

## Alleviating adverse effects of environmental stress in plants through chitosan application

Tahreem ARSHAD<sup>1</sup>, Wang LIHONG<sup>2\*</sup>, Hussam F. Najeeb ALAWADI<sup>3</sup>,  
Athar MAHMOOD<sup>4\*</sup>, Muhammad Anjum ZIA<sup>5</sup>, Maria NAQVE<sup>1</sup>,  
Basharat ALI<sup>6</sup>, Muhammad NAWAZ<sup>6</sup>, Muhammad Umair HASSAN<sup>7</sup>,  
Abeer HASHEM<sup>8</sup>, Elsayed Fathi ABD\_ALLAH<sup>9</sup>

<sup>1</sup>University of Agriculture Faisalabad, Department of Botany, 38000 Faisalabad, Pakistan; [tabreemarsbad108@gmail.com](mailto:tabreemarsbad108@gmail.com); [marianaqvi26@gmail.com](mailto:marianaqvi26@gmail.com)

<sup>2</sup>Baicheng Normal University, College of Tourism and Geographic Science, Baicheng, 137000, Jilin, China; [wlb19721108@163.com](mailto:wlb19721108@163.com) (\*corresponding author)

<sup>3</sup>Al-Qadisiyah University, College of Agriculture, Iraq; [hussam.alawadi@qu.edu.iq](mailto:hussam.alawadi@qu.edu.iq)

<sup>4</sup>University of Agriculture Faisalabad, Department of Agronomy, 38000 Faisalabad, Pakistan; [athar.mahmood@uaf.edu.pk](mailto:athar.mahmood@uaf.edu.pk) (\*corresponding author)

<sup>5</sup>University of Agriculture Faisalabad, Department of Biochemistry, 38000 Faisalabad, Pakistan; [anjum.zia@uaf.edu.pk](mailto:anjum.zia@uaf.edu.pk)

<sup>6</sup>Khawaja Fareed University of Engineering and Information Technology, Department of Agricultural Engineering, Rahim Yar Khan 62400, Pakistan; [basharat2018@yahoo.com](mailto:basharat2018@yahoo.com); [dmnawaz@kfueit.edu.pk](mailto:dmnawaz@kfueit.edu.pk)

<sup>7</sup>Jiangxi Agricultural University, Research Center on Ecological Sciences, Nanchang, China; [muhassanuaf@gmail.com](mailto:muhassanuaf@gmail.com)

<sup>8</sup>King Saud University, College of Science, Botany and Microbiology Department, P.O. Box. 2460, Riyadh 11451, Saudi Arabia; [habeer@ksu.edu.sa](mailto:habeer@ksu.edu.sa)

<sup>9</sup>King Saud University, College of Food and Agricultural Sciences, Plant Production Department, P.O. Box. 2460, Riyadh 11451, Saudi Arabia; [eabdallah@ksu.edu.sa](mailto:eabdallah@ksu.edu.sa)

### Abstract

Chitosan encourages the growth of plants, controls their metabolic processes and homeostasis, and activates their defence mechanisms. On one side, it hinders the ability of pathogens by preventing their growth and limiting their reproduction, so it will become a more common and ideal asset for agricultural sustainability. Additionally, cesium (Cs) stimulated the SOS1 pathway and raised a number of gene transcripts related to energy generation, phenol metabolism, proton motive force, salt compartmentalization, and other processes. However, plants exposed to salt stress were treated with cesium nanoparticles (CsNPs) and modified CsBMs, which boosted indole terpene alkaloid metabolism, defense-related genes, decreased ROS formation by boosting jasmonic acid (JA) signalling, increased essential oil, anthocyanins, membrane stability, alkaloids, and diterpene glycosides. This is the first review that specifically compares Cs/CsNPs/modified CsBMs treatment options under salt stress and offers insights about the biological and biochemical parameters of the plants. It also recommends using CsNPs and modified CsBMs rather than Cs for better plant function under salinity stress.

**Keywords:** chitosan; environmental stresses; defense response

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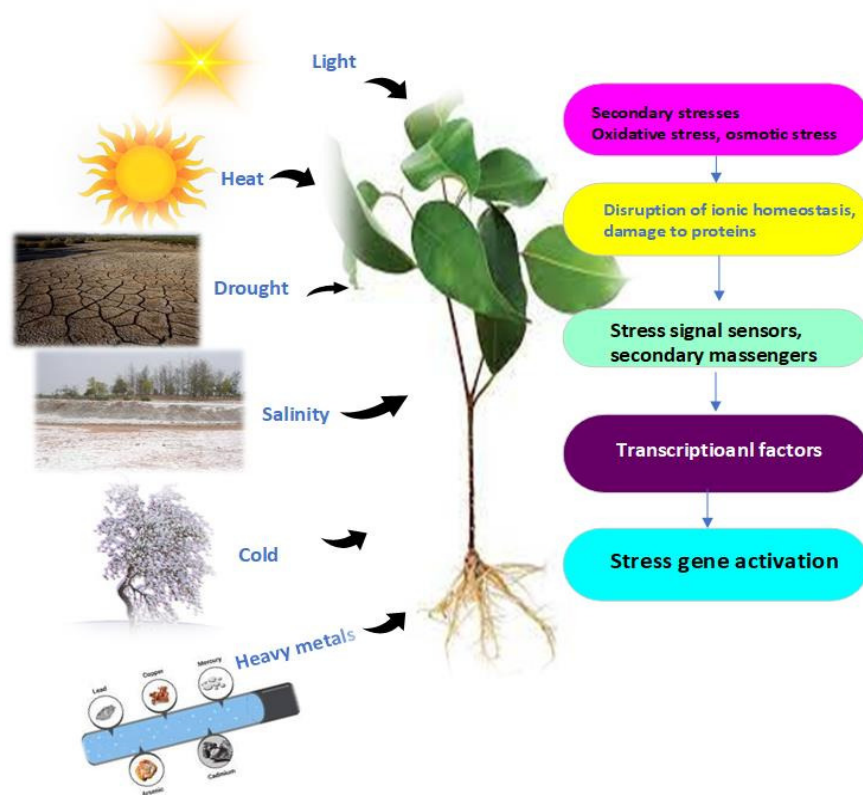
## Introduction

Infection, predation, drought, floods, excessive salinity, subzero, high, or low temperatures, as well as natural or synthetic hazardous substances, can all be stressful to plants if they last for an extended period of time. We will concentrate on plant responses that adapt to resource pressures that cause osmotic inequalities, such as part-day temperatures, temporary lack of rain, or changing sodium salinity, and set aside hazardous conditions, such as overabundance of heavy metal ions or persistent lack of water in a genuine desert. Research on environmental stressors has focused on the sensing and signalling of osmotic stress, which is converted into biochemical responses, metabolic changes, and changed physiological states, reprogramming the phase of development (Saini *et al.*, 2018). The understanding that stress signals are induced by a variety of channels and that those channels are interconnected is pertinent to the subject of stress-mediated changes in metabolism (Singh *et al.*, 2022). There are at least four routes in plants for signalling that are used to react to drought, salt, and cold temperatures as shown in Figure 1. Signals of salinity and drought are reacted to via an ABA-dependent pathway (Pastori and Foyer, 2002). Another bifurcation may be seen in a second signalling pathway that is independent of abscisic acid and exhibits divergent responses of genes that are either impacted by cold, salinity, and drought, or by salinity and drought alone (Munnik and Meijer, 2001). The focus of this article is on the biochemical processes elicited by plant counterparts of common signal transduction pathways, similar, for instance, to the yeast HOG (phosphorylation cascade)-pathway determining changes in carbohydrate allocation and analogous to the yeast phosphorylation-relay in which the amino acid phosphatase calcineurin plays an important role (Desai *et al.*, 2023), managing water and ion uptake and ion exclusion or export over environmental stress (Rose, 2023).

Early research that took into account various biotic, abiotic, and anthropogenic influences addressed the fundamental idea of physiological buildup of stress in plants (Li *et al.*, 2023). As opposed to that, molecular investigations into stress combinations in plants started around 20 years ago, with an emphasis on the combination of heat and drought stress (Percival, 2023). There are competing demands on plant physiological systems and metabolism as a result of this stressor combination has caused large production losses in agriculture (Patel *et al.*, 2023). It may also be a great illustration of the conflicting pathways that are activated in plants when several stresses are present. Stomatal regulation is a prime illustration of them. Stomata respond to heat stress by opening, allowing plants to cool themselves through transpiration, whereas they close in reaction to stress caused by drought, preventing water loss (Hassan *et al.*, 2022b). The openings of stomata on leaves remain closed as a result of the interaction of drought and heat stress, and leaf temperature rises to potentially lethal levels. While stomata on leaves close in response to the mixed impacts of heat stress and drought, stomata on flowers keep open, allowing flowers to sustain evaporation and cool the reproductive tract (representing a new acclimation strategy in plants known as “differential transpiration” (Javaid *et al.*, 2022). Many additional stress combinations of two or at most three distinct stresses applied concurrently to plants were studied after the original studies of drought and heat stress mixture (similar to the impact of multiple stresses on the Indian River lagoon ecosystem in Florida (Zandalinas and Mittler, 2022). Additional research has also looked at the impact of various stressors happening in succession on plants (in a manner akin to how storms followed by an extended drought, followed by insect assault and fires, on European woods (Coolen *et al.*, 2019).

Abiotic stress on plants causes a variety of alterations to their physiology, molecular activity, and developmental processes. These changes may increase stress sensitivity, resistance, or tolerance (Harb *et al.*, 2010). Under heat and drought extremes, detrimental consequences on plants have been recorded, including disturbances in cellular homeostasis, obstructions to growth and development, decreased yield, and plant mortality (Sharma *et al.*, 2019). Plants must react to and adapt to such pressures in order to live. However, they are today faced with challenges that go beyond their ability to adjust to existing temperature and precipitation changes brought on by climate change (physically, biochemically, and molecularly) (Rizwan *et al.*, 2019). This

is partly because plants lack the resources and energy needed to adapt to such abiotic stress circumstances; for instance, there isn't enough energy to produce stress response proteins like heat shock proteins (HSPs) or late embryogenesis abundant (LEA) proteins (Mittler, 2006).



**Figure 1.** Representation of abiotic stresses that effects the plant growth (Delezuk *et al.*, 2017)

### Chitosan

A natural, biodegradable, less poisonous and biocompatible substance is chitosan. Chitosan has attracted due to its high level of interest, physical qualities in a variety of commercial uses, including food, cosmetics, biomedicine, agriculture, preservation of the environment, and wastewater management (Morin-Crini *et al.*, 2019).

### Properties and mechanism of action

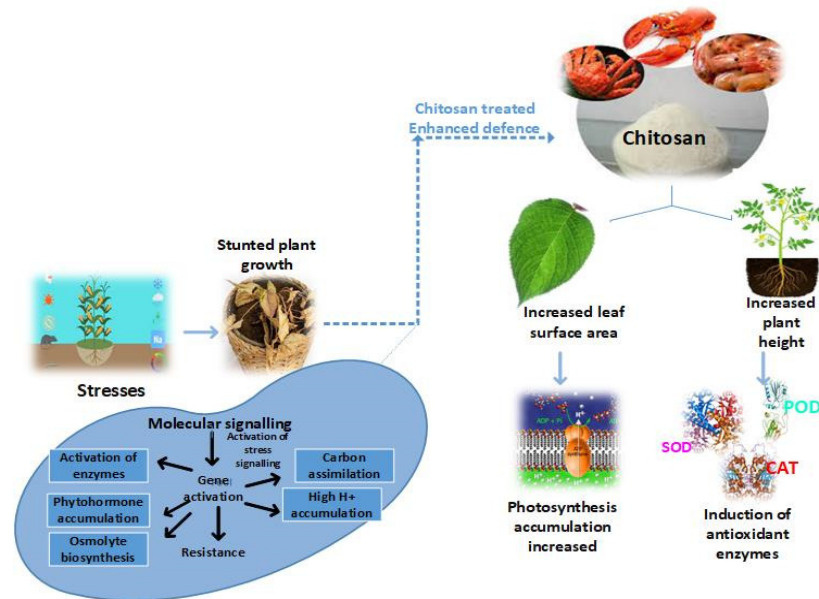
Chitin and CHT, a derivative of it, have a reputation for having the ability to act as biocontrol agents (Riseh *et al.*, 2022a). Chitin may be found in a wide range of invertebrates, including the outermost layers of insects and the exoskeletons of crustaceans. It also makes up structural polysaccharides in fungi and flexible fungal cell walls, as well as the cell walls of fungus, yeast, and algae. It accounts for roughly 16% of the organism's dry weight (Synowiecki and Al-Khateeb, 2003). Chitin is N-deacetylated using a chemical or enzymatic process to create CHT. Instead of referring to a single specific substance, the term "chitosan" designates a group of commercially available polymer chains that are varied with respect to deacetylation level, molecular mass, degree of polymerization, and acid dissociation constant (pKa value) (Peniche *et al.*, 2008). The level of deacetylation and molecular weight, in particular, affect the physicochemical qualities (such as viscosity and

solubility) and directly affect the substance's biological properties, including its impact on plants and pathogens as shown in Figure 2 (Raafat and Sahl, 2009). Chitosan has a broad range of industrial uses because of its biological (biodegradable, nontoxic, and biocompatible) and biochemical qualities (Islam *et al.*, 2017). A highly basic polysaccharide, chitosan possesses special qualities such as the capacity to form films, interact with polyanions, and chelate and remove metal ions. Furthermore, the qualities of CHT that particularly support its prospective application as a bioactive material are that it is biodegradable, nontoxic, and non-allergenic. In addition, CHT is easier to change without affecting its fundamental qualities than other biologic polymers involving chitin, cellulose, gelatin, and glucans (Kumar *et al.*, 2004). As a result, by changing its physical and chemical and biophysical characteristics, CHT has been widely employed for a variety of applications. A novel strategy for crop security is to strengthen the defence systems of the plant against diseases (Ab Rahman *et al.*, 2018). The initial description of CHT's impact on plant response was that it served as an elicitor, activating plant defence systems and enhancing plants' resistance to pathogens including bacteria and fungus (Song *et al.*, 2021). Chitosan inhibits bacterial growth, possibly as a consequence of its sensitivity for cell surfaces. Recent studies claim that CHT stimulates plant defence genes and fosters plant development and growth through the octadecanoid pathway (Arif *et al.*, 2022). Based on the protective gene induction activity, CHT was demonstrated to provide disease resistance in a variety of plants, with disease and plant cultivar specificity (Malerba and Cerana, 2016). Chitin and CHT treatment causes plants to develop chitinase, which dissolves the chitin and CHT chain into highly soluble types (Kumari and Kishor, 2020). According to Boonlertnirun *et al.* (2007), In some cases, CHT stimulates the expression of a variety of genes associated in plant defence responses, which in turn promotes the synthesis of secondary plant metabolites. Chitosan influences pathways involving jasmonic acid. Jasmonate has several behaviours that are comparable to those of the plant hormone Abscisic Acid (ABA), which is essential for controlling how much water plants utilize (de Ollas *et al.*, 2015). According to Jwa *et al.* (2006), CHT increased the expression of the rice endosperm kinase (REK) mRNA as a result of acting as a fungal elicitor. Jasmonic acid (JA), salicylic acid (SA), and hydrogen peroxide all have an effect on REK, a crucial mediator of the plant self-defense/stress response. Utilizing CHT-based compounds, a wide range of antibacterial and regulatory properties have recently been analyzed in plants. Lee *et al.* (2003) discovered that Chitosan CHT reduced the size of the stomatal aperture and inhibited light-induced stomatal opening by generating reactive oxygen species (ROS), such as super oxide and hydrogen peroxide, which inhibit stomatal opening and promote stomatal closing. According to reports, CHT possesses antifungal and antimicrobial properties (Martins *et al.*, 2014).

### **Introduction to chitosan as a potential mitigating agent for plant stress**

Chitosan, a naturally existing biological molecule and the second-most common polysaccharide after cellulose, is produced via the deacetylation of chitin. Its biocompatibility, biodegradability, nontoxicity, and wide range of antibacterial action have made it a crucial area of research for drug delivery systems. As nanotechnology has developed, chitosan-based nanoformulations have attracted a lot of interest in agricultural sciences (Gao and Wu, 2022).

Chitosan has come out as the viable solutions to minimize these difficulties without damaging agro-ecosystem and soil. Chitosan has demonstrated to have remarkable qualities such as broad range of antibacterial capabilities, anti-inflammatory, biocompatibility with other compounds. Chitosan, which is the the second-highest common polysaccharide after cellulose, is the deacetylated form of chitin. In marine species, chitin may be found in the cell walls of fungi, insects, and crab shells (Elieh-Ali-Komi and Hamblin, 2016). Chitin is converted into chitosan by the alkaline deacetylation of the linear chain of D-glucosamine and N-acetyl-D-glucosamine subunits, which are joined by glycosidic linkages. Chitosan possesses an amine group compared to chitin, which makes it easier to generate functional derivatives and change the structure. Chitosan increases plant growth and yield and triggers a variety of defence responses in plants (Pongprayoon *et al.*, 2022).



**Figure 2.** An overview of chitosan-mediated plant growth regulation under stress conditions (Chakraborty *et al.*, 2020)

Because of its beneficial qualities, which include biodegradability, biocompatibility, non-toxicity, the capacity to boost plant growth and productivity, and the ability to promote resistance against a range of biotic and abiotic problems, chitosan utilization in agriculture is receiving interest on a global scale. Numerous studies have shown that chitosan increases productivity and growth in a variety of crops, including rice, soybeans, maize, potatoes, and tomatoes (Boamah *et al.*, 2023). The capacity may be related to enhanced physiological processes, increased nutrition absorption, cell division, and protein synthesis (da Silva *et al.*, 2011). Using chitosan inhibits a wide range of bacterial, viral, fungal, and nematode infections. Examples of fungi that have been greatly decreased by chitosan treatment include *Alternaria*, *Rhizopus*, *Bortrytis*, *Fusarium*, etc. (Al-Hetar *et al.*, 2011). Additionally, resistance to powdery mildew as well as antibacterial properties against many plant pathogenic bacteria, including *Xanthomonas* spp. and *Pseudomonas* spp. and enhance tomato development (Kagale *et al.*, 2004). Chitosan increased growth and productivity while conferring resistance to the tomato mosaic virus in tomatoes (Abdelkhalek *et al.*, 2021). Numerous nematodes that cause plant disease, including *Meloidogyne* species in tomato plants, can be effectively controlled by chitosan (Asif *et al.*, 2017). The primary elements of the mechanism that results in immunity to insects, pests, and diseases are the production of defensive biomolecules and the increased expression of defense-related genes (Khalil and Badawy, 2012).

Drought, salinity, temperature, and heavy metal toxicity are examples of abiotic stresses that have been reported to be induced by chitosan and its byproducts (Hidangmayum *et al.*, 2019). They affect the physiological aspects of the plant and the gene for the stress-protective metabolite. Additionally, they can scavenge ROS, trigger defensive reactions, and eventually promote plant growth and development. As nanotechnology has developed, chitosan biomolecule has shown to be a more trustworthy choice for creating nanoparticles that are more effective and efficient than bulk chitosan. Additionally, chitosan nanoparticles have significant promise for achieving the objective of sustainable agriculture as a polymer carrier for various bioactive compounds that are useful to plants and methods for encapsulating metals (Riseh *et al.*, 2022b).

### **Chitosan NMs' essential physicochemical characteristics that contribute to their functionality**

It is crucial to comprehend the fundamental physicochemical properties of chitosan NMs in order to comprehend the cutting-edge functioning of these materials. One amino group (-NH<sub>2</sub>), two groups of hydroxyl (-OH), and three carbon atoms at the C-2, C-3, and C-6 positions, respectively, make up a chitosan polymer. Chitosan with high levels of elimination has few acetyl groups and no obvious bioactivity. Because of the significant steric resistance, C3-OH is less active than the other -OH groups; nonetheless, C6-OH is the most active due to its ease of rotation and low steric hindrance. The accessibility of -NH<sub>2</sub> and C6-OH groups on the chitosan biopolymer's strand is a consequence that renders it particularly bioactive (Wang *et al.*, 2020). Chitosan has a net positive charge due to the -NH<sub>2</sub> group, which enables it to come into contact with anionic molecules which include cell wall phospholipids and functional and structural anionic proteins. By interacting with cell receptors and accelerating metabolic processes, the -OH functional group functions as an electron acceptor and speeds up signal transmission. However, by linkage linear chitosan biopolymer substrate into tiny structures using tripolyphosphate, the chitosan polymer's functionality can be improved. Linear chitosan fragments' cationic -NH<sub>2</sub> groups are bound by anionic TPP, resulting in the formation of chitosan NMs. The resulting chitosan NMs have greater surface area compared to volume ratio and more surface functional groups, which increases their likelihood of interacting with plant cells. Due to advancements in synthesis approaches and thorough characterization, the process of implementing chitosan NMs with the required properties has become easier, leading to the synthesis of customised chitosan NMs (Azmana *et al.*, 2021). Chitosan NMs may be tailored by altering their physicochemical characteristics, such as their size, distribution of size, shape, and charge on the surface, dispersity, porousness, and rheological factors like viscosity. The bioactivity in plants is influenced by three key characteristics of chitosan NM, including its tiny particle size, dispersity, and surface electrical charge (zeta potential). Size is crucial for greater contact with physiological surfaces and intra-tissue penetrability. To guarantee product homogeneity, stability, and consistency of bioactivity, a reduced dispersity index is needed. Zeta potential influences both surface contact with biomolecules and NMs' ability to enter intracellular spaces. The physicochemical characteristics of chitosan NMs may be altered by modifying the quantity of the unprocessed product, in this case chitosan, and other physical elements involved in the synthesis process, such as pH and temperature (Saharan *et al.*, 2016). Particularly for chitosan NMs, symmetric nanoarchitecture develops, such as developing nano-fibrous, nano-spherical, or nano-porous. Therefore, they ought to be able to penetrate the size-exclusion barriers that are present in the cuticle, trichome, stomata, stigma, and hydathode, as well as through physical wounds and root connections, to enter plant tissues. These barriers range from 1 to 1000 nm (Huang *et al.*, 2021). Numerous active ingredients (AIs), such as nutrition, may connect to the functional groups of chitosan NMs via a covalent bond or electrostatic interaction (He *et al.*, 2022). Additionally, analysis of several chitosan NMs found extremely porous surface and interior layers that can accommodate a number of AIs (Kumaraswamy *et al.*, 2018). Based on the aforementioned key characteristics, chitosan NMs have been mixed with a variety of organic and inorganic substances to create chitosan nanoconjugates, which have been shown to improve plant growth and development (Prajapati *et al.*, 2022).

### **Derivatives of chitosan as biotic elicitors**

The potential use of chitosan and its associated compounds in the elicitation process is linked to the biological function of this substance, which primarily includes its ability to activate natural plant defence systems and enhance plant tolerance to stress (Ferri and Tassoni, 2011). This has been connected to various physical and biochemical changes, including oxidative stress, H<sub>2</sub>O<sub>2</sub> buildup, production of supplemental substances and development agents, as well as accumulation of lignin and callose as shown in Figure 3. Plant responses to chitosan include modifications in chromatin structure, suppression of H<sup>+</sup>-ATPase activity in the

cell membrane, stimulation of MAP kinases, and an increase in the cytosolic  $\text{Ca}^{2+}$  concentration (Hong *et al.*, 2006). Plant responses to chitosan include modifications in chromatin structure, suppression of  $\text{H}^{+}$ -ATPase activity in the cell membrane, stimulation of MAP kinases, and an increase in the cytosolic  $\text{Ca}^{2+}$  concentration. By supplying high-quality raw materials with increased levels of health-improving chemicals, it can benefit consumers and assist address issues related to the lack of bioactive compounds produced by plants to meet current needs (Yang *et al.*, 2021). The most often used chitosan salts, such as lactate or acetate, are a result of this polymer's solubility, which dictates how effectively it stimulates reactions (Stasińska-Jakubas and Hawrylak-Nowak, 2022).

The usefulness of chitosan and its byproducts in the method of elicitation has been documented in a large number of research articles. Studies on the *Curcuma longa* plant (Sathiyabama and Manikandan, 2018) shown that the plants' defensive mechanisms were activated by the foliar application of a 0.1% chitosan solution, which also had a positive effect on plant growth and the accumulation of curcumin in their rhizomes. It was also demonstrated in a study on *Stevia rebaudiana* that chitosan solutions at concentrations of 0.1% and 0.2% had a stimulating effect. Chitosan treatment enhanced biomass, phenolic compound concentration, and rebaudioside levels (Mehregan *et al.*, 2017). The usage of various chitosan oligosaccharide concentrations (50, 200, 500, or 1000 ppm) had a positive impact on plant development and the amount of polyphenolic chemicals, according to a field experiment on *Origanum vulgare* ssp. *hirtum*.



**Figure 3.** The most important effects of chitin and its derivatives' applications (Shahrajabian *et al.*, 2021)

According to the research of Gerami *et al.* (2021), it may be possible to increase *S. rebaudiana*'s resistance to salt and lessen the phytotoxic effects of salinity on these plants by using chitosan as an elicitor. Similar results were found in an experiment by Safikhan *et al.* (2018), where chitosan increased the physiological parameters of *Silybum marianum* and hastened development while reducing the harmful effects of salt stress.

Furthermore, chitosan applied to *Salvia officinalis* decreased the harmful effects of drought stress, according to a study carried out under water-scarce settings. Additionally, it improved the amount and purity of essential oils, the total amount of phenolic and flavonoid components, and the antioxidant qualities of sage extracts (Ghorbanpour, 2015). Chitosan suspension and chitosan solutions in 1% acetic acid were shown to

stimulate the synthesis of flavonoids in *Ononis arvensis* under in vitro condition. When chitosan solution in acetic acid was used as an elicitor in *Mentha piperita* suspension cultures, the accumulation of menthol rose considerably (Qiu *et al.*, 2021). Consequently, the greenhouse treatment of *M. piperita* with chitosan raised the overall concentration of phenolic and flavonoid components and improved the antioxidant capacity of the extracts (Salimgandomi and Shabrangi, 2016). Additionally, triterpenoid saponin synthesis was boosted by chitosan in *Psammosilene tunicoides* hair root cultures. *Ocimum basilicum*, *O. sanctum*, and *O. gratissimum*, three types of basil, were cultured in cell cultures, and it was discovered that the polymer had a positive impact on biomass accumulation (Ahmad *et al.*, 2019). Other studies on *O. basilicum* shown that the elicitation of chitosan was effective in stimulating biomass development, accelerating the production of total phenolic and terpene elements, increasing the quantities of rosmarinic acid and eugenol, and improving antioxidant activity. The foliar application of chitosan lactate increased the levels of rosmarinic acid, anthocyanins, and phenolic substances in plant material from *O. basilicum* and *M. officinalis* (Stasińska-Jakubas *et al.*, 2023).

### Drought stress

Reduced growth and yields are the result of drought's impact on a variety of morpho-physiological, biochemical, and molecular elements of plant development. Stress brought on by drought impairs chloroplast function, lowers chlorophyll concentration, and increases activity of enzymes involved in the photosynthesis process. Due to the stomata closing, it disrupts CO<sub>2</sub> uptake, which reduces photosynthesis and plant development (Sukhova *et al.*, 2022). Chitosan, on the other hand, causes stomatal closure and does so via an ABA-dependent route. Although the exact mechanism underlying chitosan-induced closure of stomatal pores is unknown, ABA activity has been shown to support stomatal closure and reduce transpiration (Khan *et al.*, 2023). Bean leaves treated with chitosan have been demonstrated to stimulate ABA activity, which causes stomatal closure (Iriti *et al.*, 2009). Similar to this, pepper's foliar application of chitosan has antitranspirant properties and decreases water usage by 26-43% through stomatal closure (Farouk and Amany, 2012). Similar antitranspirant properties were discovered in barley (*Hordeum vulgare*) and bean (*Phaseolus vulgaris* L.) (Hidangmayum *et al.*, 2019). Chitosan pretreatment increased the production of stress-protective phytochemicals in white clover, which reduced drought stress (Li *et al.*, 2017). Drought stress was reduced in *Thymus daenensis* with foliar application of chitosan without affecting the plant's ability to produce essential oils or its dry matter content (Emami Bistgani *et al.*, 2017). Excessive accumulation of proline in plants is a sign of an adaptive response to stress, which lowers the leaf water potential and reduces water loss. Numerous studies have noted that chitosan increased the level of proline content. For instance, in safflower and the thyme plant (ESPOSITO, 2020). Proline levels, however, are said to have little effect on castor bean (*Ricinus communis*) (Sara *et al.*, 2012). Similar outcomes were discovered in oligo-chitosan-treated blackberry plants, where neither the treated nor control plants showed any appreciable levels of proline (Yeboah *et al.*, 2020). Increased proline accumulation suggested plant stress, although a steady level might also mean that the plant had adapted to the stress (Rasheed *et al.*, 2022). As a result, it is believed that various plant species have distinct methods for treating chitosan. Chitosan stimulates a number of antioxidant enzymes and aids in the development of plants. This was demonstrated in seeds of apple, where chitosan treatment boosted SOD, CAT, and MDA activity, lowering lipid peroxidation and mitigating the effects of drought stress (Altaf *et al.*, 2022). Black poplars, sugar beets, and peas all have more soluble sugar content as a result of chitosan (Rkhaila *et al.*, 2021). These sugars, including glucose and fructose, can modify the stress response, enhance drought mitigation strategies, and foster growth and development through signal transduction. A number of stress-related genes involved to glucose transport and metabolism were also elevated in white clover after chitosan treatment, which may assist to mitigate the consequences of drought stress (Elansary *et al.*, 2020). Additionally, it was noted that chitosan treatment increased the amount of chlorophyll and photosynthetic activity (Varamin *et al.*, 2020).

Additionally, it was shown that adding chitosan to apple explants cultured on agar medium at a dosage of 40 mg/L reduced the negative effects of salt stress (Regni *et al.*, 2022). Treatment of maize, soybeans, and beans with chitin oligosaccharides has also been reported to boost photosynthetic levels (Li *et al.*, 2020a).

Relative water content (RWC), vegetative development, and yield all increased when chitosan nanoparticles were applied to barley plants in soil and epidermal forms at doses of 60 and 90 ppm to mitigate the deleterious effects of late-season drought stress (Verma *et al.*, 2022). By lowering stomatal conductance and transpiration, the foliar application of nanochitosan improved the water status of plants in pearl millet that was under salt stress (Attaran Dowom *et al.*, 2022). Increased proline buildup and antioxidative activity in periwinkle (*Cartharanthus roseus*) following foliar treatment with chitosan nanoparticles helped to reduce drought stress. Additionally, it is said to boost alkaloid quantity and activate a gene that produces defence enzymes (Tang *et al.*, 2022). Sugarcane plants treated with *S-nitrosoglutathione*, a NO donor, and encapsulated in chitosan nanoparticles have demonstrated to lessen the deleterious effects of drought stress, as seen by increased root biomass and higher rates of photosynthesis than those treated with free *S-nitrosoglutathione* alone (Silveira *et al.*, 2021). In addition, a study on wheat plants subjected to a water shortage scenario and subsequently given soil and foliar treatments with chitosan nanoparticles at 90 ppm revealed improved physiological and biochemical traits in the plants (Dolatkhah Dashtman *et al.*, 2023).

Chitosan (CTs) is one of these growth promoters. It is a biopolymer that is not poisonous, nitrogenous, and biodegradable, made by the shells of chitin of aquatic crustaceans like lobsters, crabs, prawns, and other creatures like insects. Chitosan can increase plant development by reducing the effects of environmental challenges including salt and drought when used in plant cultivation (Limpanavech *et al.*, 2008). In contrast to other biopolymers, it can also be easily manipulated without altering its basic qualities. Therefore, by altering CTs' physicochemical and biophysical characteristics, they have been widely exploited for a variety of applications. Recently, drugs based on CTs have demonstrated a variety of antibacterial and regulatory properties in plants (Singh Dhillon *et al.*, 2013).

One method to boost yield per unit area and improve product quality is to use growth stimulants that have an impact on plant growth and development (Giglou *et al.*, 2022). Growth stimulants are used to speed up plant development, particularly of the roots and leaves, and to boost stress tolerance. Plant growth promoters increase seed germination and biological activity in crops (Nardi *et al.*, 2021).

The interplay of stress from water and growth stimulation therapy on Kitoplas' physiological and morphological features had a considerable impact, as demonstrated by Torabi Giglou *et al.* (2020). The same authors demonstrated that plants treated with 10 ppm of Kitoplus<sup>®</sup> had the greatest concentration and proportion of essential oils. Chitosan, a component in the growth stimulant Kitoplus<sup>®</sup>, has been employed in the current investigation to minimize the effects of drought stress (Giglou *et al.*, 2022).

The current study also sought to determine how Fe-CTS NPs can alleviate the detrimental impacts of drought stress on peppermint. Despite the fact that many nanomaterials have been used in agriculture, the usage of iron oxide nanoparticles with chitosan coating is a novel method of giving plants the nutrients they require (Kashyap *et al.*, 2015). There has to be more study on the use of Fe-CTS NPs in medicinal and aromatic plants because there haven't been many studies done in this area. Due to the economic significance, growing demand, and widespread use of mint in many industries, as well as the knowledge gap regarding the effects of NPs in this herb under drought, the role of nanomaterials (Fe-CTS NPs) and plant growth stimulants was evaluated in this study with a view to mitigating the crucial impacts of drought stress (Giglou *et al.*, 2022).

### Salinity stress

Salinity has a big influence on how plants grow all around the planet. The expected high salinity rate for all agricultural land throughout the world is over 20% (Paul and Nair, 2008). Salinity affects arable land covering 800 million hectares, or about 6% of the total land surface, which has a detrimental impact on crop

growth and development (Selvakumar *et al.*, 2014). Salinity inhibits nutrient and water absorption across the whole plant system on a physiological and biochemical level (Nawaz *et al.*, 2022). Oxidative stress is caused by the accumulation of reactive oxygen species (ROS), which disrupts cellular function and is modulated by salt stress. Numerous investigations have shown that MDA buildup brought on by salt led to cellular membrane lipid peroxidation. However, there are important data showing that chitosan and its byproducts control and reduce stress brought on by salt (Hassan *et al.*, 2021).

The osmotic stress brought on by salinity stress in safflower (*Carthamus tinctorius*) and sunflower (*Helianthus annuus* L.) plants was able to be reduced by modest concentrations of chitosan (Mahdavi *et al.*, 2011). Furthermore, wheat, legumes such as chic lentils, isagbol, ajowan, sunflower, fenugreek, and corn have shown signs of chitosan and oligo-chitosan treatment lowering salt stress (Hidangmayum and Dwivedi, 2022). Previously, chitosan's ability to cause abiotic stress in many crops has been succinctly examined as shown in Table 1. These crops may respond better to nanochitosan because they have a bigger surface area as a result of their tiny particle size, increased adsorption capacity, nontoxicity, and ability to effectively encapsulate other compounds. When seeds are treated with chitosan nanoparticles at concentrations of 0.1%, 0.2%, and 0.3% at a salt concentration of 100 mM, research on salt-sensitive bean plants demonstrates increased seed germination (Zayed *et al.*, 2017). Nitric oxide in the chitosan domain has been shown to be more efficient than free donor NO at decreasing salt stress in maize. Additionally, they observed enhanced levels of PSII and chlorophyll in all treated plants, as well as better S-nitrosothiol concentration in the leaf and increased NO bioavailability in the plant (Mahmood *et al.*, 2022). Solid matrix pumping with nanochitosan improved plant development, the amount of chlorophyll, and protein levels in mungbean seedlings while reducing the negative effects of salt (Balusamy *et al.*, 2022). When tomato plants were exposed to salt stress followed by treatment with chitosan-polyvinyl ethanol hydrogels with or without copper nanoparticles, it was shown that the expression of genes for jasmonic acid (JA) and superoxide dismutase (SOD), which are crucial for detoxification, increased (Hidangmayum and Dwivedi, 2022).

As a result, CsBMs are often employed in a variety of biomedical applications. It has been reported that they may be produced via the reverse micellar method, emulsion droplet coalescence, ionic gelation, rainfall, screening, and spray drying (Balusamy *et al.*, 2022). However, the chitosan nanoparticles (CsNPs) utilized in the salt stress tolerance research were made using ionotropic gelatin (Mendes *et al.*, 2016). The capacity of Cs to encapsulate a variety of molecules, make nanoparticles in an extensive variety of sizes, encapsulate pharmaceuticals with medium to high effectiveness, and produce stable nanoparticles demonstrates the method's adaptability for usage in the biomedical area (Ahmed and Aljaeid, 2016).

### Heavy metal stress

There are several publications on the usage of bulk chitosan, despite the paucity of studies on the utilization of chitosan nanoparticles giving resistance against heat and heavy metal stressors (Zafar *et al.*, 2023). Maize seeds primed with chitosan nanoparticles at 15 °C were demonstrated to increase seedling characteristics with a shorter mean germination time (Boamah *et al.*, 2023). Similar outcomes were recently seen in ball pepper (*Capsicum annum* L.) treated with chitosan, which had improved germination characteristics at low temperatures as well as higher activity of the stress-defending enzymes glucanase and chitinase. Wheat exposed to oligo-chitosan at various degrees of polymerization was protected from chilling stress (Moenne and González, 2021). Similarly, oligo-chitosan protected tea plants from cold stress by activating genes involved in photosynthesis, carbon metabolism, and antioxidants (Ji *et al.*, 2022). Use of chitosan with different molecular weights 5 kDa and 1 kDa in edible rapeseed grown hydroponically led to protection from cadmium toxicity (Zong *et al.*, 2017). Additionally, applying large amounts of chitosan and zinc to late-sown *Phaseolus vulgaris* L. dry bean plants minimized the harmful effects of heat stress (Hassan *et al.*, 2022a). Due to the presence of both amino and hydroxyl groups, chitosan has shown to successfully form compounds with metal ions Pb(II),

Cu(II), and Ag(I) in soil as well as other mineral ions including Cl, K<sup>+</sup>, and NO<sub>3</sub> that are advantageous for phytoremediation and biological fortification programmes (Hidangmayum and Dwivedi, 2022). This circumstance may benefit from the use of bulk chitosan or chitosan nanomaterials, either by themselves or in combination with other potent substances known to activate defense enzymes or lessen heavy metal stress or toxicity. Additionally, chitosan nanoparticles may be more important than bulk form in terms of the adsorption, dissolution, movement, and bioactivity of the contained active components with controlled release mechanisms (Maluin and Hussein, 2020).

### **Temperature stress**

Given the swift change in the environment worldwide and growth in the usage of synthetic chemicals, extreme temperatures and metal-contaminated soil are having an impact on the world's agricultural situation and the production of food.

### **Hot stress**

Due to the fact that heat stress frequently coexists with severe drought and is challenging to assess, heat stress is frequently seen as a complex problem (McKersie and Lesheim, 2013). According to reports, late-sown plants may withstand heat stress when chitosan, zinc, and humic acid are sprayed foliarly on them (Ibrahim and Ramadan, 2015) There is a paucity of published data on the use of chitosan under heat stress. Nevertheless, other data indicate that ABA may activate genes linked to heat shock. Choi *et al.* (2016) suggest that heat stress tolerance may be mitigated by ABF3 (abscisic acid responsive-element-binding factor 3) overexpression Thus, by promoting ABA activity—which is connected to the earlier study on closing stomatal pores (Bittelli *et al.*, 2001) and further activating defense-related ABA-responsive genes, the application of chitosan might potentially mitigate the negative effects of high temperatures.

### **Cold stress**

It has been established that one of the most significant abiotic factors that lower agricultural crop productivity by affecting the condition of crops and post-harvest life is cold stress. Cold has been discovered to significantly hinder the reproductive development of many agricultural plant species, with rice demonstrating sterility when subjected to cold temperatures during anthesis as one example (Thakur *et al.*, 2010). Since plants are sessile by nature, they have developed special mechanisms to deal with changes in environment temperature (Imran *et al.*, 2021). Plants are subjected to cold and freezing temperatures in temperate climates, which are particularly detrimental to plants as a kind of stress. Through a process known as acclimatization, plants develop chilling and freezing resistance against such deadly cold shocks in order to adapt (Guy, 1990). Many significant crops, however, are still unable to adapt to the cold.

**Table 1.** Effect of chitosan to mitigate abiotic stress in various crops

Plant	Stress	Application method	Chitosan 's effect	References
Tomato	Salinity	Spray method	Enhanced morphological characteristics, photosynthetic pigments, electrolytes, total phenol, and antioxidative properties	(Eltaweil <i>et al.</i> , 2021)
Wheat	Heavy metal	Seed priming	Minimize concentration up to 0.25% ameliorated the damage found due to AI antioxidant activity	(Yu <i>et al.</i> , 2018)
Soya bean	Heavy metal	Foliar application	Lower nickel absorption and lessen nickel toxicity via increasing physiological traits, proline, and antioxidant enzymes	(Sadeghipour, 2021)
Barley	Drought	Soil treatment	Boosted morpho-physiological characteristics and antioxidant activity when combined with biochar, reducing drought stress	(Guo <i>et al.</i> , 2021)
Potato	Drought	Oligo-chitosan spray	Plant growth traits increased, alleviate drought stress	(Muley <i>et al.</i> , 2019)
Safflower	Salinity	Media supplement	Increased formation of secondary metabolites. Minimize salt stress	(ÖZKURT and BEKTAŞ, 2022)
Maize	Salinity	Soil application	Increased growth traits, antioxidant activity, combat salt stress	(Sathiyabama and Parthasarathy, 2016)
Tea	Cold	Exogenous application	Increased antioxidant activity, photosynthesis, and carbon processes, as well as the activation of genes involved in stress signalling, all reduced cold stress	(Liang <i>et al.</i> , 2017)
Chrysanthemum	Drought	Foliar spray	enhanced morphophysiological traits, antioxidant	(M Younis <i>et al.</i> , 2019)

			capacity, and stress-associated gene expression led to better resistance to drought stress.	
Marjoram	Drought	Foliar treatment	improved morpho-physiological characteristics, activity of antioxidants, and oil composition-related gene expression	(Al-Ghamdi, 2019)
Milk thistle	Drought	Foliar method	Overall growth and phytochemicals traits improved, increase in flavonoids	(Shokraei <i>et al.</i> , 2021)

### Biotic stresses

A range of biotic stresses, such as those brought on by nematodes, insects, fungus, viruses, and bacteria, are imposed on plants (Gull *et al.*, 2019). These biotic stressors reduce agricultural productivity by causing a range of illnesses, and harm to crop plants. Therefore, the use of research approaches, many methods for mitigating biotic stresses have been developed. By researching the genetic mechanisms of the agents producing these stressors, biotic stresses in plants can be mitigated (Meena *et al.*, 2017). By creating resistant kinds of agricultural plants, genetically modified plants have demonstrated to be a significant effort against biotic stressors in plants as shown in Table 2. All parts of the plant can be consumed by plant-parasitic nematodes, although they mostly harm the root system and spread disease through the soil. They produce stunting and wilting, which are symptoms of inadequate nutrition. Despite the fact that they seldom kill their hosts, viruses can harm plants both locally and systemically, producing stunting, chlorosis, and malformations in many different parts of the plant (Kumar, 2023). When insects eat or place their eggs on plants, it harms the plants. Through their stylets, piercing-sucking insects can spread viruses to plants. Fungus parasites come in two different varieties: biotrophs, which do not employ toxins to destroy host cells, and necrotrophs, which do. When coupled with bacteria, they can infect various parts of the plant and cause symptoms such as vascular wilts, leaf spots, and cankers (Cordon *et al.*, 2022).

Plants produce ROS as a result of biotic stressors brought on by insects or pathogens, for which they have honed defence and management systems. The excessive accumulation of ROS as a defence against insects or pathogens becomes hazardous to plants if it reaches baseline levels. Plants engage a highly specialized and strict scavenging mechanism for the elimination of excess ROS and maintenance of baseline levels to prevent this self-toxicity (Huang *et al.*, 2019). Effective ROS regulation is essential for plants' capacity to reduce stress, and it plays a critical role in whether or not plants can withstand biotic stress (Berrios and Rentsch, 2022).

**Table 2.** Chitosan's effect to mitigate biotic stresses in different plants

Plant Species	Features of the protective molecules and administration technique	Protective effect	Reference
Bell pepper	1% chitosan, spray method	Being resistant to <i>Phytophthora capsici</i>	(Motahharifar <i>et al.</i> , 2020)
Lemon balm	0.005, 0.01, 0.015% chitosan, shoot spraying	accumulation of phenolic chemicals and enzymes linked to defence	(Tarassoli <i>et al.</i> , 2021)
Date palm	0.1% chitosan nanoparticles, seedling irrigation	strengthening of natural immunity	(Hassani <i>et al.</i> , 2020)
Tomato	0.001, 0.01, 0.1% chitosan microparticles, exogenous application	Accumulation of enzymes involved in defence	(Sucharitha <i>et al.</i> , 2018)
Stone fruit trees	0.001% chitosan-Ag nanoparticles, foliar application	Defeat of the <i>pseudomonas syringe</i>	(Shahryari <i>et al.</i> , 2020)
Garden beet	0.2% chitosan; 0.05% nano chitosan, foliar spraying	Ability to resist <i>Pegomya hyoscyami</i>	(Muzzarelli <i>et al.</i> , 2012)
Potato	0.4% chitosan, tuber immersion	Resistance to <i>Fusarium spp.</i>	(Elshamy <i>et al.</i> , 2019)
Rice	0.3% chitosan oligosaccharide, seedlings spraying	Tolerance against <i>Fusarium oxysporum</i>	(Van Toan and Hanh, 2013)
Orange	0.05% chitin oligosaccharide, leaf infiltration	Opposition to <i>Candida Liberibacter asiaticus</i>	(Zhai <i>et al.</i> , 2018)

### Mechanisms of chitosan action in alleviating plant stress

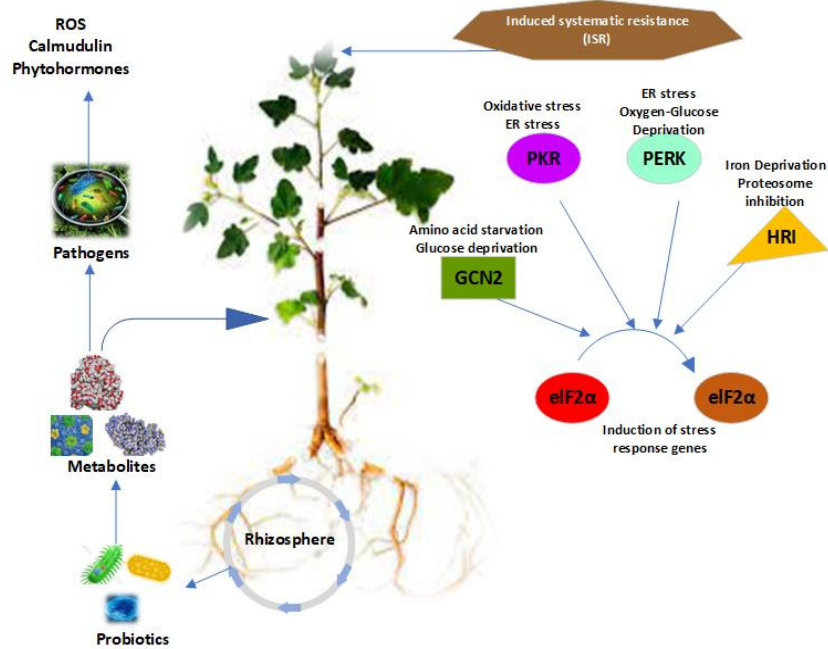
#### *Mechanism of action of chitosan*

The mechanism of chitosan in plants is currently poorly understood. But according to various accounts, chitosan prompted the plants to establish a number of defensive systems (Hidangmayum *et al.*, 2019). Chitin-specific receptors, which are known to set off defensive responses, are present in plant cell membranes. Because they mimic chemicals present in chitin-containing species, plants activate their defence systems in response to chitin-based therapies (Iriti and Faoro, 2009). Chitin elicitor binding proteins (CEBiP) have been found in a number of crops. These result in defensive responses that interact with chromatin and/or may bind to specific receptors, directly changing the different gene expression profile that is sensitive to chitosan. There is evidence that mustard (*Brassica campestris*) leaf extracts include a lectin family member that binds to chitosan. The plasma membrane H<sup>+</sup>-ATPase was also quickly activated in tests on isolated vesicles from *Mimosa pudica* and *Cassia fasciculata*, showing the presence of chitosan receptor molecules (Amborabé *et al.*, 2008). Furthermore, lysin motif receptor-like kinase, chitin elicitor receptor kinase 1 (CERK1), which may bind to both chitin and chitosan, and the MAP kinase pathway gene may all be activated by chitosan. This was carried out in an experiment with mutant knockout strains of *A. thaliana*. However, it has been found that chitosan signalling in *A. thaliana* seedlings does not need CERK1 and is detected through a CERK1-independent pathway (Povero *et al.*, 2011). Due to this, chitosan binding receptors are still thought to be “a Pathogen-Associated Molecular Pattern (PAMP) in search of a Pattern Recognition Receptor (PRR)” because their existence is unknown.

In most plant species, chitosan and its byproducts display a range of eliciting chemicals (Pichyangkura and Chadchawan, 2015). Plants responded to biotic stress by producing phytoalexin, pathogenesis-related proteins including chitinase and -glucanase, proteinase inhibiting agents, callose formation, lignin biosynthesis, and the stimulation of stress-responsive genes, among other defence mechanisms. However, it has been found that chitosan and its oligomers cause these defense-related molecules to increase, allowing for the use of chitosan and its byproducts as effective antimicrobial agents and stimulants for plant protection (Katiyar *et al.*, 2014). Chitosan treatment has been shown to induce chitinase and glucanase enzymes in a number of crops, including tomato, peach and dragon fruit. However, in *Oryza sativa* seedlings, variable molecular mass of chitosan exhibits various levels of pathogenesis-related protein, indicating chitosan has diverse functions depending on its forms. Chitinase and glucanase are substances linked to pathogen resistance (Yeh *et al.*, 2010). Additionally, chitosan with a low molecular weight (5 kDa) was able to stimulate the production of chitinase, -glucanase, lipoxygenase, phytoalexin, and other pathogenesis-related chemicals. Additionally, it was shown that changes in the content of sterol had a negative impact on insect resistance. It has been noted that seedlings' chitinase activity increases by 30-50% after being exposed to depolymerized chitosan and its fatty acids (Choudhary *et al.*, 2007).

#### *Induced systemic resistance (ISR) and enhanced disease resistance*

Both types of induced resistance, which may be broadly categorized as systemic acquired resistance (SAR) and ISR, call for preconditioning before the infection that eventually leads in resistance to a pathogen's. The plant gains improved defensive capability as a result of the induced resistance once it has been activated as shown in Figure 4. The well-known PGPR process includes the competition for niche and substrate, mineral dissolution, production of inhibited allelochemicals, and ISR against a variety of pathogens (Das *et al.*, 2019). ISR mediated by non-pathogenic rhizobacteria is comparable to pathogen-induced SAR in that both share the non-expressor of pathogenesis-related gene 1 (NPR1) signalling receptor, which eventually offers a wide range of resistance to plant diseases. In both ISR and SAR, growth regulators for plants that include salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) are crucial. Numerous elements relevant for the ISR response have been identified through experimental research. To defend *Solanum lycopersicum* plants from *Fusarium oxysporum* and *Pseudomonas corrugata*, which cause Fusarium wilt and pith necrosis, respectively, the nonpathogenic *Pseudomonas putida* strain LSW17S produces systemic immunity (Hyung *et al.*, 2016). ISR provides a system for naturally fostering resistance to plant diseases. Lipopolysaccharides, siderophores, and developmental regulators have all been identified as ISR determinants. For instance, it has been observed that the lipopeptides of *Bacillus amylolequifaciens* and plant-growth-promoting rhizobacteria promote systemic immunity in plants and aid in the control of rhizomania brought on by the sugar beet necrotic yellow vein virus. Lipopeptides from the *Bacillus amylolequifaciens* bacteria offer defence against the viral vector *Polymyxa betae*. It has been demonstrated that lipopeptides may successfully activate ISR in sugar beet's roots and leaves. Plant resistance is induced by lipopeptides such *Bacillus elicitors* fengycin and surfactin. When pepper plants were exposed to *B. pumilus* strain S2-3-2, pathogenesis-related (PR) protein genes such CaPR1, CaPR4, and CaPR10 were shown to be upregulated. Application of the *Bacillus pumilus* strain S2-3-2 resulted in the formation of indole-3-acetic acid (IAA), which facilitated the development of the tobacco plant (Li *et al.*, 2020b).



**Figure 4.** Regulation and mechanism of signaling pathways to mitigate stresses (Chakraborty *et al.*, 2020)

### Activation of defense-related genes and signaling pathways

#### *Calcium-mediated disease resistance pathway*

$\text{Ca}^{2+}$  serves as the primary mediator of plants' immunological and stress responses and is a conserved second messenger. Apparently encoding a  $\text{Ca}^{2+}$ -permeable channel is NRG1.1, a plant nucleotide-binding leucine-rich repeat receptor role in ETI, according to a recent study. As a pervasive signal molecule,  $\text{Ca}^{2+}$  governs a variety of cellular metabolic activities, such as the control of the oxidative burst, the expression of genes, and signal transmission, as well as several crucial stages of the apoptotic cycle. It is essential for the control of several stress genes that contribute to plant tolerance (Rivero *et al.*, 2022). In plant cells,  $\text{Ca}^{2+}$  is distributed in a very uneven manner. Transmembrane  $\text{Ca}^{2+}$  transport or  $\text{Ca}$  chelate modulation can both lead to changes in the cellular free  $\text{Ca}^{2+}$  level (Vercesi *et al.*, 2018). For plants to mount an immune response in response to  $\text{Ca}^{2+}$ -dependent PAMPs, the  $\text{Ca}^{2+}$  concentration is essential. The imprinted cyclic nucleotide-gated valve is a crucial factor in  $\text{Ca}^{2+}$  signalling and PTI responses brought on by PAMPs and ROS when the external  $\text{Ca}^{2+}$  concentration is high enough. The inhibitory kinase Botrytis-induced kinase 1 of the pattern-recognition receptor complex phosphorylates and activates the channel upon pathogen invasion, causing an excess quantity in the intracellular  $\text{Ca}^{2+}$  level (Wu *et al.*, 2014). Stomatal closure often happens when a plant experiences stress brought on by a disease. During immunological signal transduction, the  $\text{Ca}^{2+}$  osmotic channel OSCA1.3 of the plant *Arabidopsis thaliana* and its activation by Botrytis-induced kinase 1 can regulate closing of stomata.  $\text{Ca}^{2+}$  participation in early apoptosis is crucial, and  $\text{Ca}^{2+}$  signals are also implicated in the control of biotic/abiotic stress-induced PCD in plants (Ding *et al.*, 2022).

#### *ROS-mediated disease resistance signaling pathway*

Plants create ROS quickly and temporarily in response to biotic or abiotic stresses, which causes the cellular ROS content to be much greater than usual. This is the 'oxidative explosion' that is commonly referenced (Gechev *et al.*, 2006). In addition, pathogenic fungus and the plants they infect can cause ROS to be produced by plants and enhance cell death by the use of glucan, galactosaldehyde, peptides, and SA. There are five different kinds of ROS, with  $\text{H}_2\text{O}_2$  being the most medically significant since it is a very stable variety

and may spread into intracellular spaces (Kim *et al.*, 2015). The NADPH oxidase in plants, the principal ROS producer during innate immunity is RBOHD, and NADPH oxidase activity is probably what causes the ROS oxidative burst. To guarantee the entire elicitor-induced ROS burst, the C-terminal of RBOHD is controlled by the phosphorylation and ubiquitination of different kinases (Bardo *et al.*, 2021). A phosphorylation site mutation compromises a plant's ability to fight against pathogen invasion. However, it is still unknown how pathogens respond to ROS stress and how the ROS amount is precisely controlled to prevent cell damage caused by excessive ROS generation.

In stressful situations, ROS performs two different roles (Das and Roychoudhury, 2014). Moreover, because of their potent oxidative capabilities, ROS may harm cells, impair regular physiological processes, and even cause death by interfering with an organism's normal metabolism and degrading macromolecules (Hancock *et al.*, 2001). For instance, ROS exhibit direct toxicity towards invasive infections and can be utilised as antibacterial agents. Additionally, ROS help the cell wall generate lignin, cross-link proteins with the cell wall, and reinforce the cell wall, all of which increase the host's structural resistance to disease (Santiago *et al.*, 2013).

## Conclusions

Our data suggests that an alternate bactericide to prevent plant infections may be made using chitosan and COS. Despite the intriguing buildup of theoretical and practical evidence in recent years, more study is needed to completely comprehend the mechanisms governing the way of action of these drugs. Future research should focus on elucidating the molecular specifics of the underlying mechanisms and their significance to the antibacterial capabilities of chitosan in this specific instance of the antibiotic mechanism of action. The engagement and collaboration of businesses, government regulatory agencies, and research institutes will be essential for the bactericidal mechanism to be effective when applied widely. Therefore, additional research should concentrate on identifying their molecular details, which may reveal the unexplained biochemical activities. To solve these crucial and related issues, new fertilizers must be created that provide nutrients to plants and promote plant metabolism to withstand environmental challenges. Numerous proteomic studies describe the mechanism through which chitosan helps plants endure biotic and abiotic stressors. After a proteomic analysis of chitosan's inhibitory impact on *P. expansum*, 26 proteins were found and categorized according to their putative biological functions. The suppressive strategy of chitosan against *F. oxysporum f. sp. cucumerinum* was explained by a thorough proteome analysis of chitosan-responsive proteins. In order to understand how chitosan affects metabolic pathways, this led to the discovery of 62 expressed proteins that are involved in the obstruction of the Fusarium cell wall, disruption of DNA, and disruption of both functional and structural protein biosynthesis (Zhang *et al.*, 2020). In order to utilize chitosan as effectively as possible in sustainable agriculture, we desire that plants and pathogens treated with chitosan would undergo a lot more proteome investigations.

Natural biopolymers such as chitin, chitosan, and chitosan oligosaccharides have a wide range of functions in plants. These substances have so far been successfully used in practical applications to protect horticulture plants against diseases, and on plant productivity and growth, especially under environmental constraints which highlight its promising roles for crop cultivation under drought conditions in arid and semi-arid regions. Regarding drought, chitosan causes a variety of advantageous reactions in plants, including antitranspirant, activation of the ROS scavenging system, better stomatal conductivity, improved root growth, and improved plant development in general. It is safe for the environment and non-toxic, which will be very useful when using sustainable agriculture methods. The variability of preparation, which can significantly alter the physical characteristics of chitosan, is nevertheless unavoidable. Despite the work that has been done thus far, the exact mechanism by which chitosan acts inside the system of plants is not fully known. To improve the

use of chitosan in the control of abiotic stress, more transcriptome and proteomic investigations of genes and proteins sensitive to abiotic stress are thus required.

### Authors' Contributions

Writing the original article: T.A. and A.M.; reviewing and editing: W.H., M.A.Z., M.N., B.A., M.N., M.U.H., A.H. and E.F.A; funding acquisition: A.H. and E.F.A. All authors read and approved the final manuscript.

### Ethical approval (for researches involving animals or humans)

Not applicable.

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### Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

### References

- Ab Rahman SFS, Singh E, Pieterseand CM, Schenk PM (2018). Emerging microbial biocontrol strategies for plant pathogens. *Plant Science* 267:102-111. <https://doi.org/10.1016/j.plantsci.2017.11.012>
- Abdelkhalek A, Qari SH, Abu-Saied MAA-R, Khalil AM, Younes HA, Nehelaand Y, Behiry SI (2021). Chitosan nanoparticles inactivate alfalfa mosaic virus replication and boost innate immunity in *Nicotiana glutinosa* plants. *Plants* 10:2701. <https://doi.org/10.3390/plants10122701>
- Ahmad W, Zahir A, Nadeem M, Garros L, Drouet S, Renouard S, Doussot J, Giglioli-Guivarc'h N, Hanoand C, Abbasi BH (2019). Enhanced production of lignans and neolignans in chitosan-treated flax (*Linum usitatissimum* L.) cell cultures. *Process Biochemistry* 79:155-165. <https://doi.org/10.3390/molecules26040791>
- Ahmed TA, Aljaeid BM (2016). Preparation, characterization, and potential application of chitosan, chitosan derivatives, and chitosan metal nanoparticles in pharmaceutical drug delivery. *Drug Design, Development and Therapy* 483-507. <https://doi.org/10.2147/dddt.s99651>
- Al-Ghamdi AA (2019). Marjoram physiological and molecular performance under water stress and chitosan treatment. *Acta Physiologiae Plantarum* 41:1-8. <https://doi.org/10.1007/s11738-019-2830-0>
- Al-Hetar M, Zainal Abidin M, Sariahand M, Wong M (2011). Antifungal activity of chitosan against *Fusarium oxysporum* f. sp. *cubense*. *Journal of Applied Polymer Science* 120:2434-2439. <https://doi.org/10.1002/app.33455>
- Altaf MA, Shahid R, Ren M-X, Naz S, Altaf MM, Khan LU, Tiwari RK, Lal MK, Shahidand MA, Kumar R (2022). Melatonin improves drought stress tolerance of tomato by modulating plant growth, root architecture, photosynthesis, and antioxidant defense system. *Antioxidants* 11:309. <https://doi.org/10.3390/antiox11020309>
- Amborabé B-E, Bonmort J, Fleurat-Lessardand P, Roblin G (2008). Early events induced by chitosan on plant cells. *Journal of Experimental Botany* 59:2317-2324. <https://doi.org/10.1093/jxb/ern096>

- Arif Y, Siddiquiand H, Hayat S (2022). Role of chitosan nanoparticles in regulation of plant physiology under abiotic stress. In: Sustainable Agriculture Reviews 53: Nanoparticles: A New Tool to Enhance Stress Tolerance. Springer. pp 399-413. [https://doi.org/10.1007/978-3-030-86876-5\\_16](https://doi.org/10.1007/978-3-030-86876-5_16)
- Asif M, Ahmad F, Tariq M, Khan A, Ansari T, Khanand F, Siddiqui AM (2017). Potential of chitosan alone and in combination with agricultural wastes against the root-knot nematode, *Meloidogyne incognita* infesting eggplant. Journal of Plant Protection Research 57(3). <http://dx.doi.org/10.1515/jppr-2017-0041>
- Attaran Dowom S, Karimian Z, Mostafaei Dehnaviand M, Samiei L (2022). Chitosan nanoparticles improve physiological and biochemical responses of *Salvia abrotanoides* (Kar.) under drought stress. BMC Plant Biology 22:364. <https://doi.org/10.1186/s12870-022-03689-4>
- Azmana M, Mahmood S, Hilles AR, Rahman A, Arifinand MAB, Ahmed S (2021). A review on chitosan and chitosan-based bionanocomposites: Promising material for combatting global issues and its applications. International Journal of Biological Macromolecules 185:832-848. <https://doi.org/10.1016/j.ijbiomac.2021.07.023>
- Balusamy SR, Rahimi S, Sukweenadhi J, Sunderraj S, Shanmugam R, Thangavelu L, Mijakovicand I, Perumalsamy H (2022). Chitosan, chitosan nanoparticles and modified chitosan biomaterials, a potential tool to combat salinity stress in plants. Carbohydrate Polymers 284:119189. <https://doi.org/10.1016/j.carbpol.2022.119189>
- Bardo C, Matteo C, Sachie K, Stevens DM, Wrzaczekand M, Gitta C (2021). Stress-induced reactive oxygen species compartmentalization, perception and signalling. Nature Plants 7:403-412. <https://doi.org/10.1038/s41477-021-00887-0>
- Berrios L, Rentsch JD (2022). Linking reactive oxygen species (ROS) to abiotic and biotic feedbacks in plant microbiomes: The dose makes the poison. International Journal of Molecular Sciences 23:4402. <https://doi.org/10.3390/ijms23084402>
- Bittelli M, Flury M, Campbelland GS, Nichols EJ (2001). Reduction of transpiration through foliar application of chitosan. Agricultural and Forest Meteorology 107:167-175. [https://doi.org/10.1016/S0168-1923\(00\)00242-2](https://doi.org/10.1016/S0168-1923(00)00242-2)
- Boamah PO, Onumah J, Adugubaand WO, Santo KG (2023). Application of depolymerized chitosan in crop production: A review. International Journal of Biological Macromolecules 123858. <https://doi.org/10.1016/j.ijbiomac.2023.123858>
- Boonlertnirun S, Sarobol E, Meechouianand S, Sooksathan I (2007). Drought recovery and grain yield potential of rice after chitosan application. Agriculture and Natural Resources 41:1-6.
- Chakraborty M, Hasanuzzaman M, Rahman M, Khan MAR, Bhowmik P, Mahmud NU, Tanveerand M, Islam T (2020). Mechanism of plant growth promotion and disease suppression by chitosan biopolymer. Agriculture 10:624. <https://doi.org/10.3390/agriculture10120624>
- Choi C, Namand J-P, Nah J-W (2016). Application of chitosan and chitosan derivatives as biomaterials. Journal of Industrial and Engineering Chemistry 33:1-10. <https://doi.org/10.1016/j.jiec.2015.10.028>
- Choudhary DK, Prakashand A, Johri B (2007). Induced systemic resistance (ISR) in plants: mechanism of action. Indian Journal of Microbiology 47:289-297. <https://doi.org/10.1007/s12088-007-0054-2>
- Coolen S, Van Pelt JA, Van Weesand SC, Pieterse CM (2019). Mining the natural genetic variation in *Arabidopsis thaliana* for adaptation to sequential abiotic and biotic stresses. Planta 249:1087-1105. <https://doi.org/10.1007/s00425-018-3065-9>
- Cordon G, Andrade C, Barbaraand L, Romero AM (2022). Early detection of tomato bacterial canker by reflectance indices. Information Processing in Agriculture 9:184-194. <https://doi.org/10.1016/j.inpa.2021.06.004>
- da Silva EC, Nogueira R, da Silvaand MA, de Albuquerque MB (2011). Drought stress and plant nutrition. Plant Stress 5:32-41. <https://doi.org/10.5829/idosi.aejaes.2016.16.4.12907>
- Das K, Roychoudhury A (2014). Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. Frontiers in Environmental Science 2:53. <https://doi.org/10.3389/fenvs.2014.00053>
- Das S, Singh VK, Dwivedy AK, Chaudhari AK, Upadhyay N, Singh P, Sharmaand S, Dubey NK (2019). Encapsulation in chitosan-based nanomatrix as an efficient green technology to boost the antimicrobial, antioxidant and *in situ* efficacy of *Coriandrum sativum* essential oil. International Journal of Biological Macromolecules 133:294-305. <https://doi.org/10.1016/j.ijbiomac.2019.04.070>

- de Ollas C, Arbonaand V, GóMez-Cadenas A (2015). Jasmonoyl isoleucine accumulation is needed for abscisic acid build-up in roots of *Arabidopsis* under water stress conditions. *Plant, Cell & Environment* 38:2157-2170. <https://doi.org/10.1111/pce.12536>
- Delezuk JA, Pavinatto A, Moraes ML, Shimizu FM, Rodrigues VC, Campana-Filho SP, Ribeiroand SJ, Oliveira Jr ON (2017). Silk fibroin organization induced by chitosan in layer-by-layer films: Application as a matrix in a biosensor. *Carbohydrate Polymers* 155:146-151. <https://doi.org/10.1016/j.carbpol.2016.08.060>
- Desai N, Rana D, Salave S, Gupta R, Patel P, Karunakaran B, Sharma A, Giri J, Benivaland D, Kommineni N (2023). Chitosan: a potential biopolymer in drug delivery and biomedical applications. *Pharmaceutics* 15:1313. <https://doi.org/10.3390/pharmaceutics15041313>
- Ding L-N, Li Y-T, Wu Y-Z, Li T, Geng R, Cao J, Zhangand W, Tan X-L (2022). Plant disease resistance-related signaling pathways: recent progress and future prospects. *International Journal of Molecular Sciences* 23:16200. <https://doi.org/10.3390/ijms232416200>
- Dolatkah Dashtmian A, Hosseini Mazinianiand SM, Pazoki A (2023). Exogenous chitosan nanoparticles modulated drought stress through changing yield, biochemical attributes, and fatty acid profile of common bean (*Phaseolus vulgaris* L.) cultivars. *Gesunde Pflanzen* 1-14. <https://doi.org/10.1007%2Fs10343-023-00912-6>
- Elansary HO, Abdel-Hamid AM, Yessoufou K, Al-Mana FA, El-Ansary DO, Mahmoudand EA, Al-Yafrasi MA (2020). Physiological and molecular characterization of water-stressed *Chrysanthemum* under robinin and chitosan treatment. *Acta Physiologiae Plantarum* 42:1-14. <https://doi.org/10.1007/s11738-020-3021-8>
- Elich-Ali-Komi D, Hamblin MR (2016). Chitin and chitosan: production and application of versatile biomedical nanomaterials. *International Journal of Advanced Research* 4:411.
- Elshamy MT, Husseinyand SM, Farroh KY (2019). Application of nano-chitosan NPK fertilizer on growth and productivity of potato plant. *Journal of Scientific Research in Science* 36:424-441. <https://doi.org/10.21608/JSRS.2019.58522>
- Eltaweil AS, Omer AM, El-Aqapa HG, Gaber NM, Attia NF, El-Subruiti GM, Mohy-Eldinand MS, Abd El-Monaem EM (2021). Chitosan based adsorbents for the removal of phosphate and nitrate: A critical review. *Carbohydrate Polymers* 274:118671. <https://doi.org/10.1016/j.carbpol.2021.118671>
- Emami Bistgani Z, Siadat SA, Bakhshandeh A, Ghasemi Pirbaloutiand A, Hashemi M (2017). Morpho-physiological and phytochemical traits of (*Thymus daenensis* Celak.) in response to deficit irrigation and chitosan application. *Acta Physiologiae Plantarum* 39:1-13. <https://doi.org/10.1080/10412905.2021.1885512>
- Esposito D (2020). Advanced strategies to deliver bioactive molecules in nutraceuticals. University of Naples Federico II.
- Farouk S, Amany AR (2012). Improving growth and yield of cowpea by foliar application of chitosan under water stress. *Egyptian Journal of Biology* 14:14-16. <http://dx.doi.org/10.4314/ejb.v14i1.2>
- Ferri M, Tassoni A (2011). Chitosan as elicitor of health beneficial secondary metabolites in *in vitro* plant cell cultures. *Handbook of Chitosan Research and Applications* 389-414.
- Gao Y, Wu Y (2022). Recent advances of chitosan-based nanoparticles for biomedical and biotechnological applications. *International Journal of Biological Macromolecules* 203:379-388. <https://doi.org/10.1016/j.ijbiomac.2022.01.162>
- Gechev TS, Van Breusegem F, Stone JM, Denevand I, Laloi C (2006). Reactive oxygen species as signals that modulate plant stress responses and programmed cell death. *Bioassays* 28:1091-1101. <https://doi.org/10.1002/bies.20493>
- Gerami SE, Pourmadadi M, Fatoorehchi H, Yazdian F, Rashediand H, Nigjeh MN (2021). Preparation of pH-sensitive chitosan/polyvinylpyrrolidone/ $\alpha$ -Fe<sub>2</sub>O<sub>3</sub> nanocomposite for drug delivery application: Emphasis on ameliorating restrictions. *International Journal of Biological Macromolecules* 173:409-420. <https://doi.org/10.1016/j.ijbiomac.2021.01.067>
- Ghorbanpour M (2015). Major essential oil constituents, total phenolics and flavonoids content and antioxidant activity of *Salvia officinalis* plant in response to nano-titanium dioxide. *Indian Journal of Plant Physiology* 20:249-256. <https://doi.org/10.1007/s40502-015-0170-7>
- Giglou MT, Giglou RH, Esmacilpour B, Azarmi R, Padash A, Falakian M, Śliwka J, Gohariand G, Lajayer HM (2022). A new method in mitigation of drought stress by chitosan-coated iron oxide nanoparticles and growth stimulant in peppermint. *Industrial Crops and Products* 187:115286. <https://doi.org/10.1016/j.indcrop.2022.115286>
- Gull A, Loneand AA, Wani NUI (2019). Biotic and abiotic stresses in plants. *Abiotic and Biotic Stress in Plants* 2019:1-19. <https://doi.org/10.5772/intechopen.85832>

- Guo Q, Wu X, Ji Y, Hao Y, Liao S, Cui Z, Li J, Younasand M, He B (2021). pH-responsive nanofiltration membrane containing chitosan for dye separation. *Journal of Membrane Science* 635:119445.
- Guy CL (1990). Cold acclimation and freezing stress tolerance: role of protein metabolism. *Annual Review of Plant Biology* 41:187-223. <https://doi.org/10.1016/j.memsci.2021.119445>
- Hancock J, Desikanand R, Neill S (2001). Role of reactive oxygen species in cell signalling pathways. *Biochemical Society Transactions* 29:345-349. <https://doi.org/10.1042/0300-5127:0290345>
- Harb A, Krishnan A, Ambavaramand MM, Pereira A (2010). Molecular and physiological analysis of drought stress in *Arabidopsis* reveals early responses leading to acclimation in plant growth. *Plant Physiology* 154:1254-1271. <https://doi.org/10.1104/pp.110.161752>
- Hassan F, Ali E, Gaber A, Fetouhand M, Mazrou R (2021). Chitosan nanoparticles effectively combat salinity stress by enhancing antioxidant activity and alkaloid biosynthesis in *Catharanthus roseus* (L.) G. Don. *Plant Physiology and Biochemistry* 162:291-300. <https://doi.org/10.1016/j.plaphy.2021.03.004>
- Hassan MU, Ghareeb RY, Nawaz M, Mahmood A, Shah AN, Abdel-Mageed A, Abdelsalam NR, Hashem M, Alamriand S, Thabit MA (2022a). Melatonin: a vital protectant for crops against heat stress: mechanism and prospects. *Agronomy* 12:1116 <https://doi.org/10.3390/agronomy12051116>
- Hassan MU, Mahmood A, Awan MI, Maqbool R, Aamer M, Alhaithloul HA, Huang G, Skalicky M, Bressticand M, Pandey S (2022b). Melatonin-induced protection against plant abiotic stress: mechanism and prospects. *Frontiers in Plant Science* 13:902694. <https://doi.org/10.3389/fpls.2022.902694>
- Hassani F-ZSA, El Bourakadi K, Merghouband N, Bouhfid R (2020). Effect of chitosan/modified montmorillonite coating on the antibacterial and mechanical properties of date palm fiber trays. *International Journal of Biological Macromolecules* 148:316-323. <https://doi.org/10.1016/j.ijbiomac.2020.01.092>
- He S-B, Yang L, Yang Y, Noreldeen HA, Wu G-W, Peng H-P, Dengand H-H, Chen W (2022). Carboxylated chitosan enabled platinum nanozyme with improved stability and ascorbate oxidase-like activity for a fluorometric acid phosphatase sensor. *Carbohydrate Polymers* 298:120120. <https://doi.org/10.1016/j.carbpol.2022.120120>
- Hidangmayum A, Dwivedi P, Katiyarand D, Hemantaranjan A (2019). Application of chitosan on plant responses with special reference to abiotic stress. *Physiology and Molecular Biology of Plants* 25:313-326. <https://doi.org/10.1007/s12298-018-0633-1>
- Hidangmayum A, Dwivedi P (2022). Chitosan based nanoformulation for sustainable agriculture with special reference to abiotic stress: a review. *Journal of Polymers and the Environment* 1-20. <https://doi.org/10.1007/s10924-021-02296-y>
- Hong J, Yokomakura A, Nakano Y, Ishihara K, Kaneda M, Onodera M, Nakahama K-I, Morita I, Niikuraand K, Ahn J-W (2006). Inhibition of vacuolar-type (H<sup>+</sup>)-ATPase by the cytostatic macrolide apicularen A and its role in apicularen A-induced apoptosis in RAW 264.7 cells. *FEBS Letters* 580:2723-2730. <https://doi.org/10.1016/j.febslet.2006.04.031>
- Huang H, Ullah F, Zhou D-X, Yiand M, Zhao Y (2019). Mechanisms of ROS regulation of plant development and stress responses. *Frontiers in Plant Science* 10:800. <https://doi.org/10.3389/fpls.2019.00800>
- Huang WX, Chen XW, Wu L, Yu ZS, Gao MY, Zhao HM, Mo CH, Li YW, Caiand QY, Wong MH (2021). Root cell wall chemistry remodelling enhanced arsenic fixation of a cabbage cultivar. *Journal of Hazardous Materials* 420:126165. <https://doi.org/10.1016/j.jhazmat.2021.126165>
- Hyung J-H, Ahn C-B, Kim BI, Kimand K, Je J-Y (2016). Involvement of Nrf2-mediated heme oxygenase-1 expression in anti-inflammatory action of chitosan oligosaccharides through MAPK activation in murine macrophages. *European Journal of Pharmacology* 793:43-48. <https://doi.org/10.1016/j.ejphar.2016.11.002>
- Ibrahim EA, Ramadan WA (2015). Effect of zinc foliar spray alone and combined with humic acid or/and chitosan on growth, nutrient elements content and yield of dry bean (*Phaseolus vulgaris* L.) plants sown at different dates. *Scientia Horticulturae* 184:101-105. <https://doi.org/10.1016/j.scienta.2014.11.010>
- Imran QM, Falak N, Hussain A, Munand B-G, Yun B-W (2021). Abiotic stress in plants; stress perception to molecular response and role of biotechnological tools in stress resistance. *Agronomy* 11:1579. <https://doi.org/10.3390/agronomy11081579>
- Iriti M, Picchi V, Rossoni M, Gomasasca S, Ludwig N, Garganoand M, Faoro F (2009). Chitosan antitranspirant activity is due to abscisic acid-dependent stomatal closure. *Environmental and Experimental Botany* 66:493-500. <https://doi.org/10.1016/j.envexpbot.2009.01.004>

- Iriti M, Faoro F (2009). Chitosan as a MAMP, searching for a PRR. *Plant Signaling & Behavior* 4:66-68. <https://doi.org/10.3390/agronomy11081579>
- Islam S, Bhuiyanand MR, Islam MN (2017). Chitin and chitosan: structure, properties and applications in biomedical engineering. *Journal of Polymers and the Environment* 25:854-866. <https://doi.org/10.1007/s10924-016-0865-5>
- Javaid MM, Mahmood A, Alshaya DS, Alkahtani MD, Waheed H, Wasaya A, Khan SA, Naqve M, Haiderand I, Shahid MA (2022). Influence of environmental factors on seed germination and seedling characteristics of perennial ryegrass (*Lolium perenne* L.). *Scientific Reports* 12:9522 <https://doi.org/10.1038/s41598-022-13416-6>
- Ji D, Ou L, Ren X, Yang X, Tan Y, Zhouand X, Jin L (2022). Transcriptomic and metabolomic analysis reveal possible molecular mechanisms regulating tea plant growth elicited by chitosan oligosaccharide. *International Journal of Molecular Sciences* 23:5469. <https://doi.org/10.3390/ijms23105469>
- Jwa N-S, Agrawal GK, Tamogami S, Yonekura M, Han O, Iwashashiand H, Rakwal R (2006). Role of defense/stress-related marker genes, proteins and secondary metabolites in defining rice self-defense mechanisms. *Plant Physiology and Biochemistry* 44:261-273. <https://doi.org/10.1016/j.plaphy.2006.06.010>
- Kagale S, Marimuthu T, Thayumanavan B, Nandakumarand R, Samiyappan R (2004). Antimicrobial activity and induction of systemic resistance in rice by leaf extract of *Datura metel* against *Rhizoctonia solani* and *Xanthomonas oryzae* pv. *oryzae*. *Physiological and Molecular Plant Pathology* 65:91-100. <https://doi.org/10.1016/j.pmpp.2004.11.008>
- Kashyap PL, Xiangand X, Heiden P (2015). Chitosan nanoparticle-based delivery systems for sustainable agriculture. *International Journal of Biological Macromolecules* 77:36-51. <https://doi.org/10.1016/j.ijbiomac.2015.02.039>
- Katiyar D, Hemantaranjan A, Singhand B, Bhanu AN (2014). A future perspective in crop protection: Chitosan and its oligosaccharides. *Advances in Plants & Agriculture Research* 1:1-8. <https://doi.org/10.15406/apar.2014.01.00006>
- Khalil MS, Badawy ME (2012). Nematicidal activity of a biopolymer chitosan at different molecular weights against root-knot nematode, *Meloidogyne incognita*. *Plant Protection Science* 48:170-178. <https://doi.org/10.17221/46/2011-PPS>
- Khan W-u-D, Sharif F, Naeem MA, Farooq MA, Siddiqand Z, Imran M (2023). Chitosan polymerized silica composite as a potential silicon source: modulation on antioxidant enzymes, ionic homeostasis, and grain quality in maize plants under Na<sup>+</sup> stress. *Journal of Plant Growth Regulation* 42:2374-2388. <https://doi.org/10.1007/s00344-022-10711-4>
- Kim KS, Lee D, Songand CG, Kang PM (2015). Reactive oxygen species-activated nanomaterials as theranostic agents. *Nanomedicine* 10:2709-2723. <https://doi.org/10.2217/nmm.15.108>
- Kumar MR, Muzzarelli RA, Muzzarelli C, Sashiwaand H, Domb A (2004). Chitosan chemistry and pharmaceutical perspectives. *Chemical Reviews* 104:6017-6084. <https://doi.org/10.1021/cr030441b>
- Kumar M, Kaur S, Yadav SKR, Sundaram S (2023). Molecular, physiological and biochemical responses of plants to abiotic stress. In: *Advances in Plant Physiology*. Scientific Publishes, India, pp 93-109.
- Kumaraswamy R, Kumari S, Choudhary RC, Pal A, Raliya R, Biswasand P, Saharan V (2018). Engineered chitosan-based nanomaterials: Bioactivities, mechanisms and perspectives in plant protection and growth. *International Journal of Biological Macromolecules* 113:494-506. <https://doi.org/10.1016/j.ijbiomac.2018.02.130>
- Kumari S, Kishor R (2020). Chitin and chitosan: origin, properties, and applications. *Handbook of chitin and chitosan*. Elsevier, pp 1-33. <https://doi.org/10.1016/B978-0-12-817970-3.00001-8>
- Lee HB, Yu M-R, Yang Y, Jiand Z, Za H (2003). Reactive oxygen species-regulated signaling pathways in diabetic nephropathy. *Journal of the American Society of Nephrology* 14:S241-S245. <https://doi.org/10.1097/01.ASN.0000077410.66390.0F>
- Li K, Xing R, Liuand S, Li P (2020a). Chitin and chitosan fragments responsible for plant elicitor and growth stimulator. *Journal of Agricultural and Food Chemistry* 68:12203-12211. <https://doi.org/10.1021/acs.jafc.0c05316>
- Li Q, Dunn E, Grandmaisonand E, Goosen MF (2020b). Applications and properties of chitosan, *Applications of Chitan and Chitosan*. CRC Press, pp 3-29.
- Li S, Yan L, Venuste M, Xu F, Shi L, White PJ, Wangand X, Ding G (2023). A critical review of plant adaptation to environmental boron stress: Uptake, utilization, and interplay with other abiotic and biotic factors. *Chemosphere* 139474. <https://doi.org/10.1016/j.chemosphere.2023.139474>

- Li Z, Zhang Y, Zhang X, Merewitz E, Peng Y, Ma X, Huangand L, Yan Y (2017). Metabolic pathways regulated by chitosan contributing to drought resistance in white clover. *Journal of Proteome Research* 16:3039-3052. <https://doi.org/10.1021/acs.jproteome.7b00334>
- Liang J, Yan H, Puligundla P, Gao X, Zhouand Y, Wan X (2017). Applications of chitosan nanoparticles to enhance absorption and bioavailability of tea polyphenols: A review. *Food Hydrocolloids* 69:286-292. <https://doi.org/10.1016/j.foodhyd.2017.01.041>
- Limpanavech P, Chaiyasuta S, Vongprommek R, Pichyangkura R, Khunwasi C, Chadchawan S, Lotrakul P, Bunjongrat R, Chaideeand A, Bangyeekhun T (2008). Chitosan effects on floral production, gene expression, and anatomical changes in the *Dendrobium* orchid. *Scientia Horticulturae* 116:65-72. <https://doi.org/10.1016/j.scienta.2007.10.034>
- M Younis A, Aly-Eldeenand MA, Elkady EM (2019). Effect of different molecular weights of chitosan on the removal efficiencies of heavy metals from contaminated water. *Egyptian Journal of Aquatic Biology and Fisheries* 23:149-158. <https://doi.org/10.21608/EJABF.2019.52591>
- Mahdavi B, Modarres Sanavy SAM, Aghaalikhani M, Sharifiand M, Dolatabadian A (2011). Chitosan improves osmotic potential tolerance in safflower (*Carthamus tinctorius* L.) seedlings. *Journal of Crop Improvement* 25:728-741. <https://doi.org/10.1080/15427528.2011.606354>
- Mahmood A, Bibi S, Naqve M, Javaid MM, Zia MA, Jabbar A, Ud-Din W, Attia KA, Khanand N, Al-Doss AA (2022). Physiological, Biochemical, and yield responses of linseed (*Linum usitatissimum* L.) in  $\alpha$ -Tocopherol-mediated alleviation of salinity stress. *Frontiers in Plant Science* 13:867172. <https://doi.org/10.3389/fpls.2022.867172>
- Malerba M, Cerana R (2016). Chitosan effects on plant systems. *International Journal of Molecular Sciences* 17:996. <https://doi.org/10.3390/ijms17070996>
- Maluin FN, Hussein MZ (2020). Chitosan-based agronanochemicals as a sustainable alternative in crop protection. *Molecules* 25:161125:1611. <https://doi.org/10.3390/molecules25071611>
- Martins AF, Facchi SP, Follmann HD, Pereira AG, Rubiraand AF, Muniz EC (2014). Antimicrobial activity of chitosan derivatives containing N-quaternized moieties in its backbone: a review. *International Journal of Molecular Sciences* 15:20800-20832. <https://doi.org/10.3390/ijms151120800>
- McKersie BD, Lesheim Y (2013). Stress and stress coping in cultivated plants. Springer Science & Business Media.
- Meena KK, Sorty AM, Bitla UM, Choudhary K, Gupta P, Pareek A, Singh DP, Prabha R, Sahuand PK, Gupta VK (2017). Abiotic stress responses and microbe-mediated mitigation in plants: the omics strategies. *Frontiers in Plant Science* 8:172. <https://doi.org/10.3389/fpls.2017.00172>
- Mehregan M, Mehrafarin A, Labbafian M, Naghdi Badi H (2017). Effect of different concentrations of chitosan biostimulant on biochemical and morphophysiological traits of stevia plant (*Stevia rebaudiana* Bertoni). *Journal of Medicinal Plants* 16(62).
- Mendes J, Paschoalin R, Carmona V, Neto ARS, Marques A, Marconcini J, Mattoso L, Medeirosand E, Oliveira J (2016). Biodegradable polymer blends based on corn starch and thermoplastic chitosan processed by extrusion. *Carbohydrate Polymers* 137:452-458. <https://doi.org/10.1016/j.carbpol.2015.10.093>
- Mittler R (2006). Abiotic stress, the field environment and stress combination. *Trends in Plant Science* 11:15-19. <https://doi.org/10.1016/j.carbpol.2015.10.093>
- Moenne A, González A (2021). Chitosan-, alginate-carrageenan-derived oligosaccharides stimulate defense against biotic and abiotic stresses, and growth in plants: A historical perspective. *Carbohydrate Research* 503:108298. <https://doi.org/10.1016/j.carres.2021.108298>
- Morin-Crini N, Lichtfouse E, Torriand G, Crini G (2019). Fundamentals and applications of chitosan. *Sustainable agriculture reviews* 35: chitin and chitosan: history, fundamentals and innovations. Springer 35:49-123.
- Motahharifar N, Nasrollahzadeh M, Taheri-Kafrani A, Varmaand RS, Shokouhimehr M (2020). Magnetic chitosan-copper nanocomposite: A plant assembled catalyst for the synthesis of amino-and N-sulfonyl tetrazoles in eco-friendly media. *Carbohydrate Polymers* 232:115819. <https://doi.org/10.1016/j.carbpol.2019.115819>
- Muley AB, Shingote PR, Patil AP, Dalviand SG, Suprasanna P (2019). Gamma radiation degradation of chitosan for application in growth promotion and induction of stress tolerance in potato (*Solanum tuberosum* L.). *Carbohydrate Polymers* 210:289-301. <https://doi.org/10.1016/j.carbpol.2019.01.056>
- Munnik T, Meijer HJ (2001). Osmotic stress activates distinct lipid and MAPK signalling pathways in plants. *FEBS Letters* 498:172-178. [https://doi.org/10.1016/S0014-5793\(01\)02492-9](https://doi.org/10.1016/S0014-5793(01)02492-9)

- Muzzarelli RA, Boudrant J, Meyer D, Manno N, DeMarchisand M, Paoletti MG (2012). Current views on fungal chitin/chitosan, human chitinases, food preservation, glucans, pectins and inulin: A tribute to Henri Braconnot, precursor of the carbohydrate polymers science, on the chitin bicentennial. *Carbohydrate Polymers* 87:995-1012. <https://doi.org/10.1016/j.carbpol.2011.09.063>
- Nardi S, Schiavonand M, Francioso O (2021). Chemical structure and biological activity of humic substances define their role as plant growth promoters. *Molecules* 26:2256. <https://doi.org/10.3390/molecules26082256>
- Nawaz M, Hassan MU, Chattha MU, Mahmood A, Shah AN, Hashem M, Alamri S, Batool M, Rasheedand A, Thabit MA (2022). Trehalose: A promising osmo-protectant against salinity stress—physiological and molecular mechanisms and future prospective. *Molecular Biology Reports* 49:11255-11271. <https://doi.org/10.1007/s11033-022-07681-x>
- Özkurt N, Bektaş Y (2022). Alleviation of salt stress with chitosan foliar application and its effects on growth and development in tomato (*Solanum lycopersicum* L.). *Türkiye Tarımsal Araştırmalar Dergisi* 9:342-351. <https://doi.org/10.19159/tutad.1168393>
- Pastori GM, Foyer CH (2002). Common components, networks, and pathways of cross-tolerance to stress. The central role of “redox” and abscisic acid-mediated controls. *Plant Physiology* 129:460-468. <https://doi.org/10.1104/pp.011021>
- Patel T, Babbar A, Behera K, Katara CK, Anand KJ, Vyshnavi R, Pachoriand S, Bichewar N (2023). Exploring the potential of proximal remote sensing in plant stress phenotyping: A comprehensive review. *International Journal of Environment and Climate Change* 13:2602-2621. <https://doi.org/10.9734/ijec/2023/v13i92511>
- Paul D, Nair S (2008). Stress adaptations in a plant growth promoting rhizobacterium (PGPR) with increasing salinity in the coastal agricultural soils. *Journal of Basic Microbiology* 48:378-384. <https://doi.org/10.1002/jobm.200700365>
- Peniche C, Argüelles-Monaland W, Goycoolea F (2008). Chitin and chitosan: major sources, properties and applications, Monomers, polymers and composites from renewable resources. Elsevier, pp 517-542. <https://doi.org/10.1016/B978-0-08-045316-3.00025-9>
- Percival GC (2023). Heat tolerance of urban tree species-a review. *Urban Forestry & Urban Greening* 128021. <https://doi.org/10.1016/j.ufug.2023.128021>
- Pichyangkura R, Chadchawan S (2015). Biostimulant activity of chitosan in horticulture. *Scientia Horticulturae* 196:49-65. <https://doi.org/10.1016/j.scienta.2015.09.031>
- Pongprayoon W, Siringam T, Panyaand A, Roytrakul S (2022). Application of chitosan in plant defense responses to biotic and abiotic stresses. *Applied Science and Engineering Progress* 15. <https://doi.org/10.14416/j.asep.2020.12.007>
- Povero G, Loreti E, Pucciariello C, Santaniello A, Di Tommaso D, Di Tommaso G, Kapetis D, Zolezzi F, Piaggiesiand A, Perata P (2011). Transcript profiling of chitosan-treated *Arabidopsis* seedlings. *Journal of Plant Research* 124:619-629. <https://doi.org/10.1007/s10265-010-0399-1>
- Prajapati D, Pal A, Dimkpa C, Singh U, Devi KA, Choudharyand JL, Saharan V (2022). Chitosan nanomaterials: A prelim of next-generation fertilizers; existing and future prospects. *Carbohydrate Polymers* 288:119356. <https://doi.org/10.1016/j.carbpol.2022.119356>
- Qiu H, Su L, Wangand H, Zhang Z (2021). Chitosan elicitation of saponin accumulation in *Psammosilene tunicoides* hairy roots by modulating antioxidant activity, nitric oxide production and differential gene expression. *Plant Physiology and Biochemistry* 166:115-127. <https://doi.org/10.1016/j.plaphy.2021.05.033>
- Raafat D, Sahl HG (2009). Chitosan and its antimicrobial potential—a critical literature survey. *Microbial Biotechnology* 2:186-201. <https://doi.org/10.1111/j.1751-7915.2008.00080.x>
- Rasheed A, Li H, Tahir MM, Mahmood A, Nawaz M, Shah AN, Aslam MT, Negm S, Moustafaand M, Hassan MU (2022). The role of nanoparticles in plant biochemical, physiological, and molecular responses under drought stress: A review. *Frontiers in Plant Science* 13:976179. <https://doi.org/10.3389/fpls.2022.976179>
- Regni L, Del Buono D, Micheli M, Facchin SL, Tolisanoand C, Proietti P (2022). Effects of biogenic ZnO nanoparticles on growth, physiological, biochemical traits and antioxidants on olive tree *in vitro*. *Horticulturae* 8:161. <https://doi.org/10.3390/horticulturae8020161>
- Riseh RS, Hassanisaadi M, Vatankhah M, Soroushand F, Varma RS(2022b). Nano/microencapsulation of plant biocontrol agents by chitosan, alginate, and other important biopolymers as a novel strategy for alleviating plant

- biotic stresses. International Journal of Biological Macromolecules <https://doi.org/10.1016/j.ijbiomac.2022.09.278>
- Riseh RS, Hassanisaaadi M, Vatankhah M, Babakiand SA, Barka EA (2022a). Chitosan as potential natural compound to manage plant diseases. International Journal of Biological Macromolecules <https://doi.org/10.1016/j.ijbiomac.2022.08.109>
- Rivero RM, Mittler R, Blumwaldand E, Zandalinas SI (2022). Developing climate-resilient crops: improving plant tolerance to stress combination. The Plant Journal 109:373-389. <https://doi.org/10.1111/tpj.15483>
- Rizwan M, Ali S, ur Rehman MZ, Adrees M, Arshad M, Qayyum MF, Ali L, Hussain A, Chathaand SAS, Imran M (2019). Alleviation of cadmium accumulation in maize (*Zea mays* L.) by foliar spray of zinc oxide nanoparticles and biochar to contaminated soil. Environmental Pollution 248:358-367. <https://doi.org/10.1016/j.envpol.2019.02.031>
- Rkhaila A, Chtouki T, Erguig H, El Halouiand N, Ounine K (2021). Chemical proprieties of biopolymers (chitin/chitosan) and their synergic effects with endophytic *Bacillus* species: Unlimited applications in agriculture. Molecules 26:1117. <https://doi.org/10.3390/molecules26041117>
- Rose MA (2023). Endophytic bacteria Isolated from *Aeschynomene indica* plants and their role in nod-factor independent nodule formation and nitrogen fixation. Doctoral dissertation, The University of Texas at Arlington.
- Sadeghipour O (2021). Chitosan application improves nickel toxicity tolerance in soybean. Journal of Soil Science and Plant Nutrition 21:2096-2104. <https://doi.org/10.1007/s42729-021-00505-0>
- Safikhhan S, Khoshbakht K, Chaichi MR, Aminianand A, Motesharezadeh B (2018). Role of chitosan on the growth, physiological parameters and enzymatic activity of milk thistle (*Silybum marianum* (L.) Gaertn.) in a pot experiment. Journal of Applied Research on Medicinal and Aromatic Plants 10:49-58. <https://doi.org/10.1016/j.jarmap.2018.06.002>
- Saharan V, Kumaraswamy R, Choudhary RC, Kumari S, Pal A, Raliyaand R, Biswas P (2016). Cu-chitosan nanoparticle mediated sustainable approach to enhance seedling growth in maize by mobilizing reserved food. Journal of Agricultural and Food Chemistry 64:6148-6155. <https://doi.org/10.1021/acs.jafc.6b02239>
- Saini P, Beniwal A, Kokkiligaddaand A, Vij S (2018). Response and tolerance of yeast to changing environmental stress during ethanol fermentation. Process Biochemistry 72:1-12. <https://doi.org/10.1016/j.procbio.2018.07.001>
- Salimgandomi S, Shabrangi A (2016). The effect of chitosan on antioxidant activity and some secondary metabolites of *Mentha piperita* L. Journal of Pharmaceutical & Health Sciences 4:135-142.
- Santiago R, Barros-Riosand J, Malvar RA (2013). Impact of cell wall composition on maize resistance to pests and diseases. International Journal of Molecular Sciences 14:6960-6980. <https://doi.org/10.3390/ijms14046960>
- Sara K, Hossein A, Masoudand SJ, Hassan M (2012). Effects of water deficit and chitosan spraying on osmotic adjustment and soluble protein of cultivars castor bean (*Ricinus communis* L.). Journal of Stress Physiology & Biochemistry 8:160-169.
- Sathiyabama M, Manikandan A (2018). Application of copper-chitosan nanoparticles stimulate growth and induce resistance in finger millet (*Eleusine coracana* Gaertn.) plants against blast disease. Journal of Agricultural and Food Chemistry 66:1784-1790. <https://doi.org/10.1021/acs.jafc.7b05921>
- Sathiyabama M, Parthasarathy R (2016). Biological preparation of chitosan nanoparticles and its *in vitro* antifungal efficacy against some phytopathogenic fungi. Carbohydrate Polymers 151:321-325. <https://doi.org/10.1016/j.carbpol.2016.05.033>
- Selvakumar G, Kim K, Huand S, Sa T (2014). Effect of salinity on plants and the role of arbuscular mycorrhizal fungi and plant growth-promoting rhizobacteria in alleviation of salt stress. Physiological Mechanisms and Adaptation Strategies in Plants Under Changing Environment 1:115-144.
- Shahrajabian MH, Chaski C, Polyzos N, Tzortzakisanand N, Petropoulos SA (2021). Sustainable agriculture systems in vegetable production using chitin and chitosan as plant biostimulants. Biomolecules 11:819. <https://doi.org/10.3390/biom11060819>
- Shahryari F, Rabieianand Z, Sadighian S (2020). Antibacterial activity of synthesized silver nanoparticles by sumac aqueous extract and silver-chitosan nanocomposite against *Pseudomonas syringae* pv. *syringae*. Journal of Plant Pathology 102:469-475. <https://doi.org/10.1007/s42161-019-00478-1>

- Sharma D, Singh R, Tiwari R, Kumarand R, Gupta VK (2019). Wheat responses and tolerance to terminal heat stress: a review. *Wheat production in changing environments: responses, adaptation and tolerance* 149-173. [https://doi.org/10.1007/978-981-13-6883-7\\_7](https://doi.org/10.1007/978-981-13-6883-7_7)
- Shokraei S, Mirzaei E, Shokraei N, Derakhshan MA, Ghanbariand H, Faridi-Majidi R (2021). Fabrication and characterization of chitosan/kefiran electrospun nanofibers for tissue engineering applications. *Journal of Applied Polymer Science* 138:50547. <https://doi.org/10.1002/app.50547>
- Silveira NM, Prativiera PJ, Pieretti JC, Seabra AB, Almeida RL, Machadoand EC, Ribeiro RV (2021). Chitosan-encapsulated nitric oxide donors enhance physiological recovery of sugarcane plants after water deficit. *Environmental and Experimental Botany* 190:104593. <https://doi.org/10.1016/j.envexpbot.2021.104593>
- Singh Dhillon G, Kaur S, Jyoti Sarma S, Kaur Brar S, Vermaand M, Yadagiri Surampalli R (2013). Recent development in applications of important biopolymer chitosan in biomedicine, pharmaceuticals and personal care products. *Current Tissue Engineering (Discontinued)* 2:20-40.
- Singh A, Kukreti R, Sasoand L, Kukreti S (2022). Mechanistic insight into oxidative stress-triggered signaling pathways and type 2 diabetes. *Molecules* 27:950. <https://doi.org/10.3390/molecules27030950>
- Song X-P, Verma KK, Tian D-D, Zhang X-Q, Liang Y-J, Huang X, Liand C-N, Li Y-R (2021). Exploration of silicon functions to integrate with biotic stress tolerance and crop improvement. *Biological Research* 54:1-12. <https://doi.org/10.1186/s40659-021-00344-4>
- Stasińska-Jakubas M, Hawrylak-Nowak B, Wójciakand M, Dresler S (2023). Comparative effects of two forms of chitosan on selected phytochemical properties of *Plectranthus amboinicus* (Lour.). *Molecules* 28:376. <https://doi.org/10.3390/molecules28010376>
- Stasińska-Jakubas M, Hawrylak-Nowak B (2022). Protective, biostimulating and eliciting effects of chitosan and its derivatives on crop plants. *Molecules* 27:2801. <https://doi.org/10.3390/molecules27092801>
- Sucharitha K, Beulahand A, Ravikiran K (2018). Effect of chitosan coating on storage stability of tomatoes (*Lycopersicon esculentum* Mill). *International Food Research Journal* 25:93-99.
- Sukhova E, Ratnitsyna D, Gromovaand E, Sukhov V (2022). Development of two-dimensional model of photosynthesis in plant leaves and analysis of induction of spatial heterogeneity of CO<sub>2</sub> assimilation rate under action of excess light and drought. *Plants* 11:3285. <https://doi.org/10.3390/plants11233285>
- Synowiecki J, Al-Khateeb NA (2003). Production, properties, and some new applications of chitin and its derivatives. *Critical Reviews in Food Science and Nutrition* 43(2):145-171. <https://doi.org/10.1080/10408690390826473>
- Tang W, Liu X, Heand Y, Yang F (2022). Enhancement of vindoline and catharanthine accumulation, antioxidant enzymes activities, and gene expression levels in *Catharanthus roseus* leaves by chitoooligosaccharides elicitation. *Marine Drugs* 20:188. <https://doi.org/10.3390/md20030188>
- Tarassoli Z, Najjarand R, Amani A (2021). Formulation and optimization of lemon balm extract loaded azelaic acid-chitosan nanoparticles for antibacterial applications. *Journal of Drug Delivery Science and Technology* 65:102687. <https://doi.org/10.1016/j.jddst.2021.102687>
- Thakur P, Kumar S, Malik JA, Bergerand JD, Nayyar H (2010). Cold stress effects on reproductive development in grain crops: an overview. *Environmental and Experimental Botany* 67:429-443. <https://doi.org/10.1016/j.envexpbot.2009.09.004>
- Van Toan N, Hanh TT (2013). Application of chitosan solutions for rice production in Vietnam. *African Journal of Biotechnology* 12(4):382-384. <https://doi.org/10.5897/AJB12.2884>
- Varamin JK, Fanoodi F, Sinaki JM, Rezvanand S, Damavandi A (2020). Foliar application of chitosan and nano-magnesium fertilizers influence on seed yield, oil content, photosynthetic pigments, antioxidant enzyme activities of sesame (*Sesamum indicum* L.) under water-limited conditions. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* 48:2228-2243. <https://doi.org/10.15835/nbha48411852>
- Vercesi AE, Castilho RF, Kowaltowski AJ, de Oliveira HC, de Souza-Pinto NC, Figueiraand TR, Busanello EN (2018). Mitochondrial calcium transport and the redox nature of the calcium-induced membrane permeability transition. *Free Radical Biology and Medicine* 129:1-24. <http://dx.doi.org/10.1016/j.freeradbiomed.2018.08.034>
- Verma KK, Song X-P, Joshi A, Tian D-D, Rajput VD, Singh M, Arora J, Minkinaand T, Li Y-R (2022). Recent trends in nano-fertilizers for sustainable agriculture under climate change for global food security. *Nanomaterials* 12:173. <https://doi.org/10.3390/nano12010173>

- Wang W, Meng Q, Li Q, Liu J, Zhou M, Jinand Z, Zhao K (2020). Chitosan derivatives and their application in biomedicine. *International Journal of Molecular Sciences* 21:487. <https://doi.org/10.3390/ijms21020487>
- Wu S, Shanand L, He P (2014). Microbial signature-triggered plant defense responses and early signaling mechanisms. *Plant Science* 228:118-126. <https://doi.org/10.1016/j.plantsci.2014.03.001>
- Yang J, Shen M, Luo Y, Wu T, Chen X, Wangand Y, Xie J (2021). Advanced applications of chitosan-based hydrogels: From biosensors to intelligent food packaging system. *Trends in Food Science & Technology* 110:822-832. <https://doi.org/10.1016/j.tifs.2021.02.032>
- Yeboah A, Lu J, Yang T, Shi Y, Amoanimaa-Dede H, Boatengand CGA, Yin X (2020). Assessment of castor plant (*Ricinus communis* L.) tolerance to heavy metal stress-a review. *Phyton* 89:453. <https://doi.org/10.32604/phyton.2020.09267>
- Yeh C-H, Linand P-W, Lin Y-C (2010). Chitosan microfiber fabrication using a microfluidic chip and its application to cell cultures. *Microfluidics and Nanofluidics* 8:115-121. <https://doi.org/10.1007/s10404-009-0485-7>
- Yu D, Regenstein JM, Zang J, Xia W, Xu Y, Jiandand Q, Yang F (2018). Inhibitory effects of chitosan-based coatings on endogenous enzyme activities, proteolytic degradation and texture softening of grass carp (*Ctenopharyngodon idellus*) fillets stored at 4 °C. *Food Chemistry* 262:1-6. <https://doi.org/10.1016/j.foodchem.2018.04.070>
- Zafar S, Afzal H, Ijaz A, Mahmood A, Ayub A, Nayab A, Hussain S, Maqsood U-H, Sabirand MA, Zulfiqar U (2023). Cotton and drought stress: An updated overview for improving stress tolerance. *South African Journal of Botany* 161:258-268. <https://doi.org/10.1016/j.sajb.2023.08.029>
- Zandalinas SI, Mittler R (2022). Plant responses to multifactorial stress combination. *New Phytologist* 234:1161-1167. <https://doi.org/10.1111/nph.18087>
- Zayed M, Elkafafi S, Zedanand AM, Dawoud SF (2017). Effect of nano chitosan on growth, physiological and biochemical parameters of *Phaseolus vulgaris* under salt stress. *Journal of Plant Production* 8:577-585. <https://doi.org/10.21608/JPP.2017.40468>
- Zhai L, Bai Z, Zhu Y, Wangand B, Luo W (2018). Fabrication of chitosan microspheres for efficient adsorption of methyl orange. *Chinese Journal of Chemical Engineering* 26:657-666. <https://doi.org/10.1016/j.cjche.2017.08.015>
- Zhang S, Zhang M, Khalid AR, Li L, Chen Y, Dong P, Wangand H, Ren M (2020). Ethylcinn prevents potato late blight by disrupting protein biosynthesis of *Phytophthora infestans*. *Pathogens* 9:299. <https://doi.org/10.3390/pathogens9040299>
- Zong H, Liu S, Xing R, Chenand X, Li P (2017). Protective effect of chitosan on photosynthesis and antioxidative defense system in edible rape (*Brassica rapa* L.) in the presence of cadmium. *Ecotoxicology and Environmental Safety* 138:271-278. <https://doi.org/10.1016/j.ecoenv.2017.01.009>



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