# Role of Phenolic Metabolites in Salinity Stress Management in Plants

# 16

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## Abstract

Abiotic stress has emerged as a major threat to food security, accounting for the majority of crop and agricultural product losses worldwide. Salinity is one of the primary key variables that inhibit plant growth and productivity among other abiotic stresses. Ionic stress, osmotic stress, and the formation of reactive oxygen species (ROS) are all negative effects of high salt levels in the soil. Detoxification of ROS may play a vital role in improving the salinity stress (SS) tolerance of plants. Plants use their receptors to detect risk and activate a protective native defence system to resist ROS. The accumulation of certain protective secondary metabolites such as phenolic compounds (PCs), terpenes, and alkaloids is one of these defensive mechanisms. PCs, in particular, operate as potent antioxidants and are essential for the plant's survival under salt stress. Enhanced PC synthesis ensures the plants' survival, tenacity, competitiveness, and endurance against SS.

## Keywords

Abiotic stress · Salinity · Phenolics · Oxidative stress · ROS

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## 16.1 Introduction

Stress is defined as any unfavourable condition or substance that negatively impacts plant growth, metabolism, development, or productivity. Plants are subjected to a variety of environmental stresses (both biotic and abiotic), which inhibit their growth and alter the quality and amount of agricultural produce (Basu et al. 2016; Wang et al. 2016a, b; Anjum et al. 2017; Hussain et al. 2018). Abiotic stressors, such as drought, salt, cold, and high temperatures, affect 90% of arable lands, resulting in yield losses of up to 70% in the major food crops (Waqas et al. 2019). Drought is expected to reduce production by 17%, salinity by%, high temperature by 40%, low temperature by 15%, and other factors by 8% (Rehman et al. 2005; Ashraf et al. 2008). According to the estimates based on the combination of climate change and agricultural yield models, important crops such as rice, wheat, and maize will lose productivity even further, posing a serious threat to food security (Tigchelaar et al. 2018).

Salinity is one of the most important abiotic stresses, especially in arid and semiarid environments, where it causes several socio-economic concerns. According to reports, nearly 20% of the world's agricultural land is affected by salt (Martinez et al. 2016; Hussain et al. 2019). By 2050, it is anticipated that 50% of cultivable land will be affected by salinity (FAO 2008). A high concentration of soluble salts containing chlorides (Cl−) and sulphates of sodium ($Na_2SO_4$), calcium ($CaSO_4$), and magnesium ($MgSO_4$) characterises salinity ($MgSO_4$). Among them, sodium chloride (NaCl) is the most pervasive, soluble, and superabundant salt on the planet (Munns and Tester 2008; Fageria et al. 2012). Excess salt causes biochemical, morphological, physiological, and molecular alterations in plants, all of which have a negative impact on productivity and plant growth. SS causes disruption in ion!! homoeostasis and osmotic stress and results in the excess generation of ROS and subsequently oxidative damage (Ivanova et al. 2015; Zhu 2016). Plants have evolved an antioxidant defence mechanism that consists of enzymatic and non-enzymatic components that assist scavenge ROS to decrease the toxic effects of ROS accumulation. Among the enzymatic components, glutathione reductase (GR), peroxidase (POX), catalase (CAT), and superoxide dismutase (SOD) are the most important, while the non-enzymatic components mainly include carotenoids, PCs, and flavonoids (Almeselmani et al. 2006; Rivero et al. 2014). In plants, PCs play an important part in their response to SS (Lopez-Martínez et al. 2020). PCs have a strong ROS scavenging capacity, and their build-up is usually thought to be a beneficial self-protection mechanism in plants when they are exposed to salt-induced oxidative stress (Ahanger et al. 2017; Zhao et al. 2015). Honeysuckle leaf PCs, such as chlorogenic acid, were found to be enhanced as a mechanism for acclimatisation to SS was indicated in several studies (Yan et al. 2017). An increase in hydroxycinnamic acid content was reported in tomato plants exposed to SS (Martinez et al. 2016), although the precise role of PCs in combating oxidative stress during SS is still not clear. Therefore, much information about the protective role of plant PCs associated with the SS has been discussed in this chapter.

## 16.2 Soil Salinity

Soils containing excessive number of water-soluble salts carrying positive charge includes $Mg^{2+}$, $Ca^{2+}$, $K^+$, and $Na^+$ along with negative charge ions such as $CO_3^{2-}$, $HCO^{3-}$, $NO^{3-}$, $SO_4^{2-}$, and $Cl^-$ in the root zones are termed as salt-affected soils (Rhoades and Miyamoto 1990). Soluble salts are present in all soils and natural water, and the amount of salts present in the root zone determines whether the soil is normal or salt-affected. When salt concentrations in the root zone approach critical levels, it has a negative impact on seed germination, plant growth, and yield (Conway 2001; Denise 2003). Highly soluble salts like NaCl, $Na_2SO_4$, $NaHCO_3$, and $MgCl_2$ result in more plant stress when compared to less soluble salts such as $CaCO_3$, $MgSO_4$, and $CaSO_4$. Saline soils can be classified into five major groups based on their salinity levels (Table 16.1). Studies reported that higher NaCl concentrations (200 mM) affected the growth of rapeseed sprouts (Falcinelli et al. 2017). Kaymakanova (2009) also found that germination %, seedlings growth, and respiration rate were decreased in response to NaCl and $Na_2SO_4$ treatment in bean cultivars.

## 16.3 An Overview of Salinity Issues Globally

The land surface of the earth is nearly 13.2 × $10^9$ ha, out of which only 7 × $10^9$ ha is arable. At present, the total cultivated area is 1.5 × $10^9$ ha, out of which 0.34 × $10^9$ ha (23%) is saline and 0.56 × $10^9$ ha (37%) is sodic (Massoud 1981). The salinity problem is dynamic, affecting over 100 countries worldwide; no continent is completely free of salinity (Fig. 16.1). Abrol et al. (1988) reported in FAO soils bulletin 39 for different continents, presenting 932.2 Mha of salt-affected soils in the world (Table 16.2).

The majority of countries affected by salinisation are located in arid and semiarid regions, where poor-quality groundwater is used for agriculture (Massoud 1974; Ponnamperuma 1984). The Aral Sea basin in Central Asia, the Indo-Gangetic basin in India, the Indus basin in Pakistan, the Yellow River basin in China, the Euphrates basin in Syria and Iraq, the Murray-Darling basin in Australia, and the San Joaquin valley in the United States are just a few of the prominent regions where salinisation has been widely reported (Qadir et al. 2014). In Asia, salinity affects around 20% of India's cultivable land, primarily in coastal Gujarat, Rajasthan, and the

**Table 16.1** Classification of saline soils

| Depth of soil | Non-salinity | Weak salinity | Moderate salinity | Strongly salinity | Very strongly salinity |
|---|---|---|---|---|---|
| 0–60 cm (0–2 ft) | 2 dS/m | 2–4 dS/m | 4–8 dS/m | 8–16 dS/m | >16 dS/m |
| 60–120 cm (2–4 ft) | <4 dS/m | 4–8 dS/m | 8–16 dS/m | 16–24 dS/m | >24 dS/m |

*dS* deci-Siemens, pH of saline soil <8.5

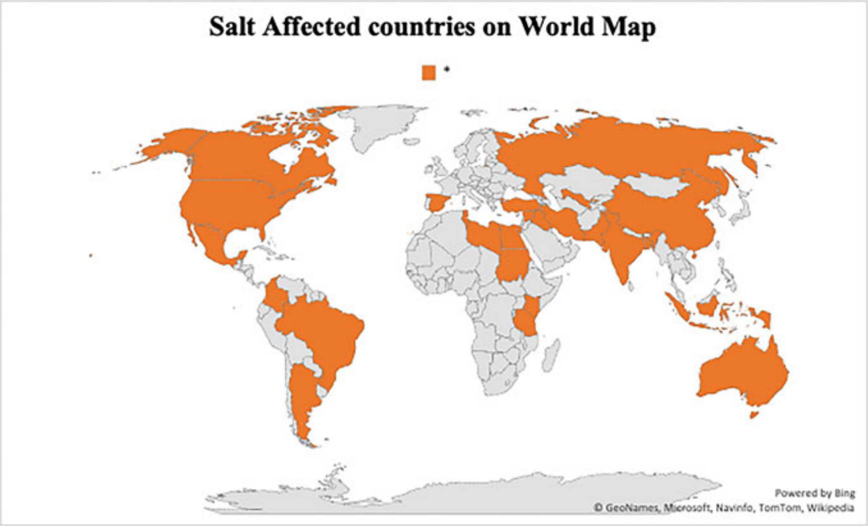


**Fig. 16.1** World map depicting countries with salinity problems (adapted and modified from Pavuluri 2014)

**Table 16.2** Worldwide distribution of salt-affected areas (Mha)

| Area | Sodic soils | Saline soils | Total | Percent |
|---|---|---|---|---|
| Europe | 22.9 | 7.8 | 30.8 | 3.30 |
| Africa | 26.9 | 53.5 | 80.4 | 8.60 |
| America | 69.3 | 77.6 | 146.9 | 15.8 |
| Asia | 121.9 | 194.7 | 316.5 | 33.9 |
| Australasia | 340.0 | 17.6 | 357.6 | 38.4 |
| World | 581.0 | 351.2 | 932.2 | 100 |

Source: Abrol et al. (1988)

Indo-Gangetic plains. According to the ICAR-Central Soil Salinity Research Institute, Karnal database, India has a salinity problem of 6.74 million hectares, with 3.78 million hectares of sodic soils and 2.96 million hectares of saline soils (Mandal et al. 2010). Table 16.3 shows the extent and distribution of salt-affected soils in various Indian states. Gujarat (2.20 Mha) and Uttar Pradesh (1.37 Mha) are the Indian states with the most salt-affected soils.

## 16.4 Causes of Soil Salinity

Because of its negative influence on agricultural production and sustainability, soil salinity is a critical global issue. Salinity issues can occur in any climate and can be caused by both natural and human-induced activities (Flowers 2004; Zaman et al. 2018). Many factors contribute to salinisation, including salt content, soil chemistry, climate, ground topography, and anthropogenic impacts (Blumwald 2000). Also, the

**Table 16.3** Distribution of the salt-affected areas in India

| State | Coastal saline soil (ha) | Alkali soils (ha) | Saline soils (ha) | Total (ha) |
|---|---|---|---|---|
| West Bengal | 441,272 | 0 | 0 | 441,272 |
| Uttar Pradesh | 0 | 1,346,971 | 21,989 | 1,368,960 |
| Tamil Nadu | 13,231 | 354,784 | 0 | 368,015 |
| Rajasthan | 0 | 179,371 | 195,571 | 374,942 |
| Punjab | 0 | 151,717 | 0 | 151,717 |
| Orissa | 147,138 | 0 | 0 | 147,138 |
| Madhya Pradesh | 0 | 139,720 | 0 | 139,720 |
| Maharashtra | 6996 | 422,670 | 177,093 | 606,759 |
| Kerala | 20,000 | 0 | 0 | 20,000 |
| Karnataka | 586 | 148,136 | 1307 | 150,029 |
| J & K* | 0 | 17,500 | 0 | 17,500 |
| Haryana | 0 | 183,399 | 49,157 | 232,556 |
| Gujarat | 462,315 | 541,430 | 1,218,255 | 2,222,000 |
| Bihar | 0 | 105,852 | 47,301 | 153,153 |
| A & N islands | 77,000 | 0 | 0 | 77,000 |
| Andhra Pradesh | 77,598 | 196,609 | 0 | 274,207 |
| Total | 1,246,136 | 3,788,159 | 1,710,673 | 6,744,968 |

Source: Mandal et al. (2010)

intensity of soil salinisation relies on the type and amount of salts, their relative abundance in the soil, degree of solubility, and effect on soil pH (Dheeravathu et al. 2018). Inherent soil salinity (weathering of rocks, parent material); use of poor-quality irrigation water as well as poor drainage; unsustainable irrigation practices (heavy irrigation); high evaporation; previous exposure of land to seawater; and dumping of industrial brine into the soil are just a few of the main causes of salinity (Shrivastava and Rajesh 2015).

## 16.5 Salinity Effects on Plants

Salinity in soil and water is major stress induced by higher levels of salts, particularly high $Na^+$ and Cl. Salt reduces plant growth and productivity at low concentrations, but at higher concentrations, it can inhibit plant growth (Parida and Das 2005). The detrimental effects of SS on the plant are related to low water potential, ion imbalance, nutritional imbalance, and toxicity. They all have negative physiological, biochemical, and molecular effects on plants (Banerjee and Roychoudhury 2018). Ion imbalance is caused by the accumulation of $Na^+$ and $Cl^-$ in tissues/plants exposed to elevated NaCl concentrations, resulting in an altered $Na^+/K^+$ ratio. External $Na^+$ limits the uptake of K+, a critical ingredient for plant growth and development, resulting in lower productivity and even death. Changes in K+ can disrupt osmotic equilibrium, stomatal function, and the operation of certain enzymes (James et al. 2011; Iqbal et al. 2015). Salinity has been shown to increase Na+ and

$Cl^-$ concentrations while decreasing the K+/Na+ ratio in *Vicia faba* in previous studies (Gadallah 1999). Under SS, the mangrove, *Bruguiera parviflora*, showed a significant rise in $Na^+$ and $Cl^-$ content (Parida and Das 2004). Salinity induces the production of ROS such as singlet oxygen ($^1O_2$), hydroxyl radical (•OH), $H_2O_2$ (hydrogen peroxide), and superoxide ($O_2^{\bullet -}$) which are toxic to plant metabolism. Salinity-induced ROS generation interferes with the cellular functions of plants and can cause oxidative damage in various macromolecules such as nucleic acids, proteins, and lipids (Gupta and Huang 2014; Del-Rio 2015). $Na^+$ concentrations above 100 mM are hazardous to cell metabolism, causing critical enzyme inhibition, membrane instability, and osmotic imbalance. SS reduces the quantum efficiency of PSII and Rubisco activity by affecting physiological and metabolic processes such as the photosynthetic pathway, photosynthetic pigments such as chlorophyll, and total carotenoid content. Other physiological functions such as respiration, glycolysis, soluble protein, nitrogen fixation, and disruption of the electron transport system (ETS) in chloroplasts and mitochondria are also affected by SS (Khan et al. 2009; Mittal et al. 2012; Iqbal et al. 2015). Disturbances in photosynthetic ETS due to SS induced the production of ROS into the cells resulting in photoinhibition and photooxidative damages (Gururani et al. 2015). Degradation of chlorophyll in crops like *Thymus* species can also indicate the negative effects of salt (Bistgani et al. 2019). Under high SS, the aminolevulinic acid synthase enzyme, which is the major precursor of chlorophyll production, is altered, resulting in a decrease in chlorophyll concentration (Santos 2004). Growth and metabolism are suppressed by SS, but tolerance limits and growth rate reduction at various toxic salt concentrations vary among plant species (Parida and Das 2005).

## 16.6 Salt Tolerance in Plants

A plant's ability to develop and complete its life cycle in a medium with a high concentration of soluble salts is known as salt tolerance. During the growth season, salt tolerance is usually quantified as the relative yield of a certain crop in salty soil compared to nonsaline circumstances (Munns 2002). Glycophytes are crop species that are extremely sensitive to soil salt and cannot grow at 100 mM NaCl. On the other hand, halophytes are highly tolerant to SS. They are native to saline soils and can grow at 250 mM NaCl (Hernandez and Almansa 2002; Flowers and Colmer 2015; Parida and Das 2005). Plants vary widely in terms of their tolerance to salinity with different growth stages. Barley (*Hordeum vulgare*), for example, is the most tolerant cereal, whereas rice (*Oryza sativa*) is the most sensitive. Plants that are sensitive to salt are divided into four categories: sensitive, moderately sensitive, moderately tolerant, and tolerant (Table 16.4).

Salinity tolerance is a complex feature that results from a combination of physiological, biochemical, and molecular interactions (Tang et al. 2015). Any changes in morphological appearance during SS are not sufficient to identify the effect and consequently design the management approaches (Ahanger et al. 2017). Plants adopt a variety of physiological, biochemical, and molecular mechanisms to deal with SS

**Table 16.4** Classification of some crops based on salt tolerance

| Sensitive | Tolerant | Moderately tolerant | Moderately sensitive |
|---|---|---|---|
| Rice | Barley | Sorghum | Chickpea |
| Sesame | Canola | Soybean | Corn and corn (forage) |
| Black bean | Cotton | Sunflower | Peanut |
| Pigeon pea | Guar | Wheat | Sugarcane |
| Walnut | Oats and forage oats | Barely (forage) | Alfalfa |
| Mango | Rye and forage rye | Guinea grass | Berseem |
| Banana | Triticale | Dhaincha | Cowpea (forage) |
| Apricot | Sugar beet | Rhodes grass | Clover |
| Banana | Asparagus | Pineapple | Lablab bean |
| Blackberry | Date palm | Wild rye | Foxtail millet |
| Carrot | Jojoba | Squash | Sesbania |
| Grapefruit | Salt grass, desert | Olive | Cassava |
| Avocado | Bermuda grass | Coconut | Broccoli |
| Apple | Wheatgrass, tall | Artichoke | Spinach |
| Orange | Natal plum | Safflower | Sweet potato |

to limit toxicity and increase yield (Koyro 2006; Stepien and Johnson 2009). To understand which physiological systems are responsible for plant salinity tolerance, it's necessary to know if the osmotic effect of salt in the soil or the toxic effect of salt within the plant suppresses growth (Munns and Tester 2008). Separation of ions, osmotic adjustment, generation of suitable solutes (proline, glycine betaine), salt exclusion or salt secretions, induction of plant hormones, induction of antioxidant enzymes (SOD, CAT, POX, GR), and accumulation of PCs are some of the biochemical techniques used (Parida and Das 2005; Zheng et al. 2010; Sharma et al. 2019). Few halophytes (*Atriplex*, *Plumbago)* and some mangrove species (*Avicennia and Acanthus*) bear multicellular salt glands which secrete excess salts at leaf surfaces (Hasanuzzaman et al. 2013). Studies on *Brassica napus* cultivars showed increased accumulation of proline during SS (Rezaei et al. 2017). A positive correlation has been noticed between the accumulation of glycine betaine and polyamine in stress tolerance in quinoa varieties (Adolf et al. 2013). Activities of different enzymes such as ascorbate peroxidase (APX), POX, CAT, and glutathione S-transferase (GST) are upregulated in response to SS in *Chenopodium quinoa* (Causin et al. 2020).

Changes in the plant transcriptome, metabolome, and proteome are among the molecular processes of salt tolerance (Banerjee and Roychoudhury 2018). Different families of transcriptional factors, such as activator protein (AP2), basic leucine zipper (bZIP), ERF, MYB, and WRKY, all show strong relationships with SS (Kumar et al. 2017). Several studies noted that different transcriptional factors induce the overexpression of many genes in response to SS. Enhanced expression of *GmDREB2*, *MtCBF4* in *Arabidopsis thaliana* (Chen et al. 2007), bZIP gene in *Tamarix hispida* (Wang et al. 2010) provides tolerance against SS.

## 16.7 PC Accumulation Under SS

PCs are a diverse group of plant secondary metabolites. PC and its derivatives including anthocyanins, coumarins, isoflavonoids, flavonoids, tannins, and lignins play pivotal roles throughout the life cycle of the plant (Tomar and Agarwal 2013). PCs are aromatic molecules with one or more hydroxyl groups that come from diverse developmental phases and environmental influences, such as shikimate and phenylpropanoid (PP) pathways (Tomar et al. 2015; Patra et al. 2013). Plants rely on PCs for growth, development, and reproduction. They act as defence compounds against abiotic and biotic stresses (Lattanzio 2013). During abiotic stress conditions, the biosynthesis of most PCs such as phenolic acids, flavonoids, lignin, and tannins increases, which helps the plant cope with environmental constraints. Under abiotic stress conditions (drought, heavy metals, salt, high/low temperature, and ultraviolet radiations), the PP biosynthetic pathway is activated, resulting in the accumulation of different PCs that can alleviate oxidative stress and scavenge damaging ROS (Rossi et al. 2016; Borges et al. 2017). Plants under SS vary in composition and PC content, which is both genetically and environmentally controlled (Awika and Rooney 2004). A literature survey reported the increase in PCs in different plant tissues during SS (Table 16.5). The higher PC contents and antioxidant activities were noticed in *Salvia mirzayanii* and red pepper plants in response to SS (Navarro et al. 2006; Valifard et al. 2014). Environmental factors have an impact on PC biosynthetic pathways, as their regulation and gene expression are altered in response to various stresses. In the case of SS, the altered activity of various key enzymes in the shikimate and PP pathways governs PC production (Lattanzio 2013; Martinez et al. 2016; Sanchita 2018). A detailed discussion on how plants manage SS through the accumulation of PCs is discussed in the following section.

## 16.8 Mechanism of Action of PCs in Salinity Stress Management

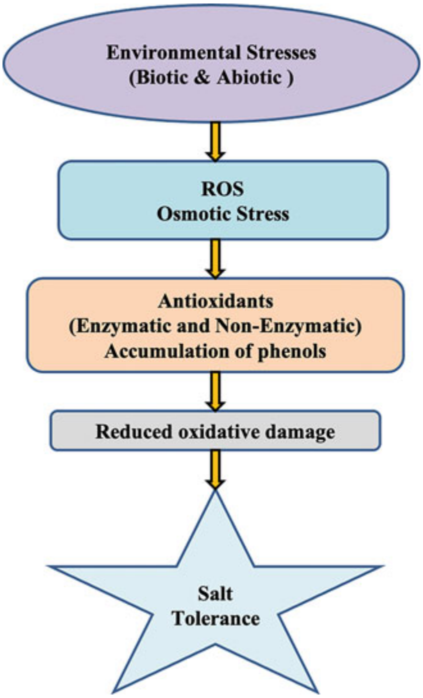
SS causes the production of ROS like $H_2O_2$, $O_2^{\bullet-}$, and •OH and requires a strong antioxidant system to combat the ROS propagation (Taibi et al. 2016). During SS, PCs act as powerful antioxidants and participate in plant protection against ROS (Bistgani et al. 2019) (Fig. 16.2).

PCs displayed an antioxidant activity by preventing the breakdown of hydroperoxides into free radicals or by deactivating the free radicals (Valifard et al. 2014). Furthermore, the changed activities of numerous important enzymes in PC biosynthetic pathways govern PC production in response to SS (Rossi et al. 2016). Upregulation of enzymes is followed by increased transcript levels of genes encoding important biosynthetic enzymes such as F3RT (flavonoid 3-O-rhamnosyltransferase), F3GT (flavonoid 3-O-glucosyltransferase), FLS (flavanol synthase), F3′H (flavonoid-3′-hydroxylase), F3H (flavanone3-hydroxylase), CHI (chalcone isomerase), CHS (chalcone synthase), C3H (cinnamate 4-hydroxylase), 4CL (4-coumarate coenzyme A ligase), C4H (cinnamate 4-hydroxylase), PAL (phenylalanine-ammonia lyase), SK (shikimate kinase), SDH (shikimate

**Table 16.5** Phenolic compounds in salinity stress management

| Plant/crop | Response of endogenous phenolics during salinity stress | References |
|---|---|---|
| *Hypericum pruinatum* | Increase of PCs, namely, chlorogenic acid, rutin, quercitrin, isoquercitrin, and hyperoside | Caliskan et al. (2017) |
| *Salvia mirzayani* | Accumulation of PCs and antioxidant activity | Valifard et al. 2014) |
| Rice (*Oryza sativa L.*) | Cell wall-bound PC ferulic acid and 4-hydroxycinnamic acid were increased | Gupta and De (2017) |
| *Thymus vulgaris* L. | Increase of PC content and radical scavenging activity | Bistgani et al. (2019) |
| Honeysuckle (*Lonicera japonica* Thunb.) | Increased production of chlorogenic acid and luteolosid | Yan et al. (2017) |
| Artichoke (*Cynara scolymus* L.) | Caffeic and chlorogenic acid accumulation increased | Rezazadeh et al. (2012) |
| *Amaranthus tricolor* | Gallic acid, vanillic acid, ferulic acid, isoquercitrin content increased | Sarker and Oba (2018) |
| *Asparagus aethiopicus* | Increased chlorogenic acid, caffeic acid, and rutin content | Al-Ghamdi and Elansary (2018) |
| *Carthamus tinctorius* | Total PC and flavonoid content increased | Wang et al. (2016a, b) |
| *Chenopodium quinoa* | Total PC and flavonoid content increased | Aloisi et al. (2016) |
| *Cynara cardunculus* | Increased gallocatechin, quercitrin, and leucocyanidin content | Lucini et al. (2016) |
| *Hordeum vulgare* | Increased total phenolic content | Ma et al. (2019) |
| *Mentha piperita* | Increased total phenolic content | Coban and GokturkBaydar (2016) |
| *Ocimum bascilicum* | Increased caffeic acids, cinnamyl malic acid, and quercetin | Scagel et al. (2019) |
| *Olea europaea* | Total phenolics, kaempferol, and quercetin | Rossi et al. (2016) |
| *Salvia mirzayanii* | Increased total phenolic content | Valifard et al. (2014) |
| *Solanum lycopersicon* | Increased total caffeoylquinic acid content | Martinez et al. (2016) |
| *Solanum villosum* | Increased caffeic acid, total phenolic, and quercetin | Ben-Abdallah et al. (2019) |
| White cabbage (*Brassica oleracea* var. capitata) | Increased hydroxycinnamic acids | Linic et al. (2019) |
| Rapeseed (*Brassica napus* var. oleifera) | Increase in contents of PCs | Falcinelli et al. (2017) |
| *Achillea fragrantissima* | Increase in contents of PCs | Abd El-Azim and Ahmed (2009) |

**Fig. 16.2** Flow chart indicating phenolic salinity stress tolerance mechanisms



dehydrogenase), and DAHPS (3-deoxy-D-arabino-heptulosonate) (Fig. 16.3). The enzyme DAHPS is highly upregulated under all stresses including salinity and is a key determinant governing the carbon flow into the shikimate pathway (Zhang et al. 2015). The other enzymes SHD and SK of shikimate pathway as well as the expression level of their transcripts were also upregulated. L-phenylalanine, an essential amino acid for the formation of hydroxycinnamic acids, is produced by the shikimate pathway. The amino acid L-phenylalanine is generated higher during SS (Hoque et al. 2020). This is also in agreement with the levels of L-phenylalanine produce several folds higher than in control in tomato plants under SS (Martinez et al. 2016). Following the shikimate pathway, L-phenylalanine is transformed into cinnamic acid, which leads to the creation of other phenolic compounds (Fig. 16.3, PP pathway). Several key enzymes, such as PAL, C4H, and 4CL, participate in the synthesis of cinnamic acid, p-coumaric acid, and p-coumaryl-CoA from L-phenylalanine (Besseau et al. 2007; Ferrer et al. 2008). The major enzyme in the PP pathway, PAL, transforms phenylalanine to cinnamic acid and is significantly upregulated in response to a variety of environmental stressors. In olive trees, the number of PAL and their transcripts increases in response to SS, according to studies (Rossi et al. 2016). Under SS, the expression levels of several enzymes such as PAL, C4H, and 4CL were many times greater and were also strongly linked with the concentrations of various substances such as cinnamic acid, p-coumaric acid, and p-coumaryl-CoA (Martinez et al. 2016). p-Coumaryl-CoA produced in PP pathway is

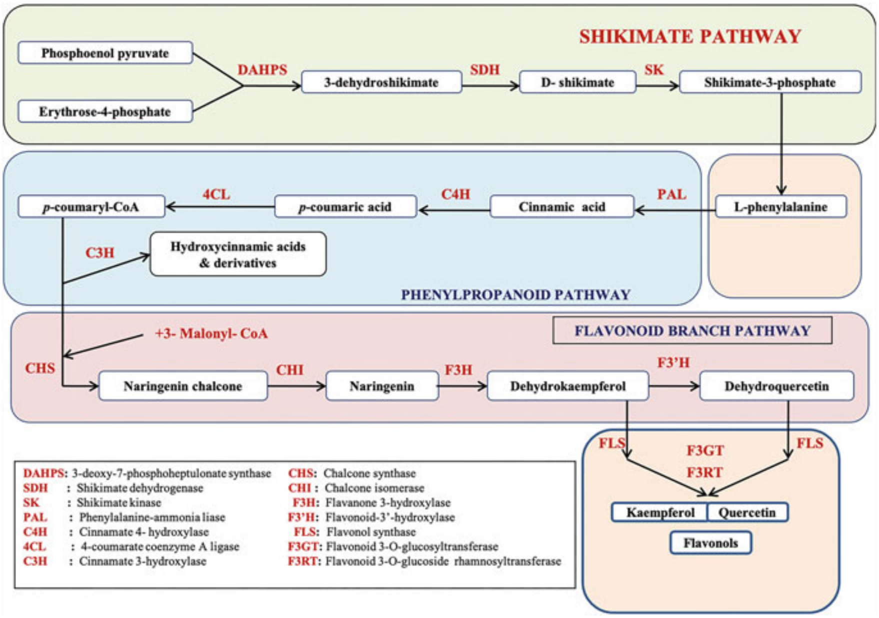


**Fig. 16.3** Schematic representation of the regulation of phenol metabolism in response to salinity stress (adapted and modified from Martinez et al. 2016)

used as a substrate for the synthesis of hydroxycinnamic acids or flavonols (flavonol-branched pathway). With the help of the enzyme C3H, p-coumaryl-CoA is transformed into hydroxycinnamic acids and derivatives (Ferrer et al. 2008). SS induces the upregulation of enzyme C3H and resulted in overaccumulation of hydroxycinnamic acids and derivatives. The major factor for flavonoid production is chalcone synthase (CHS). This enzyme CHS catalyses the conversion of p-coumaryl-CoA and three molecules of malonyl-CoA into naringenin chalcone, starting the flavonoid production process (Fig. 16.3, Flavonoid branch pathway). From naringenin chalcone, production of other compounds like naringenin, flavonols, and other derivatives is regulated by different enzymes like CHI, F3H, FLS, F3GT, and F3RT, respectively. Studies reported that higher amounts of PCs like quercetin, caffeic, ferulic, and apigenin are accumulated in response to salinity stress in *Thymus* species (Bistgani et al. 2019). Salicylic acid plays a function in increasing salinity tolerance mechanisms in a variety of crops, including *Vicia faba*, *Brassica juncea*, *Medicago sativa*, and *V. radiata* (Jini and Joseph 2017; Khan et al. 2015).

## 16.9 Conclusion and Future Prospective

Salinity has become a major environmental issue that has a negative impact on plant growth and development. Because SS impacts plant cellular activity, agricultural output suffers and the farmer loses money. A recent salt stress study has shown that PCs such as phenols, polyphenols, flavonoids, anthocyanin, and phenolic acids increase plant tolerance. PCs protect plants from salt stress in a variety of ways, including reactive oxygen species detoxification, physiological and metabolic process regulation, and cell integrity maintenance. Aside from the vast amount of information available on PCs, more study is needed to determine the involvement of specialised PCs in response to salinity stress and to define the intimal molecular process that switches from primary metabolism to activation of the PP pathway in response to SS.

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