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Carotenoids and Flavonoids in Plant Stress Management

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Abstract

Globally escalating food demand and unpredictable global warming have threatened the humanity in jeopardy. Excessive use of commercial pesticides and chemical fertilizers is providing ease of handling, but their toxic nondegradable residues are known to exert negative impacts on the plants, microbes, and even soil health. The unpredictable climate change leads to enhanced incidence of abiotic and biotic stresses in plants. Several integral approaches of fungi, microbes, plant, and their derived metabolites are used to encounter the stresses for effective crop management. The secondary metabolites are proving their immense potential and have time and again being proven to cope up the unavoidable and unpredictable changes due to adverse environmental conditions. The chapter highlights the role of both microbial and plant-based flavonoids and carotenoids as key agents for managing biotic and abiotic stress tolerance in crop plants. Moreover, such feasible and efficient biological application using plant-based composition helps to mitigate the challenges and open new gates of sustainable agriculture.

Keywords

Carotenoids · Flavonoids · Metabolites · Stress · Tolerance

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H. B. Singh et al. (eds.), *Antioxidants in Plant-Microbe Interaction*,
https://doi.org/10.1007/978-981-16-1350-0_5

5.1 Introduction

Plants as sessile organisms are constantly being affected by changes in their environmental conditions. The unfavorable or stress conditions have forced plants to change the functional aspect of powerful signaling sensors that guide them towards attaining optimal growth via manipulating their biophysical, biochemical, and molecular events (Ingle and Padole 2019; Taïbi et al. 2016; Enebe and Babalola 2018). Unpredictable and unavoidable climatic changes enforce abiotic stresses as the prime limiting factors among diverse stresses threatening agriculture and leading to decline in productivity both qualitatively and quantitatively (Grayson 2013; Nabavi et al. 2020). Majorly, diverse environmental constraints affect crop lands worldwide and only 3.5% of the global land area remains unaffected. The abiotic stresses, viz., salinity, floods, nutrient starvation, drought, heat, light intensity, cold/chilling, anaerobiosis, and acidic conditions are known to decline agricultural productivity worldwide (Meena et al. 2017). In this regard, the enormous chemical compounds have been produced in the plants which can be used as taxonomic markers and known as secondary metabolites (Bennett and Wallsgrove 1994; Tabatabaei and Ehsanzadeh 2016; Kaab et al. 2020). Secondary metabolites are attracting interest of the scientific communities owing to their indirect biological role in the growth and development of organisms. Secondary metabolites are versatile compounds often demonstrating in plant physiological processes as protectants against abiotic and biotic stresses in plants. These play a central role in various associations of plant–rhizobia, plant–microbe, soil microbes, and arbuscular mycorrhizal symbiosis and boost plant growth via the production of important biological agents (Del Valle et al. 2020).

In the last decades, the secondary metabolites are proving their immense potential in the plant stress physiology. The immobile nature of plants diverted the sieve of selection to utilize the secondary metabolites to overcome the stress constrains and help them to survive in the changing environments (Ingle and Padole 2019). Rhizospheric microbes form an interacting association with crop plants which ultimately regulates the nutrient supply to plants through varied direct mechanisms (Rob et al. 2020; Kaab et al. 2020). Studies on plant-based microbial associations at physiological, biochemical, and molecular levels recognized that microbial interactions directly affect plant responses under various stress conditions (Farrar et al. 2014). For deciphering the mysterious interaction among connections and mechanisms regarding the functional role at molecular levels with the resistance responses against abiotic stresses. The priming stimulates on antioxidant function have been found to compare with enhanced transcript levels of glutathione and ascorbate biosynthesis, enzymatic antioxidants that representing complex transcriptional alteration of the antioxidant components (Savvides et al. 2016). Different technological advancements also accelerated understanding of mutant technology, RNAi-mediated gene silencing, metabolite profiling gene editing systems, and proteomic analysis to identify capacious molecular communication that helped in enlightening our awareness of microbial-based mitigation approaches toward abiotic stresses tolerance in plants. New advances in Multiomics have appeared as integrated, holistic, and other analytical approaches for the analysis of one of the major dynamic and complex system of plants-microbial interactions that regulating the consequences progressed in the different plants to improve them to tolerate stress conditions (Luan et al. 2015).

5.2 Classical Example of Secondary Metabolites in Plant Resistance

Pigmentation is hallmark of microbial colonies rich in flavonoids and carotenoids content. These compounds protect microbes from various adverse conditions including drought, heat, cold, salinity, UV protection, and other damages (Rob et al. 2020). Carotenoids represent an important group of natural occurring pigments that are chiefly abundant in both photosynthetic (algae and plants, cyanobacteria) and nonphotosynthetic organisms (bacteria and fungi). These are synthesized within the chloroplasts of algae and plants naturally and the lycopene cyclization is major branch point in their biosynthesis. Lycopene, the product is converted by the activity of lycopene β-cyclase into β-carotene-like derivatives that plays significant roles against oxidative burst, photoprotection, salinity, drought, and salinity damages in higher plants (Paliwal et al. 2017). Quercetin is the aglycone form of ubiquitous flavonoid glycosides such as quercetin and rutin, rich in the citrus fruits, buckwheat tea, celery, broccoli, lettuce, tomatoes, *Ginkgo bioloba*, and onions (Table 5.1). They have high antioxidant potential hence fall under the category of effective antioxidants under the UV radiation, drought, salinity, cold, nitrogen deficiency, and heavy metal stress (di Ferdinando et al. 2012; Zhan et al. 2019). The apigenin is naturally occurring metabolite available in 4′, 5, 7-trihydroxyflavone form, and is found to be present in large quantities in celery, chamomile, vine spinach, oregano, and artichoke in the dried form (Table 5.1). They also have high antioxidant potential induced under the drought and UV radiation (Shukla and Gupta 2010). Fisetins are the ubiquitously present glycosylated compounds having powerful antioxidative potential (Gonçalves et al. 2018). Kaempferols are known to regulate several proteins and their functional activities such as cell growth and differentiation (Peer and Murphy 2006; Pei et al. 2020). Naringenin is widely distributed in the bergamot, tomatoes, citrus, and other fruits, which functions to interfere with the activity of the phenylpropanoid pathway enzyme, 4-coumarate: CoA ligase. It causes allelopathic impact on the growth and lessens the lignin deposition in plants (*Echinochloa oryzicola*, *Zea mays*, and *Oryza sativa*) (Deng et al. 2004). Chrysin is involved in the presymbiotic growth, i.e., spore germination, hyphal growth, branching patterns, and the formation of secondary spores, of the various arbuscular mycorrhizal fungi (*G. margarita, Gigaspora rosea*, *Glomus mosseae*, and *G. intraradices*) (Scervino et al. 2005). Apigeninidin is the anthocyanidin produced in the sorghum under the pathogen attack (Mizuno et al. 2014). Rutin is the ubiquitously present flavone enhancing the defense responses against the number of abiotic stresses in plants (Samanta et al. 2011). Catechins are the anthocyanins produced against the pathogen attack in the variety of plants (Barry et al. 2002).

Table 5.1 Secondary metabolites involved in defense reactions

No.	Metabolites	Class of secondary metabolites	Induced under type of stress	Plant source	Potential type	References
1.	Quercetin	Aglycone form	UV radiation, cold, nitrogen deficiency, heavy metal stress, drought, and salinity stress	Ubiquitously in plant	High antioxidant potential	di Ferdinando et al. (2012)
2.	Apigenin	Flavone	Drought and UV radiation	Ubiquitous	High antioxidant potential	Mekawy et al. (2018)
3.	Genistein	Isoflavone	Salt stress	Currants, raisin, and legumes	Increased photosynthesis levels, nodulation, and nitrogen fixation	Gonçalves et al. (2018); Akcin and Yalcin (2016)
4.	Fisetin	Flavonol	–	Ubiquitously in plant	Powerful antioxidative effects	Rashid et al. (2019)
5.	Kaempferol	Flavonol	Oxidative damages and UV radiation	Ubiquitously in plant	Exhibits antioxidant property by inhibiting the AOX activity	Peer and Murphy (2006)
6.	Naringenin	Flavanones	Heat stress and salinity	Citrus fruits, bergamot, and tomatoes	Allelopathic impact	Deng et al. (2004)
7.	Diadzein	Isoflavone	Pathogen attack	Leguminous plants	Intermediate signal carriers, and defense responses particularly to pathogenic attacks	Yu et al. (2000)
8.	Myricetin	Flavonols	–	Abundant in fruit, vegetables, tea, berries, and red wine	Allelopathic, antimicrobial, and antioxidant activities	Samanta et al. (2011)
9.	Chrysin	Flavone	–	Abundantly present in many plant extracts, including *Propolis*, blue passion flower	Symbiotic growth	Scervino et al. (2005)

10.	Apigeninidin	Anthocyanidin	Pathogens	Sorghum	–	Mizuno et al. (2014)
11.	Rutin	Flavone	UV light, low temperature, and desiccation	Ubiquitous	Enhancing the defense system against environmental stresses	Samanta et al. (2011)
12.	Catechin	Anthocyanins	Pathogen infection	Variety of plants	Represents the antimicrobial defenses	Barry et al. (2002)
13.	Gallic acid	Simple phenolic acid	Salt and osmotic stresses	Rice	Promoting the antioxidant response	de Klerk et al. (2011)
14.	Caffeic acid	Hydroxycinnamic acid derivatives	Soil salinity and other abiotic stresses	Legumes	Lignin synthesis, increasing cell wall thickness, and improving plants defense mechanism	Enebe and Babalola (2018)
15.	Syringic acid	Simple phenolic acid	Osmotic stress	*Vicia faba*	Stomatal closure restoration induced by ABA	Purohit et al. (1991)
16.	Vanillic acid	Simple phenolic acid	–	*Malus*	Enhances the rooting and inhibition of IAA decarboxylation	de Klerk et al. (2011)
17.	Ferulic acid	Hydroxycinnamic acid derivatives	–	*Zea mays* and *Oryza sativa*	Increases the IAA oxidase activity in seedlings, gene overexpression involved in the biosynthesis of ethylene and jasmonic, inhibition of lateral roots and root hairs formation, and reversed ABA effect	Chi et al. (2013); Purohit et al. (1991)

Gallic acid is the simple phenolic acid observed in the rice under salt and osmotic stress promoting the antioxidant responses (de Klerk et al. 2011).

Similarly, Syringic acid was observed in the *Vicia faba* under the osmotic stress involved in the stomatal closure to maintain the turgidity of plants (Purohit et al. 1991). Vanillic acid is a phenolic acid which was observed to enhance rooting in the *Malus* plant (de Klerk et al. 2011). Hydroxycinnamic acid derivatives such as ferulic acid and caffeic acid are involved in the defense responses. Caffeic acid was observed in the legume plants under the saline and abiotic stresses enhancing the cell wall thickening, lignifications, and inducing plant defense mechanisms (Enebe and Babalola 2018). Similarly, ferulic acid increases the IAA oxidase activity in seedlings, gene overexpression in the ethylene and jasmonic acid biosynthesis, and inhibition of lateral roots and root hair formation (Chi et al. 2013). The resistance provided to organisms mediated by secondary metabolites, viz., carotenoids may have ecological significance allowing organisms to colonize certain environments, for example, invasion of wounds and colonization of leaf surfaces by pigmented heterobasidiomycetous yeasts. In microbes, the knowledge of the mechanisms underlying the control of singlet oxygen species is based on few model organisms, viz., *Chlamydomonas*, *Rhodococcus sphaeroides*, *E. coli*, *Agrobacterium tumefaciens*, and *C. Crescentus*. The response to any kind of stress appears to be tightly controlled at the transcriptional and post-transcriptional levels. It appears that the response of the microbes to stress involves a complex network of regulatory factors, which will make it difficult to unravel their individual functions. Recent research on chemical priming has provided further knowledge of the complex mode of action of specific signaling molecules in plant stress tolerance.

5.3 Flavonoids and Carotenoids: New Contenders of Plant Resistance in Twenty-First Century

Flavonoids and carotenoids both of plant and microbe origin are well-known contenders providing tolerance response to higher plants in abiotic stresses (Fig. 5.1). Additionally, long-reported responses as protectors of damaging solar radiation both have been known for key roles as antioxidants by reducing the production of reactive oxygen species (ROS) after formation at primary response in stressed plant. Flavonoids are abundantly distributed in various cell organelles including chloroplast, nucleus, small vesicles endoplasmic reticulum, vacuole, cytosol, and extracellular space. Flavonoids such as flavones, flavonols, anthocyanins, and proanthocyanidins have been identified as antioxidants and function to protect plants from cellular damage under stress conditions (Clayton et al. 2018). The chloroplast-associated metabolites scavenge free radicals to maintain cellular redox. Kaempferol and Quercetin glycosides were reported abundant in chloroplasts during fungal attack, ultraviolet (UV) irradiation, salinity, drought, and function as protective antioxidants systems under stress conditions (Rob et al. 2020). According to Agati et al. (2009) flavonoids have long been accounted to be present in the cell vacuoles, epidermal cells wall, glandular, and nonsecretary trichome structures and hence have

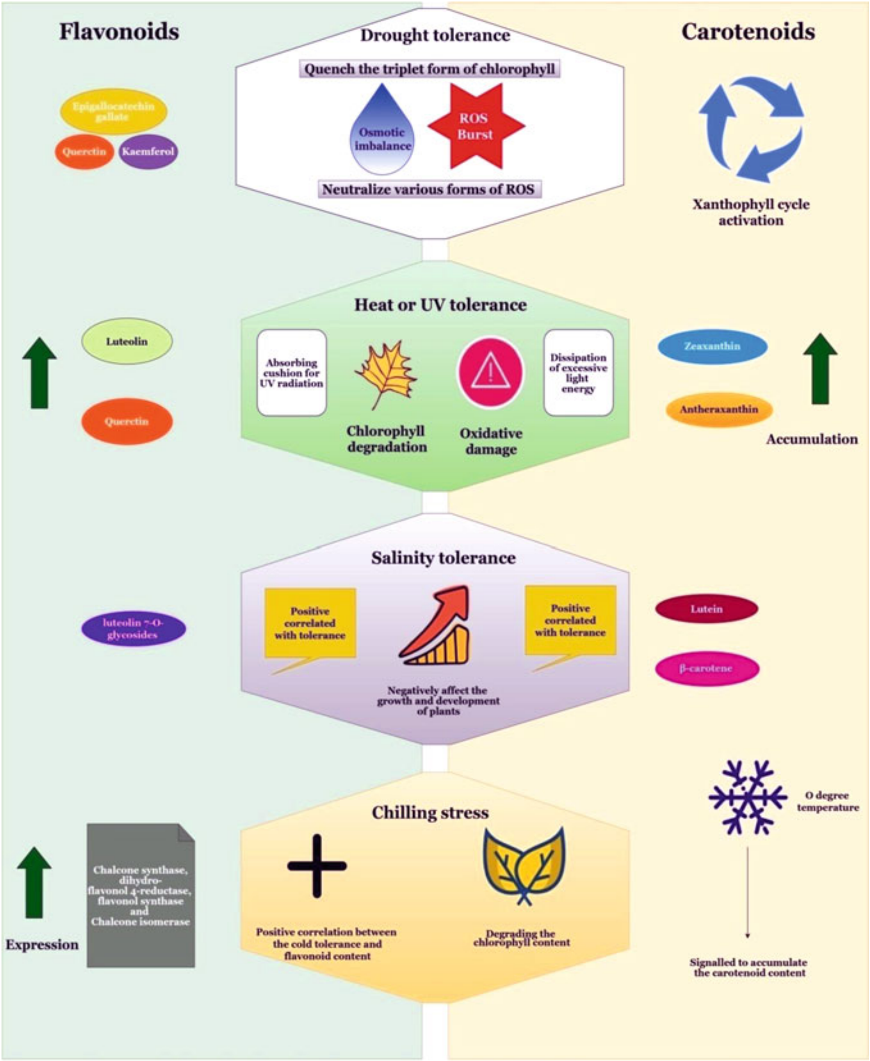

Fig. 5.1 Carotenoids and flavonoids as defense agents

been expected mainly to have the role of mitigating short ranges of solar wavelengths. Although anthocyanins have been well known to store in the vacuoles (mesophyll cells) in most of the plant species, and strongly supported by in vitro studies (Agati and Tattini 2010). However, studies confined that flavonoids may help in ROS scavenging within or towards the production sites. Microalgae species belonging to genus *Chlorella, Dunaliella, Scenedesmus*, and *Haematococcus* are considered as the key producers of commercially vital carotenoids. Many microorganisms have been reported to produce secondary metabolites such as astaxanthin, lutein, and b-carotene, etc. (Table 5.2).

Table 5.2 Diverse microbial strains as active producers of flavonoids and carotenoids

Secondary metabolite	Producer strains	References
Quercetin	*Chryseobacterium balustinum*, *Arbuscular mycorrhiza*	Lattanzio et al. (2006)
Genistein	*Gibberella fujikuroi*, *Bradyrhizobium japonicum*	Dashti et al. (2014), Cesari et al. (2019)
Naringenin	*Bradyrhizobium* sp., *Azospirillum brasilense*	Boué et al. (2000)
Diadzein	*Gibberella fujikuroi*	Hamayun et al. (2017)
Syringic	*Arthrobacter* sp.	Cesari et al. (2019)
Vanillic	*Nitrinicola lacisaponesis*	Dashti et al. (2014)
Ferulic	*Halomonas* sp.	Passari et al. (2017)
Rutin	*Bacillus endophyticus*, *Pseudomonas aeruginosa*	Kousar et al. (2020)
Catechin	AMF (*Glomus mosseae*) and PGPR (*Bacillus pumilus*)	Bhutia et al. (2012), Dashti et al. (2014)
Gallic	*Pseudomonas mendocina*	Passari et al. (2017)
Caffeic	*Bacillus pumilus*	Kousar et al. (2020)

Rutin accumulation was significantly lowered in salt susceptible species. High antioxidant (O^{-2} and H_2O_2) contents were detected in both types of rutin-reduced transgenic plants under high salt stress. Moreover, exogenous application of rutin effectively enhances the ROS scavenging and ultimately gains the salinity tolerance. The environmental stresses have multiple and complicated effect on plant growth and development. The environmental stresses altered either incrementally or rapidly. Essentially plants recognize and respond differentially to biological signals appropriately with the required pace of survival (Takahashi and Shinozaki 2019). The sophisticated networks of physiological processes in plants arise due to involvement of diverse molecular and cellular level of regulatory mechanisms required for both short- and long-term responses varying from cellular to whole plant level (Rob et al. 2020). It has been accepted that flavonoids also control movements of phytohormones like auxin, and a nuclear allocation of chalcone isomerase (CHI) and chalcone synthase (CHS) is consistent with regulation employed by flavonoid compounds on the genes transcription mediated for development changes, facilitated via the auxin-transporting facilitator proteins (ATFP) (Agati and Tattini 2010).

5.4 Stress Tolerance Responses by Flavonoids and Carotenoids

5.4.1 Drought Tolerance

Under the drought conditions, the osmotic and ROS balance are disturbed which stressed the cellular metabolism and structure (Rao et al. 2020). Plants develop array of mechanisms such as compatible solute production, antioxidant production, and other entities to withstand the unavoidable stressed conditions. The concentration of ascorbic acid and α-tocopherol and epigallocatechin gallate (flavonoids) were higher in the *Cistus clusii* grown under the drought condition (Hernandez et al. 2004). In the *A. thaliana* seedlings, the total flavonoids and the quercetin, and kaemferol (flavanols) were higher in roots (Shojaie et al. 2016). Similarly, the *Jatropha* seedlings showed higher concentration of flavonoids under the drought conditions (Lama et al. 2016). Carotenoids have ability to neutralize various forms of ROS and can quench the triplet form of chlorophyll in the leaves (Ramel et al. 2012). Under the drought conditions, the carotenoid levels increased in the olive trees, beans, and alpine plants which were considered to be associated with the xanthophyll cycle activation (Doupis et al. 2013; Buchner et al. 2017; Schweiggert et al. 2017). The increase in the zeaxanthin content was also suggested to play important role in the different abiotic stress tolerance (Wu et al. 2015). However, it has been also reported that under moderate drought conditions, carotenoid content tends to decrease (Sudrajat et al. 2015). Applications of *Rhizobium* cultures enhance N-supply and fixation process in cowpea, soybean, red-clover, pea, and alfalfa crops. The symbiosis between *Bradyrhizobium* and *Rhizobium* sp. effectively supports the nutritional strategies, ensuring an efficient N-supply in legumes, pastures, and grasses (Nagpal et al. 2020; Kumawat et al. 2019). The N-fixation, nodulation number, and growth in *Medicago sativa* improved with *R. meliloti* strain along with increased yield under water- deficient environment. In another study, *Rhizobium* strains effectively enhanced the nodulation rate in *M. sativa*, *V. faba*, *P. sativum*, and *P. vulgaris*, whereas reports support the effectiveness of plant–microbe interactions to improve drought stress in legumes via degrading phosphorus (Rob et al. 2020).

5.4.2 Heat or UV Tolerance

UV radiations are naturally imparted on the plants along with the sunlight. To which plants have to sense and respond on the basis of damage caused which depends upon the repair and acclimation response. Flavonoids provide themselves as absorbing cushion for UV radiation nullifying the ROS- induced cellular damages. The activation of photoreceptors induces the transcription factors to trigger the transcription of flavanoid biosynthetic genes. It has been observed that UV-B photoreceptor mutants (uvr8-1) and *Arabidopsis* wild plant under continuous 4 h of low-dose UV radiation depict the activation of chalcone synthase stimulation (enzyme involved in flavanoid biosynthesis) (Jenkins 2013). In several plant species, the ratio of luteolin to apigenin and quercetin to kaempferol has been enhanced under the UV light (di Ferdinando et al. 2012). The quercetin and luteolin glycosides aid in reducing the ROS production by effectively chelating with Cu and Fe ions (Brown et al. 1998; Berli et al. 2010). In the pepper plant, the compounds for UV-B absorption and antioxidants such as carotenoids have been induced under the UV-B radiation exposure (León-Chan et al. 2017). Similarly, in the tobacco plant, the carotenoid content and antioxidant capacity have been intensified after the low and high UV-B exposure (Shen et al. 2017). Moreover, the antioxidants accumulated in apical epidermal layer of leaves and stems to protect from the injuries from internal tissues against UV-B radiation. In *A. thaliana*, the kaempferol synthesis is deficient in flavone (chalcone) isomerase mutant shows much sensitivity to UV radiation. The worthy role of flavonoids is not exceptional functional of UV-protection via inducing antioxidant molecules, signal molecules, secretion of defensive compounds, and allelochemicals during exposure of UV radiation in plant. Moreover, flavonoids that accumulate in upper epidermis layer specially absorb a large amount of light ranging from 280 to 340 nm wavelengths.

Xanthophyll cycle was activated during intensive light conditions and helps in biosynthesis of zeaxanthin and proteins. According to Couso et al. (2012), the cytochrome-dependent hydroxylases and carotenes enzymes were evaluated to be up-regulated that control the xanthophyll cycle during light stress. Accumulation of zeaxanthin and antheraxanthin, and corresponding decrease in violaxanthin amounts were correlated with high light intensity resistance. This interconversion of zeaxanthin and violaxanthin is associated to a promising photoprotective role in the photosynthetic machineries indulging in dissipation of excessive light energy when exposed to intensive light stress.

In algal species, carotenoid accumulation was reported to enhance with temperature that activates cellular response or antioxidant mechanism related to enhanced activity of biosynthetic enzyme, free oxygen radical formation, and damaging effects observed at elevated temperatures. The enhanced threshold levels and carotenoid content by two-folds were reported by Juneja et al. (2013) in *Haematococcus pluvialis* and *Chlorococcum* sp., with temperature rise from 20 to 30 °C. *Dunaliella salina* (Halophytic green alga) has been noted to accumulate huge concentration of β-carotene when exposed to excessive water salt, light, and nutrient amounts in extreme conditions (Llorente et al. 2017).

The effect of ultraviolet-B radiation affected the chlorophyll content by degrading them and induced the accumulation carotenoids in *Capsicum annuum* (León-Chan et al. 2017). Enhanced level of UV-B rapidly elevates carotenoid content compared with control plants and the production of those compounds. The increased carotenoids and ROS at high UV-B radiation were reported in *Nicotiana tabacum* L. leaves play important role in tolerating the oxidative damage in plant caused by high UV-B conditions (Shen et al. 2017).

5.4.3 Salinity Tolerance

Excessive accumulation of ROS is primary cause of salinity stress usually resulting in deleterious effects on plants (Kang et al. 2018). Flavonoids and carotenoids play an important protective role against oxidative burst and injuries caused by salt stress. In *Lupinus albus* seedling, the *Chryseobacterium balustinum* Aur9 elevated total nitrogen content, root surface, germination rate, aerial growth, N-absorption, and biological N-fixation. It also promoted the systematic induced responses and helped to overcome the salt stress in soybean and *Arabidopsis* species. Under high salinity condition, strains of *Sinorhizobium fredii* were used to enhance the nitrogen fixation rate via eliciting the nodule number in significant manner (Rodríguez-Navarro et al. 2002). In *Rhizobium tropici,* salt-tolerant wild-strain, the increased antioxidant enzymes activities including dehydroascorbate reductase and superoxide dismutase resulted in salinity tolerance and were correlated to enhanced antioxidant enzymes in nodules (Tejera et al. 2004). The various nitrogen-fixing bacteria tolerant to high concentration of NaCl are *Rhizobium meliloti*, *R. leguminosarum*, and rhizobia from *Vigna unguiculata* whereas *Rhizobium fredii*, *R. meliloti*, and *Sinorhizobium fredii* show regulatory mechanism for K^+ strictly but control Mg^{2+} flux under salt stress condition. The *R. meliloti* derived from xerophytic tree species formed a symbiotic association with *M. sativa* and confirmed effective salt tolerance (Zahran 1999).

Several metabolic and physiological changes are affected by the salinity stress. On the basis of duration and intensity, the salinity stress can negatively affect the growth and development of plants. According to Zhao and Dixon (2009), a positive correlation was observed between the flavanoid biosynthesis level and the Glutathione-*S*-transferase content (role in flavonoids transportation to vacuole). Similarly, the biosynthesis of luteolin 7-*O*-glycosides was significantly enhanced under the salinity conditions (Agati et al. 2011). The seedling of *Solanum nigrum*, having lower dry biomass of leaves and roots along with the higher flavanoid contents (Abdallah et al. 2016). The accumulation of carotenoids such as β-carotene and lutein in the sweet potatoes were observed under the salinity stress. The IbZDS gene encoding β-Carotene desaturase is related with the carotenoid accumulation for tolerance whose expression induced for carotenoid biosynthesis under salinity condition (Li et al. 2017). In the *Solanum nigrum*, the expression of phytoene desaturases, zeta carotene desaturases, phytoene synthase, capsanthin/capsorubin synthase, and lycopene b-cyclase was down-regulated under the higher salt concentration in the salt sensitive *Capsicum* plants (Maurya et al. 2015).

According to Li et al. (2017), the expression of carotenoids can be up-regulated or down-regulated by overexpression or suppression of genes inducing activity of f-Carotene desaturases like enzymes and their biosynthetic pathways. The overexpression of IbZDS (*Ipommea batata*) gene is associated with ZDS, resulted in significant increases in β-carotene and lutein-related accumulation improved salinity tolerance sweet potatoes. The suppression of lycopene-cyclase (α-LCY) and lycopene β-cyclase (β-LCY) genes by RNA interference resulted in enhanced concentrations of total carotenoids, β-carotene, and ultimately stress tolerance cells of sweet potatoes (Kim et al. 2015). The findings were also supported by Kang et al. (2017) in sweet potatoes, where CHY-b suppression up-regulates the carotenoid level and enhances tolerance to stress. According to Jin et al. (2015), salinity stress tolerance observed to be associated with LCY-β and α-LCY genes in *Nicotiana tabacum* in which suppression of α-LCY and overexpression of LCY-β play role for enhanced salinity tolerance. The variations reported in species level depend upon the complexity in regulation of carotenoids. However, the transcriptional control regulating genes interaction that is all involved in regulating level of carotenes compounds during stress tolerance. The expression of phytoene synthase 2 and LCYB genes was associated with the enhanced level of lutein and carotene observed in *Solanum nigrum*. The expression of lycopene β-cyclase, zeta carotene desaturases, phytoene desaturases, phytoene synthase, and capsorubin/capsanthin synthase in capsicum sp. was down-regulated with increase in salinity level (Maurya et al. 2015; Ben Abdallah et al. 2016).

Elevated levels of copper induce the production of ROS and carotenoids formation; in *Vicia faba*, subjected to elevating the amount of copper were reported to be concentration-dependent. The increased carotenoid levels could be result of enhanced activity of nonenzymatic antioxidant system related to secondary metabolic compounds (Abdel-Latef and Abu-Alhmad 2013). In *Cicer arietinum*, cadmium (Cd) stress caused significant enhancement in level of carotenoids. The carotenoid synthesis lowered ROS damage induced by cadmium toxicity (Ahmad et al. 2016) whereas, phosphorus (P) or nitrogen (N) repletion was observed to elevate the carotenoid levels in algae and increased levels of thiobarbituric acid (TBA) and H_2O_2 reactive species along with decreased SOD activity (Moussa et al. 2017). In microalgae, Zhang et al. (2017) studied enhanced carotenoid accumulation in unfavorable conditions. The findings showed that nitrogen depletion facilitated the synthesis of carotenoids, compared to chlorophylls and demonstrated that carotenoids were highly sensitive to N stress. Comparatively declined chlorophyll content was observed with progressed nitrogen stress. These findings showed that the carotenoid content in *Chlorella vulgaris* varied over time with different salinity environmental conditions (Zhang et al. 2017).

5.4.4 Chilling Stress

The low temperature can affect the plant growth cycle with each stage from its germination to the maturity. Plants respond differentially based on their genetic potential to tolerate chilling stress. Many plant species either tropical or subtropical (rice, maize, and tobacco) fail to survive under chilling temperature; however, some overwintering cereals and *Arabidopsis* can continue to survive and grow (Liu et al. 2018). The increase in flavonoid content was noticed with the lowering in temperature reported in the epidermal cells of many plant species (Bilger et al. 2007). In the *A. thaliana* accessions, the positive correlation was recorded between the cold tolerance and the level of flavonoid content (Korn et al. 2008). Many biosynthetic genes such as chalcone synthase, dihydroflavonol 4-reductase, flavonol synthase, and chalcone isomerase for flavonoids were expressed higher in the cold tolerant plants (having higher anthocynin and quercetin derivative content) than the sensitive ones (Hannah et al. 2006). The higher flavonoids in the fruits of *Phoenix dactylifera* L. were reported at the 0 °C temperature condition along with the no any kind of chilling injury symptoms observed (El-Rayes 2009). The low temperature resulted in decline in chlorophyll content and signaled to accumulation of carotenoids in the *Capsicum annuum* (León-Chan et al. 2017).

5.5 Biotic Stress Tolerance: A Feasible and Efficient Biological Application

The microbial inoculants and their secondary metabolites are proved to be efficient agents and act as biofungicide, bioherbicides, and biopesticides. Microbial inoculants play important role as biocontrol approach could be driven by elevating phosphorus solubilization, improve biological nitrogen fixation, nutrient absorption at rhizospheric region, systemic acquired resistance, and production of synergetic secondary metabolites in low concentration provides toxicity to pathogens. Moreover, the toxic effect could be overcome by production of regenerative hormones (ethylene and auxin) at damage site. Several fungi and microbe inoculation of *Aspergillus niger*, *Penicillium citrinum*, *Aspergillus fumigatus*, *Penicillium funiculosum*, *Penicillium aurantiogriseum*, *Trichoderma koningii*, *Phytophthora infestans*, *Sporolactobacillus inulinus*, *Amphibacillus xylanus*, *Bacillus amyloliquefaciens*, *Microbacterium oleovorans* release inhibitory compounds against fungal pathogens (Nesci et al. 2005; Pereira et al. 2007; Etcheverry et al. 2009). Strains of *Bacillus* spp. secrete inhibitory compounds and used as biological controlling agent in wide range of fungal infections in plants. *Bacillus subtilis* was used to be control production of aflatoxin and *Aspergillus flavus* in field condition, whereas Pseudomonads and rhizobia are effectively known to suppress the growth of *Fusarium* and *Pythium* sp. (Antoun and Prévost 2005; Cepeda 2012; Alori and Babalola 2018). Moreover, both microbes and plants employed alternative mechanism in form of antibiotics or phytoalexins containing flavonols, carotenoids, alkaloids substance to control the plant pathogens. The compounds show antagonistic effect at rhizosphere and exhibit biocidal properties on soil-borne pathogens. The properties can be altered by formulation, cultivation, and application methods of PGPR under stress responses (Glick 2012, 2015; Raaijmakers and Mazzola 2012; Grobelak et al. 2015; Bhattacharyya et al. 2016; Olanrewaju et al. 2017). Certain classical examples for PGPR producing bactericidal effects are *Pseudomonas* spp. and *Bacillus* that have been identified to liberate aerugine, azomycin, bacilysin, butyrolactones, bacillaene, cepaciamide A, cepafungins, chlorotetain, 2,4-diacetyl phloroglucinol, fengycin, tas A, karalicin, phenazine-1-carboxylic acid, rhamnolipids, iturin, pseudomonic subtilin, subtilosin, sublancin, oomycin A, zwittermycin A, kanosamine, and pyrrolnitrin (Alori and Babalola 2018). The total phenols, carotenoids, and anthocyanin content observed to be enhanced in lettuce via exogenous application of inoculation containing *Glomus fasciculatum* and *Azotobacter chroococcum* (Baslam et al. 2011). Similarly, flavonoid content was reported to be increased with inoculation of *Glomus mosseae* and *G. fasciculatum* in lettuce (Baslam et al. 2011). Arbuscular mycorrhizal fungi (AMF) speed up antioxidant biosynthesis upto 75% significantly through rhizobacterial inoculation in soybean seedlings. The above findings are well supported by the inoculation studies of *Bacillus megaterium* and *Pseudomonas fluorescens* in catharanthus under stress conditions (Alori and Babalola 2018).

5.5.1 Fungal Tolerance

Different bacterial strains of PGPR including *Bacillus subtilis*, *Bacillus licheniformis*, *Chryseobacterium*, *Balustinum*, and *Pseudomonas* sp. when combined enhance significant level of resistance against soil-borne diseases in tomato and pepper under in vitro conditions. The genes isolated from *Lycium chinensis* such as carotene isomerase (LcCRTISO), phytoene desaturase (LcPDS), and β-carotene desaturase (LcZDS) via carotenoid biosynthesis are significantly enhanced making the tobacco plant salinity resistant (Lattanzio et al. 2006; Domenech et al. 2006). *Pseudomonas mendocina*, *Nitrinicola lacisaponensis*, *Bacillus pumilus*, *Halomonas* sp., and *Arthrobacter* sp., isolated from salinity conditions showed siderophore, indole acetic acid (IAA), ammonia production, P-solubilization, and other plant growth-effecting traits. Studies on bacterial inoculation of above isolates enhanced presence of flavonoid quercetin and phenolics compounds cinnamic, ferulic, gallic, vanillic, syringic, and caffeic, acids in the rhizosphere soil. The high concentration of phenolics, quercetin, and IAA in rhizosphere soil zone exhibited a cumulative synergistic function that supported elevated salinity stress tolerance in wheat (Venkidasamy et al. 2018; Pathan et al. 2020; Tiwari et al. 2011; Mahmoudi et al. 2019).

5.5.2 Bacterial Tolerance

Bacillus cereus (strain BS107) against *Xanthomonas axonopodis* pv. v*esicatoria* in pepper leaves shows induction of induced systematic response where, ISR-elicited responses of *Bacillus* spp. was also reported against root-knot nematodes, viral, bacterial, and fungal pathogens. Yang and Yen (2000) reported molecular evidences in favor of priming effect of Rhizobacterium strains on the up-regulation of ISR and defense genes in pepper plant.

5.5.3 Insect and Nematode Tolerance

The flavonoids and isoflavonoids are lethal to the insect pests by altering the behavior, growth, and development of target insects (War et al. 2013; Melo et al. 2017). The flavones 5-hydroxyisoderricin, 5-methoxyisoronchocarpin, and 7-methoxy-8- (3- methylbutadienyl)-flavanone are present in *Tephrosia villosa* (L.), *T. vogelii*, and *T. purpurea* (L.), respectively, which can be used to repell *Spodoptera exempta* and *S. littoralis* (Simmonds et al. 1990). The overexpression of transcriptional factors required for flavonoid production confers the resistance in *Arabidopsis* against the *Spodoptera frugiperda* (Johnson and Dowd 2004). The chickpea plant was showing antifeedent activity against the Helicoverpa armigera by mean of maackiain, judaicin, 2-methoxyjudaicin, and judaicin-7-*O*-glucoside isoflavonoid productions (Simmonds and Stevenson 2001). The alliarinoside, cyanopropenyl glycoside, and isovitexin-600-D-β-glucopyranoside interfere with the feeding activity of Pieris napi oleracea (native American butterfly) (Renwick et al. 2001). The overexpression of CCD1 leads to the β-ionone (carotenoid) in *Arabidopsis* plant increases the emission of β-ionone to prevent the damage induced by the insect attack (Wei et al. 2010).

5.6 Recent Advancement in Functional Aspect of Flavonoids and Carotenoids in Crop Improvement

Recently, many reports published on the functional aspect of flavonoids and carotenoids in term of stress tolerance in crop plants (Liu et al. 2015; Kudoyarova et al. 2019). The sulfoquinovosyl transferase enzyme induces glycosylation of flavonoid that elevates tolerance to osmotic stress in rice (Zhan et al. 2019). Application of soil – organic matter enhances the efficacy of secondary metabolites including flavonoids and microbes- based communication (Del Valle et al. 2020). Identification of allelochemicals and phytotoxic activity induce tolerance from *Schumannianthus dichotomus* observed by Rob et al. (2020). The overexpression of the cytochrome CYP82A3 gene derived from *Glycine max* improves drought and salinity tolerance and also proves a strong resistance against *Botrytis cinerea* and *Phytophthora parasitica* in transgenic tobacco (*Nicotiana benthamiana*) species (Yan et al. 2016; Tian et al. 2017). Rhizosphere acts as hotspot for allelochemicals, PGPR, and secondary metabolites production based on soil-plant –microbe interaction inducing cycling of nitrogen and carbon in soil (Del Valle et al. 2020). Enhanced level of Arbuscular mycorrhiza (AMF) induces production of root flavonoids, shows colonization in invasive tree species reported by Pei et al. (2020). Screening of tunisian plant extract formulation shows bioherbicide properties and in *Cynara cardunculus* (Kaab et al. 2020). In sweet potato, enhanced lutein and β-carotene level through suppression or down-regulation of the β-carotene hydroxylase gene and increase abiotic stress tolerance in transgenic stress tolerance (Li et al. 2017). Similarly, findings reported by Kea et al., showed enhanced β-carotene amount, lycopene β-cyclase gene (IbLCYB2), and suppression of lycopene ε-cyclase expression in sweet potatoes (Li et al. 2017; Kang et al. 2018). Multiple stress conditions impose more beneficial impacts on plants compared to that posed in presence of individual stress alone (Liu et al. 2015). Combination of stresses ultimately reduces the detrimental effect of each other thereby, increasing the probability of better survival of plants. The cumulative impact of drought and accumulation of ozone (O_3) in plants resulted in better tolerance. The combined affect was attributed to decreased values of stomatal conductance. Elevated concentration of reduced glutathione and ascorbic acid effectively scavenge ROS, thereby causing a considerable drop in the total ROS content. Several mechanisms highlighting the role of microbes in abiotic stress alleviation have been proposed (Kumar et al. 2019; Ke et al. 2019; Khan et al. 2020). Soil-inhabiting microbes belonging to genera *Achromobacter*, *Azospirillum*, *Variovorax*, *Bacillus*, *Enterobacter*, *Azotobacter*, *Aeromonas*, *Klebsiella*, and *Pseudomonas* have been shown to enhance plant growth even under unfavorable environmental conditions (Kaushal and Wani 2016; Sorty et al. 2016) (Fig. 5.2).

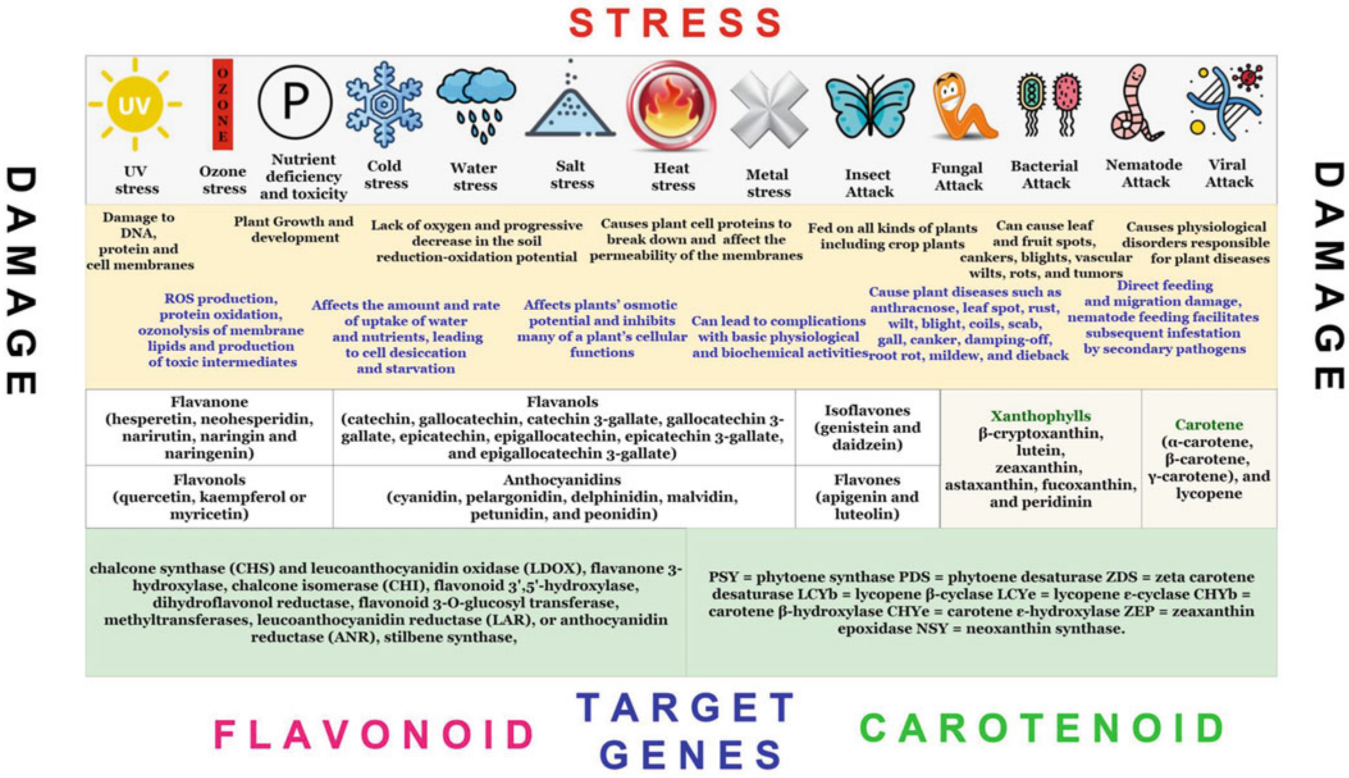

Fig. 5.2 The defense mechanism mediated by microbial carotenoids and flavonoids to combat varied biotic and abiotic stresses in plants

5.7 Conclusion and Future Remarks

Presently, greatest interest is towards new prospective of microbial and their secondary products including carotenoids and flavonoids that can be used in plant stress tolerance and crop improvement under climate change scenario. Looking into application of crop production without compromising yield loss due to severity of biotic and abiotic using microbial-based inoculants become more efficient and effective. Moreover, the PGPR, microbial and plants-based metabolites having both biological as well as ecofriendly approaches in term of sustainable crop improvement, stress management, and promoting soil health are common. Enhanced flavonoids and carotenoids level in plants are significantly relayed to the elevated light-dependant oxidative damages and promoting antioxidant systems in plants. Morphological structures including specialized glandular trichomes and stomatal guard cells may be conveniently noted to investigate the functional-localization interaction of flavonoids in photoprotection systems. It is evident that high concentration of carotenoids and flavonoids in rhizosphere increases bacterial-mediated growth-promoting responses in root exudates and leaves confirmed growth and resistance in plants. These play a central role in various associations of plant–rhizobia, plant–microbe, soil microbes, and arbuscular mycorrhizal symbiosis and boost plant growth via the production of important biological agents. These microbial-based inoculations may lead to the identification of new signaling molecules and decipher the pathways responsible for triggering stress resistance in challenging environment.

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