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Plant Phenolics in Sustainable Agriculture

Volume 1

 Springer



Plant Phenolics Under Water-Deficit Conditions: Biosynthesis, Accumulation, and Physiological Roles in Water Stress Alleviation

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Abstract

Phenolic compounds play important role as a structural component of secondary cell wall and non-enzymatic antioxidant system of the plants. The encounter to the drought stress conditions bring about the imbalance in the rate of ROS (reactive oxygen species) production and their quenching by antioxidant machinery of plants which puts plant under oxidative stress. The plant phenolics specially flavonoids play important role in neutralizing these harmful ROS and protect the plant from oxidative damage of ROS. Further, the controlled imposition of drought stress to plants is successfully used as a strategy to enhance the content of the bioactive compounds and phenylpropanoids in economically important food and medicinal plants. In this chapter we present the overview of phenylpropanoids biosynthesis and also present a brief account of the protective roles of phenolics specially flavonoids in drought stress alleviation. A concise description of the molecular interventions attempted so far, to regulate the synthesis of phenylpropanoids in different plants, is also presented.

Keywords

Phenylpropanoids · ROS (reactive oxygen species) · Flavonoids · PAL (phenylalanine ammonia-lyase) · Chalcone synthase · Drought stress

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R. Lone et al. (eds.), *Plant Phenolics in Sustainable Agriculture*,
https://doi.org/10.1007/978-981-15-4890-1_19

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19.1 Introduction

Plants synthesize several thousand phenol derivatives collectively referred to as plant phenolics. The common structural feature of the diverse plant phenolics is the presence of hydroxy-substituted benzene ring within their chemical structure. In fact, the expression “plant phenolics” encompasses a highly diverse group with enormous structural diversity that includes multitudes of plant secondary metabolites like flavonoids, stilbenes, tannins, and many cell wall components like lignin, lignans, suberin, and cutins. Due to their vast structural diversity and their very broad range of physiological functions as cell wall structural component and as secondary metabolites, the straightforward definition of plant phenolics becomes evasive. However, Quideau et al. have suggested the use of the term “plant phenolics” strictly for secondary natural metabolites synthesized via shikimate/phenylpropanoid pathway, forming phenylpropanoids or the “polyketide” acetate/malonate pathway, which can produce simple phenols, or both of them (Quideau et al. 2011).

The polyphenols are known to play diverse roles in all the plant forms including primitive forms as bryophytes to most advanced angiosperms. In fact, phenolic compounds do not play a direct role in primary photosynthetic or respiratory metabolism of plants but still have an important role in plant survival. The diverse physiological roles played by the plant phenolic compounds include their role as fungicides (stilbenes), natural pesticides (tannins), signaling molecules for establishing symbiotic associations, attracting the pollinators, cell wall constituent (lignin), and forming impermeable layers of the cell wall (suberin and cutin). Moreover, the flavonoids like chalcones, flavones, and flavonols are known to absorb UV light and have been reported to act as UV photo screens (Hertweck 2009). In addition to their important role for the survival of plants, the plant phenolics act as bioactive compounds having great human health benefits and better nutraceutical properties. The occurrence of the low-molecular-weight plant phenolics is universal in higher plants; however, some of them are species-specific phenolics and thus are of great taxonomic relevance and also exploited as plant species/family-specific biomarkers (Ishimaru et al. 1987; Veit et al. 1995; Almaraz-Abarca et al. 2006; Kharazian 2014; Ávila-Reyes et al. 2018).

The production of the phenolic compounds by plants is often affected by the external environmental conditions like exposure to UV light, an encounter with a pathogen, wounding, the growth conditions like moisture status of the soil, soil pH and salinity, and many other biotic and abiotic factors. A great deal of information has been generated about the effect of the water stress on primary metabolism (photosynthesis and respiration), but the information regarding flavonoid metabolism in response to drought stress remains fragmented. In this chapter, we discuss various aspects of phenolics biosynthesis under water stress condition. We here also present the description of the physiological role played by plant phenolics in drought stress alleviation.

19.2 Biosynthesis of Plant Phenolics: An Overview

Biosynthesis of the plant phenolics takes place through the extension of the shikimate pathway. The synthesis of plant phenolic compounds (phenylpropanoids) does take place either through the shikimate/chorismate pathway or malonate pathway or involving both of them (Knaggs 2001). The aromatic terpenoids are also synthesized by acetate/mevalonate pathway (Bhattacharya et al. 2010), but it will not be dealt with in this description. The phenylalanine, an aromatic amino acid, synthesized in the shikimic acid pathway, is the common precursor of all phenylpropanoid compounds. The aromatic amino acid phenylalanine synthesized through the shikimic acid pathway is deaminated to cinnamic acid by the action of the phenylalanine ammonia-lyase (PAL). This step catalyzed by the phenylalanine ammonia-lyase (PAL) is the committed step in the phenylpropanoid biosynthesis pathway. The PAL is the most intensively studied enzyme of the plant secondary metabolism. Subsequently, the hydroxylation (introduction of the hydroxyl group at carbon 4) of the phenyl ring of the cinnamic acid is catalyzed by P₄₅₀-monooxygenase to generate p-coumaric acid. The p-coumaric acid further undergoes hydroxylation and methylation of the newly added hydroxyl group at positions 3 and 5 by the sequential enzymatic action of the P₄₅₀-monooxygenase (hydroxylation) and O-methyl transferases (methylation) to generate the ferulic acid and sinapic acid.

The carboxyl groups of the p-coumaric acid, ferulic acid, and sinapic acid are reduced to their corresponding alcohol forms in a multistep conversion to generate the alcohol, namely, p-coumarin alcohol, coniferyl alcohol, and the sinapyl alcohol, respectively. These alcohol forms are collectively known as monolignols. This conversion basically involves the activation of the COOH group of p-coumaric acid, ferulic acid, and sinapic acid by the corresponding *hydroxycinnamate: CoA ligase* at the expense of CoASH and ATP resulting in the formation of thioester to produce p-coumaroyl-CoA, coniferyl-CoA acid, and sinapyl-CoA, respectively.

The thioester p-coumaroyl-CoA serves as a branch point from which other metabolic pathways in the phenylpropanoid, network diverge (Vogt 2010). At this branch point, the generated thioester can either be used by a lignin-specific branch of the phenylpropanoid pathway forming p-coumaryl, coniferyl, and sinapyl alcohol or else may be diverted to the flavonoid biosynthesis through malonate pathway (Fig. 19.1).

For lignin biosynthesis, the generated thioesters are further reduced to the corresponding alcohol by the sequential action of NADP oxidoreductase and the corresponding dehydrogenase where two molecules of NADPH⁺ + H⁺ are used to produce corresponding alcohols. The coumaryl alcohol, coniferyl alcohol, and sinapyl alcohol are commonly referred to as “monolignols.” The monolignols are essential building block for the subsequent synthesis of the structural phenylpropanoids like lignin, lignan, suberin, and cutin.

The lignans are the dimerization product of monolignols. The monolignols can undergo dimerization supposed to be mediated through the formation of free radicals resulting in the formation of lignans. The lignans mainly involve the formation of the linkage either through their side chains (e.g., as in pinosresinol) or the linkage

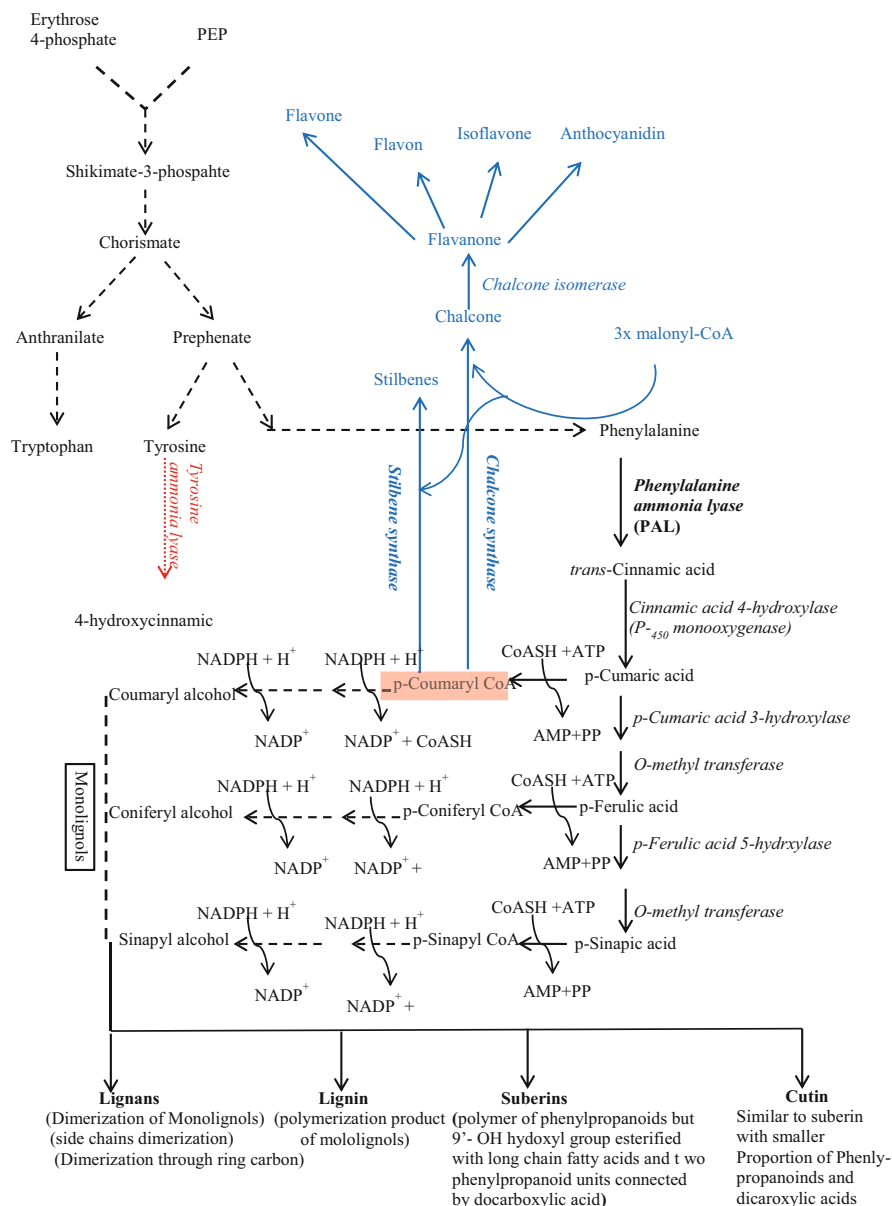


Fig. 19.1 An overview of the biosynthesis of phenylpropanoids in plants. The lignin-specific branch of phenyl propanoids diverge at p-coumaryl-CoA (highlighted in enclosed red color box), while the flavonoid branch is shown with blue color arrows and labels. The dotted arrow indicates that the actual biosynthetic steps are summed up, and only key steps are shown for establishing the context. The details of these steps are omitted for sake of presenting precise overview:

involving phenyl ring carbons (e.g., as in malagnol). Unlike lignans which are the product of dimerization of monolignol units, the lignin is the polymerization product of monolignols where polymerization is supposedly mediated by laccases and peroxidases, resulting in the formation of lignin. Lignin is the second most abundant plant polymer after cellulose. Hence, 40% of the total flux of organic compounds circulating in the biosphere is being channeled through phenylpropanoid biosynthesis (Zhang and Liu 2015). In suberins, monolignols are connected in a manner similar to lignin, but the 9'-OH group is esterified with long-chain fatty acids, and two phenylpropanoid units are also connected by dicarboxylic acids forming ester linkage.

Flavonoids, which include a vast array of low-weight phenolics, are synthesized through the malonate pathway. The p-Coumaroyl-CoA, (a thioester of coumaric acid) and three molecules of malonyl-CoA are used to form a molecule of chalcone (contain two phenyl rings) by the enzymatic action of the chalcone synthase (Verweridis et al. 2007). Chalcone synthase has low catalytic activity and hence plant cells produce a higher quantity of the chalcone synthase. Chalcone is acted upon by chalcone isomerase to form flavanone which serves as the precursor of so many flavonoids (refer Fig. 19.1). Some plants like peanut and grapevine have another enzyme stilbene synthase which also uses p-Coumaroyl-CoA and three molecules of malonyl-CoA to form stilbenes. Some stilbenes like resveratrol and vinifera are known to have very strong antifungal activity and thus play an important role in plant protection (Lee and Lee 2015; Gabaston et al. 2017).

19.3 Phenylpropanoids and Their Role in Water Stress Alleviation

Water stress is one of the most significant abiotic stresses that affect the many physiological and biochemical processes of plants and phenylpropanoid metabolism is no exception to this. Under water stress conditions, there is increased in the production of reactive oxygen species (ROS) like superoxide anion O_2^- , hydrogen peroxide H_2O_2 , singlet oxygen O , and hydroxyl radical OH (Zhang and Kirkham 1994). These reactive oxygen species may cause lipid peroxidation, membrane damage, protein degradation, breakage of DNA, and cell mortality, if not taken care by the antioxidant system of plants (Shao et al. 2008). The detoxification of ROS in plants is mediated by enzymatic and non-enzymatic antioxidant system. The enzymatic antioxidant system includes the action of many enzymes like *superoxide dismutase* (SOD), *ascorbate peroxidase* (APX), *catalase* (CAT), and *peroxidase* (POD) to neutralize the deleterious effect of the ROS. The non-enzymatic antioxidant includes the vitamin C, tocopherols, carotenoids, glutathione, and phenol derivatives (Ashraf et al. 2019). The enhanced production of phenolics (a prominent component of non-enzymatic antioxidant system of plants) under water-deficit condition is obvious physiological demand of the plant under water stress exposure.

The overproduction of the ROS (reactive oxygen species) under water stress is counterbalanced by the induction of phenylpropanoid pathway resulting in increased flavonoid biosynthesis and other phenolics. For instance, the increased accumulation of flavonoids under drought stress conditions has been reported in willow leaves (Akula and Ravishankar 2011) and *Arabidopsis* (Nakabayashi et al. 2014). The Nakabayashi and coworkers measured the anthocyanin and flavonol levels in *Arabidopsis* plants at intermittent intervals of 2 days under imposed drought stress conditions and noticed the increase in the content of anthocyanin and flavonol in response to drought. In particular, anthocyanins A5, A8, A9, A10, and A11 and flavonols F6 and F8 were first to accumulate under water-deficit conditions, while flavonols F1, F2, and F3 accumulated later stage of drought (Nakabayashi et al. 2014). Plant tissues containing a higher accumulation of phenolics like anthocyanins exhibit better desiccation tolerance.

The changes in the accumulation of a higher amount of phenolics under water-deficit conditions are often brought about by the altered activity of enzymes of the phenylpropanoid biosynthesis pathway or increased de novo synthesis of these enzymes. The concentration of flavonoids in plant cell often exceeds 1 mM and may even reach up to 10 mM under water stress in some specialized cells (Larson 1988). Phenylalanine ammonia-lyase (PAL) is the gateway enzyme of phenylpropanoid biosynthesis which diverts the central flux of carbon from the primary metabolism to the synthesis of a vast array of phenolics like lignin, anthocyanin and flavonoids, pigments, and phytoalexins. PAL is also used as a biochemical marker whose overexpression indicates the onset of plant antioxidant defense mechanism in response to biotic and abiotic stresses. PAL activity does exist in all the higher plants, and in some fungi and a few bacteria, but have not been reported in animals (Xiang and Moore 2005). PAL activity may be regulated by feedback inhibition by its own product, cinnamic acid, which may also modify the expression of the PAL gene (Boudet 2007). Hence, any change in the enzymatic activity of PAL or the change in expression of genes encoding PAL (de novo synthesis of PAL) leads to the changes in phenolic content of the plant. In fact, there is an ample number of reports describing the multilevel regulation of PAL including change in enzymatic activity of PAL, altered gene expression, de novo synthesis, and post-translational modifications in response to certain external environmental variable. The increased activity of PAL under water stress conditions and consequent increased production of phenolic compounds like ferulic acid has been shown in the leaves of maize (Hura et al. 2008) and fruit of the capsicum (Phimchan et al. 2014). However, there are contrary reports also which have shown the marked decrease in the activity of the PAL in response to the water-deficit condition in maize (Bardzik et al. 1971).

The increased expression of another important enzyme of flavonoid biosynthesis pathway, chalcone synthase, has also been reported in *Arabidopsis* under water stress conditions (Nakabayashi et al. 2014). In fact, chalcone synthase (CHS), chalcone isomerase (CHI), and flavanone 3-hydroxylase (F3H) are the three key enzymes of flavonoids biosynthesis. Chalcone synthase acts on the CoA-ester of cinnamic acid and uses three molecules of malonyl-CoA to form chalcone. Chalcone

is further isomerized to flavanone by the enzyme chalcone flavanone isomerase (CHI). This flavanone is the precursor for the synthesis of a myriad of flavonoid compounds. The increased expression of the chalcone synthase under water-deficit conditions confirms its role in water stress alleviation. The proteomic studies have also shown the changes in the flavonoid biosynthesis enzymes, namely, chalcone isomerase (CHI) and dihydroflavonol-4-reductase in response to drought stress conditions. The synthesis of dihydroflavonol-4-reductase, an important enzyme of flavonoid biosynthesis pathway, has been reported to decrease in drought-sensitive *Z. mays* cultivar but was higher in the tolerant genotype of the *Z. mays* (Benesova et al. 2012). Pandey and coworker reported a decrease in levels of CHI (chalcone isomerase), a key enzyme of flavonoid biosynthesis in *O. sativa* under drought stress conditions (Pandey et al. 2010). The changes in the enzyme activity/gene expression/de novo synthesis of key enzymes of phenylpropanoid biosynthesis in drought stress response have been summarized in Table 19.1.

19.4 Controlled Drought Stress for Enhancing Antioxidant Potential of Food and Medicinal Plants

The food substances rich in flavonoids and phenolic content are considered as nutraceuticals. Such antioxidants-rich foods impart the protection against many serious human ailments like arthritis, emphysema, retinopathy, neurodegenerative cardiovascular diseases, atherosclerosis, cataracts, and even cancer (Repo-Carrasco-Valencia et al. 2010). The food items with a high content of flavonoids are regarded as functional foods. The deliberate controlled imposition of the water stress has been shown to enhance the overall content of the bioactive compounds in medicinal plants (Kleinwachter and Selmar 2014). The accumulation of the higher amount of plant phenolics under water stress conditions in fruits, vegetable, and even cereals crops is widely reported (Gharibi et al. 2016; Siracusa et al. 2017). The natural drought stress-tolerant plants accumulate a good amount of antioxidants including flavonoids and other phenolics. For instance, the leafy vegetables like *Amaranthus tricolor* are well acclimated to drought stress and hence accumulate good amount of flavonoids (Sarker and Oba 2018). The higher metabolic plasticity and increased accumulation of flavonoids in the leaves has been attributed to the capability of plants like *Moringa oleifera* to establish in xeric and water-scarce environments (Brunetti et al. 2018b). Even the drought-sensitive plants grown under the arid or semiarid conditions often accumulate a higher amount of the flavonoids and other phenols compared to the same plants grown under moderate conditions. The phenolic compounds play an important role as an antioxidant system for neutralizing the deleterious effect of the ROS produced under water stress conditions.

As a primary physiological response to the drought stress conditions, plants tend to partially close their stomata to reduce the water losses through transpiration. As a consequence of this, the CO₂ uptake and fixation through Calvin cycle also decreases in the leaves. The NADPH⁺+H⁺ produced during the light reaction of the photosynthesis starts accumulating making the internal environment of the plant

Table 19.1 The effect of the drought stress on the enzymatic activity/gene expression/de novo synthesis of the key enzymes of phenylpropanoid biosynthesis pathway in different crops

S. No.	Type of function studied	Crop/plant	Plant part assayed	Salient finding	Reference
1	PAL enzymatic activity	<i>Olea europaea</i> L (olive)	Fruit	PAL activity increased with water deficit	Tovar et al. (2002)
2	PAL enzymatic activity	<i>Zea mays</i> (maize)	Leaf	PAL activity increased with deficit irrigation and correlated well with ferulic acid content	Hura et al. (2008)
3	PAL enzymatic activity	<i>Trifolium repens</i> (white clover)	Leaf	PAL activity increased with drought	Lee et al. (2007)
4	PAL enzymatic activity	<i>Triticum aestivum</i> (wheat)	Seedling	PAL activity increased with water deficit	Tian and Lei (2006)
5	PAL enzymatic activity	<i>Labisia pumila</i> (kacip fatimah)	Leaf	PAL activity increased with water deficit	Jaafar et al. (2012)
6	PAL enzymatic activity	<i>Capsicum annum</i> (Capsicum)	Fruit	PAL activity increased with water deficit	Phimchan et al. (2014)
7	^a PAL enzymatic activity	<i>Zea mays</i> (maize)	Leaf	10% to 20% water deficit resulted in decreased activity of PAL	Bardzik et al. (1971)
8	PAL enzymatic activity	<i>Zea mays</i> (maize)	Leaf and root	The PAL activity sharply increased in leaves during drought stress but remained constant in root	Gholizadeh (2011),
9	PAL gene expression (<i>pal</i> gene)	<i>Betula pendula</i> (birch)	Leaf	Drought stress induced PAL gene expression	Paakkonen et al. (1998)
10	Chalcone synthase (<i>chs</i>) gene expression	<i>Achillea pачycephala</i>	Leaf	The CHS gene expression increased with drought stress	Gharibi et al. (2019)
11	Chalcone synthase gene expression (<i>chs</i> gene)	<i>Triticum aestivum</i> (wheat)	Leaf	The <i>chs</i> gene expression increased under water stress	Ma et al. (2014)

(continued)

Table 19.1 (continued)

S. No.	Type of function studied	Crop/plant	Plant part assayed	Salient finding	Reference
12	Chalcone isomerase (<i>chi</i>) expression	<i>Chrysanthemum morifolium</i>	Leaf	The <i>chi</i> gene expression increased under water stress	Hodaiei et al. (2018)
13	Flavanone 3-hydroxylase <i>f3h</i> gene expression	<i>Chrysanthemum morifolium</i>	Leaf	The <i>f3h</i> gene expression increased under water stress	Hodaiei et al. (2018)
14	Flavanone 3-hydroxylase <i>f3h</i> gene expression	<i>Vitis vinifera</i>	Berry skin	The <i>f3h</i> gene expression increased under water stress	Castellarin et al. (2007)
15	Dihydroflavonol 4-reductase (<i>DFR</i>) gene expression	<i>Vitis vinifera</i>	Berry skin	<i>DFR</i> gene was upregulated under early season water deficit	Castellarin et al. (2007)
16	Flavonol synthase (<i>FLS</i>) gene expression	<i>Triticum aestivum</i> (wheat)	Leaf	<i>fls</i> gene expression increased under drought stress	Ma et al. (2014)
17	Flavone synthase (<i>FNS</i>) gene expression	<i>Triticum aestivum</i> (wheat)	Leaf	<i>fns</i> gene upregulated post drought stress	Ma et al. (2014)
18	Anthocyanidin synthase (<i>ANS</i>) gene expression	<i>Triticum aestivum</i> (wheat)	Leaf	Higher expression level of <i>ans</i> gene under drought stress conditions	Ma et al. (2014)

^aIndicates unexpected trend

cell highly reducing. As a consequence of reduced uptake of CO₂ and elevated concentrations of NADPH+H⁺ in leaves, the metabolic processes are pushed toward the synthesis of highly reduced compounds, like isoprenoids, phenols, or alkaloids (Selmar and Kleinwächter 2013). However, there exist few contradictory reports also which suggest the reduced level of phenolic compounds like caffeic acid, *p*-coumaric acid, and ferulic acid during water stress in grapevine (Król et al. 2014). Nonetheless, the increased accumulation of antioxidant has been reported in many crops including wheat (Keleş and Öncel 2002), *Lavender* (Munné-Bosch et al. 2001), *Ligustrum vulgare* (Tattini et al. 2004).

However, the application of drought stress for enhancing the antioxidants and phytochemicals is not without risk. The application of the deliberate water stress, its intensity, frequency, and intervals is crucial to attaining the desired level of accumulation of bioactive compounds. In lettuce (*Lactuca sativa*), the exposure of plants to

multiple water stress resulted in a significant reduction in shoot growth, whereas mild stress imposed before harvest resulted in an enhanced concentration of phytochemical (Oh et al. 2010).

In real field conditions, drought stress is often accompanied by higher temperatures. The increased accumulation of the bioactive compounds and plant phenolics under heat conditions has also been reported in major cereal grains. For instance, Shewry et al. (2010) evaluated 26 wheat cultivars by growing them at 6 different locations spread across Hungary, France, Poland, and the UK for 2 years and found that the phytochemicals like stanols, alkylresorcinols, and bound phenolic acids had strong positive correlations with the mean temperature between heading and harvest. The whole-wheat grain does contain significant amounts of antioxidants like carotenoids and polyphenols that can effectively scavenge many free radicals formed during various metabolic reactions. Particularly the polyphenols of the wheat have hydroxyl groups linked to the aromatic rings that can react and stabilize free radicals. The effect of environmental conditions is generally more pronounced on the soluble fraction of phenolic compounds compared to bound forms of polyphenols in wheat grain (Di Silvestro et al. 2017). In addition to the wheat, barley is also considered a good source of bioactive phenols. Martinez et al. evaluated 27 barley genotypes (*Hordeum vulgare* L.) under two different environmental regimes in the Czech Republic and Spain and reported the good amount of tocopherols (ranging between 39.9 and 81.6 $\mu\text{g/g}$) in barley (Martinez et al. 2017). Phytochemicals present in barley are categorized into several major classes, like polyphenols, flavonoids, phytosterols, lignans, tocols, and folates. Authors identified 64 bioactive compounds in the barley that included 19 phenolic acids and aldehydes, 9 flavan 3-ols, 9 flavone glycosides, and 27 anthocyanins indicating barley as the good source of antioxidants.

19.5 Trickling Phenylpropanoids Biosynthesis Pathway for Enhancing Drought Stress Tolerance

In the past decade, there is a growing demand for the food rich in flavonoids and other antioxidants. This has attracted the attention of the researcher to increase the flavonoid content in the food item. Further, the increased production of the non-enzymatic antioxidants particularly flavonoids is also seen as the pragmatic strategy to combat the deleterious effects of water stress on plant growth and development. Earlier, structural and regulatory genes of the maize were transferred into rice, which resulted in the increased expression of the genes of the anthocyanin pathway (Gandikota et al. 2001).

Due to the fine understanding of the biochemical pathways of phenylpropanoid metabolism, the efforts are on to trickle this pathway at the molecular level for enhanced production of flavonoids. The transgenic modifications targeted at phenylpropanoid biosynthesis are likely to be the most direct way of enhancing flavonoid biosynthesis. The scientific study across diverse systems reflects the role of transcription factors in the regulation of flavonoid biosynthesis. The transcription

factors often regulate the gene expression of multiple genes and hence targeted for transgenic research. For instance, Naing and coworkers recently reported the enhanced drought stress tolerance in transgenic tobacco by overexpressing snapdragon-derived *Ros1* (Naing et al. 2018). The overexpression of *Ros1* resulted in enhanced anthocyanin accumulation and elevated expression of stress-responsive genes in tobacco plants. The overexpression of *SbMYB8* gene derived from *Scutellaria baicalensis* (a traditional Chinese medicinal plant) in tobacco has been shown to regulate the chalcone synthase activity for increased production of flavonoid like caffeoylquinic acid. The *SbMYB8* transgenic tobacco plants synthesized higher amount of flavonoids, displayed higher gene expression of flavonoid synthesis genes, and displayed better drought tolerance compared to wild-type plants (Yuan et al. 2015). Very recently, the transgenic Arabidopsis for *SsMAX2 gene* (a key component of strigolactones signaling) has been shown to accumulate higher anthocyanin content under drought stress conditions leading to significant improvement in drought stress tolerance compared to wild-type plants (Wang et al. 2019).

The genetic manipulations of the phenylpropanoid biosynthesis pathway have been a prime target of researchers engaged in biofuel research for engineering plants for low lignin content. The thioester p-coumaroyl-CoA serves as a branch point in the phenylpropanoid pathway from which lignin-specific branch and flavonoid-specific branch of the phenylpropanoid network diverge (Vogt 2010). At this branch point, the generated thioester can either be used by a lignin-specific branch of the phenylpropanoid pathway forming p-coumaryl, coniferyl, and sinapyl alcohol monolignols or else may be diverted to the flavonoid biosynthesis through malonate pathway. The downregulation of genes of lignin-specific branch can alter the carbon flux through the phenylpropanoid pathway possibly toward flavonoid biosynthesis and can also modulate the synthesis of other secondary metabolites. For producing the plant material with better pulp properties, the downregulation/knockdown of the genes of lignin biosynthesis is attempted. The lignin modification has been shown to be associated with activation of the genes involved in oxidative stress in tobacco, poplar, and Arabidopsis (Baxter and Stewart Jr 2013). However, the lignin is important component of plant secondary cell wall. The reduction in the lignin content of the plant cell wall may not only negatively affect the drought stress tolerance of the plant but also increase the possibility of pathogen attack.

19.6 Conclusion and Future Perspectives

The unavailability of the required amount of water is the major constraint in achieving the ideal threshold yields in any agricultural or horticultural cropping system. Plants are often confronted with the limited supply of the water at some stage of their life cycle. However, some plants are evolutionary well adapted to water scarce conditions and have the natural ability to tackle the drought-induced dysregulation of metabolism often indicated by the abrupt generation of a large number of reactive oxygen species (ROS). Such tolerant plants are equipped with higher levels of enzymatic (peroxidases, superoxide dismutase, and catalase) and

non-enzymatic antioxidant (phytochemicals) system as a physiological weapon for quenching of the ROS produced during the drought stress. The plant phenolics have been a subject of scientific investigation for the last many decades. The plant phenolics represent the most abundant and the most versatile natural products of plants. The understanding of the plant phenolics biosynthesis, accumulation, and its regulation is of utmost importance for devising the strategy to minimize the severe losses caused due to the various abiotic stresses. Extensive research has unraveled the molecular mechanisms of drought and desiccation tolerance with more emphasis on the role of plant flavonoids and other antioxidants. In response to water stress, plants typically accumulate a wide range of antioxidants, including enzymatic antioxidants and non-enzymatic. By now, a great deal of information has been generated concerning the biosynthesis, regulation, and genetic manipulation of plant phenolics. Therefore, there are many opportunities to exploit accumulated information to overcome the great agricultural losses by enhancing the phenylpropanoid contents ensuring the minimal trade-off for primary metabolites.

Does the role of flavonoids are simply limited to the chemical quenching of ROS, or they play a more versatile role in plants? This is the question which is pertinent mainly because of the exhaustive chemical diversity of the flavonoids in nature. It is biologically irrational that plants would channel 40% of the total carbon flux through phenylpropanoid biosynthesis pathways for the mere quenching of the ROS species if the other enzymatic antioxidant system is also operational under stress conditions. The vast chemical diversity of flavonoids (more than 7000) that plant has evolved also suggest about their multifaceted role, else such great chemical diversity was not required for ROS detoxification. The role of the flavonoids as signaling molecules is also being discussed in plants. Recently, the flavonoids like quercetin derivatives and their role in signaling cascades that regulate cell growth have been discussed (Hou and Kumamoto 2010). It is also proposed that the flavonoids modulate the phytohormone signaling by inhibiting the activity of a wide range of protein kinases, including mitogen-activated protein kinases, that operate downstream of ROS in the regulation of cell growth and differentiation (Brunetti et al. 2018a). With the continuously expanding knowledge about the chemical diversity of flavonoids and their proposed wider role in modulating the phytohormones signaling and cell growth, the plant flavonoids research would continue to assume central focal theme for plant abiotic stress tolerance, even in remaining part of twenty-first century.

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