Review Article



A review on abiotic stress resistance in maize: effect, resistance mechanism and management

Zabeehullah Burhan¹, Hina Nazir^{1*}, Ayesha Arif¹, Ehsan Ullah², Ansar Abbas³, Ammara Shoukat¹, Abid Ali¹, Qurat Ul Ain⁴

¹Department of Botany, University of Agriculture, Faisalabad, Pakistan.

*Correspondence

Hina Nazir

nazirkhan8032@gmail.com

Volume: 2, Issue: 1, Pages: 36-44

DOI: https://doi.org/10.37446/corbio/ra/2.1.2024.36-44

Received: 10 November 2023 / Accepted: 30 January 2024 / Published: 31 March 2024

Maize (*Zea mays* L.), a fundamental global staple, faces increasing threats to productivity due to two major abiotic stresses: drought and salt stress. This review synthesizes current research on the stresses on maize, elucidates the underlying resistance mechanisms, and explores management strategies to enhance stress resilience. The review first delineates the damaging effects of drought and salt stress on the growth of maize, development, and its yield. By consolidating information from diverse research areas, this review offers a comprehensive overview of drought and salt stress resistance in maize. The insights provided are valuable for researchers, breeders, and policymakers working towards sustainable maize production in the face of increasing environmental challenges. A holistic understanding of the intricate interplay between drought, salt stress, resistance mechanisms, and effective management strategies is essential for developing resilient maize varieties and ensuring global food security in a changing climate.

Keywords: climate change, productivity, resistance mechanisms, signal transduction, epigenetic modification, maize

Introduction

Maize (Zea mays L.) is a prominent main cereal crop that is cultivated all over the globe for the purpose of providing people with sustenance, feeding animals, and producing biofuel (Miao et al., 2017). After rice and wheat, it is the 3rd leading crop that is grown for agricultural purposes (Xie et al., 2017). It has been shown via study that the production of maize in emerging countries has to significantly increase in order to meet the growing request for the human and animal feeding. The best temperature range for the production is between 28 and 32 degrees Celsius, and the amount of water required to complete the life cycle is between 500 and 800 millimeters. The characteristics of the surrounding environment have significant effect on the development of crops (Xie et al., 2017). The genotypes of plants are responsible for controlling their production as well as other qualities, while the environment also has a significant influence on plants. For plants to successfully finish their life cycle in their natural habitat, they must go through a number of phases. There have been recent shifts in climate factors like as precipitation and temperature, which have resulted in extended periods of drought and temperature variations that are far higher than what would be considered desirable. Agricultural production has been affected as a result of these differences. Agricultural productivity has grown over the last twenty years; nevertheless, the exposure of plants to abiotic stress presents a new challenge in terms of maintaining an increase in crop yield in the face of a changing climate (Mao et al., 2015). Environmental elements have a significant effect on the amount of crop production. Plant genotypes have an effect on yield as well as other features, whereas environmental circumstances have an important influence on these traits. For the purpose of completing their whole life cycle in the wild, plants go through a number of phases. Due to the fact that climate features such as rainfall

²Biological Sciences, University of Sargodha, Pakistan.

³Department of Biological Sciences, Thal University, Bhakkar, Pakistan.

⁴Institute of Soil and Environmental Science, University of Agriculture, Faisalabad, Pakistan.

and temperature have become more unpredictable in recent years, there has been a protracted period of drought and temperature changes that are greater than what would be considered desirable. As a result of these changes, crop production has been negatively impacted. Over the course of the last two decades, there has been a rise crops yield. The sensitivity of the plants to abiotic stress, on the other hand, presents a new obstacle to the maintenance of improvements in agricultural productivity in the face of altering climatic patterns (Mao et al., 2015).

In the future, it may be necessary to cultivate crops that are able to withstand abiotic stress in order to maintain agricultural productivity (Duvick, 2005). Plant cells activate signaling pathways for the purpose of responding to a wide variety of stimuli. These pathways include hormones derived from plants, signal transducers and transcription regulators. (Zandalinas et al., 2018). In the future, it may be necessary to cultivate crops that are able to withstand abiotic stress in order to maintain agricultural productivity (Duvick, 2005). Plant cells activate signaling pathways for the purpose of responding to a wide variety of stimuli. These pathways include hormones derived from plants, transcription regulators, and signal transducers. All of these signals work together to affect stress-induced genes, which in turn cause the production of enzymes and proteins that have important role in stress metabolism (Zandalinas et al., 2018). A rise in droughts ranging from moderate to intense, an increase in air temperatures, and a raise in the occurrence of rainfall all pose a threat to maize production (Lobell et al., 2014). Research on maize is now mostly concentrated on developing characteristics that increase its tolerance to abiotic stress. Making a determination about the genetic components that tolerate these stresses is a challenging task (Mao et al., 2015). There are a number of complex quantitative features that are responsible for abiotic tolerance, and these attributes may be connected with other physiological and developmental aspects. Numerous qualitative trait loci (QTL) regulate these features, with only a little effect on the trait's total expression. Additionally, this makes the process of identification and modification more difficult. A number of different abiotic stresses will be evaluated in this review with the intention of determining how they affect maize production (Miao et al., 2017)

Zea mays and abiotic stress

Abiotic challenges such as dryness and nutritional limits are climbing higher on the list of restraints, which is the reason why the worldwide drop in annual crop grain yield is accelerating (Mueller et al., 2012). It would seem that maize is the crop that is most susceptible to the effects on the production of agricultural due to change in climate. The most important environmental factors that have a detrimental influence on maize output across the world include high levels of salt, excessive heat, drought, and nutritional deficiencies (Tebaldi & Lobell, 2018). Certain factors that have a detrimental influence on maize's development and output include waterlogging, excessive heat or cold, and severe droughts (Ahuja et al., 2010). Furthermore, it is projected that alternation in climate will have an effect on the temperature of the surrounding environment, which will in turn have an effect on the severity and frequency of droughts in various regions of the globe that are responsible for the cultivation of maize (Yang et al., 2014). It has been shown that the unpredictability of climatic factors in the Indo-Gangetic and Sub-Saharan Africa is responsible for over fifty percent of the total changing in the crop yields of maize in these areas (Ray et al., 2015). Particularly drought and generally abiotic stress are very harmful to maize yields (Bänzinger, 2000). This is true regardless of the germplasm and stress that the plant is subjected to during the embryonic stage of the plant. According the findings by the number of research, the maturity periods in the most important maize-producing areas of the globe may get shorter if temperatures continue to rise. Increasing temperatures, on the other hand, will have an effect on metabolism, which will result in a decrease in the absorption of carbon, as a consequence, a decrease in the pollination and grain set (Iqbal & Arif, 2010; Moriondo et al., 2011). Furthermore, high temperatures may cause drought condition due to the falling water content in soil, in addition to other broad-scale climatic changes that influence the patterns of rainfall (Lobell & Field, 2007; Challinor et al., 2010). This is because the soil's water content decreases when temperatures are high. According to the findings of the researchers, the yield of maize throughout the globe decreased by 8.3 percent for every °C that the temperature increased between 1961 and 2002. There were a few factors that contributed to these oscillations, including variations in the amount of precipitation and the maximum and lowest temperatures. Maize yields are forecasted to decrease by 10-20% by the end of the twenty-first century as a result of significant climate change. This prediction holds true even if the crop obtains all of the water that it requires (Xu et al., 2016). The agricultural sector of the global economy must simultaneously provide around 70 percent of the food that is required to feed a population that is probable rise at least nine billion people by the year 2050 (Smith & Gregory, 2013).

Drought stress

It has been compared to cancer in human biology (Pennisi, 2008) because drought is so much more intricate and harmful to plant biology than it is to human biology. (Wang et al., 2016). Especially when it is at a crucial phase that is vulnerable to drought (Figure 1), which is especially true when it is in the seedling stage. Maize may be cultivated in a broad variety of climates, ranging from semi-arid to temperate zones. This even includes regions that are prone to

drought, such as those in North and South America, Africa, Europe, and Asia (Xie et al., 2017). Drought stress during vegetative development, particularly during the period of time between V1 and V5, is associated with a reduction in the development of plants (Aslam & Maqbool, 2015).



Figure 1. A maize field with drought effect

The description of this method may be broken down into three primary components. These three strategies are known as drought tolerance, drought prevention, and drought escape. The resilience to drought is the result of the combined effects of these methods. The drought resistance refers to the capacity of plants to sustain a good balance of water and turgidity status even when they are subjected to water stress situations (Osmolovskaya et al., 2018). Plants are able to finish their life cycle prior to the beginning of drought, which is a method known as drought escape (Figure 2). They exhibit seasonal fluctuations (Osmolovskaya et al., 2018; Basu et al., 2016).

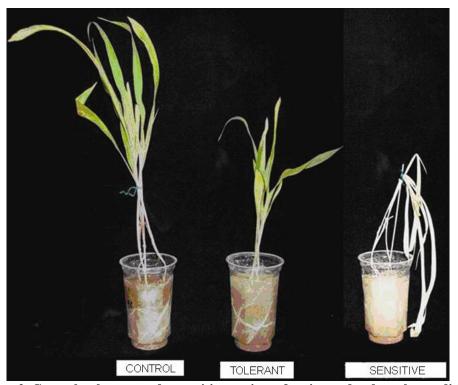


Figure 2. Control, tolerant, and a sensitive variety of maize under drought conditions

Morphological and physiological alterations occur in plants when they are subjected to drought stress. Three main headings describe this procedure. You can either flee the drought or you can learn to live through it. Drought resilience is the result of combining these techniques. To find cultivars that can withstand drought, many studies have been carried out (Osmolovskaya et al., 2018). The focus of research has transitioned from studying the physical characteristics of organisms to discovering the specific genes that play a crucial role in drought resistance, in line with technological improvements (Figure 2). One of plants' primary metabolic pathways, photosynthesis, is both affected by and

contributes to the plant's reaction to drought (Meng et al., 2016). Drought reduces plant photosynthesis efficiency by damaging photosynthetic pigments. Even while closing stomata is a step in the right direction for drought mitigation, doing so lowers evaporation, which in turn lowers root absorption and the assimilation of carbon response (Xie et al., 2017).

Drought effects on photosynthetic activity

Researchers discovered that dryness reduced photosynthesis and that endosperm cell division, which leads to grain development, is more drought sensitive than starch deposition in the seed. Drought has a more profound effect on photosystem-II than on photo-system I in the photosynthetic pathway. The process results in the production of free, high-energy electrons inside the leaf. The photo-oxidation of chlorophyll is the process that leads to the loss of photosynthetic capability. It is the motion of unpaired electrons that causes this discharge. Stress from dryness decreases enzyme activity. As acid invertase activity declines, starch is less efficiently formed from sucrose in grain. The preservation of photosynthesis and the formation of dry matter are critically dependent on the optimal development of leaf area. Particularly for light capture and reduced power output, photosynthetic pigments find widespread usage. Soil moisture affects the efficiency of chlorophyll a and chlorophyll b, and carotenoids are compounds that help plants deal with drought. Factors like as leaf relative water content and water potential are critical to photosynthesis (Farooq *et al.*, 2009). The question of whether the reduction in photosynthesis is caused by the closing of stomata or the loss of metabolism is still being debated among plant scientists (Anjum et al., 2003; Lawson et al., 2003). However, the primary cause of drought stress has been thought to be stomatal closure or other factors that reduce photosynthetic rate (Farooq et al., 2009).

Salt stress

Possible consequences of salt stress on crop development include uneven nutrition as a result of disruptions in the absorption and transportation of vital nutrients, ion toxicity from sodium and/or chloride, and high osmotic stress as a result of a low external water potential. The second one could take some time to take effect since plants might reassert some of their stored nutrients (Munns et al., 2006; Flowers & Flowers, 2005). Damage to subcellular organelles and biological membranes, stunted growth, aberrant development, and eventual plant death may result from sodium toxicity in plant tissues (Davenport et al., 2005). Crop yields drop when grown in salty environments because of the effects on respiration, photosynthesis, nitrogen fixation, and starch metabolism, among other physiological processes (Quintero et al., 2007). Salt resistance refers to a plant's capacity to withstand salt stress and yet generate harvestable yields. For plants to thrive in salty environments, they go to great lengths to adapt to the conditions, including regulating stomatal openings, maintaining ion homeostasis, balancing hormones, activating their antioxidant defense system, adjusting osmosis, adjusting tissue water status, and more (Conventional breeding in conjunction with biotechnology, marker-assisted selection, nutrient management, and to successfully grow maize in soils impacted by salt, it may be required to apply external growth regulators or osmoprotectants. (Janmohammadi et al., 2008; Gunes et al., 2007; Eker et al., 2006; Li et al., 2010; Kaya et al., 2010;).

Salt stress effects

While salinity does have an effect on maize development and growth, plant responses vary with stress level and the developmental stage of the crop. The 1st stage of salinity, which is caused by osmotic stress, affects the development of maize plants when exposed to the stress for a short period of time (Sümer et al., 2004).

Germination and plant growth

When growing crops on soils impacted by salt, the success of the germination process is the most important step in establishing the seedlings. The germination events are often spread out more widely, start to germinate at a slower pace, and are delayed when exposed to salt stress (Farsiani & Ghobadi, 2009; Ashraf & Foolad, 2005). In contrast to later phases of development, salinity has a greater impact on germination and early seedling growth. To a large extent, salt stress affects production by dropping the soil solution's osmotic potential, which in turn slows the seeds' ability to absorb water, by making the embryo poisonous to Na and Cl, or by change the production of proteins (Hasegawa et al., 2000; Farsiani & Ghobadi, 2009; Khaje Hosseini et al., 2003). Salt stress slows down development of shoot by reducing leaf extension and initiation, rate of leaf abscission, and internode growth (Akram et al., 2010a; Rios-Gonzalez et al., 2002; Qu et al., 2012). Salt stress drastically impedes the growth of leaves rate via falling either the quantity or velocity of elongating cells (Szalai & Janda, 2009).

Resistance methods

Maize plants have a range of modifications at the sub-cellular, cellular level, and organ levels in order to thrive in saline conditions. The development of resistance to salt in maize plants is intricate, involving multiple adaptations such as the regulation of stomata, alterations in hormonal balancing, activation of antioxidants, osmotic regulation, preservation of the tissue water contents, and various mechanisms to exclude toxic ions when exposed to salinity. Below is a concise overview of the salt resistance systems present in maize plants at different stages.

Osmoregulation and osmoprotection

Osmotic adjustment, also known as oxygen regulation, is a crucial cellular response in plants that helps mitigate the adverse impacts of drought stress caused by high salinity levels. This adaptation is particularly important during the first stage of salt stress. Osmoregulation is mostly achieved by the accumulation of both inorganic and organic solutes in response to the high salt or drought conditions, which reduces water potential without reducing the actual amount of water (Serraj & Sinclair, 2002). The primary osmolytes are sugar alcohols, soluble sugars, proline, trehalose, organic acids, and glycine betaine. Salinity increase in the buildup of proline in maize plants (de Azevedo et al., in 2004). In a similar manner, Mansour et al. (2005) observed a rise in the addition of glycine betaine and proline in *Zea mays* plants when exposed to salt stress (Kaya et al., 2010).

Apoplastic acidification

Cell apoplast acidity is necessary for the extensibility of cell walls, since it requires a lower pH in the apoplast to activate the enzymes responsible for loosening the cell wall, known as expansins. Inefficient plasma membrane H+ - pumping by ATPase, caused by poor cell wall acidification, hampers the development of maize seedlings during the 1st stage of salinity. This inefficiency may be attributed to alterations in gene expression (Zörb et al., 2005). This ability is crucial for relaxing the cell wall and promoting development in the presence of salt stress (Pitann et al., 2009c; Wakeel et al., 2011a).

Hormonal regulation

Hormone production, which occurs in minute amounts but is sufficient to control plant growth, is what regulates the growth and development of plants. Gibberellins, auxins, ethylene, cytokinins, and abscisic acid are the primary phytohormones, with the former three stimulating growth and the latter inhibiting growth. Maize plants undergoing salinity exhibit specific alterations in the production of these growth chemicals. Salt stress in maize resulted in elevated levels of abscisic acid and reduced levels of indole acetic acid (auxins). This change in hormone levels may cause the stomata to close, reducing loss of water caused by salinity (Younis et al., 2003). Root tips are the first sensors of reduced availability of water in a saline environment, since the osmotic impact triggers a signal to the shoots, prompting adjustments in the overall metabolic processes of the whole plant (Schubert, 2009).

Conclusion

In conclusion, in order to ensure global food safety, mainly in light of climate alteration, it is crucial to understand and solve the issue of drought and salt stress resistance in maize. Significant yield losses in maize may be caused by these stresses, which threatens agricultural output. But We have made significant progress in understanding the mechanisms of resistance that enable maize plants to endure such types of stressors. Extensive research on the molecular and physiological responses of maize to salt stress and drought has revealed a web of adaptation mechanisms. Some examples of this include improving antioxidant systems, synthesizing osmoprotectants, and activating genes that respond to stress. Root design and water-use efficiency are other important factors that contribute to a plant's ability to withstand these stresses. Reduce the damage that drought and salt stress do to maize crops by using effective management techniques. One potential course of action is the creation and widespread use of drought- and salt-tolerant maize cultivars using conventional breeding methods or innovative biotechnological techniques. The effective use of water may be achieved via integrated water management approaches including rainwater collection and precision irrigation. To make maize more resistant to stress, agronomic methods and soil amendments that increase nutrient availability and improve soil structure may be used. Finally, to combat the growing environmental pressures, sustainable maize production requires a multifaceted strategy that integrates genetics, agronomy, and technology. Ensuring food security and livelihoods for communities depending on maize farming requires ongoing study, collaboration, and the sharing of information. This will lead to the development of robust maize varieties and the implementation of appropriate management practices.

Author contributions

All authors contributed to the study's conception and design. Author Hina Nazir was responsible for creating the study and writing the protocol. Hina Nazir and Zabeehullah Burhan handled the preparation of the materials, data collection, and analysis. Hina Nazir wrote the first draft of the manuscript, and Ayesha Arif provided feedback on earlier iterations. Author EHSANULLAH, Ansar Abbas, Ammara Shoukat the literature searches and contributed a lot in Strategies Portion. The final part of the manuscript is Hinder Hunger written by Abid Ali and Qurat Ul Ain. Hina Nazir was in charge of managing the references and citations. All authors read and approved the final manuscript.

Funding

No funding

Conflict of interest

The author declares no conflict of interest. The manuscript has not been submitted for publication in other journal.

Ethics approval

Not applicable

Availability of data and material

The datasets generated and/or analysed during the current study available from the corresponding author on reasonable request.

Competing Interests

The author declares no conflict of interest. The manuscript has not been submitted for publication in other journal.

References

Ahuja, I., de Vos, R. C., Bones, A. M., & Hall, R. D. (2010). Plant molecular stress responses face climate change. *Trends in plant science*, *15*(12), 664-674.

Akram, M., Ashraf, M. Y., Ahmad, R., Rafiq, M., Ahmad, I., & Iqbal, J. (2010). Allometry and yield components of maize (*Zea mays* L.) hybrids to various potassium levels under saline conditions. *Archives of Biological Sciences*, 62(4), 1053-1061. Doi: 10.2298/ABS1004053A

Anjum, F., Yaseen, M., Rasul, E., Wahid, A., & Anjum, S. (2003). Water stress in barley (*Hordeum vulgare* L.). II. Effect on chemical composition and chlorophyll contents. *Pak. J. Agric. Sci*, 40(1-2), 45-49.

Ashraf, M., & Foolad, M. R. (2005). Pre-sowing seed treatment—A shotgun approach to improve germination, plant growth, and crop yield under saline and non-saline conditions. *Advances in agronomy*, 88, 223-271. Doi: 10.1016/S0065-2113(05)88006-X

Aslam, M., Maqbool, M. A., & Cengiz, R. (2015). Drought stress in maize (*Zea mays* L.) Effects, resistance mechanisms, global achievements and. *Cham: Springer*.

Bänzinger, M. (2000). Breeding for drought and nitrogen stress tolerance in maize: from theory to practice. Cimmyt.

Basu, S., Ramegowda, V., Kumar, A., & Pereira, A. (2016). Plant adaptation to drought stress. F1000Research, 5.

Challinor, A. J., Simelton, E. S., Fraser, E. D., Hemming, D., & Collins, M. (2010). Increased crop failure due to climate change: assessing adaptation options using models and socio-economic data for wheat in China. *Environmental Research Letters*, 5(3), 034012.

Cosgrove, D. J. (2000). Loosening of plant cell walls by expansins. *Nature*, 407(6802), 321-326. Doi: 10.1038/35030000

Davenport, R., James, R. A., Zakrisson-Plogander, A., Tester, M., & Munns, R. (2005). Control of sodium transport in durum wheat. *Plant physiology*, *137*(3), 807-818. Doi: 10.1104/pp. 104.057307

Duvick, D. N. (2005). The contribution of breeding to yield advances in maize (Zea mays L.). Advances in agronomy, 86, 83-145.

Eker, S., Cömertpay, G., Konuşkan, Ö., Ülger, A. C., Öztürk, L., & Çakmak, İ. (2006). Effect of salinity stress on dry matter production and ion accumulation in hybrid maize varieties. *Turkish journal of agriculture and forestry*, 30(5), 365-373.

El-Bassiouny, H. M. S., & Bekheta, M. A. (2005). Role of putrescine on growth, regulation of stomatal aperture, ionic contents and yield by two wheat cultivars under salinity stress.

Farooq, M., Wahid, A., Kobayashi, N. S. M. A., Fujita, D. B. S. M. A., & Basra, S. M. A. (2009). Plant drought stress: effects, mechanisms and management. *Sustainable agriculture*, 153-188.

Farsiani, A., & Ghobadi, M. E. (2009). Effects of PEG and NaCl stress on two cultivars of corn (Zea mays L.) at germination and early seedling stages. *International Journal of Agricultural and Biosystems Engineering*, 3(9), 442-445.

Flowers, T. J., & Flowers, S. A. (2005). Why does salinity pose such a difficult problem for plant breeders?. *Agricultural water management*, 78(1-2), 15-24. Doi: 10. 1016/j.agwat.2005.04.015

Gunes, A., Inal, A., Alpaslam, M., Erslan, F., Bagsi, E.G., Cicek, N. (2007). Salicylic acid induced changes on some physiological parameters symptomatic for oxidative stress and mineral nutrition in maize (*Zea mays L.*) grown under salinity. *J Plant Physiol* 164,728–736. Doi: 10.1016/j.jplph.2005.12.009

Hager, A. (2003). Role of the plasma membrane H+-ATPase in auxin-induced elongation growth: historical and new aspects. *Journal of plant research*, *116*, 483-505. Doi: 10.1007/s10265-003-0110-x

Hasegawa, P. M., Bressan, R. A., Zhu, J. K., & Bohnert, H. J. (2000). Plant cellular and molecular responses to high salinity. *Annual review of plant biology*, *51*(1), 463-499. doi: 1040-2519/00/0601-0463

Hichem, H., & Mounir, D. (2009). Differential responses of two maize (*Zea mays* L.) varieties to salt stress: changes on polyphenols composition of foliage and oxidative damages. *Industrial crops and Products*, 30(1), 144-151. doi:10.1016/j.indcrop.2009.03.003

Iqbal, M. M., Goheer, M. A., & Khan, A. M. (2009). Climate-change aspersions on food security of Pakistan. *Science Vision*, 15(1), 15-23.

Jafar, M. Z., Farooq, M., Cheema, M. A., Afzal, I., Basra, S. M. A., Wahid, M. A., ... & Shahid, M. (2012). Improving the performance of wheat by seed priming under saline conditions. *Journal of Agronomy and Crop Science*, 198(1), 38-45. doi: 10.1111/j.1439-037x.2011.00487.x

Janmohammadi, M., Dezfuli, P. M., & Sharifzadeh, F. (2008). Seed invigoration techniques to improve germination and early growth of inbred line of maize under salinity and drought stress. *Gen Appl Plant Physiol*, 34(3-4), 215-226.

Kaya, C., Tuna, A. L., & Okant, A. M. (2010). Effect of foliar applied kinetin and indole acetic acid on maize plants grown under saline conditions. *Turkish Journal of Agriculture and Forestry*, 34(6), 529-538. doi: 10.3906/tar-0906-173

Khajeh-Hosseini, M., Powell, A. A., & Bingham, I. J. (2003). The interaction between salinity stress and seed vigour during germination of soyabean seeds. *Seed Science and technology*, *31*(3), 715-725.

Lawson, T., Oxborough, K., Morison, J. I., & Baker, N. R. (2003). The responses of guard and mesophyll cell photosynthesis to CO2, O2, light, and water stress in a range of species are similar. *Journal of experimental botany*, 54(388), 1743-1752.

- Li, B., Li, N., Duan, X., Wei, A., Yang, A., & Zhang, J. (2010). Generation of marker-free transgenic maize with improved salt tolerance using the FLP/FRT recombination system. *Journal of Biotechnology*, *145*(2), 206-213. doi:10.1016/j.jbiotec.2009.11.010
- Lobell, D. B., & Field, C. B. (2007). Global scale climate—crop yield relationships and the impacts of recent warming. *Environmental research letters*, 2(1), 014002.
- Lobell, D. B., Roberts, M. J., Schlenker, W., Braun, N., Little, B. B., Rejesus, R. M., & Hammer, G. L. (2014). Greater sensitivity to drought accompanies maize yield increase in the US Midwest. *Science*, *344*(6183), 516-519.
- Mao, H., Wang, H., Liu, S., Li, Z., Yang, X., Yan, J., ... & Qin, F. (2015). A transposable element in a NAC gene is associated with drought tolerance in maize seedlings. *Nature communications*, 6(1), 8326.

Menezes-Benavente, L., Kernodle, S. P., Margis-Pinheiro, M., & Scandalios, J. G. (2004). Salt-induced antioxidant metabolism defenses in maize (*Zea mays* L.) seedlings. *Redox report*, 9(1), 29-36. doi: 10.1179/135100004225003888

Meng QingFeng, M. Q., Chen XinPing, C. X., Lobell, D. B., Cui ZhenLing, C. Z., Zhang Yi, Z. Y., Yang HaiShun, Y. H., & Zhang FuSuo, Z. F. (2017). Growing sensitivity of maize to water scarcity under climate change.

Miao Zhen Yan, M. Z., Han Zhao Xue, H. Z., Zhang Ting, Z. T., Chen Si Yuan, C. S., & Ma Chuang, M. C. (2019). A systems approach to a spatio-temporal understanding of the drought stress response in maize.

Miao Zhen Yan, M. Z., Han Zhao Xue, H. Z., Zhang Ting, Z. T., Chen Si Yuan, C. S., & Ma Chuang, M. C. (2019). A systems approach to a spatio-temporal understanding of the drought stress response in maize.

Moriondo, M., Giannakopoulos, C., & Bindi, M. (2011). Climate change impact assessment: the role of climate extremes in crop yield simulation. *Climatic change*, 104(3-4), 679-701.

Mueller, N. D., Gerber, J. S., Johnston, M., Ray, D. K., Ramankutty, N., & Foley, J. A. (2012). Closing yield gaps through nutrient and water management. *Nature*, 490(7419), 254-257.

Munns, R., James, R. A., & Läuchli, A. (2006). Approaches to increasing the salt tolerance of wheat and other cereals. *Journal of experimental botany*, *57*(5), 1025-1043. doi: 10.1093/jxb/erj100

Osmolovskaya, N., Shumilina, J., Kim, A., Didio, A., Grishina, T., Bilova, T., ... & Wessjohann, L. A. (2018). Methodology of drought stress research: Experimental setup and physiological characterization. *International journal of molecular sciences*, 19(12), 4089.

Pennisi, E. (2008). The blue revolution, drop by drop, gene by gene. Science, 320(5873), 171-173.

Pitann, B., Zörb, C., & Mühling, K. H. (2009). Comparative proteome analysis of maize (Zea mays L.) expansins under salinity. *Journal of Plant Nutrition and Soil Science*, 172(1), 75-77. doi:10.1002/jpln.200800265

Qu, C., Liu, C., Gong, X., Li, C., Hong, M., Wang, L., & Hong, F. (2012). Impairment of maize seedling photosynthesis caused by a combination of potassium deficiency and salt stress. *Environmental and experimental botany*, 75, 134-141. doi:10.1016/j.envexpbot.2011.08.019

Quintero, J. M., Fournier, J. M., & Benlloch, M. (2007). Na+ accumulation in shoot is related to water transport in K+starved sunflower plants but not in plants with a normal K+ status. *Journal of plant physiology*, *164*(1), 60-67. doi:10.1016/j.jplph.2005.10.010

Ray, D. K., Gerber, J. S., MacDonald, G. K., & West, P. C. (2015). Climate variation explains a third of global crop yield variability. *Nature communications*, 6(1), 5989.

Rios-Gonzalez, K., Erdei, L., & Lips, S. H. (2002). The activity of antioxidant enzymes in maize and sunflower seedlings as affected by salinity and different nitrogen sources. *Plant Science*, *162*(6), 923-930. doi: 10.1016/S0168-9452(02)00040-7

Schubert, S. (2009). Advances in alleviating growth limitations of maize under salt stress.

- Schubert, S., Neubert, A., Schierholt, A., Sümer, A., & Zörb, C. (2009). Development of salt-resistant maize hybrids: the combination of physiological strategies using conventional breeding methods. *Plant Science*, 177(3), 196-202. doi:10.1016/j.plantsci.2009.05.011
- Serraj, R. A. C. H. I. D., & Sinclair, T. R. (2002). Osmolyte accumulation: can it really help increase crop yield under drought conditions?. *Plant, cell & environment*, 25(2), 333-341. doi:10.1046/j.1365-3040.2002.0075.x
- Smith, P., Gregory, P,J. (2013). Climate change and sustainable food production. *Proceedings of the Nutrition Society*, 72(1), 21-28.
- Szalai, G., & Janda, T. (2009). Effect of salt stress on the salicylic acid synthesis in young maize (*Zea mays* L.) plants. *Journal of agronomy and crop science*, 195(3), 165-171. doi:10.1111/j.1439-037x.2008.00352.x
- Tebaldi, C., & Lobell, D. (2018). Differences, or lack thereof, in wheat and maize yields under three low-warming scenarios. *Environmental Research Letters*, 13(6), 065001.
- Wakeel, A., Sümer, A., Hanstein, S., Yan, F., & Schubert, S. (2011). In vitro effect of Na+/K+ ratios on the hydrolytic and pumping activity of the plasma membrane H+-ATPase from maize (Zea mays L.) and sugar beet (Beta vulgaris L.) shoot. *Plant Physiology and Biochemistry*, 49, 341-345. doi:10.1016/j.plaphy.2011.01.006
- Wang, X., Wang, H., Liu, S., Ferjani, A., Li, J., Yan, J., ... & Qin, F. (2016). Genetic variation in ZmVPP1 contributes to drought tolerance in maize seedlings. *Nature genetics*, 48(10), 1233-1241.
- Xie, T., Gu, W., Meng, Y., Li, J., Li, L., Wang, Y., ... & Wei, S. (2017). Exogenous DCPTA ameliorates simulated drought conditions by improving the growth and photosynthetic capacity of maize seedlings. *Scientific Reports*, 7(1), 12684.
- Xie, T., Gu, W., Meng, Y., Li, J., Li, L., Wang, Y., ... & Wei, S. (2017). Exogenous DCPTA ameliorates simulated drought conditions by improving the growth and photosynthetic capacity of maize seedlings. *Scientific Reports*, 7(1), 12684.
- Xu, H., Twine, T. E., & Girvetz, E. (2016). Climate change and maize yield in Iowa. PloS one, 11(5), e0156083.
- Yang, J., Sicher, R. C., Kim, M. S., & Reddy, V. R. (2014). Carbon dioxide enrichment restrains the impact of drought on three maize hybrids differing in water stress tolerance in water stressed environments. *International Journal of Plant Biology*, *5*(1), 5535. Doi: 10.4081/pb.2014.5535
- Younis, M.E., El-Shahaby, O.A., Nematalla, M.M., El-Basrawisy, Z.M. (2003). Kinetin alleviates the influence of waterlogging and salinity on growth and affects the production of plant growth regulators in *Vigna sinensis* and *Zea mays. Agronomie*, 23, 277–285.
- Zandalinas, S. I., Mittler, R., Balfagón, D., Arbona, V., & Gómez-Cadenas, A. (2018). Plant adaptations to the combination of drought and high temperatures. *Physiologia plantarum*, 162(1), 2-12.
- Zörb, C., Stracke, B., Tramnitz, B., Denter, D., Sümer, A., Mühling, K. H., ... & Schubert, S. (2005). Does H+ pumping by plasmalemma ATPase limit leaf growth of maize (Zea mays) during the first phase of salt stress?. *Journal of Plant Nutrition and Soil Science*, 168(4), 550-557. Doi:10.1002/jpln.200520503