



Plant Phenolics: As Antioxidants and Potent Compounds Under Multiple Stresses 11

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Abstract

Reactive species are categorized into two broad sub-categories, reactive oxygen species (ROS) and reactive nitrogen species (RNS), possessing either a free radical with an unpaired electron in the valence shell or a neutral molecule. Free radicals are classified as one of the crucial steps in stress signaling which often cause unavoidable impairment to the essential biomolecules as a result of which the cell experiences various regulatory impairments. Redox homeostasis between the oxidants and antioxidants is the key to ensure normal cell functioning. As far as the current scientific evidence is concerned, almost all the plants possess natural antioxidants distributed throughout different parts of the plants. Different antioxidant assays show the potentiality of plant phenolics as an effective radical scavenger. Multiple hydroxyl and carbonyl groups of polyphenols help in the establishment of stable metal- and protein–polyphenol

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215

R. Lone et al. (eds.), *Plant Phenolics in Abiotic Stress Management*,
https://doi.org/10.1007/978-981-19-6426-8_11

complex thereby restricting the development of free radicals. Phenols are known to work harmonious with other antioxidants thereby escalating the overall radical scavenging activity. A plentiful of research is evident on the propensity of plant phenolics as antioxidants but two things limit their current usability as food antioxidants. First, plant phenols are secondary metabolites and their continuous biotransformation inside the cells and tissues is an obvious event making their bioavailability difficult. Second, there are a few pieces of evidence on the toxicity and/or carcinogenicity of plant phenolics which restricts the considerations for the acceptability of such antioxidants as food additives. By considering the before-mentioned facts, this chapter compiles the emerging roles of phenolic compounds as antioxidant and impacts of multiple stressors on plant processes and stress managements through phenolic compounds.

Keywords

Phenolics · Antioxidants · ROS · Multiple stress · Stress management

11.1 Introduction

The basic life functions of a typical plant involve production and utilization of various plant metabolites which are categorized into primary and secondary metabolites (SMs). The latter is a derivative of primary metabolite and often described as an intermediate or end product of metabolic pathway. A great proportion of organic compounds do not participate directly in growth and development. Unlike primary metabolites, the presence or absence of these metabolites does not strictly impair the organism's established functionality. However, majority of the plant SMs are naturally constitutive and exist in their biologically active forms leaving few as inactive precursors. Damages to the plants caused by several biotic and abiotic factors trigger the activation and modulation of these inactive precursors. Complex metabolic pathway often involves overlapped intermediates of primary and secondary metabolism indicating common pathway being shared by primary and secondary metabolisms (Verpoorte et al. 2000; Yeoman and Yeoman 1996). There are three distinguished groups of SMs, includes terpenes, phenolics and nitrogen, sulphur compounds (Jamwal et al. 2018).

Phenolic compounds have one aromatic ring with one (phenol) or more (polyphenol) -OH^- groups. These SMs often exist in the form of different functional derivatives (esters, methyl ethers, glycosides, etc.) synthesized either through the shikimic acid pathway or through the malonate/acetate pathway. Phenolics are broadly classified into simple phenolics (such as phenolic acids), polyphenols (such as tannins, flavonoids), lignans, coumarins, lignins, resveratrol, etc. on the basis of their carbon backbone (Harborne 1964; Cheynier et al. 2013). Solubility of simple phenolics can be changed from polar organic solvent to water through esterification and glycosylation with further facilitation through the increased number of hydroxyl groups in case of polyphenols. Even though phenolic compounds are

abundant in plant kingdom but their allocated amount varies from one another depending on the selectionary advantage conferred to an individual plant during the course of evolution. Plant phenolics are divided in two classes such as preformed phenolics (synthesized during the normal development of plant) (Pridham 1960) and induced phenolics (elicitor mediated synthesis by plants during stressed environment) (Nicholson and Hammerschmidt 1992).

Plants being sessile experience multitudinous stresses ceaselessly throughout their growth and development due to the ever-changing environment (Singhal et al. 2017). Plants have no/little options to adapt with the changing conditions. One of the adaptive responses of plants is synthesize SMS, especially phenolic compounds. Phenolic compounds have been shown very effective under multiple abiotic and biotic stress and unfavorable climatic conditions and provide tolerance via antioxidant activity. This chapter compiles the overview of phenolic compounds and their role under multiple stressors.

11.2 Overview of Plant Phenolics and Its Role

11.2.1 Primary Function of Plant Phenolics as Antioxidants

Research in the field of plant ecology and plant physiology to explore the potential of plant phenolics has gained the pace by virtue of antioxidant and free radical scavenging properties of plant phenolics. Presence of more than one acidic hydroxyl groups in the phenyl ring of polyphenols makes them good donors of hydrogen or electron and hence the ability to confer free radical reduction (chain-breaking function) and termination of the Fenton reaction through the phenoxy radical intermediates. These phenoxy radical intermediates can also act as pro-oxidants at a higher pH in the presence of higher concentration of phenolic compounds and redox-active metals (copper, iron). Certain phenolics like flavonoids impede the membrane lipid peroxidation through altered membrane lipid packing. This alteration causes drastic loss of membrane fluidity and thus prevents free radical diffusion (Rice-Evans et al. 1997). Stimulatory role of phenolics cause amplification of cellular antioxidant capacity through host antioxidant enzyme responses (Shetty and Wahlqvist 2004). Phenolic coupling followed by oligomerization in case of complex polymeric phenolics (viz. tannins) escalates the antioxidant ability (Bors and Michel 2002).

11.2.2 Additional Functions of Phenolics in Plants

Phyllospheric and rhizospheric exudates containing polyphenols in the form of leachates can act as signaling compounds which when enter the soil cause alteration in the rates of decomposition and nutrient cycling through direct or indirect effects caused to soil microbial (decomposer) community (soil–microbe interaction). Flower and fruit pigmentation are also aided by phenolics (viz. flavonoids). This

gives the plant a blessing in disguise for its own propagation through pollinator-mediated seed dispersal. Cross-linking among cell wall polymers ordinarily imparts the long-term maintenance of structural integrity. In this regard, hydroxycinnamate, a phenolic compound, plays a significant role making it difficult for the approaching pathogens to penetrate the cell wall. Among other physiological role of plant phenolics includes integral signal during plant–fungus interaction, maintain fruit quality and aroma, primary barrier during herbivores attack, synthesis of plant growth promoting substances, bioremediation, water and mineral absorption, chlorophyll content, pigment composition, and as allelochemicals (Zaprometov 1992; Sharma et al. 2019; Kumar et al. 2020a, b, c).

11.2.3 Impacts of Plant Phenolics on Plant Physiological, Biochemical, Reproductive, and Yield Traits

Wide distribution and as a part of key product of secondary metabolism, phenolics are known to influence various growth- and development-related physiological process in plants. Be it in normal or stress condition, plants get constant amelioration in the suboptimal conditions through phenolics-mediated tolerance and adaptation. As mentioned earlier, phenolics have diverse direct or indirect roles in nutrient mobilization through signal transduction (viz. flavonoid and salicylic acid signaling), allelopathy, plant growth promotion through plant growth promoting rhizobacteria (PGPR), pigmentation, etc. apart from their active role as antioxidants. Phenolics are involved in functional pollen development (Van Der Meer et al. 1992; Taylor and Grotewold 2005) and imbibition mediated boosting of seed germination rate (Shankar et al. 2009). Photosynthetic activity and biosynthesis of assimilatory pigments (chlorophyll *a* and *b*) can be amplified in C₃ (sunflower) and C₄ (maize) plants through polyphenols (Tanase et al. 2015).

11.2.3.1 Antioxidants: Definition, Classification, General Mechanism of Action

Antioxidants are the substances which stop the oxidation of any substance and counteract the free radicals at the same time generated during oxidative stress even with relatively low concentrations. Antioxidants discontinue these sequence reactions by eliminate free radical intermediates and obstruct other reactions by being oxidized themselves.

11.2.4 Classification of Antioxidants

Antioxidants can be grouped into natural and synthetic antioxidant system. Natural antioxidants are further categorized into enzymatic and non-enzymatic antioxidants. Enzymatic antioxidants include superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPX), glutathione reductase (GR), and glucose-6-phosphate dehydrogenase. Enzymatic antioxidants are produced endogenously where as

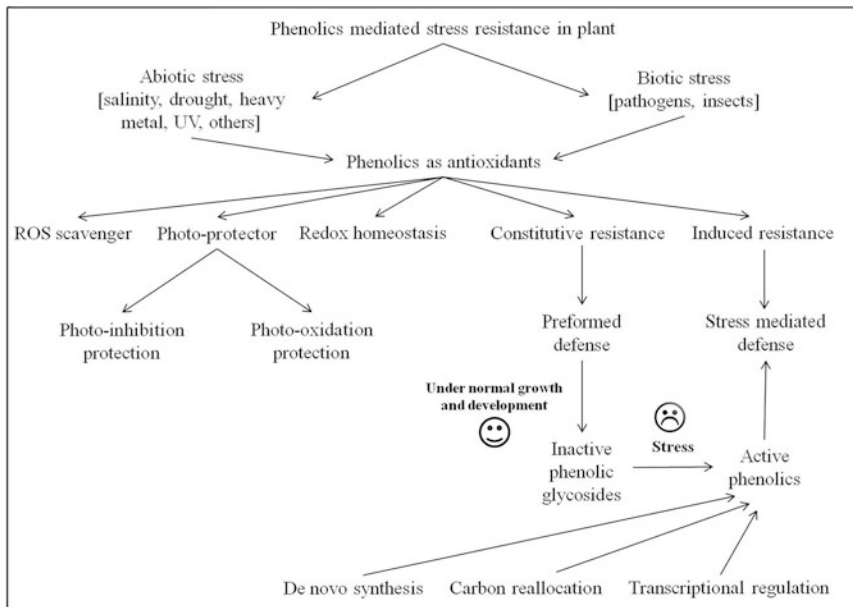


Fig. 11.1 Plant stress mitigation through phenolics-mediated resistance

non-enzymatic antioxidants are mostly from dietary origin. Non-enzymatic antioxidants include minerals (zinc, selenium), carotenoids (β -carotene, zeaxanthin, lycopene), vitamins (vit. A, C, E, K), some antioxidant cofactors (coenzyme Q_{10}), and phenolics (Bunaciu et al. 2012) of which polyphenols is the largest class (Liu 2004). On the other hand, synthetic antioxidants (given in Fig. 11.1) are man-made compounds synthesized chemically. When stressed, plants generate singlet and triplet oxygen species, peroxides, harmful enzymes. The role of antioxidant system is to scavenge these toxic radicals as singlet and triplet oxygen quenchers, synergists, enzyme inhibitors, and peroxide decomposers (Manach et al. 1998). Some of the analytical methods to measure antioxidant content and capacity of plant extracts are based on assays involving hydrogen atom, assays involving electron transfer, chemiluminescence, etc. (Huang et al. 2005).

11.2.5 Stress-Mediated ROS Generation and Redox Signaling: Good or Bad?

Exposure to various abiotic and biotic stresses leads to an imbalance in cellular redox homeostasis followed by generation of reactive oxygen species (ROS), which sooner or later leads to the oxidative stress and damage of plant cell organelles. For plant stress mitigation, optimal level of ROS acts as a priming step in the activation of antioxidant system through ROS-mediated redox signaling. On the contrary, over

production of ROS leads to disruption of normal cell functions leading to the plant immune system failure (Hussain et al. 2019). Hence, generation of ROS can be considered as a necessary evil. Stress-mediated ROS generation has several impacts on plants both physiologically and biochemically through protein disruption, reduced CO₂ fixation in chloroplasts, photooxidative damage to the photosynthetic complexes (principally PSII), membrane peroxidation ultimately leading to programmed cell death (PCD) (Amist et al. 2019).

ROS-mediated redox signaling is a cascade of event where redox-sensitive signaling proteins and metabolic enzymes undergo reversible oxidation/reduction to execute cellular functions via either regulating or amplifying the downstream signaling components, such as kinases, phosphatases, and transcription factors (Suzuki et al. 2012). Physiological events in the plants are regulated by phytohormones to a large extent. ROS acts as secondary messenger in the hormone signaling pathways and can impose hormonal regulation feedback or feedforward mechanism (Noctor et al. 2018). As a consequence of this cross-linked signaling between ROS and hormone, plants undergo modified root architecture triggering lateral root emergence with enhanced root hair growth (Du and Scheres 2018).

11.3 Abiotic Stress Response Through Phenolics

Challenges from ever transforming environment coupled with increased anthropogenic activities force plants to undergo a plethora of biotic and abiotic stresses throughout their life. These create a major setback in terms of their growth, development, and yield attributes.

Plants endure this unfavorable condition through different inherent mechanisms and acclimatize in the hostile environment surrounding them. In this regard, the chapter elaborates the role of antioxidant systems with a specific reference to phenolics (plant SM) to mitigate various abiotic and biotic stresses along with the basics of the mechanism underlying.

Plant SMs are believed to be considered as by-products until the scientific evidences regarding the active involvement of plant phenolics in maintaining a harmony between plant and its surrounded environment whether for stress mitigation or growth and developmental process have popped up. The fascinating fact about plant phenolics are they not only involved in the obliteration of harmful organisms associated with the abnormal growth and metabolism of plants but also playing a crucial role in maintaining the healthy population of beneficial symbiotic microorganisms around rhizosphere. The defensive action and expression of plant phenolics against biotic stresses (pathogenic microbes, insects, etc.) are something bestowed to plants during the natural evolution process. This built-in basal level of constitutive expression plus an induced expression of phenolics through stress-mediated signaling provides two-layered protection to the plants. Counteracting mechanism of phenolics against insects or pathogens can be direct or indirect (toxicity through induced changes in phenolic profiles) (Tyagi et al. 2020; Tak and Kumar 2020; Wagay et al. 2020). Among different schemes of the

phenolics-mediated plant stress tolerance, the most noticeable is the activation of antioxidant systems which is synergistic to almost all the defense mechanisms in the plants. In fact, phenolics itself can act as an antioxidant to scavenge ROS (Amarowicz et al. 2010) and hinder the activities of specific oxidizing enzymes (Elavarthi and Martin 2010). Cross negotiation among various factors such as phytohormone production, biosynthetic pathway modulation occurs by virtue of the radical scavenging ability of antioxidant system and through optimized ROS signaling.

Physiological and molecular mechanisms concerning SMs production are deeply concatenated with the interactions between signaling molecules (salicylic acid, jasmonic acid, their derivatives, etc.) and enzymes for phenolics biosynthetic (phenylpropanoid) pathway (do Nascimento and Fett-Neto 2010; Cheyner et al. 2013). There is an absolute certitude that stress mitigation through phenolics is a resultant of one or more enzymatic (phenylalanine ammonia lyase; PAL, chalcone synthase; CHS, dihydroflavonol 4-reductase; DFR, cinnamate-4-hydroxylase; C4H, flavanone 3-hydroxylase; F3H, flavonol synthase; FLS, isoflavone synthase; IFS, isoflavone reductase; IFR, UDP flavonoid glycosyltransferase; UFGT) modulation (s) involved in phenolic biosynthetic pathway (Sharma et al. 2016, 2019; Ashraf et al. 2018; Naikoo et al. 2019).

11.3.1 Phenolics-Mediated Resistance Towards Salinity Stress

Phenylpropanoid-mediated synthesis of phenolics helps in scavenging ROS effectively in osmotic and ionic mismatches during salt stress (Rossi et al. 2016; Al-Ghamdi and Elansary 2018). Up-regulation of flavonoid biosynthetic genes like VvbHLH1, NtCHS1, GmFNSII-1, GmFNSII-2, etc. helps in accumulation of flavonoid thereby aiding phenolic-mediated ROS scavenging (Tanase et al. 2014; Wang et al. 2016; Zheng et al. 2017). Similarly, enhanced transcript levels of PAL, C4H, F3H, DFR, FLS facilitate tolerance mechanism to the plants under salt stress (Perin et al. 2019). In Brassicaceae (Chinese cabbage, white cabbage, and kale), short-term adaption to salinity stress is species specific and phenolic compound hydroxycinnamic acid is higher in tolerant species. In this case, phenolic compounds provide tolerance via maintaining of higher levels of SM, osmoprotectants, and suffer less from metabolic imbalance or disorders (Linić et al. 2019)

11.3.2 Phenolics-Mediated Resistance Towards Drought Stress

Reports suggest under water deficit conditions both the accumulation and synergism of phenolics (such as flavonoids) with other antioxidant systems go hand in hand resulting in plant resistance against drought stress (Sánchez-Rodríguez et al. 2011). Water scarcity induces closure of stomata resulting in less CO₂ diffusion through stomatal pores. At this point, cell utilizes less reducing power (NADPH + H⁺) and ATP to synthesize carbohydrate as there is lower concentration of CO₂ to be fixed.

The lack of CO₂ also leads to impaired Calvin cycle making it almost difficult for the conversion of NADPH + H⁺ and ATP to NADP⁺ and ADP + Pi. The non-utilization of vast number of free electrons possessed inside the reducing equivalent may then be able to break redox homeostasis through ROS generation inside the cell. Xanthophyll cycle play two key roles in drought stress. First, it helps in reverting the excess NADPH + H⁺ and ATP into NADP⁺ and ADP + Pi even in the absence of Calvin cycle. Second, it forms excess of SMs among which phenolics occupy the major proportion thus contributing towards the cellular redox homeostasis by scavenging ROS in the system if any (Gnanasekaran and Kalavathy 2017).

11.3.3 Phenolics-Mediated Resistance Towards Heavy Metal Stress

Transcriptional regulation of phenylpropanoid pathway enzymes (phenylalanine ammonia-lyase, chalcone synthase (CS), shikimate dehydrogenase, (SKDH) cinnamyl alcohol dehydrogenase (CAD), and polyphenol oxidase (PPO)) (Zafari et al. 2016; Chen et al. 2019) causes up-regulation in their activity under metal stress (Handa et al. 2019). This up-regulation is the main cause of phenolic (flavonoid)-mediated metal stress tolerance and their subsequent metal chelation process (Kisa et al. 2016) with an ultimatum of protecting the plants from oxidative stress and ROS.

11.3.4 Phenolics-Mediated Resistance Towards UV Stress

Light/UV stimulated flavonoid biosynthetic pathways and their corresponding gene transcript levels (Naikoo et al. 2019; Chen et al. 2019; Ghasemi et al. 2019) are the key to protect plant and its photosynthetic apparatus against high-intensity light and UV radiations by absorbing them (Lattanzio 2013; Landi et al. 2015). This modulation of the flavonoid biosynthetic pathway can either be a dependent or independent process on hormone (ABA) and/or jasmonic acid (Demkura et al. 2010; Berli et al. 2015).

Other abiotic factors like excess application of insecticides (Sharma et al. 2016), heat stress (Świeca 2015), chilling stress (Zhou et al. 2019; Wang et al. 2019), etc. invigorate cells' ability to accumulate phenolic compounds by up-regulating biosynthetic pathway enzymes for quenching the reactive radicals. Plant cell wall thickening through lignification and suberization enhances freezing stress tolerance (Griffith and Yaish 2004).

11.4 Plant Phenolics and Biotic Stress: Beyond Antioxidant Role

The generalized scheme of plant stress mitigation through phenolics is depicted in Fig. 11.1. Like abiotic stresses, plants have to undergo multiple biotic stresses caused by diverse living micro or macroscopic organisms. Even though plants

contain a diverse group of protective molecules such as preformed peptides, proteins, and SMs against these biotic factors but the concentrations of these molecules are often at basal levels. However, pathogenic attack causes genetic reprogramming followed by elevation to their levels through elicitor-induced expressions as documented in case of phenolics where plant accumulate higher levels of phenolics through elicitor-mediated up-regulation in the activities of biosynthetic enzymes such as phenylalanine ammonia lyase and chalcone synthase (Campos et al. 2003; Yedidia et al. 2003).

Detection of potential assailants can activate the plant defense response which is otherwise kept under tight genetic control in normal condition to maintain equilibrium between primary and secondary metabolism. The sudden surging in the SMs expression levels is due to the plant signal perception in the form of damages caused due to the toxins produced by pathogens and is evident from an increased levels of phenolics under fungal infection (Verma and Shukla 2015). In fact, preformed phenolic compounds are stored as antibiotic phenolics in inactive bound forms and get activated rapidly upon pathogen attack. The beauty of plant system having SMs (phenolics) is that there is no requirement of additional transcriptional activation for their expression but mere breakage of compartmentalization is enough to create a protective shield against biotic stresses (Osborn 1996).

Phenolics-mediated oxidative reactions consume excess oxygen making a toxic environment for the pathogen survival. Presence of acidic hydroxyl groups in polyphenols has made them suitable candidates to penetrate biological membranes of fungus, while multiple hydroxyl groups help in uncoupling of oxidative phosphorylation (Siqueira et al. 1991; Parvez et al. 2004). Complex natural phenolics such as tannins and lignans can reduce the *in vitro* growth of fungal mycelium through their inhibitory action on the extracellular fungal enzymes which are essential for host tissue penetration (MacRae and Towers 1984). Mechanical penetration and survival of fungal pathogens are restricted via elicitor-mediated lignifications of plant cell wall which impede the movement of water and other diffusible molecules for pathogen survival (Garcia-Brugger et al. 2006; Houston et al. 2016). In this regard, flavonoid can also serve as low-molecular weight phytoalexins which are antimicrobial in nature (Samanta et al. 2011).

11.5 Factors Affecting the Regulation of Phenolic Biosynthesis

11.5.1 Proline Accumulation Under Stress

A key linkage between environmental stress and adaptive responses of plants towards stress is discussed here. Both biotic stresses and abiotic stresses induce the accumulation of a large quantity of free proline through reduced oxidation of the amino acids. This temporary proline accumulation through proline-D1 pyrroline-5-carboxylate (P5C) cycle generates a pool of NADP⁺ and regulates cellular redox potential (Kaur and Asthir 2015). Pentose phosphate pathway (PPP) is an established pathway for phenolic biosynthesis among others (Shetty and Wahlqvist 2004). Since

NADP⁺ is the cofactor for the enzyme (glucose-6-phosphate dehydrogenase; G6PDH) catalyzing rate limiting step of PPP, proline-mediated high-NADP⁺/NADPH flux may augment phenolic biosynthesis (Cheynier et al. 2013) along with other phenolic precursor forming pathways like glycolysis (Maeda and Dudareva 2012) and calvin cycle (Lattanzio et al. 2009).

11.5.2 Cellular Compartmentalization

Synthesis of plant phenolics in thylakoids of chloroplasts and their subsequent storage (as inactive phenolic glycosides) in cell vacuoles manifest that the compartmentalization is a necessary physiological event to pile the reduced form of phenolics (Wink 1997). Stress-triggered de-compartmentalization (Beckman 2000) can cause mixing up of glycosidase enzyme with its inactive substrate (phenolic glycosides) resulting in clip off of glucose moiety thus making active phenolics ready for stress response (Dai et al. 1996).

11.5.3 Carbon Reallocation: As a Function of Growth vs Defense

Tolerance and resistance mechanisms of plants come with a high cost of resource allocation for the synthesis of defensive metabolites. Therefore, plants do not synthesize these metabolites unless they are threatened with potential harm above their threshold level. Unlike a stressed plant, a healthy plant only relies on the preformed or constitutive defenses (Morrissey and Osbourn 1999; Wittstock and Gershenzon 2002; Koricheva et al. 2004). Plant's decision whether to grow or defend drives the quantitative (constitutive expression) and qualitative (de novo synthesis) synthesis phenolics through either carbon reallocation (production of defensive SMs instead of developmental primary metabolite like sucrose) or enzyme kinetics alteration at transcriptional level (Henkes et al. 2001; Nakane et al. 2003; Lloyd and Zakhleniuk 2004; Leser and Treutter 2005; Fritz et al. 2006; Walters and Heil 2007; Akula and Ravishankar 2011; Vos et al. 2013 represented in Fig. 11.2).

11.5.4 Theory of Photo-Protection and Co-evolution: Blessings in Disguise

Red to reddish-orange color of the deciduous tree leaves are due to the storing of anthocyanin, a class of flavonoids inside the acidic vacuole, a specialized leaf compartment. These color cues due to the presence of anthocyanin solve two major problems of the plants. First, it provides protection against photo-inhibition and photo-oxidation of photosynthetic pigments through light attenuation (green sunlight interception). Second, the red color might serve as a representation of plants poor nutrient status and hence not preferred by the insects and hence a low-insect

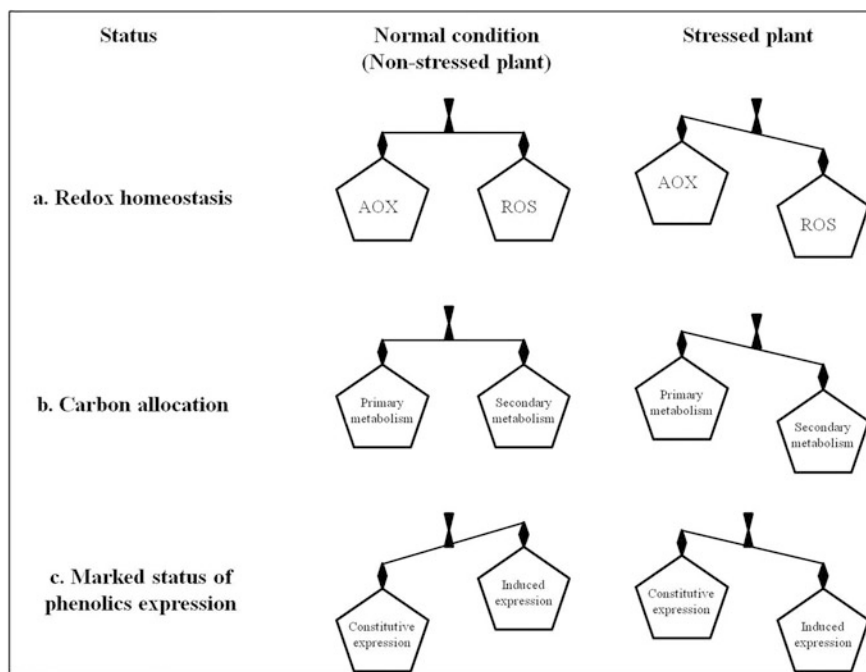


Fig. 11.2 Status of normal (non-stressed) and stressed plants. (a) Redox homeostasis (*AOX* antioxidant, *ROS* reactive oxygen species); (b) carbon allocation (primary metabolism, secondary metabolism); (c) marked status of phenolics expression (constitutive expression, induced expression)

load (Archetti 2009; Archetti et al. 2009; Nikiforou and Manetas 2010; Hughes 2011).

11.6 Plant Physiological, Genetical, Biochemical and Molecular Approaches to Improve Phenolic Compounds and Stress Mitigation

In terms of plant physiology, stress is defined as any abiotic or biotic factors which affect plant functioning and development. Nearly every plant has to undergo various forms of stress during their life cycle as a result of which it affects the growth and yield of the plant. Plants accumulate phenolic compounds as a defense strategy against stress. Though it provides a defense to plants during adverse conditions but the trade-off between growth and defense has certain limitations. Since resources are limiting, the strategy of mitigating stress by improving the phenolic compound comes with certain restrictions. Three different approaches can achieve the engineering of improving phenolic content.

11.6.1 Biochemical Strategies of Phenolic Compounds to Mitigate Stress Tolerance

Growth regulators, nutrients, and fertilizers on phenolic development have crucial role in balancing of plant redox equilibrium. Treatment of grape leaf and fruit by sucrose and abscisic acid was found to be highly correlated with total phenolic content (Gambetta et al. 2010). Spayd et al. (1994) observed that nitrogen used to have an inhibitory effect on phenolic content. Under low nitrogen, the canopy was lighter and exposed for better light-enhancing phenolic accumulation. Phenolic content and metabolism have diversely been affected by growth regulators. Berhow (2000) studied that ABA had a little effect on the flavonon responsible for the bitterness of the grapefruit. Whereas GA reduced the flavonon content lowering the bitterness of grape. A plethora of literature suggests that the induction of biotic and abiotic stress response in plants is mediated by signaling molecules such as jasmonic acid, salicylic acid, and their derivatives. Such defensive phenolic compounds play a vital role when plants are infected with microbial pathogens. Lauvergeat et al. (2001) demonstrated that the application of salicylic acid in *Arabidopsis* resulting in accumulation of defense phenolic compounds. North et al. (2012) demonstrated that NAA and six BAP significantly increased phenolic exudation during micro-propagation. Several other studies showed that application of methyl jasmonate resulted in decreased phenolic content due to decreased gene expression of phenylalanine ammonia-lyase (PAL) important enzyme in chlorogenic acid biosynthesis. Ruiz et al. (2003) reported that calcium induces the activity of PAL. Due to the increase in total calcium content PAL activity increased, resulting in decreased phenolic content. Similarly, boron was found to have an inhibitory effect on phenols. Ruiz et al. (1998) reported that deficiency of boron leads to increase phenolic content. As provided from the information here, various biochemical factors play a significant role in increasing the accumulation in plants and hence crucial for mitigating abiotic stress.

11.6.2 Genetic/Metabolic Engineering of Phenolic Compounds to Mitigate Stress Tolerance

Flavonoids and carotenoids are one of the largest classes of plant phenolics. Both play an essential role in both abiotic and biotic stress response. Necessarily, the alteration in the biosynthetic pathway of phenolic compounds can optimize and regulate the production of flavonoids. The genetic and metabolic engineering of flavonoids and carotenoids can be achieved through following different approaches.

11.6.2.1 Blocking the Biosynthetic Pathway (RNAi Pathway)

In this technique, the RNA nucleotide, which is identical with the transcript sequence, is used. It is commonly known as the antisense RNA technique. Davuluri et al. (2005) reported that the operation of specific promoters using RNA technology

increase the level of carotenoids. Casacuberta et al. (2015) reported that DET 1 gene was regulated using RNAi technology resulting in an enhanced level of flavonoids.

11.6.2.2 Endogenous Synthesis of Biochemical Compounds Using Structural and Regulatory Genes

The engineering of structural genes in the fruit peel of tomato resulted in a 70-fold elevation in flavonol (Bovy et al. 2007). CHS, CHI, F3H, and FLS are the four most essential enzymes flavonoid biosynthesis pathway. The overexpression of this for genes resulted in flavonoid production both in the peel (primary quercetin glycosides) and flesh (primary kampferol glycosides).

11.6.2.3 Inserting New Branches: The Pathway for the Production of Novel Flavonoids

Stilbene synthase is a key enzyme involved in trans-resveratrol biosynthesis. Trans-resveratrol is a phenolic compound with antioxidant properties. Bovy et al. (2007) reported that introduction of *Stsy* gene in lettuce enhanced the synthesis of revarstatol in transgenic lettuce. Shih et al. (2008) reported that engineering of soybean isoflavone synthase genes resulted in increased phenolic content. Through this genetic manipulation, neither the content of other phenolic compounds was altered or had any side effects.

11.6.3 Physiological Strategies of Phenolic Compounds to Mitigate Stress Tolerance

In the context of improving plant phenolics for abiotic stress tolerance, physiological strategy including screening based on mechanical wounding, chlorophyll pigment, osmolyte, nutrient stress, UV irradiation, and heat shock are essential (Godara et al. 2016). Among these various approaches, solar radiation plays a crucial role in increasing phenolic content in plants. Analysis of the metabolomics-based phenotyping of compounds, regulating physiological processes in plants, revealed that carotenoids and flavonoid content variation in different varieties could provide insight into an effective strategy for mitigating abiotic stress. For increasing the content of flavonoids and carotenoids, environmental factors play a crucial role. This happens due to the significant role of environment in modulating the physiological processes in plants. A list of environmental factors, which can be included in improving the phenolic content in the plant are enlisted below in Table 11.1.

11.7 Conclusion

In conclusion, phenolic compounds are ubiquitous in nature and have very crucial role in plant growth and developments. In the field conditions, plant faces a number of adverse situations like biotic and abiotic stresses at different growth stages and responsible for production of high ROS. These ROS are highly reactive, cause the

Table 11.1 Plant biochemical changes upon abiotic stress exposure

Sl. no.	Environmental factors	Response	Reference
1.	Sun exposure	Increase in anthocyanin content	Downey et al. (2004)
2.	Sun exposure	Increase in flavonol content	Spayd et al. (2002)
3.	UV-B exposure	Increase in flavonol and stilbene content	Booij-James et al. (2000)
4.	UV-B exposure	Increase in flavonoid content and cinnamic acid	Reuber et al. (1996), Zucker (1965)
5.	Temperature	Decrease of anthocyanin content at high temperature (30–35 °C)	Mori et al. (2005)
6.	Temperature	Decrease of cinnamic acid content under heat stress	Fletcher et al. (2005)
7.	Irrigation	Deficiency of water leads to an increase in phenolic content	Marsilio et al. (2006)
8.	Irrigation	Root zone during leads to an increase in total phenolic compounds	Santos et al. (2005)
9.	Heavy metals	Upregulation of PAL, chalcone synthase, SKDH, CAD, and PPO	Zafari et al. (2016), Chen et al. (2019)
10.	Salinity	Up-regulation of flavonoid biosynthetic genes like VvbHLH1, NtCHS1, GmFNSII-1, GmFNSII-2, etc. help in accumulation of flavonoid	Sharma et al. (2019)

membrane disruption of cell organelles, and disturb the functions of normal cell machinery. Phenolic compounds have important role in maintaining the cell functions under these situations by reducing ROS, provide structural integrity, signaling and change at biochemical and molecular levels. This chapter clearly concluded about the functions of phenolic compounds and impact of different stressors on physiological and biochemical levels of plants. Additionally, this chapter gives insight on the physiological, biochemical, and molecular mechanism of phenolic compounds under these circumstances. Therefore, a proper insight of the biochemical, physiological, and molecular understanding along with genomics, metabolomics, transcriptomics, and phenomics approach will enhance the opportunity of improving the phenolic content for mitigating multiple stress response in plants.

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