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Role of Oxylipins in Salinity Stress: A Review

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ABSTRACT

The presence of excess concentration of salt in soil adversely affects the growth of plants and their developmental processes like germination, growth, flowering, fruit set and ultimately causes decline in agricultural yield. These deleterious impacts of salt stress can be mitigated by the exogenous application of oxylipins. Through this review, we analyze the functions of oxylipins in plants growing under saline stress.

Figures : 02 References : 41 Table : 00

KEY WORDS : Defence mechanisms, Jasmonic acid (JA), Methyl jasmonate (MeJA), Oxylipins, Salt stress, Salt tolerance

Introduction

Salinity is among one of the most deleterious factors which adversely affects the economic yield of agricultural crops in different parts of the world. This abiotic factor causes extensive stress conditions for plants leading to oxidative damage. As a result, salinity stress affects several physiological processes like germination ability, length of radicle and plumule, fresh and dry mass, economic yield, nutritional quality of seed, content of various metabolites (chlorophyll, protein and sugar), activity of enzymatic antioxidants together with nodulation in plants.[14,23] It ultimately leads to decline in plant growth, together with lower yield and harvest quality.

The common causes behind soil salinity are either natural or anthropogenic.[41] Natural salinization or primary salinization occurs due to disintegration of rocks and deposition of salts carried out by oceanic waves by wind and rain. Secondary salinization results due to anthropogenic interference. Activities by humans change the hydrological balance of soil which disturbs the delicate natural balance which exists between water applied to soil in the form of rainfall or irrigation and water which is used by crops in transpiration.[27] Most common such anthropogenic activities involve:

1) Clearing of land/ deforestation.
2) Using annual crops to replace perennial vegetation.
3) Making use of irrigation schemes which either have insufficient drainage or use salt-rich water for irrigation.
4) Chemical contamination of soil by making use of intensive agricultural systems, especially in green houses and intensive farming systems.

Environmental stresses steer towards excessive generation and/or accumulation of reactive oxygen species (ROS) within living cells/tissues. Excess of ROS is deleterious to plants. Therefore, to cope with such variable environmental cues, plants adopt many alterations in their morphology, physiology, development as well as biochemical processes to sustain their optimal growth rate and productivity even in stressful conditions.[31, 38] Plants have developed a complex combination of detoxification mechanisms (both enzymatic and non-enzymatic), to counter the oxidative damage caused because of unrestricted generation/accumulation of ROS. The enzymatic antioxidants comprise superoxide dismutase (SOD), glutathione peroxidase (GPX),

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ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), dehydroascorbate reductase (DHAR), and mono-hydro ascorbate reductase (MDAR). Nonenzymatic antioxidants comprise carotenoids, glutathione, flavonoids and tocopherols. Both enzymatic and non-enzymatic types of antioxidants are crucial for ROS homeostasis.

Oxylipins are bioactive lipid molecules which are generated in plant cells through the oxidative transformation of polyunsaturated fatty acids (PUFAs) from various metabolic pathways *viz,* cyclooxygenase (COX), lipoxygenase, and cytochrome P450 pathways. They act as signaling molecules to regulate development, growth, senescence and programmed cell death in plants. They also play a key role in determining sex of reproductive organs, and in providing defense mechanism against both biotic and abiotic types of stresses.[6] There are numerous studies available which provide convincing evidences which prove that these oxygenated lipid metabolites have an active participation in plant defense mechanisms.[4] Earlier studies in this arena focused only on jasmonic acid (branch of C18 polyunsaturated fatty acid metabolism) and its involvement in plant defense-signaling pathways. However recently, oxylipins other than jasmonates have also been inspected to participate in the main defence mechanisms employed by plants.[4, 18] Similarly, Methyl jasmonate (MeJA) and 12-oxo phytodienoic acid (OPDA), are signaling molecules that are involved in defence mechanisms.[8]

Formation of Oxylipins is carried out by the action of various lipoxygenase (LOX) enzymes which initiate the oxygenation of polyunsaturated fatty acids to form fatty acid hydroperoxides.[11] Further, these fatty acid hydroperoxides are converted into a cluster of bioactive compounds, called oxylipins by the action of several enzymes.[11] The oxylipin family consists of keto fatty acids, oxo fatty acids, fatty acid hydroperoxides, hydroxy fatty acids, volatile aldehydes and the plant hormone-jasmonic acid together with its biosynthetic precursor *viz.*12-oxo-phytodienoic acid (OPDA).[40] Plant oxylipins/ Phytooxylipins are mainly derived from oxygenized fatty acid precursors (mainly C16 and C18 fatty acids). The enzyme lipoxygenases (LOX) attach molecular oxygen either at C9 position of linoleic acid or C13 position of á-linolenic acid (most common substrates) resulting in formation of 9- and 13-hydroperoxy fatty acids

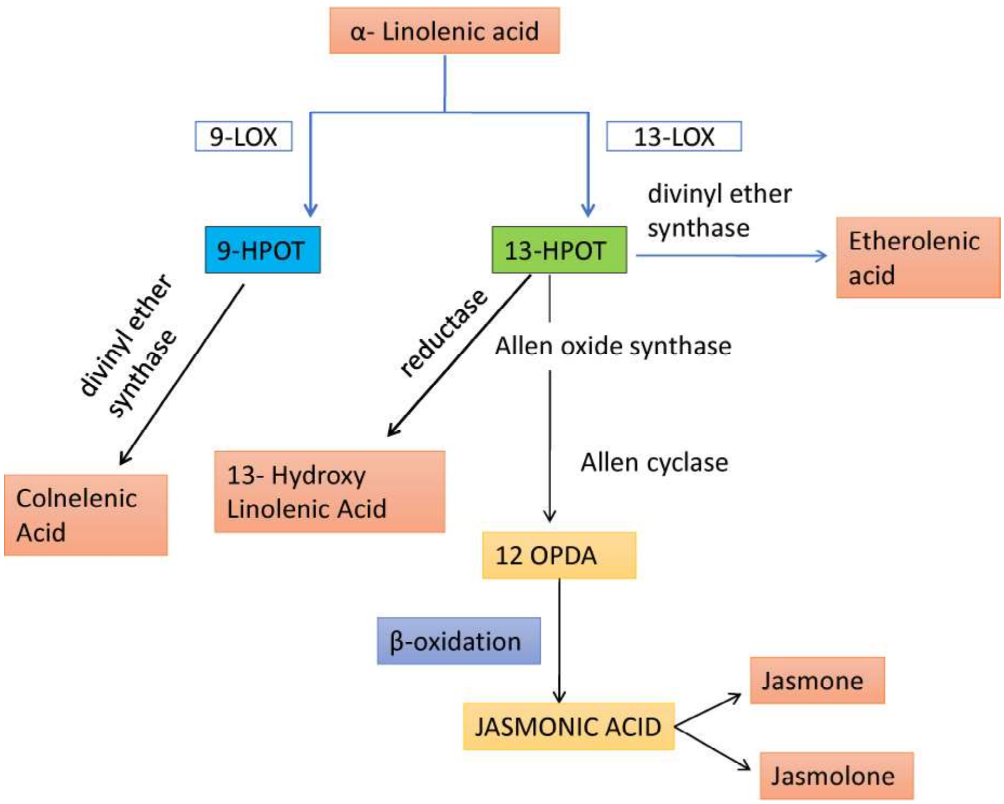

Fig. 1: The LOX pathway.[5] The dioxygenation of fatty acids like linolenic acid (18:3), catalyzed by 9-LOXs and 13-LOXs, results in formation of several derivatives performing different functions in the plant. (13-HPOT-(13S)-hydroperoxy-(9Z,11E)-octadecadienoic acid; 9-HPOT-(9S)-hydroperoxy-(10E, 12Z)-octadecadienoic acid).

respectively.[11] There are different types of LOX isoforms present in plants:

Type I: includes 9-LOX isoenzymes, found outside the plastid

Type II: includes 13-LOX isoenzymes which are localized inside the plastid[29]

Lipoxygenases are nonheme iron-containing dioxygenases found in plant and animal cells. These enzymes catalyze the addition of molecular oxygen to polyunsaturated fatty acids to produce an unsaturated fatty acid hydroperoxide which ultimately is converted into oxylipins *via* various enzymatic reactions.[34] The hydroperoxy fatty acid products formed by the action of LOX enzymes are further converted to various other compounds by different enzymes (Fig. 1).

Physiological role of oxylipins in salinity stress

Oxylipins play a crucial role in providing defense against both abiotic and biotic stress tolerance.[32] Various reports narrate about oxylipin role in plants under biotic stress, but in case of abiotic stress, the role of oxylipins is still not very clear especially with respect to salinity stress.[32] Oxylipin such as methyl jasmonate (MeJA) is reported to reduce the deleterious effect of NaCl stress on photosynthetic rate and simultaneously enhance plant growth.[19, 20] Exogenous application of jasmonic acid (JA) mitigated the negative effects of high salt concentrations on photosynthetic rate and growth rate in barley.[37] Exogenous pretreatment of JA is reported to ameliorate salt-stress induced negative effects in rice seedlings and cause remarkable decline in sodium concentration especially in salt-sensitive cultivars.[22] The plant metabolism gets disturbed due to salt stress which results in oxidative stress, malnutrition, loss of membrane integrity together with genotoxicity.[35,21] These deleterious effects can be mitigated by exogenous application of JA.[9] "In tomato, endogenous JA levels played a crucial role in enhancing salt tolerance through homeostasis maintenance of reactive oxygen species (ROS) generated due to oxidative stress.[1] In addition, exogenous JA treatments have shown to reduce injury in plants caused due to salinity stress by increasing the photosynthetic rates and stimulating the proline contents and abscisic acid (ABA) levels.[3] Such ameliorative effects of JA could be attributed to increase enzymatic antioxidant activity or reduced rate of Na^+ accumulation in shoots.[25,39] Exogenous application of JA caused enhancement in Na^+ exclusion by roots due to reduced Na^+ uptake and *via* providing surface salt stress tolerance in two maize genotypes.[33] Studies suggest that exogenous oxylipin treatment increases the activities of catalase (CAT)[10, 26], superoxide dismutase (SOD)[13, 26], glutathione reductase (GR)[2] and ascorbate peroxidase (APX) thus enhancing the ROS scavenging ability and alleviating the oxidative damage caused by salt stress. A simultaneous decrease in the concentrations of malondialdehyde (MDA) and hydrogen peroxide (H_2O_2) has been reported in response to oxylipin treatment.[28] JA can upregulate several genes which involved in defense mechanisms.[30]

Mechanism behind oxylipin induced amelioration of salinity stress

During salinity stress conditions oxylipins induce the biosynthesis of various secondary metabolites including phenylpropanoids, alkaloids, terpenoids, and glucosinolates which provide defensive mechanisms.[12,15] Endogenous as well as exogenous levels of JA augment plant salt stress tolerance by the mechanism described[9] (Fig. 2). Salinity stress in plants generates osmotic stress due to increasing salt concentration in plant cells, ultimately upregulating biosynthesis of abscisic acid, jasmonic acid and 12-oxo-phytodienoic acid[16, 36], while the Gibberellic Acid biosynthesis is downregulated.[7] When JA is applied exogenously or produced endogenously during salt stress, the JAZ (JASMONATE ZIM- DOMAIN) repressor is degraded, such that the transcription factor MYC2 is activated. The transcription factor MYC2 acts as a signaling molecule which is positively regulated by the hormone abscisic acid.[24] Under stress conditions, biosynthesis of GA is repressed and resultantly, DELLA proteins would accumulate. The accumulated DELLA proteins interact with JAZ proteins and thus MYC2 is relieved from JAZ repression, which in turn triggers secondary plant metabolic pathways.[17] Subsequently, the synthesis of flavonoids and terpenoids is upregulated which are required for adaptation of plants under stressful environments.

Current status and Conclusion

Salinity is an abiotic stress condition which hampers production in field, affecting not only agricultural output but also food security. Therefore, plants have developed certain complex multicomponent signaling regulatory networks to adapt themselves under external environmental stressful conditions. Oxylipin based signaling systems are the most important components of this network. Oxylipins are lipid-derived compounds including the phytohormone jasmonic acid and related jasmonate metabolites like cis-(+)-12-oxo-phytodienoic acid (cis-OPDA), methyl jasmonate (MeJA), and jasmonoyl-L-isoleucine (JA-Ile) which act as signals in the plant response to biotic and abiotic stress. During salinity stress conditions, oxylipin mediated responses in plants ensure maximum fitness of plants and provide tolerance. Since very few studies have been done till date in this field of oxylipin induced abiotic stress tolerance,

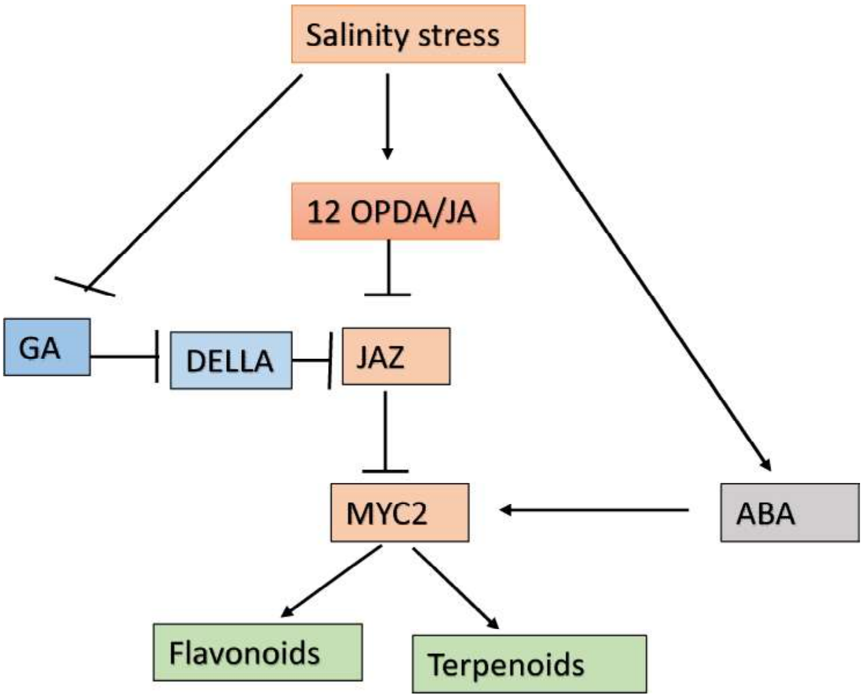

Fig.2 : Schematic diagram of the mechanism behind oxylipin induced amelioration of salinity stress

very few data and analysis are available. For future perspective, it is an important challenge to establish the role played by oxylipin signaling in enhancing productivity of crops/plants under environmental stress conditions. A few transgenic plants with altered lipid metabolism have already been generated which provide tolerance against abiotic and biotic stress conditions. A lot still remains to be discovered using this line as a tool for improving plant health and agricultural yield.

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