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Deciphering physiological, biochemical, and molecular responses of potato under salinity stress: A comprehensive review

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Abstract

Among abiotic factors, salinity poses a serious danger to agriculture on a worldwide scale, seriously impairing crop productivity. Salinity has a significant impact on food security, making potato (*Solanum tuberosum*) a promising crop for the future. Due to ion toxicity brought on by osmotic stress during salt stress, potato plant growth is impeded. High salinity levels induce osmotic stress, significantly disrupting the overall physiological health of plants. This disruption manifests in various ways, including the onset of nutritional imbalances, hindrance in detoxifying reactive oxygen species (ROS), membrane impairment, and decreased photosynthetic activity. The broad spectrum of impact adversely influences crucial physiological and biochemical processes in plants. These encompass maintaining water balance, regulating transpiration and respiration, optimizing water usage efficiency, preserving hormonal balance, controlling leaf area, overseeing germination, and hindering the production

of antioxidants. The increased permeability of the plasma membrane and subsequent chemical leakage due to ROS during salinity stress result in water imbalance and plasmolysis. However, potato plants effectively manage oxidative stress induced by salinity by upregulating both enzymatic and non-enzymatic antioxidant activities. In response to counteracting the detrimental effects of salinity, plants synthesize osmoprotectants such as proline, polyols (including sorbitol, mannitol, xylitol, lactitol, and maltitol), and quaternary ammonium compounds such as glycine betaine. Many proteins and their interactions regulate the complex and varied pathways that contribute to the salt response and tolerance. This review intends to refocus emphasis on the need to investigate the physiological, biochemical, and molecular responses now in place and subsequently create viable mitigating solutions for salt stress in potatoes. © 2018 The Author(s)

Keywords: Antioxidant activities, Osmoprotectants, Overexpression, Potato, Reactive oxygen species, Salt stress

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Introduction

The potato, scientifically known as *Solanum tuberosum* L. is a significant member of the Solanaceae family. It stands as one of the most crucial vegetable crops globally which is highly regarded for its economic significance. It is considered as a main food for many people of the world as it is a good source of energy, rich in carbohydrates and starch, in addition to containing many minerals, vitamins and amino acids (Matlob et al., 1989). Potato crop is one of the important crops, with its consumption increasing, focusing on its quality and increasing its productivity. Due to their great nutritional content and outstanding productivity potential, the potato ranks fourth after rice, wheat and maize among the leading food crops globally (FAO, 2008). It is a crucial part of the global sustainable food framework since it produces more food energy on a smaller area of land than maize, wheat, and rice (Saha & Hossain, 2011). Potato production has increased, making it a crucial crop for reducing food shortages. A substantial portion exceeding half of the global potato supply originates from developing nations, which are also

regarded as important sources of food and money for many farmers (Sabur & Gangwar, 2005; Scott, 2011). The growth and production of plants are negatively impacted by a variety of environmental conditions because they are sessile, sensitive beings that experience diverse environmental pressures throughout their life cycle (Khan & Singh, 2008; Tuteja & Sopory, 2008; Yadav et al., 2012). According to Rengasamy (2006), environmental factors including salt, drought, cold, and UV have a negative impact on crop production in a number of regions of the world. By 2050, the population of the globe is predicted to be close to 10 billion, which will result in severe food shortages. To feed the growing global population, adaptable crops should be designed specifically for stress-prone areas (Gill & Tuteja, 2010).

Salinity of soils is one of the biggest ecological challenges to world agriculture (Zhang et al., 2007). It causes an imbalance in physiological processes in plants and has an effect on the quantity and quality of potatoes produced, especially in semi-arid growing regions. Moreover, salinity creates an adverse hydrological environment that prevents crops from growing normally (Amin et al., 2008). Anticipated trends indicate that the rising salinization of arable land will

result in significant global consequences, potentially causing a 30% reduction in usable land within the next 25 years and a potential 50% decrease by the middle of the 21st century (Wang et al., 2003). As per the United Nations Environment Program, approximately 50% of all cropland and 20% of agricultural land worldwide are currently affected by salt stress (Yokoi et al., 2002). Salinity exerts a detrimental effect on potato growth and yield, particularly during the initial growth stages (Katerji et al., 2003). The primary mechanism significantly affected by salinity is photosynthesis (Hayat et al., 2010). Furthermore, salt stress worsens respiration rates, ion toxicity, and membrane instability, collectively contributing to stunted plant growth (Gupta et al., 2002). Increased salt concentrations inhibit the growth and yield of potato by disrupting vital physiological processes, such as ion balance, water status, stomatal function, mineral nutrition, and photosynthetic efficiency (Munns, 2002).

Salinity stands as a primary abiotic stress that significantly diminishes both crop productivity and quality. The rehabilitation of salt-affected soil can be accomplished through good management of water and land (Bernstein, 1975), but the most practical and cost-effective method is to grow crops that can thrive and produce on such soils. Consequently, managing the effects of salinity on plants can also be done biologically (Rains, 1972). The effect of salinity on productivity may be mitigated by identifying plant genotypes with enhanced resistance to salt and incorporating these desirable features into commercially viable varieties. The practice of using living things or their byproducts for the benefit of humans or other living things is known as biotechnology. It combines tissue culture with genetic engineering. In genetic engineering, desired genes can be isolated from one organism and transform to same or other species. Genes can be transmitted from an organism in one kingdom to another. Biotechnology is considered as broad sense of gene pool. Biotechnology has emerged as a promising solution to address the salinity problem. In this approach, diverse plant species are rigorously evaluated for their stress tolerance capabilities. For plants susceptible to salinity, genetic transformation techniques are employed to introduce genes conferring resistance against salinity-induced stress.

The enhancement of abiotic stress resistance is now highly valued throughout the entire world; nevertheless, some effort has been concentrated in Pakistan on abiotic stress in potatoes, specifically salinity stress. Numerous studies have been conducted to address salinity challenges in agricultural regions by exploring methods such as irrigating with fresh water and implementing measures to prevent soil drainage through the enhancement of water courses. Poor and small landowners cannot employ these approaches because they are too expensive. It is challenging to create a variety for these abiotic challenges because of the autotetraploidy and polygenic quantitative inheritance of the potato's complex genetic composition. Evaluation of potato cultivars for salt stress using *in vitro*

methods and micropropagation is a very quick and contemporary method (Byun et al., 2007). Cutting-edge approaches to develop resilient crop plants particularly those capable of withstanding environmental stress like salinity integrate the application of plant tissue culture methods together traditional breeding and biotechnology (Rahman et al., 2008). A successful and quick strategy appears to be the investigation of plant salt tolerance to determine crop susceptibility (Zhu, 2007). According to Rengasamy (2006), environmental pressures like salt, drought, cold, and UV are affecting various parts of the world and reducing crop productivity. By 2050, it's predicted that there will be a significant food shortage when the world population approaches 10 billion. As a result, it is essential to develop adaptable crops specifically engineered for regions prone to stress, to sustain and nourish the increasing global population (Gill & Tuteja 2010).

Salinity

Salinity refers to the concentration of dissolved salts in a body of water, typically measured as the amount of salt (such as sodium chloride, magnesium sulfate, potassium nitrate, and sodium bicarbonate) present in one kilogram (1,000 grams) of seawater. These salts dissolve into ions, contributing to the overall salinity of the water. The electrical conductivity of a solution collected from a soil paste that has been soaked with water can be used to calculate the salinity of the soil. Salination is another term for the process of boosting the salt content in water. Salinity is the abiotic stress that causes the most harm (Gupta & Huang, 2014). Electrical conductivity of the extract, or EC_e, is the acronym for salinity. Its values are decisiemens per metre (dS/m) or millimhos per centimetre (mmhos/cm). Both units have the same numerical value and are equivalent in terms of measurement. Several plants are susceptible to soil salinity, and today's soils are becoming more salinized. Salinity develops when salt builds up on the soil's surface and rises to the soil's surface due to evaporation and capillary action. Salinity rises as a result of using potassium fertiliser incorrectly. The amount of salt in the soil has a significant impact on plant growth and development (Vidal et al., 2009). According to reports, nearly 25% of the world's irrigated land is harmed by salinity (Cuartero et al., 2006). Three direct mechanisms cause salt stress to simultaneously affect plant development and yield. First, salinity prevents the intake of water, which results in water stress, also known as osmotic stress due to the ion uptake in leaves, which causes a reduction in growth. Na⁺ was found to be more harmful than other ions (Lopez-Climent et al., 2008).

A study was carried out to assess how various soil salinities (sulfate-hydrochloric, sulfate-sodium, and hydrochloric-sulfate) at different stress levels impact the regeneration of the potato cultivar Tollocan (Bernal et al., 2013). This study was performed in controlled greenhouse conditions with selected tubers exposed to saline water treatments. The salinity levels were maintained between 0 and 15.0 dSm⁻¹ closely resembling field conditions. The regenerated tubers exhibited stunted

growth, and their yield was severely compromised. The combination of sulphate-hydrochloric and hydrochloric-sulphate with an electrical conductivity of 6.0 dSm^{-1} significantly hindered potato plant growth. This study led to the conclusion that potatoes are highly sensitive to sodium salinity. Homayoun et al. (2011) examined the salinity tolerance of potato varieties Agria and Marphona by subjecting them to different NaCl concentrations (0, 50, 100 and 150 mg l^{-1}) in a greenhouse setting. The experiment involved transferring potato plantlets, initially grown without growth hormones in plain MS medium in an incubation room, to 30 cm pots filled with disinfected sand-based soil. These pots were then moved to greenhouse conditions to induce salinity stress at the specified levels. The plantlets were exposed to two-month exposure to stress before being extracted from the pots to record multiple morphological parameters. The findings revealed a significant response from both potato varieties when subjected to induced salinity stress. Agria demonstrated a higher number of minitubers, but the size and quantity of buds on minitubers decreased with increasing salinity stress levels.

Khenifi et al. (2011) investigated the impact of salt stress on the micropropagation of six potato cultivars (Bartina, Spunta, Cardinal, Desiree, Timate, and Fabula) to determine their tolerance to NaCl. They exposed single-node cuttings from each cultivar to NaCl at concentrations of 0, 40, 80 mM, and 120 mM in MS medium for duration of four weeks. This experiment was repeated twice for both varieties. The researchers also examined data related to shoot length, root length, fresh weight, and dry weight to assess the differences in vitality and vigor among the genotypes. The results showed that salt stress had a pronounced impact on the fresh weight, shoot length, root length, and root weight, especially at higher NaCl levels (20-80 mM). In this study, the Bartina variety emerged as the more salt-tolerant variety producing greater shoot length across all tested salt concentrations.

Screening of potato cultivars against salinity

Salt stress conditions trigger the activation of numerous genes encoding complicated protein structures depending upon the plant species' genetic traits (Culha & Cakirlar, 2011). Under conditions of salt stress, diverse metabolic and physiological alterations take place in potatoes, where genes and transcription factors play crucial roles in coordinating these processes (Batelli et al., 2012). Prior research has demonstrated that salt stress dramatically reduces tuber yield and its associated components in field-grown potato crops (Ghosh et al., 2001; Elkhatab et al., 2006). Selecting salt-tolerant varieties through field trials is a prolonged, expensive and challenging process to replicate. *In vitro* cell and tissue culture techniques offer a

rapid, reliable, and contemporary approach for screening potato varieties for salt tolerance (Ashraf & Wu, 1994). *In vitro* conditions offer a quicker and more precise method for assessing plant growth under saline and drought stresses (Banu et al., 2015). Rahman et al. (2008) conducted experiments examining the salinity effect on three Bangladeshi potato cultivars using single-node cuttings. *In vitro* assessments of NaCl or mixed salt stress effects on potato genotypes have been proposed as feasible alternatives to the expensive, labor-intensive, and occasionally difficult field-based evaluations (Albiski et al., 2012). The impact of salinity stress on potatoes has been investigated using various methods such as single-node cuttings (Naik & Widholm, 1993), five-node cuttings (Morpurgo, 1991), and root tip segments or suspension cultures as explored by Naik & Widholm (1993). Their findings allowed for the determination of the relative tolerance of cultivars by conducting a multivariate analysis of six growth parameters in *in vitro* plantlets across different salinity levels.

In vitro screening offers an efficient alternative for selecting materials based on their response to salinity stress. Specifically, *in vitro* microtubers derived from potato plants have been proved to be invaluable resources for disease-free long-term preservation, genetic material transport, germplasm evaluation, and *in vitro* selection. This method of *in vitro* microtuberization not only facilitates physiological studies and germplasm selection in potatoes but also serves as a crucial source of explants for assessing potato plants' salt tolerance. The primary objective of this experiment was to employ *in vitro* screening to assess the salt tolerance of potato varieties commonly grown in semi-arid regions worldwide. This evaluation was based on morphological, growth, and developmental parameters.

Plant responses and mechanisms of salinity tolerance

To comprehend the physiological mechanisms responsible for salinity tolerance, it becomes essential to determine whether the reduction in growth arises from the osmotic impact of soil salt (osmotic phase) or the toxic influence of salt within the plant (ionic phase). The osmotic phase initiates once the salt concentration around the roots surpasses a certain threshold, leading to a decreased rate of shoot growth. Most plants exhibit a threshold level of 40 mM NaCl. This leads to slower development of new leaves and lateral buds resulting in fewer branches or lateral shoots (Munns & Tester, 2008). Conversely, it is logical for a plant under these conditions to maintain root structures or even extend root length to explore deeper soil layers for water, mitigating the effects of evaporation and reduced photosynthesis. The ionic phase occurs as salt reaches toxic levels in older leaves causing their death. When the rate of new leaf production lags behind leaf loss, the plant experiences reduced photosynthetic activity and slowed growth. Initially, osmotic stress significantly impacts growth, exerting a more pronounced influence on growth rates than ionic stress. Ionic stress affects growth at a later stage

with comparatively less intensity than osmotic stress (Munns & Tester, 2008). Nevertheless, in conditions of high salinity or in species unable to regulate Na^+ transport effectively, the ionic effect predominates over the osmotic effect (Munns & Tester, 2008).

Salinity tolerance can be categorized into three distinct mechanisms. The first mechanism involves tolerance to osmotic stress. Osmotic stress negatively impacts turgor pressure resulting in reduced cell expansion and consequently reduced growth. Enhanced tolerance to osmotic stress leads to greater leaf growth and increased stomatal conductance primarily benefiting plants with adequate soil moisture. Second is the exclusion of Na^+ by the roots preventing the buildup of toxic Na^+ concentrations in the leaves (Munns & Tester, 2008). Sodium (Na^+) is absorbed by the roots and then moves to the shoot through the transpiration stream. It's suggested that modifying the Na^+ transport processes in the root's plasma membrane could potentially exclude Na^+ from the shoot (Moller et al., 2009). Another approach involves tissue tolerance, where cells have the ability to endure the accumulation of Na^+ by separating Na^+ and Cl^- at both cellular and intracellular levels. This separation assists in preventing the cytoplasm from reaching toxic concentrations. Over time, toxicity becomes noticeable due to the gradual buildup of Na^+ to elevated levels, particularly evident in older leaves (Munns & Tester, 2008).

Functional exploration and utilization of *NHX1* genes for enhancing salt tolerance

Tang et al. (2010) conducted a research study involving the cloning of the sodium proton antiporter gene *TrNHX1* from *Trifolium repens* L., a forage legume. They not only isolated the gene but also assessed its integration and expression patterns. To accomplish this, they employed reverse transcriptase Polymerase Chain Reaction (PCR) and RACE (Rapid Amplification of cDNA Ends) techniques, utilizing degenerate oligonucleotide primers. Their investigation unveiled that *TrNHX1* possessed a nucleotide sequence having 2,394 bases, harboring an open-reading frame (ORF) with 1,626 nucleotides, ultimately encoding a protein of 541 amino acids, with a molecular weight of 59.5 kDa. The amino acid sequence of *TrNHX1* exhibited a substantial 78% homology with *AtNHX1*, a vacuolar Na^+/H^+ antiporter. This homology encompassed the presence of a consensus amiloride-binding domain. Notably, the functionality of *TrNHX1* was demonstrated through its capacity to ameliorate salt-sensitive phenotypes in yeast mutants Δnhx1 and $\Delta\text{ena1-4}\Delta\text{nhx1}$, as well as its ability to confer resistance to hygromycin-sensitive yeast mutants. Furthermore, the expression of *TrNHX1* in *T. repens* was significantly upregulated under elevated levels of NaCl (150 mM), underscoring its role in responding to salt stress. Tang et al. (2010) reported that *TrNHX1* serves a parallel role to the

vacuolar Na^+/H^+ antiporter gene, contributing to improved salt tolerance via ion homeostasis. Similarly, the functional exploration of *AtNHX1* gene was carried out by introducing it into soybean via *Agrobacterium tumefaciens*-mediated transformation (Xing et al., 2010). Through a comprehensive evaluation process encompassing integration, sustainability, and gene performance, they precisely analyzed the transgenic lines up to the T6 generation. Notably, within the pool of transgenics, two lines exhibited maximal expression of *AtNHX1*, encouraging the researchers to subject these lines to further scrutiny throughout the T5 generations. To ascertain the successful integration of the gene, polymerase chain reaction (PCR) techniques were effectively employed. The assessment of gene expression in all T5 progenies was achieved through Reverse Transcription PCR (RT-PCR). Remarkably, the T5 progeny plants displayed heightened tolerance to salt stress, underscoring the crucial role of the introduced gene in conferring salt tolerance. These collective outcomes emphasize the potential utility of the *AtNHX1* gene for enhancing salt-stressed lands' agricultural productivity.

The researchers investigated *TrNHX1* integration and its expression using reverse transcriptase polymerase chain reaction (RT-PCR) and Rapid Amplification of cDNA Ends (RACE) techniques employing degenerate oligonucleotide primers (Tang et al., 2010). Their discoveries unveiled that *TrNHX1* consisted of a 2394-nucleotide sequence and an open-reading frame (ORF) with 1626 nucleotides. This frame encoded a 541-amino acid protein weighing 59.5 kDa. Crucially, *TrNHX1* displayed a 78% homology with the vacuolar Na^+/H^+ antiporter, *AtNHX1* and possessed a consensus amiloride-binding domain. *TrNHX1* effectively mitigated salt sensitivity induced by both NaCl and KCl , in yeast mutants Δnhx1 and $\Delta\text{ena1-4}\Delta\text{nhx1}$. Furthermore, the expression of *TrNHX1* in *T. repens* increased significantly at elevated NaCl levels (150 mM), indicating its role in ion homeostasis. This study concluded that *TrNHX1* functioned similarly to the vacuolar Na^+/H^+ antiporter gene, thus enhancing salt tolerance through ion homeostasis. Similarly, Zhou et al. (2010) characterized the ubiquitin-conjugating enzyme gene, *GmUBC2*, after successfully cloning it from soybean crops. Following its isolation, this gene was introduced into soybean plants under conditions of drought and high salt levels. Transgenic Arabidopsis plants containing *GmUBC2* demonstrated improved resilience to both salt-induced stress and drought in contrast to their non-transgenic counterparts. The research further indicated that the increased expression of *AtNHX1* and *AtCLCa* (antiporters) prompted the activation of key genes associated with proline biosynthesis (*AtP5CS*) and the gene responsible for the copper chaperone for superoxide dismutase (*AtCCS*). These genes displayed significantly increased expression levels in the transgenic plants. It was concluded that *GmUBC2* upregulated ion homeostasis, osmolyte synthesis, and antioxidant tolerance. They additionally suggested that modifying and characterizing the ubiquitination pathway stands as a dependable strategy for augmenting salt and drought tolerance in crop plants using biotechnological and genetic engineering methodologies.

Conclusion

The emergence of abiotic stresses including heat, drought, and salinity poses a significant threat to potato cultivation. Among these stresses, salt stress is detrimental to potato production and productivity. Human activities such as groundwater deterioration, environmental pollution, and the disposal of industrial and sewage waste contribute to intensifying challenge of soil salinity placing substantial burdens on potato breeders. Salinity greatly affects the potato crop impacting various aspects such as yield, root and shoot formation, dry weight, and biomass production. Salt stress disrupts the osmotic balance, water regulation, nutrient equilibrium, and cellular and morphological processes in potato plants. Several essential physiological mechanisms, including source-sink interaction, hormonal regulation, antioxidant production and enzymatic activity are hampered by salinity stress in potatoes. The screening of potato cultivars has revealed that salt tolerance and sensitivity are genotype-dependent rather than epigenetic adaptations to stress conditions. *In vitro* screening offers a practical, quick and reproducible alternative to field trials for identifying and selecting salt-tolerant potato genotypes that facilitates further improvement through biotechnological and breeding methods. However, it is clear that more extensive research is needed to fully understand the mechanisms behind salt tolerance in potatoes. To overcome salinity stress challenge, a collaborative approach involving conventional, molecular, genomic, and transgenic methods is essential, with a particular focus on identifying salt-tolerant sources and incorporating them into breeding programs. This comprehensive research strategy is imperative to secure the future of sustainable potato cultivation in the face of growing salinity challenges.

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