Temperate plants face two types of cold stress: chilling stress

(0-15°C) and freezing (0°C). Temperate plants can tolerate extreme temperatures[118] but tropical plants are vulnerable to cooling shock and do not possess a cold adaptation mechanism. The reproductive development of plants is also slowed by exposure to low temperature.

Plants detect cold via the plasmalemma receptor, and a signal is sent to activate genes that respond to cold and transcription factors that mediate stress tolerance.[119] Cold stress is mediated by salicylic acid (SA), abscisic acid (ABA), brassinosteroids (BRs), and other phytohormones.[120] Phytohormones, such as GAI and JAZ7, regulate the expression of low-temperature-inducible genes in cassava.[121] Cold stress inhibits gibberellins and cytokinins, which promote the expression of CBF1 and CBF3. The upregulation of these genes protects plants from freezing temperatures.[122] This causes an increase in the expression of the cold-responsive genes. JA also boosts cold tolerance by interacting with other hormone signaling pathways.[86] *ESK1, GIGANTEA (GI), HOS9, AtHAP5A,* and *AtXTH21* genes found in Arabidopsis provide tolerance to low temperatures without using the CBF pathway.[123]

LEA proteins are important for membrane stabilization. These proteins also prevent protein aggregation.[124] *CuCOR19*, a citrus *LEA* gene, improves cold tolerance in transgenic tobacco.[125] Other genes, such as wheat dehydrin *WCS19* and *Arabidopsis COR15a* (Artus *et al.*)[126] enhance the freezing resistance of transgenic *Arabidopsis* plants. Dehydrins such as wheat *WCOR410*,[127] barley *DHN5*,[128] have highly resistant to cold stress. These heat shock proteins (HSPs) are induced by low temperatures and function to prevent membrane refolding, denaturing protein, and hindering protein aggregation.[129]

CONCLUSION

Phenolic chemicals are abundant in plants and provide a variety of activities such as protection against biotic and abiotic stresses. Phenolics are found in various plants and fruits. They are categorized into several classes based on their structure and are classified as phenolics, stilbenoids, flavonoids, and lignans based on their chemical structures. In general, phenolics can be seen as free forms in plants, but they are mostly conjugated to sugar residues linked to a hydroxyl group (O-glycosides) or an aromatic ring carbon atom (C-glycosides) by a glycosidic bond. Plants experience both biotic and abiotic stresses, and phenolic chemicals play a crucial role in plant growth and defence mechanisms, allowing them to endure different stresses. The potential role of phenolics in abiotic stress tolerance is promising, and holds great potential for shaping the future of agriculture and environmental sustainability. To enhance the resistance of crops to environmental stressors, such as drought, extreme temperatures, and nutrient deficiencies, crops with increased phenolic production can be developed through genetic engineering or biotechnological approaches. Utilize phenolic-rich plant extracts or compounds for eco-friendly stress management strategies in agriculture to reduce reliance on chemical interventions. Integrate the role of phenolics in sustainable agricultural practices, promoting a balance between high crop yields and environmental conservation. To investigate the potential of phenolic-rich plants for phytoremediation, they were used to detoxify and rehabilitate soil and water contaminated by pollutants. Phenolic compounds play a crucial role in enhancing plant performance under adverse conditions by synthesizing pigments, maintaining structural integrity, producing secondary metabolites, acting as antioxidants, and contributing to biochemical defense. Plants have a range of genes that are activated when exposed to various stressors, enabling them to endure stressful situations.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTION

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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DATA AVAILABILITY

All datasets generated or analyzed during this study are included in the manuscript.

ETHICS STATEMENT

Not applicable.

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