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Soil Salinisation and Salt Stress in Crop Production

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1. Introduction

For optimal grow and development, cultivated plants require balanced presence of water and dissolved minerals (salts) in their rhizosphere. In that respect, quality and availability of two natural resources, water and soils, are crucial in cultivation. Although Earth abounds in water, an almost negligible portion (~2.5% or 35 million km³) is fresh or with low salt concentration (<1 dS/m) (Shiklomanov & Rodda, 2003; Ondrasek et al., 2010), i.e. water that may be conditionally used for irrigation in crop production, whereas the rest is salty and therefore unsuitable for irrigation. However, irrigated agriculture consumes ~70% (and >90% in many developing countries) of total water withdrawal to produce ~36% of global food (Howell, 2001). According to recent estimates (ICID, 2009), almost 300 million ha in the world are irrigated, with ~2/3 of that in most populated and the fast growing Asian countries. In many irrigated agricultural areas, especially in developing countries, water scarcity is pronounced because of environmental conditions (e.g. arid and semiarid climate zones) and the rising population (i.e. food demand). As a consequence, there is an increasing trend of inappropriate use of restricted water (e.g. over/pumping of salinised aquifers) and continuous degradation of land resources (e.g. salt-affected soils), representing a large burden to human food supply and natural ecosystems.

Some of the most produced and widely used crops in human/animal nutrition such as cereals (rice, maize), forages (clover) or horticultural crops (potatoes, tomatoes) usually require irrigation practices, but are relatively susceptible to excessive concentration of salts either dissolved in irrigation water or present in soil (rhizosphere) solution. In a majority of cultivated plants, yields start declining even at relatively low salinity in irrigation water ($EC_w > 0.8$ dS/m) (e.g. Ayers & Westcot, 1994) or soil ($EC_{se} > 1$ dS/m in saturated soil extracts) (see Table 1 in Chinnusamy et al., 2005). Increased soil salinity may induce various primary and secondary salt stress effects in cultivated plants (section 4.3.1). Salt stress as one of the most widespread abiotic constraints in food production may also result in the negative ecological, social and/or economic outcomes. For instance, recent deposition of toxic salt sediments and sea intrusion in tsunami-affected areas of Maldives damaged >70% of agriculture land, destroyed >370,000 fruit trees and affected around 15,000 farmers, with

costs estimated at around AU\$6.5 million (FAO, 2005). Successful remediation of salt-degraded areas for crop production, besides using relatively salt-tolerant species/genotypes, is highly dependent on sustainable management practices that are usually costly, time consuming and may be difficult or impossible to implement fully in certain ecological situations (e.g. seepage soil salinity; section 3.1). Accordingly, in response to the salinity issue, Australia's National Action Plan for Salinity and Water Quality from 2000, resulted in investments of about AU\$1.4 billion over 7 years to support actions by communities and land managers in salt-affected regions (Williams, 2010). However, recent advances in plant breeding and molecular biology technologies suggest that increasing salt tolerance in cultivated plants could be one of the most promising and effective strategies for food production in salt-affected environments.

2. Salinisation - A global land degradation issue

Different types of physical, chemical and/or biological land degradation processes (e.g. compaction, inorganic/organic contamination, diminished microbial activity/diversity), mostly under excessive anthropogenic pressures during the last century, have resulted in serious consequences to global natural resources. Among them, soil salinisation, arising from either natural or human-induced causes, led to an increase in concentration of dissolved salts in the soil profile to a level that impairs food production, environmental health and socio-economic wellbeing (Ondrasek et al., 2009a; Rengasamy, 2006). Despite numerous adverse environmental consequences (e.g. crop yield/quality decline, disruption of soil aggregates/structure, desertification), areas already affected by salinity are among the most intensively exploited ones in global agriculture. Salinisation is among the three soil degradation processes [in addition to organic matter (OM) decline and contamination] recognized as the main threats to environmental resources and human health in EU (Ondrasek et al., submitted a) and many other developed (Helal et al., 1999) or developing countries (Rengasamy, 2006), affecting almost 1 billion ha worldwide.

3. Soil salinisation processes

Depending on soils, the extracted solutions differ in the content of dissolved salts (cations/anions); if total salt concentration, i.e. electrical conductivity (EC_{se}), exceeds 20 mM (~ 2 dS/m), they can be categorised as salt-affected (e.g. Abrol et al., 1988). The underlying salinisation processes may be primary (natural) and secondary (anthropogenic) (Ghassemi et al., 1995). Main driving forces of naturally-induced (inherent) soil salinity are: i) intrusion of highly salinised water in coastal (oceans, sea) or continental (e.g. fossil salt aquifers) regions, ii) aeolian i.e. wind borne salt from salt surface waters (oceans, lakes) deposited inland, and iii) dissolution of soil parent minerals. In contrast, some agricultural practices (fertigation, application of inorganic/organic soil amendments) may contribute to secondary salinisation processes. In contrast to that categorised classification, soils salinisation principally inherent to Australian environmental conditions is different (Biggs et al., 2010; Rengasamy, 2006).

3.1 An Australian example

Australia is the most salt-affected continent with $\sim 1/3$ (~ 260 million ha) of total global salinised area, and $\sim 1/2$ of total world's alkaline area (e.g. Szabolcs, 1989). The most

widespread Australian soil salinity (>250 million ha), called subsoil or transient, is present in alkaline (pH >8.5) and Na-enriched soils (e.g. ESP \geq 6) (Rengasamy, 2002) and specific climatic surrounding, where evapotranspiration demand frequently exceeds rainfall by multi-fold. Transient salinity occurs preferentially in higher ecobiotopes (e.g. slight uplifts and terraces), in illuvial subsoil (B) horizons (20-100 cm from the soil surface) enriched with topsoil-leached Na salts (EC_{se} 4-16 dS/m) and dispersed clay particles (e.g. Rengasamy, 2002, 2006). In such subsoil circumstances, whereby excessive Na⁺ presence disturbs soil structure and hydraulic properties (e.g. Ondrasek et al., 2010), after watering i.e. during wet season, dissolved salt ions fluctuate over the solum and cause its salinisation. Therefore, subsoil salinity is triggered by water/solute flux and hydraulic conductivity of (sub)pedosphere (e.g. Rengasamy, 2002), rather than by the fluctuation of salinised groundwater that is the main cause of second most abundant type of salinisation in Australian soils.

Groundwater-induced (seepage, dryland) salinity, in contrast to transient salinity, occurs in the lowest positions in the landscape (e.g. base of slopes/valleys). In this type, also called catena form - type 1, water flows relatively easily through the lighter textured soils in upslope locations, but cannot move as quickly through the heavy soils in the footslope, causing waterlogging and seepage (Biggs et al., 2010). It is induced by upwards intrusion and/or capillary rising of highly saline (EC_w up to 150 dS/m) and relatively superficial (<2 m from land surface) watertable, even up to topsoils strongly salinising them (EC_{se} up to 80 dS/m) by secondary processes (Rengasamy, 2002). From economical/ecological perspective, soils affected by dryland salinity are more adversely affected than transiently saline subsoils, are highly restricted for cultivation and could be high costly to remediate.

Total annual cost to Australian economy caused by dryland/transient salinity and associated subsoil constraints (e.g. excessive pH, Na, Cl, B, Al, carbonates; see review by Dang et al., 2006) are estimated at more than A\$1.6 billion (e.g. Rengasamy, 2002). One of relatively cost-effective and widely used strategies in coping with groundwater salinity in Australia is lowering/controlling of watertables (e.g. around 1 m from soil surface) by withdrawing from underlying salt-affected aquifers and using the water in irrigated agriculture (directly or after mixing with fresh water), thus enables salt leaching and improved permeability in the rhizosphere (e.g. Bethune & Batey, 2002). Also, a short-term use of slightly to moderately salinised water for irrigation of perennial pastures (EC_w 0.8-2.4 dS/m) or legume lucerne crops (EC_w 2.5 dS/m) would have little effect on their production (e.g. Burrow et al., 2002; Rogers, 2001).

However, over the long-term period, such irrigation practices will most likely induce (among other constrains discussed later) irrigation salinity as a widespread soil degradation problem. In many similar arable, (semi)arid areas around the world, secondary salinisation induced with inappropriate irrigation/drainage practices (e.g. re/using of saline ground/surface waters, using of industrial/municipal waste waters/effluents, over-pumping of coastal aquifers, lacking/improper subsoil drainage, etc) affects ~50% of global irrigated areas, with an annually increment of up to 500,000 ha (e.g. Martinez-Beltran & Manzur, 2005; Ondrasek et al., 2009a), representing a serious threat to sustainable food production and deterioration of natural terrestrial resources.

Recently, ICID (2009) estimated that >20% of water used in Australia is derived from groundwater sources, and out of that the most is used for irrigation of totally ~2.55 million ha irrigated land area. A substantial part of that land is probably exposed to secondary irrigation salinisation because (re)using of saline groundwater for crop irrigation is one of common

strategies in Australian soil salinity management (Bethune & Batey, 2002). According to the same authors, irrigated pastures, mostly developed on lands with highly salinised watertables, are spread on around 30% or 0.7 million ha of irrigated land in Australia.

There are many other types of primary/secondary land (water) salinisation processes (see report by Biggs et al., 2010) such as i) closed depression salinity i.e. primary salinity that occurs in natural deep depressions (e.g. lakes, swamps, etc: Figure 1a) with restricted leaching and pronounced surface (10-30 mm) salt encrustation i.e. crystallisation (Figure 1c), and ii) so-called dam-form salinity, occurring in many water storage areas (Figure 1b).

3.2 An European (Croatian) example

Soil degradation processes are widespread in European countries (e.g. wind/water erosion on ~160 million ha or ~15% of total Europe's area; compaction on ~36% of European subsoils, etc) and have been either driven or exacerbated by human activities (European



Fig. 1. Closed depression (a, c) and dam (b) type salinity with the white surface salt encrustation (a, b, c) in the Lake Grace area, Western Australia (Photos taken by G. Ondrasek, 2011).

Commission, 2006). According to the same source, total annual costs of some of the most important land degradations (erosion, OM decline, salinisation, landslides and contamination) that could be estimated amount to AU\$52 billion, and do not include the damage to the soil ecological functions as these are exceedingly difficult to quantify. Among continents, Europe has the lowest portion of degraded soils by excessive salinity (~31 million ha), ~8-fold lower compared to the most salt-affected Australia (e.g. Szabolcs, 1989). According to General Soil Map of Croatia (1:50,000) permanent halomorphic soil classes (Solonchak and Solonetz) are minor i.e. distributed on <600 ha or 0.01% of total land area (Bogunovic et al., 1998). However, recent multidisciplinary studies, related to environmental salinisation processes (land/water) and their influence on irrigated agriculture and natural ecosystems of intensively agro-exploited coastal estuaries (Ondrasek et al., 2010; Romić et al., submitted) suggest potentially large influence of salinisation in Mediterranean areas of Croatia. Also, seems that substantial portion of salinised land areas is still fortunately periodically characterised because of specific geo(pedo)logical and climate interactions. From geological perspective, along coastline of Adriatic Sea there are many fertile and arable karstified fields and alluvial estuaries with similar properties and exposure to salinisation processes as can be explained in case of Neretva River delta (Figure 2).

The geological parent material in down stream of Neretva river consists of: i) Mesozoic and Paleogene carbonates with certain Paleogene flysch materials (creating the basement of the fractured and deeply karstified valley that is very susceptible to sea water intrusion; Figure 2a), and ii) Quaternary sediment and poorly lithified deposits (with heterogeneous water permeability and other hydraulic properties) representing surface of lito(pedo)sphere underlain by clay, sand and/or gravel alluvial (Holocene) fractions as well as Pleistocene conglomerates (Romić et al., submitted). Also, direct sea water intrusion, in the shape of salty wedge, through Neretva river and its natural/artificial tributaries is possible even up to several tens of kilometres upstream, depending on river watertable and seasonal (dry/wet) conditions (Figure 2b). Irrespective of which way seepage of salty water is manifested (directly through porous karstified materials or via river flows, laterally or upwardly through alluvial deposits), salty water is mixing with groundwater, restricting its usage for agriculture or as drinking water (Figure 2c).

As confirmed by chemical analyses of surface and groundwater sources and topsoil saturation extracts, primary and/or potential secondary salinisation processes are present on >2,500 ha of irrigated land in Neretva River estuary, given that EC_w/EC_{se} and/or SAR (Sodium Adsorption Ratio) values exceed those recommended for agriculture by FAO (e.g. Abrol et al., 1988; Ayers & Westcot, 1994; Ondrasek et al., 2010). Detected processes of primary salinization caused by the capillary rising of highly salinised groundwater (e.g. $EC_w > 23$ dS/m at <4 m depth) may initiate salt accumulation in (sub)soil horizons (Ondrasek et al., 2010). Also, multi-annual monitoring of quality of surface water sources (ameliorative drainage channel network, Romić & Vranjes, 2010) confirmed their periodically strong salinisation and serious restrictions of their irrigation usage (i.e. $EC_w > 3$ dS/m) (Ayers & Westcot, 1994). Meanwhile, at most analysed locations, surface water is used in intensive horticultural production employing drip/micro sprinkler fertigation practices (Romić et al., 2008), inducing secondary soil salinisation. However, favourable climate and soil conditions such as i) intensive rainfall (>650 mm) in between two vegetation seasons, ii) relatively homogenous/stable solum structure, and iii) light soil texture and therefore good water permeability of majority of alluvial sediments, enable leaching of accumulated topsoil salts

into deeper horizons (below the root zone) and underpin resilience of these agricultural ecosystems (Ondrasek et al., 2010). Finally, recently initiated monitoring of salinisation downstream of Neretva River estuary (Romic & Vranjes, 2010 and references therein) will provide new insights into the subsoil constrains in this area (e.g. salinity/sodicity).

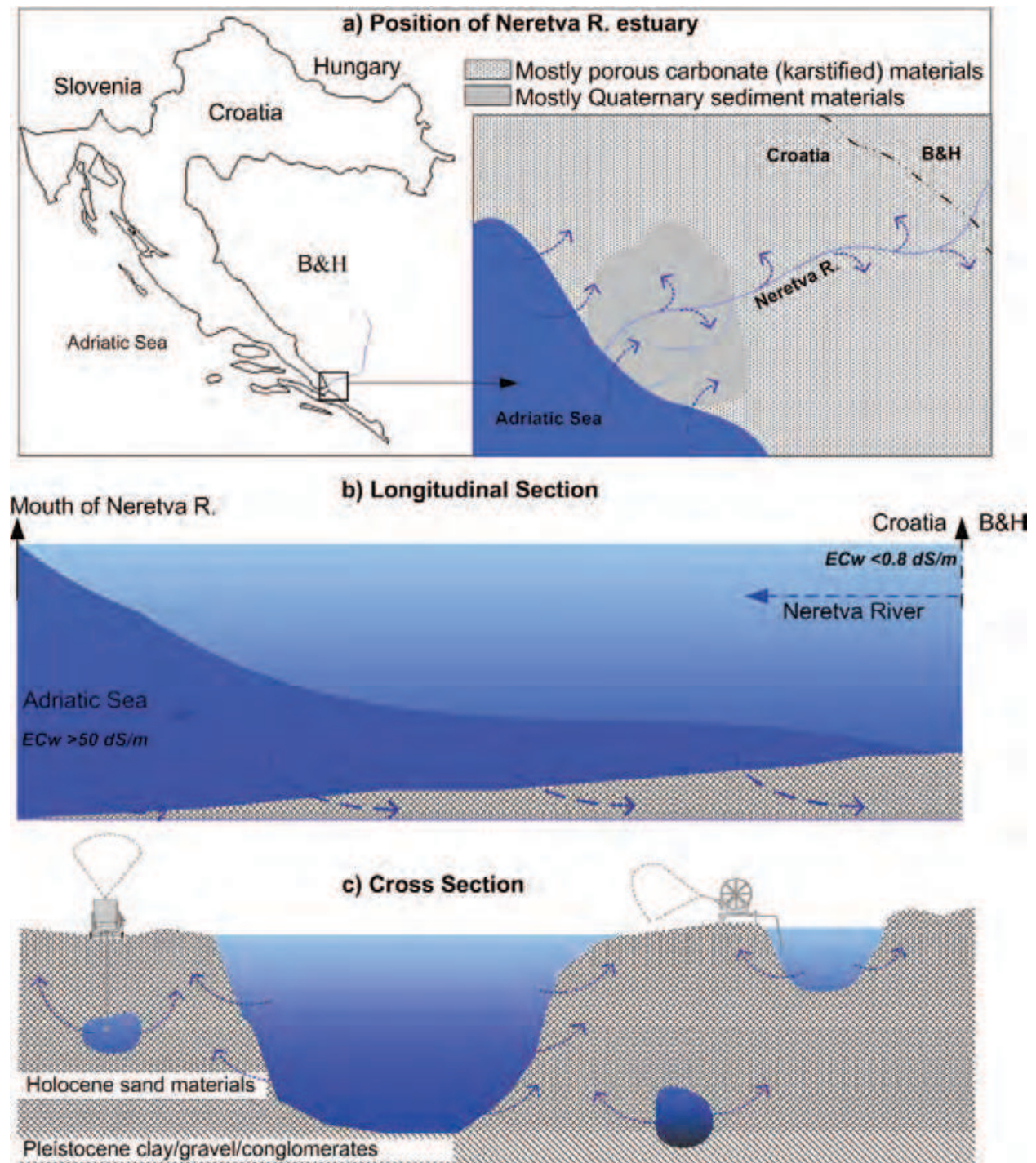


Fig. 2. Salinisation processes in Neretva river estuary, Croatia, adopted from Ondrasek, 2008; Romic et al., submitted and references therein (dashed arrows represent intrusion of sea/salted water, whereas the straight arrows are main flow directions of river/sea)

4. Environmental consequences of soil salinity

4.1 Impact on pedosphere

Soil salinity is often accompanied by a wide range of pedosferic (low soil fertility, high exposure to erosion processes), atmospheric (high air temperature, low precipitation and air humidity) and/or hydrospheric (water scarcity) constraints, which negatively influence agricultural production. However, secondary consequences of salinity, such as those due to long-term usage of salinised water for irrigation, may cause permanent soil degradation because of dispersion of soil aggregates. Sodium (Na^+), as the most frequent causative agents of salinity, is the most pronounced destructor (by dispersion) of secondary clay minerals. Dispersion occurs because of Na^+ replacement of calcium (Ca^{2+}) and other coagulants (Mg^{2+} , OM) adsorbed on the surface and/or inter-layers of soil aggregates (e.g. Ondrasek et al., 2010 and references therein). The replacement is mainly caused by specific physical characteristics, such as ionic radii, electrical charge and hydration ability of particular elements, whereas some chemical properties (e.g. increased pH) may facilitate the clay dispersion process.

For instance, 6-co-ordinated Ca^{2+} and Mg^{2+} ions have radii of 0.100 and 0.072 nm, respectively, whereas that of Na^+ is 0.102 nm (Shannon, 1976). Also, single-charged Na has lower clay-binding ability than double-charged Ca (or Mg), which in turn is not so strongly hydrated as Na (Rashad & Dultz, 2007). Thus, after Ca^{2+} (Mg^{2+}) replacement by Na^+ and its intrusion into secondary clay minerals (e.g. 1:1 or 2:1 phyllosilicate sheets) and watering (i.e. hydration), interlamellar space increases and may cause decoupling of lamellae (sheets), i.e. clay dispersion. Finally, under alkaline conditions ($\text{pH} > 8$) rate of dissolution (dispersion) of silicate minerals increases because excessive OH^- interacts with the clay interface and generates strong negative charge (e.g. Rashad & Dultz, 2007).

Dispersed clay particles undergo leaching through the soil and may accumulate and block pores, especially in fine-textured soil horizons (Burrow et al., 2002) i.e. cause pedosferic waterlogging. Furthermore, dispersion of clay usually induces topsoil crusting, thus reducing infiltration, enhancing surface runoff and other related degradation processes (soil erosion/desertification, surface waterlogging, nutrient leaching, etc). Over time, in saline (sodic) soils crusted surface layer (Figure 3b) constrains hydraulic properties (water permeability, infiltration rate, etc) as well as aeration of topsoil horizons and the root zone.

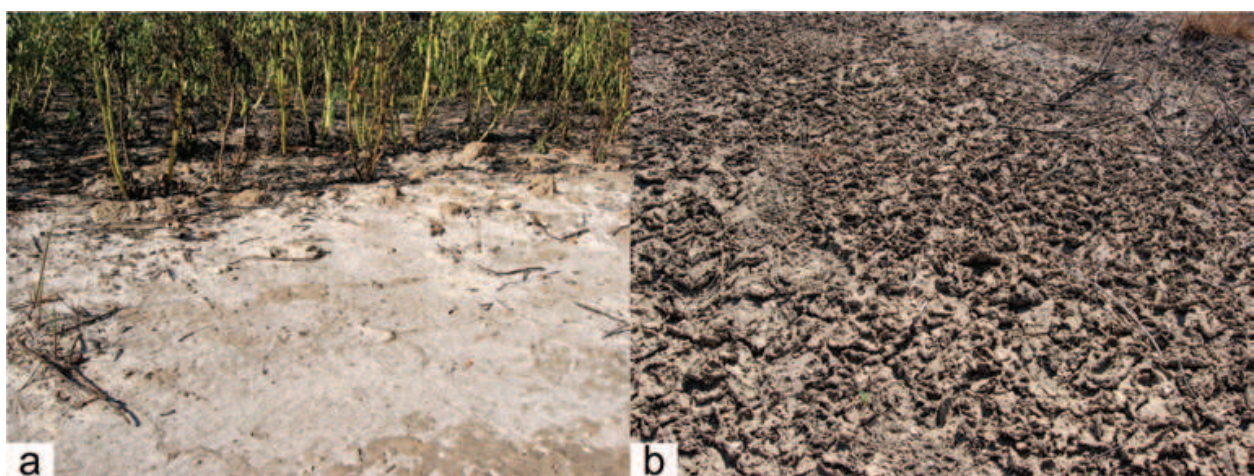


Fig. 3. Surface salt crystallisation (a) and topsoil crusting (b) in a faba bean paddock (Esperance area, W. Australia) (Photos taken by G. Ondrasek, 2010)

During the dry periods, salts accumulated in the soil profile or on the soil surface (Figure 3a) may further affect soil properties. For instance, ground observations and radiometric measurements confirmed that quantity and quality (i.e. mineralogy) of salts, together with soil moisture, colour, and roughness, affect the soil surface reflectance (Metternicht & Zinck, 2003), and consequently influence the topsoil physical properties (e.g. warming). It was shown that abundance of Na_2SO_4 (puffy crusts) or NaCl (smooth crusts) increases reflectance in the visible and near-infrared wavelengths compared with the nonsaline soil surface (e.g. Metternicht & Zinck, 2003). According to the same authors, the surface of saline soils is brighter compared to sodic (alkaline) soils due to OM dispersion in the latter.

4.2 Impact on hydrosphere

Increased salinity in soil solution, especially increased concentrations of Na^+ and Cl^- ions, significantly influence solubility i.e. mobility of potentially toxic trace elements (Helal et al., 1999; Khoshgoftar et al. 2004; Khoshgoftarmanesh et al., 2006; Ondrasek et al., 2009a, 2009b; Weggler et al., 2004). Excessive salinity may cause desorption of particular metal and other cations from the soil adsorption matrix, increasing concentration of bioavailable forms in the soil solution. In particular, an exposure to increasing NaCl salinity increased concentration of trace elements (e.g. Cu , Zn , Cr and/or Cd) in the rhizosphere soil solution (Helal et al., 1999; Khoshgoftar et al. 2004; Ondrasek et al., submitted b) or in unplanted humic solution (Lores & Pennock, 1998). Namely, organic (humics, black carbon) and inorganic (clay, hydroxides) surfaces, mostly negatively charged, compete with salt anions (Cl^- , SO_4^{2-}) for metal cations (Cu^{2+} , Al^{3+}) via adsorption and complexation reactions (e.g. Adriano et al., 2004). Therefore, under excessive concentrations of Na^+ , it is really expected displacement of weakly bound metal forms (Cd^{2+} , Zn^{2+}) and their accelerate release from soil solids to solution and enhance their mobility i.e. expose surrounding aquatic ecosystems to increased metals contamination (Ondrasek et al., submitted a).

4.3 Impact on biosphere, particularly plants

In general, bulk and rhizosphere soil, as well surface and subsurface soil profiles, differ in their chemical, physical and biological properties (pH, salinity, redox potential, porosity, water retention, abundance and diversity of microbial species, etc). Increased salinity/sodicity (EC/Na) in the rhizosphere affects root exudation (e.g. of low-molecular-weight organic substances) and biochemical transformations i.e. decomposition of organic matter by microorganisms (Ondrasek et al., submitted b). Contradictory effects of increased EC and Na on soil biological processes (e.g. OM decomposition) have been reported (Li et al., 2006 and references therein). Recently, Ondrasek et al. (submitted a) observed a decrease in dissolved OM (dependent on soil microbe-root interactions) of 5% (at ~ 4 dS/m and 20 mM Na) and $>20\%$ (at ~ 8 dS/m and 60 mM Na) compared to control (~ 2 dS/m and 1.5 mM Na). Similar observation were reported by Li et al. (2006), who noticed significant negative correlations between soil EC and total CO_2 emission or microbial biomass C, suggesting that salinity had an adverse effect on microbial biomass and activity. Therefore, naturally-occurring soil OM decomposers may be sensitive to salt-induced stress.

4.3.1 Salt stress in crop production

4.3.1.1 Background

A majority of cultivated plant species, especially widely grown horticultural and cereal crops (e.g. Table 1 from Chinnusamy et al., 2005), are glycophytes i.e. susceptible to

excessive concentration of dissolved ions (e.g. >30 mM or >3.0 dS/m) in the rhizosphere solution. Depending on salt concentration and the length of exposure, the stage of growth/development and the environmental conditions (e.g. humidity, temperature, insolation, soil moisture, etc), in glycophytes increased salinity may induce different physiological malfunctions, such as osmotic, ionic and different secondary (e.g. oxidative) disorders (Zhu, 2001), generally known as salt stress. Osmotic stress, as primary reaction triggered by relatively low/moderate salinity levels, decreases soil water potential i.e. reduces water uptake and causes possible cell dehydration (Ondrasek et al., 2009a and references therein). For instance, increased concentration of dissolved salts may reduce soil water potential from -1 to -2.5 (-5 in extreme cases) MPa (Flowers & Flowers, 2005), whereas at water field capacity its potential is 0.033 MPa. In saline conditions, osmotic pressure in the rhizosphere solution exceeds that in root cells, influencing water and nutrient uptake. Further plant responses to osmotic stress are stomata closure (partially or fully) i.e. transpiration/C assimilation reduction, decrease in cell growth and development, reduced leaf area and chlorophyll content, accelerated defoliation and senescence i.e. mortality of plant organism (Shannon & Grieve, 1999).

An increase in concentration of certain dissolved ions, such as those in relatively shallow Australian Na-subsoils solution, will enhance their uptake i.e. ionic stress, and ultimately cause phytotoxic effects (e.g. Cl⁻, B, Al toxicity). Specific ionic stresses disrupt integrity/selectivity of root plasma membrane, homeostasis of essential ions and numerous metabolic activities (e.g. Zhu, 2001). For instance, in rice, as one of the most widely grown cereals, salinity is the main limiting variable of mineral nutrition (Marschner, 1995). Moreover, approximately half of global saline (i.e. alkaline) soils used for cereal production are overlain on soils with low levels of plant-available Zn i.e. Zn-deficient soils, due to Zn complexation/competition with dissolved salts (CO₃S, SO₄S, Na⁺) at alkaline pHs (Ondrasek et al., submitted b). Therefore, given that the food crop consumption is the principal route of most essential minerals into the human organism, salinity may indirectly contribute to mineral deficiency in billions of people.

The primary salinity effects give rise to numerous secondary ones such as oxidative stress, characterised by accumulation of reactive oxygen species (ROS, e.g. H₂O₂, O₂⁻, ·OH), potentially harmful to biomembranes, proteins, nucleic acids and enzymes (Gomez et al., 2004) (see 5.2. section). Antioxidative enzymes such as superoxide dismutase (SOD), catalases, peroxidises, etc enhance detoxication of ROS. The relatively salt-tolerant species (e.g. pea genotypes) have increased activities of certain antioxidative enzymes (e.g. SOD; Hernandez et al., 2001), whereas in salt-sensitive species (e.g. cowpea) Na⁺ causes a stronger inhibition effect on particular SOD forms than Cl⁻ ions (Hernandez et al., 1994).

4.3.1.2 Nutrient uptake under salt stress - Impact on food production

Two most important ions that induce salt stress in plants are Na⁺ and Cl⁻. Sodium is nonessential but beneficial element, whereas Cl is essential phytomicronutrient (Marschner, 1995); however, both are potentially toxic in excessive concentrations, triggering specific disorders and causing substantial damages to crops. Under excessive Na⁺ and Cl⁻ rhizosphere concentration (activity), there are competitive interactions with other nutrient ions (e.g. K⁺, NO₃⁻, H₂PO₄⁻) for binding sites and transport proteins in root cells, and thereafter for (re)translocation, deposition and partitioning within the plant (see reviews by Grattan & Grieve, 1999; Tester & Davenport, 2003; White & Broadley, 2001). Significantly enhanced uptake and accumulation of Na and Cl (from 11-fold in radish up to >100-fold in

strawberry and muskmelon leaves), accompanied with a decrease in K concentration in the same tissues (from ~30% in strawberry and ~40% in radish to 4-fold in muskmelon) was obtained under moderate (60 mM) NaCl salinity (Ondrasek et al., 2009a, 2009b; unpublished). In the same studies, salinity stress reduced all vegetative parameters (e.g. number of strawberry runners by up to 7-fold and length of the longest runner by 3-fold), decreased total fruit yield (in radish by 35%, muskmelon by 50% and strawberry by 60%), accelerated leaf senescence and reduced the strawberry growing period by up to 22 days i.e. induced plant mortality after 65-day treatment with salinised (60 mM NaCl) nutrient solution.

The high K/Na and Ca/Na ratios are essential for normal plant functioning (e.g. Chinnusamy et al., 2005). The Ca/Na declined under salinity by 13-fold in radish, 113-fold in strawberry and 150-fold in muskmelon leaf tissue (Ondrasek et al., 2009a, 2009b; unpublished). It appears that disturbance of cytosolic Ca²⁺ homeostases in root cells is one of the fastest signals in glycophytes to increasing salinity; hence, a decrease in Ca/Na could be one of the most reliable salt-stress indicators (reviewed by Rengel, 1992). An addition of Ca may significantly mitigate certain salt stress-induced dysfunctions in crops that may be used as one of management strategies in salt-affected agro-ecosystems (section 5.1).

Crops with perturbed nutrients relations (e.g. Ca/Na, K/Na etc) are more susceptible to invasion of different pathogenic (micro)organisms and/or physiological dysfunctions (e.g. blossom-end rot, blackheart), whereas their edible parts have markedly less economic and nutritional value due to reduced fruit size and shelf life, non-uniform fruit shape, decreased vitamin content, etc. (Ondrasek, 2008 and references therein). Consumption of edible crop parts grown in salt-affected and metal contaminated surrounding could pose a high risk of metals intake into the human/animal organisms (Ondrasek et al., submitted b). It was well documented that in rhizosphere/soil solution salinised by Na⁺, Cl⁻ and/or SO₄²⁻ ions, potentially toxic metals such as Cd, Zn and Cu are taken up and accumulated to a large extent in different horticultural (McLaughlin et al., 1998; Ondrasek et al., 2009a, 2009b; Smolders et al., 1997), cereal (Khoshgoftar et al. 2004; Khoshgoftarmanesh et al., 2006; Weggler et al., 2004) and forage (green manure) crops (Helal et al., 1999), although complete mechanisms are unexplained. Matrix of saline (sodic) soil is naturally poor and/or depleted in metal-binding interfaces (e.g. alumosilicate minerals, organic C), thus predisposes crops to potentially strong metal influence.

5. Options for mitigating salt stress in crop production

A majority of arable salt-affected areas are distributed in the intensively cropped food producing regions such as those in Asia and Australia. The excessive concentration (EC) and ratios (e.g. ESP, SAR) among particular salts (Na, Cl, Ca, Mg) as well pH conditions need to be taken into account when considering appropriate strategies for reclamation of salt-affected soils in crop production. Such salt-affected soils can be categorised into: i) saline (EC_e > 4 dS/m, ESP < 15 and pH < 8.5), ii) saline-sodic (EC_e > 4 dS/m, ESP > 15 and pH < 8.5) and iii) sodic (EC_e > 4 dS/m, ESP > 15 and pH > 8.5), each requiring specific approaches for reclamation (Horney et al., 2005) and sustainable land management practices, that are usually costly and difficult to implement, and may even result in further degradation.

5.1 Sustainable agricultural management in salinised conditions

Sustainable agricultural management in salt-affected conditions is principally based on two main approaches; prevention (with aim to elude further salinisation processes) and

remediation management (i.e. reclamation of existing salinised land/water), but they usually overlap (e.g. Biggs et al., 2010). In selecting the most appropriate managing approaches analysis of several critical variables should be taken into account: i) the nature of soil geochemistry (i.e. salt type and concentrations, acidity, alkalinity), ii) groundwater hydrology (e.g. watertable fluctuation), iii) climate conditions (precipitation, evapotranspiration), and iv) plant species selection.

In natural environment, indigenous flora can counteract negative influences of excessive salinity by maintaining salinised groundwater below a harmful level and/or by its genetic predisposition i.e. pronounced salinity resistance. With introduction of cultivated species, many interrelations in natural terrestrial ecosystems were disturbed. Many primary salinised areas, such as those in alluvial floodplains (e.g. section 3.2), after land amelioration by (sub)surface drainage (open channel and pipeline network) had groundwater salinity decreased to a level suitable for agricultural production (Romic et al., submitted). These authors confirmed that with proper selection of modern irrigation systems (e.g. drippers vs. micro sprinklers) and mulch cropping technology, negative ecological consequences (e.g. yield/vegetative growth declining, mortality of cultured crop, increased EC_{se}) arising from usage of salinised water for irrigation (EC_w up to 7 dS/m) may be markedly reduced (Romic et al., 2008). Thus, establishing adequate drainage and/or ensuring sufficient volume of good quality (low salinity) water for irrigation and salt leaching from the root zone may be an appropriate strategy for at least partially reclaiming saline soils. Burrow et al. (2002) used channel/rain water ($EC_w=0.1$ dS/m) to leach salts from the topsoil, but not in subsoil where another constraints were detected, i.e. increased clay dispersion and sodicity. Therefore, saline-sodic and/or sodic (sub)soils require an application of appropriate soil amendments for Na replacement to aid in remediation (e.g. Horney et al., 2005).

Application of certain amendments (inorganic or organic fertilisers, lime, gypsum, etc) to pedosphere with excessive concentration of salts/Na has multiple beneficial roles. One is cation exchange of Ca for Na (e.g. with Ca-based amendments) given that the addition of electrolyte such is Ca (also Mg) helps to maintain micro-aggregate integrity in the soil profile (discussed in 4.1). With the application of 12 t/ha of gypsum, Wheaton et al. (2002) markedly decreased the ratio of Na^+ to $Ca^{2+} + Mg^{2+}$ (i.e. SAR) and reclaimed sodic subsoil (ESP 6-10) to non-sodic. In the same study, gypsum improved physical soil properties i.e. decreased clay dispersion (i.e. increased flocculation), reduced spontaneous dispersion (air-dry aggregates) and dispersion of remoulded aggregates, increased hydraulic conductivity and probably ensured better aeration. Under acidic pHs, $CaCO_3$ application (liming) provides an electrolyte source for ensuring sufficient Ca-for-Na replacement, whereas in naturally $CaCO_3$ -sufficient soils, H_2SO_4 application (or its precursor, elemental S) in reaction with carbonates ultimately produces gypsum i.e. exchangeable Ca (e.g. Horney et al., 2005). For achieving positive effects of different soil amendments in salt-affected conditions, several critical factors need to be considered, such as: i) uniform soil incorporation (mixing), ii) adequate soil water content for their dissolution, iii) presence of certain microbial population (e.g. sulphuric bacteria for S oxidation), etc. For example, Wheaton et al. (2002) reclaimed moderately sodic subsoils by applying 12 t/ha gypsum and 2,850 mm of water (as irrigation plus rain). To be dissolved, an average gypsum dosage (~10 t/ha) would need ~1,200-1,500 mm water (Greene & Ford, 1985; Wheaton et al., 2002), an amount hardly achievable by natural precipitation in short term in (semi)arid conditions (in contrast, irrigation may be too costly to implement).

Given that excessive Na^+/Cl^- salinity mostly impairs macro/micronutrient balance (discussed before), the direct practice to recover nutrient uptake and homeostasis is by specific (e.g. Ca, K, P) fertilisation. For instance, it was shown that supplementary application of Ca may result in many benefits (e.g. reduced accumulation of Na and improved K and Ca uptake, dry matter production, yield, etc) for crops grown under saline conditions (Cuartero & Fernandez-Munoz, 1999). Also, the same authors suggested that increasing K (to 10-15 mM) and P (to 10-100 μM) in the rhizosphere solution could be recommendable for saline conditions, although the upper levels of these nutrient concentrations should be further investigated.

Application of Zn fertiliser may be beneficial in saline/sodic environment. It was confirmed that ZnSO_4 may improve salt tolerance in cereals and results in several other important benefits such as crop micronutrient enrichment (e.g. by 90% for Zn) and reduced uptake/phytoaccumulation of toxic elements (e.g. by >100% for Cd) (Khoshgoftar et al., 2004). However, Zn fertilisation is not always acceptable because of ecological/economic consequences, whereas cropping of Zn-efficient species/genotypes on such Zn-deficient soils is one possible approach for reducing land degradation and minimizing the use of fertilizers (Khoshgoftar et al., 2006; Rengel & Graham, 1995).

Cropping system adaptation i.e. opportunity cropping, is another possible and widely used strategy in combating salinity and some other accompanied (sub)soil constrains (e.g. low soil fertility and water retention capacity, water deficit, high evaporation, increased pH) or land degradations (e.g. OM depletion, desertification). It assumes implementation of conservation tillage systems to restrict loses of soil moisture, soil erosion, reduce soil compaction, disturbance and energy consumption, i.e. conserve plant-available water and OM (Ondrasek et al., submitted b). Under such land management, at least 30% of the crop residues may remain on the soil surface (e.g. straw residues and stubble between rows, Figure 4). Furthermore, opportunity cropping assumes a wide range of other measures, such as double cropping (consociation of cereals and forages), selection of crop species (e.g. perennial deep rotted, more salt-tolerant, etc.), presence of pasture and tree species (for windbreaks, controlling groundwater level), etc. (see report by Biggs et al., 2010). Lucerne, as relatively salt-tolerant and deep-rooted legume, is shown to be the most effective perennial pasture for controlling groundwater recharge, with the strongest dewatering in the soil profile within the first 18 months of establishment (Powell, 2004).

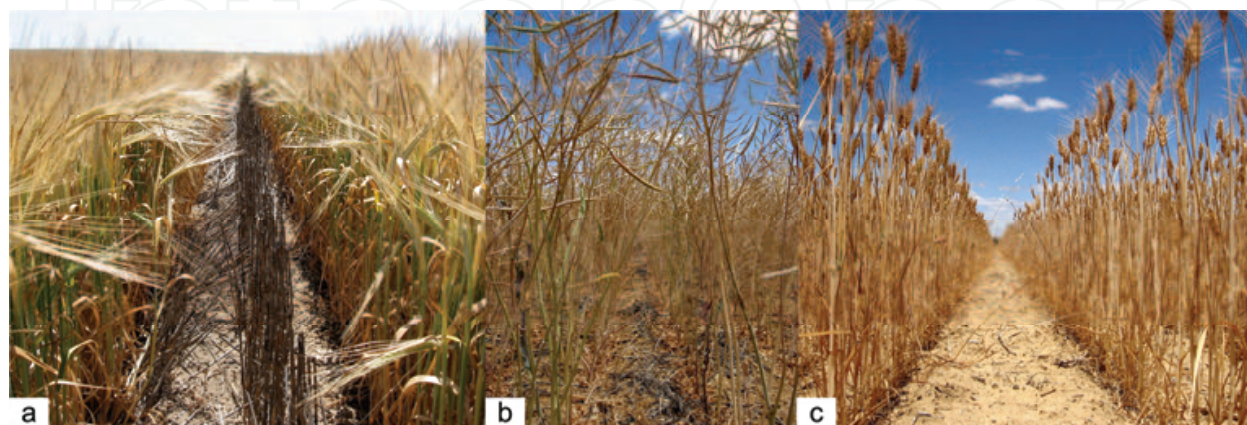


Fig. 4. Conservation tillage systems in barley (a; Esperance area, W. Australia), and canola and wheat (b, c; Dalwallinu area, W. Australia) (Photos taken by G. Ondrasek, 2010)

Grafting is a widely used technique in horticulture for asexual propagation and may also be helpful in withstand deleterious salinity effects (e.g. Cl toxicity) in crops. It was well documented that certain rootstock-scion combinations can reduce uptake and root-shoot translocation/accumulation of dissolved salts (Na⁺ and/or Cl⁻) in mango (Schmutz & Lüdders, 1999), citrus (reviewed by Storey & Walker, 1999) and grapevines (Stevens & Walker, 2002).

Several attempts have been made to improve salt tolerance by hydropriming (Basra et al., 2005a), pre-sowing chilling treatment (Basra et al., 2005b), halopriming (Kamboh et al., 2000) and ascorbate priming (Borsani et al., 2001; Afzal et al., 2006). Priming can increase the activity of free radicals scavenging enzymes, thus can reduce the damages caused by salt stress. Seed priming (osmoconditioning) with salinised (NaCl) solution prior to sowing is one of possible methods for improving salt tolerance in a wide range of relatively salt-sensitive crops (e.g. tomato, muskmelon, cucumber, etc) (e.g. Sivritepe et al., 2003, 2005). Based on literature review, Cuartero & Fernandez-Munoz (1999) recommended priming in 1 M NaCl for 36 hours in the case of direct sowing, and for seedlings conditioning in moderately saline solution or by withholding water for 20-24 hours, although specific duration and concentrations should be adapted to a particular crop.

Notwithstanding that elucidation of salt tolerance is complex with respect to its quantitative multigenic character (e.g. Flowers & Flowers, 2005), transgenic plants have been produced with high tolerance to salinity (up to 200 mM NaCl or 20 dS/m) (reviewed by Chinnusamy et al., 2005). Therefore, exploitation of genetic approaches (discussed next) in the long-term may achieve some of the most promising and effective outcomes in plant salt tolerance.

5.2 Genetic mechanisms of increasing of salt tolerance in plants

Enhanced salt tolerance in crop plants may be achieved via traditional and molecular breeding and transgenic approaches. However, genetic and physiological complexity of salinity tolerance does not lend itself easily to traditional breeding that may for example use a pedigree approach, which consists of screening germplasm for donors of salt tolerance, crossing a donor with an elite line and advancing the F1 hybrid to about the F8 generation while selecting for an elite trait. While the efficiency of this type of breeding is not sufficient (Ashraf & Akram, 2009), the use of wild relatives for breeding gives useful physiological information about the salt tolerance traits (Colmer et al., 2006). In addition, cell and tissue culture techniques are used to identify somaclonal variants (Zhu et al., 2000) and screen germplasm for salt tolerance *in vitro* (Arzani, 2008).

Molecular and transgenic breeding is more expensive than conventional, but represents an efficient way to produce salt-tolerant lines. Advances in genomics are underpinning an alternative approach in which a pre-breeding phase is used to pyramid several known genes and finely-mapped major quantitative trait loci (QTLs) for complementary aspects of salt tolerance. DNA-based selection protocols that are used to pyramid these genes are again employed during the breeding phase to transfer the entire set of genes for salt tolerance into any elite line by backcrossing (Benneth & Khush, 2003; Flowers, 2004).

Given the complexity of salt tolerance, only a few QTLs are identified within any given genome (Yeo et al., 2000). The fact that a QTL represents many genes complicates finding key loci within the QTL. Quesada et al. (2002) found five QTLs associated with salinity in *Arabidopsis* and identified the location of two of them. The other genetic approach currently used to enhance salt tolerance includes generation of transgenic plants to introduce new

genes or to alter expression levels of existing genes to affect the degree of tolerance (avoid or reduce deleterious effects, re-establish the homeostatic conditions and maintain active growth in saline environments; Zhu, 2001).

Important deleterious effects under saline conditions might be due to reactive oxygen species (ROS), which cause oxidative stress as one of the most general stress types (Lee et al., 2001). Plants under salt stress produce stress protein and specific osmolytes for scavenging ROS (Xiong & Zhu, 2002; Zhu et al., 1997). Oxidative stress tolerance is genetically controlled; improvements can be provided by conventional breeding and transgenic techniques (Asraf & Akram, 2009) or by adopting physiological approaches (Afzal et al., 2006). Most transgenic improvements in plant salt tolerance are focused on overexpressing enzymes involved in oxidative protection (Allen et al., 1997). In addition, engineering with the regulatory protein NPK1, a nitrogen-activated protein kinase that mediates oxidative stress responses, is also an efficient way for supporting antioxidant defence (Kovtun et al., 2000). Improvements provided via other proteins, like barley late embryogenesis abundant proteins and C-repeat-binding/dehydration-responsive element-binding proteins (CBF/DREBs) in transgenic plants may have ROS detoxifying effects, but are not specific for salt tolerance (Liu et al., 1998; Stockinger et al., 1997).

There are many proteins that appear related to salt stress response in plants. These proteins can directly regulate the levels of osmolytes and control ion homeostasis. Osmolytes, such as mannitol, fructans, proline and glycinebetaine, are also active in scavenging ROS. Genetic engineering of these osmolytes resulted in increasing salt tolerance (Harinasuth et al., 1996; Sahi et al., 2006; Zhu, 2001).

For improved tolerance to salinity, it is important to re-establish homeostasis by controlling Na^+ , K^+ , Cl^- transporters mediating influx and efflux to fine-tune ion concentrations in the cytoplasm (Zhu, 2001). Nonselective cation channels mediate Na^+ entry into the cell, and their molecular identity is becoming clear (Munns & Tester, 2008). Anion and cation transporters are a frequent target of genetic engineering to improve crop salt tolerance (Yamaguchi & Blumwald, 2005). Transcriptome analysis can pinpoint genes associated with regulation of RNA and protein metabolism that have a significant role in regulating salt-stress tolerance (Sahi et al., 2006). Mian et al. (2011) identified a large number of important genes using forward and reverse genetics, yeast complementation and transcriptomics. Microarray analysis has clearly shown that transcripts encoding RNA-binding proteins, helicases, cyclophilins, F-box proteins, dynamin-like proteins, and ribosomal proteins are linked to the salt-stress response in *Arabidopsis* (Sottosanto et al., 2004).

Earth is a salty planet, the problem of salinity is increasing together with the demand for food; hence, salt-tolerant crops are required. Great efforts have been made to improve salt tolerance of crops by means of conventional and more recently genetic breeding program. However, the genetic complexity of salt tolerance makes the task extremely difficult.

6. Conclusion

Soil salinisation is a widespread soil degradation process, exacerbated by a mismatch between water demands for irrigation in food production and the amount of quality (non-saline) water. Different land, crop and/or water management approaches (e.g. conservation tillage, crop selection/rotation, groundwater level control) have been used to combat salinisation processes in agro-ecosystems and mitigate salt-induced stresses in food/feed production. Although salt resistance in plants is multigenic and thus complex, breeding and

transgenic approaches to improve salinity resistance could contribute to enhancing crop production over millions of ha of salt-affected areas worldwide.

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8. References

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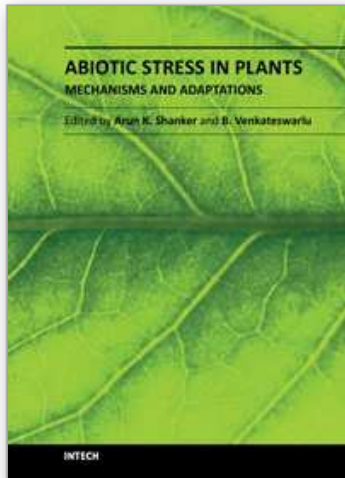
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Abiotic Stress in Plants - Mechanisms and Adaptations

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World population is growing at an alarming rate and is anticipated to reach about six billion by the end of year 2050. On the other hand, agricultural productivity is not increasing at a required rate to keep up with the food demand. The reasons for this are water shortages, depleting soil fertility and mainly various abiotic stresses. The fast pace at which developments and novel findings that are recently taking place in the cutting edge areas of molecular biology and basic genetics, have reinforced and augmented the efficiency of science outputs in dealing with plant abiotic stresses. In depth understanding of the stresses and their effects on plants is of paramount importance to evolve effective strategies to counter them. This book is broadly divided into sections on the stresses, their mechanisms and tolerance, genetics and adaptation, and focuses on the mechanic aspects in addition to touching some adaptation features. The chief objective of the book hence is to deliver state of the art information for comprehending the nature of abiotic stress in plants. We attempted here to present a judicious mixture of outlooks in order to interest workers in all areas of plant sciences.

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