Regulating Reactive Oxygen Species Concentrations in Plant Cells

Subjects: Biotechnology & Applied Microbiology

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Environmental factors, such as high light intensity, adverse temperature, drought, or soil salinity, are summarized as abiotic stresses and discriminated from biotic stresses that are exerted by pathogens and herbivores, for instance. It was an unexpected observation that overproduction of reactive oxygen species (ROS) is a common response to all kinds of stress investigated so far. ROS are important messengers in cell signaling, but exceeding a concentration threshold causes damage. This requires fine-tuning of ROS production and degradation rates. In general, there are two options to control cellular ROS levels, (I) ROS scavenging at the expense of antioxidant consumption and (II) enzyme-controlled degradation of ROS. As antioxidants are limited in quantity, the first strategy only allows temporarily buffering of a certain cellular ROS level. This way, it prevents spells of eventually damaging ROS concentrations.

Keywords: stress response ; ROS ; antioxidants

1. Introduction

Most plant species are sessile organisms. Individual plant communities can be characterized by the observed specific abundance pattern of plant species. Plant species dominating a location are optimally adapted to local growing conditions. They show a high growth rate and are able to spread and produce a high number of vigorous seeds [1]. The respective genetic potential allows plants to adapt to local growing conditions, but the growth rate is reduced if environmental factors differ from the plant's optimal demands. Such adverse factors limiting plant performance have been termed stress [2]. Thus, stress translates into "to much" or "not enough" of the respective factor. In some cases, certain stress is comprised of more than one component. This applies to salt stress, for instance: obviously, there is an ionic component affecting the membrane potential, but there is also an osmotic component because high salt concentrations inhibit water uptake [3]. Finally, if ions enter the cytosol, they can cause a secondary effect by affecting protein structure and catalytic activity of enzymes, for instance.

2. ROS Production

ROS-producing reactions can be categorized into three groups: (1) ROS production as a side reaction in metabolism, (2) ROS production as a response to pathogen attack (biotic stress response), and (3) ROS production during the abiotic stress response. In any of these cases, ROS (H_2O_2) functions as signaling compounds in addition to potentially damaging effects. Thus, ROS control cellular homeostasis and, this way, may stimulate adaptation to adverse growth conditions (contributing to the development of stress tolerance).

2.1. ROS Production in Metabolism

ROS are byproducts of metabolic activity. They are important regulators of cellular homeostasis, but their synthesis and storage have to be controlled to prevent ROS from eventually reaching toxic concentrations. In all cell compartments, non-enzymatic and enzymatic antioxidants are present to protect cell contents from ROS damage. ROS results in H_2O_2 production and is the most important component in signaling [4].

In peroxisomes and glyoxysomes, oxidase activities were found. In leaves, the glycolate oxidase is among the most active enzymes [5]. It is involved in the photorespiration pathway (**Figure 1**). Further oxidase activities are linked to fatty acid oxidation (acyl-CoA oxidase) and polyamide and purine metabolism, for instance. While photorespiration-dependent oxidase activity is dominant in green tissues in the light, high rates of H_2O_2 production can be found in glyoxysomes of germinating oil seeds.

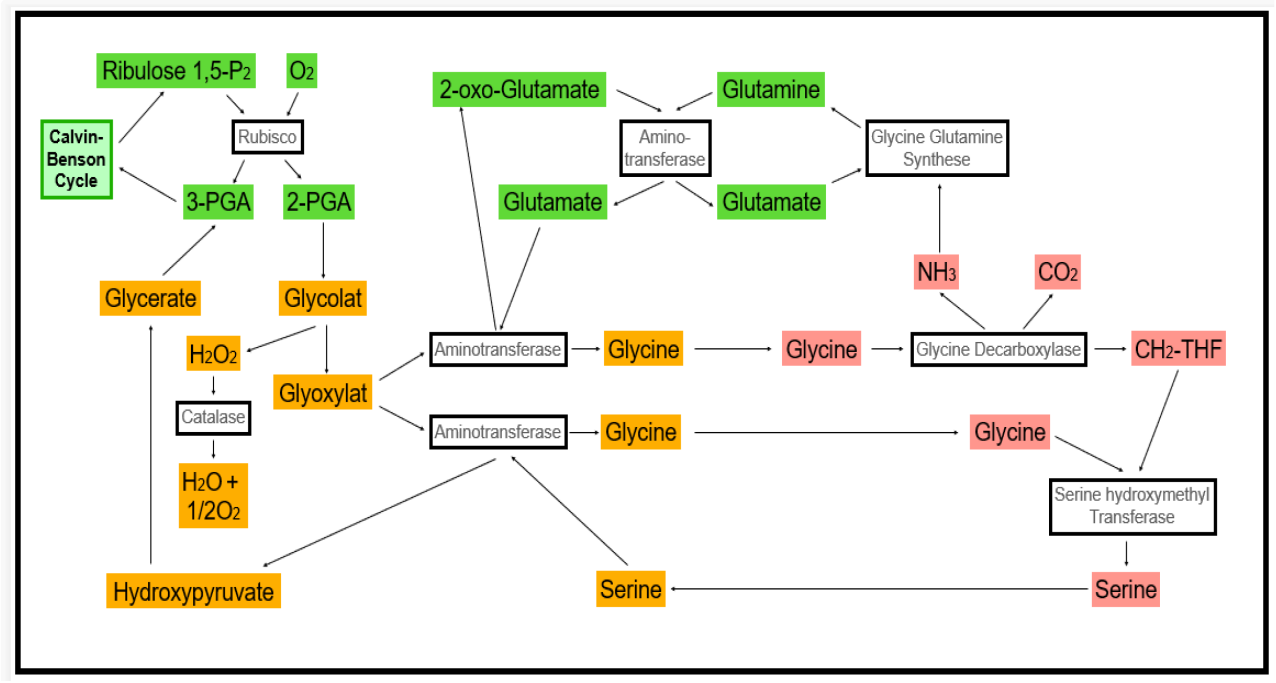

Figure 1. Metabolic interaction of cell compartments during photorespiration.

In chloroplasts and mitochondria, ROS are generated by electron transport activity (**Figure 2**). While photosynthetic electron transport and oxygen are competing for electrons released from light-activated chlorophyll in photosystem II, the Mehler reaction dominates oxygen reduction by photosystem I activity [6]. The probability of flavin-containing dehydrogenase catalyzed ROS production in mitochondria is increasing with the electron transport rate [7][8].

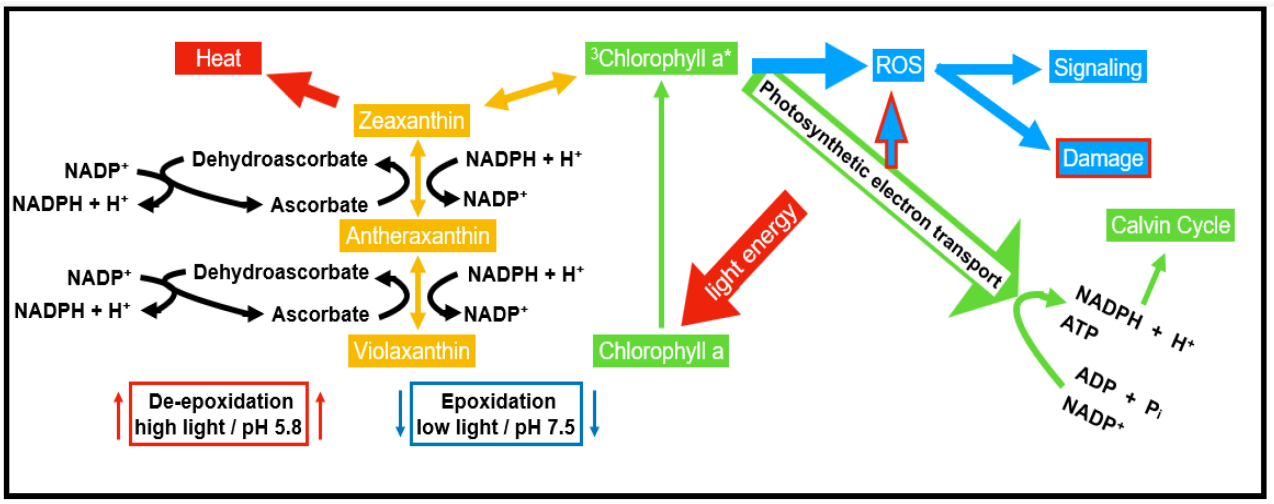

Figure 2. Absorption and display of energy in reaction centers and light-harvesting complexes. Chlorophyll a* in its triplet state is sufficiently stable to allow electron transfer reactions to redox components of the electron transport chain.

The NADPH-dependent oxidase is the most important source for ROS production at the plasma membrane. It has a major function in pathogen induce oxidative burst as described below.

2.2. ROS Production as a Response to Pathogen Attack

Plant defense reactions initiated by pathogen attacks are complex. Production of huge amounts of ROS is among the immediate observable effects [9]. The origin of produced ROS has been (and still is) a matter of debate. The observed effect has a lot in common with the well-known oxidative burst that can be observed after bacterial infection of animals [10]. For instance, it was observed that plant cells respond to ROS application with a hypersensitive response.

In this case, cell death can be microscopically observed in the infected area subsequent to the pathogen attack. This phenotype depends on the plant's biochemistry rather than the activities of the pathogen. Pathogen recognition initiates ROS production in several subcellular compartments. Apparently, this response is started by ROS released out of chloroplasts, while plasma membrane NADPH oxidase only subsequently responds [11][12]. Nevertheless, NADPH oxidase activity is important for spreading hypersensitive responses from one cell to neighboring ones [13]. Hypersensitive

response-related plant genes were named R genes by plant breeders because the respective activity was found to improve pathogen resistance [14]. Among the gene, functions are control of ROS production, control of autophagy, and coding for compounds of ROS signaling pathways.

The hypersensitive response can be suppressed in plant cell cultures by the addition of ROS scavenging enzymes, such as superoxide dismutase and catalase [15]. Thus, while the response can be clearly seen, results indicate that there are several ROS producers involved. Apparently, which of the potential producers are dominant in ROS production depends on plant species and the anatomical location of pathogen attack [16].

2.3. Abiotic Stress-Induced ROS Production

The metabolic flux, i.e., the consumption of assimilates released from chloroplasts in the light, is inhibited under stress, and the probability of light-induced ROS production increases (**Figure 1**) [17][18].

Sink regulation of photosynthetic activity is dependent on the physiological state of the plant. In other words, the plant is integrating adverse stress effects occurring at the same time on the basis of assimilating supply to sink organs [19]. Feedback inhibition of photosynthesis increases the probability of ROS production. ROS functions as messengers in retrograde gene regulation in the nucleus, but increasing ROS concentrations causes damage to cell components.

3. Components Controlling the ROS Level in Plants

3.1. Major Antioxidants Involved

3.1.1. Ascorbic Acid (Vitamin C)

Ascorbate is thought to be the most abundant antioxidant [20]. It interacts with other antioxidants, thus forming an antioxidant network (**Figure 3**) [21]. Phosphorylated sugars and nucleotide-linked sugars of the cytosolic carbohydrate pool are substrates for ascorbate synthesis, while the last steps of ascorbate synthesis take place inside the mitochondria [22]. Several pathways leading to ascorbate formation were identified, but it is generally agreed that the Smirnow–Wheeler pathway is the most important one for ascorbate biosynthesis in plants (**Figure 4**) [23].

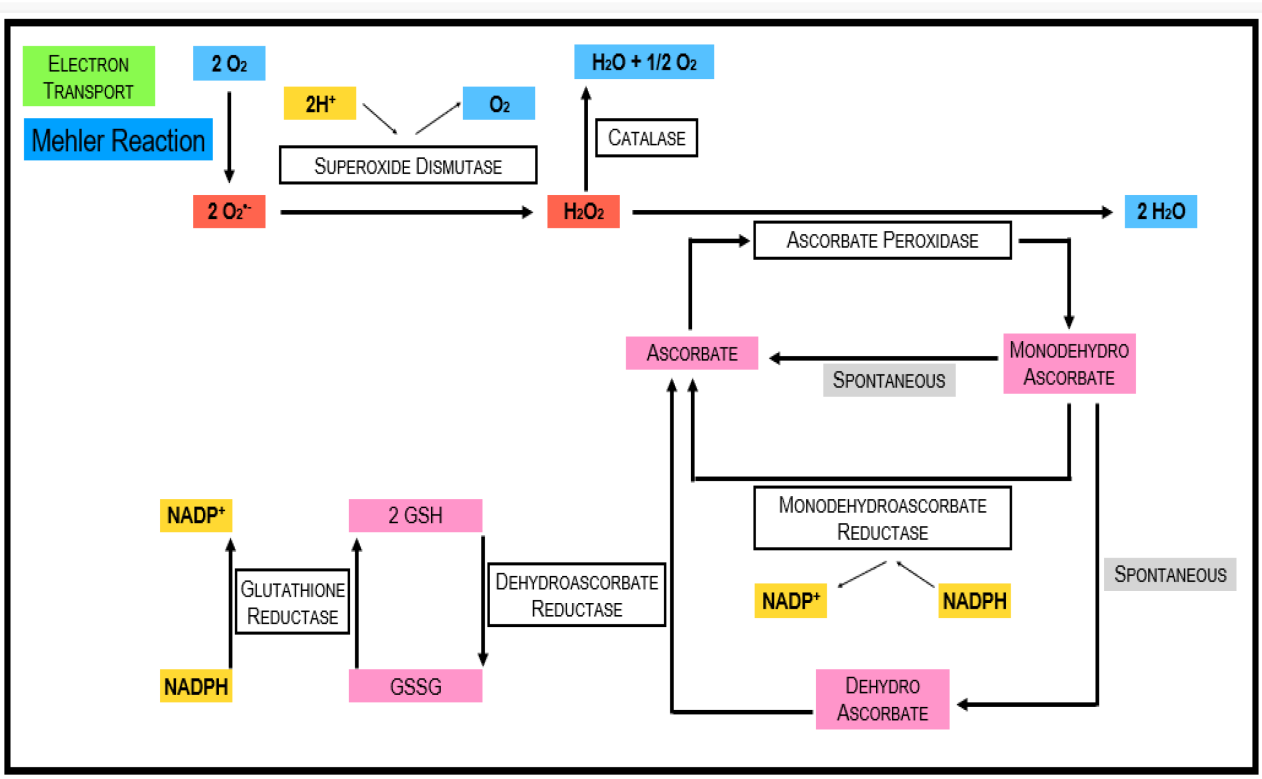

Figure 3. Scavenging of ROS. The figure demonstrates two alternative pathways to scavenge ROS produced by the Mehler Reaction: (i) the SOD-CAT pathway (top left) and (ii) the interplay of antioxidant enzymes in the ascorbate–glutathione cycle.

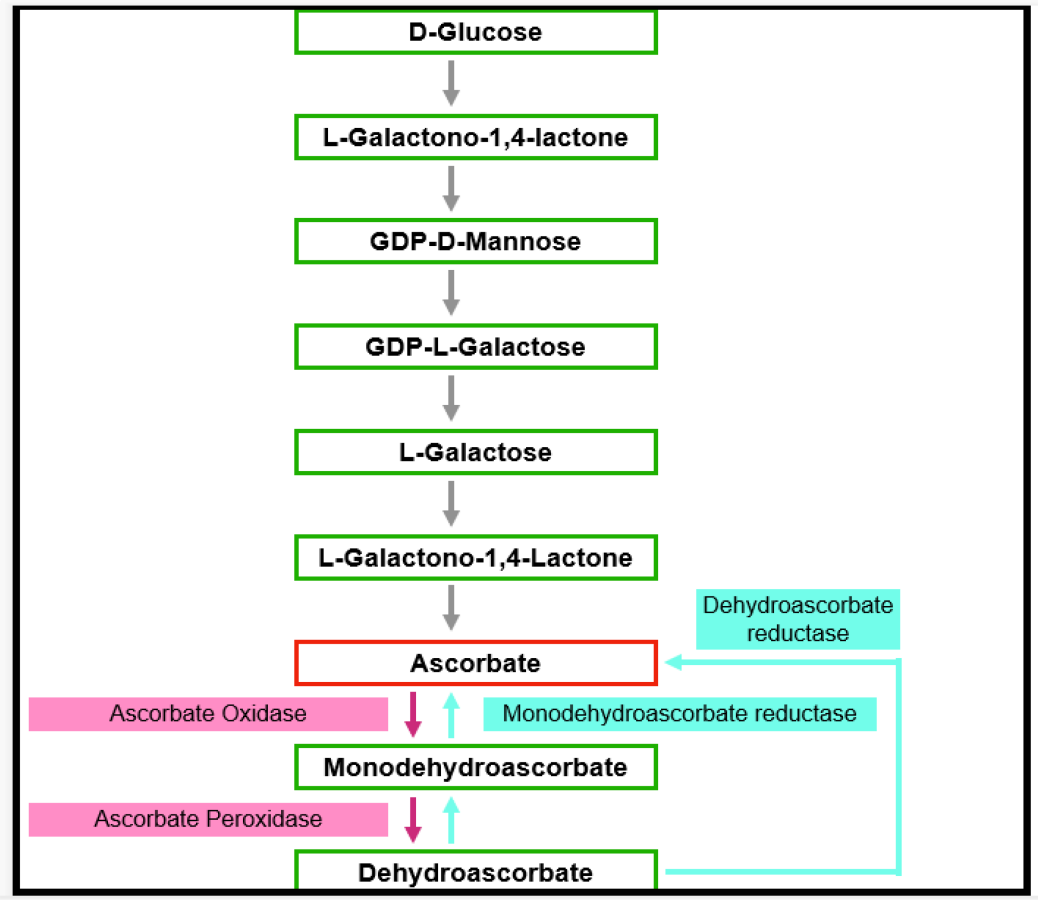

Figure 4. Outline of the pathway of ascorbate biosynthesis in plants. Ascorbate is a major antioxidant found in all plant tissues. The pathway of biosynthesis may vary due to the availability of precursors.

3.1.2. α-Tocopherol

Tocopherols are a group of antioxidants that are present in all parts of a plant [24]. α-tocopherol (vitamin E) is the most biologically active antioxidant among the four isomers (α, β, γ, and δ). Protection of membrane lipids from oxidative damage is among the most important functions. High tocopherol concentrations are found in the chloroplasts. This is the site of tocopherol synthesis from precursors deriving from the shikimate and mevalonate pathways [25]. Surprisingly it was found that the origin of intermediates of the pathways of tocopherol and carotenoid biosynthesis changes during the maturation of chloroplasts. While young, still developing chloroplasts are autonomous, intermediates of these two pathways are imported from the cytosol into mature chloroplasts [26]. This puzzling observation was made by feeding isolated plastids with radioactively labeled intermediates. It nicely explains contradictory results on the compartmentation of enzymes involved in tocopherol synthesis because, in the experiments with Arabidopsis mutants, populations of plastids of the different developmental stages had to be used [27][28]. One hundred and twenty singlet oxygen particles can be killed by a single α-tocopherol molecule. α-Tocopherols additionally work as recyclable chain reaction terminators of PUFA (Polyunsaturated fatty acids) radicals created by lipid oxidation [29]. In this sequence, α-tocopherol first interacts with lipid peroxy radicals. Subsequently, the reaction is terminated by ascorbate to yield tocopheroxyl [30]. The most credited function of tocopherols is their contribution to different mechanisms in the protection of PUFAs from oxidation [31]. ROS produced as a byproduct of metabolism and photosynthesis are sources of lipid peroxidation in cells of plants; α-tocopherol levels were found to increase in photosynthetic tissues of plants responding to a number of abiotic stresses [32].

3.1.3. Glutathione

Glutathione is a tripeptide (γ-glutamyl-cysteinyl glycine), which was found in essentially all cell compartments such as cytosol, vacuoles, chloroplasts, mitochondria, and endoplasmic reticulum [33]. It is engaged with a wide scope of processes such as cell differentiation, cell development/division, cell death, senescence, detoxification of xenobiotics, formation of metabolites, regulation of enzymatic action, synthesis of proteins, and nucleotides, lastly, articulation of stress-responsive genes [34]. The reactivity of the thiol group of glutathione makes it especially appropriate to serve a wide scope of biochemical capacities in all living beings. The nucleophilic nature of the thiol is significant in the development of mercaptide bonds with metals and for reacting with individual electrophiles [35]. For both enzymatically and non-enzymatically reduction of DHA (dehydroascorbate), GSH is used. In these reactions, two GSH molecules are oxidized to

GSSG (oxidized glutathione). Glutathione reductase and NADPH are utilized for the regeneration of GSSG to recycle 2 GSH.

3.1.4. Carotenoids

Carotenoids have a place within a group of lipophilic antioxidants, which are confined in the plastids of both photosynthetic and non-photosynthetic plant tissues. They are tracked down not just in plants but also found in microorganisms. Carotenoids show their antioxidative property by securing the photosynthetic apparatus in four ways, (a) responding with LPO items to end the radical chain reaction, (b) interacting with $^1O_2$ and creating heat as a byproduct, (c) preventing light-dependent production of $^1O_2$ by reacting with $^3Chl^*$ and exciting chlorophyll (Chl^*), and (d) interacting with xanthophylls to allow transfer of excitation energy. This reaction allows the release of surplus energy as heat through the xanthophyll cycle [36].

3.1.5. Flavonoids

Flavonoids are generally found in the plant kingdom preferentially in the leaves, flower organs, and pollen grains. Flavonoids can be ordered into four classes based on their structure, flavonols, flavones, isoflavones, and anthocyanins. They were considered a secondary ROS scavenging system in plants. They likewise interact with $^1O_2$, and this way reduces the risk of peroxidation of membrane lipids [37].

Flavonoids are the only antioxidant biomolecules that possess the capacity to absorb UV radiation. Absorbed energy quanta result in a generation of ROS. The ROS generation from certain flavonoids was studied using fluorescence probes. Flavonoids generate three ROS types: the superoxide anion radical ($O_2^{\bullet-}$), the hydroxyl radical ($^\bullet OH$), and singlet oxygen ($^1O_2$). This is based on the presence of the 2,3 double bond found in all flavonoids.

3.2. Enzymes Catalyzing ROS Removal

3.2.1. Superoxide Dismutase (SOD; EC.1.15.1)

The superoxide dismutase enzyme family is arranged into three categories Cu/Zn-SOD, Fe-SOD, and Mn-SOD. They are protecting from damage by dismutating $O_2^{\bullet-}$ into O_2 and H_2O_2 and lessening the probability of $^\bullet OH$ formation [38]. Cu/ZnSOD is present in chloroplasts and the cytosol of the plant cell, and MnSOD is present in peroxisomes and the mitochondrial matrix. The upregulation of SODs is part of the oxidative stress response and is crucial for the survival of plants.

3.2.2. Catalases (CAT; EC 1.11.1.6)

Catalases are preferentially found in peroxisomes. They are tetrameric heme-containing enzymes that convert 2 H_2O_2 to $O_2 + 2H_2O$ [24]. Many plants have different catalase isozymes. Six were found in Arabidopsis, two in castor bean [39]. They can dismutate H_2O_2 or, on the other hand, can oxidize substrates such as ethanol, methanol, formic acid, and formaldehyde. Plant catalases can be grouped into three classes: class I catalases are generally noticeable in photosynthetic tissues and are associated with the expulsion of H_2O_2 delivered during photorespiration; class II catalases are produced in vascular tissues and may assume a part in lignification, and their accurate biological function stays obscure; class III catalases are profoundly plentiful in seeds, and young plants and their function connect with the removal of excessive H_2O_2 delivered during unsaturated fat degradation in the glyoxylate cycle in glyoxysomes [40].

3.2.3. Ascorbate Peroxidase (APX; E.C. 1.1.11.1)

APX is an essential part of the Ascorbate–Glutathione (ASC-GSH) cycle. While CAT preferentially scavenges H_2O_2 in the peroxisomes, APX fills a similar role in the chloroplast and cytosol. Ascorbic acid is used as a reducing agent to reduce H_2O_2 to H_2O and also DHA. The APX family comprises at minimum five distinct isoforms, including thylakoid and microsomal membrane-bound structures, just as dissolvable stromal, cytosolic, and also apoplastic enzymes [41][42][43]. APX is a more efficient scavenger of H_2O_2 in times of stress because it is widely distributed and has a better affinity for H_2O_2 than CAT. The isoform that is more responsive to light-mediated oxidative stress is APX1. This is due to the suppression of tylEX. An enhanced stress tolerance could be observed when the expression of tylAPX was stimulated [43].

3.2.4. Monodehydroascorbate Reductase (MDHAR; E.C. 1.6.5.4)

MDHAR is liable for recovering ascorbic acid (AA) from the fleeting MDHA, involving NADPH as a reducing agent, ultimately renewing the cell AA pool. Since it recovers AA, it is co-localized with the APX in the mitochondria and peroxisomes, where APX rummages H_2O_2 and oxidizes AA in the process [44]. MDHAR has a few isozymes that are bound in chloroplast, glyoxysomes, mitochondria, cytosol, and peroxisomes.

3.2.5. Glutathione Peroxidases (GPX, EC 1.11.1.9)

Glutathione peroxidases are a group of numerous isozymes which catalyze the reduction in H_2O_2 [45][46][47]. It assumes an essential part in the biosynthesis of lignin, just as guards against biotic stress by debasing indole acetic acid (IAA) and using H_2O_2 all the while. GPX favors fragrant aromatic compounds such as guaiacol and pyrogallol [48] as electron donors. GPxs in plants are characterized into three kinds: selenium-subordinate (GPx, EC 1.11.1.19), the non-selenium-subordinate phospholipids hydroperoxide GPx (PHGPX), and glutathione transferases (GST, EC 2.5.1.18) showing GPx movement (GST-GPx). Due to its presence in cytosol and vacuole, it is considered a vital enzyme in the evacuation of H_2O_2.

PHGPx was displayed to react to salt stress [46], and this increment in action was seen in catalase deficient tobacco plants [45]. In citrus, PHGPx protein and the gene encoding were isolated and characterized.

4. Regulating ROS Concentrations in Plant Cells

4.1. Stress Perception and Signaling

Several forms of abiotic stress are indirectly linked to water deficit stress. This applies to ionic stresses (salt/sodic stress, high nutrient stress, etc.) and cold stress, for instance [49][50]. As a result, responses of cell turgor are observed, and the cellular concentration of ABA increases [51]. ABA-dependent and ABA-independent responses were described [52]. Due to ABA transport, respective effects can be observed in the whole plant. Stomata closure is among the most obvious ABA responses. By using molecular methods, the expression of ABA-responsive genes was observed [41][42][43][44][45][46][47][48][49][50][51][52][53][54][55][56]. Gene products can be categorized into compatible solutes and compounds conferring protection from osmotic and ionic damage. As shown in **Figure 5**, metabolites of primary carbohydrate and amino acid pathways function as substrates for the respective catalysis of these compounds. Among the second type of products are signaling compounds and transcription factors regulating further genes [57][58][59].

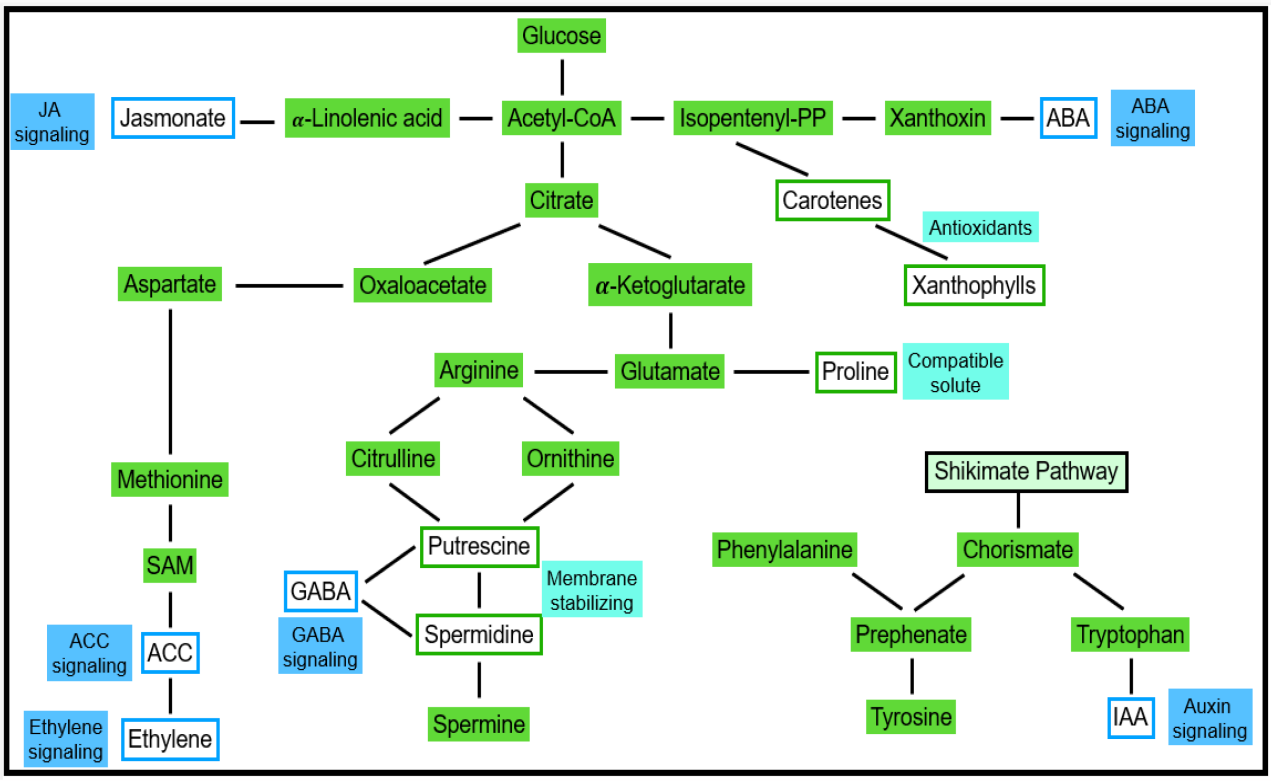

Figure 5. The synthesis of compatible compounds and signaling molecules integrating into plant metabolism. Depending on the respective genetic potential, plants differ in the expression of metabolic pathways. Moreover, these preferences may vary during a plant's life cycle. This has consequences for the preferences to produce individual compounds such as compatible solutes, hormones, and other signaling molecules. Levels of these molecules depend on both availabilities of substrates (precursors) and the activities of enzymes involved in biosynthesis.

4.2. ROS in Signaling Events

Reactive oxygen species are not only toxic side products of aerobic metabolism but also are important signaling compounds tuning metabolism as well as plant development. There is a tightly knit network of ROS signaling pathways,

Ca signaling, and ethylene signaling. During optimal growth conditions, ROS synthesis rate and ROS degradation rate are balanced, allowing a constant cellular ROS level. ROS scavenging occurs by interaction with antioxidant molecules as well as enzyme-controlled degradation at the expense of the cellular ascorbate/dehydroascorbate and glutathione (GSH/GSSG) redox pools [60].

4.3. Regulating the Activity of ROS Scavenging Enzymes

Typically it is observed that the activity of ROS scavenging enzymes increases as a response to environmental stress. When comparing genotypes differing in the degree of stress tolerance, the more tolerant genotype shows a more pronounced increase in ROS scavenging activity as compared to the more sensitive one [61]. It was also generally observed that the expression and activities of antioxidant enzymes not only differ between roots and shoots but also vary during the phase of stress adaptation [62].

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