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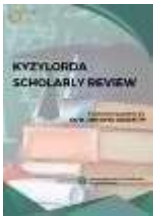

Responses to Salt Stress in Terms of Morpho-Physiological, Leaf, Mineral Composition .L Zea Mays: A Review

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Abstract. Salinization is spreading in soil, and on current estimates, about half of the world's arable land could be salt-affected by 2050. Maize (Zea mays L.) is one of the crops that is among the most heavily liable to lose. It sustains widespread populations in arid and semi-arid areas, for example in the Middle East and North Africa, and as a moderately salt-sensitive C4 cereal, it occupies an uneasy middle path not collapsing immediately like a glycophyte, but losing yield relatively steadily as EC is increased. This review synthesizes what is known about how yellow maize responds to salt stress, from morphology down to ion and redox biochemistry. The morphological picture is the same for all studies. Germination appears to be retarded and reduced. Plant height, leaf area, root and shoot biomass also decrease, with the amount of drop depending on genotype, salt concentration, and growth stage. There are two things happening physiologically in parallel, as well. Stomata close, decreasing CO_2 supply, and PSII suffers non-stomatal injury, so chlorophyll declines, and net photosynthesis decreases more rapidly than stomatal conductance would lead one to expect. Tolerance is largely determined in ion relations. Na^+ and Cl^- accumulate to toxic concentrations and compete with K^+, Ca^{2+}, and Mg^{2+} on membrane and tissue levels. Most screening work relies on the shoot K^+/Na^+ ratio, not Na^+, as it is the ability to keep K^+ in the cytosol whilst excluding or compartmentalizing Na^+ that separates the tolerant lines from those that are sensitive. The ionic and osmotic disturbance contributes to a secondary issue, ROS accumulation, which maize counterbalances with the usual enzymatic defences (SOD, POD and CAT) and with osmolytes and antioxidant metabolites, including proline and phenolic compounds. Tolerant genotypes also typically have anatomical features that contribute: greater root cortical aerenchyma and a tighter regulation of Na^+ loading into the xylem. Research on mitigation has broadened well beyond gypsum-and-leaching. Measurable improvements in ion homeostasis and antioxidant activity in maize under salt have been proven in plant growth-promoting microbes, exogenous phytohormones, and diverse organic and inorganic amendments to soil. The catch is that most of that evidence relies on short pot trials with NaCl alone, usually at the seedling stage. When field salinity does exist, it is seldom a single salt, so the stress is not typically for a very short period of time and seedling tolerance often does not relate to yield at the grain level. For Iraqi and regional farming in particular, the gap that matters is that between a healthy-looking 21-day seedling grown in the greenhouse and an ear of maize grown at harvest in a saline field.

Keywords: Zea mays L.; Salinity stress; Ionic homeostasis; Photosynthetic apparatus.

1. Introduction

University Salinization in soils has become one of the most widespread abiotic constraints on agriculture and one of the immediate constraints on food security globally. The soil in salt-affected areas is around 17 million km² worldwide and it continues to increase. Climate-induced aridification, sea-level rise, secondary salinization from poorly managed irrigation and inappropriate fertilization, among others, drive the same direction. Estimates of annual loss of arable land to salt accumulation are currently between 1.5 and 2.5 million hectares, and without serious mitigation, approximately half the world's cultivated area is expected to be salt compromised by 2050 [1]. The pressure is greatest in arid and semi-arid areas with high evapotranspiration and poor drainage and often brackish irrigation water, which collectively exceed the salt tolerance limit for the cultivation of most plants. Maize (Zea mays L.) remains stuck in that frame. It is the world’s most consumed cereal and is a key component in food, feed, and bio-industrial production systems, yet grain, silage, and biofuel feedstock have driven its cultivation onto marginal and salt-prone soils [2]. While its C4-photosynthesis, with carbon fixation separated in mesophyll and bundle-sheath cells, allows more water-use efficiency than most cereals, it is still a glycophyte, and is only moderately salt-tolerant. The most early-developmental sensitive stages of this crop are germination, emergence, and early vegetative growth, and what happens during those weeks usually decides whether the crop will enter a productive reproductive stage at all under saline environments [3]. Maize salt injury is typically divided into two overlapping parts. The earliest osmotic phase starts within hours to days of exposure: solutes build up around the root, reducing soil water potential and restricting the uptake of water. The ionic stage forms at a more gradual pace, occurring over weeks, and involves accumulation of Na^+ and Cl^- in the tissues of transpiring plants that distorts the cytosolic K^+/Na^+ ratio, displaces Ca^{2+} from membrane binding sites, and induces earlier senescence in older leaves before younger leaves are affected [4]. The predictable outcome from both stages is production of excessive amount of ROS (superoxide, H_2O_2, hydroxyl radicals) in chloroplasts, mitochondria and peroxisomes. ROS oxidize membrane lipids, denature proteins and destroy nucleic acids, and also activate the enzymatic antioxidant system (superoxide dismutase, peroxidase, ascorbate peroxidase, catalase) and the non-enzymatic scavengers such as ascorbate, glutathione, proline and phenolic compounds [5]. Those biochemical changes are visible on the machinery of photosynthesis. As guard cells lose turgor and ABA signaling increases, stomatal conductance and net CO_2 assimilation decrease. Photosystem II suffers more than Photosystem I, and electron transport efficiency (Fv/Fm) drops and chlorophyll a, chlorophyll b, and total carotenoid contents decrease, depending on cultivar, salt concentration and stress duration [6]. It’s the same disruptions that ripple out through the plant. Plant height, leaf area, root and shoot biomass (fresh and dry), leaf number, and final grain yield decrease more or less with respect to salinity. Tolerant genotypes are characterized almost entirely by root characteristics: increased cortical aerenchyma production, increased cortical cells, decreased Na^+ loading to the xylem and thus the shoot, and enhanced plasma membrane selectivity for K^+ over Na^+ [7]. In alleviating these complex effects, a number of recent studies have been focused on the several parallel approaches, such as the exogenous application of phytohormones like salicylic acid, gibberellic acid and melatonin, the use of plant-growth promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi, seed priming protocols, organic and inorganic soil amendments, nanomaterial-mediated foliar applications—activities that principally work by elevating antioxidant defences, restoring ion homeostasis, and maintaining water relations when subjected to stress [8]. However, in light of this expanding literature, a synthetic view of the interplay of morpho-physiological, biochemical and mineral-composition responses to salt stress in maize and on how these interactions become yield-relevant indicators at the field scale is yet to be had, in general, due to limited studies considering isolated parameters, rather than integrated whole-plant responses [9]. Thus, the current review has focused on unifying new findings on (i) the physio-biochemical processes involved in salt tolerance in maize, (ii) salinity intensity and yield-related morphological and leaf features, (iii) dynamics of mineral composition and ion homeostasis under saline conditions, and (iv) the most relevant research questions in seed-enhancement, phytohormone applications, microbial inoculation, and genetic improvement for saline environments, with a special focus on arid-region agriculture [10].

2. Literature Review

2.1 Yellow Maize (Zea mays L.) and Its Economic and Food Importance

Yellow maize (Zea mays L.) is a member of the Poaceae family, and the world's third most produced cereal after wheat and rice, used as human food, livestock feed, and as feedstock for the starch, oil, and bioethanol industries. In 2020, global production was about 1.21 billion tons from 205 million hectares spread over more than 115 countries and 170 climatic zones, which is an unusual reach for any single crop and points to a wide adaptability to different agricultural environments (Alhammad et al., 2023). Maize is a C4 plant, which has a high carbon fixation efficiency due to cooperation between mesophyll cells and bundle sheath cells. This makes it more water and radiation use efficient than C3 plants. Yet this physiological capability does not lessen its sensitivity to abiotic stresses; maize is described as moderately salt-sensitive (Farooq et al., 2015; EL Sabagh et al., 2021) and salinity stress clearly impacts germination processes and early vegetative growth. Due to the rapid increase in soil salinization worldwide, there is an urgent need to elucidate maize response to salinity physiologically, morphologically, and at the mineral level. Such an understanding will be used to develop more tolerant genetic constructs suitable for saline lands, and to devise appropriate agricultural strategies. Therefore, this review aims to present the most recent evidence in terms of the mechanisms of response published in peer-reviewed articles in the literature in recent years on Zea mays L. to salt stress.

2.2 Salinity Stress, Its Global and Regional Spread

Soil salinization represents a major type of environmental degradation that endangers food security. Now about one billion hectares of land are affected, with agricultural areas losing between 1.5 and 2.5×10^5 hectares per year to salt accumulation, and estimates suggest over 50% of arable land could be salt-affected by 2050 unless significant mitigation is considered. Strategic crops such as maize are directly in the path of this trend (Wang et al., 2023). The Middle East and North Africa are among the hardest-hit, driven by both climatic and structural factors: low rainfall, high evaporation, weak drainage networks, and the regular use of saline irrigation water. Iraq is a clear example. About 70% of its irrigated land is salt-affected, with about 25,000 hectares lost each year due to continued poor irrigation and drainage infrastructure. Most of that damage is concentrated in central and southern governorates — historically the country’s food basket (Zoidou et al., 2026). There are two ways that salinity harms plants. It is osmotic stress that strikes first: soil water potential drops and roots have difficulty taking in water. Ionic stress ensues when Na^+ and Cl^- build up in plant tissues to toxic, and eventually lethal concentrations. In addition to this, nutritional imbalances and high ROS levels will oxidise membranes, proteins, and nucleic acids, which ultimately impair photosynthesis and water-use efficiency (Munns and Tester, 2008).

2.3 Morphological and Physiological Responses of Yellow Maize Under Salinity Stress

Salt stress drives a succession of morphological alterations in maize that starts from germination and persists throughout vegetative and reproductive stages. Wang et al. (2024) analysed 41 local cultivars at 60, 120 and 180 mM NaCl, which showed a significant reduction in stem thickness, embryo length, radicle length, leaf area, germination percentage, germination index, salt tolerance index, and seed vigor index with the increase of salinity and significant differences among cultivars. The seedling stage is the most sensitive window in maize and the loss of this time will extend to later growth stages as well as final yield. The physiological aspect is consistent. Habib et al. (2024) treated maize seedlings with 250 mM NaCl for 4 weeks and observed a decline in leaf RWC, stem and root length, fresh and dry biomass, leaf area, and chlorophyll and carotenoid contents. Tissue Na^+ increased and K^+ decreased, and this is the classic indicator of salinity-modified ionic imbalance; consequently, tolerant genotypes are associated with a comparatively high K^+/Na^+ ratio relative to sensitive ones. Ahmed et al. (2023) offered the same argument in a different way: with a 30-day hydroponic experiment on 15 genotypes grown at 0, 50 and 100 mM NaCl, with clear divisions into tolerant (4), moderately tolerant (6) and sensitive lines (5). The tolerant group also demonstrated a relatively large shoot dry weight and higher Chl a, Chl b, total chlorophyll and carotenoid content, making leaf greenness and chloroplast integrity useful screening properties for use even in salt tolerance breeding. Roots suffer the most, since they directly encounter the saline soil. Zhao et al. (2022) demonstrated lower leaf RWC, photochemical efficiency, and catalase activity under salinity, as well as higher SOD and POD activity, greater MDA, and increased Na^+ uptake and transport from root to shoot. If anything, the anatomical aspect of the same study was more useful for breeders: the tolerant genotype JNY658 developed more root cortical aerenchyma, larger cortical cells, and fewer cell rows, all of which led to a lower metabolic cost associated with maintaining cortical tissue and improved oxygen transport under the saline environment. Pan et al. (2023) had a helpful methodological disclaimer. Gradual salinity and salt shock are not equivalent experimental treatments. Under salt shock, osmotic stress, water deficit, and Na^+ toxicity also affected the plant at the same time and the specific sequential phases observed under gradual salinity collapse into a single compound stress. In their work, the tolerant genotypes exhibited early activation of antioxidants, early superoxide signalling and slow root-to-shoot Na^+ translocation. Lastly, Mukhtar et al. (2023) demonstrated in their study that maize inoculation with Bacillus sp. PM31 resulted in significantly better stem and root length, plant height, fresh and dry biomass and leaf area results, in comparison to those in the non-inoculated controls, suggesting that symbioses between plants and microbes can be considered as a potentially useful element for the management of salinity.

2.4 Effect of Salinity Stress on Leaves and the Photosynthetic Process

Salinity damage is most damaging to leaves, and leaves are the easiest place to read it visually and physiologically. Stress manifests as yellowing, stunting, and decreased total leaf area. Pinheiro et al. (2014) exposed maize to 50 and 100 mM NaCl and observed a distinct reduction in total leaf area and dry weight with leaf water potential decrease at the higher concentration. Photosynthetic rate decreased at 100 mM NaCl while stomatal conductance (gs) decreased at either concentration, as expected, since stomatal closure does most of the initial cutting in photosynthesis under salt, and non-stomatal limitations only become important under higher salinity. This is supported by the photosystem-level data. Hussain et al. (2021) compared maize (Zea mays) and sorghum at 150 and 200 mM NaCl, and found that ΦPSII in maize dropped by 60–72%, against only 40% in sorghum. The increase in electrolyte leakage and lower Fv/Fm in maize indicated structural damage at PSII and confirmed that maize thylakoids were more sensitive than those of sorghum. Ali et al. (2024) expanded the image concerning the field-relevant scales of 4, 7, and 10 dS/m; when 10 dS/m was used, chlorophyll was reduced by 80.4%, stem length by 55.4%, and stem fresh weight by 54%. Their PCA selected root-to-shoot ratio, chlorophyll content, root fresh weight, stomatal conductance, leaf area, and relative water content as the most informative traits for screening salt-resilient genotypes — a handy checklist for breeding programs looking to keep the trait list in check. The biochemical layer gives a surprising wrinkle to leaf age. AbdElgawad et al. (2016) treated maize seedlings with 75 and 150 mM NaCl for three weeks, and observed increased total phenolics in mature leaves, flavonoids, total antioxidant capacity (TAC), tocopherols, and proline, while electrolyte leakage, MDA, and H_2O_2 rose only at the higher concentration. This indicates that younger leaves are better guarded than older leaves and that non-enzymatic antioxidants come online earlier than the classical oxidative damage markers. Khalid et al. (2024) found the same trend at the enzyme level, whereby SOD and POD activity increased as Na^+ concentrations increased from 25 to 150 mM, and tight control of ascorbate peroxidase (APX) regulated H_2O_2 and MDA levels in maize leaves. Liu et al. (2025) applied the question to the transcriptome and reported 11,074 DEGs under salinity, with specific regulation of carbohydrate metabolism, MAPK signalling, and phenolic biosynthesis. The image they describe is similar to a molecular stress memory that might help maize get through repeated salinity episodes.

2.5 Mineral Composition and Ionic Homeostasis Response Under Salinity Stress

Mineral imbalance is among the most obvious physiological features of salinity in maize. Na^+ competes with K^+, Ca^{2+} and Mg^{2+} in roots for absorption sites or binding sites on proteins/enzymes. Farooq et al. (2015), in a large systematic review, reported that high Na^+ and Cl^- concentrations in the root zone decrease N, K, Ca, Mg and Fe uptake by the plant. In the short run, toxic Na^+ damages biological membranes and subcellular organelles, retards plant growth and causes abnormal development before plant death. Maize is also more sensitive than some other cereals; it accumulates relatively high Na^+ in its leaves, rather than efficiently sequestering it in the roots, they found. Akram et al. (2019) examined 3 maize cultivars grown at 0–140 mM NaCl and monitored the ions separately. The uptake of Cl^- by roots and shoots grew steadily up to 105 mM, followed by a slight decrease thereafter. Na^+ was mostly in roots while Cl^- was more prevalent in vegetative tissues. Na^+/K^+ ratios increased as salinity became high, and the ionic imbalance associated with growth decreases was maintained throughout the process. This principle is essential for employing the Na^+/K^+ ratio as the main screening criterion for tolerant genotypes. Turan et al. (2010) also found the same impact in cultivar RX947 at 100 mM NaCl: increased Na^+ and Cl^-, less overall chlorophyll, more stomatal resistance, and increased proline—the textbook maize combination of stomatal closure and osmotic adjustment. The mitigation literature points in a single direction from several angles. Wang et al. (2021) showed that arbuscular mycorrhizal fungi (AMF) decreased the root-to-leaf Na^+/K^+ gradient in maize under salinity; thus, maintaining a controlled Na^+/K^+ gradient became a key tolerance mechanism, where Na^+ was found to be the major toxic ion. Ahmad et al. (2023) inoculated maize with Aspergillus welwitschiae BK under saline conditions and indicated higher tissue N, P, Ca^{2+}, K^+, and Mg^{2+}, lower Na^+ and Cl^-, and lower Na^+/K^+ and Na^+/Ca^{2+} ratios. Khan et al. (2018) tackled the phenomenon with an unusual approach and demonstrated that phosphorus depletion enhanced salt tolerance via increased tissue mass density, accumulation of sugars and proline, and decreased Na^+ absorption. Ahmed et al. (2019) found the effectiveness of soil amendments: calcium-fortified compost decreased shoot Na^+/K^+ ratio by 70–85% across EC levels of 1.6, 5, and 10 dS m^{-1}, with a parallel increase in N, P, and K uptake. On the applied side, Latef et al. (2018) sprayed Zn and Cu on a tolerant and a sensitive cultivar, and reported lower Na and Cl, higher P, N, Ca, K, Mn, Fe, Zn, and Cu, and higher water potential, stomatal conductance, and photosynthesis.

2.6 Oxidative Stress and the Role of Enzymatic and Non-Enzymatic Antioxidants

Salinity stress in maize is associated with ROS production, such as the superoxide anion (O_2^-) and hydrogen peroxide (H_2O_2), which induces membrane lipid peroxidation and degrades proteins and nucleic acids. Plants respond to this with a dual defence system: enzymatic antioxidants (SOD, CAT, POD, APX, GR) and non-enzymatic scavengers (ascorbic acid, ASA; glutathione, GSH; proline; polyphenols). Saleem et al. (2024) compared four maize genotypes (two tolerant, two sensitive) at 12 dS m^{-1}. Tolerant lines had higher relative water content, higher ASA, GSH and proline, and stronger POD, GPX and MDHAR activity. Sensitive lines exhibited higher ROS, MDA and LOX activity; essentially the reverse of the tolerant profile. Islam et al. (2024) further described maize salt tolerance as a coordinated response between antioxidant capacity, phytohormone signalling, and ionic homeostasis. In this system, proline does multiple things at once: osmotic adjustment, protection of the enzymes and membranes, and scavenging of ROS, making it accumulate extensively in tolerant lines. Furthermore, on the molecular level, numerous key salt-tolerance genes have been identified in maize: ZmPIF3, ZmHAK1, ZmNHX1, and ZmSTG1. Now Genome-Wide Association Studies (GWAS) and CRISPR/Cas9 technology are being used to extract genetic markers and tolerance mechanisms. These will feed directly into breeding programmes.

Conclusion

Salt stress hits maize on multiple fronts. It slows growth, lowers photosynthesis, distorts ion balance, and produces oxidative damage. Tolerance does not come down to one trait. It is the joint product of morpho-physiological adaptations, ion homeostasis, and antioxidant defence, and the genotypes that perform well usually do well across all three. Integrated mitigation and breeding strategies have moved the field forward, but the gaps that matter most are still the same two: long-term field trials under realistic mixed-salt conditions, and a credible link from seedling-stage screening data to reproductive-stage yield. For arid regions like Iraq, where most field salinity is mixed-salt, perennial, and on land that already has degraded drainage, closing those two gaps is the precondition for turning any of this work into yield in the bag.

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