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Fortified organic manure improves stress tolerance in plants: Linking to antioxidants and MAPK signaling

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Abstract:
Stress conditions caused by both biotic and abiotic factors are a serious problem in crop productivity. This is achieved by increasing resistance to stress for sustainable agriculture. Organic and fortified organic manures containing essential nutrients and bioactive compounds are a potential, eco-friendly option to reduce the effects of stress. Hence, it is of interest to review the physiological, biochemical and molecular basis of increased stress tolerance. Thus the application of fortified organic manure, with special focus on antioxidant defense and mitogen-activated protein kinase (MAPK) signaling is of interest. Fortified organic manure provides a well-balanced supply of nutrients and bioactive molecules that stimulate enzymatic and non-enzymatic antioxidant systems, maintain cellular redox homeostasis, and modulate the MAPK signaling pathway, an important pathway in plant stress responses. This triggers a systemically induced signaling response that may prepare plants to better withstand stress. The complex interplay between fortified organic manure, antioxidants and MAPK signaling under stress conditions contributes to the design of sustainable farming practices that ensure the resilience and productivity of crops during environmental change. Thus, the possibilities, issues and prospects of soil enrichment with nutrients for sustainable crop production are reviewed.

Keywords: Fortified organic manure; mitogen-activated protein kinase (MAPK) signaling; antioxidants; stress tolerance; crop productivity

Background:
The world is a complex network of life, bound together through the dynamic interplay of species and environment. All aspects of life, human and plant are greatly influenced by environmental conditions **[1]**. Through this multifaceted mosaic, stress situations are a recurring theme, a characteristic of retarded growth and yield of crops. Plant stress tolerance is an important factor in the plant–environment interaction, determining plant survival and economic viability **[2]**. Plants' response to an adaptation to different stressors, caused by biotic or abiotic factors, have a significant impact on the overall health, productivity and ecological resilience of the plants **[3]**. Stress conditions involve a variety of abiotic and biotic factors that may have a negative effect on organisms, especially plants. The abiotic factors are temperature extremes, availability of water, soil composition and light intensity, and the biotic factors are interactions with other living organisms including pathogens, herbivores and competitors **[4]**. Stress conditions may be very variable, depending, *e.g.,* on geographical location and type of ecosystem. Some stressors cause stress to plants in similar ways, such as causing oxidative stress or damaging certain plant cell structures, while others cause stress in different ways, such as by triggering specific molecular pathways in response to different kinds of pathogens or herbivores **[5]**. It is essential to comprehend the mechanism of these stress factors in order to formulate successful strategies for resilience and adaptation of plants in a wide range of environments. About 50% of crop loss is attributable to abiotic stresses, of which 10% is due to drought and 20% is due to heat stress. Moreover, tolerance to stress plays a key role in the quality and yield of agricultural products and has important implications for global food security **[6]**. Plants are subjected to many constraints, such as drought, extreme temperatures, soil salinity and various pathogens. Plants have advanced defense responses when challenged by the environment, in which stress-responsive pathways such as antioxidant signaling and the mitogen-activated protein kinase (MAPK) pathway are triggered **[7]**. Cellular antioxidants are critical protectors of cellular homeostasis. Furthermore, MAPK signaling is identified as an important regulator in the complex signaling networks that control plant responses to stress **[8]**. Once activated, MAPKs trigger a cascade of signaling events, culminating in the activation of stress-responsive genes and the co-ordination of physiological changes that increase stress tolerance. The MAPK signaling pathway is a dynamic and versatile biochemical event in the plant in response to environmental challenges, and is capable of integrating and transducing a variety of stress signals **[9]**. Fortified organic manures are usually organic manures fortified or enriched with additional nutrient(s) to give a better balanced and complete nutrient package for plant growth **[10]**. Fortification is the process of providing plants with additional nutrients to address their nutrient requirements. The aim of fortified organic manure is to supply a wider spectrum of nutrients to plants by adding minerals and microorganisms to organic manure **[11]**. Available data shows that fortified organic manure can help plants to resist stress. Hence, the antioxidant and MAPK signaling pathway-mediated role of fortified organic manure in the regulation of stress tolerance in plants is of interest **[12]**.

Organic manure:
Organic manure is a critical part of sustainable farming practices, promoting the principles of environmental protection and soil health. Organic manure does not provide artificial plant nutrients as synthetic fertilizers often do, but rather supplies the soil with required nutrients from natural sources. It is an important component of organic farming systems, promoting a holistic approach to agriculture that emphasizes the connection of soil, plants and the environment **[13]**. Organic manure consists of organic matter from plant and animal resources. These materials are broken down by microorganisms into a rich nutrient substance that increases the fertility of the soil **[14]**. The basic purpose of organic manure is to provide a balanced and sustainable supply of essential elements to plants, so that they are able to grow well without causing stress to the environment. Organic manure also helps to structure the soil, fix water and increase microbial activity. The organic manures' unique characteristic is their effect on soil health, biodiversity and soil contaminants **[15]**. In organic farming, organic manure is generally used. The characteristics and properties of conventional manure and organic manure have not been well

defined. A few studies have found differences between conventional and organic manures. The differences are in three dimensions: (i) microbiological content and antibiotic contamination, (ii) greenhouse gas emission, and (iii) chemical composition and characterization. Usually, the use of conventional manure on cropland is referred to as an "organic amendment". An assessment of the long-term effects of conventional and organic manures on soil salinity, trace elements and heavy metals is required, as higher concentrations of these chemicals can affect the yield of crops and have negative impacts on soil organisms such as earthworms **[16]**. In India and other countries, organic farming has been expanding as an alternative model of crop farming to make it more economical and environmentally friendly. One of the major principles of organic farming is that natural resources are recycled efficiently and safely on the farm, in order to compensate for the negative impact of agrochemicals and to preserve ecological balance and biodiversity. To substitute for the chemical inputs that are essential resources in conventional agriculture, organic agriculture uses composts and manures of "true" organic origin, quality and standards. Additionally, cow dung and urine, which could provide both organic matter and microbial consortia, are not necessarily from in-house dairy farms with conventional (non-organic) farming systems and therefore are not considered to be "true" organic manure. Thus, animal husbandry—poultry and fish—has also become an integral part of this ecological type of farming, known as organic animal husbandry **[17]**. In the United States, as well as in other countries including India, the certification process for organic products and farms is constantly evolving to ensure "true" organic standards in complex food chains. Organic manure, through decomposition by microbes, eventually results in the enhancement of soil humic content. Humic substances (HSs) can produce beneficial effects on a wide range of agricultural, ornamental and medicinal crops, affecting growth and development parameters, physiology and response to stress. HSs can also mitigate abiotic and biotic stresses and activate growth and development of plants, thus improving yields and agricultural production. Physiological conditions lead to the regulation of ROS levels through the synthesis of redox enzymes in plants. This mechanism of action stimulates root proliferation and helps plants to resist stress **[18]**.

Fortified organic manure:

One of the significant developments in the use of organic manure is the development of fortified organic manure. This pioneering technique is based on the main concept of organic farming, which is to add complementary nutrients to the organic matrix, giving rise to an effective synergy whereby the plant's nutritional needs are met. Fortified organic manure is made from organic manure with mineral additives, a compost mixture of nitrogen- and carbon-rich material, microbial inoculants, seaweed extracts, fish emulsion and more **[19]**. Fortified organic manure is a strategic addition to the methods of organic agriculture. Organic manure is known for its ability to nourish crops and improve soil structure, while adding extra nutrients to fortified formulations increases its ability to support crop growth, particularly in stressful environments. These formulations are specially designed to deliver a more balanced and precise nutrient profile, supporting the best possible plant growth even under less favourable soil and climatic conditions. The fortification process is associated with the addition of nutrients (N, P, K and the micronutrients Ca, Mg, S, B, Zn, Fe, Cu, Co, Se and Si). Incorporation of microbes with organic manure boosts nitrogen fixation and cellulolytic degradation, stimulates the synthesis of phytohormones and raises the level of secondary metabolites, which boost plant growth **[20]**. Fortified organic manure decreases the emissions of greenhouse gases and NH_3 from animal production, improving nitrogen availability to crop plants. Fortified organic manure is designed to meet the needs of different crops, thus offering a well-balanced and customized soil-enrichment method **(Figure 1; Table 1)**. Fortified organic manure not only has environmental advantages but also supplies the nutrients needed to address specific nutrient deficiencies, which significantly increases the stress tolerance of plants and agricultural productivity **[21]**.

Table 1: List of fortified organic manure types

Sl. No	Fortified organic manure	Enriched with	Reference
1	NPK-enriched organic manure	Nitrogen, phosphorus and potassium	**[3]**
2	Micronutrient-enriched organic manure	Iron / zinc / copper / manganese / boron / molybdenum	**[35, 49]**
3	Ca^{2+}–Mg^{2+} enriched organic manure	Calcium and magnesium	**[16]**
4	Biofortified organic manure	Bioactive compounds	**[67]**
5	pH-adjusted organic manure	Adjusted according to soil conditions	**[68]**
6	Customized crop-specific organic manure	Nutrient requirement-based enrichment	**[3]**
7	Nanobiochar-based nutrient amendment	Nano-enabled nutrient / carbon amendment	**[41]**
8	Nano-fertilizer	ZnO nanoparticles with fortified rice-residue compost	**[44]**

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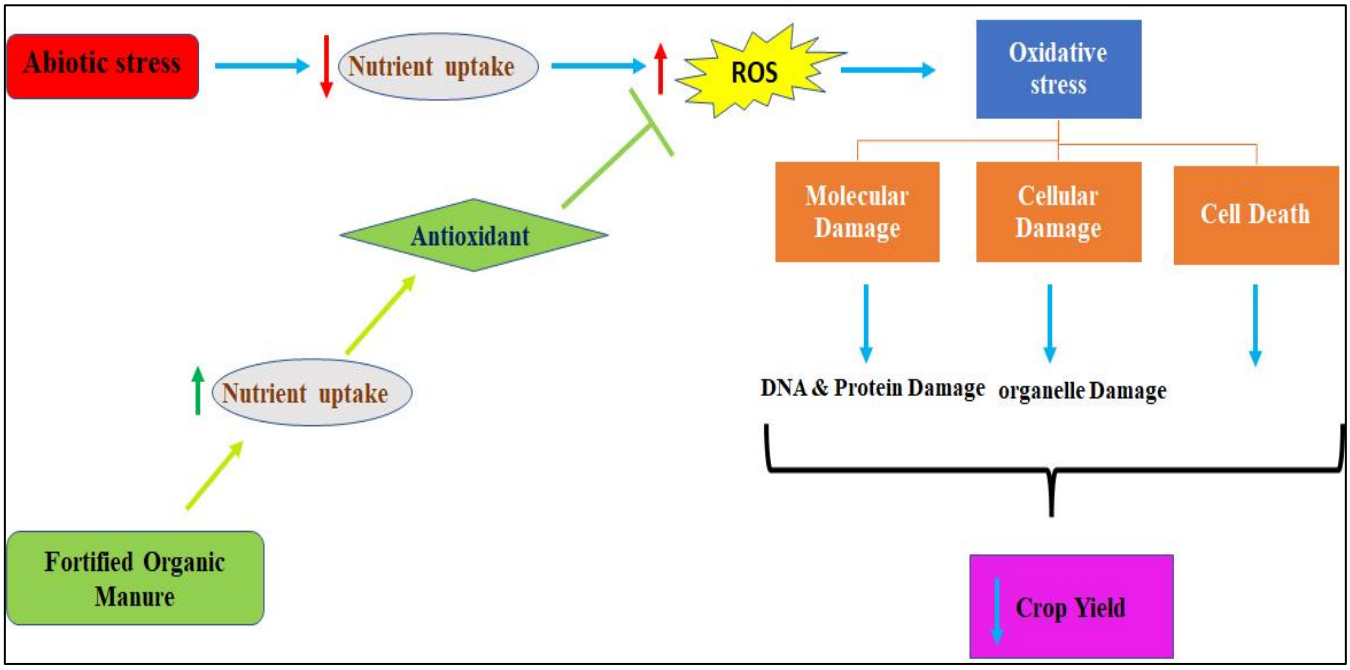


Figure 1: Overview of fortified organic manure involved in stress tolerance via antioxidant mechanisms. Abiotic stress causes water scarcity, which leads to inadequate nutrient intake. Loss of nutrient intake can lead to the accumulation of reactive oxygen species within cells, causing molecular and cellular damage, and the yield of a crop declines. In contrast, the use of fortified organic manure supplies the necessary nutrients and water to the plant for maintaining cellular homeostasis through increased antioxidant activity

Antioxidants and stress tolerance:

Reactive oxygen species (ROS) serve as triggers that activate signaling pathways involved in the initiation of biological processes. The major processes involved in signal translation that occur by redox reaction are oxidation and reduction of biomolecules. Decreasing the negative effects of ROS and oxidative stress on plants is a major role of antioxidants in improving plant stress tolerance. ROS are often produced by plants as a natural by-product of cellular processes in response to environmental constraints, including drought, high temperature, salt and infection by pathogens. When the production of ROS is too high, it can lead to oxidative stress, cell damage and metabolic disruption in plants. The primary defence against these damaging effects are the antioxidants, both enzymatic and non-enzymatic **[22]**. Enzymatic antioxidants such as superoxide dismutase, catalase and peroxidase neutralize and scavenge ROS. They prevent the generation of harmful free radicals, keeping plant cells in good structure and integrity. Enzymatic antioxidant defenses are supplemented by non-enzymatic antioxidants, mainly ascorbic acid, tocopherols and glutathione. These antioxidants help plants maintain a delicate balance of oxidized and reduced molecules, and play a role in plants' antioxidant capacity. Another important role of antioxidants is to protect cell membranes against the damaging effects of lipid peroxidation triggered by ROS. Lipid-soluble antioxidants, such as vitamin E, act as membrane stabilizers and help to maintain the integrity of cell structures. Moreover, antioxidants play a role in controlling the redox balance inside the cell, which enables the functioning of plant biological systems under stressful conditions **[23]**. Plants regulate stress-signaling pathways through the antioxidant system. Plants can adapt to stressors through the expression of stress-responsive genes; for instance, ascorbic acid has been shown to be an important player in this regard. Antioxidants also induce the activity of other antioxidant enzymes, creating a positive feedback effect and augmenting the plant's defense systems. Antioxidants play an important role in sustaining photosynthetic efficiency. They help to preserve the chloroplasts and other photosynthetic elements from oxidative damage so that they can keep producing energy even when the environment presents challenges **[24]**. Antioxidants also help in the development of roots and soil absorption, providing plants with the necessary nutrients in the soil. Antioxidants can be used to improve the overall stress tolerance of plants and can thereby help plants to withstand abiotic and biotic stress **[25]**. This role is diverse and relevant to the study of plant biology and serves as an example of the growing significance of antioxidants as a possibility to develop strategies for more resilient and productive crops under various and challenging conditions.

Oxidative stress and defense:

In plants, environmental stress causes an imbalance between the production of reactive oxygen species (ROS) and the antioxidant defense. Lipid peroxidation and membrane damage could be caused by ROS, such as superoxide ($O_2^{\bullet -}$) and hydroxyl radicals ($^{\bullet}OH$) **[25]**. They also oxidize proteins, changing the structure and function of enzymes, break DNA strands and modify the bases **[26]**. The relationship between ROS generation and

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antioxidant defense is shown in **Figure 1**. ROS overproduction occurs in response to abiotic stresses including drought, high temperature and salinity. Water shortage and high temperatures induce water deficits that slow down nutrient transport and intake, resulting in nutrient imbalances and increased production of ROS **[27]**. Salinity also disrupts the cell's physiology and induces stress-signaling pathways. Too much salt leads to the build-up of Na^+, K^+ and Cl^-, which disturbs the balance of ions and osmosis and causes the production of $O_2\bullet^-$, H_2O_2 and •OH [26]. An optimal K^+/Na^+ ratio increases the salt tolerance of the crop. Saline soils can be improved by beneficial microbes, organic materials and micronutrients combined as fortified organic manure, which increases organic carbon, humus and nutrient availability. The use of calcium-fortified composted animal manure (CF-CAM) has been found to limit the oxidative stress caused by salinity and also to enhance the growth, nutrition and physiological performance of canola **[28]**. These amendments can also promote biodiversity in the soil and improve plant resistance. NADPH oxidases, specifically respiratory burst oxidase homologs (RBOHs) **[29]**, are activated by salinity stress; stomatal conductance is reduced and photosynthetic enzymes and photosystems are impaired, leading to a build-up of ROS **[30]**. The production of ROS is also associated with plasma-membrane NADPH oxidases and apoplastic diamine oxidases. In wheat, salinity causes ROS production, lipid peroxidation and electrolyte leakage, which are greater in tolerant cultivars. H_2O_2 and malondialdehyde (MDA) also accumulate more in the salt-sensitive cultivars of *Brassica juncea* than in the tolerant cultivars. Ca^{2+}-dependent mitogen-activated protein kinase (MAPK) signaling pathways are also activated by salinity **[31].** ROS are also produced when plants are stressed by biotic agents, such as pathogens. Pathogen-associated molecular patterns (PAMPs) are recognized by pattern-recognition receptors (PRRs), which trigger PAMP-triggered immunity (PTI) and intracellular signaling cascades leading to the production of ROS **[32]**. RBOHs are important sources of the oxidative burst, transferring electrons from NADPH to oxygen to generate superoxide radicals, which are part of the pathogen-restriction mechanism. ROS and MAPK signaling also regulate other pathways, such as light-responsive pathways. Environmental stress also activates stress-response genes coding for antioxidant enzyme proteins such as superoxide dismutase (SOD), catalase (CAT), peroxidase, ascorbate peroxidase (APX) and glutathione reductase (GR) **[33, 34]**. SODs such as Cu, Zn-SOD, Fe-SOD and Mn-SOD transform superoxide to H_2O_2 and oxygen. CAT, APX and GR are additional enzymes that further detoxify H_2O_2 and help maintain redox balance. APX is involved in the AsA–GSH pathway, while GR is involved in the reduction of oxidized glutathione (GSSG) to reduced glutathione (GSH) with NADPH as electron donor **[33]**. Peroxiredoxins (Prxs) detoxify peroxide substrates and modulate ROS-dependent signaling **(Figure 2)**. If there is severe stress, the antioxidant capacity may be reduced, and the accumulation of ROS, oxidative bursts and cell damage may occur. The formation of ROS is carefully controlled within certain cellular compartments. Photosynthetic electron-transport chains, plasma-membrane NADPH oxidases and apoplastic peroxidases are the main sources **[34]**. Abiotic stress can induce a ROS burst and retrograde signaling, which can lead to ROS production in organelles and damage to proteins and enzymes **(Figure 3)**. In chloroplasts, singlet oxygen ($^1O_2$), superoxide radical ($O_2\bullet^-$), hydrogen peroxide (H_2O_2) and hydroxyl radical (•OH) are generated through processes including the excitation of chlorophyll (Chl) in the electron-transport chain (ETC) at photosystems I and II (Mehler's reaction), dismutation of $O_2\bullet^-$ by superoxide dismutase (SOD), and the Fenton reaction involving reduced iron (Fe^{2+}) and copper (Cu^+). Peroxisomes produce $O_2\bullet^-$ and H_2O_2 via photorespiration (glycolate), enzymatic reactions and NADH-dependent small ETC. The mitochondrial ETC contributes to $O_2\bullet^-$ production, which is then converted to H_2O_2 by SOD. In the cytosol, NADPH induces the conversion of O_2 into $O_2\bullet^-$ via plasma-membrane NADPH oxidase, followed by dismutation into H_2O_2 in the apoplast by SOD. ROS generated in different organelles under abiotic stress conditions mediate signaling pathways at low to moderate concentrations or induce oxidative stress at high concentrations (Source: Sachdev *et al.* **[20]**).

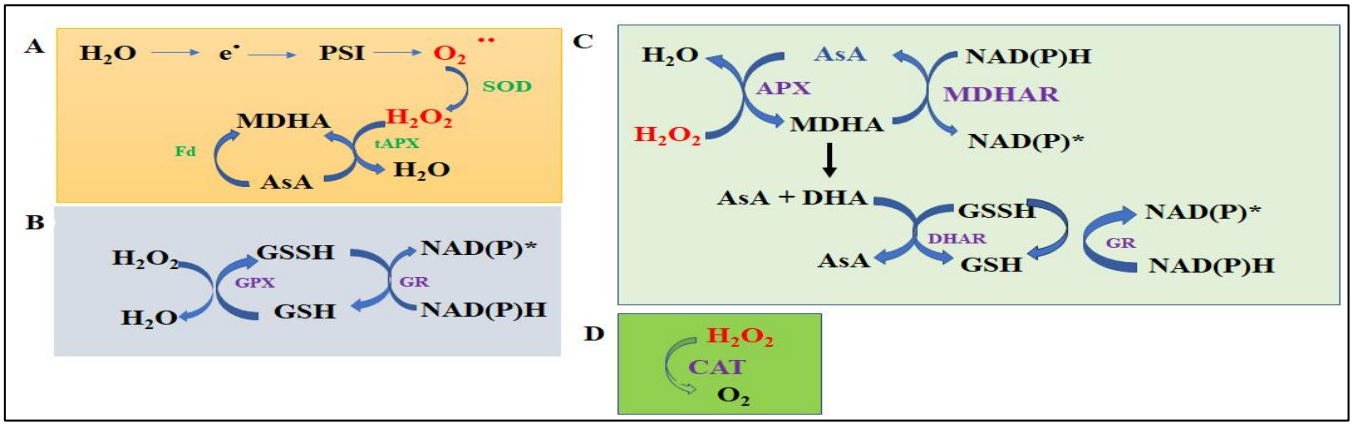


Figure 2: Catalytic reaction of antioxidant enzymes. SOD, superoxide dismutase; CAT, catalase; Prxs, peroxiredoxins; O_2, molecular oxygen; H_2O_2, hydrogen peroxide; $O_2\bullet^-$, superoxide radicals. (Source: Racchi **[69]**.)

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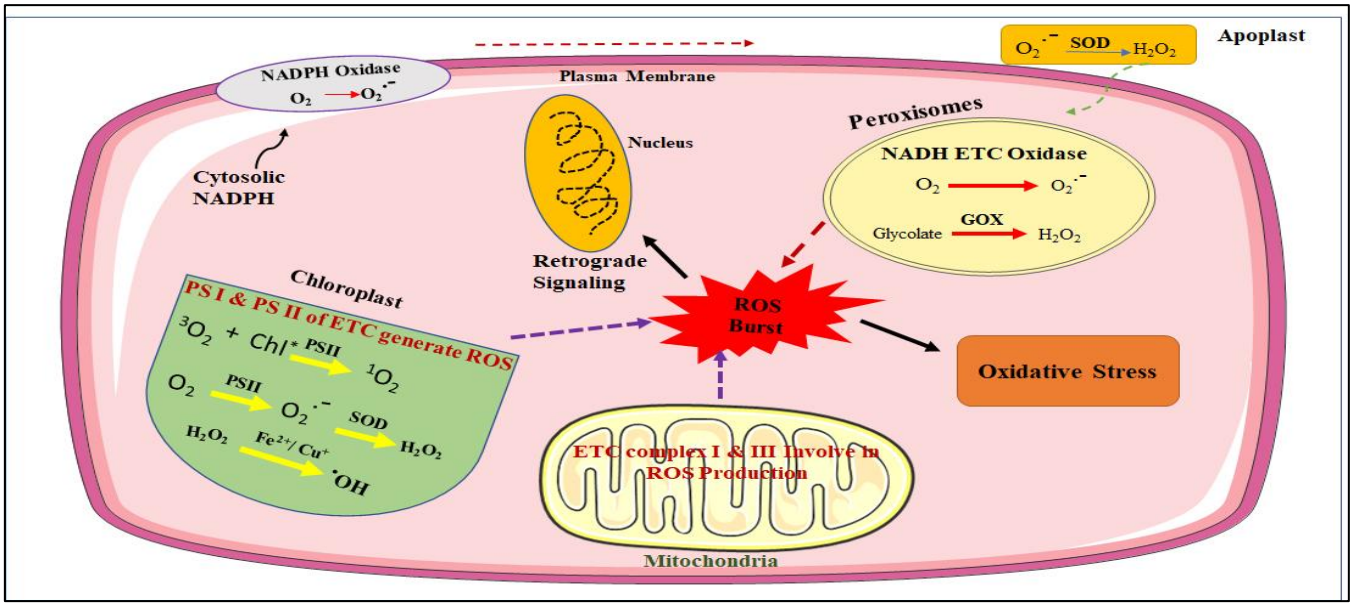


Figure 3: Abiotic stresses trigger the production of reactive oxygen species (ROS) within various organelles of plant cells, initiating either signaling (retrograde) pathways or oxidative stress

Influence of fortified organic manure on defense systems:

Under stress conditions, fortified organic manure is beneficial in providing nutrients and antioxidant defenses to plants. Antioxidant enzymes require micronutrients such as Fe, Zn, Cu, Mn and Se as cofactors. Fe is needed for catalase and peroxidase, while Mn is needed for superoxide dismutase (SOD). These can therefore be added to organic fertilizers to improve antioxidant enzyme activity and stress resistance **[35, 36]**. Organic manure can also affect phytohormonal signaling, as it may contain high levels of nutrients. Two crucial plant growth and stress-response regulators are abscisic acid (ABA) and jasmonic acid (JA). ABA-receptor activation in turn inhibits PP2C and stimulates SnRK2 kinases, which regulate the ABF transcription factors that mediate stomatal responses **[37]**. In response to drought and salinity stress, *GhABF2*, an ABA-responsive bZIP transcription factor, activates many ABA-responsive genes and improves drought and salinity tolerance. It has been shown to be associated with high proline levels and stimulation of SOD and catalase (CAT) activity in cotton, which helps to lower oxidative stress. JA signaling also controls stress defense through JA-Ile–COI1-mediated degradation of JAZ repressors, which releases transcription factors such as MYC2. This pathway is associated with plant defence and secondary-metabolite production (alkaloids, terpenoids) **[38]**. Under various stresses, fortified organic manure has shown positive effects on growth and production. It improved the growth and yield of mash bean under cadmium (Cd) stress. Maize growth was enhanced in saline-sodic soils with calcium-fortified compost, which not only increased NPK uptake but also decreased the Na^+/K^+ ratio, thus improving growth, yield, physiology and nutrient uptake. Bio-inoculants added to growing media can also increase the uptake and translocation of nutrients, thus increasing fruit yield and quality **[39]**. Fruit crops also show the potential of arbuscular mycorrhizal (AM) fungal consortia to enhance the growth, yield and quality of the crop **[40]**. Nanomaterials have the potential to enter plants through the apoplastic or symplastic route and affect plant metabolism. Carbon nanoparticles, having a larger surface area and microporosity, can be used as promoters of plant growth **[41]**. An improvement in the growth and metabolism of *Vigna radiata* was obtained by using engineered carbon nanoparticles **[42]**. Nano-nutrients and nanobiochar resulted in significant improvement in growth parameters and biomass under drought stress by reducing ROS levels and lipid peroxidation and enhancing the membrane stability of tomato. The foliar application of nano-nutrients also enhanced the activities of antioxidant enzymes, secondary metabolites and osmolytes **[43]**. The use of ZnO nanoparticles with fortified organic manure boosted rice productivity in nutrient-poor soils **[44]**, and iron- and zinc-fortified nanobiochar increased rice yield and nutrient levels **[45]**.

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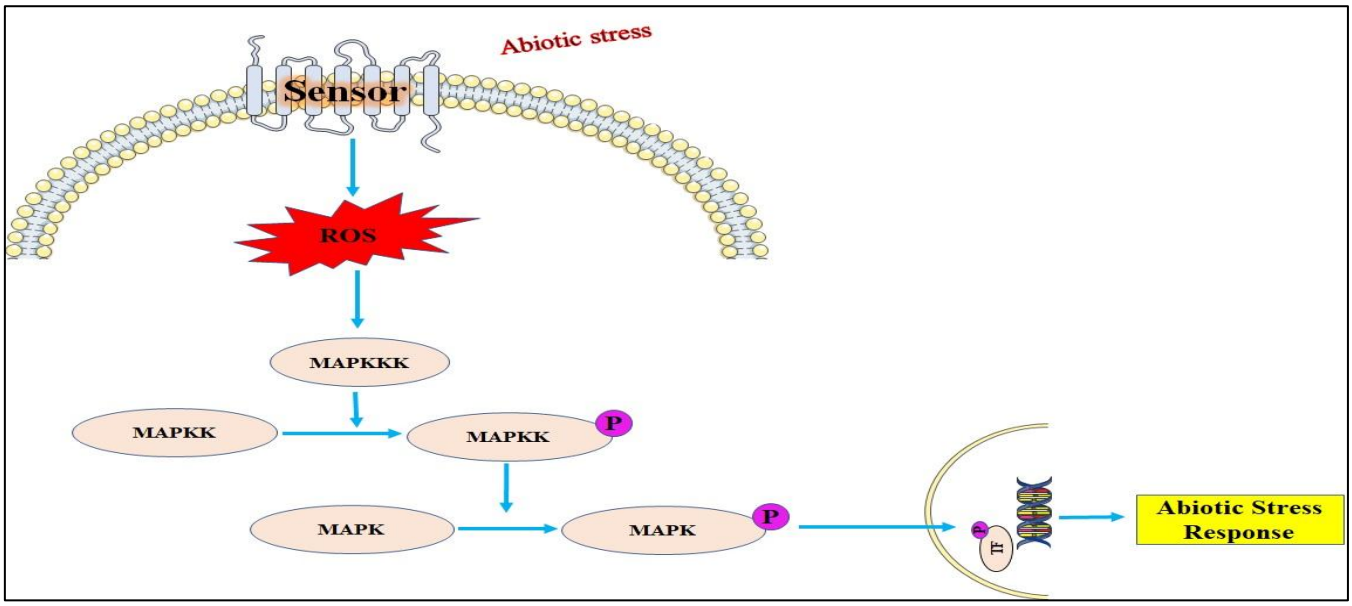


Figure 4A: MAPK signaling pathway during stress conditions in plants

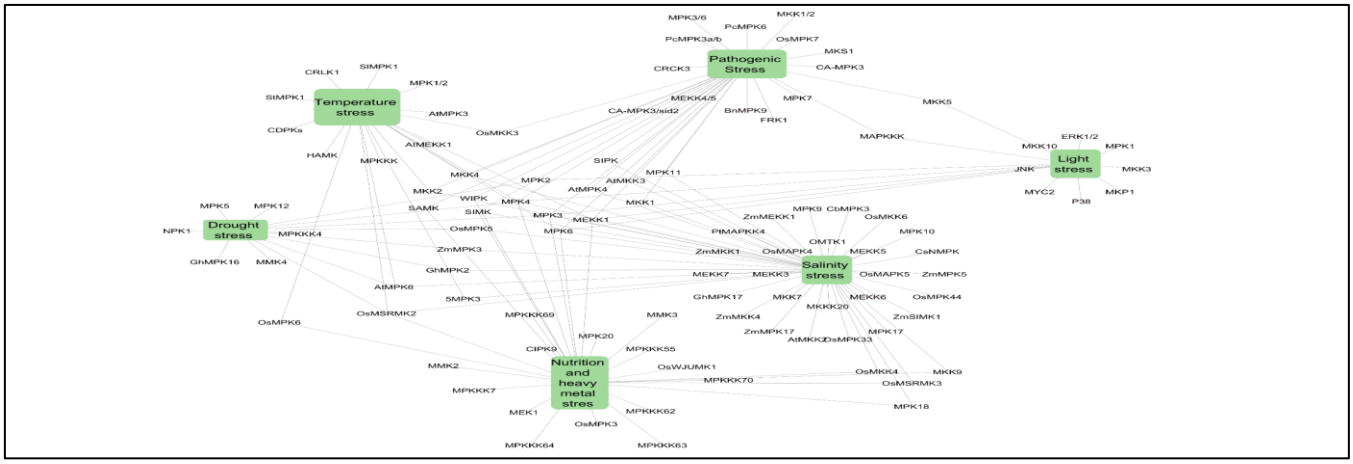


Figure 4B: Major MAPK signaling-linked genes that are expressed during different stress conditions in plants

Table 2: MAPK signaling involved in stress response

S. No	Plant species	MAPK genes	Role in stress	Reference
1	*Malus* spp. (Apple)	*MaMAPK*	Highest expression in drought	**[50]**
2	*Malus domestica* (Apple)	*MAPKKK* Raf-like group gene	Overexpression of MdRaf5	**[51]**
3	Apple seedling	*MdMAPK16-2, MdMAPK17, MdMAPK20-1*	Expression increased during drought; enhanced by AMF inoculation	**[47]**
4	*Brassica napus* (Rapeseed)	BnMAPK1	Related to drought-stress response; overexpression enhances tolerance	**[52]**
5	*Cucumis sativus* (Cucumber)	*CsMAPKs*	Initially downregulated, then significantly upregulated	**[53]**
6	*Fragaria vesca* (Strawberry)	*FvMAPK5, FvMAPK8*	Important for abiotic stress responses; transcriptionally activated	**[54]**
7	*Poncirus trifoliata* (Trifoliate orange)	*PtrMAPK*	Transcript levels increased by dehydration; overexpression improves tolerance	**[55]**
8	*Morus* spp. (Mulberry)	*MnMAPKs*	Positive regulation, particularly *MnMAPK7*	**[56]**
9	*Manihot esculenta* (Cassava)	*MeMAPKs*	Potential role in water uptake and drought response	**[57]**
10	*Vitis vinifera* (Grapevine)	*VviMAPKKKs*	Expression significantly increased	**[58]**
11	*Brachypodium distachyon*	MAPK cascade genes	90% induced under cold stress; 60% induced under heat stress	**[59]**
12	*Solanum lycopersicum* (Tomato)	*SlMPK1, SlMPK2, SlMPK3*	*SlMPK1*: negative regulator of thermotolerance; *SlMPK3* responsive to cold	**[60]**
13	*Cucumis sativus* (Cucumber)	*CsMAPKs*	Most upregulated	**[53]**

14	*Fragaria vesca* (Strawberry)	*FvMAPKs, FvMAPKKs*	Upregulated	**[54]**
15	*Morus* spp. (Mulberry)	*MnMAPKs*	Differential regulation	**[56]**
16	*Chrysanthemum morifolium*	*CmMPKs*	Decreased or unchanged after heat shock	**[62]**
17	*Mentha piperita* (Peppermint)	MAPK protein	Promotes V-H^+-ATPase expression; enhances tolerance	**[63]**
18	*Musa* spp. (Banana)	Not specified	MAPK cascade more active in tolerant species	**[65]**
19	*Morus* spp. (Mulberry)	*MnMAPKs*	Upregulated; differential regulation	**[56]**
20	*Chrysanthemum morifolium*	*CmMPKs, CmMKKs*	Involved in regulating salt tolerance	**[62]**
21	*Manihot esculenta* (Cassava)	*MeMAPKs*	Some upregulated, others downregulated	**[57]**
22	*Actinidia chinensis* (Kiwifruit)	*AcMAPKs*	Upregulated	**[66]**
23	*Fragaria vesca* (Strawberry)	*FvMAPKs, FvMAPKKs*	Upregulated	**[54]**

MAPK signaling pathway in stress response:

The mitogen-activated protein kinase (MAPK) signaling pathway is one of the most important pathways in cells, involved in growth, differentiation, survival and environmental response. In plants, MAPK cascades are responsible for signaling events in response to pathogenic, light, temperature, drought, salinity, nutritional and heavy-metal stresses **(Figure 4A and 4B)**. Most cascades involve MAP3Ks/MEKKs, MAP2Ks/MEKs/MKKs and MAPKs. Upstream MAP3Ks or MAP4Ks are activated by stress perception, and sequential phosphorylation of MAP2Ks and MAPKs occurs. MAP2Ks are enzymes that phosphorylate MAPKs at the conserved T-X-Y motif. The activated MAPKs phosphorylate a variety of proteins such as transcription factors or other kinases, and MAPK phosphatases (MKPs) stop the signal and modulate its duration **[46]**. The reactive oxygen species (ROS)-mediated mitogen-activated protein kinase (MAPK) signaling pathway under abiotic stress conditions. Abiotic stress is perceived by membrane-bound sensor proteins, leading to the generation of ROS, which act as secondary messengers to activate the MAPK cascade. The signaling cascade involves sequential phosphorylation and activation of MAP kinase kinase kinase (MAPKKK), MAP kinase kinase (MAPKK) and MAP kinase (MAPK). Activated MAPK translocates to the nucleus, where it phosphorylates transcription factors, resulting in the regulation of stress-responsive genes and the induction of abiotic stress responses. "P" denotes phosphorylation. Network of MAPK genes involved during pathogenic stress, light stress, temperature stress, drought stress, salinity stress, and nutrition and heavy-metal stress conditions. The network of stress-related genes was identified using CYTOSCAPE 3.10.2 software. MAPK pathways also play a role in nutrient signaling, which is regulated by nutrients such as sugar, nitrogen, phosphate, iron and potassium. The *GhMAP3K14–GhMKK11–GhMPK31* cascade has been identified as a key regulator of drought-stress responses in cotton **[46]**. These results show that MAPK signaling events are involved in integrating the environmental and physiological cues that control plant adaptation. Under oxidative stress, the ROS and MAPK signaling pathways are tightly linked. Antioxidants that block the accumulation of ROS may inhibit MAPK activation, and ROS may in turn activate the MAPK pathway. One example is that H_2O_2 can modify signaling proteins through oxidation, thereby activating MAPK signaling. This means that ROS may act as signaling molecules and alter important protein residues, triggering downstream kinase cascades **[48]**. Further evidence from apple species indicates that MAPK signaling is involved in drought tolerance. Twelve MAPKKKs were significantly regulated in response to polyethylene-glycol-induced drought stress, and overexpression of *MdRaf5* resulted in decreased transpiration and reduced stomatal aperture in transgenic *Arabidopsis*, leading to increased drought tolerance **[51]**. Arbuscular mycorrhizal fungi (AMF) are also involved in MAPK-mediated drought tolerance in apple plants. Under drought conditions, AMF inoculation significantly upregulated *MdMAPK16-2*, *MdMAPK17* and *MdMAPK20-1* **[47]**. MAPKs also play a role in drought responses in strawberry and mulberry. *FvMAPK5* and *FvMAPK8* have been shown to be induced by drought **[54]**, while six MAPKs were upregulated during drought in mulberry (*MnMAPK3*, *MnMAPK4*, *MnMAPK6*, *MnMAPK7*, *MnMAPK8* and *MnMAPK9*) **[56]**. In *Brachypodium distachyon*, MAPK genes are also induced by temperature stress, with ~90% of them induced by cold and ~60% by heat stress **[59] (Table 2)**. In tomato, silencing of *SlMPK1* enhances heat tolerance and decreases the accumulation of ROS, while its overexpression results in higher accumulation of H_2O_2 and MDA. In contrast, *SlMPK3* promotes cold tolerance by boosting antioxidant activity, proline levels, soluble sugars, germination and root growth. Overall, MAPK cascades regulate ROS signaling, antioxidant defence and stress-responsive gene expression, thus playing a crucial role in plant resilience under environmental stress **[60]**.

Fortified organic manure regulates MAPK signaling pathways:

The ability of fortified organic manure to modulate MAPKs is an intriguing topic in plant signaling and sustainable farming. Fortified with nutrients and bioactive compounds, fortified organic manure has a strong impact on the complex MAPK signaling network in plants. Fortified organic manure delivers nutrients such as zinc, manganese and copper into the plant, which in turn modulate the molecular pathways leading to MAPK activation **[64]**. The mechanisms involve specific recognition of enriched organic components by plant receptors, which may affect the activation of MAPKs. Thus, the expression of stress-sensitive genes and the control of several physiological processes are regulated **[46]**. Owing to its balanced content of organic matter, micronutrients and beneficial microbes, fortified organic manure acts as both a signaling modulator and a nutrient source **[18]**. It is thought that this modulation of the MAPK pathway helps plants to better withstand the environment, take up nutrients more efficiently, and grow and develop more effectively. The molecular interaction between enriched organic manure and MAPK signaling is an interesting research area that could benefit sustainable agriculture, although it is not yet fully understood. There are potential opportunities to tailor organic amendments to optimize plant health, productivity and agroecosystem sustainability by modulating this stress-response

pathway. A key benefit is that further research in this area may lead to the discovery of additional targets for precision agriculture **[61]**.

Conclusion:
Available data on the role of the MAPK cascade in stress response, gained from studies in different plant species, offers significant insights for crafting strategies to enhance stress tolerance and boost the resilience of crops under variable environmental conditions. The potential to harness the regulatory capacity of MAPK signaling pathways for sustainable agriculture and for the development of crops able to withstand harsh environmental conditions is vast. Additionally, fortified organic manure appears to be an effective means of improving plant stress resistance, antioxidant activity and sustainable agriculture by controlling MAPK signaling pathways. Its bioactive compounds, combined with nutritional enrichment, offer a comprehensive solution that supports plant health and resilience in the presence of environmental challenges, ensuring resilient and productive agricultural crops.

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R. Singaravel: Conceptualization, Methodology, Investigation, Writing – original draft, Writing – review & editing.

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References:
[1] Zia R *et al. Microbiol. Res.* 2021 **242**:126626. [PMID: 33189069].
[2] Majeed Y *et al. Front. Plant Sci.* 2023 **14**:932923. [DOI: 10.3389/fpls.2023.932923].
[3] Zhou Z *et al. Front. Environ. Sci.* 2022 **10**:1058071. [DOI: 10.3389/fenvs.2022.1058071].
[4] Babcock-Jackson L *et al. J. Agric. Food Chem*. 2023 **22**:8265. [PMID: 37219570]
[5] Chaudhary P *et al. Front. Plant Sci.* 2022 **13**:930340. [PMID: 36082294]
[6] file:///C:/Users/User/Downloads/E-02-03-88-299-303AgriArticlepublished.pdf
[7] Köninger J *et al. Agric. Syst.* 2021 **194**:10325. [DOI: 10.1016/j.agsy.2021.103251].
[8] Lehmann J *et al.* N*at. Rev. Earth Environ*. 2020 **1**:544. [PMID: 33015639].
[9] Bhanwaria R *et al. Plants*. 2022 **11**:722. [PMID: 35336604].
[10] Das S *et al. Food Qual. Saf.* 2020 **4**:69. [DOI: 10.1093/fqsafe/fyaa018].
[11] Castro B *et al. Nat. Plants.* 2021 **7**:403. [PMID: 33846592].
[12] De Castro J *et al. Agronomy.* 2022 **12**:780. [DOI: 10.3390/agronomy12040780].
[13] De Hita D *et al. Front. Plant Sci.* 2020 **11**:493. [DOI: 10.3389/fpls.2020.00493].
[14] Tellen VA & Mbiseh SJ, *Agric. Ecol. Res. Int.* 2020 **21**:30. [DOI: 10.9734/jaeri/2020/v21i730155]
[15] Greff B *et al. J. Environ. Manage*. 2022 **302**:114088. [PMID: 34798585].
[16] Yang S *et al. Agronomy.* 2023 **13**:969. [DOI: 10.3390/agronomy13040969].
[17] Ahuja I *et al. Waste Manag*. 2020 **115**:95. [PMID: 32736033].
[18] Ahmed T *et al. Plants*. 2023 **12**:3550. [DOI: 10.3390/plants12203550].
[19] Seleiman MF *et al. Plants*. 2021 **10**:259. [PMID: 33525688].
[20] Sachdev S *et al. Antioxidants*. 2021 **10**:277. [PMID: 33670123].
[21] Andrés Juan C *et al. Int. J. Mol. Sci.* 2021 **22**:4642. [PMID: 33924958].
[22] Kumari VV *et al. Int. J. Mol. Sci.* 2022 **23**:8519. [PMID: 35955651].
[23] Shabbir R *et al. Agronomy*. 2022 **12**:2795. [DOI: 10.3390/agronomy12112795].
[24] Singhal RK *et al. Front. Plant Sci.* 2021 **12**:670369. [PMID: 34484254].
[25] Hasanuzzaman M *et al. Int. J. Mol. Sci*. 2021 **22**:9326. [PMID: 34502233].
[26] Alharbi K. *ACS Omega.* 2022 **24**:20819. [PMID: 35755363].
[27] Biswas S *et al. Plant Stress.* 2023 **9**:100186. [DOI: 10.1016/j.stress.2023.100186].
[28] Naveed M *et al. Sustainability*. 2020 **12**:846. [DOI: 10.3390/su12030846].
[29] Kabała K *et al. Antioxidants*. 2022 **11**:1534. [PMID: 36009253].
[30] Hasanuzzaman M *et al. Antioxidants.* 2020 **9**:681. [PMID: 32751256].
[31] Fu H & Yang Y, *Curr. Issues Mol. Biol.* 2023 **45**:5914. [DOI: 10.3390/cimb45070374].
[32] Iqbal Z *et al. Front. Plant Sci*. 2021 **12**:631810. [PMID: 33763093].
[33] Rajput VD *et al. Biology.* 2021 **10**:267. [PMID: 33810535].
[34] Trono D & Pecchioni N, *Plants.* 2022 **11**:3358. [DOI: 10.3390/plants11233358].
[35] Ahmed N *et al. Sci. Hortic.* 2024 **323**:112512. [DOI: 10.1016/j.scienta.2023.112512].
[36] https://www.sciencedirect.com/science/chapter/edited-volume/abs/pii/B9780323904520000438
[37] Lim J *et al. Front. Plant Sci.* 2022 **13**:895698. [PMID: 35712559].

[38] Umer Chattha M *et al. Agronomy*. 2021 **11**:2152. [DOI: 10.3390/agronomy11112152].
[39] Arora R *et al. Agric. Res. J.* 2022 **58**:1065. [DOI: 10.5958/2395-146X.2021.00150.2].
[40] https://link.springer.com/chapter/10.1007/978-981-15-6895-4_9
[41] Ramanayaka S *et al. Environ. Sci. Nano.* 2020 **7**:3279. [DOI: 10.1039/d0en00486c].
[42] Manna M *et al. Plant Cell Environ*. 2023 **46**:2277[PMID: 37157977]
[43] Mubashir A *et al. Front. Plant Sci*. 2023 **13**:1066790. [PMID: 36714778].
[44] Singaravel R *et al. J. Plant Nutr.* 2023 **46**:4063. [DOI: 10.1080/01904167.2023.2212722].
[45] Danquah A *et al. Biotechnol Adv.* 2014 **32**:40[PMID: 24091291]
[46] Lin L *et al. Int J Mol Sci*. 2021 **22**:1543. [PMID: 33546499]
[47] Huang D *et al. Plant Physiol. Biochem.* 2020 **149**:245. [PMID: 32087536].
[48] Khan F *et al. Plants*. 2023 **12**:2861. [DOI: 10.3390/plants12152861].
[49] Ali MA *et al. Front. Plant Sci*. 2021 **12**:743378. [DOI: 10.3389/fpls.2021.743378].
[50] Peng LX *et al. Acta Biochim. Biophys. Sin*. 2006 **38**:281. [DOI: 10.1093/abbs/38.4.281].
[51] Sun M *et al. Sci. Rep*. 2017 **7**:13511. [PMID: 29044159].
[52] Weng CM *et al. J. Integr. Agric*. 2014 **13**:2407. [DOI: 10.1016/S2095-3119(13)60696-6].
[53] Wang J *et al. BMC Genomics.* 2015 **16**:386. [PMID: 25976104].
[54] Zhou H *et al. Int. J. Mol. Sci*. 2017 **18**:1766. [DOI: 10.3390/ijms18081766].
[55] Huang XS *et al. J. Exp. Bot*. 2011 **62**:5191. [PMID: 21778184].
[56] Wei C *et al. Plant Physiol. Biochem*. 2014 **77**:108. [PMID: 24583344].
[57] Yan Y *et al. Front. Plant Sci*. 2016 **7**:1294. [DOI: 10.3389/fpls.2016.01294].
[58] Wang G *et al. BMC Plant Biol*. 2014 **14**:219. [PMID: 25158790].
[59] Jiang M *et al. BMC Genomics.* 2015 **16**:228. [PMID: 25886731].
[60] Ding H *et al. Plant Physiol*. 2018 **177**:633 [DOI: 10.1104/pp.18.00067].
[61] Wei W *et al. PLoS One.* 2017 **12**:e0178596. [DOI: 10.1371/journal.pone.0178596].
[62] Song A *et al. PeerJ*. 2018 **6**:e5037. [DOI: 10.7717/peerj.5037].
[63] Li Z *et al. Protoplasma.* 2016 **253**:553. [DOI: 10.1007/s00709-015-0834-1].
[64] Li Z *et al. Protoplasma.* 2016 **253**:1541. [PMID: 26631016].
[65] Wang L *et al. Sci. Rep.* 2017 **7**:1159. [PMID: 28442729].
[66] Wang G *et al. Int. J. Mol. Sci.* 2018 1**9**:2510 [PMID: 30149559].
[67] Naveed S *et al. Int. J. Recycl. Org. Waste Agric.* 2018 **7**:189. [DOI: 10.1007/s40093-018-0205-y].
[68] Thepsilvisut O e*t al. Horticulturae*. 2023 **9**:259 [DOI: 10.3390/horticulturae9020259]
[69] Racchi ML. *Antioxidants*. 2013 **2**:340 [DOI: 10.3390/antiox2040340].

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