ANSF
APPLIED AND NATURAL SCIENCE FOUNDATION

Journal of Applied and Natural Science
14(2), 582 - 599 (2022)
ISSN : 0974-9411 (Print), 2231-5209 (Online)
journals.ansfoundation.org

Review Article

Role of Brassinosteroids in plants responses to salinity stress: A review

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Article Info
https://doi.org/10.31018/jans.v14i2.3466
Received: April 14, 2022
Revised: June 1, 2022
Accepted: June 7, 2022

How to Cite
Vikram *et al.* (2022). Role of Brassinosteroids in plants responses to salinity stress: A review. *Journal of Applied and Natural Science*, 14(2), 582 - 599. https://doi.org/10.31018/jans.v14i2.3466

Abstract
Brassinosteroid emerges as an essential phytohormone that helps the plant to maintain plant growth and development. It also helps the plants grow well under adverse conditions along with normal conditions. In this review article, we have discussed the functional role of brassinosteroid (BRS) in plants under salinity stress conditions. Salinity stress is one of the most devastating abiotic stresses which adversely affect plant growth by disturbing their metabolic pathway. This article also comprises the occurrence, structure and signalling pathway of the brassinosteroid. Application of brassinosteroid improves the plant status under salinity by enhancing the antioxidant enzyme activity in plants. Moreover, we also reported the different growth parameters enhanced by brassinosteroid application in plants under salinity. BRSs also maintain plant growth through the regulation of expression of various genes whose products are involved in various biochemical and physiological processes. This review is based on the various aspects in much detail which are required to understand the proper mechanism of BRS, such as i) the role of BRS signaling pathways in providing tolerance to the plants, ii) changes due to the presence or absence of BRS in plants under stress conditions, iii) BRSs application on the regulation of different genes and transcriptional factor, iv) regulation in ion homeostasis, v) reduction of oxidative stress via different mechanisms under salinity stress. However, a lot of knowledge is required to understand the role of BRS in alleviating salinity stress and needs future research work on BRS with its different derivatives in the alleviation of salt stress.

Keywords: Brassinosteroid, Gene expression, Oxidative stress, Salt stress, Signaling pathway

INTRODUCTION

Brassinosteroids (BRSs) are a class of plant regulating steroidal hormones that regulate plant growth at different stages of the life cycle. BRS plays different essential functions in both biotic and abiotic stresses. BRS control different physiological and biochemical processes of plants under stress and non-stress conditions. It interacts with other hormones in the different physiological processes to control their response. Salinity has emerged as a major threat to agricultural sector in recent times. In India, around 6.727 million hectares of area is salinity affected which represent around 2% of the total geographical area of the country (Arora *et al*., 2016; Arora and Sharma, 2017). Ahanger *et al*. (2020) reported that BRS treatment helps plants to alleviate the deleterious effects of salinity.

Occurrence and structure of BRSs

Brassinolide (BL) ($C_{28}H_{48}O_6$) was the first BRS, isolated from pollen of the rape plant in 1979, after which a second BRS was isolated from *Catanea crenata* in 1982, named castasterone (Grove *et al*., 1979; Yokota *et al*., 1982). BRS are found in all divisions of the plant kingdom, including angiosperms, gymnosperms, algae, bryophytes and pteridophytes (Fujioka, 1999; Hayat and Ahmad, 2010). Pollens and immature seeds contain a high concentration of BRSs as compared to vegetative cells like stem or leaf. BL and castasterone are the most widely found BRSs in plants, present in 22 and 33 species. Most of the BRSs are found only in a restricted number of species (Fujioka & Sakurai, 1997).

However, BRSs are rarely found in algae and till now only two BRSs of C28 group are reported in algae named 24-epicastasterone and 28-homocastasterone in *Hydrodictyon reticulatum* (Camoni *et al*., 2018). Liu *et al*. (2017) reported 81 natural BRS in plants along with 137 analogs and 8 metabolites.

BRASSINOSTEROID SIGNALING PATHWAY

In BRS signaling pathway, the receptor for BRS is present on the surface of the cell, named BRI1 (brassinosteroid insensitive 1). BKI1 (BRI1 Kinase Inhibitor 1) acts as an inhibitory protein that binds to BRI1 receptor and restricts its activity. BRS binds to the BRI1 receptor via its C-terminal domain, which leads to different events like auto-phosphorylation and detachment of BKI1, which means that BRI1 now becomes active. Apart from BRI1, another receptor named BAK1 (BRI1-associated receptor kinase 1) is found in the membrane. Both BAK1 and BRI1 are leucine-rich region receptor-like kinase (LRR-RLK), which can add phosphate ions. On getting activated by the BRS binding, BRI1 binds to the BAK1 and forms a heterodimer (Li and Nam, 2002; Wang and Chory, 2006). This binding initiated a phosphorylation cascade in which one intermediate molecule phosphorylates the next molecule present in the signaling pathway. BIN2 (brassinosteroid -insensitive 2) plays a key role in this cascade pathway. It acts as a regulatory molecule that regulates the activity of BZR1 (brassinazole-resistant 1) and BES1 (bri1-EMS-suppressor 1). These regulatory molecules act as a transcriptional factor that regulates the transcription of BRS-regulated genes. In BRS absence, BIN2 remains activated and phosphorylates both BES1 and BZR1 (Li and Nam, 2002; Vert and Chory, 2006). In the phosphorylated state, BES1 and BZR1 can't bind to the DNA, due to which BRS-regulated gene remains inactive. While in the case of binding of BRS with BRI1,

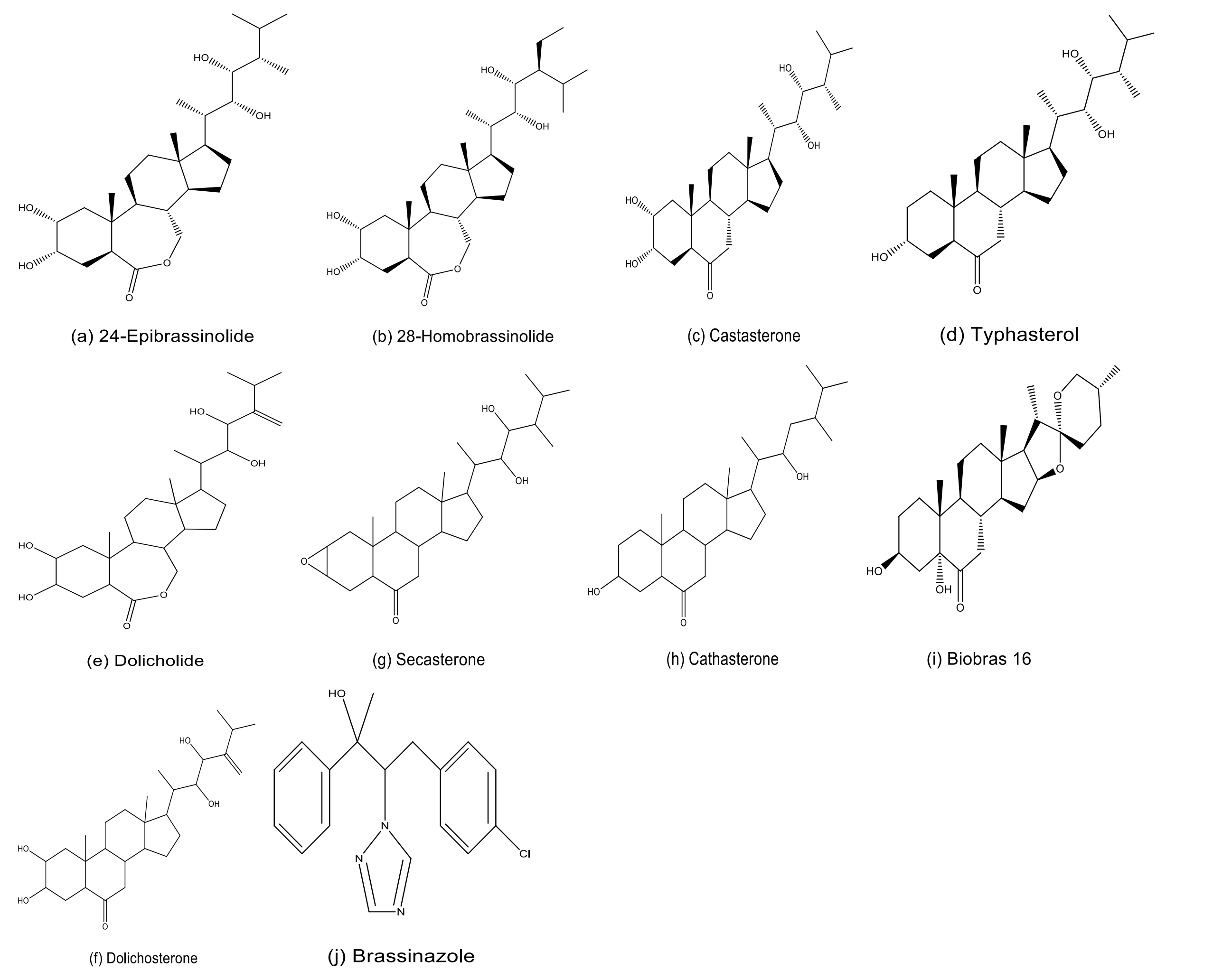

Fig. 1. *Structures of different BRSs, analogues and inhibitor. (a) 24-epibrassinolide (b) 28-homobrassinolide (c) Castasterone (d) Typhasterol (e) Dolicholide (f) Dolichosterone (g) Secasterone (h) Cathasterone (a-h are natural BRs) (i) Biobras-16 (brassinosteroid analogue) (j) brassinazole (brassinosteroid biosynthesis inhibitors) (Sources: Fujioka & Sakurai, 1997; Díaz et al., 2003; Asami et al., 2000).*

BIN2 becomes inactivated while other signaling cascade molecule, named BSU1 (bri1 suppressor 1), becomes activated. BSU1 acts as dephosphorylase, which removes the phosphate group from the next signaling molecule (Mora-García *et al*., 2004). It is also documented that in the phosphorylated state, both BZR1 and BES1 undergo degradation in the proteasome (Gampala *et al*., 2007). Another protein molecule, named 14-3-3 protein, binds with phosphorylated BZR1 and BES1 complex and exports this complex in the cytosol. In the unphosphorylated state, BES1 and BZR1 bind to DNA, which ultimately leads to the transcription of BRS-regulated genes. In conclusion, when BRS does not bind with its receptor, that will ultimately lead to phosphorylation of BES1 and BZR1, which inhibits the BRS regulated genes while in BRS presence, BES1 and BZR1 get dephosphorylated and BRS regulated genes get expressed (He *et al*., 2005; Yin *et al*., 2005). Planas-Riverola *et al*. (2019) reported that BRS helps the plant to grow normally when subjected to stress conditions via maintaining a balance between plant growth and plant resistivity to particular stress. They further added that BRS maintains this balance independently or through crosstalk via ABA. Different mechanisms are reported to explain the involvement of BRS in alleviating various stress conditions like heat, cold, and drought. These mechanisms are: enhanced synthesis of osmoprotectant (Fàbregas *et al*., 2018), antioxidant machinery activation (Kim *et al*., 2012; Lima and Lobato, 2017; Tunc-Ozdemir and Jones, 2017; Xia *et al*., 2009; Zou *et al*., 2018) and fine-tuning stress-responsive transcript machinery (Ye *et al*., 2017).

Salt stress

Stress is stated as the environmental conditions, including both biotic and abiotic, which cause an adverse impact on vegetative and reproductive stages of life and affect the growth as well as the development of plants. Biotic stress includes the adverse impact caused by the living factors like microorganisms or herbivores, while abiotic stress is caused by non-living factors like different environmental factors, including temperature, drought, salinity, etc. According to Grime (1977), stress is the external condition that decreases the photosynthetic ability of plants. At present, when the world's total population is more than 7.9 billion, the demand for food is also high, so we need to focus on enhancing food productivity on a global scale. But the major limitation to approaching this target is generated by different stress conditions that negatively affect plant growth through different physiological functions, which decrease the quality as well as quantity of food production. Biotic stress can be controlled at plant levels or by preventing the growth of the biotic factor with different pesticides, insecticides, etc. But in the case of abiotic stress, we can control it only at the plant level by enhancing the tolerance level of the plant.

Salinity stress can be defined as negative impacts caused by the high concentration of minerals like sodium or potassium ions (Munns, 2005). Among the abiotic stress, salinity becomes a major limiting factor because approx. 45 million hectares of irrigated land is badly damaged by salt stress (Shrivastava and Kumar, 2015) which is around 20% of total irrigated land. Irrigation is considered the major reason for salinity (Zhu, 2001). Szabolcs (1974) categorizes saline soil into saline soil and sodic soil. In saline soils, NaCl and Na_2SO_4, while in sodic soil, $NaCO_3$ is considered the chief salt. On the basis of causing agent, salt stress is categorized into two sub-parts: (A) Natural salt stress: it is the gathering of salts in soil or water for a longer duration via a natural process, (B) Anthropogenic salt stress: it is caused as a result of human activities like irrigation. Natural causes of salt stress include rock weathering, rainfall or evaporation, etc. Replacement of perennial crops with annual vegetation is also the main reason for salinity stress.

Salinity is considered the most affecting abiotic stress, which causes a great loss of crop yield worldwide. It reduces the plant's yield by affecting different growth parameters. Each plant can withstand a particular range of salinity, after which its growth will reduce, and at extreme salinity, it even results in the death of the plant. On the basis of the plant's threshold capacity, plants are divided into two main categories: salt tolerant and salt sensitive. Salinity affects the plant in both the vegetative phase as well as reproductive phase. In the vegetative stage, it causes a negative impact on seed germination. It is studied that presence of salt in plant-soil environment decreases capability of the seed to absorb water which reduces the growth rate. Along with this, salinity also causes injuries in leaves, which affect the photosynthetic ability of plants, due to which plant growth reduces. This process is known as the salt-specific effect of salt stress (Greenway and Munns, 1980). Salt stress negatively affects the plant's growth, measured via different morphological and physiological parameters. Petretto *et al*. (2019) reported a significant reduction in various parameters in *Eruca sativa Mill.* and *Diplotax tenuifolia* L. under salinity stress. They recorded that shoot biomass, leaf area, and plant height were significantly decreased under saline conditions. Salinity stress also affects the germination process and decrease germination percentage, seedling root and shoot length, germination index, and seedling fresh and dry weight in sorghum plant (Rajabi Dehnavi *et al*., 2020).

EFFECT OF BRSs ON SEED GERMINATION UNDER SALINITY STRESS

Salinity stress affects a plant via disturbing water balance, ion homeostasis, and ion toxicity, leading to reduced plant growth. Salinity negatively affects the germination process; with the enhancement in salt concentration in soil, germination percent decreases. Decreased germination percentage is reported under salinity stress conditions in *Oryza sativa* (Xu *et al*., 2011) and *Brassica juncea* (Ibrar *et al*., 2003). Salinity stress affects the osmotic balance among seeds and germination media, which changes the water absorption process of seeds (Ḵẖān *et al*., 2006). It is believed that alteration in the seed imbibition process alters the behavior of enzymes involved in nucleic acids metabolism (Gomes-Filho *et al*., 2008). Similar results were found in tomatoes (Kaveh *et al*., 2011). Seeds of *Brassica napus* also show decreased seed germination under high salt stress conditions (Bybordi, 2010).

Wang *et al*. (2011) conducted an experiment on cucum-

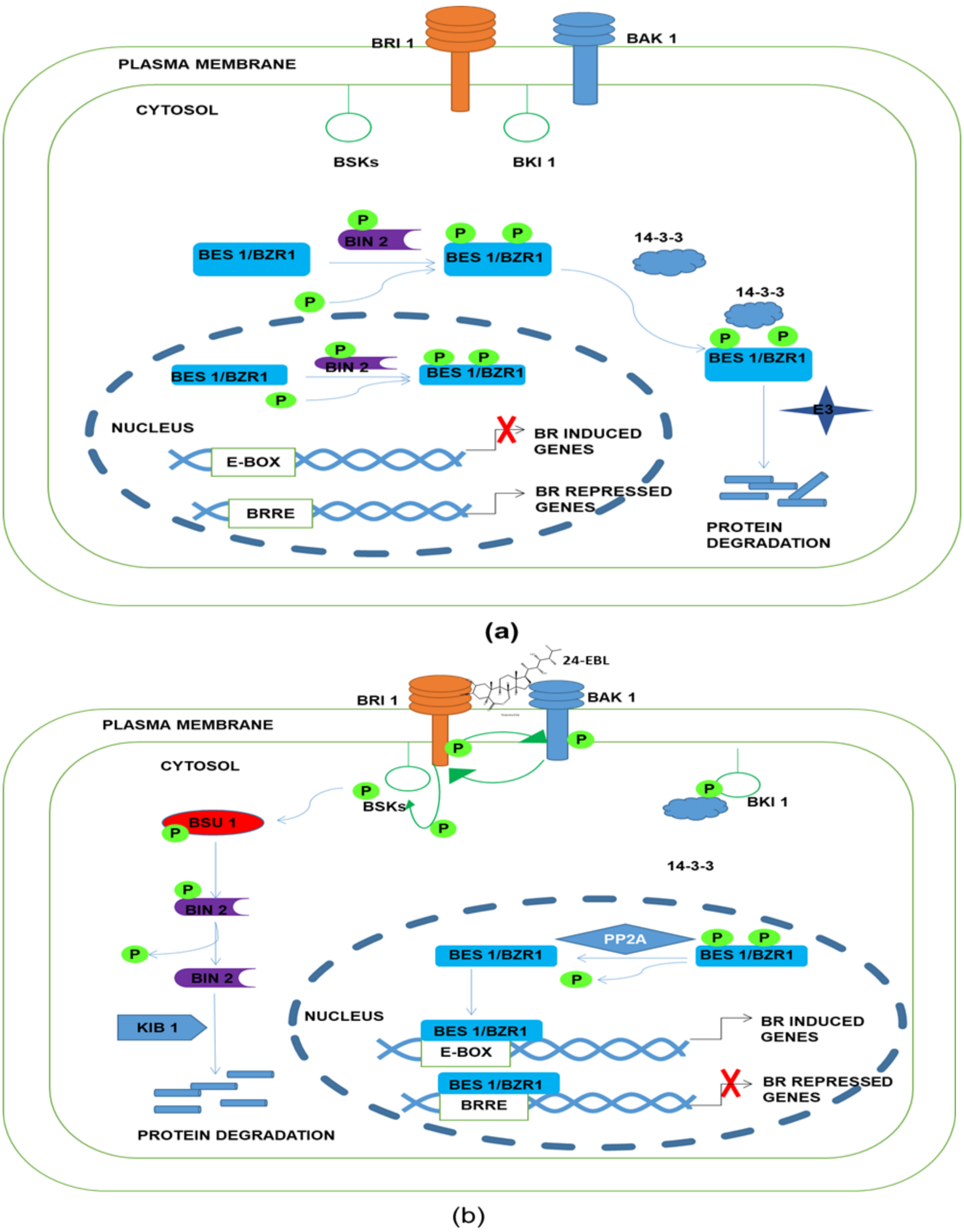

Fig. 2. *Brassinosteroid signaling pathway (a) without brassinosteroid (b) with brassinosteroid (Mao and Li, 2020). In the absence of 24-EBL, BES1/BZR1 protein undergoes degradation which results in repression of BR induced genes (a). In the presence of 24-EBL, BIN2 undergoes degradation and BES1/BZR1 bind to DNA and causes the expression of BR induced genes (b).*

bers to examine the role of BRS on seed germination under salinity stress and reported that BRSs ameliorate the harmful effects of salinity stress in cucumbers in the seed germination process. They further concluded that BRSs enhance seed germination by improving ethylene synthesis via enhancing the expression of *CsACO1 and CsACO2*. It is suggested that BRSs enhance the salt tolerance efficiency of plants by modulation of putrescine metabolism, which improves the germination process. It is reported that a proper concentration of BRS can improve the stress tolerance efficiency in plants. However, a high concentration of BRS can be harmful for plants similar to its deficiency (Liu *et al*., 2020).

EFFECT OF BRSs ON PLANT LENGTH UNDER SALINITY STRESS

Khodarahmpour *et al*. (2012) studied different growth parameters of *Zea mays* under salt stress conditions. At a high salt concentration (240mM NaCl), different growth parameters like length of plumule and radicles and seed vigor were observed. Similar results were also recorded in *Oenanthe javanica* (Kumar *et al*., 2021). They found a reduction in plant height, branches and leaves number, fresh and dry weight of root and shoot under increased salinity stress. Sensitive cultivars of coriander were more affected by salinity stress than tolerant cultivars (Meriem *et al*., 2014). It is believed that salinity stress results in osmotic stress in plants, disturbing the water balance and transport that ultimately affects different physiological and biochemical processes. Researchers believe that salt stress decreases the growth of plants because the energy produced in plants is diverted to maintain homeostasis (Atkin and Macherel, 2009; Sarker and Oba, 2020). During salt stress conditions, there is an elevation in the synthesis of reactive oxygen species (ROS) that disturbs the enzyme activity of cells. It also disturbs biomembrane stability, which results in reduced biomass (Ali *et al*., 2017; Alzahrani *et al*., 2019).

The harmful impacts of salinity on plant length can be alleviated with the application of epibrassinolide (EBL). EBL neutralizes the harmful impacts of saline conditions on length and biomass. It also improves the root and shoots length and number of roots (Sharma *et al*., 2013). Similar results were also recorded in *Medicago sativa* (Zhang *et al*., 2007) and *Zea mays* (Arora *et al.,* 2008). It is believed that in rice and Arabidopsis, plant height is controlled by the interaction between BRs and GAs. This interaction between BRs-GAs was found to be involved in regulating cell elongation. (Che *et al*., 2015; Sun *et al*., 2015). BZR1, a component of BRS signaling pathway, interacts with DELLA protein (negative regulator of GAs signalling) and forms a complex, which inhibits the DNA-binding ability of BZR1. On application of GA, DELLA proteins degrade, which causes the release of BZR1 and induces plant growth by improving the expression of genes whose product controls the cell elongation. (Bai *et al*., 2012; Gallego-Bartolome' *et al*., 2012; Li *et al*., 2012). It is reported that in BRS-related rice mutants, BRS application improved the level of GA. Further, it is observed that it also enhances the expression level of genes, which are involved in GA metabolism, like GA20ox-2/SD1 and GA3ox-2/D18 (Tong *et al*., 2014). BRS also improved the expression of the GA3ox-2 enzyme that converts the inactive form GA20 to the active form GA1. Expression of the GA2ox-3 gene is repressed by BRS, which is involved in GA inactivation, which indicates the positive involvement of BRS in plant growth (Castorina and Consonni, 2020).

EFFECT OF BRSs ON PLANT BIOMASS UNDER SALINITY STRESS

Biomass of a plant define by two major components, including root and shoot weight of the plant. In terms of growth parameters, plant biomass gives an idea about the level of severity of a stress condition. Foolad (2004) studied the impact of salinity on plants and reported that at lower salt stress conditions, plant growth reduces due to low availability of nutrients to plant, while at higher salinity, plant growth reduces due to different factors like ion imbalance, nutrient imbalance osmotic stress which disturbs the functioning of a plant at the cellular level. A significant reduction in the dry weight of root as well as of the shoot was observed in some selected rice varieties (Puvanitha and Mahendran, 2017). This reduction in dry weight may be due to high metabolic energy costs, which leads to decreased carbon content (Netondo *et al*., 2004). This decrease in dry weight is caused due to high ion toxicity that affects the nutrient uptake in the seedling (Datta *et al*., 2009).

A significant elevation in fresh weight of both root and shoot has been observed in Lucerne on priming the seeds with EBL (Zhang *et al*., 2007). It is reported that BRS application improves growth of plants by enhancing cell division and cell elongation in *Liriodendron tulipifera*. BRSs also modify the carbohydrate content of the cell wall, which depicts the positive role of BRSs in plant growth that are subjected to stress (Jin *et al*., 2014). There is an increase in shoot biomass in the wheat plant by applying BRS under salinity stress (Shahbaz and Ashraf, 2007). Similarly, BRS application also improves soybean biomass accumulation under salinity stress (Soliman *et al*., 2020). Sousa *et al*. (2021) reported that EBR spray-on salinity exposed tomato plant enhances the dry matter of different plant parts like root and shoot. According to Steffens (1991), BRSs affect plant growth by controlling the cell division and cell enlargement process. BRSs application also improves plant growth during zinc stress in radish plants (Ramakrishna and Rao, 2015) and in *Phaseolus vulgaris* L. under salinity and cadmium stress (Rady, 2011). BRs also reported enhancing cell division in parenchyma cells of *Helianthus tuberosus* (Clouse and Zurek, 1991). BRSs are known to be involved in wall loosening of epicotyl (Zurek *et al*., 1994) and hypocotyl of *Brassica chinensis* and *Cucurbita maxima* (Wang *et al*., 2001), which indicates the positive role of BRSs in maintaining plant biomass.

EFFECT OF BRSs ON PHOTOSYNTHETIC PIGMENTS UNDER SALINITY STRESS

Salinity has a negative effect on photosynthetic pigment, which ultimately affects the photosynthesis process. The major reason for photosynthesis inhibition via salinity is disturbed water potential (Betzen *et al*., 2019). It is believed that in salt stress conditions, there is an increased accumulation of Na^+/Cl^- in the chloroplast, which directly inhibits the photosynthesis process in plants (Slabu *et al*., 2009). Similar results were also observed in rice plants (Amirjani, 2011). They concluded that chlorophyll-b concentration was more affected as compared to chlorophyll-a. Saha *et al*. (2010) and Chutipaijit *et al*. (2011) also found a reduction in chlorophyll content under salt stress in *Vigna radiata* and *Oryza sativa,* respectively. It is reported that the decrease in chlorophyll content of sunflower under salinity is due to salinity-induced chlorophyll degradation or reduced synthesis of chlorophyll. Reduced production of 5-aminolaevulinic acid, which acts as a precursor of chlorophyll biosynthesis, ultimately leads to reduced chlorophyll synthesis (Santos, 2004; Parida *et al*., 2002). Fang *et al*. (1998) stated that during the process of chlorophyll degradation, there is a conversion of chlorophyll-a into chlorophyll-b. Reduction in chlorophyll content can also be linked with the increased ROS concentration, which leads to photosynthetic pigment oxidation. Enhanced activity of chlorophyllase also results in decreased chlorophyll content (Kato *et al*., 1985).

A decrease in photosynthetic pigment can be alleviated with the treatment of EBL by regulating the transcription as well as translational processes of photosynthetic pigment formation. EBL application also decreases the rate of chlorophyll degradation (Bajguz and Piotrowska-Niczyporuk, 2014; Honnerová *et al*., 2010). The use of BRSs improves the photosynthetic efficiency of plants via regulating the chlorophyll concentration and decreasing the ROS content to ameliorate the deleterious effects of salinity stress (Wu *et al*., 2017). EBL application also improved the chlorophyll content in *Pisum sativum* L. (Shahid *et al*., 2011) and *Brassica oleracea*e L. under salt stress (Çağ *et al*., 2007). Siddiqui *et al*. (2018) also reported the increase in chlorophyll content of *Brassica juncea* L. by treating the plants with 28-HBL and 24-EBL. Behnamnia *et al*. (2009a) suggested that BRS treatment improves the light-capturing efficiency of plant and enhances both the transcriptional and translational process of the enzymes involved in the chlorophyll biosynthesis. BRS shows a significant positive effect on the chlorophyll content including both chlorophylls a and b of *Robinia pseudoacacia* L. under salinity (Yue *et al*., 2019). BRs improve the chlorophyll content in *Brassica juncea* by enhancing the gene expression involved in the synthesis of enzymes, leading to chlorophyll synthesis (Hayat *et al*., 2007). It is also suggested that BRS improves the chlorophyll content via retarding the process of chlorophyll degradation and other proteins related to this protein primarily associated with the light-harvesting complex (Holá, 2011). However, the exact mechanism is still unknown, and a lot of study on this topic needs to be done.

EFFECT OF BRSs ON PHOTOSYNTHESIS UNDER SALINITY STRESS

Photosynthesis is the major physiological process that occurs in plants. This process indicates the physiological status of the plant. Out of these two photosystems, photosystem-II is considered more sensitive to salt stress (Allakhverdiev *et al*., 2000). Stepien and Klobus (2005) reported that reduced efficiency of photosystem-II under salt stress conditions, leading to reduced photosynthetic performance. This reduction in photosynthesis leads to decreased plant biomass production as well as storage (Demetriou *et al*., 2007). Salt stress alters the process of oxygen-evolving in barley by affecting the photosystem-II functioning and reducing plant growth (Kalaji *et al*., 2011). Similar results were also recorded in *Brassica juncea* (Mittal *et al*., 2012). They suggested that reduced photosynthetic activity is due to alteration in D1 protein of photosystem-II and rate of electron transport. It is also reported that during salt stress, there is a reduction in the ability of electron transfer in photosystem-II. During salinity stress conditions, alteration at both donor and acceptor side of photosystem-II occurs, resulting in decreased electron transport efficiency (Lu and Vonshak, 2002).

BRSs application enhances the photosynthetic rate of plants by enhancing the RuBisCo activity and other main enzymes included in the Calvin cycle (Yin *et al*., 2021). BRSs also improve the uptake of CO_2 that enhance the stomatal conductance (Siddiqui *et al*., 2018b). Fariduddin *et al*. (2014 a) and Yusuf *et al*. (2017) suggested that BRS application improved the formation and activity of RuBisCo enzyme, enhancing the gaseous exchange parameters under salinity stress. It promotes the photosynthetic efficiency in plants by improving the repair process of D1 protein and enhance its stabilization. BRs protect the plant from the damage resulting from the excess energy excitation in the reaction center. It is also suggested that EBL treatment increases the activity of different antioxidant enzymes like superoxide dismutase (SOD), ascorbate peroxidase (APX), and glutathione peroxidase (GPX), which reduces the concentration of ROS and protects the photosynthetic apparatus and synthesis of pre-D1 protein from the inhibitory effect of H_2O_2 (Xia *et al*., 2009). EBL also improves the expression of the different gene that encodes peroxidase, ATP24a, and ATP2 (Goda *et al*., 2002). Siddiqui *et al*. (2018c) informed that BRS regulates photosynthesis process via maintaining the development of stomatal and chloroplast structures. They further revealed that BRS regulates the photosynthesis process under stress as well as non-stress conditions. The efficiency of PSII (ϕPSII) indicates the overall photosynthesis state. It is reported to increase with the application of BRS (Yu et al., 2004; Jiang et al., 2012a; Hu et al *al*., 2013a, b; Li *et al*., 2016). BRS enhances the net photosynthetic rate by elevating the concentration of CO_2 assimilation and improving the stomatal conductance and RuBisCo activity (Gruszka, 2013).

EFFECT OF BRSs ON PROTEIN CONTENT UNDER SALINITY STRESS

Proteins are considered the major biomolecules globally and play a wide range of different functions in plants. They play both functional as well as structural roles in plants. Both positive and negative impacts of salinity stress on protein content have been recorded in various studies. A negative impact of salinity on different rice varieties has been reported which causes a significant loss of protein content in rice. Salt stress causes a great reduction in the water potential of plants which results in a decreased protein formation (Jamil *et al*., 2012). Along with it, salt stress also causes the dissociation of poly-ribosomal units ultimately leading to decreased protein content in plants (Bardzik *et al*., 1971; Jones, 1996). However, contrasting results were found in tomato (Chao *et al*., 1999) and clover plants (Sibole *et al*., 2003).

Rattan *et al*. (2012) studied the growth of maize (*Zea mays*) plants subjected to salinity stress and then treated these plants with BRS and observed that BRS mitigates the impacts of salinity via enhancing the level of protein concentration and different compatible solutes. Similar results were also reported in *Wolffia arrhiza*, which shows the positive role of BRSs in maintaining the accumulation and synthesis of protein. BRSs improve the protein content by enhancing the rate of translation that leads to enhanced protein formation (Chmur and Bajguz, 2021; Bajguz and Asami, 2005). Similarly, Bajguz and Piotrowska-Niczyporuk (2014) also reported the higher protein content in *Chlorella vulgaris on BRS treatment. According to them, BRS improve protein content by enhancing the expression of target genes.* BRSs increase the total soluble protein content in the rice by enhancing the Hill reaction efficiency, which leads to an increased accumulation of photosynthetic pigments (Maibangsa *et al*., 2000). Under stress conditions, BRS is reported to improve the activity of proteins and membrane-related enzymes via regulating the protein folding or by enhancing the interaction of proteins with sterols (Lindsey *et al*., 2003). However, contrast results were recorded in *Malus hupehensis*. It is documented that level of soluble protein content is elevated in *M. hupehensis* under salinity stress conditions significantly, but BRS application does not have any significant positive impact on protein content (Su *et al*., 2020).

EFFECT OF BRSs ON PROLINE CONTENT UNDER SALINITY STRESS

Proline is a common amino acid that acts as one of the major osmolytes. It is accumulated in plants under stress conditions and helps the plant maintain its osmotic status. High concentration levels of proline occur under saline conditions, which reflects the positive role of proline in stress conditions (Sharma *et al*., 2013). This increase in proline content, along with other organic molecules, prevents the cell from different toxic or inhibitory processes, including maintenance of turgidity of cells, providing enzyme stability, and regulating ROS activity (Szabados and Savouré, 2010). Proline also stabilizes the cell membrane and protein structure and helps regulate redox potential in plants (Ashraf and Orooj, 2006). Increased proline content in *Clerodendron inerme* was recorded under salinity stress conditions (Silambarasan and Natarajan, 2014). Similar results were also observed in rice (Demiral and Türkan, 2006), *Brassica juncea* (Madan *et al*., 1995). Different researchers have different views to justify increased content of proline under salinity stress. It is suggested that it could be due to the prevention of feedback inhibition of proline biosynthetic pathway (Widholm, 1988). It is also believed that increased proline content is due to decreased activity of proline degrading enzymes (Kandpal *et al*., 1981).

Zeng *et al*. (2010) observed that if there were a mutation in the BRSs synthetic pathway or its signaling pathway, plants would show increased sensitivity to salt stress. It is suggested to occur due to decreased transcriptional activity of proline-producing enzymes. This indicates the positive involvement of BRSs and proline in improving salinity tolerance.

An enhancement in proline content was also recorded by 24-EBL application in *Lycopersicum esculentum* cultivars under drought stress (Behnamnia *et al*., 2009b). 24-EBL treatment increases the proline content under salinity stress which defines the protective role of BRSs during salinity. It is suggested that BRSs increase proline content due to improved expression of proline biosynthesis (Özdemir *et al*., 2004). BRs treatment increases the proline content in cucumber, which helps the plant to mediate the adverse impact of autotoxicity stress by maintaining the cell membrane stability (Yang *et al*., 2019). Kutby *et al*. (2020) observed the increase in proline content in tomatoes under salinity stress which further increased under BRS application. According to them, proline aids the plants to alleviate the osmotic stress by reducing the uptake of toxic ions (Hayat *et al*., 2012). Wani *et al*. (2019) also observed the elevation in proline content via BRS application in mustard. Similar results were also recorded in cowpea under salinity stress (Cardoso *et al*., 2019). Elevation in proline content through BRS application was also observed in soybean under salt stress (Alam *et al*., 2019).

EFFECT OF BRSs ON MDA CONTENT UNDER SALINITY STRESS

Lipid peroxidation is believed to be the major process, which defines the metabolic state of membranes. It gives an idea of the overall status of membrane fluidity, membrane permeability, and separation of membrane protein that regulates the distribution of ions across the cell membrane. Malondialdehyde (MDA) content represents the status of the extent of lipid peroxidation in a plant. MDA content in sunflower was reported to be elevated under salt stress conditions, which shows the negative impact of salinity on membrane (Ebrahimian and Bybordi, 2012). Under the salinity stress conditions, there is an increased concentration of ROS, which leads to lipid peroxidation and increases the MDA content of plants. However, after the application of EBL, a decline in the level of MDA was observed. This signifies that under salinity stress conditions, treatment of EBL increases the activity of antioxidant enzymes, which reduces the ROS content and prevents lipid peroxidation (Ahammed *et al*., 2013). EBL application also helps to maintain membrane integrity by regulating the MDA content of the cell, which prevents the cell membrane from being damaged (Sharma *et al*. 2013). Rajewska *et al*. (2016) believed that BRs treatment helps the plant in the adjustment of cell redox potential via maintaining the lipid peroxidation level in the cell membrane by BRs. It is reported that both endogenous and exogenous BRs protect the plant from oxidative stress by improving the stress tolerance efficiency of maize plants. Further, it is found that *vp14* gene is an important gene involved in the abscisic acid (ABA) biosynthesis pathway and BRs upregulate this gene expression in the leaves of maize plants. This indicates that BRs enhance the stress tolerance to oxidative stress by maintaining the synthesis of ABA (Zhang *et al*., 2011). A decline in MDA content in EBL and HBL treated maize plants was observed under salinity stress (Rattan *et al*., 2020). This reduction in MDA content involves the enhanced scavenging of ROS, which decreases the membrane damage due to lipid peroxidation (Tanveer *et al*., 2018). Amraee *et al*. (2020) observed the NaCl treatment causes an increase in MDA content in tolerant variety of flax, whereas no significant change was recorded in sensitive varieties. However, BRS application declines the total MDA content in both tolerant and sensitive varieties. Similar results were also recorded in potatoes through BRS priming subjected to salinity stress which indicates the positive role of BRS in metigating the negative impact of salt stress on lipid peroxidation level (Efimova *et al*., 2018). Yue *et al*. (2018) also reported that pretreatment of BRS declines the MDA content in *Robinia pseudoacacia* L. under salinity stress.

EFFECT OF BRSs ON ANTIOXIDANT ENZYMES UNDER SALINITY STRESS

All plants produce different ROS via various metabolic processes. To protect the excess ROS accumulation, these plants produce different antioxidant enzymes like catalase (CAT), SOD, peroxidase (POD), etc. (Foyer *et al*., 1994). Enhanced level of antioxidant enzymes has been reported in many plants like maize and wheat (Lewis *et al*., 1989), rice (Fadzilla *et al*., 1997), and *Catharanthus roseus* (Misra and Gupta, 2006) in response to salinity stress. To increase the salt tolerance of a plant, it is necessary that the formation and scavenging of ROS must be regulated in the chloroplast (Miller *et al*., 2010). BRSs enhance the activities of various antioxidant enzymes that help the plant to diminish the harmful effect of accumulated ROS, which ultimately improve their stress tolerance efficiency (Vázquez *et al*., 2019). BL has been reported to mitigate the harmful effects of salinity stress in maize plants by improving the activity of antioxidant enzymes (El-Khallal *et al*., 2009). 28-HBL improves the activity of different antioxidant enzymes under salt conditions (Arora *et al*., 2008). Vardhini (2011) also reported similar results in sorghum. Along with the enhanced activity of glutathione reductase (GR), SOD, and CAT, they also observed the declined activity of two other antioxidant enzymes, named POD and polyphenol oxidase (PPO). Exogenous application of BRs increases the activity of antioxidant enzymes, leading to improved stress tolerance efficiency and increasing the accumulation of proline and sugar (Qingmao *et al*., 2006). Similar results were also obtained by pre-treating the seeds with BL sowing (Zhang *et al*., 2007). The application of BRs enhances the storage of apoplastic hydrogen peroxide (H_2O_2), which improves the antioxidant system of the plant and leads to enhanced tolerance efficiency of plant species to oxidative stress (Jiang *et al*., 2012b; Fariduddin *et al*., 2014b). Sharma *et al*. (2013) also observed similar results and found that EBL treatment increases the overall activity of different antioxidant enzymes like SOD, CAT and APX except for GR and monodehydroascorbate reductase (MDHAR), which indicates the significant role of EBL in controlling the level of ROS activity. Similar results were also obtained in cucumber (Xiao-min and Wei, 2013), eggplant (Ding *et al*., 2012), and *Lycopersicon esculentum* (Ogweno *et al*., 2008). Application of 24-EBL increases the expression of *osBRI1* and *OsDWF4* in the plants, which are involved in BRS receptor and BRS biosynthesis, respectively, which ultimately leads to improved activity of antioxidant enzymes (Sharma *et al*., 2013).

Jiang *et al*. (2012c) also believed that the stress tolerance induced via BRS application is facilitated through enhanced expression of different antioxidant enzymes. This stress tolerance mechanism is facilitated by increased synthesis and storage of H_2O_2, which acts as a signaling molecule. This enhanced concentration of H_2O_2 improves the activity of antioxidant enzymes, proteins and different transcription factors that improve the ROS scavenging activity at the cellular level and ultimately leads to enhancing the efficiency of plants to tolerate the harmful effects of abiotic stress (Xia *et al*., 2009; Cui *et al*., 2011; Zhu *et al*., 2013). Nie *et al*. (2013) studied the role of BRSs in H_2O_2 accumulation in tomatoes and in improving stress tolerance in plants. It suggested role of *respiratory burst oxidase homolog1* (RBOH1), and mitogen-activated protein kinase 1/2 (MPK 1/2) in the accumulation of H_2O_2 in the apoplast. They reveal that MPK2 plays a more significant role in its H2O2 accumulation than MPK1. When the activity of RBOH1 is silenced in *Nicotiana benthamiana*, it is observed that ROS scavenging activity is reduced which leads to decreased stress tolerance efficiency of the plant (Deng *et al*., 2015). BRS application also improves the activity of antioxidant enzymes like CAT, SOD, APX and POX in *Eucalyptus urophylla* plants that are subjected to salinity (Oliveira *et al*., 2019). Singh *et al*. (2020) observed that different antioxidant enzymes like CAT, SOD, and others increased under salinity stress conditions which were further elevated by the application of EBL. It is documented that application of 28-HBL improves the stress tolerance efficiency in *Brassica juncea* via improving the ROS scavenging activity of different antioxidant enzymes (Kaur *et al*., 2018).

EFFECT OF BRSs ON ION HOMEOSTASIS UNDER SALINITY STRESS

An appropriate ratio of ions is necessary for the normal growth and development of plant (Wang *et al*., 2003). It is suggested that enhanced absorption of ions Na^+ and Cl^- reduced the uptake of other nutrients like nitrogen, which are important for the proper growth of plants (Zhu, 2001). Along with this, there are also many other harmful effects of sodium accumulation in plants like disturbed membrane stability as well as also membrane structure (Kurth *et al*. 1986). Khan *et al*. (2000) recorded effect of salinity on *Atriplex griffithii* and suggested that with the increase of salinity, there is an elevation in the level of Na^+ and Cl^- in root, stem and leaves. On the other hand, a reduction in the level of Ca^{2+} and Mg^{2+} concentration is observed in stems and leaves. High concentration of Cl^- is the primary reason for the reduced growth of plants. A decrease in the photosynthetic efficiency of plants is observed due to elevated levels of Na^+ because it reduces the stomatal conductance of leaves by reducing the uptake of Ca^+ and K^+. In contrary to Na^+, a higher concentration of Cl^- inhibits photosynthesis by degrading chlorophyll molecules (Tavakkoli *et al*., 2011).

In a study, when canola plant was grown under salt stress with the application of BRSs, it is found that BRSs helps the plants to maintain the osmotic potential in leaves and also regulates the level of different ions which helps the canola plant to attain ionic homeostasis (Liu *et al*., 2014). Application of HBL and EBL under salinity maintains ionic balance in seedlings by reducing the concentration of Na^+ and restoring the level of K^+ (Rattan *et al*., 2020). It is believed that BRS application maintains the ionic homeostasis in plants by decreasing the transportation of Na^+ (Eleiwa *et al*., 2011). Exogenous application of 24-EBL enhances the activity of nitrate reductase, nitrite reductase, glutamine synthase and glutamate synthase, which helps to maintain the ionic balance in tomato seedlings. Further, BRSs treatment also maintains the electrochemical gradient in root and leaves of plant, which help the plants alleviate the stress conditions (Shu *et al*., 2016). Talaat and Shawky (2013) observed that BRS application in wheat plant under salinity stress conditions maintain the ionic balance in plant cell by regulating the uptake of different ions like Na^+, K^+, Ca^{2+}, Mg^{2+}, N and P. BRSs enhances the uptake of all ions except Na^+. They also observe the elevation in the organic content of plant by BRSs application. A positive co-relation is reported between Ca^{2+} and Calcium/calmodulin-dependent protein kinase (CCaMK) under BRSs treatment in plants. An increase in Ca^{2+} concentration is observed during BRS treatment, which enhances the activity of CCaMK. They also revealed that this increased activity of CCaMK

Table 1. Regulation of different genes and transcriptional factors with the application of BRs.

Gene/Transcriptional factors	Plant	Response	Effect of EBL	Reference
MhSOS1	*Malus hupehensis*	Maintaining cytoplasmic Na^+ concentration	Increasing gene expression	Su *et al*., (2020)
MhNHX1-3, *MhNHX4-1*, *MhNHX4-2*	*Malus hupehensis*	Maintaining cytoplasmic K^+ concentration	Increasing gene expression	Su *et al*., (2020)
CsAOX, CsACO1, CsACO2, CsACS1, CsACS2 CsACS3	*Cucumis sativus*, tomato	Enhance salt tolerance	Increase gene expression	Li *et al*., (2013), Zhu *et al*., (2016)
ERF115 PSK5	Arabidopsis	Enhance quiescent cell division	Regulate gene expression	Yang et al., (2001), Kutschmart et al., (2009), Heyman et al., (2013), Wei & Li (2016)

further increases the concentration of Ca^{2+} in the cytosol (Yan *et al*., 2015). Otie *et al*. (2021) reported that an exogenous application of BL improves the uptake of different ions like K^+, Ca^{2+}, and Mg^{2+} in soybean plants subjected to salinity stress. They also recorded that BL application reduces the concentration of Na^+ in the soybean leaves. It is observed that BL application under salinity stress causes the modification of plasma membrane, enhancing the plant's ability to uptake and assimilate the different nutrients (Ali *et al*., 2008). Various reports suggested that BL reverses the negative impact of NaCl on K^+ leakage in the root and shoot region of the plant (Azhar *et al*., 2017). BL treatment also alleviates the Na^+ toxicity by maintaining the K^+/Na^+ ratio (Dong *et al*., 2017).

Conclusion

The review clearly shows that salinity has a great negative effect on crop plants. Salinity stress is one of the most common abiotic stress that affects crop production in the soil. The physiological and biochemical processes in plants are badly affected by the increased concentration of salinity. Various approaches have been developed to counter the negative impact of salinity until now, but the situation is almost the same. So, there is a great need for attention to sustainable agricultural production. BRS is the most important plant hormone in relation to various stresses. BRS help the plant to alleviate the harmful salt stress and provide tolerance to the particular stress. It also enhances the antioxidant enzyme activities and regulates the ROS formation in the plant cell under salt stress conditions. BRSs act as a signaling molecule in the plant during stress conditions and activate all the defense mechanisms to face the stressed condition. The BRSs response in plants activates various enzymes involved in the defense mechanism. With the application of BRSs, plants gain much resistance to cope with the stress and improve their processes under salinity. BRSs play a great role in the improvement in yield production under salinity. There has been much research on the molecular level of BRS under salinity but there is a lack of proper mechanism and a better understanding of how it reduces salt stress in plants. Much research is needed to clearly understand its mechanism in salt stress alleviation.

Conflict of interest

The authors declare that they have no conflict of interest.

REFERENCES

1. Ahammed, G. J., Choudhary, S. P., Chen, S., Xia, X., Shi, K., Zhou, Y. & Yu, J. (2013). Role of brassinosteroids in alleviation of phenanthrene–cadmium co-contamination-induced photosynthetic inhibition and oxidative stress in tomato. *Journal of Experimental Botany*, *64*(1), 199-213. DOI: 10.1093/jxb/ers323
2. Ahanger, M. A., Mir, R. A., Alyemeni, M. N. & Ahmad, P. (2020). Combined effects of brassinosteroid and kinetin mitigates salinity stress in tomato through the modulation of antioxidant and osmolyte metabolism. *Plant Physiology and Biochemistry*, *147*, 31-42. DOI: 10.1016/j.plaphy.2019.12.007
3. Alam, P., Albalawi, T.H., Altalayan, F.H., Bakht, M.A., Ahanger, M.A., Raja, V., Ashraf, M. & Ahmad, P. (2019). 24-Epibrassinolide (EBR) confers tolerance against NaCl stress in soybean plants by up-regulating antioxidant system, ascorbate-glutathione cycle, and glyoxalase system. *Biomolecules*, *9*(11), 640. DOI: 10.3390/biom9110640
4. Ali, B., Hayat, S., Fariduddin, Q., & Ahmad, A. (2008). 24-

Epibrassinolide protects against the stress generated by salinity and nickel in Brassica juncea. *Chemosphere*, *72* (9), 1387-1392. DOI: 10.1016/j.chemosphere.2008.04.012

5. Ali, Q., Daud, M.K., Haider, M.Z., Ali, S., Rizwan, M., Aslam, N., Noman, A., Iqbal, N., Shahzad, F., Deeba, F. & Ali, I. (2017). Seed priming by sodium nitroprusside improves salt tolerance in wheat (Triticum aestivum L.) by enhancing physiological and biochemical parameters. *Plant Physiology and Biochemistry*, *119*, 50-58. DOI: 10.1016/j.plaphy.2017.08.010
6. Allakhverdiev, S. I., Sakamoto, A., Nishiyama, Y., Inaba, M. & Murata, N. (2000). Ionic and osmotic effects of NaCl-induced inactivation of photosystems I and II in Synechococcus sp. *Plant physiology*, *123*(3), 1047-1056. DOI: 10.1104/pp.123.3.1047
7. Alzahrani, S. M., Alaraidh, I. A., Migdadi, H., Alghamdi, S., Khan, M. A. & Ahmad, P. (2019). Physiological, biochemical, and antioxidant properties of two genotypes of Vicia faba grown under salinity stress. *Pakistan Journal of Botany, 51*(3), 786-798. DOI: 10.30848/pjb2019-3(3)
8. Amirjani, M. R. (2011). Effect of salinity stress on growth, sugar content, pigments and enzyme activity of rice. *International Journal of Botany*, *7*(1), 73-81. DOI: 10.3923/ijb.2011.73.81
9. Amraee, L., Rahmani, F. & Mandoulakani, B. A. (2020). Exogenous application of 24-epibrassinosteroid mitigates NaCl toxicity in flax by modifying free amino acids profile and antioxidant defence system. *Functional Plant Biology*, *47*(6), 565-575. DOI: 10.1071/FP19191
10. Arora, N., Bhardwaj, R., Sharma, P. & Arora, H. K. (2008). Effects of 28-homobrassinolide on growth, lipid peroxidation and antioxidative enzyme activities in seedlings of Zea mays L. under salinity stress. *Acta Physiologiae Plantarum*, *30*(6), 833-839. DOI: 10.3923/ajps.2007.765.772
11. Arora, S., & Sharma, V. (2017). Reclamation and management of salt-affected soils for safeguarding agricultural productivity. *Journal of Safe Agriculture*, *1*(1), 1-10.
12. Arora, S., Singh, Y. P., Vanza, M. & Sahni, D. (2016). Bioremediation of saline and sodic soils through halophilic bacteria to enhance agricultural production. *Journal of Soil and Water Conservation*, *15*(4), 302-305. DOI:10.5958/2455-7145.2016.00027.8
13. Asami, T., Min, Y.K., Nagata, N., Yamagishi, K., Takatsuto, S., Fujioka, S., Murofushi, N., Yamaguchi, I. & Yoshida, S. (2000). Characterization of brassinazole, a triazole-type brassinosteroid biosynthesis inhibitor. *Plant physiology*, *123*(1), 93-100. DOI: 10.1104/pp.123.1.93
14. Ashraf, M. & Orooj, A. (2006). Salt stress effects on growth, ion accumulation and seed oil concentration in an arid zone traditional medicinal plant ajwain (Trachyspermum ammi [L.] Sprague). *Journal of Arid Environments*, *64*(2), 209-220. https://doi.org/10.1016/j.jaridenv.2005.04.015
15. Atkin, O. K. & Macherel, D. (2009). The crucial role of plant mitochondria in orchestrating drought tolerance. *Annals of botany*, *103*(4), 581-597. DOI: 10.1093/aob/mcn094
16. Azhar, N., Su, N., Shabala, L., & Shabala, S. (2017). Exogenously applied 24-epibrassinolide (EBL) ameliorates detrimental effects of salinity by reducing K+ efflux via depolarization-activated K+ channels. *Plant and Cell Physiology*, *58*(4), 802-810. DOI: 10.1093/pcp/pcx026
17. Bai, M.Y., Shang, J.X., Oh, E., Fan, M., Bai, Y., Zentella, R., Sun, T.P. & Wang, Z.Y. (2012). Brassinosteroid, gibberellin and phytochrome impinge on a common transcription module in Arabidopsis. *Nature cell biology*, *14*(8), 810-817. DOI: 10.1038/ncb2546
18. Bajguz, A. & Asami, T. (2005). Suppression of Wolffia arrhiza growth by brassinazole, an inhibitor of brassinosteroid biosynthesis and its restoration by endogenous 24-epibrassinolide. *Phytochemistry*, *66*(15), 1787-1796. DOI: 10.1016/j.phytochem.2005.06.005
19. Bajguz, A. & Piotrowska-Niczyporuk, A. (2014). Interactive effect of brassinosteroids and cytokinins on growth, chlorophyll, monosaccharide and protein content in the green alga Chlorella vulgaris (Trebouxiophyceae). *Plant Physiology and Biochemistry*, *80*, 176-183. DOI: 10.1016/j.plaphy.2014.04.009
20. Bardzik, J. M., Marsh Jr, H. V. & Havis, J. R. (1971). Effects of water stress on the activities of three enzymes in maize seedlings. *Plant Physiology*, *47*(6), 828-831. DOI: 10.1104/pp.47.6.828
21. Behnamnia, M., Kalantari, K. M. & Ziaie, J. (2009a). The effects of brassinosteroid on the induction of biochemical changes in Lycopersicon esculentum under drought stress. *Turkish Journal of Botany*, *33*(6), 417-428. DOI:10.3906/bot-0806-12
22. Behnamnia, M., Kalantari, K. M. & Rezanejad, F. (2009b) Exogenous application of brassinosteroid alleviates drought-induced oxidative stress in *Lycopersicon esculentum* L. *General and Applied Plant Physiology*, *35*, 22–34
23. Betzen, B. M., Smart, C. M., Maricle, K. L. & MariCle, B. R. (2019). Effects of increasing salinity on photosynthesis and plant water potential in Kansas salt marsh species. *Transactions of the Kansas Academy of Science*, *122*(1-2), 49-58. DOI:10.1660/062.122.0105
24. Bybordi, A. (2010). The influence of salt stress on seed germination, growth and yield of canola cultivars. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, *38*(1), 128-133. https://doi.org/10.15835/nbha3813572
25. Çağ, S., Gören-Sağlam, N., Çıngıl-Barış, Ç. & Kaplan, E. (2007). The effect of different concentration of epibrassinolide on chlorophyll, protein and anthocyanin content and peroxidase activity in excised red cabbage (Brassica oleraceae L.) cotyledons. *Biotechnology & Biotechnological Equipment*, *21*(4), 422-425. https://doi.org/10.1080/13102818.2007.10817487
26. Camoni, L., Visconti, S., Aducci, P. & Marra, M. (2018). 14-3-3 proteins in plant hormone signaling: doing several things at once. *Frontiers in Plant Science*, *9*, 297. https://doi.org/10.3389/fpls.2018.00297
27. Cardoso, K.P.S., Silva Conceicao, S., de Araújo Brito, A.E., da Silva Martins, J.T., Machado, L.C., Correa Costa, T., dos Santos Nogueira, G.A., do Nascimento, V.R., da Silva, R.P.P., Costa Paiva, R. & Correa Barbosa, A.V. (2019). Biochemical metabolism of two cultivars of cowpea treated with 24-Epibrassinolide and subjected to saline stress. *Australian Journal of Crop Science*, *13*(3), 444-451.
28. Castorina, G. & Consonni, G. (2020). The role of brassinosteroids in controlling plant height in Poaceae: A genetic perspective. *International Journal of Molecular Sciences*, *21*(4), 1191. https://doi.org/10.3390/ijms21041191

29. Chao, W. S., Gu, Y. Q., Pautot, V., Bray, E. A. & Walling, L. L. (1999). Leucine aminopeptidase RNAs, proteins, and activities increase in response to water deficit, salinity, and the wound signals systemin, methyl jasmonate, and abscisic acid. *Plant Physiology*, *120*(4), 979-992. DOI: 10.1104/pp.120.4.979
30. Che, R., Tong, H., Shi, B., Liu, Y., Fang, S., Liu, D., Xiao, Y., Hu, B., Liu, L., Wang, H. & Zhao, M. (2015). Control of grain size and rice yield by GL2-mediated brassinosteroid responses. *Nature plants*, *2*(1), 1-8. DOI: 10.1038/ nplants.2015.195
31. Chmur, M. & Bajguz, A. (2021). Brassinolide Enhances the Level of Brassinosteroids, Protein, Pigments, and Monosaccharides in Wolffia arrhiza Treated with Brassinazole. *Plants*, *10*(7), 1311. https://doi.org/10.3390/ plants10071311
32. Chutipaijit, S., Cha-um, S. & Sompornpailin, K. (2011). High contents of proline and anthocyanin increase protective response to salinity in'Oryza sativa'L. spp.'indica'. *Australian Journal of Crop Science*, *5*(10), 1191-1198.
33. Clouse, S. D. & Zurek, D. (1991). Molecular analysis of brassinolide action in plant growth and development.
34. Cui, J.X., Zhou, Y.H., Ding, J.G., Xia, X.J., Shi, K.A.I., Chen, S.C., Asami, T., Chen, Z. & YU, J.Q. (2011). Role of nitric oxide in hydrogen peroxide□dependent induction of abiotic stress tolerance by brassinosteroids in cucumber. *Plant, Cell & Environment*, *34*(2), 347-358. DOI: 10.1111/j.1365-3040.2010.02248.x
35. Datta, J. K., Nag, S., Banerjee, A. & Mondai, N. K. (2009). Impact of salt stress on five varieties of Wheat (Triticum aestivum L.) cultivars under laboratory condition. *Journal of Applied Sciences and Environmental Management*, *13* (3). DOI: 10.4314/jasem.v13i3.55372
36. de Oliveira, V. P., Lima, M. D. R., da Silva, B. R. S., Batista, B. L. & da Silva Lobato, A. K. (2019). Brassinosteroids confer tolerance to salt stress in Eucalyptus urophylla plants enhancing homeostasis, antioxidant metabolism and leaf anatomy. *Journal of Plant Growth Regulation*, *38* (2), 557-573.
37. Demetriou, G., Neonaki, C., Navakoudis, E., & Kotzabasis, K. (2007). Salt stress impact on the molecular structure and function of the photosynthetic apparatus—the protective role of polyamines. *Biochimica et Biophysica Acta (BBA)-Bioenergetics*, *1767*(4), 272-280. DOI: 10.1016/j.bbabio.2007.02.020
38. Demiral, T. & Türkan, I. (2006). Exogenous glycinebetaine affects growth and proline accumulation and retards senescence in two rice cultivars under NaCl stress. *Environmental and Experimental Botany*, *56*(1), 72 -79. DOI: 10.1016/j.envexpbot.2005.01.005
39. Deng, X. G., Zhu, T., Zhang, D. W. & Lin, H. H. (2015). The alternative respiratory pathway is involved in brassinosteroid-induced environmental stress tolerance in Nicotiana benthamiana. *Journal of experimental botany*, *66* (20), 6219-6232. DOI: 10.1093/jxb/erv328
40. Díaz, S. H., Morejón, R. & Núñez, M. (2003). Effects of BIOBRAS-16 on rice (Oryza sativa L.) yield and other characters. *Cultivos Tropicales*, *24*(2), 35-40.
41. Ding, H. D., Zhu, X. H., Zhu, Z. W., Yang, S. J., Zha, D. S. & Wu, X. X. (2012). Amelioration of salt-induced oxidative stress in eggplant by application of 24-epibrassinolide. *Biologia plantarum*, *56*(4), 767-770. DOI: 10.1007/s10535-012-0108-0
42. Dong, Y., Wang, W., Hu, G., Chen, W., Zhuge, Y., Wang, Z., & He, M. R. (2017). Role of exogenous 24-epibrassinolide in enhancing the salt tolerance of wheat seedlings. *Journal of soil science and plant nutrition*, *17* (3), 554-569. DOI:10.4067/S0718-95162017000300001
43. Ebrahimian, E. & Bybordi, A. (2012). Effect of salinity, salicylic acid, silicium and ascorbic acid on lipid peroxidation, antioxidant enzyme activity and fatty acid content of sunflower. *African Journal of Agricultural Research*, *7*(25), 3685-3694. DOI: 10.5897// AJAR11.799
44. Efimova, M.V., Khripach, V.A., Boyko, E.V., Malofii, M.K., Kolomeichuk, L.V., Murgan, O.K., Vidershpun, A.N., Mukhamatdinova, E.A. & Kuznetsov, V.V. (2018). The priming of potato plants induced by brassinosteroids reduces oxidative stress and increases salt tolerance. In *Doklady Biological Sciences* (Vol. 478, (1),33-36. Pleiades Publishing. DOI: 10.1134/S0012496618010106
45. Eleiwa, M. E., Bafeel, S. O. & Ibrahim, S. A. (2011). Influence of brassinosteroids on wheat plant (Triticum aestivum L.) production under salinity stress conditions. I-Growth parameters and photosynthetic pigments. *Australian Journal of Basic and Applied Sciences*, *5*(5), 58-65.
46. El-Khallal, S. M., Hathout, T. A., Ahsour, A. E. R. A. & Kerrit, A. A. A. (2009). Brassinolide and salicylic acid induced antioxidant enzymes, hormonal balance and protein profile of maize plants grown under salt stress. *Research Journal of Agriculture and Biological Sciences*, *5*(4), 391-402.
47. Fàbregas, N., Lozano-Elena, F., Blasco-Escámez, D., Tohge, T., Martínez-Andújar, C., Albacete, A., Osorio, S., Bustamante, M., Riechmann, J.L., Nomura, T. & Yokota, T. (2018). Overexpression of the vascular brassinosteroid receptor BRL3 confers drought resistance without penalizing plant growth. *Nature communications*, *9*(1), 1-13. DOI: 10.1038/s41467-018-06861-3
48. Fadzilla, N. A. M., Finch, R. P. & Burdon, R. H. (1997). Salinity, oxidative stress and antioxidant responses in shoot cultures of rice. *Journal of Experimental Botany*, *48* (2), 325-331. DOI:10.1093/JXB/48.2.325
49. Fang, Z., Bouwkamp, J. C. & Solomos, T. (1998). Chlorophyllase activities and chlorophyll degradation during leaf senescence in non-yellowing mutant and wild type of Phaseolus vulgaris L. *Journal of Experimental Botany*, *49* (320), 503-510. http://dx.doi.org/10.1093/jxb/49.320.503
50. Fariduddin, Q., Mir, B. A., Yusuf, M. & Ahmad, A. (2014a). 24-epibrassinolide and/or putrescine trigger physiological and biochemical responses for the salt stress mitigation in Cucumis sativus L. *Photosynthetica*, *52*(3), 464-474. DOI: 10.1007/s11099-014-0052-7
51. Fariduddin, Q., Yusuf, M., Ahmad, I. & Ahmad, A. (2014b). Brassinosteroids and their role in response of plants to abiotic stresses. *Biologia Plantarum*, *58*(1), 9-17. DOI: 10.1007/s10535-013-0374-5
52. Foolad, M. R. (2004). Recent advances in genetics of salt tolerance in tomato. *Plant Cell, tissue and organ culture*, *76*(2), 101-119. DOI:10.1023/ B:TICU.0000007308.47608.88
53. Foyer, C. H., Lelandais, M. & Kunert, K. J. (1994). Photooxidative stress in plants. https://doi.org/10.1111/j.1399

-3054.1994.tb03042.x

54. Fujioka, S. (1999). Brassinosteroids: Steroidal plant hormones.
55. Fujioka, S., & Sakurai, A. (1997). Brassinosteroids. *Natural Product Reports*, *14*(1), 1-10. DOI: 10.1039/NP9971400001
56. Gallego-Bartolomé, J., Minguet, E.G., Grau-Enguix, F., Abbas, M., Locascio, A., Thomas, S.G., Alabadí, D. & Blázquez, M.A. (2012). Molecular mechanism for the interaction between gibberellin and brassinosteroid signaling pathways in Arabidopsis. *Proceedings of the National Academy of Sciences*, *109*(33), 13446-13451. DOI: 10.1073/pnas.1119992109
57. Gampala, S.S., Kim, T.W., He, J.X., Tang, W., Deng, Z., Bai, M.Y., Guan, S., Lalonde, S., Sun, Y., Gendron, J.M. & Chen, H. (2007). An essential role for 14-3-3 proteins in brassinosteroid signal transduction in Arabidopsis. *Developmental cell*, *13*(2), 177-189. DOI: 10.1016/j.devcel.2007.06.009
58. Goda, H., Shimada, Y., Asami, T., Fujioka, S. & Yoshida, S. (2002). Microarray analysis of brassinosteroid-regulated genes in Arabidopsis. *Plant physiology*, *130*(3), 1319-1334. DOI: 10.1104/pp.011254
59. Gomes-Filho, E., Lima, C. R. F. M., Costa, J. H., da Silva, A. C. M., da Guia Silva Lima, M., de Lacerda, C. F. & Prisco, J. T. (2008). Cowpea ribonuclease: properties and effect of NaCl-salinity on its activation during seed germination and seedling establishment. *Plant Cell Reports*, *27* (1), 147-157. DOI: 10.1007/s00299-007-0433-5
60. Greenway, H. & Munns, R. (1980). Mechanisms of salt tolerance in nonhalophytes. *Annual review of plant physiology*, *31*(1), 149-190. https://doi.org/10.1146/annurev.pp.31.060180.001053
61. Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The american naturalist*, *111* (982), 1169-1194. https://doi.org/10.1086/283244
62. Grove, M.D., Spencer, G.F., Rohwedder, W.K., Mandava, N., Worley, J.F., Warthen, J.D., Steffens, G.L., Flippen-Anderson, J.L. & Cook, J.C. (1979). Brassinolide, a plant growth-promoting steroid isolated from Brassica napus pollen. *Nature*, *281*(5728), 216-217.
63. Gruszka, D. (2013). The brassinosteroid signaling pathway—New key players and interconnections with other signaling networks crucial for plant development and stress tolerance. *International Journal of Molecular Sciences*, *14*(5), 8740-8774. DOI: 10.3390/ijms14058740
64. Hayat, S. & Ahmad, A. (Eds.). (2010). *Brassinosteroids: a class of plant hormone*. Springer Science & Business Media.
65. Hayat, S., Ali, B., Hasan, S. A. & Ahmad, A. (2007). Brassinosteroid enhanced the level of antioxidants under cadmium stress in Brassica juncea. Environmental *and Experimental Botany*, *60*(1), 33-41. DOI:10.1016/j.envexpbot.2006.06.002
66. Hayat, S., Hayat, Q., Alyemeni, M. N., Wani, A. S., Pichtel, J. & Ahmad, A. (2012). Role of proline under changing environments: a review. *Plant signaling & behavior*, *7*(11), 1456-1466. DOI: 10.4161/psb.21949
67. He, J. X., Gendron, J. M., Sun, Y., Gampala, S. S., Gendron, N., Sun, C. Q. & Wang, Z. Y. (2005). BZR1 is a transcriptional repressor with dual roles in brassinosteroid homeostasis and growth responses. *Science*, *307*(5715), 1634-1638. DOI: 10.1126/science.1107580
68. Heyman, J., Cools, T., Vandenbussche, F., Heyndrickx, K.S., Van Leene, J., Vercauteren, I., Vanderauwera, S., Vandepoele, K., De Jaeger, G., Van Der Straeten, D. & De Veylder, L., (2013). ERF115 controls root quiescent center cell division and stem cell replenishment. *Science*, *342*(6160), 860-863. DOI: 10.1126/science.1240667
69. Holá, D. (2011). Brassinosteroids and photosynthesis. In *Brassinosteroids: A class of plant hormone* (pp. 143-192). Springer, Dordrecht.
70. Honnerová, J., Rothová, O., Holá, D., Kočová, M., Kohout, L. & Kvasnica, M. (2010). The exogenous application of brassinosteroids to Zea mays (L.) stressed by long-term chilling does not affect the activities of photosystem 1 or 2. *Journal of Plant Growth Regulation*, *29*(4), 500-505. DOI:10.1007/s00344-010-9153-0
71. Houimli, S. I. M., Denden, M. & Mouhandes, B. D. (2010). Effects of 24-epibrassinolide on growth, chlorophyll, electrolyte leakage and proline by pepper plants under NaCl-stress. *EurAsian Journal of BioSciences*, *4*. DOI:10.5053/ejobios.2010.4.0.12
72. Hu, W. H., Yan, X. H., Xiao, Y. A., Zeng, J. J., Qi, H. J., & Ogweno, J. O. (2013a). 24-Epibrassinosteroid alleviate drought-induced inhibition of photosynthesis in Capsicum annuum. *Scientia Horticulturae*, *150*, 232-237. DOI : 10.1016/j.scienta.2012.11.012
73. Hu, Y. J., Shi, L. X., Sun, W. & Guo, J. X. (2013b). Effects of abscisic acid and brassinolide on photosynthetic characteristics of Leymus chinensis from Songnen Plain grassland in Northeast China. *Botanical Studies*, *54*(1), 1-9. DOI: 10.1186/1999-3110-54-42
74. Ibrar, M., Jabeen, M., Tabassum, J., Hussain, F. & Ilahi, I. (2003). Salt tolerance potential of Brassica juncea Linn. *Journal of Science and Technology (Peshawar)*, *27* (1-2), 79-84.
75. Jamil, M., Bashir, S., Anwar, S., Bibi, S., Bangash, A., Ullah, F., & Rha, E. S. (2012). Effect of salinity on physiological and biochemical characteristics of different varieties of rice. *Pakistan Journal of Botany*, *44*(1), 7-13.
76. Jiang, Y. P., Cheng, F., Zhou, Y. H., Xia, X. J., Shi, K. & Yu, J. Q. (2012a). Interactive effects of CO2 enrichment and brassinosteroid on CO2 assimilation and photosynthetic electron transport in Cucumis sativus. *Environmental and Experimental Botany*, *75*, 98-106. DOI: 10.1016/j.envexpbot.2011.09.002
77. Jiang, Y.P., Cheng, F., Zhou, Y.H., Xia, X.J., Mao, W.H., Shi, K., Chen, Z. & Yu, J.Q. (2012b). Cellular glutathione redox homeostasis plays an important role in the brassinosteroid□induced increase in CO2 assimilation in Cucumis sativus. *New Phytologist*, *194*(4), 932-943. DOI: 10.1111/j.1469-8137.2012.04111.x
78. Jiang, Y.P., Cheng, F., Zhou, Y.H., Xia, X.J., Mao, W.H., Shi, K., Chen, Z.X. & Yu, J.Q. (2012c). Hydrogen peroxide functions as a secondary messenger for brassinosteroids-induced CO2 assimilation and carbohydrate metabolism in Cucumis sativus. *Journal of Zhejiang University Science B*, *13*(10), 811-823. DOI: 10.1631/jzus.B1200130
79. Jin, H., Do, J., Shin, S. J., Choi, J. W., Im Choi, Y., Kim, W. & Kwon, M. (2014). Exogenously applied 24-epi brassinolide reduces lignification and alters cell wall car-

bohydrate biosynthesis in the secondary xylem of Liriodendron tulipifera. *Phytochemistry*, *101*, 40-51. DOI: 10.1016/j.phytochem.2014.02.003

80. Jones, G.H. 1996. Plants and microclimate. Cambridge USA. Ed. 2: 72-108.
81. Kalaji, H. M., Bosa, K., Kościelniak, J. & Żuk-Gołaszewska, K. (2011). Effects of salt stress on photosystem II efficiency and CO2 assimilation of two Syrian barley landraces. *Environmental and Experimental Botany*, *73*, 64-72.
82. Kandpal, R. P., Vaidyanathan, C. S., Kumar, M. U., Sastry, K. S. & Rao, N. A. (1981). Alterations in the activities of the enzymes of proline metabolism in Ragi (Eleusine coracana) leaves during water stress. *Journal of biosciences*, *3*(4), 361-370. http://dx.doi.org/10.1007/BF02702623
83. Kato, M., & Shimizu, S. (1985). Chlorophyll metabolism in higher plants VI. Involvement of peroxidase in chlorophyll degradation. *Plant and cell physiology*, *26*(7), 1291-1301. https://doi.org/10.1093/oxfordjournals.pcp.a077029
84. Kaur, H., Sirhindi, G., Bhardwaj, R., Alyemeni, M. N., Siddique, K. H. & Ahmad, P. (2018). 28-homobrassinolide regulates antioxidant enzyme activities and gene expression in response to salt-and temperature-induced oxidative stress in Brassica juncea. *Scientific Reports*, *8*(1), 1-13. DOI: 10.1038/s41598-018-27032-w
85. Kaveh, H., Nemati, H., Farsi, M. & Jartoodeh, S. V. (2011). How salinity affect germination and emergence of tomato lines. *Journal* of *Biological* & *Environmental* Sciences, *5*(15), 159-163.
86. Ḵẖān, M. A., Khan, M. A. & Weber, D. J. (Eds.). (2006). *Ecophysiology of high salinity tolerant plants* (Vol. 40). Springer Science & Business Media.
87. Khan, M. A., Ungar, I. A. & Showalter, A. M. (2000). Effects of salinity on growth, water relations and ion accumulation of the subtropical perennial halophyte, Atriplex griffithii var. stocksii. *Annals of Botany*, *85*(2), 225-232. https://doi.org/10.1006/anbo.1999.1022
88. Kim, B. H., Kim, S. Y. & Nam, K. H. (2012). Genes encoding plant-specific class III peroxidases are responsible for increased cold tolerance of the brassinosteroid-insensitive 1 mutant. *Molecules and cells*, *34*(6), 539-548. DOI: 10.1007/s10059-012-0230-z
89. Kulaeva, O. N., Burkhanova, E. A., Fedina, A. B., Khokhlova, V. A., Bokebayeva, G. A., Vorbrodt, H. M. & Adam, G. (1991). Effect of brassinosteroids on protein synthesis and plant-cell ultrastructure under stress conditions. DOI: 10.1021/bk-1991-0474.ch012
90. Kumar, S., Li, G., Yang, J., Huang, X., Ji, Q., Liu, Z., Ke, W. & Hou, H. (2021). Effect of salt stress on growth, physiological parameters, and ionic concentration of water dropwort (Oenanthe javanica) cultivars. *Frontiers in plant science*, *12*. https://doi.org/10.3389/fpls.2021.660409
91. Kurth, E., Cramer, G. R., Läuchli, A. & Epstein, E. (1986). Effects of NaCl and CaCl2 on cell enlargement and cell production in cotton roots. *Plant Physiology*, *82*(4), 1102-1106. DOI: 10.1104/pp.82.4.1102
92. Kutby, A. M., Al-Zahrani, H. S., & Hakeem, K. R. Role of Magnetic Field and Brassinosteroids in Mitigating Salinity Stress in Tomato (Lycopersicon Esculentum L.).
93. Kutschmar, A., Rzewuski, G., Stührwohldt, N., Beemster, G. T., Inzé, D. & Sauter, M. (2009). PSK□α promotes root growth in Arabidopsis. *New Phytologist*, *181*(4), 820-831. DOI: 10.1111/j.1469-8137.2008.02710.x
94. Lewis, O. A. M., Leidi, E. O. & Lips, S. H. (1989). Effect of nitrogen source on growth response to salinity stress in maize and wheat. *New Phytologist*, *111*(2), 155-160. DOI: 10.1111/j.1469-8137.1989.tb00676.x
95. Li, J. & Nam, K. H. (2002). Regulation of brassinosteroid signaling by a GSK3/SHAGGY-like kinase. *Science*, *295* (5558), 1299-1301. DOI: 10.1126/science.1065769
96. Li, P. Chen, L., Zhou, Y., Xia, X., Shi, K., Chen, Z., & Yu, J. (2013). Brassinosteroids-induced systemic stress tolerance was associated with increased transcripts of several defence-related genes in the phloem in Cucumis sativus. *PLoS One*, *8*(6), e66582. https://doi.org/10.1371/journal.pone.0066582
97. Li, Q. F., Wang, C., Jiang, L., Li, S., Sun, S. S. & He, J. X. (2012). An interaction between BZR1 and DELLAs mediates direct signaling crosstalk between brassinosteroids and gibberellins in Arabidopsis. *Science signaling*, *5*(244), ra72-ra72. DOI: 10.1126/scisignal.2002908
98. Li, X. J., Guo, X., Zhou, Y. H., Shi, K., Zhou, J., Yu, J. Q. & Xia, X. J. (2016). Overexpression of a brassinosteroid biosynthetic gene Dwarf enhances photosynthetic capacity through activation of Calvin cycle enzymes in tomato. *BMC plant biology*, *16*(1), 1-12. DOI:10.1186/s12870-016-0715-6
99. Lima, J. V. & Lobato, A. K. S. (2017). Brassinosteroids improve photosystem II efficiency, gas exchange, antioxidant enzymes and growth of cowpea plants exposed to water deficit. *Physiology and Molecular Biology of Plants*, *23*(1), 59-72. DOI: 10.1007/s12298-016-0410-y
100. Lindsey, K., Pullen, M. L. & Topping, J. F. (2003). Importance of plant sterols in pattern formation and hormone signalling. *Trends in plant science*, *8*(11), 521-525. DOI: 10.1016/j.tplants.2003.09.012
101. Liu, J., Gao, H., Wang, X., Zheng, Q., Wang, C., Wang, X., & Wang, Q. (2014). Effects of 24□epibrassinolide on plant growth, osmotic regulation and ion homeostasis of salt□stressed canola. *Plant biology*, *16*(2), 440-450. DOI: 10.1111/plb.12052
102. Liu, J., Yang, R., Jian, N., Wei, L., Ye, L., Wang, R., Gao, H. & Zheng, Q. (2020). Putrescine metabolism modulates the biphasic effects of brassinosteroids on canola and Arabidopsis salt tolerance. *Plant, Cell & Environment*, *43* (6), 1348-1359. DOI: 10.1111/pce.13757
103. Liu, J., Zhang, D., Sun, X., Ding, T., Lei, B. & Zhang, C. (2017). Structure-activity relationship of brassinosteroids and their agricultural practical usages. *Steroids*, *124*, 1-17. DOI: 10.1016/j.steroids.2017.05.005
104. Lu, C. & Vonshak, A. (2002). Effects of salinity stress on photosystem II function in cyanobacterial Spirulina platensis cells. *Physiologia plantarum*, *114*(3), 405-413. DOI: 10.1034/j.1399-3054.2002.1140310.x
105. Madan, S., Nainawatee, H. S., Jain, R. K. & Chowdhury, J. B. (1995). Proline and proline metabolising enzymes in in-vitro selected NaCl-tolerant Brassica juncea L. under salt stress. *Annals of Botany*, *76*(1), 51-57. https://doi.org/10.1006/anbo.1995.1077
106.
107. Maibangsa, S., Thangaraj, M., & Stephen, R. (2000). Effect of brassinosteroid and salicylic acid on rice (Oryza

sativa L.) grown under low irradiance condtion. *Indian Journal of Agricultural Research*, *34*(4), 258-260.

108.Mao, J. & Li, J. (2020). Regulation of Three Key Kinases of Brassinosteroid Signaling Pathway. *International Journal of Molecular Sciences*, *21*(12), 4340. https://doi.org/10.3390/ijms21124340

109.Meriem, B. F., Kaouther, Z., Chérif, H., Tijani, M. & André, B. (2014). Effect of priming on growth, biochemical parameters and mineral composition of different cultivars of coriander (Coriandrum sativum L.) under salt stress. *Journal of Stress Physiology & Biochemistry*, *10* (3), 84-109.

110.Miller, G. A. D., Suzuki, N., Ciftci□Yilmaz, S. U. L. T. A. N., & Mittler, R. O. N. (2010). Reactive oxygen species homeostasis and signalling during drought and salinity stresses. *Plant, cell & environment*, *33*(4), 453-467. DOI: 10.1111/j.1365-3040.2009.02041.x

111.Misra, N. & Gupta, A. K. (2006). Effect of salinity and different nitrogen sources on the activity of antioxidant enzymes and indole alkaloid content in Catharanthus roseus seedlings. *Journal of plant physiology*, *163*(1), 11-18. DOI: 10.1016/j.jplph.2005.02.011

112.Mittal, S., Kumari, N. & Sharma, V. (2012). Differential response of salt stress on Brassica juncea: photosynthetic performance, pigment, proline, D1 and antioxidant enzymes. *Plant Physiology and Biochemistry*, *54*, 17-26. DOI: 10.1016/j.plaphy.2012.02.003

113.Mora-García, S., Vert, G., Yin, Y., Caño-Delgado, A., Cheong, H. & Chory, J. (2004). Nuclear protein phosphatases with Kelch-repeat domains modulate the response to brassinosteroids in Arabidopsis. *Genes & development*, *18*(4), 448-460. DOI: 10.1101/gad.1174204

114.Munns, R. (2005). Genes and salt tolerance: bringing them together. *New phytologist*, *167*(3), 645-663. https://doi.org/10.1111/j.1469-8137.2005.01487.x

115.Netondo, G. W., Onyango, J. C., & Beck, E. (2004). Sorghum and salinity: II. Gas exchange and chlorophyll fluorescence of sorghum under salt stress. *Crop science*, *44* (3), 806-811. https://doi.org/10.2135/cropsci2004.8060

116.Nie, W. F., Wang, M. M., Xia, X. J., Zhou, Y. H., Shi, K., Chen, Z. & Yu, J. Q. (2013). Silencing of tomato RBOH1 and MPK2 abolishes brassinosteroid□induced H2O2 generation and stress tolerance. *Plant, Cell & Environment*, *36*(4), 789-803. DOI: 10.1111/pce.12014

117.Ogweno, J.O., Song, X.S., Shi, K., Hu, W.H., Mao, W.H., Zhou, Y.H., Yu, J.Q. & Nogués, S. (2008). Brassinosteroids alleviate heat-induced inhibition of photosynthesis by increasing carboxylation efficiency and enhancing antioxidant systems in Lycopersicon esculentum. *Journal of Plant Growth Regulation*, *27*(1), 49-57. DOI:10.1007/s00344-007-9030-7

118.Otie, V., Udo, I., Shao, Y., Itam, M. O., Okamoto, H., An, P. & Eneji, E. A. (2021). Salinity effects on morpho-physiological and yield traits of soybean (Glycine max L.) as mediated by foliar spray with brassinolide. *Plants*, *10* (3), 541. https://doi.org/10.3390/plants10030541

119.Özdemir, F., Bor, M., Demiral, T. & Türkan, İ. (2004). Effects of 24-epibrassinolide on seed germination, seedling growth, lipid peroxidation, proline content and antioxidative system of rice (Oryza sativa L.) under salinity stress. *Plant growth regulation*, *42*(3), 203-211. DOI:10.1023/B:GROW.0000026509.25995.13

120.Parida, A., Das, A. B. & Das, P. (2002). NaCl stress causes changes in photosynthetic pigments, proteins, and other metabolic components in the leaves of a true mangrove, Bruguiera parviflora, in hydroponic cultures. *Journal of Plant Biology*, *45*(1), 28-36. DOI:10.1007/BF03030429

121.Petretto, G. L., Urgeghe, P. P., Massa, D. & Melito, S. (2019). Effect of salinity (NaCl) on plant growth, nutrient content, and glucosinolate hydrolysis products trends in rocket genotypes. *Plant Physiology and Biochemistry*, *141*, 30-39. DOI: 10.1016/j.plaphy.2019.05.012

122.Planas-Riverola, A., Gupta, A., Betegón-Putze, I., Bosch, N., Ibañes, M. & Caño-Delgado, A. I. (2019). Brassinosteroid signaling in plant development and adaptation to stress. *Development*, *146*(5), dev151894. DOI: 10.1242/dev.151894

123.Puvanitha, S. & Mahendran, S. (2017). Effect of salinity on plant height, shoot and root dry weight of selected rice cultivars. *Scholars Journal of Agriculture and Veterinary Sciences*, *4*(4), 126-131. DOI:10.13140/RG.2.2.10540.72322

124.Qingmao, S., Shiqing, S. & Zhigang, Z. (2006). Exogenous brassinosteroid induced the salt resistance of cucumber (Cucumis sativus L.) seedlings. *Scientia Agricultura Sinica*.

125.Rady, M. M. (2011). Effect of 24-epibrassinolide on growth, yield, antioxidant system and cadmium content of bean (Phaseolus vulgaris L.) plants under salinity and cadmium stress. *Scientia Horticulturae*, *129*(2), 232-237. DOI:10.1016/j.scienta.2011.03.035

126.Rajabi Dehnavi, A., Zahedi, M., Ludwiczak, A., Cardenas Perez, S. & Piernik, A. (2020). Effect of salinity on seed germination and seedling development of sorghum (Sorghum bicolor (L.) Moench) genotypes. *Agronomy*, *10* (6), 859. https://doi.org/10.3390/agronomy10060859

127.Rajewska, I., Talarek, M. & Bajguz, A. (2016). Brassinosteroids and response of plants to heavy metals action. *Frontiers in plant science*, *7*, 629. https://doi.org/10.3389/fpls.2016.00629

128.Ramakrishna, B., & Rao, S. (2015). Foliar application of brassinosteroids alleviates adverse effects of zinc toxicity in radish (Raphanus sativus L.) plants. *Protoplasma*, *252* (2), 665-677. DOI: 10.1007/s00709-014-0714-0

129.Rattan, A., Kapoor, N. & Bhardwaj, R. (2012). Role of brassinosteroids in osmolytes accumulation under salinity stress in Zea mays plants. *International Journal of Science and Research*, *3*(9), 1822-1827.

130.Rattan, A., Kapoor, D., Kapoor, N., Bhardwaj, R. & Sharma, A. (2020). Brassinosteroids regulate functional components of antioxidative defense system in salt stressed maize seedlings. *Journal of Plant Growth Regulation*, *39* (4), 1465-1475. DOI:10.1007/s00344-020-10097-1

131.Saha, P., Chatterjee, P. & Biswas, A. K. (2010). NaCl pretreatment alleviates salt stress by enhancement of antioxidant defense system and osmolyte accumulation in mungbean (Vigna radiata L. Wilczek).

132.Saini, S., Sharma, I. & Pati, P. K. (2015). Versatile roles of brassinosteroid in plants in the context of its homoeostasis, signaling and crosstalks. *Frontiers in plant science*, *6*, 950. https://doi.org/10.3389/fpls.2015.00950

133.Sairam, R. K. (1994). Effects of homobrassinolide application on plant metabolism and grain yield under irrigated and moisture-stress conditions of two wheat varieties. *Plant Growth Regulation*, *14*(2), 173-181. DOI:10.1007/BF00025220

134. Santos, C. V. (2004). Regulation of chlorophyll biosynthesis and degradation by salt stress in sunflower leaves. *Scientia Horticulturae*, *103*(1), 93-99. DOI:10.1016/j.scienta.2004.04.009
135. Sarker, U. & Oba, S. (2020). The response of salinity stress-induced A. tricolor to growth, anatomy, physiology, non-enzymatic and enzymatic antioxidants. *Frontiers in Plant Science*, 1354. https://doi.org/10.3389/fpls.2020.559876
136. Shahbaz, M. & Ashraf, M. (2007). Influence of exogenous application of brassinosteroid on growth and mineral nutrients of wheat (Triticum aestivum L.) under saline conditions. *Pakistan Journal of Botany*, *39*(2), 513.
137. Shahid, M.A., Pervez, M.A., Balal, R.M., Mattson, N.S., Rashid, A., Ahmad, R., Ayyub, C.M. & Abbas, T. (2011). Brassinosteroid (24-epibrassinolide) enhances growth and alleviates the deleterious effects induced by salt stress in pea ('Pisum sativum' L.). *Australian Journal of Crop Science*, *5*(5), 500-510.
138. Sharma, I., Ching, E., Saini, S., Bhardwaj, R. & Pati, P. K. (2013). Exogenous application of brassinosteroid offers tolerance to salinity by altering stress responses in rice variety Pusa Basmati-1. *Plant Physiology and Biochemistry*, *69*, 17-26. DOI: 10.1016/j.plaphy.2013.04.013
139. Shrivastava, P. & Kumar, R. (2015). Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. *Saudi Journal of Biological Sciences*, *22*(2), 123-131. https://doi.org/10.1016/j.sjbs.2014.12.001
140. Shu, S., Tang, Y., Yuan, Y., Sun, J., Zhong, M. & Guo, S. (2016). The role of 24-epibrassinolide in the regulation of photosynthetic characteristics and nitrogen metabolism of tomato seedlings under a combined low temperature and weak light stress. *Plant physiology and biochemistry*, *107*, 344-353. DOI: 10.1016/j.plaphy.2016.06.021
141. Sibole, J. V., Cabot, C., Poschenrieder, C. & Barceló, J. (2003). Efficient leaf ion partitioning, an overriding condition for abscisic acid□controlled stomatal and leaf growth responses to NaCl salinization in two legumes. *Journal of Experimental Botany*, *54*(390), 2111-2119. https://doi.org/10.1093/jxb/erg231
142. Siddiqui, H., Ahmed, K. B. M. & Hayat, S. (2018a). Comparative effect of 28-homobrassinolide and 24-epibrassinolide on the performance of different components influencing the photosynthetic machinery in Brassica juncea L. *Plant Physiology and Biochemistry*, *129*, 198-212. DOI: 10.1016/j.plaphy.2018.05.027
143. Siddiqui, H., Hayat, S. & Bajguz, A. (2018b). Regulation of photosynthesis by brassinosteroids in plants. *Acta Physiologiae Plantarum*, *40*(3), 1-15. DOI:10.1007/s11738-018-2639-2
144. Silambarasan, N. & Natarajan, S. (2014). Biochemical responses of Sankankuppi (Clerodendron inerme L.) to salinity stress. *African Journal of Agricultural Research*, *9*(15), 1151-1160. DOI:10.5897/AJAR2013.7629
145. Singh, S., Jakhar, S., & Rao, S. (2020). Improvement in salt tolerance of Vigna mungo (L.) Hepper by exogenously applied 24-epibrassinolide. *Legume Research-An International Journal*, *43*(5), 647-652. **DOI:** 10.18805/LR-4019
146. Slabu, C., Zörb, C., Steffens, D. & Schubert, S. (2009). Is salt stress of faba bean (Vicia faba) caused by Na+ or Cl– toxicity?. *Journal of Plant Nutrition and Soil Science*, *172*(5), 644-651. https://doi.org/10.1002/jpln.200900052
147. Soliman, M., Elkelish, A., Souad, T., Alhaithloul, H. & Farooq, M. (2020). Brassinosteroid seed priming with nitrogen supplementation improves salt tolerance in soybean. *Physiology and Molecular Biology of Plants*, *26*(3), 501-511. DOI: 10.1007/s12298-020-00765-7
148. Sousa, V.Q., Messias, W.F.S., Pereira, Y.C., da Silva, B.R.S., Lobato, E.M.S.G., Alyemeni, M.N., Ahmad, P. & Lobato, A.K.D.S. (2021). Pretreatment with 24-Epibrassinolide Synergistically Protects Root Structures and Chloroplastic Pigments and Upregulates Antioxidant Enzymes and Biomass in Na+-Stressed Tomato Plants. *Journal of Plant Growth Regulation*, 1-17.
149. Steffens, F.E. (1991). Relationship between seeding response and environmental variables in Bethlehem, 8th Annual SASAS Conference.
150. Stepien, P. & Klobus, G. (2005). Antioxidant defense in the leaves of C3 and C4 plants under salinity stress. *Physiologia plantarum*, *125*(1), 31-40. https://doi.org/10.1111/j.1399-3054.2005.00534.x
151. Su, Q., Zheng, X., Tian, Y. & Wang, C. (2020). Exogenous brassinolide alleviates salt stress in Malus hupehensis Rehd. by regulating the transcription of NHX-Type Na+ (K+)/H+ antiporters. *Frontiers in plant science*, *11*, 38. https://doi.org/10.3389/fpls.2020.00038
152. Sun, S., Chen, D., Li, X., Qiao, S., Shi, C., Li, C., Shen, H. & Wang, X. (2015). Brassinosteroid signaling regulates leaf erectness in Oryza sativa via the control of a specific U-type cyclin and cell proliferation. *Developmental Cell*, *34*(2), 220-228. https://doi.org/10.1016/j.devcel.2015.05.019
153. Szabados, L. & Savouré, A. (2010). Proline: a multifunctional amino acid. *Trends in plant science*, *15*(2), 89-97. DOI: 10.1016/j.tplants.2009.11.009
154. Szabolcs, I. (1974). Salt affected soils in Europe. Martinus Nijhoff. *Research Institute for Soil Science and Agricultural Chemistry of the Hungarian Academy of Sciences.*
155. Talaat, N. B. & Shawky, B. T. (2013). 24-Epibrassinolide alleviates salt-induced inhibition of productivity by increasing nutrients and compatible solutes accumulation and enhancing antioxidant system in wheat (Triticum aestivum L.). *Acta Physiologiae Plantarum*, *35*(3), 729-740. DOI:10.1007/s11738-012-1113-9
156. Tanveer, M., Shahzad, B., Sharma, A., Biju, S. & Bhardwaj, R. (2018). 24-Epibrassinolide; an active brassinolide and its role in salt stress tolerance in plants: a review. *Plant Physiology and Biochemistry*, *130*, 69-79. https://doi.org/10.1016/j.plaphy.2018.06.035
157. Tavakkoli, E., Fatehi, F., Coventry, S., Rengasamy, P. & McDonald, G. K. (2011). Additive effects of Na+ and Cl– ions on barley growth under salinity stress. *Journal of Experimental Botany*, *62*(6), 2189-2203. https://doi.org/10.1093/jxb/erq422
158. Tong, H., Xiao, Y., Liu, D., Gao, S., Liu, L., Yin, Y., Jin, Y., Qian, Q. & Chu, C. (2014). Brassinosteroid regulates cell elongation by modulating gibberellin metabolism in rice. *The Plant Cell*, *26*(11), 4376-4393. DOI: 10.1105/tpc.114.132092
159. Tunc-Ozdemir, M. & Jones, A. M. (2017). BRL3 and AtRGS1 cooperate to fine tune growth inhibition and ROS

activation. *PloS one*, *12*(5), e0177400. https://doi.org/10.1371/journal.pone.0177400

160.Vardhini, B. V. (2011). Studies on the effect of brassinolide on the antioxidative system of two varieties of sorghum grown in saline soils of Karaikal. *Asian and Australasian Journal of Plant Science and Biotechnology*, *5*(1), 31-34.

161.Vázquez, M. N., Guerrero, Y. R., de la Noval, W. T., Gonzalez, L. M. & Zullo, M. A. T. (2019). Advances on exogenous applications of brassinosteroids and their analogs to enhance plant tolerance to salinity: a review. *Australian Journal of Crop Science*, *13*(1), 115-121. DOI: 10.21475/ajcs.19.13.01.p1404

162.Vert, G. & Chory, J. (2006). Downstream nuclear events in brassinosteroid signalling. *Nature*, *441*(7089), 96-100. DOI: 10.1038/nature04681

163.Wang, B., Zhang, J., Xia, X. & Zhang, W. H. (2011). Ameliorative effect of brassinosteroid and ethylene on germination of cucumber seeds in the presence of sodium chloride. *Plant Growth Regulation*, *65*(2), 407-413. DOI:10.1007/s10725-011-9595-9

164.Wang, W., Vinocur, B. & Altman, A. (2003). Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. *Planta*, *218*(1), 1-14. DOI: 10.1007/s00425-003-1105-5

165.Wang, X. & Chory, J. (2006). Brassinosteroids regulate dissociation of BKI1, a negative regulator of BRI1 signaling, from the plasma membrane. *Science*, *313*(5790), 1118-1122. DOI: 10.1126/science.1127593

166.Wang, Z. Y., Seto, H., Fujioka, S., Yoshida, S. & Chory, J. (2001). BRI1 is a critical component of a plasma-membrane receptor for plant steroids. *Nature*, *410*(6826), 380-383. DOI: 10.1038/35066597

167.Wani, A. S., Ahmad, A., Hayat, S., & Tahir, I. (2019). Epibrassinolide and proline alleviate the photosynthetic and yield inhibition under salt stress by acting on antioxidant system in mustard. *Plant physiology and biochemistry*, *135*, 385-394.

168.Wei, Z. & Li, J. (2016). Brassinosteroids regulate root growth, development, and symbiosis. *Molecular plant*, *9*(1), 86-100. https://doi.org/10.1016/j.molp.2015.12.003

169.Widholm, J. M. (1988). In vitro selection with plant cell and tissue cultures: an overview. *Iowa state journal of research (USA)*.

170.Wu, W., Zhang, Q., Ervin, E., Yang, Z. & Zhang, X. (2017). Physiological mechanism of enhancing salt stress tolerance of perennial ryegrass by 24-epibrassinolide. *Frontiers in plant science*, *8*, 1017. https://doi.org/10.3389/fpls.2017.01017

171.Xia, X.J., Huang, L.F., Zhou, Y.H., Mao, W.H., Shi, K., Wu, J.X., Asami, T., Chen, Z. & Yu, J.Q. (2009). Brassinosteroids promote photosynthesis and growth by enhancing activation of Rubisco and expression of photosynthetic genes in Cucumis sativus. *Planta*, *230*(6), 1185-1196. DOI: 10.1007/s00425-009-1016-1

172.Xia, X.J., Huang, L.F., Zhou, Y.H., Mao, W.H., Shi, K., Wu, J.X., Asami, T., Chen, Z. & Yu, J.Q. (2009). Brassinosteroids promote photosynthesis and growth by enhancing activation of Rubisco and expression of photosynthetic genes in Cucumis sativus. *Planta*, *230*(6), 1185-1196. DOI: 10.1007/s00425-009-1016-1

173.Xiao-min, L. U. & Wei, Y. A. N. G. (2013). Alleviation effects of brassinolide on cucumber seedlings under NaCl stress. *Yingyong Shengtai Xuebao*, *24*(5).

174.Xu, S., Hu, B., He, Z., Ma, F., Feng, J., Shen, W. & Yang, J. (2011). Enhancement of salinity tolerance during rice seed germination by presoaking with hemoglobin. *International Journal of Molecular Sciences*, *12*(4), 2488-2501. https://doi.org/10.3390/ijms12042488

175.Yan, J., Guan, L., Sun, Y., Zhu, Y., Liu, L., Lu, R., Jiang, M., Tan, M. & Zhang, A. (2015). Calcium and ZmCCaMK are involved in brassinosteroid-induced antioxidant defense in maize leaves. *Plant and Cell Physiology*, *56*(5), 883-896. DOI: 10.1093/pcp/pcv014

176.Yang, H., Matsubayashi, Y., Nakamura, K. & Sakagami, Y. (2001). Diversity of Arabidopsis genes encoding precursors for phytosulfokine, a peptide growth factor. *Plant Physiology*, *127*(3), 842-851. https://doi.org/10.1104/pp.010452

177.Yang, P., Azher Nawaz, M., Li, F., Bai, L. & Li, J. (2019). Brassinosteroids regulate antioxidant system and protect chloroplast ultrastructure of autotoxicity-stressed cucumber (Cucumis sativus L.) seedlings. *Agronomy*, *9*(5), 265. https://doi.org/10.3390/agronomy9050265

178.Ye, H., Liu, S., Tang, B., Chen, J., Xie, Z., Nolan, T.M., Jiang, H., Guo, H., Lin, H.Y., Li, L. & Wang, Y. (2017). RD26 mediates crosstalk between drought and brassinosteroid signalling pathways. *Nature Communications*, *8*(1), 1-13. DOI: 10.1038/ncomms14573

179.Yin, X., Tang, M., Xia, X. & Yu, J. (2021). BRASSINAZOLE RESISTANT 1 Mediates Brassinosteroid-Induced Calvin Cycle to Promote Photosynthesis in Tomato. *Frontiers in Plant Science*, *12*, 811948-811948. https://doi.org/10.3389/fpls.2021.811948

180.Yin, Y., Vafeados, D., Tao, Y., Yoshida, S., Asami, T. & Chory, J. (2005). A new class of transcription factors mediates brassinosteroid-regulated gene expression in Arabidopsis. *Cell*, *120*(2), 249-259. DOI: 10.1016/j.cell.2004.11.044

181.Yokota, T., Arima, M. & Takahashi, N. (1982). Castasterone, a new phytosterol with plant-hormone potency, from chestnut insect gall. *Tetrahedron Letters*, *23*(12), 1275-1278. https://doi.org/10.1016/S0040-4039(00)87081-1

182.Yu, J. Q., Huang, L. F., Hu, W. H., Zhou, Y. H., Mao, W. H., Ye, S. F. & Nogués, S. (2004). A role for brassinosteroids in the regulation of photosynthesis in Cucumis sativus. *Journal of experimental botany*, *55*(399), 1135-1143. DOI: 10.1093/jxb/erh124

183.Yue, J., Fu, Z., Zhang, L., Zhang, Z. & Zhang, J. (2018). The positive effect of different 24-epiBL pretreatments on salinity tolerance in Robinia pseudoacacia L. seedlings. *Forests*, *10*(1), 4. https://doi.org/10.3390/f10010004

184.Yue, J., You, Y., Zhang, L., Fu, Z., Wang, J., Zhang, J. & Guy, R. D. (2019). Exogenous 24-epibrassinolide alleviates effects of salt stress on chloroplasts and photosynthesis in Robinia pseudoacacia L. seedlings. *Journal of Plant Growth Regulation*, *38*(2), 669-682.

185.Yusuf, M., Fariduddin, Q., Khan, T. A. & Hayat, S. (2017). Epibrassinolide reverses the stress generated by combination of excess aluminum and salt in two wheat cultivars through altered proline metabolism and antioxidants. *South African journal of botany*, *112*, 391-398.https://doi.org/10.1016/j.sajb.2017.06.034

186.Zeng, H., Tang, Q. & Hua, X. (2010). Arabidopsis brassinosteroid mutants det2-1 and bin2-1 display altered salt tolerance. *Journal of Plant Growth Regulation*, *29*(1), 44-52. DOI:10.1007/s00344-009-9111-x

187.Zhang, A., Zhang, J., Zhang, J., Ye, N., Zhang, H., Tan, M. & Jiang, M. (2011). Nitric oxide mediates brassinosteroid-induced ABA biosynthesis involved in oxidative stress tolerance in maize leaves. *Plant and Cell Physiology*, *52* (1), 181-192. https://doi.org/10.1093/pcp/pcq187

188.Zhang, S., Hu, J., Zhang, Y., Xie, X. J. & Knapp, A. (2007). Seed priming with brassinolide improves lucerne (*Medicago sativa* L.) seed germination and seedling growth in relation to physiological changes under salinity stress. *Australian Journal of Agricultural Research*, *58*(8), 811-815. DOI:10.1071/AR06253

189.Zhu, J. K. (2001). Plant salt tolerance. *Trends in plant science*, *6*(2), 66-71. DOI: 10.1016/s1360-1385(00)01838-0

190.Zhu, J. Y., Sae-Seaw, J., & Wang, Z. Y. (2013). Brassinosteroid signalling. *Development*, *140*(8), 1615-1620. https://doi.org/10.1242/dev.060590

191.Zhu, T., Deng, X., Zhou, X., Zhu, L., Zou, L., Li, P., Zhang, D. and Lin, H., (2016). Ethylene and hydrogen peroxide are involved in brassinosteroid-induced salt tolerance in tomato. *Scientific reports*, *6*(1), 1-15. DOI: 10.1038/srep35392

192.Zou, L.J., Deng, X.G., Zhang, L.E., Zhu, T., Tan, W.R., Muhammad, A., Zhu, L.J., Zhang, C., Zhang, D.W. and Lin, H.H. (2018). Nitric oxide as a signaling molecule in brassinosteroid-mediated virus resistance to Cucumber mosaic virus in Arabidopsis thaliana. *Physiologia plantarum*, *163*(2), 196-210. DOI: 10.1111/ppl.12677

193.Zurek, D. M., Rayle, D. L., McMorris, T. C., & Clouse, S. D. (1994). Investigation of gene expression, growth kinetics, and wall extensibility during brassinosteroid-regulated stem elongation. *Plant Physiology*, *104*(2), 505-513. DOI: 10.1104/pp.104.2.505