



Redox Signaling and Metabolic Plasticity in Crops Under Combined Abiotic Stresses

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Abstract: -

Climate change is exposing crops to a combination or sequential abiotic stresses. An example is drought and heat, salinity and cold, and flooding and drought coincide with each other. This complicates the natural process of crop adaptation to these stresses in the conventional way. Redox signaling is a key regulatory process where reactive oxygen species (ROS) and antioxidant systems mediate a process where crops sense, absorb, and respond appropriately to more complex stress interactions controlling metabolic plasticity. The dangers of reactive oxygen species (ROS) are not confined to mere byproducts, but they are also vital signaling molecules. The combinations of stress produce different patterns of ROS, which induce the appropriate acclimatory responses. Enzyme antioxidant systems (superoxide dismutases, SOD, catalase, CAT and ascorbate peroxidases, APX, etc.) are rapidly activated once subjected to stress conditions. This prevents excessive accumulation of ROS and yet provides the opportunity to conduct signaling. Metabolic plasticity the capacity to reorganize the functioning of the primary and secondary metabolism allows plants to redirect resources between growth and stress tolerance by producing osmolytes, proline, and other secondary metabolites to aid them in overcoming stress. Redox signaling pathways combined with an epigenetic response, hormone signaling (particularly, abscisic acid) and calcium-dependent responses produces a complex stress-sensing and response system. This paper will discuss redox signaling pathways, the degradation of the antioxidants, the metabolic response when multiple stressors are combined and how this can assist us to display crops that can be able to withstand the alterations in climate.

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Introduction:

There is an increasingly observed paradox to agricultural productivity: the breeding and agronomic practices were developed under relatively constant climatic conditions, and nowadays the new and complicated stress environment is being formed because of climate change. Throughout the time, crops are increasingly exposed to multiple stresses or rapid succession as compared to discrete individual stresses, which can be highly detrimental to the crop. The weather changes between summer where one field experiences drought and heat stress simultaneously on the same day and another field experiences flooding then finally drought. In coastal agricultural regions where sea water is intruding, heat stress is exacerbated by salinity stress. The results of these combinations of stress are extremely contrasting as compared to each of the stresses alone. In order to understand the response of crops to integrated stresses it becomes necessary to study the molecular and cellular pathways that regulate stress perception and adaptation. Single stresses of plants have been studied in decades, with methods of plants adapting to drought, heat, or salinity independently. But it is becoming established that in cases of two or more stresses, they lead to non-additive interactions. A crop with slight impact of moderate drought may fail

altogether in case its stress is combined with heat stress. These cumulative effects are more terrible than the combination of the individual stress effects.

On a molecular scale, redox signaling biochemical signaling through reactive oxygen species (ROS) and antioxidant systems represents a hub or central regulatory point that integrates perception of stress and adaptive response. Reactive oxygen species (ROS) that were once seen as harmful products of aerobic metabolism are now recognized as important signaling molecules. Various abiotic stresses induce "ROS signature," and these are characteristic patterns of ROS accumulation in some regions of cells. These signatures make the plant react in a manner that is appropriate to the particular combination of stresses that the plant is experiencing. Simultaneously, the plasticity of metabolism the capacity to rearrange metabolism, redistribute resources and synthesize novel compounds assists crops to adjust to environmental adaptations. This paper examines redox signaling, antioxidant metabolism and metabolic plasticity. It discusses how they interact with each other to assist crops to become adapted to various forms of abiotic stress and the implications of this in producing climate-resistant varieties.

Redox Signaling RedoxOS as Regulatory Molecules

Reactive oxygen species like superoxide (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH^-) are normal products of aerobic metabolism, particularly in photosynthesis and respiration. In the absence of diseases and pathologies, the scavenging and creation of ROS remains balanced and thus there is a low steady-state of ROS. One balance is altered when you are stressed: production of ROS increases in a variety of ways, and the capacity to scavenge ROS increases temporarily beyond the capacity of antioxidants to manage. Previously, excessive accumulation of ROS was merely regarded as a deleterious oxidative stress. But the latest literature is a much more complex picture. At non-toxic concentrations of ROS, they are major signaling molecules which initiate adaptive reactions. Various types of stress generate distinct ROS signatures based on the type of stress. Indicatively, drought stress leads to increased concentrations of H_2O_2 , predominantly in chloroplasts, and stomata avert the supply of CO_2 and increase the difficulty of photosynthetic electron transport. The patterns of ROS produced by heat stress reveal mitochondrial superoxide due to the rupture of the electron transfer chains. Salinity stress causes ROS by various mechanisms including perturbation of electron-transport and activation of NADPH oxidases. These stress-specific ROS signals activate various

signal transduction pathways. H_2O_2 functions as a secondary messenger and causes calcium to enter the cytoplasm stimulating calcium-dependent protein kinases (CDPKs) that add phosphate groups to transcription factors following it. Different reactive oxygen species (ROS) in different compartments of the cell can trigger specific signaling cascades, which enable plants to respond to different kinds of stress differently. The given specificity allows the accurate calibration of acclimatory reactions to particular stresses. The Redox signaling is coupled with the hormone signaling, particularly abscisic acid (ABA), which accumulates when the body is under stress and interacts with the ROS signaling to enhance the strength of stress responses. ROS and ABA interact: ROS are generated, ABA accumulates and when ABA is signaled, it enhances gene expression which is sensitive to ROS. Similarly, ROS connects to calcium signaling, nitric oxide signaling and sugar sensing thus forming a single system that is capable of detecting a broad spectrum of stress-related cues.

Defense and Regulation Antioxidant Metabolism

Redox signaling involves the utilization of ROS as regulatory molecules thus excess ROS is also damaging that leads to protein damage, lipid damage, DNA damage, and cell damage. To ensure that ROS signaling

is useful but not damaging, plants have evolved complex antioxidant systems comprising of both enzymatic and non-enzymatic components.

Enzymatic Antioxidants: The antioxidant enzyme system is a defense system based on levels of protection. Superoxide dismutase (SOD) is present in different cellular locales as well as in isoforms, and is necessary in the disproportionation of superoxide to H_2O_2 and oxygen. The enzyme catalase (CAT) is predominantly located in peroxisomes and is rapid in breaking-down H_2O_2 to produce water and oxygen. Ascorbate peroxidase (APX) uses ascorbate as electrons donor to reduce H_2O_2 producing oxidized ascorbate. Similarly, the glutathione peroxidase (GPX) utilizes the reduced glutathione (GSH) to accelerate the rate at which the ROS reduction occurs. Antioxidant enzyme activities increase rapidly and largely when they are stressed. Studies show that the functions of SOD, CAT, APX and POX enzymes increase up to 2-5 times in the hours after stress exposure. This rapid activation is because of the transcriptional upregulation (Increased expression of enzyme genes) as well as the post-translational modification (Activation of the already present enzyme molecules). Enzyme activation varies depending on the form of stress and the type of crop which is dependent on the ability of the

plant to sustain the stress. Stress-tolerant varieties often have naturally high levels of antioxidant enzyme activities, without any form of stress, and thus, they respond rapidly to new stressor events. This low base shows that there are genotypic differences in the control of antioxidant system, which has been selected as a trait to breed and select.

Non-Enzymatic Antioxidants: The ascorbate-glutathione (AsA-GSH) system is a significant non-enzymatic antioxidant system. Ascorbate (vitamin C) is abundant in plant cells, and glutathione is low and directly relieves ROS, and is replenished with the help of enzyme reactions. Under stress the levels of these low-molecular-weight antioxidants increase significantly, and this increases their antioxidant capacity. The accumulation of secondary metabolites such as carotenoids, tocopherols and flavonoid occurs under stress. These materials are anti-oxidants and additional protective agents. Proline is an amino acid, which accumulates in the presence of high levels of stress and protects proteins and membranes, as well as provides osmotic adjustment. These are secondary metabolites that point to metabolic reprogramming responses that are attended to later.

Metabolic Plasticity: Stresses Reallocation and Reprogramming

Along with direct antioxidant reactions, stressed plants experience widespread

metabolic reprogramming of resources, shifting them out of growth and into stress resistance. It is a fundamental adaptation mechanism to changing environments that enable organisms to survive in harsh conditions. In optimal conditions, the metabolism of plants is focused on growth and the division of cells, the growth of tissues, and the accumulation of biomass are oriented to allocate the energy and resources. Stress results in decreased growth processes and faster stress-response processes. This is brought about by the hormones particularly the ABA and the ABA-dependent signaling cascades activated by redox signaling. This redistribution of metabolism is advantageous as it safeguards the resources against growth and helps the processes needed to survive, including the synthesis of osmolytes, stabilization of membranes, and the repair of damage that occurs due to stress.

Osmolyte Synthesis and Accumulation: One of the primary metabolic reactions is the heightened synthesis of organic solutes, called osmolytes, which are proline, glycine betaine and sugars, such as trehalose and mannitol. The osmolytes accumulate in cells to high levels, reducing the water potential of the cells and preventing them to uptake water when it becomes unavailable. Simultaneously, osmolytes stabilize the proteins and membranes, interacting with

them, and forming a hydration layer, which protects them in numerous aspects. An example is that on a presence of stress due to drought or salinity, cellular proline levels increase 10 to 30 times. This occurs due to ABA-dependent transcriptional biosynthetic enzyme proline biosynthesis.

Sugar Reallocation and Secondary Metabolism: During stress, the carbon distribution in primary metabolism is redirected to secondary metabolism and biosynthesis that provide body defense. When a person is under extreme stress, non-structural carbohydrates will decrease since respiration will rise, although, initially, it will raise their level, as starch is transported to supply substrates to secondary metabolism. The overexpression of genes encoding enzymes involved in the synthesis of flavonoids, anthocyanins, and other secondary metabolites protecting cells increase the synthesis of phenolic compounds. The substances are resistant to free radicals and can also be used in the protection against UV rays and bacteria.

Alterations in Nitrogen Metabolism: Stress leads to reduced synthesis of proteins in cells, and increased synthesis of stress related proteins in cells such as heat shock proteins, late embryogenesis abundant (LEA) proteins and dehydrins. The release of nitrogen by the process of reduced protein production is diverted to proline and other defensive amino

acids. Such a selective translation indicates that factors of translation initiation and ribosomal specialization have evolved, such that now preferential synthesis of stress-response proteins is possible. The metabolic plasticity is particularly useful when plants experience a significant amount of stress simultaneously as they have to respond to a large number of various, and even competing, demands simultaneously. A plant that is experiencing a drought and heat stress at the same time must also be able to maximize the water loss through stomatal closure and maintain photoprotection in the face of reduced transpirational cooling. Metabolic reprogramming allows the allocation of resources to two challenges, but the scale and orientation of metabolic changes might not be the same as compared to single stresses.

Integration: Redox Signaling and Metabolic Plasticity during Integrated Stress Responses

One of the most recent stress physiology revelations is the realization that redox signaling and metabolic plasticity act in synergy, and redox cues orchestrate metabolic reprogramming. Perception of stress gives rise to ROS Signatures that initiate transcriptional cascades that activate genes involved in metabolic reallocation. The upregulation of the genes encoding osmolytes and stress response is regulated by ABA signaling that is

activated and enhanced by ROS signals. Also, the metabolic byproducts also give feedback to control redox signaling. Other osmolytes such as proline alter the mechanism of ROS scavenging by acting by directly scavenging ROS, and altering the activity of antioxidant enzymes. When cells accumulate secondary metabolites in case they are stressed, the cells are safeguarded against oxidative damage and the enzyme systems interact. This feedback forms dynamic regulation where changes in metabolism are initiated due to the redox signaling which in turn alters redox status.

This is a regulatory framework which enables a sophisticated context-modulated adaptation to stress. This combination is required in case of multiple stresses. In case of drought and heat stress, there is an emission of integrated ROS signals that prompt the body to react to both drought and heat stress simultaneously.

The metabolic reallocation is concerned with osmotic adjustment (drought) and with membrane protection (heat). It achieves this through integrated redox signaling. Plants are basically an integration of various stress signals into adaptation responses and these are making sense and interacting.

Stress-Specific Metabolic Signatures: Separating between Stress Combinations

Recent research suggests that stress combinations do have a distinct different metabolic signature compared to the metabolic

signature that is caused by individual stresses. Drought stress causes build-up of proline and glycine betaine, which assists in osmotic accommodation. The secondary metabolites are oriented towards prevention of oxidative stress. Heat stress leads to an enormous upsurge in heat shock protein and chaperone concentrations and secondary metabolism is oriented towards light damage protection. The drought and heat stress result in a metabolic profile that incorporates: (1) osmolyte accumulation as in the case of drought alone, but with different amino acid profiles indicating that heat stress is more significant; (2) higher concentration of heat shock proteins as in the case of heat stress alone, which indicates is a greater risk of protein denaturation; and (3) faster secondary metabolism, including anthocyanins and other pigments which protect plants against UV light and antioxidants. As this distinct profile indicates, there is something more than mere addition of the two stresses at work. Similarly, salinity-cold stress combinations generate distinct metabolic profiles. An example is that cold stress will lead to the accumulation of carbohydrates and salt stress will lead to the production of osmolytes. This forms metabolic set ups that are optimal to that particular combination. The understanding of these stress-specific metabolic signatures offers opportunities in developing selection criteria

and breeding strategy in respect to particular stress combinations of regional importance.

Crop Development and Climate Adaptation Implication

The insights into redox signaling and metabolic plasticity in the development of crops are useful in determining how to combine stress tolerance in a secondary manner. Selection and Breeding: Stress tolerance is shown in varieties with inherently high antioxidant enzyme reactions, high sensitivity to ROS-signaling, or faster metabolic reprogramming capacity. The identification and breeding of stress-tolerant varieties can be made possible by using antioxidant enzyme activity, redox-sensitive reporter genes or metabolic profiling as a selection criterion. Agronomic Interventions: Pre-stress redox signaling and metabolic reprogramming can be triggered by the application of abscisic acid, cytokinins or other stress-priming agents, before the stress occurs, and this will enhance the subsequent tolerance to stress. Stress-priming therapy helps plants to be ready to respond promptly and intensely in case of stress. Biofortification through Secondary Metabolism: There is an accumulation of secondary metabolites through metabolic plasticity response. To produce crops with higher nutritional content, alterations in stress or genetic background can be used to increase the production of

secondary metabolites, and in particular antioxidants and micronutrients, by crops. **Multi-Stress Resilience:** In learning the metabolic signatures and redox signaling architecture in response to various forms of stress, we have the opportunity to breed and develop varieties that can respond to more than one form of stress simultaneously. Breeders do not need to breed separately to be able to select plants that will tolerate heat and drought simultaneously.

Difficulties and Future Projections

Although the mechanisms have made a great development, there are still gaps in critical research

Complexity on the Systems Level:

Despite increasing understanding of individual redox signaling pathways and metabolism, the association between these processes at scales ranging between molecular and cellular to organismal and beyond is poorly defined. Integrative complexity can be captured in systems approach which integrates transcriptomics, proteomics, metabolomics and phenomics.

Field Testing: There is much research on redox signaling and metabolic plasticity conducted in controlled environments. Testing of fields with realistic combinations of stresses which vary naturally remains limited. The conversion of knowledge into practical breeding and farming practices requires field

studies relating to the molecular level processes to achieve results.

Regulatory and Farmer Adoption:

Depending on whether genetic engineering has an impact on redox signaling or any metabolic path, various countries and markets have varying rules regarding it. One should still understand what farmers require and ensure that new varieties suit their requirements and agronomical systems.

Conclusion

Redox signaling and metabolic plasticity are both interrelated processes used to enable crops to adapt to the growing occurrence of combined abiotic stresses as a result of climate change. Reactive oxygen species (ROS) are not only harmful byproducts, but also essential signaling molecules, which help to perceive a specific combination of stressors and to start the appropriate acclimatory response. The redox homeostasis is maintained by balancing protective signaling systems against oxidative stress through antioxidant enzyme systems. Metabolic plasticity enables the reallocation of developmental resources to stress resistance, enabling the production of osmolytes, secondary metabolites and stress-protective peptides. Redox signaling together with metabolic reprogramming provides plants with a full-fledged adaptive framework which enables them to detect, process and react

appropriately to an extensive variety of stressors. The specific patterns of metabolic response to stress, including the accumulation of osmolytes, secondary metabolism, and gene expression, can distinguish among different combinations of stresses and cause the body to react appropriately. The current understanding of such mechanisms is offering potential solutions to developing climate-resilient crops through the choice of better antioxidant capacities, faster response to redox signals, and increased metabolic plasticity. The capacity to manage or cope with various stressors is increasingly becoming significant in global food security as the climate change continues to increase. The strategies of redox signaling and metabolic plasticity in crop development can be applied to produce agricultural systems that can continue to produce food despite the stress levels being elevated and diffusing with the progression of the next several decades.

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