

Revisiting Carotenoids and Their Role in Plant Stress Responses: From Biosynthesis to Plant Signaling Mechanisms During Stress

Virgílio Gavicho Uarrota, Deivid Luis Vieira Stefen,
Lucieli Santini Leolato, Diego Medeiros Gindri and Daniele Nerling

Abstract Stress in plants can be defined as any external factor that negatively influences plant growth, productivity, reproductive capacity or survival. As with any living organism, plants have an optimal temperature range at which growth and crop yield are best. Plants also require a certain amount of water for optimal survival; too much water (flooding stress) can cause plant cells to swell and burst, whereas drought stress (too little water) can cause the plant to dry up—a condition called desiccation. If the temperature is too cold for the plant, it can lead to cold stress, also called chilling stress. Cold temperatures can affect the amount and rate of uptake of water and nutrients, leading to cell desiccation and starvation. Hot weather can affect plants adversely, too. Intense heat can cause plant cell proteins to break down, a process called denaturation. Cell walls and membranes can also ‘melt’ under extremely high temperatures, and the permeability of the membranes is affected. Other abiotic stresses are less obvious, but can be equally as lethal. In farming systems, the use of agrochemicals such as fertilizers and pesticides, either in excess or in deficit, can also cause abiotic stress to the plant. The plant is affected through an imbalance of nutrition or via toxicity. High amounts of salt taken up by a plant can lead to cell desiccation, since elevated levels of salt outside a plant cell will cause water to leave the cell, a process called osmosis. Plant uptake of heavy metals can lead to complications with basic physiological and biochemical activities such as photosynthesis. Soil salinization also affects plants’ osmotic potential and

V. G. Uarrota (✉) · D. M. Gindri · D. Nerling
Laboratory of Seed Analysis, Department of Agronomy, Agro-Veterinary Science Center,
Santa Catarina State University, Luiz de Camões Avenue 2090, Lages 88520000,
Santa Catarina, Brazil
e-mail: uaceleste@yahoo.com.br

V. G. Uarrota · D. L. V. Stefen · L. S. Leolato
Laboratory of Crop Plants, Department of Agronomy, Agro-Veterinary Science Center,
Santa Catarina State University, Luiz de Camões Avenue 2090, Lages 88520000,
Santa Catarina, Brazil

D. M. Gindri
Department of Plant Protection, Integrated Company of Agricultural Development
of Santa Catarina, João José Godinho S/N., Lages 88502970, Santa Catarina, Brazil

inhibits many of a plant's cellular functions including photosynthesis and stomatal opening. Such different types of stresses can ultimately cause closure of stomata, disrupt the membrane-bound electron transport system, damage of photosynthetic machinery and the production of toxic active oxygen species. Over generations, many plants have mutated and evolved with different mechanisms to counter stress effects. These include a range of different mechanisms such as facultative inducible metabolic adaptations (i.e., excretion of organic acids; osmotic adjustment; accumulation of sugars, amino acids and polyols; induction of glycolytic enzymes; γ -aminobutyrate (GABA) accumulation; induction of fatty acid desaturases and heat shock proteins; activation of phytochelatin synthase and metallothioneins; activation of alternative respiratory pathways; induction of polyamine synthesis; production of antioxidant enzymes such as superoxide dismutase, ascorbate peroxidase, catalase, monodehydroascorbate and glutathione reductases) and eco-physiological (carbon assimilation) adaptations such as increased isoprene synthesis, which includes the large and crucial group of carotenoids. Carotenoids are essential in different plant processes and are potential antioxidants during plant stress. They act as light harvesters, quenchers and scavengers of triplate state chlorophylls and singlet oxygen species, dissipators of excess harmful energy during stress condition and membrane stabilizers.

Keywords Carotenoids • Water deficit • Temperature • Light • Greenhouse gases
Chemicals • Salt stress

1 Introduction

Plants are constantly being affected by changes in their environment (i.e., positively or negatively—so-called ‘stress conditions’) and cannot move away to a favorable condition due to their sessile nature, but they have powerful sensors or signal transduction mechanisms that connect biophysical stimuli and biochemical events that guide them toward optimal growth and development. In this regard, carotenoids represent one of the chemical interfaces between plants and the surrounding environment (Rhodes and Nadolska-Orczyk 2001; Esmon et al. 2005; Uarrota et al. 2011; Schenck et al. 2013; Smirnov 2014).

Carotenoids play important roles in living organisms. Their ubiquity is imperative for the crucial roles they play in nature. In photosynthetic organisms, they act as light harvesters by dissipating the excess energy as heat; they also act in photoprotection, structure stabilization (Frank and Cogdell 1996; Berera et al. 2006, 2009, 2010) and are precursors for the production of apocarotenoid hormones such as abscisic acid and strigolactones (Ruiz-Sola and Rodríguez-Concepción 2012). Unique in their diversity of function, carotenoids are of vital importance for the survival of photosynthetic organisms because of photoprotective role they play, which prevents over excitation of the photosystem II (PSII). Carotenoids are quenchers of chlorophylls in triplet state and chlorophyll singlet excited states

under conditions of excess light illumination (non-photochemical quenching—NPQ) and are scavengers of singlet oxygen ($^1\text{O}_2$) due to its low triplet state energy (Griffiths et al. 1995; Frank and Cogdell 1996; Berera et al. 2006, 2009, 2010).

In summary, carotenoids have at least five different roles in photosynthetic organisms: (1) accessory light-harvesting pigments via singlet state energy transfer, effectively extending the range of light absorbed by the photosynthetic apparatus; (2) quenchers and (3) scavengers of triplet state chlorophylls and $^1\text{O}_2$ and other toxic oxygen species formed within the chloroplast; (4) excess energy dissipation; and (5) structure organization or stabilization (Griffiths et al. 1995; Frank and Cogdell 1996; Polivka and Sundstrom 2004). An additional protective role is related to the carotenoid zeaxanthin, which involves the dissipation of harmful excess excitation energy under stress conditions via de novo synthesis or enzymatic de-epoxidation of the carotenoid violaxanthin during long-term stress (the xanthophyll cycle). The ability of a plant to respond to light-mediated environmental stress by producing zeaxanthin could therefore be species dependent, and ultimately could affect the ability of such species to inhabit or colonize certain habitats (Young 1991).

2 The Building Blocks of Carotenoids and Biosynthesis

Carotenoids are isoprenoids, terpenoids or terpenes, a class of natural products built from two isoprene units, isopentenyl diphosphate (IPP) and dimethylallyl diphosphate (DMAPP). See Fig. 1a, b for detailed chemical structure (Zhao L et al. 2013). DMAPP is an intermediate of both mevalonic acid pathway (MVA) and methyl erythritol phosphate pathway (MEP) and is an isomer of IPP (Pulido et al. 2012; Seemann et al. 2006; Phillips et al. 2008; Tritsch et al. 2009; National Center for Biotechnology Information, NCBI 2017), while glyceraldehyde-3-phosphate (G3P) and pyruvate (PYR) act as initial substrates to produce 1-deoxy-D-xylulose-5-phosphate (DXP), which is then isomerized to methyl erythritol phosphate (MEP). Subsequent coupling between MEP and cytidine-5-triphosphate (CTP) produces (CDP-ME), which is then phosphorylated and results in 4-diphosphocytidyl-2-C-methyl-D-erythritol-2-phosphate (CDP-MEP). The cycling of this last compound forms methylerythritol cyclodiphosphate (MEcPP) and hydroxy methyl butenyl diphosphate (HMBPP). Although, initially, only the MVA pathway was thought to be the route for the biosynthesis of IPP and DMAPP, later it was found that MEP pathway also contributes to the biogenesis of IPP and DMAPP. The cytosolic MVA and plastidial MEP pathways are two different strategies that are employed by nature to synthesize the five carbon isoprene units (Zhao L et al. 2013; Zhao Q et al. 2013). Plants are unique in that they have both MEP and MVA pathways (Seemann et al. 2006; Phillips et al. 2008; Tritsch et al. 2009; Pulido et al. 2012).

The MEP pathway produces both IPP and DMAPP from G3P (carbohydrate derivatives that originates from glucose metabolism/or Calvin cycle intermediates) and MVA only produces IPP from acetyl-Coenzyme ‘A,’ which is then converted into DMAPP by IPP isomerase. MEP enzymes are encoded by nuclear genome and

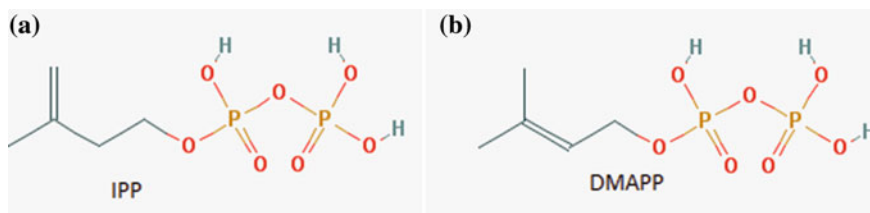


Fig. 1 The initial substrates leading to the synthesis of geranylgeranyl diphosphate (GGPP) toward carotenoid biosynthesis. **a** Isopentenyl diphosphate (IPP); and **b** dimethylallyl diphosphate (DMAPP)

imported into plastids whereas MVA enzymes can be found in the cytosol and peroxisomes (Eisenreich et al. 2001; Joyard et al. 2009; Flores-Pérez et al. 2010; Tritsch et al. 2009; Pulido et al. 2012; Vranová et al. 2013; Lipko and Swiezewska 2017). Despite the subcellular compartmentalization synthesis of IPP and DMAPP in plant cells, studies have shown that an exchange of the isoprenoid precursors can happen in different cellular locations (Flores-Pérez et al. 2010; Pulido et al. 2012; Vranová et al. 2013). Light and sugars have been correlated to downregulate the cytosol-peroxisome pathway (MVA) and upregulate the plastid (MEP) pathway (Flores-Pérez et al. 2010; Pulido et al. 2012; Vranová et al. 2013). Using both (MVA and MEP) pathways, plants have an advantage through the facilitation of molecular interactions with their surrounding environment, thereby overcoming their sessile lifestyle constraints (Ahn and Pai 2008; Joyard et al. 2009; Flores-Pérez et al. 2010; Vranová et al. 2013; Kuzuyama and Seto 2012). This also enables them to separate the synthesis of isoprenoids for various functions (Odom 2011; Chang et al. 2013; Vranová et al. 2013). The main enzymes involved in the MVA pathway are: acetoacetyl-CoA thiolase (AACT), 3-hydroxy-3-methylglutaryl CoA synthase (HMGS) and reductase (HMGR), mevalonate kinase (MVK), 5-phosphomevalonate kinase (PMK) and 5-phosphomevalonate decarboxylase (MVD). The MEP pathway is undertaken due to the action of the following enzymes: 1-deoxy-xylulose-5-phosphate synthase (DXS); 1-deoxy-xylulose-5-phosphate reductoisomerase (DXR); 2-C-methyl-D-erythritol-4-phosphatecytidyltransferase (MCT); 4-(cytidine 5'-diphospho)-2-C-methyl-D-erythritol kinase (CMK); 2-C-methyl-D-erythritol-2,4-cyclodiphosphate synthase (MDS); and 1-hydroxy-2-methyl-2-butenyl-4-diphosphosphate synthase and reductase (HDS and HDR respectively) (Phillips et al. 2008; Pulido et al. 2012; Vranová et al. 2013). It has been suggested that photosynthetic eukaryotes inherited their genes for IPP synthesis through the MEP pathway from a prokaryote endosymbiont. But this is not a unique source—an independent lateral gene transfer from other eubacterial organisms have provided some of the MEP genes in plants (e.g., DXS from α -proteobacteria, MCT and CMK from *Chlamydia*s, and MDS from *Aquifex*) (Kuzuyama and Seto 2012; Vranová et al. 2013; Zhao L et al. 2013).

Efforts in understanding the building blocks of carotenoids have been successful and are well documented in the literature (Gómez-García and Ochoa-Alejo 2013;

Corniani et al. 2014; Rodríguez-Concepción 2014; Nisar et al. 2015; Bai et al. 2016; Kiokias et al. 2016; Majer et al. 2017). In addition, all of them reinforce the same point of view. A simplified diagram of the biosynthetic pathway of carotenoids is presented in Fig. 2. As can be observed, and as stated above, carotenoids are derived from the plastid-localized MEP pathway from basic isoprene units IPP and DMAPP (Gómez-García and Ochoa-Alejo 2013; Zhao L et al. 2013; Zhao Q et al. 2013; Corniani et al. 2014; Rodríguez-Concepción 2014; Nisar et al. 2015; Bai et al. 2016; Kiokias et al. 2016; Majer et al. 2017), which then leads to the synthesis of geranylgeranyl diphosphate (GGPP). DMAPP is used as an active substrate for the addition of IPP to synthesize the short-chain branching points of isoprenoid biosynthesis (geranyl diphosphate-GPP (C₁₀), farnesyl diphosphate (C₁₅)-FPP and GGPP-C₂₀). Figure 2 outlines the main events in carotenoid biosynthesis. It seems that a ratio of 3:1 (IPP and DMAPP, respectively) is sufficient for the biosynthesis of GGPP and the condensation of two molecules of GGPP leads to formation of phytoene (Ruiz-Sola and Rodríguez-Concepción 2012).

The condensation of two molecules of GGPP leads to the formation of the first carotenoid phytoene, and phytoene synthase (PSY) is generally accepted as the most important regulatory enzyme in the pathway (Zhao L et al. 2013). The production of all-trans-lycopene from phytoene requires a complex set of reactions requiring phytoene desaturase (PDS), zeta-carotene isomerase (Z-ISO), zeta-carotene desaturase (ZDS), carotenoid isomerase (CRTISO) and light (Zhao L et al. 2013). Carotenoid biosynthesis bifurcates after lycopene to produce ϵ - and β -carotenoids by enzymatic activity of the two lycopene cyclases (ϵ -LCY and β -LCY) and this branch point has a major regulatory role in modulating the ratio of the most abundant carotenoid, lutein to β -carotenoids (Gómez-García and Ochoa-Alejo 2013; Zhao L et al. 2013; Zhao Q et al. 2013; Corniani et al. 2014; Rodríguez-Concepción 2014; Nisar et al. 2015; Bai et al. 2016; Kiokias et al. 2016; Majer et al. 2017).

2.1 Main Genes, Enzymes and Events During Carotenogenesis

The first important event in carotenogenesis is the production of phytoene from condensation of two GGPP molecules, a reaction catalyzed by PSY. Phytoene is then desaturated to create a conjugated double bond chain that forms a ‘spine’ of plant carotenoids and determines their physico-biological properties (Ruiz-Sola and Rodríguez-Concepción 2012). The addition of three molecules of IPP to DMAPP by GGPP synthase (GGPS) leads to the formation of GGPP, which is an intermediate for carotenoids, gibberellins, chlorophylls, tocopherols, phylloquinones and plastoquinone (Ruiz-Sola and Rodríguez-Concepción 2012). The synthesis of phytoene by GGPP is catalyzed by PSY by condensation. Phytoene is an uncolored carotenoid. Four sequential dehydrogenation and two isomerization increase the conjugated double bonds and transforms 15-cis-phytoene into all-trans-lycopene, a pink colored carotenoid. In summary, during desaturation, phytoene is transformed

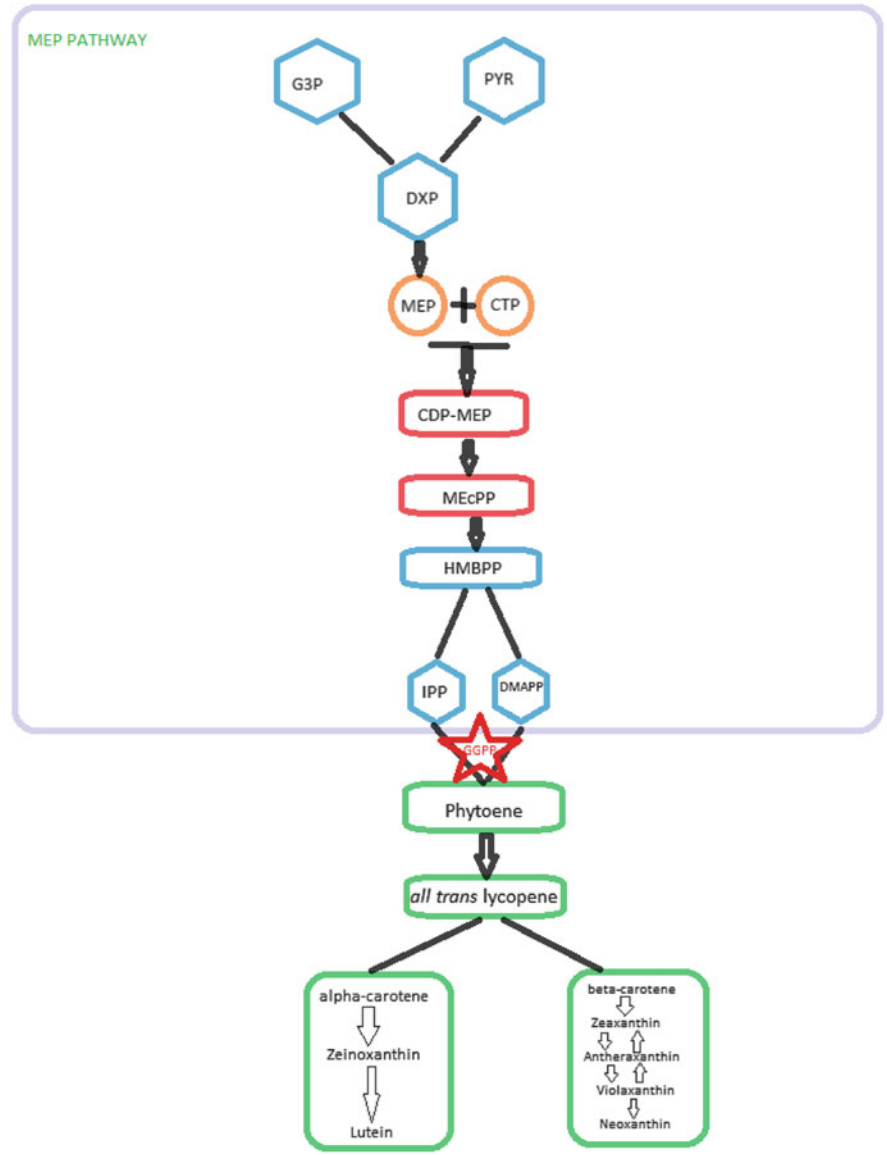


Fig. 2 Major reactions in higher plant carotenoid biosynthetic pathway. To simplify, the enzymes that catalyze the reactions are not presented in the diagram

to phytofluene, ζ -carotene, neurosporene and lycopene, respectively; and phytoene desaturase (PDS), 15-*cis*- ζ -carotene isomerase (Z-ISO), ζ -carotene desaturase (ZDS) and carotenoid isomerase (CRTISO), respectively, are the enzymes involved in these reactions. An increase in conjugated double-bond chain increases the

absorption of polyene chain towards longer wavelengths (Ruiz-Sola and Rodríguez-Concepción 2012). Cyclization of one or both ends of *all-trans*-lycopene marks the first branching point in the pathway; one branch leads to carotenoids with two β rings (β -carotene and xanthophylls (oxygenated derivatives) such as zeaxanthin, violaxanthin and neoxanthin), whereas the other branch leads to carotenoids with one β ring and one ϵ ring (α -carotene and xanthophylls such as lutein). Carotenoids with an ϵ ring are uncommon in the plant kingdom (Ruiz-Sola and Rodríguez-Concepción 2012). Xanthophylls (zeaxanthin and lutein) are produced by the hydroxylation of cyclic carotenes (α - and β -carotenes). Epoxydations of zeaxanthin yields violaxanthin, which can be transformed back into zeaxanthin by de-epoxydation (xanthophyll cycle) or converted to neoxanthin by opening the cyclohexenyl-5-6-epoxide ring. The hydroxylation of β rings is catalyzed by two enzymes (non-heme di-iron BCH type) and cyanobacteria enzyme (Crt-B) and the hydroxylation of β and ϵ rings by cytochrome P450 enzymes (CYP97 type) (Ruiz-Sola and Rodríguez-Concepción 2012).

3 Role of Carotenoids in Plant Stress: Water Deficit and Excess

Soil water availability is one of the strongest influencing factors on plant growth, development and photosynthetic capacity (Wang et al. 2012). Plants have evolved complex mechanisms to sense water availability in their environment. Cellular reprogramming for metabolism and growth in response to drought and flooding stress leads to a series of physiological, biochemical and morphological changes at the molecular and whole-plant level (Zhao et al. 2014). Some of these include stomatal closure, reduced shoot growth, leaf senescence, dormancy and carotenogenesis (Zhao et al. 2014).

Drought and waterlogging are accompanied by an increased production of reactive oxygen species (ROS) such as superoxide radical ($O_2^{\cdot-}$), singlet oxygen (1O_2), hydrogen peroxide (H_2O_2) and hydroxyl radicals ($\cdot OH$) (Ashraf 2012; Choudhury et al. 2013). Carotenoids are antioxidants that are able to detoxify various forms of ROS and also directly quench triplet chlorophylls that are sources of 1O_2 in leaves (Ramel et al. 2012). De-epoxidation of violaxanthin to zeaxanthin, in addition, avoids the formation of triplet chlorophyll (3Chl*) from singlet chlorophyll (S^*1 , via NPQ), reinforces rigidity to thylakoid membranes and prevents lipid peroxidation. Carotenoids also participate in the quenching of 1O_2 by dissipating the highly energetic molecular oxygen ($^1O_2 \rightarrow ^3O_2$ transition) and direct 1O_2 -oxidation of β -carotene and zeaxanthin (Brunetti et al. 2015).

Water deficits and prolonged waterlogging cause changes in carotenoid levels. Its regulation is highly dependent on the species, as well as the duration and intensity of the restriction or flooding period. In drought stress conditions, a reduction in the content of carotenoids have been reported in cherry tomatoes,

wheat, sorghum, sunflower and some plants of the family *Asteraceae* (Hammad and Ali 2014; Manivannan et al. 2014; Yadav et al. 2014; Al Hassan et al. 2015, 2016, 2017; Arivalagan and Somasundaram 2015; Cicevan et al. 2016).

The reduction of carotenoid content during waterlogging was observed in wheat, and white and red clover (Simova-Stoilova et al. 2012; Ozcubukcu and Ergun 2013). Both an increase and reduction of carotenoid levels was reported by Jain et al. (2017) in 24 sugarcane genotypes and in four cultivars of mung bean (Kumar et al. 2013).

It is likely that carotenoid contents tend to decrease under moderate flood and drought but increase slightly under severe drought stress (Sudrajat et al. 2015). The increase of the carotenoid concentration was observed in beans, olive trees and alpine plants (Doupis et al. 2013; Ramalho et al. 2014; Buchner et al. 2017). An increase in carotenoid levels in response to water stress could be associated with the activation of the xanthophyll cycle (Ma et al. 2013; Mattos and Moretti 2016; Schweiggert et al. 2017). Increases in zeaxanthin content were reported in African eggplants (Mibei et al. 2016) and vine berries (Savoi et al. 2016) during water deficit. Violaxanthin is transformed to antheraxanthin allowing the excess energy of the light to be dissipated (Buchner et al. 2017). The increase in zeaxanthin contents may also have a role in the improvement of plant tolerance to different abiotic stresses (Wu et al. 2015).

4 Role of Carotenoids in Plant Stress: Nutritional or Chemical

In addition to the already known functions of carotenoids, a new function has recently emerged that relates to the response of plants to environmental stresses (Havaux 2013). Plants can induce defensive responses against oxidative stress by activating non-enzymatic antioxidants, which represent the second line of defense against ROS. Oxidative stress stimulates the synthesis of carotenoids in the leaves.

Carotenoids are categorized into lipophilic antioxidant groups and have the ability to eliminate various forms of ROS, such as $^1\text{O}_2$. They act as precursors of signaling molecules that have a positive impact on the growth and development of plants and in plant responses to nutritional stress (Abdel-Latef and Abu-Alhmad 2013).

Copper is an essential micronutrient for plants; however, excess copper induces the formation of ROS. Elevated levels of carotenoids in *Vicia faba* subjected to increasing concentration of copper were found to be dose dependent. The increase in carotenoids levels could be attributed to the non-enzymatic antioxidant activity of these compounds (Abdel-Latef and Abu-Alhmad 2013).

Cicer arietinum, subjected to cadmium (Cd) stress significantly increased the content of carotenoids. The synthesis of carotenoids decreased oxidative damage induced by the toxicity of the Cd (Ahmad et al. 2016). Phosphorus and potassium

deficiencies were also reported to increase carotenoid content in spinach (Xu and Mou 2016).

Nitrogen or phosphorus repletion was reported to increase the levels of carotenoids in algae *T. marina*, decrease SOD activity and increase levels of H₂O₂ and thiobarbituric acid reactive substances (TBARS). The increases in carotenoids are related to its antioxidant role against nutrient deficiency (Moussa et al. 2017). In other research by Zhang et al. (2017), it was reported that stressful conditions can stimulate the accumulation of carotenoids in some microalgae. The results showed that nitrogen depletion facilitated the synthesis of carotenoids, while at the same time, excessive nitrogen stress led to lower proliferative and photosynthetic activity (Zhang et al. 2017). Compared with carotenoids, chlorophylls were more sensitive to nitrogen stress; chlorophylls declined dramatically as nitrogen stress progressed. These results demonstrated that the unicellular carotenoid content of *Chlorella vulgaris* presented different patterns over time under different nitrogen concentration conditions. Carotenogenesis is dependent on the degree of stress and nitrogen availability. Under such conditions, carotenogenesis cannot proceed due to a lack of enzymes, which cannot be synthesized without nitrogen availability (Moussa et al. 2017).

Percival (2017), studying the effect of glyphosate application in three *Acer* species, reported that carotenoids are accumulated in leaves with the application of glyphosate and suggested that the higher levels of carotenoids found is a tolerance mechanism against glyphosate. The increase in carotenoid levels found demonstrated that carotenoids play an important role in protecting foliar tissue against glyphosate.

5 Role of Carotenoids in Plant Stress: Temperature and Light

Carotenoids are an important group of natural pigments that are found in all photosynthetic organisms (plants, algae and cyanobacteria) and several species of non-photosynthetic bacteria and fungi. These isoprenoid derived pigments play essential roles in photosynthesis, nutrition and protection against photo-oxidative damage in higher plants. Carotenoids are synthesized via the general biosynthetic pathway within the chloroplasts of plants and algae and the cyclization of lycopene is an important branch point in this pathway. Lycopene, the product of the sequential desaturations of phytoene, is converted into β -carotene by the action of lycopene β -cyclase (Lcy- β) (Ramos et al. 2008; Paliwal et al. 2017).

Light intensity and temperature are primary environmental factors affecting the growth and development of plants. Changes in light intensity, range and duration can lead to acclimation responses, cellular damage and ultimately to the death of plants. Plants have evolved several efficient protective mechanisms that make it possible for them to survive under unfavorable light and temperature conditions

(Szymańska et al. 2017). Under stress conditions, elevated levels of ROS are produced, which in addition to deleterious effects also show signaling functions (Szymańska et al. 2017). In response to enhanced ROS formation, different low-molecular weight non-enzymatic antioxidants are synthesized, as well as antioxidant enzymes. Depending on the stress intensity and duration, the content of synthesized antioxidants varies. Under severe, short light/temperature stress, the contents of antioxidants, such as ascorbate, glutathione and prenyl lipids, tend to decrease. Under longer exposure to unfavorable light and temperature conditions, the contents of antioxidants gradually increase as a result of acclimation during long-term responses. Studies on plant antioxidant responses indicate that a crucial part of the antioxidant network operates in chloroplasts and their action shows a high level of interdependence that can be influenced by plant stress tolerance, which is also species-dependent (Szymańska et al. 2017).

The regulation of the carotenoid pathway at the transcript level seems to be related to the stress (e.g., high light) response and, in some cases, correlated with carotenoid accumulation. High light has been reported to enhance the steady-state transcript levels of PSY and PDS carotenogenic enzymes under nutrient deprivation. Highest β -*LCY* steady-state mRNA levels were obtained in cells exposed to high light ($500 \mu\text{mol m}^{-2} \text{s}^{-1}$) or low ($45 \mu\text{mol m}^{-2} \text{s}^{-1}$) combined with nutrient depletion. A similar pattern was also observed in cellular β -carotene content, and accumulation was faster in the case of exposure to high light conditions. The highest values of β -carotene accumulation were observed in cells under nutritional stress at both light intensities. However, under these conditions, the cells exposed to high light accumulated approximately twice the value obtained in cells exposed to low light conditions. Halotolerant green alga *Dunaliella salina* has been reported to accumulate large amounts of β -carotene when exposed to various [salt, light and nutrient depletion (NaCl concentrations and water)] stress conditions (Ramos et al. 2008).

According to Couso et al. (2012), the xanthophyll cycle was activated in response to high light. In high light conditions, one of the two possible routes for zeaxanthin synthesis (de novo synthesis or interconversion of violaxanthin and zeaxanthin—xanthophyll cycle) was found to be dependent on protein synthesis. Cytochrome-dependent carotenes and hydroxylases were observed to be upregulated at high light conditions, implicating the role of these enzymes in regulation of xanthophyll cycle during light stress (Couso et al. 2012). Accumulation of zeaxanthin and antheraxanthin, and the corresponding decrease in violaxanthin were correlated with high light intensity (Couso et al. 2012).

Microarray and proteomic approaches used to identify genes and proteins induced by high light in *Chlamydomonas* revealed an induction of both PSY and PDS. Lycopene- ϵ -cyclase (ϵ -*LCY*) and lycopene- β -cyclase (β -*LCY*), involved in the cyclization of lycopene to yield carotene, showed a slight reduction in their mRNA level. Zeaxanthin epoxidase (ZEP), which catalyzes the synthesis of violaxanthin and is directly involved in the xanthophyll cycle, decreased slightly in its transcription levels during high illumination condition. Expression of the P450

cytochrome-dependent and cytochrome ring carotene hydroxylase genes were also found (Couso et al. 2012).

Elevated temperatures were also studied by Wong et al. (2015) in polar microalgae. Higher carotenoid content was found at elevated temperatures. Jackson (2015) also studied the elevated temperature effects on carotenoid biosynthesis in the diploid strawberry using biochemical and genomic analysis. Gene expression and metabolite accumulation were reported to be tissue-specific at elevated temperature stress (Jackson 2015).

Temperature is one of the most important environmental factors that influence algal growth rate, cell size, biochemical composition and nutrient requirements and has a significant effect on carotenogenesis. Carotenoid accumulation in algal species was found to increase with temperature and this was claimed to be an antioxidant mechanism or cellular response related to increased oxidative free oxygen radical formation or increased biosynthetic enzyme activity and photo damaging effects observed at elevated temperatures. A threefold increase in astaxanthin formation in the green alga *Haematococcus pluvialis* with an increase of temperature from 20 to 30 °C was reported. In green alga, *Chlorococcum* sp., a twofold increase in total carotenoid content was also found when the cultivation temperature was changed from 20 to 35 °C under conditions of nitrogen deprivation (Juneja et al. 2013).

It has been demonstrated that organisms deficient in carotenoids suffer from photodamage because carotenoids have an essential role in the dissipation of excess absorbed energy and in the antioxidant activity. Under environmental stresses, the transcription of carotenoid biosynthetic genes are upregulated (leading to higher levels of carotenoids) to mediate redox balance (Esteban et al. 2015).

García-Plazaola et al. (2017) studied the carotenoid cleavage products upon heat shock and wounding stress (β -cyclocitral, β -CC), and concluded that heat and wounding stresses induces a loss of carotenoids and increased volatile end products. The rate of carotenoid losses was found to be three orders of magnitude higher than the increase of volatile compounds (García-Plazaola et al. 2017).

Physiological responses of *Scaevola aemula* seedlings to a short-term (a three-day period) high temperature (HT) stress were investigated by He et al. (2017) in order to examine the adaptation of *S. aemula* to the thermal environment. Increases in photosynthetic pigments, soluble sugars, SOD activity, and a reduction in soluble proteins, proline and catalase activity were observed in seedlings (He et al. 2017). Severe excess light stress was also studied by Brunetti et al. (2015). Isoprenes, carotenoids and flavonoids may complement the function of primary antioxidants to avoid irreversible oxidative damage, when plants experience intense transient stress events. The effectiveness of ROS-detoxifying compounds under sunlight and temperature was reported to be highly altered (Brunetti et al. 2015).

Changes in xanthophyll composition during dark-to-light transition allow carotenoids to serve strikingly different functions from light harvesting to its dissipation through non-photochemical quenching (NPQ) (Brunetti et al. 2015), thus equipping leaves with flexible mechanisms to properly manage radiant energy reaching PSII. De-epoxidation of violaxanthin to zeaxanthin may have, however, a

subtler role in chloroplasts suffering from a severe excess of radiant energy. There is compelling evidence that zeaxanthin may play antioxidant functions when the photosynthetic capacity of leaves grown in high light is severely constrained by concurrent stress agents, such as drought and salinity (Brunetti et al. 2015).

Light stimulates the biosynthesis of carotenoids and regulates the development of plastid structures to accommodate these photoprotective pigments. Carotenoid biosynthesis and storage with photosynthetic development during de-etiolation and shade is coordinated by molecular factors, when underground seedlings emerge to the light. While light positively impacts carotenoid production and accumulation in most cases, total carotenoid levels were found to decrease in roots of colored carrot cultivars when illuminated; this was attributed to the photomorphogenic characteristic of the investigated cultivars (Llorente et al. 2017).

León-Chan et al. (2017) reported that low temperature and ultraviolet-B radiation affected the chlorophyll content by degrading them and induced the accumulation of UV-B absorbing and antioxidant compounds (i.e., carotenoids) in bell pepper (*Capsicum annuum*) plants (León-Chan et al. 2017).

Shen et al. (2017) also studied the effect of increased UV-B radiation ($+9.75 \text{ mW cm}^{-2}$ was considered low UV-B and $+20.76 \text{ mW cm}^{-2}$ was considered high UV-B) on carotenoid accumulation and total antioxidant capacity in tobacco (*Nicotiana tabacum* L.) leaves. Higher levels of UV-B rapidly increased carotenoid contents compared with control plants and the production of those compounds was attributed to the excess ROS at high UV-B radiation; carotenoids were reported to play a role in protecting the plant to oxidative damage caused by UV-B stress (Shen et al. 2017).

Carotenoids are light-harvesting complexes and absorb light energy in the 400–500 nm region, which is not accessible to the chlorophyll molecules and extends the absorption range for photosynthesis. Energy is then transferred from the carotenoid to chlorophyll molecules. When they are illuminated and excited, the chlorophyll fluorescence can be observed and indicates energy transfer from carotenoid to chlorophyll (Young 1991).

On illumination, the level of the carotenoid violaxanthin in the leaves decreases. This is accompanied by an increase in the levels of the carotenoids, antheraxanthin and zeaxanthin. Subsequent return of these light-treated leaves to low light or to darkness resulted in recovery in the levels of violaxanthin, at the expense of antheraxanthin and zeaxanthin. This process is termed the xanthophyll cycle or violaxanthin cycle. The cyclic interconversion of violaxanthin and zeaxanthin is linked to a novel photoprotective process in the photosynthetic apparatus involving the dissipation of excess excitation energy when photosynthetic tissues (leaves) are exposed to light levels in excess of that which can usefully be used in photosynthesis (Young 1991).

When the light excitation energy of exposed leaves exceeds the capacity of dissipation of the photosynthetic system, photoinhibition can occur. During photoinhibition, a reduction in the efficiency of photon utilization by photosystem II (PSII) can be observed. Photoinhibition was also observed into two distinct situations: (1) when shade-adapted leaves or plants grown at low light were exposed to

high light and (2) when leaves acclimated to natural sunlight were exposed to additional environmental stresses such as unfavorably low and high temperatures, water deficit, and salt stresses. Under these conditions, a given light level that was previously not excessive becomes inhibitory because the utilization of energy through photosynthesis is decreased by the additional stress conditions. Under normal conditions, the light energy absorbed by the pigments organized in chlorophyll–protein complexes of PSII and photosystem I (PSI) is utilized in a controlled manner, leading to the generation of NADPH and ATP. However, under photoinhibitory conditions, this process is not able to dissipate all the available energy resulting from the decreased efficiency of the photosynthetic system in utilizing the energy. Other energy dissipation mechanisms playing important protective roles for PSII reaction centers and photoinhibition have been also reported and include carotenoids, photorespiration, reducing substances and SOD (Sharma and Hall 1993).

6 Role of Carotenoids in Plant Stress: Salt Stress

Salinity stress is responsible for changes in various physiological and metabolic processes. Depending on the intensity and its duration, salinity stress can inhibit productivity by inhibiting plant growth and development. One of the most damaging effects of this stress is the accumulation of Na^+ and Cl^- in the tissues of plants, when exposed to soils with high concentrations of NaCl. The entry of these ions into the cell causes imbalance and excessive absorption resulting in significant physiological disorders. The elevated Na^+ concentration inhibits the absorption of K^+ , which is an essential element for the growth and development of the plant. During salinity stress, an increase in ROS production (e.g., $^1\text{O}_2$, O_2^- , $^{\bullet}\text{OH}$ and H_2O_2) are observed and these ultimately cause oxidative damage to various cellular components (proteins, lipids and DNA), which in turn can disrupt important plant functions related to its survival (Gupta and Huang 2014). Under salinity stress, carotenoids can act as defense mechanism and their effectiveness is dependent by the presence of conjugated chains which is essentially for light absorption in photosynthetic organisms and (photo) protection in all living organisms. This function depends on their structure and chemical properties (Fiedor and Burda 2014). Carotenoids have a dual system of conjugate carbon that may be involved with energy transfer reactions (Telfer 2014; Perlik et al. 2015). According to the energy transfer reactions, carotenoids provoke thermal deactivation by fighting $^1\text{O}_2$, in addition to eliminating O_2^- and H_2O_2 formed during salinity stress (Jin et al. 2015; Kang et al. 2017).

The response of plants to salinity stress varies depending on the exposure time. A decrease in carotenoid levels in plants under salinity stress was reported in many species, including *Triticum aestivum* (Tabatabaei and Ehsanzadeh 2016; Tian et al. 2017), *Capsicum annuum* (Melo et al. 2017), *Zea mays* (Liu et al. 2015; Gul et al. 2017), *Phaseolus vulgaris* (Taïbi et al. 2016), *Cicer arietinum* (Shankar et al. 2015),

Picea abies (Schiop et al. 2015), *Nicotiana tabacum* (wild type) (Shi et al. 2015a, b), *Salicorniana prostrata* and *Suaeda prostrata* (Akcin and Yalcin 2016).

The form and functions of various organs can undergo significant changes and the plant's ability to react to salinity stress depends on genes that are expressed in the development stage during which stress is imposed. The ROS participate in a sophisticated network of signaling pathways in plants, in response to stress situations. These chemical species have influence on the expression of various genes involved in metabolism and transduction pathways, acting as signaling molecules (Li et al. 2017).

Carotenoids levels can be increased or decreased by overexpression or suppression of genes involved in biosynthetic pathways. ζ -Carotene desaturases (ZDS) are key enzymes in the pathway of the biosynthesis of carotenoids. The *IbZDS* gene is associated with this enzyme, and was related to the accumulation of carotenoids in sweet potatoes; its overexpression resulted in significant increases in β -carotene and lutein and improved the tolerance of potatoes to salinity stress (Li et al. 2017).

The other important group of genes is related to lycopene β -cyclase (β -LCY) and lycopene ϵ -cyclase (ϵ -LCY). The suppression of these genes by RNA interference resulted in increased levels of β -carotene, total carotenoids and salinity stress tolerance in sweet potato cells (Kim et al. 2013, 2014). Also in sweet potato, the suppression of *CHY- β* was responsible for enhancing carotenoids, and consequently increased salinity stress tolerance (Kang et al. 2017).

In *Solanum nigrum*, the expression of the genes *LCYB* and *phytoene synthase 2* was associated with the largest quantity of β -carotene and lutein (Ben Abdallah et al. 2016). The expression of phytoene synthase, phytoene desaturases, zeta carotene desaturases, lycopene β -cyclase and capsanthin/capsorubin synthase in *Capsicum* was downregulated as salt concentration increased (Maurya et al. 2015).

In *Nicotiana tabacum*, salinity stress tolerance appeared to be associated with genes *ϵ -LCY* and *LCYB*. The overexpression of *LCYB* and the suppression of *ϵ -LCY* were responsible for increased salinity tolerance in transgenic *N. tabacum* (Jin et al. 2015; Shi et al. 2015a, b). The differences observed in each species can be explained by the complex nature of the regulation of carotenoids, the negative and positive interaction of genes and the transcriptional control, which are all involved in regulating abundance of α and β -carotene compounds.

7 Role of Carotenoids in Plant Stress: Elevated Greenhouse Gases

The four most common greenhouse gases are carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O) and ozone (O_3). Greenhouse gases have a major indirect impact on crop growth and development through their effect on climate change but also may have direct effects on plant growth and development. The current atmospheric CO_2 concentration is approximately 400 ppm and is expected to reach

between 730 and 1020 ppm near the end of this century unless effective measures of reversal are implemented. These higher levels are already having direct effects on plant growth and development, as well as indirect effects such as rising temperatures, which in turn have their own secondary effects including less predictable rainfall (BGS 2017).

Since the start of the industrial revolution in the mid-eighteenth century, human activities have greatly increased the concentrations of greenhouse gases in the atmosphere due to burning fossil fuels, farming and forestry, cement manufacture and aerosols. CO₂ levels are substantially higher now than at any time in the last 750,000 years. Concentrations are increasing at a rate of about 2–3 ppm year⁻¹ (Maryland et al. 2008; Boden et al. 2010; BGS 2017). Since 1751, approximately 337 billion metric tons of carbon have been released to the atmosphere from the consumption of fossil fuels and cement production. The 2007 global fossil-fuel carbon emission estimate of 8365 million metric tons of carbon represents an all-time high and a 1.7% increase from 2006. Globally, liquid and solid fuels accounted for 76.3% of the emissions from fossil fuel burning and cement production in 2007, 18.5% from natural gas fuels (1551 million metric tons of carbon) and reflect a gradually increasing global utilization of natural gas. Cement production accounts for around 5% of total global industrial and energy CO₂ emissions. According to the Intergovernmental Panel on Climate Change, IPCC, for every tonne of cement produced there is a one and a quarter tonnes equivalent of CO₂ released. 4.1 billion metric tonnes of world cement production in 2017 multiplied by 1.25 tonnes of CO₂ per tonne of cement produced gives an eye watering 5.1 billion tonnes of CO₂ emitted from cement production in 2017 (Statistica 2018; Rammed Earth Consulting 2018; Worrell 2001) from fossil-fuel burning and cement production (Maryland et al. 2008; Boden et al. 2010). The increases reported here are also projected to reach a range from 535 to 983 ppm in the atmosphere by the end of the twenty first century. Together with the rising emissions of methane and other greenhouse gases, and the associated feedback effects, it is suggested that these changes may possibly cause an increase of 1.4–5.6 °C (BGS 2017). The elevated greenhouse gases are impacting plant development and carotenoids plays an important role in plant survival.

Greene et al. (2010), studying the chloroplast response in the face of environmental factors such as elevated CO₂, elevated O₃ and abiotic stress, reported that these gases affect plant cells initially by interfering with photosynthesis. Antioxidant defense systems including carotenoids play a role in alleviating plant stress caused by excess greenhouse gases (Greene et al. 2010; Rebeiz et al. 2010).

Elevated CO₂ was also reported to improve vitamin C, sugars, acids and carotenoids in tomato. Positive effects of CO₂ were observed on the total antioxidant capacity of phenols and anthocyanins, but it was found to cause a reduction in protein and mineral content. The study's authors claimed that there is a possibility that the additional carbon fixed by plant due to high CO₂ may be inverted in protective antioxidant compounds such as ascorbate and phenolics (Choudhary et al. 2015). According to Karnosky et al. (2001), chlorophylls and carotenoids are affected by climatic factors including air pollutants. A decreased stability of the

light-harvesting complex and reduced photosynthesis were observed as consequences of O₃ exposure. A reduction of chlorophyll and carotenoids may occur, while β -carotene, a component of photosynthetic center, is only slightly affected. The sum of the pigments of xanthophyll cycle is elevated under various elevated O₃ profiles and an increase in the violaxanthin/antheraxanthin ratio was also found, suggesting an impaired activity of epoxidase enzyme (Karnosky et al. 2001). A CO₂ increase was also reported to increase photosynthetic efficiency and lipid production in Antarctic algae (Wong et al. 2015).

8 Role of Carotenoids in Plant Stress: Plant Competition and Allelopathy

According to Ferreira (2004), the interference can be caused by competition (abiotic factors) and allelopathy (chemical factors produced by another individual). A number of plants have been reported to possess inhibitory effects on the growth and population of neighboring or successional plants by releasing allelochemicals into the soil, either as exudates from living plant tissues or by decomposition of plant residues (Dayan et al. 2000).

Organic substances (allelochemicals) can affect cytological and ultrastructural structures, concentration and hormonal balance, permeability and selectivity of cell membranes, mineral absorption, movement of stomata, synthesis of pigments, photosynthesis, respiration, protein synthesis, enzymatic activity, water relations, and changes in DNA and RNA (Rizvi et al. 1992; Abu-Romman et al. 2010; Hussain and Reigosa 2011). These processes constitute the results of the action of the allelochemicals, which act directly, or, in the signaling of cell degradation processes, through the production and accumulation of ROS resulting in cellular oxidative stress (Bogatek and Gniazdowska 2007; Qian et al. 2009). Carotenoids are pigments responsible for the quenching of ¹O₂ (Knox and Dodge 1985).

Ibrahim et al. (2013) reported that the carotenoid content was significantly decreased in wheat in the presence of aqueous extract of *Zea mays*. Root exudates from sorghum were reported to inhibit the activity of hydroxyphenyl pyruvate dioxygenase, which resulted in plastoquinone deficiency and, therefore, disrupted the biosynthesis of carotenoids (Meazza et al. 2002). Romagni et al. (2000) reported that usnic acid is a strong inhibitor of the PDS enzyme, which converts phytoene to carotenoids.

Ladhari et al. (2014) reported aqueous extracts of leaves from *Capparis spinosa* L. and the siliquae of *Cleome arabica* L. exhibited a cytotoxic effect in root tip cells, with a morphological modification and necrosis phenomena, which correlated with a drastic reduction of mitotic index in lettuce; the photosynthetic pigments, including chlorophyll and carotenoids, were maintained by the functional regulation of proline in the cellular levels.

Algandaby and El-Darier (2016) tested the biological activity of aqueous extracts of *Achillea santolina* L., *Artemisia monosperma* Del., and *Thymus capitatus* L. on germination of *Medicago polymorpha* seeds and showed inhibitory

activity in the leaf area index, total photosynthetic pigment and chlorophyll a, while carotenoids exhibited a slight increase. Allelochemicals present in *Sesamum indicum* leachate inhibited sprouting of tubers of the *Cyperus rotundus* L. In the pot culture, the numbers of leaves, plant height, dry weight, photosynthetic pigments chlorophyll a, b and carotenoids and protein decreased with the increase in the concentration of *S. indicum* leaf leachate (Hussain et al. 2017).

Hydroquinone, a phytotoxin, is toxic to rice. The hydroquinone at lethal concentration caused loss of cellular membrane integrity, loss of macromolecules (including chlorophyll and carotenoids, and enzyme activity) resulting in a drastic reduction in key metabolic processes (Pandey et al. 2005).

9 Signaling Mechanisms of Carotenoids During Plant Stress

9.1 Signaling and Bio-communication

Carotenoids are sources of bioactive compounds in different organisms. These compounds serve as signaling molecules and have been implicated to have a role in the interactions of plants with their surrounding environment (Esteban et al. 2015). Carotenoids play an important role in sensing and signaling oxidative stress, such as chemical oxidation of β -carotene by $^1\text{O}_2$, forming a wide variety of products. Among these compounds, those with small chains are volatile carotene derivatives, including: β -Cyc, β -ionone, α -ionone and dihydroactinidiolide (Esteban et al. 2015). At least two of them, β -Cyc and dihydroactinidiolide, are involved in the $^1\text{O}_2$ -induced changes in gene expression associated with an increased tolerance to photo-oxidative stress and photo-acclimation (Esteban et al. 2015). Because β -carotene oxidation in the reaction centers is an early event during light stress, these volatile oxidation metabolites are primary sensors of high light stress in plants. The presence of β -Cyc around cyanobacteria colonies (*Microcystis*) has been identified as repellent of the grazing behaviour of *Daphnia*. Some phytohormones are also carotenoid derivatives, such as ABA and strigolactones. The role of ABA on seed germination, maturation and acclimation to environmental stresses has been previously reported. On the other hand, strigolactones, previously known as seed germination stimulants of parasitic weeds (Esteban et al. 2015), have recently been proposed to be novel phytohormones, due to their regulatory functions involved in the control of root-hair formation, shoot branching and the interaction with other hormones. However, when exuded into the rhizosphere, they play some other roles regulating both parasitic and recognition signals in the symbiotic association between plants and arbuscular mycorrhizal (AM) fungi. Other volatile apocarotenoids such as cyclohexenone and mycorradicins derivatives play a role as attractors of seed dispersers and pollinators in fruits and flowers. In roots, their fungi toxic and antimicrobial properties control the functionality of AM

symbiosis, by regulating the turnover of arbuscules, the nutrient-exchange structures of AM fungi in root cells (Esteban et al. 2015). Other volatile carotenoid derivatives, such as 3-hydroxy- β -ionone, play significant roles as allelochemicals in biotic interactions. In plants, β -ionone has a role as antimicrobial metabolite and it regulates plant and herbivorous insect interaction acting as feeding deterrents. Plant signals of color, fragrance and flavor of flowers and fruit are also due to molecules derived from carotenoids oxidation. The color of fruits can be a signal of ripeness or nutritional value, but it also could be a reward itself for some frugivores, since carotenoids are visual signals in some animals for tegument pigmentation (Esteban et al. 2015).

A first level of regulation of carotenoid accumulation in plants is the control of the transcription of biosynthetic genes. Recent reports have shown that the expression of the *Arabidopsis thaliana* gene encoding PHYTOENE SYNTHASE (PSY), the first and main rate-determining enzyme of the carotenoid pathway (Ruiz-Sola and Rodríguez-Concepción 2012), is under the direct control of two transcription factors involved in the transduction of light signals: PHYTOCHROME-INTERACTING FACTOR1 (PIF1) and LONG HYPOCOTYL5 (HY5; Toledo-Ortiz et al. 2010, 2014). PIF1, a basic helix-loop-helix (bHLH) protein, and other members of the so-called PIF quartet (formed of PIF1, PIF3, PIF4 and PIF5, collectively referred to as PIFq), accumulates in the dark and is degraded in the light (Leivar et al. 2008; Leivar and Quail 2011). However, HY5 belongs to the basic Leucine zipper (bZIP) family, accumulates in light, and is degraded in the dark (Lau and Deng 2010). PIFq and HY5 act antagonistically for a broad set of responses (Kami et al. 2010; Lau and Deng 2010; Leivar and Quail 2011; Chen et al. 2013), including the control of PSY expression and carotenoid biosynthesis (Toledo-Ortiz et al. 2010, 2014). PIF1 (repressor) and HY5 (activator) were demonstrated to bind to the same G-box motif in the promoter of PSY, forming a dynamic repression–activation transcriptional module that provides robustness in response to light but also to temperature cues (Toledo-Ortiz et al. 2014).

Bou-Torrent et al. (2015) found that PIF1 promotes the shade-triggered decrease in carotenoid accumulation. While HY5 does not appear to be required for this process, other known PIF antagonists were found to modulate the expression of *A. thaliana* PSY gene and the biosynthesis of carotenoids early after exposure to shade. In particular, PHYTOCHROME-RAPIDLY REGULATED1, a transcriptional cofactor that prevents the binding of true transcription factors to their target promoters, was found to interact with PIF1 and hence directly induce PSY expression. By contrast, a change in the levels of the transcriptional cofactor LONG HYPOCOTYL IN FAR RED1, which also binds to PIF1 and other PIFs to regulate shade-related elongation responses, did not impact PSY expression or carotenoid accumulation. Our data suggest that the fine-regulation of carotenoid biosynthesis in response to shade relies on specific modules of antagonistic transcriptional factors and cofactors.

10 Future Perspectives and Concluding Remarks

An understanding of crop growth and development under different kinds of stress is fundamental to improving crop productivity and sustainability through both breeding and management, and especially for the dramatic adaptations that will be needed to confront climate change. In this regard, carotenoids are and will continue to play a great importance for plant survival. More direct research is needed in order to attain a better understanding the role of carotenoids in each type of plant stress discussed in this study. Special attention must be given to the effect of greenhouse gases in carotenoid signaling.

References

- Abdel-Latef AAH, Abu-Alhmad MF (2013) Strategies of copper tolerance in root and shoot of broad bean (*Vicia faba* L.). Pak J Agri Sci 50:223–328
- Abu-Romman S, Shatnawi M, Shibli R (2010) Allelopathic effects of spurge (*Euphorbia hierosolymitana*) on wheat (*Triticum durum*). Am Eur J Agri Environ Sci 7:298–302
- Ahmad P, Latef AAA, Abdallah EF, Hashem A, Sarwat M, Anjum NA, Gucel S (2016) Calcium and potassium supplementation enhanced growth, osmolyte secondary metabolite production, and enzymatic antioxidant machinery in cadmium-exposed chickpea (*Cicer arietinum* L.). Front Plant Sci 7:513
- Ahn C, Pai H (2008) Physiological function of IspE, a plastid MEP pathway gene for isoprenoid biosynthesis, in organelle biogenesis and cell morphogenesis in *Nicotiana benthamiana*. Plant Mol Biol 66:503–517
- Akcin A, Yalcin E (2016) Effect of salinity stress on chlorophyll, carotenoid content, and proline in *Salicornia prostrata* Pall. and *Suaeda prostrata* Pall. subsp. *prostrata* (Amaranthaceae). Braz J Bot 39:101–106
- Al Hassan M, Martínez Fuertes M, Ramos Sánchez FJ, Vicente O, Boscaiu M (2015) Effects of salt and water stress on plant growth and on accumulation of osmolytes and antioxidant compounds in cherry tomato. Notul Bot Horti Agrobotanici Cluj-Napoca 43:1–11
- Al Hassan M, Lopez-Gresa MP, Boscaiu M, Vicente O (2016) Stress tolerance mechanisms in *Juncus*: responses to salinity and drought in three *Juncus* species adapted to different natural environments. Funct Plant Biol 43:949–960
- Al Hassan M, Chaura J, Donat-Torres M, Boscaiu M, Vicente O (2017) Antioxidant responses under salinity and drought in three closely related wild monocots with different ecological optima. AoB Plant 9(2)
- Algandaby M, El-Darier S (2016) Management of the noxious weed; *Medicago polymorpha* L. via allelopathy of some medicinal plants from Taif region, Saudi Arabia. Saud J Biol Sci <https://doi.org/10.1016/j.sjbs.2016.02.013>
- Arivalagan M, Somasundaram R (2015) Effect of popiconazole and salicylic acid on the growth and photosynthetic pigments variations in *Sorghum bicolor* L. under drought condition. J Plant Stress Physiol 7:17–23
- Ashraf MA (2012) Waterlogging stress in plants: a review. Afr J Agri Res 7:1976–1981
- Bai C, Capell T, Berman J, Medina V, Sandmann G, Christou P, Zhu C (2016) Bottlenecks in carotenoid biosynthesis and accumulation in rice endosperm are influenced by the precursor-product balance. Plant Biotechnol J 15:195–205

- Ben Abdallah S, Aung B, Amyot L, Lalin I, Lachâal M, Karray-Bouraoui N, Hannoufa A (2016) Salt stress (NaCl) affects plant growth and branch pathways of carotenoid and flavonoid biosyntheses in *Solanum nigrum*. *Acta Physiol Plant* 38:72
- Berera R, Herrero C, van Stokkum I, Vengris M, Kodis G, Palacios RE, van Amerongen H, van Grondelle R, Gust D, Moore TA, Moore AL, Kennis JTM (2006) A simple artificial light-harvesting dyad as a model for excess energy dissipation in oxygenic photosynthesis. *Proc Natl Acad Sci USA* 103:5343–5348
- Berera R, van Stokkum I, d'Haene S, Kennis J, van Grondelle R, Dekker J (2009) A mechanism of energy dissipation in Cyanobacteria. *Biophys J* 96:2261–2267
- Berera R, van Stokkum I, Kennis J, Grondelle R, Dekker J (2010) The light-harvesting function of carotenoids in the cyanobacterial stress-inducible IsiA complex. *Chem Phys* 373:65–70
- BGS (2017) Man-made (anthropogenic) greenhouse gases | CCS | Climate change | Discovering Geology | British Geological Survey (BGS). [online] Bgs.ac.uk. Available at: <http://www.bgs.ac.uk/discoveringGeology/climateChange/CCS/Anthropogenic.html>. Accessed 19 Aug 2017
- Boden TA, Marland G, Andres RJ (2010) Global, regional, and national fossil-fuel CO₂ emissions. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., U.S.A.
- Bogatek R, Gniazdowska A (2007) ROS and phytohormones in plant-plant allelopathic interaction. *Plant Signal Behav* 2:317–318
- Bou-Torrent J, Toledo-Ortiz G, Ortiz-Alcaide M, Cifuentes-Esquivel N, Halliday K, Martinez-Garcia J, Rodriguez-Concepcion M (2015) Regulation of carotenoid biosynthesis by shade relies on specific subsets of antagonistic transcription factors and co-factors. *Plant Physiol* 169:1584–1594
- Brunetti C, Guidi L, Sebastiani F, Tattini M (2015) Isoprenoids and phenylpropanoids are key components of the antioxidant defense system of plants facing severe excess light stress. *Environ Exp Bot* 119:54–62
- Buchner O, Roach T, Gertzen J, Schenk S, Karadar M, Stöggel W, Miller R, Bertel C, Neuner G, Kranner I (2017) Drought affects the heat-hardening capacity of alpine plants as indicated by changes in xanthophyll cycle pigments, singlet oxygen scavenging, α -tocopherol and plant hormones. *Environ Exp Bot* 133:159–175
- Chang W, Song H, Liu H, Liu P (2013) Current development in isoprenoid precursor biosynthesis and regulation. *Curr Opin Chem Biol* 17:571–579
- Chen D, Xu G, Tang W, Jing Y, Ji Q, Fei Z, Lin R (2013) Antagonistic basic Helix-Loop-Helix/bZIP transcription factors form transcriptional modules that integrate light and reactive oxygen species signaling in Arabidopsis. *Plant Cell* 25:1657–1673
- Choudhary ML, Patel VB, Siddiqui WM, Verma RB (2015) Climate dynamics in horticultural science. Apple Academic Press, Oakville
- Choudhury S, Panda P, Sahoo L, Panda SK (2013) Reactive oxygen species signaling in plants under abiotic stress. *Plant Signal Behav* 8:e23681
- Cicevan R, Al Hassan M, Sestras A, Prohens J, Vicente O, Sestras R, Boscaiu M (2016) Screening for drought tolerance in cultivars of the ornamental genus *Tagetes* (Asteraceae). *Peer J* 4:e2133
- Corniani N, Velini E, Silva F, Nanayakkara N, Witschel M, Dayan F (2014) Novel bioassay for the discovery of inhibitors of the 2-C-Methyl-D-erythritol 4-Phosphate (MEP) and Terpenoid Pathways leading to carotenoid biosynthesis. *PLoS ONE* 9:e103704
- Couso I, Vila M, Vigarà J, Cordero B, Vargas M, Rodríguez H, León R (2012) Synthesis of carotenoids and regulation of the carotenoid biosynthesis pathway in response to high light stress in the unicellular microalga *Chlamydomonas reinhardtii*. *Europ J Phycol* 47:223–232
- Dayan FE, Romagni JG, Duke SO (2000) Investigation of the mode of action of natural phytotoxins. *J Chem Ecol* 26:2079–2094
- Doupis G, Bertaki M, Psarras G, Kasapakis I, Chartzoulakis K (2013) Water relations, physiological behavior and antioxidant defence mechanism of olive plants subjected to different irrigation regimes. *Scient Horticult* 153:150–156
- Eisenreich W, Rohdich F, Bacher A (2001) Deoxyxylulose phosphate pathway to terpenoids. *Trend Plant Sci* 6:78–84

- Esmon C, Pedmale U, Liscum E (2005) Plant tropisms: providing the power of movement to a sessile organism. *Int J Develop Biol* 49:665–674
- Esteban R, Moran J, Becerril J, García-Plazaola J (2015) Versatility of carotenoids: an integrated view on diversity, evolution, functional roles and environmental interactions. *Environ Exp Bot* 119:63–75
- Ferreira AG (2004) Interferência: competição e alelopatia. In: Ferreira AG, Borghetti F (eds) *Germinação: Do básico ao aplicado*. Artmed, Porto Alegre, pp 251–262
- Fiedor J, Burda K (2014) Potential role of carotenoids as antioxidants in human health and disease. *Nutrients* 6:466–488
- Flores-Pérez Ú, Pérez-Gil J, Closa M, Wright L, Botella-Pavía P, Phillips MA, Ferrer A, Gershenzon J, Rodríguez-Concepción M (2010) Pleiotropic regulatory Locus 1 (PRL1) integrates the regulation of sugar responses with Isoprenoid metabolism in *Arabidopsis*. *Mol Plant* 3:101–112
- Frank H, Cogdell R (1996) Carotenoids in photosynthesis. *Photochem Photobiol* 63:257–264
- García-Plazaola J, Portillo-Estrada M, Fernández-Marín B, Kännaste A, Niinemets Ü (2017) Emissions of carotenoid cleavage products upon heat shock and mechanical wounding from a foliose lichen. *Environ Exp Bot* 133:87–97
- Gómez-García M, Ochoa-Alejo N (2013) Biochemistry and molecular biology of carotenoid biosynthesis in Chili Peppers (*Capsicum* spp.). *Int J Mol Sci* 14:19025–19053
- Grene R, Li P, Bohnert H (2010) Elevated CO₂ and ozone: their effects on photosynthesis. In: Rebeiz C, Benning C, Bohnert H, Daniell H, Hooper J, Lichtenthaler H, Portis A, Tripathy B (eds) *The chloroplast: basics and applications*. Springer, Berlin, pp 323–346
- Griffiths M, Sistrom W, Cohen-Bazire G, Stanier R (1995) Function of carotenoids in photosynthesis. *Nature* 176:1211–1214
- Gul H, Kinza S, Shinwari ZK, Hamayun M (2017) Effect of selenium on the biochemistry of *Zea mays* under salt stress. *Pak J Bot* 49:25–32
- Gupta B, Huang B (2014) Mechanism of salinity tolerance in plants: physiological, biochemical, and molecular characterization. *Int J Genom Article ID:701596*
- Hammad SAR, Ali OAM (2014) Physiological and studies on drought tolerance of wheat plants by application of amino acids and yeast extract. *Ann Agric Sci* 59:133–145
- Havaux M (2013) Carotenoid oxidation products as stress signals in plants. *Plant J* 79:597–606
- He B, Guo T, Huang H, Xi W, Chen X (2017) Physiological responses of *Scaevola aemula* seedlings under high temperature stress. *S Afr J Bot* 112:203–209
- Hussain MI, Reigosa MJ (2011) Allelochemical stress inhibits growth, leaf water relations, PSII photochemistry, non-photochemical fluorescence quenching, and heat energy dissipation in three C3 perennial species. *J Exp Bot* 62:453–4545
- Hussain I, Singh N, Singh A, Singh H (2017) Allelopathic potential of sesame plant leachate against *Cyperus rotundus* L. *Ann Agrar Sci* 15:141–147
- Ibrahim M, Ahmad N, Shinwari-Khan Z, Bano A, Ullah F (2013) Allelopathic assessment of genetically modified and non-modified maize (*Zea mays* L.) on physiology of wheat (*Triticum aestivum* L.). *Pak J Bot* 45:235–240
- Jackson M (2015) Elevated temperature effects on carotenoid biosynthesis in the diploid strawberry, *Fragaria vesca*. Ph.D. Thesis, University of Maryland, USA
- Jain R, Singh A, Singh S, Singh SP, Srivastava VK, Chandra A, Pathak AD, Solomon S (2017) Physio-Biochemical characterization of sugarcane genotypes for waterlogging tolerance. *World J Agric Sci* 13:90–97
- Jin C, Ji J, Zhao Q, Ma R, Guan C, Wang G (2015) Characterization of lycopene β -cyclase gene from *Lycium chinense* conferring salt tolerance by increasing carotenoids synthesis and oxidative stress resistance in tobacco. *Mol Breed* 35:228
- Joyard J, Ferro M, Masselon C, Seigneurin-Berny D, Salvi D, Garin J, Rolland N (2009) Chloroplast proteomics and the compartmentation of plastidial isoprenoid biosynthetic pathways. *Mol Plant* 2:1154–1180

- Juneja A, Ceballos R, Murthy G (2013) Effects of environmental factors and nutrient availability on the biochemical composition of algae for biofuels production: a review. *Energies* 6:4607–4638
- Kami C, Lorrain S, Hornitschek P, Fankhauser C (2010) Light-regulated plant growth and development. *Curr Top Develop Biol* 91:29–66
- Kang L, Ji CY, Kim SH, Ke Q, Park SC, Kim HS, Lee HU, Lee JS, Park WS, Ahn MJ, Lee HS, Deng X, Kwak SS (2017) Suppression of the β -carotene hydroxylase gene increases β -carotene content and tolerance to abiotic stress in transgenic sweetpotato plants. *Plant Physiol Biochem* 117:24–33
- Karnosky D, Ceulemans R, Scarascia-Mugnozza G, Innes J (2001) The impact of carbon dioxide and other greenhouse gases on forest ecosystems. IUFRO Series, No. 8. CAB International, Wallingford
- Kim SH, Kim YH, Ahn YO, Ahn MJ, Jeong JC, Lee HS, Kwak SS (2013) Downregulation of the lycopene ϵ {lunate}-cyclase gene increases carotenoid synthesis via the β -branch-specific pathway and enhances salt-stress tolerance in sweet potato transgenic calli. *Physiol Plant* 147:432–442
- Kim SH, Jeong JC, Park S, Bae JY, Ahn MJ, Lee HS, Kwak SS (2014) Down-regulation of sweetpotato lycopene β -cyclase gene enhances tolerance to abiotic stress in transgenic calli. *Mol Biol Rep* 41:8137–8148
- Kiokias S, Proestos C, Varzakas T (2016) A review of the structure, biosynthesis, absorption of carotenoids-analysis and properties of their common natural extracts. *Curr Res Nutr Food Sci* 4:25–37
- Knox J, Dodge A (1985) Isolation and activity of the photodynamic pigment hypericin. *Plant Cell Environ* 8:19–25
- Kumar P, Pal M, Joshi R, Sairam RK (2013) Yield, growth and physiological responses of mung bean [*Vigna radiate* (L.) Wilczek] genotypes to waterlogging at vegetative stage. *Physiol Mol Biol Plant* 19:209–220
- Kuzuyama T, Seto H (2012) Two distinct pathways for essential metabolic precursors for isoprenoid biosynthesis. *Proc Japan Acad Ser B* 88:41–52
- Ladhari A, Omezzine F, Haouala R (2014) The impact of Tunisian Capparidaceae species on cytological, physiological and biochemical mechanisms in lettuce. *S Afr J Bot* 93:222–230
- Lau O, Deng X (2010) Plant hormone signaling lightens up: integrators of light and hormones. *Curr Opin Plant Biol* 13:571–577
- Leivar P, Quail P (2011) PIFs: pivotal components in a cellular signaling hub. *Trend Plant Sci* 16:19–28
- Leivar P, Monte E, Al-Sady B, Carle C, Storer A, Alonso J, Ecker JR, Quail PH (2008) The Arabidopsis phytochrome-interacting factor PIF7, together with PIF3 and PIF4, regulates responses to prolonged red light by modulating phyB levels. *Plant Cell* 20:337–352
- León-Chan R, López-Meyer M, Osuna-Enciso T, Sañudo-Barajas J, Heredia J, León-Félix J (2017) Low temperature and ultraviolet-B radiation affect chlorophyll content and induce the accumulation of UV-B-absorbing and antioxidant compounds in bell pepper (*Capsicum annuum*) plants. *Environ Exp Bot* 139:143–151
- Li R, Kang C, Song X, Yu L, Liu D, He S, Zhai H, Liu Q (2017) A ζ -carotene desaturase gene, *IbZDS*, increases β -carotene and lutein contents and enhances salt tolerance in transgenic sweetpotato. *Plant Sci* 262:39–51
- Lipko A, Swiezewska E (2017) Isoprenoid generating systems in plants-A handy toolbox how to assess contribution of the mevalonate and methylerythritol phosphate pathways to the biosynthetic process. *Prog Lipid Res* 63:70–92
- Liu RQ, Xu XJ, Wang S, Shan CJ (2015) Lanthanum improves salt tolerance of maize seedlings. *Photosynthetica* 54:148–151
- Llorente B, Martínez-García J, Stange C, Rodríguez-Concepción M (2017) Illuminating colors: regulation of carotenoid biosynthesis and accumulation by light. *Curr Opin Plant Biol* 37:49–55

- Ma G, Zhang L, Matsuta A, Matsutani K, Yamawaki K, Yahata M, Wahyudi A, Motohashi R, Kato M (2013) Enzymatic formation of citraurin from Cryptoxanthin and Zeaxanthin by carotenoid cleavage dioxygenase4 in the flavedo of citrus fruit. *Plant Physiol* 163:682–695
- Majer E, Llorente B, Rodríguez-Concepción M, Daròs J (2017) Rewiring carotenoid biosynthesis in plants using a viral vector. *Sci Rep* 7:41645
- Manivannan P, Rabert GA, Rajasekar M, Somasundaram R (2014) Drought stress-induced modification on growth and pigments composition in different genotypes of *Helianthus annuus* L. *Curr Bot* 5:7–13
- Maryland G, Boden TA, Andres RJ (2008) Global, regional and national fossil fuel CO₂ emissions. In: Trends: a compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tenn., USA
- Mattos LM, Moretti CL (2016) Oxidative stress in plants under drought conditions and the role of different enzymes. *Enzym Eng* 5:136
- Maurya KV, Srinivasan R, Ramesh N, Anbalagan M, Gothandam KM (2015) Expression of carotenoid pathway genes in three capsicum varieties under salt stress. *Asian J Crop Sci* 7:286–294
- Meazza G, Scheffler BE, Tellez MR, Rimando AM, Nanayakkara NPD, Khan IA, Abourashed EA, Romagni JG, Duke SO, Dayan FE (2002) The inhibitory activity of natural products on plant *p*-hydroxyphenylpyruvate dioxygenase. *Phytochemistry* 59:281–288
- Melo HF, de Souza ER, Duarte HHF, Cunha JC, Santos HRB (2017) Gas exchange and photosynthetic pigments in bell pepper irrigated with saline water. *Revist Brasil Engen Agrícola Ambient* 21:38–43
- Mibei E, Ambuko J, Giovannoni J, Onyango A, Owino W (2016) Carotenoid profiling of the leaves of selected African eggplant accessions subjected to drought stress. *Food Sci Nutr* 5:113–122
- Moussa ID, Chtourou H, Karray F, Sayadi S, Dhoubi A (2017) Nitrogen or phosphorus repletion strategies for enhancing lipid or carotenoid production from *Tetraselmis marina*. *Biores Technol* 238:325–332
- NCBI (2017) National Center for Biotechnology Information. U.S. National Library of Medicine, 8600 Rockville Pike, Bethesda, MD20894, USA. Available at: https://pubchem.ncbi.nlm.nih.gov/compound/isopentenyl_pyrophosphate#section=Chemical-and-Physical-Properties. Accessed on 13-06-2017
- Nisar N, Li L, Lu S, Khin N, Pogson B (2015) Carotenoid metabolism in plants. *Mol Plant* 8:68–82
- Odom A (2011) Five Questions about non-mevalonate isoprenoid biosynthesis. *PLoS Patho* 7: e1002323
- Ozcubukcu S, Ergun N (2013) Effects of waterlogging and nitric oxide on chlorophyll and carotenoid pigments of wheat. *J Food Agric Environ* 11:2319–2323
- Paliwal C, Mitra M, Bhayani K, Bharadwaj S, Ghosh T, Dubey S, Mishra S (2017) Abiotic stresses as tools for metabolites in microalgae. *Biores Technol* 244:1216–1226
- Pandey D, Mishra N, Singh P (2005) Relative phytotoxicity of hydroquinone on rice (*Oryza sativa* L.) and associated aquatic weed green musk chara (*Chara zeylanica* Wild.). *Pest Biochem Physiol* 83:82–96
- Percival G (2017) The influence of glyphosate on carotenoid pigments, reactive oxygen species scavenging enzymes and secondary stress metabolites within leaf tissue of three *Acer* species. *Urban Forest Urban Green* 24:19–25
- Perlík V, Seibt J, Cranston L, Cogdell R, Lincoln C, Savolainen J, Sanda F, Mancal T, Hauer J (2015) Vibronic coupling explains the ultrafast carotenoid-to-bacteriochlorophyll energy transfer in natural and artificial light harvesters. *J Chem Phys* 142:212434
- Phillips M, Leon P, Boronat A, Rodríguez-Concepción M (2008) The plastidial MEP pathway: unified nomenclature and resources. *Trend Plant Sci* 13:619–623
- Polivka T, Sundstrom V (2004) Ultrafast dynamics of carotenoid excited states-from solution to natural and artificial systems. *Chem Inform* 35(24)

- Pulido P, Perello C, Rodriguez-Concepcion M (2012) New insights into plant Isoprenoid metabolism. *Mol Plant* 5:964–967
- Qian H, Xu X, Chen W, Jiang H, Jin Y, Liu W, Fu Z (2009) Allelochemical stress causes oxidative damage and inhibition of photosynthesis in *Chlorella vulgaris*. *Chemosphere* 75:368–375
- Ramvalho JC, Zlatev ZS, Leitão AE, Pais IP, Fortunato AS, Lidon FC (2014) Moderate water stress causes different stomatal and non-stomatal changes in the photosynthetic functioning of *Phaseolus vulgaris* L. genotypes. *Plant Biol* 16:133–146
- Ramel F, Birtic S, Cuine S, Triantaphylides C, Ravanat JL, Havaux M (2012) Chemical quenching of singlet oxygen by carotenoids in plants. *Plant Physiol* 158:1267–1278
- Ramos A, Coesel S, Marques A, Rodrigues M, Baumgartner A, Noronha J, Rauter A, Brenig B, Varela J (2008) Isolation and characterization of a stress-inducible *Dunaliella salina* Lcy- β gene encoding a functional lycopene β -cyclase. *App Microbiol Biotechnol* 79:819–828
- Rebeiz C, Benning C, Bohnert H, Daniell H, Hoober K, Lichtenthaler H, Portis A (2010) The chloroplast. Springer, Berlin
- Rhodes D, Nadolska-Orczyk A (2001) Plant stress physiology. In: Encyclopedia of life sciences. Wiley, Chichester
- Rizvi SJH, Haque H, Singh UK, Rizvi V (1992) A discipline called allelopathy. In: Rizvi SJH, Rizvi H (eds) Allelopathy: basic and applied aspects. Chapman & Hall, London, pp 1–10
- Rodríguez-Concepción M (2014) Plant isoprenoids: a general overview. In: Concepcion MR (ed) Plants isoprenoids: method and protocols. Springer, Berlin, pp 1–5
- Romagni J, Duke S, Dayan F (2000) Inhibition of plant asparagine synthetase by monoterpene cineoles. *Plant Physiol* 123:725–732
- Ruiz-Sola M, Rodríguez-Concepción M (2012) Carotenoid biosynthesis in Arabidopsis: a colorful pathway. *Arab Book* 10:e0158
- Savoi S, Wong DCJ, Arapitsas P, Miculan M, Bucchetti B, Peterlunger E, Fait A, Mattivi F, Castellarin SD (2016) Transcriptome and metabolite profiling reveals that prolonged drought modulates the phenylpropanoid and terpenoid pathway in white grapes (*Vitis vinifera* L.). *BMC Plant Biol* 16:67
- Schenck C, Nadella V, Clay S, Lindner J, Abrams Z, Wyatt S (2013) A proteomics approach identifies novel proteins involved in gravitropic signal transduction. *Amer J Bot* 100:194–202
- Schiop S, Al Hassan M, Sestras A, Boscaiu M, Sestras R, Vicente O (2015) Identification of salt stress biomarkers in Romanian Carpathian populations of *Picea abies* (L.) Karst. *PLoS ONE* 10:e0135419
- Schweiggert R, Ziegler J, Metwali E, Mohamed F, Almaghrabi O, Kadasa N, Carle R (2017) Carotenoids in mature green and ripe red fruits of tomato (*Solanum lycopersicum* L.) grown under different levels of irrigation. *Arch Biol Sci* 69:305–314
- Seemann M, Tse Sum Bui B, Wolff M, Miginiac-Maslow M, Rohmer M (2006) Isoprenoid biosynthesis in plant chloroplasts via the MEP pathway: Direct thylakoid/ferredoxin-dependent photoreduction of GcpE/IspG. *FEBS Lett* 580:1547–1552
- Shankar V, Kumar D, Agrawal V (2015) Assessment of antioxidant enzyme activity and mineral nutrients in response to NaCl stress and its amelioration through glutathione in chickpea. *Appl Biochem Biotechnol* 178:267–284
- Sharma P, Hall D (1993) The role of carotenoids in protection against photoinhibition. In: Photosynthesis: Photoreactions to Plant Productivity [online], pp 469–478. Available at: . Accessed 19 Aug 2017
- Shen J, Jiang C, Yan Y, Liu B, Zu C (2017) Effect of increased UV-B radiation on carotenoid accumulation and total antioxidant capacity in tobacco (*Nicotiana tabacum* L.) leaves. *Genet Mol Res* 16(1)
- Shi Y, Guo J, Zhang W, Jin L, Liu P, Chen X, Li F, Wei P, Li Z, Li W, Wei C, Zheng Q, Chen Q, Zhang J, Lin L, Snyder JH, Wang R (2015a) Cloning of the Lycopene β -cyclase gene in *Nicotiana tabacum* and its overexpression confers salt and drought tolerance. *Int J Mol Sci* 16:30438–30457

- Shi Y, Liu P, Xia Y, Wei P, Li W, Zhang W, Chen X, Cao P, Xu Y, Jin L, Li F, Luo Z, Wei C, Zhang J, Xie X (2015b) Downregulation of the lycopene ϵ -cyclase gene confers tolerance to salt and drought stress in *Nicotiana tabacum*. *Acta Physiol Plant* 37:210
- Simova-Stoilova L, Demirevska K, Kingston-Smith A, Feller U (2012) Involvement of the leaf antioxidant system in the response to soil flooding in two *Trifolium* genotypes differing in their tolerance to waterlogging. *Plant Sci* 183:43–49
- Smirnoff N (2014) Plant stress physiology. In: *Encyclopedia of life sciences*. Wiley, Chichester
- Sudrajat DJ, Siregar IZ, Khumaida N, Siregar UJ, Mansur I (2015) Adaptability of White Jabon (*Anthocephalus cadamba* MIQ.) seedling from 12 populations to drought and waterlogging. *Agrivita* 37:130–143
- Szymańska R, Ślesak I, Orzechowska A, Kruk J (2017) Physiological and biochemical responses to high light and temperature stress in plants. *Environ Exp Bot* 139:165–177
- Tabatabaei S, Ehsanzadeh P (2016) Photosynthetic pigments, ionic and antioxidative behaviour of hulled tetraploid wheat in response to NaCl. *Photosynthetica* 54:340–350
- Taïbi K, Taïbi F, Abderrahim LA, Ennajah A, Belkhdja M, Mulet JM (2016) Effect of salt stress on growth, chlorophyll content, lipid peroxidation and antioxidant defence systems in *Phaseolus vulgaris* L. *South Afr J Bot* 105:306–312
- Telfer A (2014) Singlet oxygen production by PSII under light stress: mechanism, detection and the protective role of β -Carotene. *Plant Cell Physiol* 55:1216–1223
- Tian F, Wang W, Liang C, Wang X, Wang G, Wang W (2017) Over accumulation of glycine betaine makes the function of the thylakoid membrane better in wheat under salt stress. *Crop J* 5:73–82
- Toledo-Ortiz G, Huq E, Rodriguez-Concepcion M (2010) Direct regulation of phytoene synthase gene expression and carotenoid biosynthesis by phytochrome-interacting factors. *Proc Natl Acad Sci USA* 107:11626–11631
- Toledo-Ortiz G, Johansson H, Lee K, Bou-Torrent J, Stewart K, Steel G, Rodriguez-Concepcion M, Halliday KJ (2014) The HY5-PIF regulatory module coordinates light and temperature control of photosynthetic gene transcription. *PLoS Genet* 10:e1004416
- Tritsch D, Hemmerlin A, Bach T, Rohmer M (2009) Plant isoprenoid biosynthesis via the MEP pathway: in vivo IPP/DMAPP ratio produced by (E)-4-hydroxy-3-methylbut-2-enyl diphosphate reductase in tobacco BY-2 cell cultures. *FEBS Lett* 584:129–134
- Statistica (2018) Cement production globally and in the U.S. from 2010 to 2017 (in million metric tons). Available at: <http://www.statista.com/statistics/219343/cement-production-worldwide> accessed on 11/02/2018
- Rammed Earth Consulting (2018) Cement and CO₂ Emissions. Available at: <http://rammedearthconsulting.com/rammed-earth-cement-co2.htm>. Accessed on 11/02/2018
- Uarrotta V, Severino R, Maraschin M (2011) Maize landraces (*Zea mays* L.): a new prospective source for secondary metabolite production. *Int J Agric Res* 6:218–226
- Vranová E, Coman D, Grussem W (2013) Network analysis of the MVA and MEP pathways for isoprenoid synthesis. *Annu Rev Plant Biol* 64:665–700
- Wang M, Shi S, Lin F, Hao Z, Jiang P, Dai G (2012) Effects of soil water and nitrogen on growth and photosynthetic response of manchurian ash (*Fraxinus mandshurica*) seedlings in Northeastern China. *PLoS ONE* 7:e30754
- Wong C, Teoh M, Phang S, Lim P, Beardall J (2015) Interactive effects of temperature and UV radiation on photosynthesis of *Chlorella* strains from Polar, temperate and tropical environments: differential impacts on damage and repair. *PLoS ONE* 10:e0139469
- Worrell E, Price L, Martin N, Hendriks C, Meida L (2001) Carbon dioxide emissions from the global cement industry. *Annu Rev Energy Environ* 26:303–329
- Wu J, Ji J, Wang G, Wu G, Diao J, Li Z, Chen X, Chen Y, Luo L (2015) Ecotopic expression of the *Lycium barbarum* β -carotene hydroxylase gene (*chyb*) enhances drought and salt stress resistance by increasing xanthophyll cycle pool in tobacco. *Plant Cell Tiss Organ Cult* 121:559–569
- Xu C, Mou B (2016) Responses of spinach to salinity and nutrient deficiency in growth, physiology, and nutritional value. *J Am Soc Hort Sci* 141:12–21

- Yadav RK, Sangwan RS, Sabir F, Srivastava AK, Sangwan NS (2014) Effect of prolonged water stress on specialized secondary metabolites, peltate glandular trichomes, and pathway gene expression in *Artemisia annua* L. *Plant Physiol Biochem* 74:70–83
- Young A (1991) The photoprotective role of carotenoids in higher plants. *Physiol Plant* 83:702–708
- Zhang P, Li Z, Lu L, Xiao Y, Liu J, Guo J, Fang F (2017) Effects of stepwise nitrogen depletion on carotenoid content, fluorescence parameters and the cellular stoichiometry of *Chlorella vulgaris*. *Spectrochim Acta Part A Mol Biomol Spectro* 181:30–38
- Zhao L, Chang W, Xiao Y, Liu H, Liu P (2013a) Methylerythritol phosphate pathway of isoprenoid biosynthesis. *Ann Rev Biochem* 82:497–530
- Zhao Q, Wang G, Ji J, Jin C, Wu W, Zhao J (2013) Over-expression of *Arabidopsis thaliana* β -carotene hydroxylase (*chyB*) gene enhances drought tolerance in transgenic tobacco. *J Plant Biochem Biotechnol* 23:190–198
- Zhao P, Liu P, Shao J, Li C, Wang B, Guo X, Yan B, Xia Y, Peng M (2014) Analysis of different strategies adapted by two cassava cultivars in response to drought stress: ensuring survival or continuing growth. *J Exp Bot* 66:1477–1488