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Ecology and Physiology of Plant growth in relation to soil salinity

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A B S T R A C T

This work is intended as a review of soil salinity as one common abiotic stress in ecological systems that adversely affect plant growth**.** In arid and semi arid areas, saline areas or areas irrigated with saline waters, most plant species exhibit reductions in growth and yield. The degree of salinization is a function of several factors including, the length of time over which the salts have been deposited, frequency of deposition, salt content of ground water, chemical composition and permeability of the underlying parent rock. Understanding the ecology of plant growth in relation to salinity is paramount for breeding and genetic engineering of salt tolerant plants. Exploitation of natural genetic variations and generation of transgenic plants with novel genes or altered expression levels of the existing genes are two major approaches being used to improve stress tolerance in plants. This paper reviews the occurrence and effects of salinity on growth of plants.

Key words: *Salt tolerance, salt stress; soil salinity, plant growth*

Introduction

Soil salinization is an increasing problem that affects crop production worldwide (Musyimi et al., 2008; Panta et al., 2014). Soil salt accumulation can vary with time and place, and it is a function of climatic variability, soil management, water quality, and irrigation method (Hessini et al., 2015; Salpeter et al., 2012; Seemann and Sharkey, 1986). The over salinity of the soil is one of the main factors that limits the spread of plants in their natural habitats. It is an ever- increasing problem in arid and semi arid regions (Ziska et al., 1989). Salinity refers to the occurrence of high concentrations of dissolved major inorganic ions in solution; including Na^+, Mg^{2+}, Ca^{2+}, K^+, HCO_3^-, SO_4^{2-} and Cl^- (Mwai, 2001). Saline soils are formed under hot, arid conditions due to an accumulation of salts in the topsoil and form naturally or as a result of poorly managed irrigation (Giller and Wilson, 1991; Landon, 1991; Mwai, 2001). Soil salinity implies that there is a high concentration of dissolved salts in the soil. Saline soils occur where the supply of salts, for example from rock weathering capillary rise, rainfall or flooding, exceeds their removal; for example by leaching or flooding (Landon, 1991). Salinization due to injudicious irrigation is recognized as being responsible for the loss of large tracts of agricultural land for cultivation (Mwai, 2001). The most common ions in the soil and at high concentrations are Na^+ and Cl^- (Rozema, 1991; Soussi et al., 1998).

Salinity has been recognized as the largest single soil toxicity problem (Pierce, 1990; Rozema, 1991). In saline areas or areas irrigated with saline waters, most crop plant species exhibit reductions in growth and yield (Belkhodja et al., 1994; Reinhardt and Rost, 1995; Rozema, 1991). The conductivity leading to 50 % decreases in yield (EC 50) is often used as an index of salinity tolerance. Plants are most sensitive to salinity during seedling growth (Reinhardt and Rost, 1995). When salinity is increased, growth will be suppressed, for sensitive species already at low salt concentration and for tolerant species at a high salinity (Rozema, 1991).It is generally accepted that there are major hazards associated with saline habitats. These may be described as: -Water stress arising from the more negative water potential (elevated osmotic pressure) of the rooting medium (Hessini et al., 2015).Specific ion toxicity usually associated with either excessive chloride or sodium intake (Hessini et al., 2015; Musyimi et al., 2008).Nutrient ion imbalance when the excess of sodium or chloride leads to a diminished uptake of potassium, nitrate or phosphate or to impaired internal distribution of one or another of these ions (Hessini et al., 2015). Salinity stress can also affect plant growth indirectly due to effects of salts on the soil (Levitt, 1980).

Dynamics of soil salinization

Soil salinization refers to the accumulation of soluble salts in the rooting region of the soil (rhizosphere) to concentrations that are high enough to affect plant growth and development (Mwai, 2001). The process and occurrence of salinization of soils is located primarily, although not exclusively, in arid and semi- arid regions of the world. The degree of salinization is an important determinant on whether soil is agriculturally productive or not, especially in the irrigated lands and in arid and semi arid regions (Pierce, 1990; Yeo, 1983). The degree to which soil has been salinized is a function of several factors such as the length of time over which the salts have been deposited, frequency of deposition, salt content of ground water, chemical composition and permeability of the underlying parent rock (Mwai, 2001; Pierce, 1990).

Soluble salts in groundwater can be traced to the composition of the parent material, to weathering and to sea-spray (Plaut and Federmann, 1991). Soil salinization may occur either naturally or artificially as a result of human activity. Under natural conditions, saline soils occur where drainage is sluggish, for example low lying lands such as the flood plain of rivers, low lying shores of lakes, in poorly drained depressions, and in arid climates (Mwai, 2001), due to high evaporation rates coupled with low precipitation and impeded drainage (Giller and Wilson, 1991). Soil salinity has also developed as a result of faulty irrigation, especially in the tropical arid and semi-arid regions where the only arable land has to be irrigated and the water available for irrigation is usually salt rich. Furthermore, soils in these regions are usually rich in salts (Giller and Wilson, 1991; Mwai, 2001).

Modern agriculture management practices often worsen the extent of salinity by remobilizing salts from deep soil layers (Belkhodja et al., 1994; Rozema, 1991). Problems of salinity occur as well in non-irrigated environments. Dry land salinity, which occurs through the process of saline seep, also reflects a change in the quantity and movement of groundwater. Modifications of the vegetative cover (perennials to annuals), certain cultivation practices such as summer fallow, and the management of surface water, including snowmelts are responsible for these changes (Landon, 1991; Plaut and Federmann, 1991).

Secondary salinization and alkalinization occur when the natural drainage system is unable to accommodate the additional water input, causing a rise in ground water levels. Problems of salinity and alkalinity also occur because of the application of brackish, saline and alkaline waters (Mwai, 2001; Plaut and Federmann, 1991).

Classification of saline soils

Salinity is commonly measured as electrical conductivity (EC) and soils are classified as saline, if the EC is greater than 4 d SM^{-1} (Giller and Wilson, 1991; Rozema, 1991) and an exchangeable sodium percentage (ESP) less than 15; sodic soils (non- saline alkali soils with an EPS greater than 15 and with an EC less than 4 millimhos / cm (Rozema, 1991; Landon, 1991). The high ESP modifies the physical and chemical properties of the soil. Saline alkali soil refers to soil with an EPS >15 and EC > 4 millimhos / cm. Salt in saline soils consist of a mixture of Na, Mg, Ca, as cations, and chloride and Sulphate as anions. Sodium and chloride are the main ions (Rozema, 1991).

Salt-affected soils are commonly divided into two main groups namely; the saline group, which refers to soils affected by sodium salts such as sodium chloride and sodium sulphate; and an alkali group, which indicate soils affected by sodium salts capable of alkaline-hydrolysis such as bicarbonate and sodium carbonate (Plaut and Federmann, 1991). Soils may be both saline and alkaline at the same time, depending on the proportion of sodium to calcium and magnesium in the salts (Plaut and Federmann, 1991). The properties of these soils depend on the ratio of soluble salts and exchangeable sodium. Properties of sodic soils may be amended by the application of $CaSO_4$ or $CaCl_2$ improving permeability drainage and aeration (Rozema, 1991; Robinson et al., 1983; Salpeter et al., 2012).

The following are some of the ways by which salts may accumulate in the soil: -

- Irrigating an area with restricted drainage due to hard pans, poor soil structure, or an unweathered impermeable rock layer. This would raise the water table sufficiently to establish capillary contact with the surface soil (Mwai, 2001).
- Man-made salination of arable land may occur as a result of irrigation practices in semi arid areas. Insufficient application of irrigation water leads to insufficient leaching of the salts imported either in the irrigation water or otherwise, and hence accumulation in the soil (Mwai, 2001).
- Diversion of irrigation canals from the lower reaches of rivers and streams, which are already salt loaded may lead to seepage and return flow of salts collected from irrigated land upstream (Mwai, 2001).
- Use of poor quality irrigation water, which has excess concentration of soluble salts (Perera et al., 1997).
- Surface run-off from irrigated cropland which is often contaminated with salts; and the growth in reservoirs and canals for irrigation purposes, which exposes the water to evaporation and therefore increasing salt concentrations (Perera et al., 1997).

Relative salinity tolerance of plants

Most terrestrial plant species are not capable of growing well at a salt concentration in a nutrient solution of 50 mM NaCl or higher. Only a small group of halophytic plant species, that posses a highly specialized type of physiology and morphology shows good growth under saline conditions, up to the salinity of sea water, that is 500 mM NaCl (Robinson et al., 1983).

Plant species in general, including crop plants differ with regard to their tolerance to salinity; it may also be that crop plants are tolerant to salinity at one growth stage but sensitive during another stage of the life cycle (Gorrham et al., 1985; Levitt, 1980). The ability of a species to recover after harsh conditions, like salinity, drought, or waterlogging, is related to the stress intensity (level and duration) and the damage induced by the stress (Hessini et al., 2015). Most crops tolerate higher salt concentration under cool humid conditions (Robinson et al., 1983; 1985), compared to hot and dry conditions. In most saline soils potassium is found in far lower concentrations than Na^+, which competes with K^+ by a low affinity mechanism; hence a Na^+-induced K^+ deficiency is produced (Mckersie and Leshem, 1994). Rozema (1991) has noted that complete reclamation of salinated land requires replacement of the accumulated sodium by calcium. Fertilization of soil will increase yields of saline soils proportionally more than of non-saline soils (Mckersie and Leshem, 1994). Salt tolerance during germination and emergence, is based on survival of early seedlings and also salt tolerance of older plants may be based on a decrease of growth rate or yield (Robinson et al., 1983).

Salinity stress and plant responses

Movement of salt into roots and to shoots is a product of the transpirational flux required to maintain the water status of the plant (Hasegawa et al., 2000). Prolonged transpiration brings large amounts of salt into the shoot, especially into the old leaves, thus killing them. This process eventually limit the supply of assimilates to the growing regions and might be the main factor determining yield (Munns and Termaat, 1986). Upon salinization, Na^+ moves first to the older, expanded leaves and not to the young developing leaves (Yeo and Flowers, 1986). As the concentration of a nutrient ion in the external medium increases, so does its rate of uptake by the plant. To protect actively growing and metabolizing cells, plants regulate ion movement into tissues (Hasegawa et al., 2000; Levitt, 1980).

The main barrier to passive Na^+ and Cl^- flow to the shoots is almost certainly the suberized endodermis (Flowers and Yeo, 1992; Greenway and Munns, 1980). High ion concentrations in leaves could be prevented if ions were removed from the xylem during upward transport, and this occurs for Na^+ in some salt-sensitive species (Munns, 2002). The accumulation of large quantities of ions in mature and old leaves which then senesces has often been observed under salt stress (Flowers and Yeo, 1992). Measurements of ions in phloem sap have indicated that the more salt tolerant species exclude Na^+ and Cl^- from the phloem to a large extent, whereas less tolerant ones do not have the same restriction (Munns, 2002).

Abscisic acid (ABA), cytokinin and other hormones apparently control root and integrated plant growth in response to environmental stress like salinity (Pierce, 1990). Abscisic acid takes part in the adjustment of leaf metabolism to decrease in water activity and regulates stomatal conductance under stress conditions (Seemann and Critchley, 1985). The accumulation of ABA in leaves generally provides reasonably strong evidence that ABA modulates stomatal aperture in leaves under environmental stress (Bradford, 1983; Seemann and Critchley, 1985). Abscisic acid is a plant growth substance known to influence stomatal behavior (Bradford, 1983). Farquhar and Sharkey (1982) have suggested that irradiance of mesophyll tissue should reduce the amount of ABA available via the free space to the guard cells and enhance stomatal opening.

Studies indicate ABA inhibitory to root growth and extension (Robertson, 1985). Increases in ABA level in roots may directly affect growth and development at the root apex (Bradford, 1983). Root apex has the capacity to perceive and respond directly to stress (Robertson, 1985). ABA may have a more direct effect on root development during environmental stress.

Cytokinins have been reported to play a role in preventing stomatal closure and possibly ameliorating the effect of stress on assimilative capacity of plants (Bradford, 1983; Itai and Vaadia, 1971). Bradford (1983) suggests that cytokinins may be involved in the maintenance of photosynthetic capacity. Severe salinity stress can inhibit leaf photosynthesis through stomatal closure (Marler and Zozor, 1996; Micklebart and Arpaia, 2002). Also salinity inhibits non-stomatal processes (Plaut and Federmann, 1991; Yeo, 1983).

Salt taken up by plants may not directly control their growth by affecting turgor pressure, photosynthesis or enzyme activities; rather the build of salt in old leaves may hasten leaf death (Belkhodja et al., 1999; Munns, 2002). This may in turn affect the supply of assimilates or hormones to the growing regions thereby affecting growth. An increase in the cytokinin supply from the roots (perhaps signaling increased root growth) could affect photosynthesis by stimulating chlorophyll formation and protein synthesis, and at the same time promote stomatal opening during the early stages of osmotic adjustment to salinity stress (Farquhar and Sharkey, 1982).

Cytokinins can promote synthesis of photosynthetic enzymes and electron components in expanding leaves (Itai and Vaadia, 1971). Accumulations of apoplastic solutes have been shown to affect stomatal aperture according to Sibole et al. (2003). For some species Na^+ could contribute to stomatal closure (Landon, 1991; Marler and Zozor, 1996; Sharma and Hall, 1992). Perera et al. (1997) found a direct response of the stomata of *Aster tripolium* to Na^+ which was not ABA-mediated and hypothesized that such sensory system is useful to control the amount of salt delivered to the leaf by the transpiration stream. It is important to establish that varietal differences in ion concentration could merely be consequences of growth inhibitions or injury (Netondo, 1999; Perera et al., 1997).

Salt stress avoidance and salt stress tolerance are the two major kinds of salt resistance (Levitt, 1980). Salinity stress avoidance is achieved by the maintenance of low salt concentration in the cells either in a passive excretion or dilution mechanism (Gorrham et al., 1985; Hasegawa et al., 2000). Glycophytes restrict ion movements to the shoot by attempting to control ion efflux into the roots xylem (Hasegawa et al., 2000). Some halophytes exclude Na^+ and Cl^- through glands and bladders (Gorrham et al., 1985; Mckersie and Leshem, 1994). Plants ultimately survive and grow in saline environments because of osmotic adjustment through intracellular compartmentation that partitions toxic ions away from the cytoplasm through energy dependent transport into the vacuole (Alian et al., 2000; Hasegawa et al., 2000).

General considerations of salinity stress on plant growth

Plants are considered to be under stress when they experience a relatively severe shortage of an essential constituent or an excess of a potentially toxic or damaging substance. When soils contain high amounts of soluble salts or high amounts of sodium, they develop unfavourable characters, which hamper both cultivation operations and plant growth (Mwai, 2001).

Salinity effects on plant growth and yield depend in part on factors that affect acquisition of carbon (Yeo, 1983). Photosynthesis is usually lower in plants exposed to salinity and may decline with time of exposure (Munns and Termaat, 1986; Netondo, 1999). The degree of inhibition by saline conditions varies greatly among species, as do the mechanisms involved in inhibition (Mckersie and Leshem, 1994). Like many other crop plants; citrus leaves are sensitive to salt injury when saline solutions come into contact with leaves (Romero-Aranda and Syvertesen, 1996). Marler and Zozer (1996) indicated that salinity reduced CO_2 and light efficiency.

Plants can withstand high chloride concentrations by restricting chloride uptake and transport to leaves or by an increased ability of their leaf tissue to tolerate high chloride concentrations (Bar et al., 1996; Musyimi et al., 2008). Tolerance by citrus trees to chloride is attributed to rate of chloride transport from the soil to the leaves (Bañuls and Primo-Millo, 1992). Bar *et al.* (1996) have reported chloride uptake by avocado trees to be high at low concentrations of nitrate in the soil.

Reduction of leaf growth due to salinity has been reported in many plant species including, Spider plant and sorghum among others (Richardson and McCree, 1985; Musyimi et al., 2008; Netondo, 1999). Mwai (2001) reported inhibition of the leaf initiation, emergence and growth of new leaves in highly stressed spider plants due to salinity. According to Yeo and Flowers (1986), salinity has little effect upon leaf initiation, but accelerates senescence. The overall effect of salinity is to reduce the life span of expanded leaves. The distribution of Na^+ from leaf to leaf is not related to their transpiration rates (Ziska et al., 1989).

Salinity reduces photosynthesis, stomatal conductance and water potential in leaves of citrus trees (Bañuls and Primo-Millo, 1992). Improved potassium nutrition has been reported to cause reduced transpiration rate of wheat by more complete closing of the stomata (Mishra et al., 1991). Potassium also plays important role in photosynthesis, and up to 50 % of the total quantities of this element in leaves are in chloroplasts.

In glycophytes, soil moisture deficit and soil salinity each result in reduced leaf expansion rates and lower photosynthetic rates per unit of leaf area (Richardson and McCree, 1985; Reinhardt and Rost, 1995). Any loss of water can be potentially harmful for plants growing in saline areas (Nobel, 1983).

Stomata play an important role since they are the routes through which water vapor leaves and carbon dioxide and oxygen required for photosynthesis and respiration enter into the leaf (Netondo, 1991). The stomata remain open whenever the guard cells have sufficient turgor pressure and so the plant loses water by transpiration (Netondo, 1991). Salt accumulation in plants interferes directly with photosynthesis in non-halophytes (Panta et al., 2014).

According to studies by Bañuls and Primo-Millo (1992) analysis of photosynthetic response to changes in foliar Cl^- and Na^+ concentrations indicated the predominant role of chloride in reducing gas exchange of Hamlin orange leaves. Decrease in dry matter production and leaf content of potassium, magnesium and calcium have been reported in spinach and lettuce due to sodium salts (Levitt, 1980).

Salinity can seriously change the photosynthetic carbon metabolism, leaf-chlorophyll content, as well as photosynthetic efficiency (Netondo, 1999; Sibole et al., 2003). Salt promotes the accumulation of ammonium, nitrate and free amino acids in plants (Sibole et al., 2003). Proline and carbohydrate are accumulated in plant tissues under saline stress, and these substances are suspected of contributing to osmotic adjustment (Sibole et al., 2003; Qados, 2011).

Salt stress may cause a rate limitation in the photosynthetic system, thereby, disposing the photosynthetic system to over-energinazation even at low light (Seemann and Sharkey, 1986). Greater inhibition of CO_2 assimilation may indicate that the dissipation of excess energy is less efficient (Seemann and Sharkey, 1986).

Photosynthesis as a major plant process, which contributes to plant growth and productivity, may be reduced by stomatal closure restricting the supply of CO_2 to the photosynthetic apparatus in leaves (Netondo, 1991). Closure therefore limits photosynthetic activity, thereby influencing total plant dry matter accumulation. A further reduction of photosynthesis results from non-stomatal factors, which becomes effective under severe salinity stress conditions (Ashraf et al., 2002; Robinson et al., 1983; 1985).

Decrease in photosynthesis could be an indirect consequence of impaired physiology of plants growing under salinity stress (Munns, 2002; Reinhardt and Rost, 1995). Growth of plants is ultimately reduced by salinity but species vary in the salt concentration they can tolerate before growth is impaired (Robinson et al., 1983). The reduction in growth is often accompanied by decreased rate of photosynthesis. Reduction in photosynthetic capacity with salt stress is associated with decreased stomatal conductance (Belkhodja et al., 1999; Netondo et al., 2004). However recent studies have reported that non-stomatal factors such as inhibition of CO_2 fixation by the chloroplasts during stress may account for decreases of photosynthetic activity (Musyimi et al., 2008). Different studies have reported a relationship between non-stomatal effects and the presence of high leaf Na^+/ Cl^- concentrations (Seemann and Critchley, 1985; Sibole et al., 2003). Tolerant cultivars are expected to exhibit fewer disturbances in the photosynthetic processes when growing under salinity (Belkhodja et al., 1999).

Osmotic adjustment involves net accumulation of solutes in a cell in response to falls in water potential of its environment. As a consequence, cell osmotic potential is diminished, which in turn attracts water into the cell and so tends to maintain turgor pressure. Several compounds, like sugars, glycerol, amino acids (such as proline, quaternary ammonium, sulfonium compounds (e.g., glycinebetaine), polyols, and sugar alcohols contribute to osmotic adjustment (Hessini et al., 2015). Some of the tolerant plants accumulate Na^+ and Cl^- for osmotic adjustment, but that ions are at least partially excluded from the cytoplasm where they may inhibit metabolic functions (Robinson et al., 1983). Reduction of osmotic potential by solute accumulation has been regarded as a fundamental process for turgor and hence growth maintenance for plants under environmental stress (Reinhardt and Rost, 1995; Robinson et al., 1983). Many plants lower their osmotic potentials in order to maintain turgor during salinity stress. This osmotic adjustment may involve uptake and accumulation of inorganic ions or the synthesis of organic solutes (Robinson et al., 1983). Excess salinity decreases the osmotic potential of the available soil water, hence reduction in the energy gradient of water flow through the soil-plant-atmosphere continuum (Qados, 2011). Reduction of the water flow through plants may, in turn, result in leaf-water deficits that adversely affect leaf turgor or stomatal conductance (Bañuls and Primo-Millo, 1992). Most tree crops are considered salt sensitive, especially in regards to chloride; however, it is not clear how much of this sensitivity is due to changes in leaf water status.

Conclusions

Salinity is a major ecological problem which needs to be addressed. There is clear and urgent need to develop salt tolerant plants that can cope with the changing climate and environmental changes. A call is made to ecologists, ecophysiologists, plant breeders, environmental scientists, and plant biochemists to intensify their research in solving salinity problem.

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