

Chapter 19

Plant Secondary Metabolites in Stress Tolerance



Esra Koç and Belgizar Karayiğit

Abstract Secondary metabolites are natural defense elements that play a vital role in plant defense against adverse environmental conditions. The amounts of secondary metabolites increase significantly to adapt to harsh conditions. The increase in the synthesis and accumulation of plant secondary metabolites to cope with abiotic and biotic stress indicates a strong link between secondary metabolites and biotic and abiotic stress tolerance. In this chapter, the contribution of secondary metabolites to plant defense against biotic and abiotic stress factors such as salinity, drought, heat and cold, heavy metals, and UV is discussed.

Keywords Abiotic and biotic stress · Antioxidants · Oxidative stress · Phytochemicals · Plant secondary metabolites

1 Introduction

The lack of an immune system and active mobility of plants makes it very difficult for plants to resist environmental stresses (Meena et al. 2017). Therefore, plants develop a variety of defense responses, including secondary metabolites (SMs), to cope with the stresses that arise under variable growing conditions (Fig. 19.1). Although plant SMs do not directly affect plant metabolism and growth, they play an important role in the plant defense. Secondary metabolites are primary metabolite derivative compounds produced in plants when various physiological changes occur (Zandalinas et al. 2017). The SMs are substances produced by the plants to protect themselves in case of exposure to any stress condition (Isah 2019). Secondary metabolites play a role in alleviating biotic stresses such as fungi, viruses, and bacteria, as well as abiotic stresses (Jan et al. 2021). When plants are exposed to abiotic and biotic stress conditions, they can

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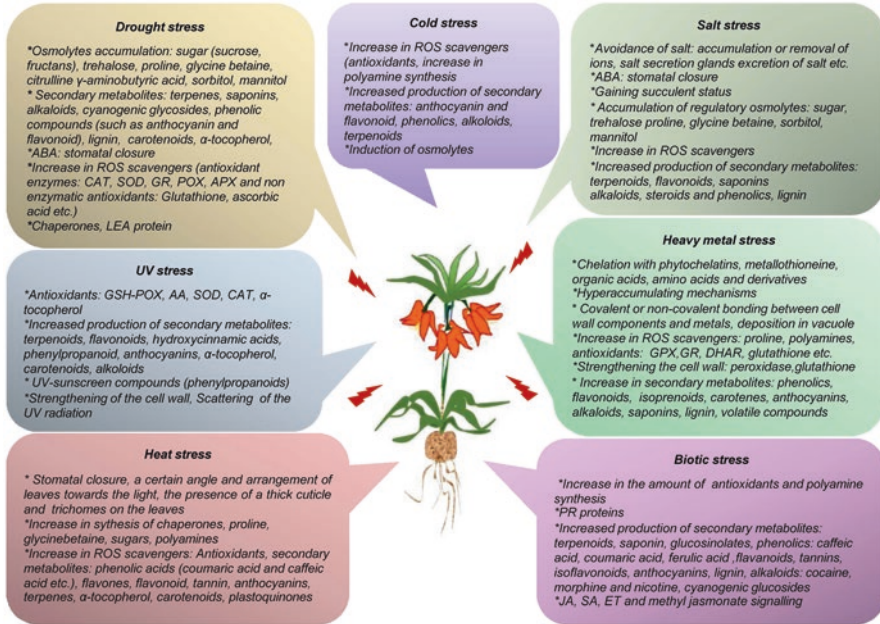


Fig. 19.1 Plant defense responses to stresses

produce more than one hundred thousand SMs through different metabolic pathways (Meena et al. 2017). The biosynthesis and accumulation of SMs vary depending on abiotic and biotic stress. In plants, SMs are classified as N-containing compounds, phenolic compounds (phenolic acids, lignin, flavonoids, stilbenes, coumarins, tannins), terpenes (sterol, carotenoids, glycosides, volatiles), and S-containing compounds (glutathione, glucosinolates, phytoalexins, thionins, defensins, alliin) (Fang et al. 2011; Ashraf et al. 2018; Jamwal et al. 2018; Isah 2019). Various SMs are synthesized by alternative mechanisms in plants. Mono-, di-, and tetraterpenes, phytol, plastoquinone, and carotenoids are synthesized from the methylerythritol phosphate pathway; sterols, sesquiterpenes, and triterpenes are synthesized from the mevalonate pathway; phenolic compounds are synthesized from the shikimic acid and malonic acid pathway; and N-containing compounds are synthesized from the tricarboxylic acid pathway (Jamwal et al. 2018). Additionally, SMs have different chemical structures such as aliphatic (polyamine, isoprene, ethylene), aromatic (phenolic acid), hydroaromatic (terpenoid, jasmonic acid), and heterocyclic (flavonoid) that enable them to perform different functions (Edreva et al. 2008; Ahanger et al. 2020). Phenolics are compounds synthesized in plants during normal development or when the plant is exposed to biotic or abiotic stress (Xiao et al. 2019). Phenolics are aromatic plant SMs that have a phenyl ring attached to one or more hydroxyl groups (Mathew et al. 2015). In plants, it generally accumulates in the vacuoles located in the center of epidermal cells and in the cells under the epidermis in the leaves and shoots. Some phenolic compounds are covalently bound to the plant cell wall, while others are found on the outer surfaces of the cuticle or plant organs. However, in some tree species, flavonoids accumulate in the nucleus,

and this causes the formation of a DNA-flavonoid complex, which protects against oxidative damage (Falcone Ferreyra et al. 2012). The most well-known property of phenolics is the scavenging of reactive oxygen species (ROS). Phenolic compounds such as esters, flavonoids, lignins, and tannins act as antioxidants under abiotic stress conditions (Selmar 2008). Terpenes consist only of isoprene units, whereas terpenoids have isoprene units as well as additional units such as ketone, heterocyclic, and hydroxyl. Terpenoids are one of the important secondary metabolites that play a role in defense against both abiotic and biotic stress factors in plants (Porres-Martinez et al. 2016). Due to their antioxidant activities, terpenes can prevent abiotic-induced oxidative stress (Blanch et al. 2009). Like carotenoids, terpenoids protect plants against photodamage and oxidative stress by promoting photorespiration (Bartwal et al. 2013). ROS formed due to photoinhibition are scavenged by antioxidants such as tocopherols and carotenoids (Goh et al. 2011). It is assumed that the isoprene units in the structure of terpenes can alleviate stress conditions, as large protein complexes increase the interaction between themselves or with membrane lipids, providing the stability of the membrane structure (Sharkey and Yeh 2001). Phytohormones stimulate the synthesis of volatile terpenes as signal compounds in plant defense and stress responses (Wani et al. 2016). Phytoalexins are one of the compounds that play a role in the defense mechanism in plants. Diterpenes and sesquiterpenes function as phytoalexins (Hwang and Sung 1989). Most plant SMs contain nitrogen (N) in their structure. Alkaloids, cyanogenic glycosides, glucosinolates, and nonprotein amino acids are mainly nitrogen-containing SMs. Alkaloids have antifungal, anti-insecticidal, and antibacterial effects (Singh 2018). The inhibitory effects of alkaloids on glycosidase metabolism deter herbivores and provide protection owing to their singlet reactive oxygen scavenging properties (Mithöfer and Boland 2012). Cyanogenic glycosides are involved in plant defense against both herbivores and phytopathogens, while glucosinolates are involved in plant defense against biotic agents (Ballhorn 2011). Nonprotein amino acids have different roles, including antiherbivore, antimicrobial, and allelochemical activities (Mcsweeney et al. 2008).

Studies have shown that the amount of plant SMs generally increases during abiotic and biotic stresses. This demonstrates the importance of accumulation of secondary metabolites in improving stress tolerance. In this chapter, the role of SMs against various stress factors such as salt, drought, cold, high temperature, heavy metals, UV, and pathogens to which plants are exposed has been discussed.

2 Abiotic Stress and Secondary Metabolites

2.1 *Secondary Metabolites in the Salt Stress Tolerance of Plants*

Salt stress is one of the important abiotic factors limiting the growth and development of plants worldwide (Yang et al. 2018). Salinity causes osmotic stress, which causes dehydration, oxidative stress, ionic stress, and physiological drought in plant

cells. This situation causes a decrease in cytosolic and vacuolar volumes, a decrease in photosynthesis and growth rate, the inability of plants to take water despite the presence of water, and a decrease in nutrient uptake (Ashraf et al. 2015). Plants exposed to salt stress accumulate sugar alcohols such as sorbitol, mannitol, pinitol, and carbohydrates such as fructose, glucose, sucrose, trehalose, raffinose, and stachyose. These osmolytes stabilize the cell membranes against lipid peroxidation and maintain turgor pressure (Slama et al. 2015). Trehalose has an important role in the regulation of ionic balance and redox state. Additionally, raffinose and galactinol accumulations were detected in the intercellular space of plants exposed to stress (Yan S et al. 2022). It has been reported that raffinose and galactinol protect cells against oxidative damage by scavenging the hydroxyl radical (Nishizawa et al. 2008). In addition to their osmolyte function, amino acids have cellular functions such as scavenging ROS and controlling the transport of ions. For example, proline not only acts as an osmolyte in plants under salt stress but also protects plants against oxidative damage as a ROS scavenger with its antioxidant property. A positive correlation was found between proline accumulation and salinity tolerance in *L. esculentum*, *M. sativa*, and *A. corniculatum* plants. An increase in phenolic levels was detected in *A. fragrantissima*, *C. annuum*, and *C. tinctorius* exposed to salt stress (Navarro et al. 2006; Verma and Shukla 2015; Golkar and Taghizadeh 2018). In addition to proline, increases in the levels of amino acids such as phenylalanine, aspartic acid, valine, arginine, cysteine, citrulline, alanine, arginine, and glutamine were determined in plants under salt stress (Cao et al. 2017). Glycine betaine, which is an osmoprotectant and also acts as a ROS scavenger, reduces lipid peroxidation by improving the activities of glutathione *S*-transferase (GST) and glutathione peroxidase (GPX) enzymes. It protects the 3D structures of proteins by preventing protein carbonylation (Hoque et al. 2007; Hasanuzzaman et al. 2014).

Plants provide a maximum tolerance to salt stress by increasing or decreasing the secondary metabolite production (Golkar and Taghizadeh 2018). Corn, wheat, rice, and potato plants exposed to salt stress produce secondary compounds such as terpenoids, flavonoids, alkaloids, steroids, and phenolics (Jan et al. 2021). It has been reported that high alkaloid and phenolic concentrations in plants are effective in scavenging ROS caused by salt stress. They are compounds with high antioxidant properties (Chunthaburee et al. 2015). Again, the increase in flavonoid levels under stress shows that their antioxidant properties are effective in increasing tolerance to oxidative damage as a ROS scavenger. The amounts of chlorogenic acid, caffeic acid, ellagic acid, ferulic acid, gallic acid, syringic acid, vanillic acid, and *p*-coumaric acid increase under salinity conditions to maintain redox homeostasis (Razieh et al. 2021). Similarly, the increase in terpene accumulation in plants under salt stress showed that these compounds act as ROS scavengers with their antioxidant properties against oxidative stress (Dahham et al. 2015; Porres-Martinez et al. 2016). Salt stress increased the concentrations of various alkaloids and essential oils in *Solanum nigrum*, *Catharanthus roseus*, *Rauvolfia tetraphylla*, *A. fragrantissima*, *Oryza sativa*, and *Datura innoxia* (Said-Al and Omer 2011; Chunthaburee et al. 2015; Verma and Shukla 2015). Again, in *S. nigrum* seedlings exposed to salt stress, increases in the expression of flavonoid genes and genes related to carotenoids were

determined (Ben Abdallah et al. 2016). Hyoscyamine 6 β -hydroxylase is known to act as the factor responsible for alkaloid synthesis in plants exposed to salt stress (Schlesinger et al. 2019). Salinity stress in *Matricaria chamomilla* increased the concentration of various phenolics such as caffeic, chlorogenic, and protocatechuic acid (Kováčik et al. 2009). Oliveira et al. (2020) reported that the accumulation of cellulose, lignin, and matrix polysaccharides in stem and root tissues of maize (*Zea mays*) under salt stress and the expression of genes from phenylpropanoid biosynthesis and the activities of enzymes were stimulated. Another study reported that *M. pulegium* and *N. sativa* increased the amount of phenolic compounds under salinity stress (Oueslati et al. 2010). Similarly, in *M. pulegium* exposed to salt stress, an increase was detected in the amount of pulegone, but no change was observed in the amount of another terpene, neomenthol (Karray et al. 2009). Additionally, in a study conducted on *H. annuus* L. exposed to salt stress, significant increases in the polyamine content of the roots of the plant were observed (Chiapusio et al. 2016). Some SMs produced in different plants exposed to salt stress are detailed in Table 19.1.

Many natural and synthetic metabolites have been used exogenously to increase plant tolerance to salt stress as osmoregulatory and ROS scavengers. Various amino acids (proline, glycine betaine, etc.), hormones (salicylic acid, methyl jasmonate, benzyl aminopurine, melatonin), sugars (trehalose), polyamines (spermine, spermidine, putrescine), and vitamins are among these metabolites (Patel et al. 2020). These exogenous applications are suggested as a promising approach to increasing tolerance to salt stress. Another promising approach to increasing salt tolerance is the manipulation of genes involved in the synthesis of SMs with protective properties.

2.2 *The Role of Secondary Metabolites in Reducing Drought Stress Damage in Plants*

Drought stress, which is one of the stresses that mostly affect agricultural productivity in the world, has been reported by the World Health Organization as a factor that will cause 700 million people to migrate to different regions by 2030 (WHO 2020). Drought stress occurs when the amount of water available in the soil cannot meet the needs of the plants and when atmospheric. This situation causes physiological, morphological, biochemical, precipitation is insufficient ecological, and molecular changes in plants by affecting many metabolic processes, such as the growth and development of plants, amount of biomass, photosynthesis and transpiration rate, stomatal conductance, and cellular dehydration (Xu et al. 2010; Mashilo et al. 2017). Drought stress causes the production of ROS such as superoxide, hydroxyl and singlet oxide, and hydrogen peroxide, which are quite toxic and reactive in plants. Reactive oxygen species, on the other hand, cause disruption of cellular homeostasis by damaging protein, carbohydrate, lipid, and DNA (Anjum et al. 2017; Ibrahim et al. 2019). However, plants induce an enhanced SM production,

Table 19.1 SMs accumulate in different plants under salts stress

Plant	SMs	Function	References
<i>Matricaria chamomilla</i>	Caffeic acid (hydroxycinnamic acid)	Antioxidant activity	El Mihaoui et al. (2022)
<i>Solanum lycopersicum</i>	Polyamine	H ₂ O ₂ -mediated signaling	Raziq et al. (2022)
<i>Olea europaea</i>	Oleuropein (polyphenolic)	Antioxidant activity	Araújo et al. (2021)
<i>Achillea fragrantissima</i>	Alkaloid	Antioxidant activity	Elsharkawy et al. (2021)
<i>Medicago sativa</i> , <i>Medicago arborea</i>	Medicagenic acid and zahnic acid (saponins), hydroxycinnamic acids	Fortification of plant membranes, ROS scavenger, lignin formation	Sarri et al. (2021)
Cotton	Gossypol and tannin	With these metabolites, which increase with salt stress, slower growth of cotton aphids and reduction of reproduction rate	Ma et al. (2021)
<i>Helianthus annuum</i>	Chlorogenic acid (polyphenol)	ROS scavengers	Ma et al. (2020)
<i>Solanum lycopersicum</i>	Flavonoid	Antioxidant activity	Martínez et al. (2020)
<i>Matricaria chamomilla</i>	Chlorogenic acid (polyphenol)	Antioxidant activity (participate in the nonenzymatic detoxification of oxygen radicals and lipid peroxidation products)	Petrulova et al. (2020)
<i>Apocynum venetum</i>	Quercetin, kaempferol	Antioxidant activity	Xu et al. (2020)
<i>Fragilariopsis cylindrus</i>	Dimethylsulfoniopropionate, dimethylsulfoxide (dimethylsulfonium compounds)	Osmoregulators	Wittek et al. (2020)
<i>Lycopersicon esculentum</i>	Glycine betaine	Protective effect on the plant growth	Civelek & Yildirim (2019)
<i>Datura innoxia</i>	Hyoscyamine, scopolamine (alkaloids)	Antioxidant activity	Schlesinger et al. (2019)
<i>Ocimum basilicum</i>	Rosmarinic acid, caffeic acid, caftaric acid, cinnamyl malic acid, feruloyl tartaric acid, quercetin (phenolics)	Antioxidant activity, ROS scavengers, maintaining redox homeostasis	Scagel et al. (2019)
<i>Datura innoxia</i>	Hyoscyamine, scopolamine (alkaloids)	Antioxidant activity	Schlesinger et al. (2019)

(continued)

Table 19.1 (continued)

Plant	SMs	Function	References
Iranian licorice	Glycyrrhizin, betulinic acid, soyasaponins, and phytosterols (triterpenoids)	Antioxidant activity	Shirazi et al. (2019)
<i>Salicornia brachiata</i>	3,6-Dihyronicotine, portulacaxanthin II, papaverine, and secoberbine (alkaloids)	Antioxidant activity: ROS scavengers	Benjamin et al. (2019)
<i>Salicornia brachiata</i> (in root and leaves)	3- β -D-Glucuronoside-28--glucoside, taxol, glycyrrhetinate (oleanolate) Desoxyhemigossypol-6-methyl ether, costunolide, heliespirone C (sesquiterpenoids)	Antioxidant activity, ROS scavengers	Benjamin et al. (2019)
<i>Salvia mirzayanii</i>	1,8-Cineole and linalyl acetate (increased), bicyclogermacrene (decreased) (terpenoids)	Antioxidant activity	Valifard et al. (2019)
<i>Carthamus tinctorius</i>	Proline	Antioxidant activity	Golkar and Taghizadeh (2018)
<i>Solanum lycopersicum</i>	Tomaditine (alkaloid)	ROS scavengers	Rivero et al. (2018)
<i>Prosopis farcta</i>	Caffeic acid (hydroxycinnamic acid)	Antioxidant: ROS scavengers	Sarker and Oba (2018)
<i>Rauvolfia tetraphylla</i>	Reserpine (alkaloid)	Antioxidant: ROS scavengers	Sytar et al. (2018)
<i>Artemisia annua</i>	Artemisinin (terpenoid)	ROS scavengers	Vashisth et al. (2018)
<i>Chenopodium quinoa</i> Willd.	Saponin	ROS scavengers, seed germination stimulant	Yang et al. (2017)
<i>Triticum aestivum</i>	Glycine betaine	Antioxidant, osmolyte	Tian et al. (2017)
<i>Oryza sativa</i>	Ferulic acid, p-coumaric acid (phenolic)	Antioxidant activity, ROS scavengers	Minh et al. (2016)
<i>Citrus aurantium L.</i>	Linalool, linalyl acetate, neryl acetate, geranyl acetate and α -terpineol, limonene and trans- β -ocimene	ROS scavengers	Eirini et al. (2017)
<i>Catharanthus roseus</i>	Vincristine, vinblastine, ajmalicine (alkaloids)	Antioxidant activity	Fatima et al. (2015)
<i>Gossypium</i>	Tannic acid	Antioxidant activity	Wang et al. (2015)
<i>Brassica oleracea</i>	Sinigrin (aliphatic glucosinolate)	Plant water balance, involving aquaporins under salt stress, antioxidant activity	Martínez-Ballesta et al. (2015)

(continued)

Table 19.1 (continued)

Plant	SMs	Function	References
<i>Solanum nigrum</i>	Solamargine, solasonine (glycol alkaloids)	Salt stress enhanced production of total alkaloids	Muthulakshmi et al. (2013)
<i>Plantago ovata</i>	Saponins flavonoids	ROS scavengers	Zahra et al. (2012)
<i>Capsicum annuum</i>	Capsaicin	Reducing the negative effects of osmotic stress	Arrowsmith et al. (2012)
<i>Fagopyrum esculentum</i>	Rutin, orientin, isoorientin, vitexin	ROS scavengers	Lim et al. (2012)
<i>Nicotiana tabacum</i>	Proline, myo-inositol, GABA	Osmolyte, ROS scavengers	Zhang et al. (2011)
<i>Glycine max</i>	Abscisic acid	Stomatal closure	Gao et al. (2011)

phytohormonal response, and osmotic regulation to increase tolerance to drought stress (Larson 2018; Jogawat et al. 2021; Yadav et al. 2021a). Secondary metabolites reduce membrane lipid peroxidation with their antioxidant properties and serve as cell wall components to strengthen the cell wall against stress factors (Yang et al. 2018). Plants try to cope with drought conditions by increasing the amounts of SMs such as terpenes, saponins, alkaloids, and phenolics (anthocyanins and flavonoids) (Chen et al. 2011; Jaafar et al. 2012; Isah 2019). Generally, drought stress increases the concentrations of phenolic compounds by stimulating key genes in the phenylpropanoid pathway. Flavonoids, polyphenols, and terpenoids or isoprenoids are secondary compounds that are effective in scavenging increased ROS due to drought (Trembl and Smejkal 2016). For example, increases in the levels of phenolic compounds were determined in *H. brasiliense*, *P. sativum*, *Chrysanthemum* sp., and *Salix* sp., which were exposed to drought stress (Dawid and Hille 2018; Hodaei et al. 2018; Larson 2018). In studies on cotton and potato, it has been determined that drought stress increases terpene and flavonoid synthesis (Payton et al. 2011; Zhang et al. 2014). In another study, it was determined that drought stress increased the amounts of glycosides, monoterpenes, terpenoids, and carotenoids in rosemary and grapes (Liu et al. 2014; Savoi et al. 2016). It has been reported that there is an increase in rosmarinic, ursolic, and oleanolic acid production in *P. vulgaris* and an increase in betulinic acid content in *H. brasiliense* (Chen et al. 2011; Jaafar et al. 2012). Razavizadeh and Komatsu (2018) found significant increases in the amounts of thymol, γ -terpinene, proline, and carbohydrates in seedlings exposed to mannitol-induced drought stress. Wang et al. (2019) found significant increases in the amounts of flavonoids, proanthocyanidins, and phenolics and in the activities of antioxidant enzymes in *Matteuccia struthiopteris* (L.) Todar. and *A. multidentatum* (Doll.) exposed to drought stress. Drought stress significantly increased the lignin and pectin content in the roots of soybean (Al-Hakimi 2006). Mazloom et al. (2020) reported that the treatment of lignin-based hydrogel reduced electrolyte leakage while increasing the water content and proline amount. The other groups of SMs

produced in response to drought stress are N- and S-containing compounds. Increases in the amounts of alkaloids such as catharanthine, vindoline, capsaicinoid, vincristine, and vinblastine were determined in *C. roseus* under drought stress (Phimchan et al. 2012; Zhang et al. 2012). Cyanogenic glycosides act as antioxidants in water deficiency conditions, and the released hydrogen cyanide increases the amount of endogenous salicylic acid (SA) (Sun et al. 2018). Amino acids such as citrulline γ -aminobutyric acid, β -aminobutyric acid, β -alanine, and ornithine act as both antioxidants and osmolytes (Vranova et al. 2011). Glutathione and thionine are compounds that serve to scavenge ROS as powerful antioxidants. For some SMs produced in different plants exposed to drought stress, refer to Table 19.2. All these studies have shown that genes responsible for the biosynthesis of SMs can be used to increase drought tolerance. For example, overexpression of chalcone synthase in tobacco plant increased the amount of flavonoids (Zhao et al. 2019), and overexpression of the *GH4CL7* gene in *G. hirsutum* and increase in lignin biosynthesis increased resistance to drought stress (Sun et al. 2020). In another study, it was determined that overexpression of *IAA5*, *IAA6*, and *IAA19* genes in *Arabidopsis thaliana* stimulated glucosinolate accumulation (Salehin et al. 2019). It has been reported that overexpression of phosphoenolpyruvate carboxylase and an increase in anthocyanin biosynthesis in transgenic rice increase resistance to drought stress (He and Sheffield 2020). Therefore, manipulation and overexpression of genes related to the synthesis pathway of these metabolites to increase the amount of SMs have been suggested as one of the effective strategies to increase the resistance of plants to various stresses, including drought stress (Yadav et al. 2021b).

2.3 Cold Stress Alters Secondary Metabolism

Plants must grow at suitable temperatures to complete their growth and development. Both high and low temperatures require plants to cope with various challenges. A low temperature is one of the most detrimental stresses for plants living in temperate regions (Janská et al. 2010; Peng et al. 2015). Cold stress is divided into two classes: chilling stress, which is low temperatures between 0 and 15 °C without freezing (Chen L et al. 2020), and freezing stress, which is temperatures below 0 °C (Zhang et al. 2020). Freezing stress is more harmful to plants than chilling stress. It causes many damages such as chilling stress, a decrease in photosynthesis, osmotic damage, desiccation, oxidative stress, inhibition of protein synthesis and enzyme activities, a decrease in membrane permeability, ion leakage, and dehydration in cells and tissues (Ramakrishna and Ravishankar 2011). Low temperatures significantly affect plant growth and development by causing reduced root length, leaf loss, reduced leaf expansion, symptoms such as chlorosis and necrosis, and damage to reproductive organs such as pollen and pollen tube (Lyons 1973). Freezing stress causes the formation of ice crystals in both the intracellular and intercellular spaces. The ice crystal formation in the intercellular space causes dehydration and the withdrawal of water from the cell due to the decreasing water potential in the apoplastic

Table 19.2 Some SMs synthesized in plants exposed to drought stress

Plant	SMs	Function	References
<i>Papaver somniferum</i>	Narcotine (alkaloid)	Responses to oxidative stress	Kundrářová et al. (2021)
<i>Pisum sativum</i>	Phenolic compounds	Antioxidant: neutralizes free radical damage	Sutulienė et al. (2021)
<i>Hypericum perforatum</i>	Pseudohypericin, hyperforin, hypericin	Antioxidant activity	Torun et al. (2021)
<i>Oryza sativa</i>	Spermine (polyamine)	Maintain water balance, stabilize cell membranes, improve water use efficiently	Li Z et al. (2020)
<i>Salvia officinalis</i>	Carnosic acid (diterpenes)	Antioxidative protection	Pavić et al. (2019)
<i>Vitis vinifera</i>	Ferulic acid (hydroxycinnamic acid)	Antioxidant activity	Hodaei (2018)
<i>Cola acuminata, P. somniferum camptothecin</i>	Narcotine, morphine, and codeine (alkaloids)	ROS scavengers, antioxidant activity	Yang et al. (2018)
<i>Chrysanthemum morifolium</i>	Apigenin (phenolic compound)	Antioxidant activity	Hodaei et al. (2018)
<i>Glycyrrhiza glabra</i>	Glycyrrhizin	ROS scavengers Antioxidant activity	Hosseini et al. (2018)
<i>Amaranthus tricolor</i>	Hydroxybenzoic acids, hydroxycinnamic acids (flavonoids)	Antioxidant activity	Sarker and Oba (2018)
<i>Mentha</i> sp.	Cineole (monoterpenes)	Antioxidant activity	Llorens and Vacas (2017)
<i>Thymus vulgaris</i>	Cineole (monoterpene)	Antioxidant activity Electron-donating	Llorens and Vacas (2017)
<i>Salvia officinalis</i>	Monoterpenes	Antioxidant Massively increased in respond to drought stress	Radwan et al. (2017)
<i>Pinus sylvestris</i>	Abietic acid (terpenoids)	Resistance of water deficit	Sancho-Knapik et al. (2017)
<i>Hypericum brasiliense</i>	Quercetin (phenolic)	Antioxidant activity	Selmar et al. (2017)
<i>Catharanthus roseus</i>	Vinblastine (alkaloid)	Enhancing the activities of antioxidant enzymes	Liu et al. (2017)
<i>Camellia sinensis</i>	Catechins (phenolics)	Antioxidant activity	Wang et al. (2016)
<i>Oryza sativa</i>	Polyamines	Antioxidant activity	Berberich et al. (2015)
<i>Zea mays</i>	Zealexins and kauralexins	Osmotic stress tolerance	Vaughan et al. (2015)
<i>Gossypium hirsutum</i>	Ascorbic acid, glutathione and α -tocopherol	Antioxidant activity	Hussien et al. (2015)

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Table 19.2 (continued)

Plant	SMs	Function	References
<i>Eucomis autumnalis</i>	Iridoids (monoterpenes)	Antioxidant activity	Masondo et al. (2014)
<i>Triticum aestivum</i>	Glutathione, homotaurine	ROS scavengers: against oxidative damage Maintain of cellular redox balance	Zechmann (2014)
<i>Hypericum brasiliense</i>	Rutin (phenolic)	Antioxidant activity	Dal Belo (2013)
<i>Salvia officinalis</i>	Monoterpenes	Promoting reactions which consume NADPH-H ⁺ Increased activity of enzyme corresponding in this reaction	Selmar and Kleinwachter (2013)
<i>Labisia pumila</i>	Phenolic compound	Induction in activity of PAL Increased in photosynthesis and quantum yields	Jaafar et al. (2012)
<i>Catharanthus roseus</i>	Vinblastine, vincristine, vindoline, catharanthine (alkaloids)	Regulating nitrogen content	Zhang et al. (2012)
<i>Triticum aestivum</i>	Spermine (polyamine)	Increased cell water status Osmoprotectants	Alcázar et al. (2010)
<i>Citrus reticulata</i>	Spermine (polyamine)	Antioxidant: ROS scavengers	Shi et al. (2010)
<i>N. tabacum</i>	Nicotine (alkaloid)	Ripening in leaves	Cakir and Cebi (2010)
<i>Scrophularia ningpoensis</i>	Catalpol, harpagide, aucubin, harpagoside (glycosides)	Antioxidant: ROS scavengers enhancing the activities of antioxidant enzymes	Wang et al. (2010)

space. Intracellular ice formation often leads to cell death, as it causes membrane rupture, changes in membrane permeability, mechanical deterioration in the protoplasm, and deformation of the cell wall (Levitt 1980; Steponkus 1984). The damage to the cell membrane of the cold is largely due to dehydration. A low temperature causes changes in the lipid content of the cell membrane, with an increase in phospholipid content and a decrease in the ratio of cerebrosides in general. Fatty acid saturation of the cell membrane of plant species and its sensitivity to cold are inter-related (Uemura and Steponkus 1999). Since the ratio of saturated fatty acids is higher in the membranes of plants that are sensitive to cold, membrane leaks occur as the membrane tends to pass from the liquid mosaic phase to the solid gel form during cold stress. Cold-tolerant plants has a lower transition temperature (the temperature at which it changes from the liquid mosaic phase to the gel phase) since it has higher unsaturated fatty acids (Wang et al. 2006). The organelle that is firstly and most severely affected by cold stress is chloroplasts (Liu et al. 2018). It causes changes in the structure of thylakoids and swelling (Kratsch and Wise 2000).

Additionally, low temperatures also decrease photosynthesis due to the reduction of stomatal opening and the inhibition of CO₂ exchange. However, since the photosynthetic apparatus captures more photons than necessary, PS II inhibits electron transport and causes photoinhibition, and photodamage occurs with the degradation of the D1 reaction center protein (Szilard et al. 2005; Yang et al. 2017). Under stress conditions, ROS are produced in the chloroplasts, mitochondria, and peroxisome and apoplasmic regions of plants (Xie et al. 2019). The main reason for the formation of ROS in chloroplasts is stomatal closure, as well as restrictions in CO₂ fixation due to disruptions in the electron transport chain (ETC) (Mignolet-Spruyt et al. 2016). Similarly, disruptions in the ETC in the mitochondria cause ROS production. ROS induce lipid peroxidation; deterioration of DNA, lipid, and carbohydrate structure; and inactivation of enzymes (Foyer and Noctor 2005). Plants increase the biosynthesis of different SMs to be protected from these damages. In a study conducted on *O. basilicum* L., it was determined that the application of 4 °C cold stress increased the amounts of camphor, bornyl acetate, eugenol, methyl chavicol, and methyl eugenol, as well as the activity of superoxide dismutase (SOD) and GPX antioxidant enzymes (Rezaie et al. 2020). In the study, it was also determined that the total phenolic and flavonoid amounts were increased compared with the control group. These increases in the activities of antioxidant enzymes and the amounts of total phenolic and flavonoid levels have been associated with protection against ROS toxicity. This high increase in the amount of phenolic compounds was attributed to the increase in phenylalanine ammonia-lyase (PAL) activity. Phenolic compounds are SMs with the potential to scavenge ROS and prevent lipid peroxidation as electron and hydrogen atom donors (Huang et al. 2019). While flavonoids and phenolics serve as scavengers, unsaturated fatty acids also help increase tolerance to cold by improving cell membrane fluidity (Li J et al. 2019; Li Q 2020).

Sun et al. (2021) detected increases in the amount of free fatty acids, lysophosphatidylcholines, and lysophosphatidylethanolamine, which are biomarkers of freezing damage, in cold stress-tolerant and cold stress-sensitive *A. arguta*. These accumulations indicate membrane damage caused by cold stress. It was determined that the amounts of phenolic compounds, such as hydroxytyrosol, tyrosol, and oleuropein, and the enzyme activities of PAL and polyphenol oxidase increased in the leaves of olive trees exposed to -7 °C (Ortega-García and Peragon 2009). The authors associated polyphenol oxidase and oleuropein with the antioxidant defense system. Additionally, it was determined that the accumulation of anthocyanin and flavonoid in *A. thaliana*, *Petunia hybrid*, and *Z. mays* plants exposed to cold stress (Janas et al. 2002; Yang et al. 2018); the total phenol concentrations and particularly the genistein amount in the roots of *Glycine max* plant (Janas et al. 2002); and the chlorogenic acid production in *M. domestica* tree were increased. It has been reported that low-temperature stress also increases the synthesis of phenolic compounds, which participate in the structuring of the cell wall and serve in the biosynthesis of lignin and suberin (Griffith and Yaish 2004). However, Krol et al. (2015) reported that long-term cold stress decreases the amount of phenolic compounds, and this may be related to the slowing down of some elements of the secondary metabolism. More phenolic reduction was found in the cold-sensitive *V. vinifera*

cultivar than the cold-tolerant cultivar. However, it was also determined that the total level of phenolic compounds and antioxidant activity in the cold-resistant cultivar were higher than that in the susceptible cultivar. Glycosylated terpenoids are SMs that play a role in increasing tolerance to cold stress (Yeshe et al. 2022). Zhou et al. (2017) found an increase in the amount of nerolidol in frost-damaged tea and suggested that this increase is a response to cold stress. Zhao et al. (2020) reported that increases in the level of glycosylated sesquiterpene and nerolidol glucoside, which have antioxidant and ROS scavenging ability, in the tea under cold stress may be effective in increasing tolerance to cold stress. Additionally, with the effect of cold stress, terpenoids, such as β -phellandrene, (E)- β -ocimene, δ -elemene, α -humulene, β -caryophyllene, withanolide A, withaferin A, and nerolidol glucoside, and increases in the concentration of phenolics, such as pelargonidin, anthocyanins, anthocyanidins, genistein, and daidzein, and alkaloids, such as vindoline, were detected (Janas et al. 2002; Dutta et al. 2007; Copolovici et al. 2012; Mir et al. 2015; Jeon et al. 2018; Zhao et al. 2020).

Data obtained from studies on different plants indicate that polyamines are also effective in increasing tolerance to cold stress. It is stated that the polyamine levels of plants such as *T. aestivum*, *M. sativa*, and *P. antiscorbutica* increase considerably under cold stress, and this increase in the amount of polyamine may be related to cold tolerance (Akula and Ravishankar 2011; Kovacs et al. 2011). In a similar study, it was reported that putrescine and polyamines of spermine and melatonin synthesized in the *D. carota* plant protect against apoptosis caused by cold stress (Lei et al. 2004). In another study, it was stated that the plant *S. tuberosum* produces polyamine to eliminate the harmful effects of ROS formed by the effect of cold stress (Kou et al. 2018). It increases tolerance to cold by preventing cytolysis by binding to phospholipids in the cell membranes of polyamines (Li and He 2012). Some other SMs under cold stress are mentioned in Table 19.3.

Another response used by plants against cold stress is carbohydrate metabolism. Carbohydrates serve to retain water in cells, stabilize cell membranes, and scavenge ROS. While the decrease in temperature decreased the water potential and starch amount, it increased the amount of soluble sugar, sucrose, mannitol, and osmotin (PR-5 protein) (Antognozzi et al. 1993; D'Angeli and Altamura 2007; Eris et al. 2007). Amino acids such as betaine, arginine, and proline also act as osmoprotectants in increasing tolerance to cold stress (Meilong et al. 2020).

With the activation of genes responsible for the synthesis of SMs, the tolerance level and adaptation of plants to various stress conditions can be achieved (Jan et al. 2021). Determining the genetic responses of plants to stress is one of the important research areas for developing cold stress-tolerant plants. *GOLS1*, *GOLS3*, *GR-RBP3*, *HYDROLASE22*, *RHL41*, *CAU1*, *PME41*, *DREB26*, and *CRK45* are necessary genes for increasing the tolerance of *Camellia sinensis* to cold stress (Samarina et al. 2020). In the study of *O. basilicum* L., it was determined that cold stress (4 °C) increased the amounts of methyl eugenol and methyl chavicol and that these metabolites were in a positive correlation with the expression levels of eugenol synthase 1 (*EGS1*) and eugenol O-methyl transferase (*EOMT*) genes. Therefore, *EGS1* and *EOMT* genes have been proposed as candidate genes for genetic manipulation of the

Table 19.3 Different SMs synthesized in plants under cold stress

Plant	SMs	Function	References
<i>Camellia weiningensis</i> , <i>Camellia oleifera</i>	ABA, IAA, prenol lipids, organooxygen compounds, fatty acyls	Stomatal closure and decreasing water loss Signal transduction, energy storage	Xu et al. (2022)
<i>Camellia sinensis</i>	Catechin, dihydroxyphenylacetic acid, procyanidin B2, galactose	ROS scavengers Osmotic regulatory	Yan F et al. (2022)
<i>Zea mays</i>	ABA, raffinose, trehalose-6-phosphate, proline, monosaccharides	ABA: upregulation of <i>LEA</i> genes Raffinose: protecting the photosynthetic apparatus from oxidative damage, osmoprotectants	Guo et al. (2021)
<i>Triticum aestivum</i>	Putrescine, spermine, spermidine (polyamines)	Antioxidant: ROS scavengers	Alcázar et al. (2020)
<i>Saccharum spontaneum</i>	Trehalose (sugars), brassinosteroids	Osmotic regulatory, signal transduction	Yang et al. (2020)
<i>Glycine max</i>	Phenolics	Antioxidant: ROS scavengers, redox properties, inhibitors of lipid peroxidation in cell membrane	Ozfidan-Konakçı et al. (2019)
<i>Artemisia annua</i>	Artemisinin (terpenoid)	ROS scavengers Stimulation of SOD activity	Vashisth et al. (2018)
<i>Fagopyrum tartaricum</i>	Anthocyanins, proanthocyanidins	Antioxidant: ROS scavengers	Jeon et al. (2018)
<i>Brassica oleracea</i> L. var. <i>italica</i> Plenck cv. 'Lord'	Glucosinolates, flavonols, and vitamin C	Antioxidative properties	Mølmann et al. (2015)
<i>Withania somnifera</i>	Withanolide A , withaferin A	Antioxidant: ROS scavengers	Mir et al. (2015)
<i>Centella asiatica</i> L.	Asiaticoside, madecassoside (triterpene glycosides)	Plant cell adaptation	Plengmuankhae and Tantitadapitak (2015)
<i>Vitis vinifera</i>	Caffeic, ferulic acid, <i>p</i> -coumaric acid	Antioxidant: ROS scavengers	Krol et al. (2015)
<i>Artemisia annua</i>	Artemisinin (sesquiterpene)	Antioxidant: ROS scavengers	Brown (2010)
<i>Capsicum annuum</i> L.	Total phenolic, proline, total protein	Antioxidant: ROS scavengers	Koç et al. (2010)

phenylpropanoid biosynthesis pathway in increasing the cold tolerance of *O. basilicum* (Rezaie et al. 2020). It was determined that cold stress increased the levels of steroidal alkaloids, glycoalkaloids, phenolic acids, and flavonoids in *S. viarum*, a medicinal plant (Patel et al. 2022). It has been reported that there is a correlation

between the transcription levels of genes involved in the biosynthesis of glycoalkaloids and flavonoids and the amounts of these metabolites. Recent research confirmed the expression and posttranslational modifications of genes that control the production of SMs to increase plant tolerance to such stresses.

2.4 *Production of Plant Secondary Metabolites Under Heat Stress*

In the last five decades, increases in CO₂ and other greenhouse gases because of human activities have caused the world to warm by approximately 0.85 °C (Bein et al. 2020). This degree may seem small, but it is not. Even an increase of 1 °C is the beginning of the road to disaster. When an increase of 2 °C is reached, the temperatures normally seen once every decade will begin to be seen every 2 years. When it reaches 1.5 °C, this temperature increase will be seen almost every 5 years. Similar results will be valid for excessive precipitation and drought. Therefore, heat stress is one of the important factors affecting the growth and development of plants now and in the future. High temperatures cause deterioration of membrane integrity of plants, a decrease in photosynthesis rate, and premature aging of plants. Seed germination inhibition, growth reduction, and excessive ROS production are among their main adverse effects (Hasanuzzaman et al. 2013). Heat stress induces the production of alkaloid and phenolic compounds in various plant species (Ramakrishna and Ravishankar 2011). It has been stated that *F. vesca*, *S. officinarum*, and *L. sativa* plants exposed to heat stress produce high amounts of phenolic acids, antioxidants, flavones, and anthocyanins (Wu et al. 2007). α -Tocopherol and plastoquinone, which are synthesized in high amounts in *L. esculentum* plant under heat stress, facilitate photosynthesis by acting as antioxidants and electron carriers (Havaux 2020). Similarly, the continuous synthesis and emission of terpenes are effective in countering the damage caused by heat stress (Korankye et al. 2017). With the effect of heat stress, increases in the concentrations of terpenoids such as β -phellandrene, 2-carene, α -phellandrene, limonene in *S. lycopersicum* and α -caryophyllene, and β -farnesene in *D. carota* were determined. Additionally, a high amount of flavonoid production has been reported in the *O. basilicum* plant, which is exposed to high-temperature stress (Al-Huqail et al. 2020). Isoprenes synthesized from the mevalonate pathway in plants help to heal the photosynthetic apparatus damaged by the effect of heat shock and to improve thermotolerance (Li and Sharkey 2013). Similarly, increases in the concentration of isoprene terpenoids were detected in *Q. rubra* exposed to heat stress (Hanson and Sharkey 2001). Carotenoids and phenolic compounds such as flavonoid, lignin, and tannin show antioxidant properties under heat stress, scavenge ROS, and protect against oxidative damage (Sehgal et al. 2016). There has been an increase in the amount of anthocyanin, coumaric acid, and caffeic acid phenolics in *D. carota* with the effect of heat stress (Commisso et al. 2016). Alterations in the amount of different SMs under heat stress are mentioned in

Table 19.4 Different SMs synthesized in plants under heat stress

Plant	SMs	Function	References
<i>Arabidopsis thaliana</i>	Carbohydrate modifications, cutin, wax, heat shock proteins	Oxidative stress resistance, cell wall remodelling	Xiang and Rathinasabapathi (2022)
<i>Heracleum sosnowskyi</i>	Furanocoumarin (xanthotoxin, bergapten, isopimpinellin), proline, anthocyanins (osmolytes)	Antioxidant activity	Rysiak et al. (2021)
<i>Solanum lycopersicum</i>	Gibberellins	Thermotolerance and delayed leaf senescence	Jahan et al. (2021)
<i>Medicago sativa</i>	Flavonoid	Powerful antioxidant capacity	Chen S et al. (2020)
<i>Lepidium sativum</i>	Anthocyanin, carotenoid	Antioxidant activity	Al-Sammarraie et al. (2020)
<i>Daucus carota</i>	Terpenoids, phenolics	Antioxidant activity: ROS scavengers	Ahmad et al. (2019)
<i>Artemisia sieberi alba</i>	Flavonoid, tannins, phenols, alkaloid, terpenoids, steroid, proline, mannitol, inositol, and sorbitol (osmolyte)	Antioxidant activity: ROS scavengers, osmoprotectants	Alhaithloul (2019)
<i>Salix</i> spp. hybrid “ <i>Terra Nova</i> ”	Increase in isoprene, decrease in flavonoid	Antioxidant activity, thermotolerance properties	Austen et al. (2019)
<i>Elodea nuttallii</i> , <i>Potamogeton crispus</i> , <i>Vallisneria asiatica</i>	Carotenoids	Deactivation of H ₂ O ₂	De Silva and Asaeda (2017)
<i>Psychotria brachyceras</i>	Brachycerine (monoterpene-indole alkaloid)	Antioxidant activity against singlet oxygen hydroxyl and superoxide radicals	Da Silva Magedans et al. (2017)
<i>Solanum lycopersicum</i> cv. Mato	α-Phellandrene; β-caryophyllene, 2-carene, limonene (terpenoids)	Antioxidant activity	Copolovici et al. (2012)
<i>Solanum lycopersicum</i>	Volatile isoprenoids	ROS scavengers	Vickers et al. (2009)

Table 19.4. Under heat stress, the synthesis of SMs generally increases, leading to the protection of cellular structures from oxidative damage (Sehgal et al. 2016), but there are also reports emphasizing a decrease in the concentration of SMs in plants under heat stress. Temperature is an important environmental factor affecting anthocyanin metabolism in plants. In some studies, it has been reported that high temperatures inhibit the expression of genes that control anthocyanin synthesis and the accumulation of activators (Wang et al. 2016; Rehman et al. 2017). It has been reported that there is a decrease in the levels of anthocyanins and carotenoids in many species such as *V. vinifera* and Brassicaceae, due to partial pigment degradation and reduced gene transcription in plants under the

high-temperature stress (Yang et al. 2018). Again, in a recent study, Liu et al. (2019) reported that a high temperature decreased the amount of anthocyanin in the *S. tuberosum*. Authors pointed out that the reason for this decrease was the directing of the flow to lignin and chlorogenic acid biosynthesis of isoprene, a more beneficial metabolite with antioxidant and thermotolerance properties (Wahid et al. 2012; Austen et al. 2019).

Plant survival strategies against high temperatures include osmoprotectants such as chaperones, proline, glycine betaine, sugars, and polyamines (Sakamoto and Murata 2002; Gepstein et al. 2005; Chen et al. 2007). In the study conducted on *V. aconitifolia* exposed to 42 °C for 7 days, increases in the amount of proline and total sugar and the activities of antioxidant enzymes were shown as evidence of thermotolerance (Harsh et al. 2016).

2.5 Plant Secondary Metabolites Produced in Response to Heavy Metal Stress

Heavy metal stress is one of the main abiotic stress factors that prevent metabolic processes in plants due to reasons such as contamination of soil, air, and water, high bioaccumulation, toxicity, and lowering the quality of natural products produced by plants (Keunen et al. 2016; Sahay and Gupta 2017). Heavy metal stress causes changes in the conformation of chloroplasts in plants and increases the efficiency of various signaling (ethylene and jasmonic acid) pathways that stimulate aging (Keunen et al. 2016). They produce ROS and damage DNA, RNA, and protein by causing oxidative stress (Kumar and Sharma 2018). They decrease the amount of chlorophyll *a* and *b* due to the inhibition of enzymes involved in the biosynthesis of pigments (Rai et al. 2016). For example, it has been reported that Pb stress decreases the amount of photosynthetic pigments even in *B. juncea*, which is used in heavy metal phytoremediation (Chandra and Kang 2016). Plants protect themselves from the toxicity of metals by various mechanisms. These mechanisms include antioxidant defense, binding to the cell wall or deposition in the vacuole, returning the metal ions in free form or complex form to the rhizosphere, synthesis of low molecular weight organic acids, accumulation of osmoprotectants, chelate formation with sulfur donor phytochelatins and metallothioneins, and production of SMs such as isoprenoids, phenolics, flavonoids, and carotenes (Dalvi and Bhalariao 2013; Umar et al. 2013; Khare et al. 2020). All these studies indicate that SMs can be an effective strategy for reducing the toxicity of heavy metals (Table 19.5). Since the cell wall is the first barrier that metals encounter, cell wall components protect the protoplast by binding to metals. For example, the functional groups of lignin bind more than one metal ion to itself. Phenolic compounds such as lignin, quercetin, coumaric acid, catechin, ferulic acid, and myricetin protect the cell against metal stress by contributing to the increase in cell wall thickness (Guo et al. 2008; Krzesłowska 2011). The

Table 19.5 Biosynthesis of some SMs in plants under heavy metal stress

Plant/metal	SMs	Function	References
<i>Hypericum perforatum</i> /Se	Hypericin, hyperforin (essential oil) phenolic	Antioxidant activity	Nazari et al. (2022)
<i>Salvia sclarea</i> /Cd	Phenolic, anthocyanins, carotenoids	ROS scavengers, carotenoids reduce oxidative stress in chloroplasts	Dobrikova et al. (2021)
<i>Imperata cylindrical</i> /Cu	Hydroxycinnamic acid, cyanidins, flavons	Antioxidant activity, cyanidins protect the photosynthetic complex	Vidal et al. (2020)
<i>Belamcanda chinensis</i> /Cu	Tectorigenin, tectoridin, iristectorigenin A, (flavonoids)	ROS scavengers, antioxidant activity	Zhu et al. (2020)
<i>Radish sativus</i> /Cd, Cr, Pb	Glutathione	ROS detoxification, phytochelatin synthesis, chelation of metals	Gao et al. (2020)
<i>Solanum lycopersicum</i> /Ni	Phenols, anthocyanins, flavonoids	ROS scavengers	Jahan et al. (2020)
<i>Medicago sativa</i> /Cd	Xylogalacturonan	Strengthening cell wall (with pectin methylation)	Gutsch et al. (2019)
<i>Tagetes minuta</i> L./Pb	Sabinene, limonene, b-ocimene, b-citral, verbenone (volatile compounds)	ROS scavengers, activation of defense genes	Pazcel et al. (2018)
<i>Oryza sativa</i> /Cd	Phenylalanine, methionine, histidine, lysine	Mitigating levels of metal ions	Fu et al. (2018)
<i>Oryza sativa</i> /Cr	p-Coumaric, caffeic, and gallic acids, protocatechuic, p-hydroxybenzoic	Antioxidant activity, chelation	Dubey et al. (2018)
<i>Corylus avellana</i> /AgNPs	Taxol, baccatin II (taxanes)	Antioxidant activity	Jamshidi and Ghanati (2017)
<i>Zea mays</i> /Cd, Cu, Pb	Chlorogenic acid, vanillic acid (phenolic)	Antioxidant activity	Kisa et al. (2016)
<i>Vigna radiata</i> /Cd	Alkaloids	Antioxidant activity	Nahar et al. (2016)
<i>Vaccinium corymbosum</i> /Cd	Phenolics	Antioxidant activity	Manquían-Cerda et al. (2016)
<i>Tagetes minuta</i> L./Pb	β -Ocimene, α -thujone (volatile compounds)	Activation of defense genes	Sosa et al. (2016)
<i>Prosopis farcta</i> /Pb	Salicylic acid, ferulic acid, vitexin, daidzein, phenolic acids	Signaling molecules Metal chelation ROS scavengers	Zafari et al. (2016)
<i>Vitis vinifera</i>	Flavonoids	Antioxidant activity	Leng et al. (2015)
<i>Solanum nigrum</i> , <i>Parthenium hysterophorus</i> /Cr	Malic and citric acid	Metal binding	UdDin et al. (2015)

(continued)

Table 19.5 (continued)

Plant/metal	SMs	Function	References
<i>Abelmoschus esculentus</i> /Cd, Pb, Zn	Nonprotein thiols	Antioxidant activity	Kandzióra-Ciupa et al. (2013)
<i>Vitis vinifera</i> /Co, Ag, Cd	Resveratrol, sesquiterpenoid, phytoalexin	Antioxidant activity	Cai et al. (2013)
<i>Lepidium sativum</i> /As	Lepidine, proline, ascorbic acid	Chelation antioxidant activity	Umar et al. (2013)
<i>Helianthus annuus</i> /Cu	<i>p</i> -Coumaric acid	Metal precipitation	Meier et al. (2012)
<i>Artemisia annual</i> /As	Artemisinin	Antioxidant activity	Rai et al. (2011)
<i>Phaseolus vulgaris</i>	Phenolic	ROS scavengers: against oxidative damage, hydrogen donors, metal-chelating capacity, reducing agents	Hamid et al. (2010)
<i>Matricaria chamomilla</i> /Cd, Cu	Caffeic acid, ferulic acid, <i>p</i> -coumaric acid, chlorogenic acid, salicylic acid, vanillic acid, <i>p</i> -OH benzoic acid, syringic acid	Antioxidant activity, ROS scavengers, chelation	Kováčik et al. (2009)

peroxidase (POX) oxidizes monolignols to radicals that combine with the lignin polymer. These radicals then combine to form the lignin polymer and thus contribute to the strengthening of the cell wall (Wang et al. 2013). Moreover, phenols, alkaloids, and saponins can prevent the harmful effects of metal toxicity by forming stable complexes with different metals or by chelation with metals (Berni et al. 2019; Nobahar et al. 2021). Plants exposed to metal stress secrete root exudate, which includes metabolites such as phenolics, amino acids and derivatives, sugar and organic acids, and proteins, and mucilage into the soil. These metabolites chelate metals in the rhizosphere and apoplast, preventing them from entering the symplast and reducing the toxicity in the cytoplasm (Nigam et al. 2001). Histidine and nicotinamide are amino acids that play an important role in the chelation of heavy metals. Nicotianamine, a free amino acid, can bind metals such as iron (Fe), copper (Cu), and nickel (Ni) (Higuchi et al. 1999). Histidine, which is chelator-like nicotinamide, also forms a complex with zinc (Zn) and Ni, reducing heavy metal toxicity (Salt et al. 1999; Richau et al. 2009). Proline, another amino acid, acts as an osmoregulator in the regulation of the water balance disorder that occurs during heavy metal stress. It also detoxifies $\cdot\text{OH}$ and $^1\text{O}_2$ and increases the activities of intracellular antioxidant enzymes (Mourato et al. 2012). Organic acids such as malate, malonate, oxalate, tartrate, citrate, and aconitate reduce toxicity by forming chelates with metals in the cytosol (Anjitha et al. 2021). Metallothioneins, which are rich in cysteine, reduce metal toxicity by binding to metals with the thiol group of cysteine (Zhou and Goldsbrough 1994). They also increase tolerance to oxidative stress by acting in ROS detoxification. Glutathione is an important ROS and methylglyoxal (a

cytotoxic compound) scavenger and an antioxidant effective in the chelation of metals (Saito et al. 2011). Additionally, phytochelatins, a cysteine-rich polypeptide family that plays an important role in reducing metal toxicity, are also synthesized from glutathione (Yang et al. 2005). Like metallothioneins, the heavy metal is accumulated in the vacuole by forming a complex with the heavy metal with the thiol groups they have, and its free circulation in the cytosol is limited (Sanit'a Di Toppi and Gabbrielli 1999). Anthocyanins (cyanidin, delphinidin, petunidin, etc.) with adjacent hydroxyl groups have strong metal-chelating effects (Tang and Giusti 2020). Janeesha et al. (2020) found a high accumulation of anthocyanins in maize under Zn stress. Cyanidin gained electrons and formed a complex with zinc, increasing the tolerance to high Zn stress. The phenolic and flavonoid compounds in *G. pseudo-china* plants chelate Zn and Cd metals. It has also been reported that *Cinchona* alkaloids can form complexes with different metals, such as Fe, lead (Pb), Cu, and cobalt (Co), and that phenolic compounds such as catechin and juglone can form complexes with Fe (Chobot and Hadacek 2010). It has been determined that tannins extracted from plant seeds can chelate metals such as Zn, Fe, and Cu (Karamac 2009). Many studies conducted to date show that various SMs synthesized under heavy metal stress play an active role in reducing the damage of heavy metals in the cytoplasm by forming chelates with metals.

Antioxidants such as tocopherol, carotenoids, glutathione, ascorbate, and phenolic compounds, such as coumarin, tannin, lignin, anthocyanin, and flavonoids, act as ROS scavengers in plants exposed to heavy metal stress (Maleki et al. 2017). Phenolic compounds and flavonoids, which act as antioxidant compounds due to their hydrogen atom or electron-donating abilities, can directly scavenge ROS (Okem et al. 2015). Phenolic compounds and flavonoids with redox properties act as antioxidants and ROS scavengers and can chelate metals (Rice-Evans and Paganga 1996). For example, it was determined that increased phenolic compounds in *P. vulgaris* exposed to Pb stress scavenge ROS and reduce lipid peroxidation and oxidative damage (Neelofer et al. 2010). The increase in phenolic, flavonoid, and anthocyanin concentrations in *Salvia sclarea* increased its tolerance to Cd metal (Dobrikova et al. 2021). These metabolites have been reported to act as ROS scavengers. It has been determined that Cu metal increases the production of phenolic and lignin compounds in *P. ginseng* and *W. somnifera* plants (Khatun et al. 2008), and Cu²⁺ and Cd²⁺ metals stimulate the biosynthesis of betalain, shikonin, and digitalin (Trejo et al. 2001). Zn²⁺ metal increased lepidine production in *L. sativa* plant (Saba et al. 2000). Thomas et al. (2011) reported that Cd and Co metals stimulated diosgenin accumulation in *T. foenum-graecum*. AgNO₃ and CdCl₂ increased the concentration of scopolamine and hyoscyamine, and Pb increased the synthesis of phenolic compounds (Winkel-Shirley 2001). The downregulation of the hyoscyamine 6β-hydroxylase enzyme responsible for the synthesis of scopolamine by silver ions increased the amount of scopolamine (Pitta et al. 2000). Winkel-Shirley (2001) reported that plants grown on aluminum-containing soils have a high flavonoid content, and this may help reduce damage caused by oxidative stress.

2.6 UV Stress Affects the Production of Secondary Metabolites in Plants

Light is an important abiotic factor that can affect plant growth, production, and quality of SMs. The responses of different plant species to UV stress differ depending on the signal transmission mechanism, the amount and intensity of light, and the effect of gene expression (Parikrama and Esyanti 2014). UV-B radiation causes the formation of ROS such as H_2O_2 in plants, damaging DNA and chloroplasts, specifically photosystem II (Del Valle et al. 2020). Plants can adapt to UV changes by accumulating various SMs such as terpenoids, flavonoids (flavonols, anthocyanins, catechins, etc.), hydroxycinnamic acids, phenylpropanoids, tannins, cyanogenic glycosides, α -tocopherol, glucosinolates, carotenoids, and alkaloids (Morales et al. 2010; Jan et al. 2021). Ferulic acid, caffeic acid, and *p*-coumaric acid are the most effective phenolics for reducing the harmful effects of UV. Most phenols, such as hydrocinnamic acids, *p*-coumaric acid, and ferulic acid, help in cell wall formation and represent the beginning of lignification (Antonova et al. 2012). Some other SMs in different plants exposed to UV stress and their defense effects are presented in Table 19.6.

SMs accumulated in the epidermal layers of the cells of plants exposed to UV-B stress protect the underlying sensitive tissues against the harmful effects of stress. However, Zhao et al. (2013) reported that long-term exposure to UV-B stress may decrease the protectiveness of these metabolites due to less photosynthate production. The photosensitive and highly stable cellular components absorb excess UV-B and prevent photodamage. UV-B and UV-C stimulate flavonoid synthesis and synthesis of compounds synthesized from the phenylpropanoid pathway (Warren et al. 2003). Flavonoids and phenylpropanoid derivatives, deposited in the epidermal cells, significantly inhibit the effect of UV stress as a UV-absorbing sunscreen (Mazza et al. 2000). In addition to flavonoids, compounds such as carotenoids and anthocyanins accumulate in the upper epidermis of the leaves and form UV-B blocks as UV absorbers and prevent the formation of ROS (Hideg et al. 2013). Flavonoids alleviate photoinhibition and photooxidative damage by eliminating the harmful effects of ROS, owing to their radiation absorption (UV-absorbing) properties (Jordan 2002). UV-B stress increases the concentration of flavonoid content in *H. vulgare*, *P. incarnata*, *P. quadrangularis*, *P. edulis*, and *K. pinnata*, polyamines in *C. sativus*, and flavonols in *P. abies* (Antognoni et al. 2007). As it is known, the cell wall of plants is the largest carbon source in the biosphere. The cell wall consists of polysaccharides such as cellulose and hemicellulose, as well as pectin, lignin, structural proteins, and other compounds. Some studies have shown that while UV-B increases the level of phenolic compounds in the structure of the cell wall, it causes relaxation in the cell wall with the release of $-CH_4$ from pectin (Ruhland et al. 2005; Messenger et al. 2009). In another study, Cuzzuol et al. (2020) determined that UV-B increased polyphenols such as flavonoids and lignins and the total antioxidant capacity in sun-tolerant *Paubrasilia echinata*. However, it was found that there was an increase in lignin content despite the decrease in hemicelluloses in

Table 19.6 Different SMs synthesized in plants exposed to UV stress

Plant	SMs	Function	References
<i>Amaranthus tricolor</i> L.	Phenolic compounds, flavonoids, anthocyanin, ascorbic acid, betalain	Antioxidant activity, UV-B-absorbing compounds	Wittayathanarattana et al. (2022)
<i>Fagopyrum esculentum</i>	Phenolics	Antioxidant activity	Hornýák et al. (2022)
<i>Solanum lycopersicum</i>	Diterpenes	Antioxidant activity increased when plant exposed to UV stress	Mannucci et al. (2022)
<i>Arabidopsis thaliana</i>	α -Tocopherol	UV-B photoprotection, ROS scavengers	Badmus et al. (2022)
<i>Hordeum vulgare</i>	Flavonoids	Antioxidant activity	Gromkowska-Kępką et al. (2021)
<i>Artemisia annua</i>	Artemisinin (sesquiterpene)	Antioxidant activity	Wani et al. (2021)
<i>Capsicum annuum</i>	Cynaroside (flavonoid)	ROS scavengers	Ellenberger et al. (2020)
<i>Nymphoides humboldtiana</i>	Flavonoid	Antioxidant activity, ROS scavengers	Nocchi et al. (2020)
<i>Psychotria brachyceras</i>	Brachycerine (alkaloid)	UV-screening, prevention of UV-energy absorption, antioxidant activity, detoxification of hydroxyl and superoxide radicals	Porto et al. (2020)
<i>Cuminum cuminum</i>	Terpenoids, flavonoids, anthocyanins, phenols, alkaloids, β -carotene, lycopene	UV-absorbing compounds, carotenoids: receptors of reactive oxygen species, antioxidant activity	Ghasemi et al. (2019)
<i>Trigonella foenum-graecum</i> L.	Phenolics, flavonoids, anthocyanins, aromatic oil compounds	UV-B-absorbing compounds, antioxidant capacity	Sebastian et al. (2018)
<i>Zingiber officinale</i>	Gingerol, zingiberene	Antioxidant activity, longevity, and stress resistance	Lee et al. (2018)
<i>Alternanthera sessilis</i> , <i>Alternanthera brasiliana</i>	Betacyanin (alkaloid), betaxanthin	Antioxidant capacity	Klein et al. (2018)
<i>Prunella vulgaris</i>	Caffeic acid, rosmarinic acid, flavonoids, hyperoside, salviaflaside	Antioxidant activity, high accumulation in vegetative, flowering, and fruiting stages	Chen et al. (2018)
<i>Fagopyrum esculentum</i>	Rutin catechin (flavonoid)	Antioxidant activity	Zheng et al. (2017)
<i>Bixa orellana</i>	β -Carotene	Antioxidant activity	Sankari et al. (2017)

(continued)

Table 19.6 (continued)

Plant	SMs	Function	References
<i>Brassica oleracea</i>	Glucosinolates, phenolics, carotenoids, chlorophyll	Signaling molecules, antioxidant activity	Moreira-Rodríguez et al. (2017)
<i>Fagopyrum esculentum</i>	Quercetin (flavonoid)	Antioxidant activity	Huang et al. (2016)
<i>Coleus forskohlii</i>	Trimethyl citrate, methyl stearate, cadina-1,4-diene, δ -cadinene, cadinene, α -pinene, d-borneol, camphene, etc.	ROS scavengers	Takshak and Agarwal (2016)
<i>Catharanthus roseus</i>	Alkaloids	ROS scavengers	Zhu et al. (2015)
<i>Psychotria brachyceras</i>	Brachycerine	Antioxidant and antimutagenic activity	Nascimento et al. (2015)
<i>Artemisia annua</i>	Artemisinin	ROS scavengers	Pandey and Panday Rai (2014)
<i>Catharanthus roseus</i>	Vinblastine, vindoline, catharanthine	UV-B-absorbing compounds	Guo et al. (2014)
<i>Vitis vinifera</i>	Terpenes	Antioxidant activity	Marchive et al. (2013)
<i>Fagopyrum tataricum</i>	Catechin, quercetin rutin	Antioxidant activity	Regvar et al. (2012)
<i>Ipomoea batatas</i>	Hydroxybenzoic acids, hydroxycinnamic, flavonols, anthocyanins, catechins	Antioxidant activity	Carvalho et al. (2010)
<i>Mentha x piperita</i>	Menthol, limonene, 1,8-cineole	Signaling molecules	Behn et al. (2010)

sun-resistant ecotypes. The increases in lignin and flavonoid content strengthen the cell wall and increase mechanical resistance, thus reducing the UV-B transfer from the leaf surface to the mesophyll and increasing tolerance to stress (Cuzzuol et al. 2020). Additionally, epidermal cuticle configurations are capable of scattering some of the UV radiation, although small reflectivity may be required for UV scattering.

Antioxidants are compounds that protect against oxidative stress caused by various stress factors. Metabolites such as ascorbic acid, phenolic compounds, carotenoids, glutathione, flavonoids, and α -tocopherol, which are nonenzymatic antioxidants, serve to scavenge ROS species and prevent lipid peroxidation (Miret and Munné-Bosch 2015). Moreover, phenolic acids such as hydrocinnamic acid, anthocyanins, stilbenes, and various other phenylpropanoid pathway compounds also have a high antioxidant activity (Agati and Tattini 2010). For example, the concentration of phenolics, a compound with antioxidant properties, increases with the effect of UV-B stress. However, these antioxidant capacities of SMs vary not only from their concentrations but also from their biochemical structures and the cellular regions (cell walls, vacuoles of epidermal and mesophyll cells, chloroplasts, trichomes) where they are synthesized and accumulated. For example,

monohydroxylated B-ringed flavonoids containing a single -OH group absorb more UV-B than dihydroxy B-ringed flavonoids containing two -OH groups (Agati and Tattini 2010). It was found that flavonoids with the catechol group in the B ring showed better antioxidant properties (Agati et al. 2009). It has also been stated that light increases the biosynthesis of terpenoid indole alkaloids in *C. roseus* (Liu et al. 2018). Increases in the amount of carbonic acid, a diterpene, were also determined in *R. officinalis* under UV-B stress (Luis et al. 2007). It has been reported that carbonic acid, an antioxidant, prevents the deterioration of the structure of the cell membrane by preventing lipid peroxidation against UV-B stress (Munne-Bosch and Alegre 2002). Carotenoids, which act as photosynthetic pigments, were also increased in plants exposed to UV stress (Sankari et al. 2017). It protects the thylakoid membrane lipids of carotenoids and some terpenoids against high light damage. Xanthophylls and tetraterpene carotenoids increase photosynthesis by preventing photooxidative damage in the photosynthetic apparatus (Jahns and Holzwarth 2012; Pattanaik and Lindberg 2015).

Carotenoids act as ROS scavengers during stress and protect thylakoid membranes and proteins. They prevent free radical chain reactions by reacting with the products formed because of lipid peroxidation and protect the photosynthetic apparatus (Niyogi et al. 2001; Swapnil et al. 2021). UV stress causes anthocyanin accumulation in *P. avium*, *M. domestica*, *P. frutescens*, *D. carota*, and *F. vesca* (Winkel-Shirley 2001; Ramakrishna and Ravishankar 2011). In a study investigating the effects of anthocyanins accumulated in the mesophyll and epidermis against UV stress, it was determined that the antioxidant activity of anthocyanins accumulated in the mesophyll against oxidative damage was more effective than their sunscreen properties (Kytridis and Manetas 2006). In plants exposed to UV-B stress, an increase in alkaloid biosynthesis was determined by the effect of the tryptophan decarboxylase enzyme and WRKY6 factor (Mehrotra et al. 2018). In a similar study with *P. brachyceras* leaves under UV stress, alkaloid increases were detected due to the increase in the expression of genes encoding the enzyme that produces tryptamine, the indole precursor of alkaloid synthesis (Nascimento et al. 2015).

3 Plant Secondary Metabolite Synthesis Under Biotic Stress

Nematodes, fungi, viruses, insects, viroids, and bacteria cause serious damage by affecting the growth and development of plants. Plants have developed various defense mechanisms against pathogens. Phytochemicals with antimicrobial effects, such as phenolics, flavonoids, coumarins, terpenoids, lignins, alkaloids, stilbenes, and glucosinolates, are important metabolites of defense responses in plants. The first barrier against pathogens in plant defense is the cuticle and cell walls (Berto et al. 1999). The accumulation of cutins or waxes increases resistance to the pathogen (Xu et al. 2022). Cuticles, which are rich in cutin, prevent the germination of spores of fungi and mycelial growth due to their hydrophobic properties. Additionally, triterpenoids, the main components of cuticular wax, confer chemical

resistance to fungal pathogens. It has been determined that 16-hentriacontanone (palmitone), which is the main component of the cuticular wax of *A. squamosa*, shows resistance and antifungal activity (Shanker et al. 2007). The SMs associated with defense in plants are generally divided into two groups: phytoanticipins and phytoalexins (Mansfield 1999). Phytoalexins and phytoanticipins are SMs with antimicrobial properties against insect, microorganism, and herbivorous attacks (Morant et al. 2008). Phytoanticipins such as saponin, glucosinolates, and cyanogenic glucosides are low molecular weight antimicrobial compounds, which exist in plants before infection or also occur after infection.

Phytoanticipins can accumulate in dead cells or be excreted into the rhizosphere. The inactive forms are stored in the vacuole. When necessary, they are hydrolyzed and become active, that is, toxic. For example, quinone, catechol, and protocatechuic acid have inhibited the germination of the spores of *C. circinans* and *B. cinerea*. Glycosides and glucosinolates are synthesized in healthy tissues before infection but are activated when tissue damage occurs. Although found at higher levels in healthy plants, saponins with surfactant properties are glycosides that impair the integrity and function of the membrane by binding to the sterols in the cell membranes of some pathogens (Tiku 2020). It has been determined that avenacins localized in the roots of the oat plant prevent *G. graminis* var. *tritici* infection (Osbourn 1996). However, it was determined that 26-desglucoavenacosides A and B, which are active forms of avenacosides localized in the leaves and shoots of the oat plant, have antifungal properties (Gus-Mayer et al. 1994a, b; Osbourn et al. 1994). Since some saponins bind to proteins and inhibit proteinases, they impair digestion in the guts of insects (Amtul and Shakoori 2014). Newman (2014) reported that saponins isolated from *B. vulgaris* leaves have a deterrent activity against *P. xylostella*. α -Tomatine, which is the main saponin of tomato and is found at high levels in the flowers, leaves, and fruits of the tomato plant, provided a high resistance against fungi such as *F. oxysporum* f. sp. *lycopersici* and *V. albo-atrum* (Smith and MacHardy 1982; Pegg and Woodward 1986). However, α -tomatine has been reported to be active at a certain pH. For example, since *A. solani* lowers the pH at the infection site, α -tomatine becomes inactive, so the pathogen cell membrane cannot break down, and the antifungal effect disappears (Roddick and Drysdale 1984). Cyanogenic glycosides containing nitrogen are degraded by hydrolytic enzymes such as β -glycosidases and hydroxy nitrile lyases, released by plants after infection to produce hydrogen cyanide, which is highly toxic to pathogens (animals, insects, etc.) (Poulton and Li 1994; Tiku 2020). Hydrogen cyanide binds to and inhibits cytochrome oxidase to stop electron transport, damaging the respiratory system of predators. However, plants protect themselves from the toxic effects of hydrogen cyanide with detoxification enzymes (Miller and Conn 1980). Glucosinolates, which are S-containing glycosides found in members of the Brassicaceae, are converted by myrosinase (a thioglucosidase) into different products such as nitrile, thiocyanate, and isothiocyanate, which are highly toxic to many pathogens. The toxic effects of these degradation products on pathogens such as *Alternaria* sp., *P. parasitica*, *L. maculans*, and *M. brassicicola* have been determined, and it has also been reported that they can be used as fungicides against other plant pests such

as grains (Mari et al. 1993; Angus et al. 1994). Benzoxazinoids, another phytoanticipins, are predominantly found in grains such as wheat, rye, and corn and in some dicot plants with antimicrobial properties. In response to tissue damage caused by pathogen attack, they are hydrolyzed by β -glycosidase to produce toxic BX-Glcs aglycones (Korte et al. 2015; Del Cueto et al. 2018). Various compounds synthesized from the phenylpropanoid pathway exhibit antifungal properties by inhibiting spore germination and serve as phytoanticipins. For example, caffeic acid, *p*-coumaric acid, ferulic acid, and methoxycinnamic acid induce resistance to *A. flavus* Link and *A. parasiticus* Speare (Sobolev et al. 2006). The protective effects of hesperidin against *P. digitatum*, kaempferide triglycoside and hydroxyacetophenone against *F. oxysporum*, and sakuranetin against *M. grisea* infection have been determined (Marchesini et al. 1996). Phytoalexins, which include substances synthesized through the terpenoid and phenylalanine pathway, are low molecular weight antimicrobial compounds and get accumulated in plants after infection and inhibit the growth of bacteria and fungi (Jeandet et al. 2013) and inhibit spore growth and growth of hyphae to pathogenic fungi. They are thus considered defense compounds against diseases caused by pathogens. However, the amount and rate of accumulation of phytoalexins affect the development of pathogens (Duke 2018). Stilbenoids are metabolites derived from the amino acid phenylalanine. *p*-Coumaryl-CoA and malonyl-CoA enable the production of resveratrol (3,5,4'-trihydroxy-trans-stilbene) and various flavonoids in plants. However, the activity of the stilbene synthase enzyme is required for the synthesis of these two compounds. Because of this, using a single biosynthetic gene, it is possible to obtain a phytoalexin of the stilbene type, which is an important compound for defense against fungal infection in noninfected plants. Stilbenes, which are also considered phytoalexins, have a strong antifungal activity because they accumulate in the necessary concentrations to prevent fungal infection in plants (Morales et al. 2000). An example of this is the accumulation of pinosylvin and pinosylvin 3-O-methyl ether against *C. versicolor* and *G. trabeum* infection in conifers (Schultz et al. 1992). Resveratrol, a stilbene analog and first isolated from *V. grandiflorum* in 1940, is a compound with many activities such as antibacterial, antiviral, antioxidant, and antitumor (Jeandet et al. 1995; Song et al. 2021). It was determined that resveratrol inhibits the penetration and spore germination of *V. inaequalis* in apples (Schulze et al. 2005). It has also been reported that *B. cinerea* and *P. viticola* also reduce sporangia germination (Pezet et al. 2004). Song et al. (2021) reported that resveratrol derivatives formed due to modifications such as the removal of phenolic hydroxyl groups and ester formation in the structure of resveratrol inhibit tobacco mosaic virus (TMV).

Phenols are the most well-known and common defense compounds against insects, various bacteria, and fungi (Uleberg et al. 2012). Phenol derivatives and tannins prevent the proliferation of bacteria by increasing membrane damage and permeability and inactivating metabolism (Khameneh et al. 2019). Flavonoids, tannins, isoflavonoids, anthocyanins, lignins, phytoalexins, and furanocoumarins are important phenolic compounds that act as defense compounds against pests (Rani and Jyothsna 2010). Phenolics and flavonoids inhibit pathogens by disrupting their structures by causing lipid peroxidation in the cell membrane and mitochondrial

membrane in fungi (VanEtten et al. 1994). Phenylpropanoids and flavonoids have phenolic hydroxyl groups that form ionic and hydrogen bonds with peptides and protons, causing the denaturation of proteins and enzymes, thus inhibiting the physiological activities of pathogens, including the reproductive system (Morrissey and Lou 2009). Phenolic compounds also show antibacterial properties by inhibiting enzymes such as NADH reductase and ATP synthase (Rempe et al. 2017). Flavonoids not only inhibit bacterial cell wall proteins and DNA synthesis but also cause inactivation of metabolism (Bouarab-chibane et al. 2019). Additionally, phenolics and flavonoids such as chlorogenic acid synthesized from the phenylpropanoid pathway increase the activities of defense enzymes and activate the SA signaling pathway (Jiao et al. 2018). *p*-Coumaric acid increases the activity of antioxidant enzymes and regulates the PR genes and phenylpropanoid pathway (Yuan et al. 2019). It has been reported that N-hydroxypipicolinic acid, a secondary metabolite, can induce systemic acquired resistance (SAR) during pathogen infection (Yildiz et al. 2021). Polyphenols form covalent bonds with SH, OH, or free amino groups of some proteins of phytopathogens, causing the degradation of the 3D structures of proteins and thus inactivation (Zaynab et al. 2018). Polyphenols such as catechins have been reported to be effective in defense by changing plasma membrane permeability and oxygen production in different bacterial species such as *P. aeruginosa*, *S. marcescens*, *B. bronchiseptica*, *B. subtilis*, and *S. aureus* (Wang et al. 2018). It was determined that the increase in resveratrol O-methyltransferase and resveratrol synthase 3 enzymes in soybean exposed to *R. solani* inhibited the growth of the fungus (Zernova et al. 2014). Hydroxycinnamic derivatives, oleuropein derivatives, flavonol monoglucoside, and tyrosol derivatives were found to be effective in the defense against *Fusicladium oleagineum*, which causes leaf spot disease in olive trees (Talhaoui et al. 2015). Significant differences in endogenous phenolic levels were detected in plants exposed to fungal infections by *L. angustifolius* (Verma and Shukla 2015). It was determined that the amount of phenolics such as kaempferol, quercetin, caffeic acid, and chlorogenic acid increased in plants against virus infection (Parr and Bolwell 2000). Other SMs that act as defense compounds against fungi and insects are alkaloids such as caffeine, cocaine, morphine, and nicotine (Ogbanna and Opara 2017). Cyanogenic glycosides, another N-containing compound, are also important SMs with toxic properties, which play a role in the defense against herbivores and insects (Santisree et al. 2020). The nicotine found in tobacco leaves binds to the receptors of nicotinic acetylcholine, blocks endogenous neurotransmitters, and causes paralysis and even death in insects (Dewey and Xie 2013). It has been reported that dhuririn is highly effective in deterring insects in *S. bicolor* by its effective hydrolysis and subsequent release of cyanide (Krothapalli et al. 2013). Since terpenoids have repellent properties against herbivores, they prevent larvae feeding and reduce egg laying (Maffei 2010). It has been determined that latex, which is secreted from the roots of the dandelion plant and is in the terpene group, protects the plant against *M. melolontha* larvae (Huber et al. 2016). Studies on some SMs found to be effective in the development of disease resistance to pathogens in plants are presented in Table 19.7.

Table 19.7 Some SMs synthesized against pathogens and their functions

Plant	SMs	Function	References
<i>Oryza sativa</i>	Hydroxycinnamoyl-tyramine conjugates	Antibacterial, antifungal	Shen et al. (2021)
<i>Avena strigosa</i>	Avenacins (triterpene)	Antipathogenic	Li et al. (2021)
<i>Oryza sativa</i>	Phenolamides	Antifungal	Fang et al. (2022)
<i>Solanum lycopersicum</i>	β -Phellandrene, lycosantalol (mono-diterpenes)	Antifungal	Zhou and Pichersky (2020)
<i>Citrus sinensis</i>	Hesperidin (flavanones)	Antibacterial	Soares et al. (2020)
<i>Anacardium occidentale</i>	Agathisflavone (flavonoids)	Antimicrobial	Andrade et al. (2019)
<i>Aesculus hippocastanum</i>	Aescin (saponin)	Antifungal	Trda et al. (2019)
<i>Canavalia gladiata</i>	Gallotannin (tannins)	Natural antioxidant, antibacterial agents	Gan et al. (2018)
<i>L. radiate</i>	Lycorine, colchicine, galanthamine, 3-epimacronine, deoxytazettine, N-allylnorgalanthamine (alkaloid)	Insecticidal	Yan et al. (2018)
<i>Sorghum bicolor</i> L.	Dhurrin (cyanogenic glucoside)	Antiherbivore	Emendack et al. (2018)
<i>Vitis vinifera</i>	d-Viniferin, pterostilbene	Antifungal	Viret et al. (2018)
Cotton	Phenol, gossypol	Antivirus	Mandhanıa et al. (2018)
<i>Vaccinium myrtillus</i>	Chlorogenic acid	Antiherbivore	Hernandez-Cumplido et al. (2018)
<i>Peganum harmala</i>	β -Carbolines (alkaloid)	Antibacterial	Suzuki et al. (2018)
<i>Solanum nigrum</i>	Myristic acid, veremivirine, oleuropein glucoside (alkaloids)	Antifungal	Tiku (2018)
<i>Solanum nigrum</i>	Glycoalkaloids	Insecticidal	Spochacz et al. (2018)
<i>Arabidopsis thaliana</i>	Menthol (monoterpene)	Antifungal	Lin et al. (2017)
<i>Nicotiana</i> sp.	Pyridine alkaloid (nicotine)	Antibacterial	Stevenson et al. (2017)
<i>Capsicum</i> spp.	Capsidiol	Antifungal	Lee et al. (2017)
<i>Ricinus communis</i>	Ricinine and its derivatives (alkaloid)	Antibacterial, antifungal	El-Naggar et al. (2017)

(continued)

Table 19.7 (continued)

Plant	SMs	Function	References
<i>Zanthoxylum piperitum</i>	Pellitorine (alkaloid)	Insecticidal	Kim and Ahn (2017)
<i>Waltheria indica</i>	Quinoline (alkaloid)	Antifungal	Cretton et al. (2016)
<i>Pisum sativum</i> L. cv. Arkel	Shikimic acid, gallic acid, chlorogenic acid, syringic acid, coumaric acid, cinnamic acid, salicylic acid, myricetin, quercetin, kaempferol	Antipathogenic	Jain et al. (2015)
<i>Olea europaea</i> L.	Quinic acid, cyclic polyols	Antibacterial	Luvisi et al. (2017)
<i>Citrus sinensis</i>	Hesperidin, rutin	Antibacterial	Soares et al. (2015)
<i>Hypericum perforatum</i>	Phenylpropanoid, naphthodianthrone	Antifungal	Gadzovska et al. (2015)
<i>Prunus amygdalus</i>	Cyanogenic glycosides	Antioxidant	Tiedeken et al. (2014)
<i>Psoralea corylifolia</i> L.	Psoralen (furanocoumarin)	Antipathogenic	Ahmed and Baig (2014)
<i>Cucumis sativus</i>	Cucurbitacins	Antifungal, antibacterial, antiherbivore	Shang et al. (2014)
<i>Ricinus communis</i> , <i>Euphorbia peplus</i> , <i>Jatropha curcas</i>	Casbene diterpenoids	Antifungal, antibacterial	King et al. (2014)
<i>Vitis vinifera</i>	Caftaric acid, procyanidin, quinic acid	Antibacterial	Wallis et al. (2013)
<i>Solanum lycopersicum</i>	α -Solanine, α -tomatine (steroidal glycoalkaloids)	Antifungal, antibacterial, insecticidal	Itkin et al. (2013)
<i>Oryza sativa</i>	Diterpenoid (phytoalexin)	Antifungal	Kanno et al. (2012)

In addition to these phytochemicals, SA, jasmonic acid (JA), and ethylene (ET) are critical in regulating defense responses. The JA, SA, ET, and methyl jasmonate are signal molecules that take part in the fight against pathogens and stimulate the antioxidant system and secondary metabolite. Defense against biotrophic pathogens is mediated by an SA-dependent pathway in plants, whereas neurotropic pathogens usually induce a defense system mediated by JA and ET (Fig. 19.2). Insect or pathogen attacks cause the accumulation of endogenous hormones such as SA, JA, and ET, which will activate the defense mechanisms in plants. Specific plant hormones such as SA, JA, and ET, on the other hand, are effective in the formation of hypersensitive response and SAR, by acting as stimulants in the synthesis of antioxidants that are effective in creating resistance to pathogens and harmful insects, with various SMs, phenolics, phytoalexins, and pathogen-related proteins (PR) (Jumali et al. 2011) (Fig. 19.2).

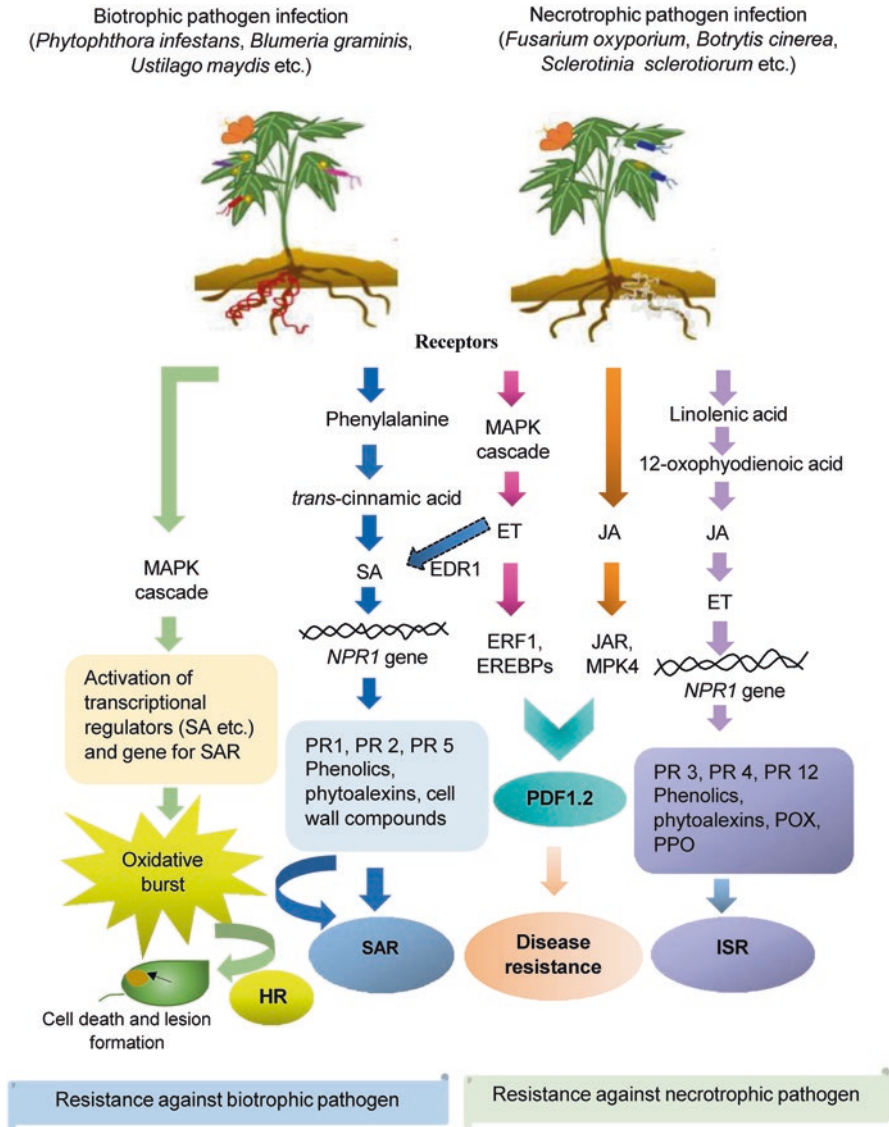


Fig. 19.2 SA, JA, and ET signal transduction pathway and disease resistance (*ET* ethylene, *EREBPS* ethylene-responsive element-binding protein, *EDR1* enhanced disease resistance 1, *ERF1* ethylene response factor, *HR* hypersensitive response, *ISR* induced systemic resistance, *JA* jasmonic acid, *MAPK* mitogen-activated protein kinase, *NPR1* nonexpressor of pathogenesis-related genes 1, *PAL* phenylalanine ammonia-lyase, *PDF1.2* plant defensin 1.2, *PR* pathogen-related proteins, *SA* salicylic acid, *SAR* systemic acquired resistance)

PR proteins, with 17 families identified in different plant species, are considered markers in SAR (Van Loon et al. 2006). Chitinases belong to the PR-3, PR-4, PR-8, and PR-11 classes and catalyze the hydrolysis of chitin, which is a component of the fungal cell wall and helps in the development of resistance to the pathogen. The hydrolysis of glucan, another structural component of the fungal cell wall, is catalyzed by glucanase, a PR-2 class protein (Van Loon et al. 1994). PR proteins show the following different functions: PR1 (antifungal), PR2 (β -1,3-glucanases), PR3 (chitinases), PR4 (class I and II chitinases), PR5 (thaumatin-like proteins), PR9 (peroxidases), PR12 (defensins), and PR13 (thionins) (Van Loon and Van Strien 1999). Studies have shown that genetically modified potato plants expressing tobacco PR-5 osmotin are more resistant to *P. infestans*, *F. solani*, and *R. solani* (Rivero et al. 2012). More resistance to *C. arachidicola* and *A. flavus* is developed in peanuts due to the overexpression of the rice chitinase gene (Prasad et al. 2013). Besides, defensin and thionine serve as effective defense responses against various phytopathogens in antimicrobial proteins rich in small cysteine (Kaur et al. 2011).

Investigation of metabolite pathways specific to a plant species, determination of biosynthetic genes, and transfer of the gene responsible for the synthesis of the metabolite to the plant that does not contain this metabolite have allowed the development of plants resistant to pathogens. The many SMs such as isoflavonoids, hydrocinnamic acid amides, terpenes, camalexin, and alkaloids besides stilbenes or genes encoding the enzymes involved in the synthesis of these metabolites can be transferred to other plants and in this way a resistance against various diseases (Muroi et al. 2012; Rook 2016). The genomic sequence of the beta-amyrin synthase enzyme involved in the biosynthesis of saponins, following the cloning from *A. strigosa*, and expressed transgenically in turf plants has developed resistance to fungal pathogens such as *F. culmorum*, *S. nodorum*, and *G. graminis* (Silva et al. 2018). Tobacco plants overexpressing heterologous phenylalanine ammonia-lyase (PAL) transgenes have been observed to show resistance to *C. nicotianae* and *P. parasitica* fungal pathogens (Way et al. 2002). It has been reported that it acts as a repellent against *M. sexta* in transgenic tobacco plants containing volatile isoprene, thereby preventing the feeding of this herbivore (Laothawornkitkul et al. 2008).

Another strategy is to increase the resistance in transgenic plants formed by transferring genes encoding polyamines such as spermine, spermidine, and putrescine, which serve to increase resistance or tolerance to biotic stresses. Hazarika and Rajam (2011) have reported that when they transferred a gene that is effective in polyamine synthesis to tomato plants, disease resistance developed in tomato plants against wilt disease caused by *F. oxysporum* and early blight caused by *A. solani* together with an increase in polyamine synthesis.

The limitations of the traditional breeding methods such as time loss and high cost have led to the development of plant tissue culture techniques such as in vitro protoplast fusion, secondary metabolite production, and haploid technology. The protoplast fusion is based on the combination of the nuclei and cytoplasm of two separate protoplasts through chemical or electrical means. The plant resulting from this combination is called somatic hybrid (Lakhani et al. 2016; Tiwari 2018). In the control of plant diseases caused by some fungi, *Trichoderma* species, known as biocontrol agents and distributed in many parts of the world, have been used. These fungal

species increase antagonistic properties by producing bioactive substances in the fight against plant diseases and stimulate SAR in plants with their hyperparasitism (Shah and Afiya 2019). The studies at a molecular genetic level have also focused on increasing the proteinase or chitinase activities acting on the pathogen cell walls or by increasing the copy number of suitable genes or combining these genes with strong promoters (*Pcbh1*, *ech42*) to increase the biocontrol ability of *Trichoderma*. The protoplast fusion is a good tool in the improvement of *Trichoderma* species and the development of hybrid strains in other filamentous fungi. It has been reported that this technique is useful for developing superior hybrid strains and enhancing the antagonistic activity of *Trichoderma* spp. against various fungal pathogens such as *F. oxysporum*, *M. phaseolina*, *R. solani*, and *S. rolfsii* (Lakhani et al. 2016).

Secondary metabolite production is another way to obtain pathogen-resistant plants using various methods in tissue cultures. SMs, such as alkaloids, phenols, flavonoids, lignins, organic acids, peptides, steroids and derivatives, tannins, terpenes, and vitamins, may be produced using cell culture techniques. These substances may be produced in vitro using a cell and tissue culture technique. Another method used in the production of SMs is elicitor application. Elicitors are stimulants that allow the plant to protect itself by producing antimicrobial substances in case of stress conditions (Narayani and Srivastava 2017). The elicitors that act as signals bind to elicitor-specific receptors on the cell membrane of the plant, and the signal is detected, activating the transduction cascade, inducing the expression of the relevant genes and transcription factors and the synthesis of the SMs (Halder et al. 2019). Oligogalacturonic acids in the plant cell wall stimulate the synthesis of phytoalexin, whereas chitin in the fungus stimulates the synthesis of phenolic compounds (Gadzovska et al. 2015). When elicitors such as SA and methyl jasmonate are used as stimulants, they induce defense against pathogens by stimulating stilbene and gymnemic acid biosynthesis (Chodisetti et al. 2015; Xu et al. 2015). It was determined that phytohormone applications such as abscisic acid, gibberellin, and ET increased the amounts of phenolic compounds (Liang et al. 2013). Tashackori et al. (2018) in their study, in which *P. indica* used the cell wall as an elicitor, found that it caused significant increases in the amounts of cinnamic acid, ferulic acid, SA, myricetin, kaempferol, diosmin, and flavonoids lignins and lignans in *Linum album* cell cultures. Significant increases were detected in the amounts of PAL, anthocyanin, carotenoid, flavonoid, phenolic, and antioxidant capacity in pepper seedlings treated with proline. The increase in the PAL activity induced by proline increased the amounts of flavonoids and anthocyanins, thus increasing the tolerance of pepper against *P. capsici* infection (Koç 2017, 2022). Kumar et al. (2008) have reported that an application of toxins created by different plant pathogens to the cultures produced with cell suspensions, somatic embryos, and organogenic and embryogenic calluses may allow the pathogen-resistant plants to be developed. It has been determined that when compounds belonging to *P. megasperma* are applied to a soybean plant in the cell cultures, they produce a secondary metabolite called glycolide, and similarly, when a compound obtained from the pathogen *P. aphanidermatum* is applied, it produces various SMs such as ajmaline, tabersonine, and catharanthine (Razdan 2003).

4 Conclusion

The biosynthetic mechanisms of SMs, one of the most important defense strategies developed by plants for survival, are regulated by various stress factors. Many studies have shown that abiotic and biotic stresses cause changes in the levels of phenolic compounds, terpenes, alkaloids, flavonoids, antioxidants, osmoregulators, carotenoids, anthocyanins, glucosinolates, and phytohormones in plants. Stress tolerance in plants can be increased by manipulating the biosynthesis and accumulation of SMs. For this, it is important to identify the genes encoding the enzymes of the secondary metabolite pathways, such as the mevalonate (MVA) and methylerythritol phosphate and (MEP) pathways for terpenoids and carotenoids, the shikimic acid and tricarboxylic acid pathways for alkaloids, and the malonic acid and the shikimic acid pathways for phenolics. Another effective option for increasing the production of SMs is elicitor application. Additionally, different strategies can be combined to produce a high amount of desired – targeted – compounds.

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