Mirza Hasanuzzaman *Editor*

Plant Ecophysiology and Adaptation under Climate Change: Mechanisms and Perspectives II

Mechanisms of Adaptation and Stress Amelioration

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This book is dedicated
to
My Mother
To me, she was a great inspiration, a great teacher, and a great philosopher.

Preface

Impact of climate change is expected to be broadly negative, including reduced water availability, salinity, flood, and infestation of pests and diseases. Due to the significant climate change over the centuries, the incidence of various abiotic stresses such as salinity, drought, extreme temperature, atmospheric pollutions, and metal toxicities regularly affect plant life and productivity. Many crops perform only at 30% of their genetic potential under adverse environmental conditions. The predictable loss of crop production is as much as 70% in an average and might be 100% in extreme cases. The resulted economic loss caused by environmental stress is a great concern in agriculture.

To sustain productivity against the environmental stresses, the crucial importance is to know and understand the plants-specific responses to the different environmental factors. Plant ecophysiology is the science of interaction of plants with the environment, and the vital underlying acclimation and adaptation processes. The off-putting effects of abiotic stresses result in alteration in plant metabolism and physiology, which challenge survival, productivity, reproductive biology, and reproducibility. These adverse effects result from structural and functional alteration of cellular components of plant. Structural alterations of cellular organelles due to environmental stresses cause alteration in physiological processes, such as water entrance and transportation, nutrient uptake, chloroplast functioning, photosynthetic efficiency, mitochondrial activity, vacuolar structure and function, and the altered structure of nucleus cause genetic modification. The physiology and adaptive mechanisms of plants are greatly varied in different species and genotypes. The ability of various plant groups to tolerate the extremes posed by natural conditions and/or chemically rich environments involves morphological and physiological adaptation as well as changes in ecological behavior to sustain in relatively protected niches within an extreme environment.

To survive under environmental extremity, plants respond at the molecular, cellular, and physiological level, which involves a complex network supporting perception and transmission of stress signals, which subsequently initiate a plethora of responses. Against different kinds of stress-induced responses, there are two broad outcomes: programmed cell death (PCD) or stress acclimation. The PCD is considered a lethal effect whereas acclimation often leads to adaptation to certain adverse environmental stresses, which sustain plant survival and productivity. A deeper understanding of the mechanisms underpinning plant stress adaptation may offer novel opportunities to develop crop plants with an enhanced ability to tolerate environmental fluctuations, which are the focal points of concern of plant ecophysiological study. In modern concept, the survival mechanism and potential of plants are not left behind as a natural process. Rather how the adaptation process can be enhanced is a great concern of scientists of the related fields. In present perspectives, scientists are manipulating the surrounding environment of target plants so that the plant can be less affected by natural environmental stresses. Use of a broad range of exogenous phytoprotectants including plant nutrients, trace elements, phytohormones, and signaling molecules, probiotic microorganisms to improve adaptation processes of plants are being explored day by day. Scientists are going through the genetic manipulation and biotechnological processes to sustain plant productivity under the adverse environmental conditions. Much progress has been gained in the last few decades in the area of plant ecophysiology research and on their adaptive mechanisms. Although there are numerous publications in journal and proceedings, there is a scarcity of a comprehensive book dealing with both ecophysiology and adaptive mechanisms of plants under climate change.

This is the second volume of the two-volume book, *Plant Ecophysiology and Adaptation under Climate Change: Mechanisms and Perspectives* that provides current state-of-the-science knowledge of plant ecophysiology, with particular emphasis on plant responses and tolerance mechanisms as well as remediation techniques. This volume will provide the reader with a wide spectrum of information, including vital references. This is done through 32 chapters written by hundreds of experts in the field of Botany, Plant Physiology, Ecology, Crop Science, and Environmental Sciences, ultimately aiming to become a useful information tool for plant biologists, crop scientists, ecologists, plant breeders as well as a guide for students in the field of Plant Science, Agriculture and Environmental Sciences.

I like to give special thanks to the authors for their outstanding and timely work in producing such fine chapters. Our profound thanks also go to Mr. Sayed Mohammad Mohsin, Dr. M.H.M. Borhannuddin Bhuyan, Ms. Khurshida Parvin, Dr. Kamrun Nahar, Khussboo Rahman, Khadeja Sultana Sathi, and Mr. Abdul Awal Chowdhury Masud, for their critical review and valuable support in formatting and incorporating all editorial changes in the manuscripts. I am highly thankful to Ms. Lee, Mei Hann, Editor (Editor, Life Science), Springer, Japan, for her prompt responses during the acquisition. I am also thankful to Sivachandran Ravanan, Project Coordinator of this book, and all other editorial staffs for their precious help in formatting and incorporating editorial changes in the manuscripts.

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About the Editor

Mirza Hasanuzzaman is Professor of Agronomy at Sher-e-Bangla Agricultural University in Dhaka, Bangladesh. He received his PhD in *Plant Stress Physiology and Antioxidant Metabolism* from the United Graduate School of Agricultural Sciences, Ehime University, Japan, as a recipient of a scholarship from the Japanese Government (MONBUKAGAKUSHO). Later, he completed his postdoctoral research at the Center of Molecular Biosciences, University of the Ryukyus, Okinawa, Japan, as a recipient of the Japan Society for the Promotion of Science (JSPS) postdoctoral fellowship. Subsequently, he received the Australian Government's Endeavour Research Fellowship for postdoctoral research as an Adjunct Senior Researcher at the Tasmanian Institute of Agriculture, University of Tasmania, Australia. Mirza Hasanuzzaman has supervised 20 MS students. His current work is focused on the physiological and molecular mechanisms of environmental stress tolerance. Prof. Hasanuzzaman has published over 120 research publications in peer-reviewed journals. He has edited 12 books and written 45 book chapters on important aspects of plant physiology, plant stress responses, and environmental problems in relation to agricultural plants. According to Scopus®, Prof. Hasanuzzaman's publications have received roughly 4800 citations with an h-index of 37 (As of April 2020). He is an editor and reviewer for more than 50 peer-reviewed international journals and was a recipient of the

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Chapter 1
Salinity Stress Management in Field Crops: An Overview of the Agronomic Approaches

Abdul Majeed and Saira Siyyar

Contents

Abstract Crop plants have defined roles in the global food supply. Cereals, pulses, beans, and grains are particularly important for their nutrients and easy availability for consumers who cannot purchase meat and dairy products. Thus, elevated production of field crops for addressing the food and energy demands of the human population is crucially necessary, and it remains one of the emerging areas of interest for agronomists. In global agriculture, a significant proportion of cultivated land is affected by soil salinity. The problem has devastating effects on crops' growth, yield, and production. The adversities of salinity stress on crops become even worse in regions with low rainfall and high evaporation rate and where substandard irrigation practices are common. Soils enriched with salinity affect the growth, physiology, and production by triggering water deficit conditions, ionic toxicity, oxidative stress, and alteration in metabolic events. To reduce the agronomical, physiological,

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and biochemical damages on crops imposed by high salinity levels, development of salt-tolerant varieties and modulation in agricultural practices seem to be ideal strategies as they would lead to attaining high yields of crops under a stressful environment. In this paper, a comprehensive review is presented about the problem of salinity and updates about management strategies in crop plants employing agronomic approaches.

Keywords Agricultural sustainability · Salt-tolerant crops · Ionic toxicity · Osmotic abnormalities · NaCl · Biotechnology

1.1 Introduction

Rice, maize, wheat, potato, pulses, beans, and several other crops are essential food commodities which are actively playing their role in global food supply and contributing to the energy needs of millions of people throughout the world. A drastic increase in human population (estimated to exceed 9 billion by 2050) will require more food and energy (Edgerton 2009; Cole et al. 2018); hence, greater efforts are required to enhance the crop productivity and reduce the gap between current and required yields. Concurrently, several biotic and abiotic challenges in global agriculture persist which hinder the production and yields of crops on which humans rely for their food and energy. Excessive burden and infestation of plant pathogens, weeds, and other pests (Korres et al. 2016; Savary et al. 2019), prevailing and anticipated changes in climate (Hasegawa et al. 2018), ozone and heavy metal pollution (Shahid et al. 2015; Tian et al. 2016), heat and drought (Daryanto et al. 2017; Fahad et al. 2017), and salinity (Parihar et al. 2015; Parmoon et al. 2018; Majeed et al. 2019) are important factors which influence negatively the production of crop plants and are expected to impart their effect on food supply in the future.

Salinity which currently affects more than 20% of agricultural land and which is expected to pose potential challenges to land degradation and agricultural production in the future is a leading global abiotic stress that affects general plants and cultivated crops adversely (Pitman and Läuchli 2002; Butcher et al. 2016). Impact of salinity on crops is direct as well as indirect. Direct and abrupt effects include osmotic stress which results from concentrated soil with salts, while the indirect and relatively slower effect is the accumulations of Na^+ and Cl^- ions inside tissues, which cause ionic toxicity (Munns and Tester 2008). Both effects correspond to physiological and growth abnormalities in challenged crops resulting in either delayed or inhibited germination, growth, and yields (Munns and Tester 2008; Hanin et al. 2016). It is widely suggested that hyper-salinity levels induce ionic toxicity, oxidative stress, and abnormalities in stomatal functionality, respiration, and mineral uptake (Han et al. 2015a, b; AbdElgawad et al. 2016). Earlier studies have clearly demonstrated that higher salt concentration affected metabolic and physiological functions, germination, growth, development, and yields in wheat

(Saboora et al. 2006; Wahid et al. 2007; Mohamed et al. 2017), rice (Zeng and Shannon 2000; Shereen et al. 2005; Vibhuti et al. 2015; Kumar and Khare 2016), maize (Akhtar et al. 2015b; AbdElgawad et al. 2016; Waheed et al. 2016), tomato (Li et al. 2015; Gharsallah et al. 2016; Zhang et al. 2016), potato (Akhtar et al. 2015a; Hu et al. 2016), sorghum (Miranda et al. 2016; Nxele et al. 2017), and several other crops. Thus there is a greater need for devising methods, which could lead to minimal adversities of salinity on crops of agronomic importance.

Sustainable measures to manage the salinity problems are achievable through successive efforts which may encompass modulation in agricultural practices and biotechnological approaches though the specified methods may have variable advantages and disadvantages depending on the type of salinity management method, responding crop species, agricultural area, and level of salinity. Modification in agronomic practices may efficiently contribute to the management of salinity stress to a varying degree. The practices may include sequencing and cultivation of relatively tolerant crop species on saline soil (Sharma and Minhas 2005), appropriate irrigation designs in saline environment (Qadir and Oster 2004; Majeed and Muhammad 2019), residue retention (Devkota et al. 2015), and employing seed priming with different priming materials and growth-promoting bacteria (Majeed et al. 2018; Majeed and Muhammad 2019). Development of salt-tolerant varieties of crops using breeding and biotechnology can further strengthen our grips on yield gap because tolerant varieties would exhibit anticipated production and yield in a salty environment (Fita et al. 2015). Identification of salinity tolerance genes and their adaptation in a specific crop, while their introgression to major crops from candidate donor is a challenging task in the field of biotechnology and progress in this field, can yield promising results toward salinity management. In this chapter, salinity and its effects on crops and different approaches exploiting agronomic tools for addressing salinity stress are discussed.

1.2 Salinity and Its Causes

Naturally, soils have different organic and inorganic materials which originate from death and decomposition of organisms and weathering processes of parent materials, respectively. The composition of organic and inorganic substances widely differs in different soils, which depends on several factors ranging from the abundance of biotic communities to depth of soil and locations. Generally, soils with fluctuating biological activities of organisms will have substantial amounts of organic matter than barren soils. Similarly, soils with considerable bulk of parent rocks and those located near coastal areas will comprise abundant minerals and salts. The presence of salt and minerals is a natural prerequisite for fertile soil and proper growth of plants; however, excessive concentrations of salts (especially NaCl) result in hyper-ionic solution in soils which hinders a conducive environment necessary for plants' establishment, growth, and development. On the basis of electrical conductivity (EC), soil is said to be affected with salinity if EC exceeds 4 dS m^{-1} (Munns and Tester 2008; Butcher et al. 2016).

The origin of agricultural salinity stems from naturally weathering materials as well as from intensive activities of human beings. Naturally, weathering processes of rocks containing Na, Ca, Mg, SO_4, and other salts add to soil salinity when a significant amount of such salts accumulate in water/soil. However, this type of salinity is more pronounced in arid regions as the water carrying these salts evaporates leaving salts in soils (Chhabra 1996). Changing patterns of rainfall in many areas are also a leading cause of salinity. Infrequent rainfall coupled with temperature fluctuations often causes drought conditions in soils which in most instances are linked with high soil salinity (Salehi-Lisar and Bakhshayeshan-Agdam 2016). To a significant extent, fossil salts (resulting from previous salt deposit or entrapments), the flow of salts from oceans to coastal areas, and low water table in some regions may also cause natural salinity and soil degradation (Chhabra 1996). Causes of salinization originating from human activities include excessive irrigation practices, land degradation, changing vegetation patterns, and poor drainage schemes (Parihar et al. 2015). Fields located near industrial zones and mining sites are prone to anthropogenic salinity because water entering into fields from such sites may carry industrial wastes and salts which lead to salinity as well as other sources of pollution. Cutting and burning of trees and other plants for domestic and commercial purposes lead to barren land, accumulation of CO_2 in the atmosphere, high evaporation rate, and reduced rainfall, which are the leading causes of salinity (Majeed and Muhammad 2019). Land cleanup and irrigation indirectly cause the rise of water table which allows salts to migrate to the upper portion of the soil making it saline (Munns and Tester 2008).

1.3 Plants' Responses to Salinity Stress

Soil salinity, whether of natural or anthropogenic origin, adversely affects plants' germination, growth, and physiological functions. Accumulation of salts in soil causes osmotic, physiological, and metabolic abnormalities both in soil and within the challenged plant (Fig. 1.1). Classical causes of salinity-induced growth and germination abnormalities in exposed plants are osmotic stress, nutrient imbalance, and toxicity of ions, which trigger water deficiency, reduced nutrient uptake and distribution, and abnormal metabolism, respectively (Gorham et al. 2010).

First and essentially drastic effects of salinity include osmotic stress which corresponds to reduced water availability in soil. High salinity results in hyperaccumulation of salts in soil with consequent changes in the water status. Water scarcity drastically affects the germination of yet-to-germinate seeds as well as the growth of already established seedlings and plants. Since water is an essential component for the germination initiation, salinity-induced osmotic stress either completely hinders the germination of the sensitive plant species or delays the processes in tolerant

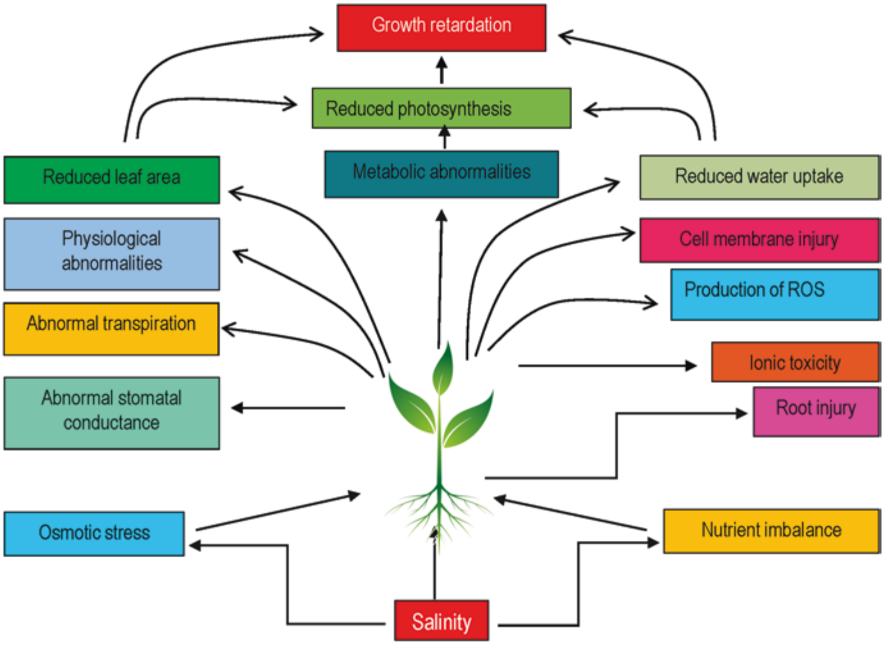

Fig. 1.1 Effect of salinity stress on physiology and growth of challenged plant. *ROS* reactive oxygen species

species. For already established plants, osmotic stress results in lower water absorption by the plant which leads to physiological wilting (Kordrostami and Rabiei 2019). Root zone saturated with salts can draw water from roots resulting in wilting and even in death of those plants which are not tolerant of salinity.

Another abnormality associated with hyper-saline conditions is a nutritional imbalance in soil and plant tissues (Gorham et al. 2010). Research on nutritional status of different plants under salinity stress has established that different nutrients such N, NO_3^-, P, Zn, Mn, etc. significantly declined in target plants due to lower uptake because in soil the compositional status and availability become imbalanced due to interactive effects of Cl^- and Na^+ ions with different minerals (Hu and Schmidhalter 2005). In studies such as those conducted by Santos et al. (2001), Grewal (2010), Wang et al. (2012), Yousif et al. (2010), and Garg and Bhandari (2016), salinity-induced nutritional imbalance in different plants was observed. The deficiency in nutrient uptake or mobilization inside host tissues results in metabolic disorders and impaired enzymatic activities which affect vital processes such as photosynthesis, respiration, and transpiration consequently leading to reduced growth and yield of the challenged plants.

Ionic toxicity, induced by salinity, is a leading factor, which severely affects several structural components and biochemical processes of plants' tissues. Hyperaccumulation of specific ions in shoots due to high salts in soils results in ionic toxicity which injures cells and tissues with negative effects on cellular machinery that promotes metabolic and physiological activities of plants (Sairam and Tyagi 2004; Machado and Serralheiro 2017). Excessive quantities of Na^+ and Cl^- in cytosol are toxic to many of the cellular processes including imbalanced ions (due to competitive replacement of Na with K, Mg, Ca, etc. and $Cl^-$for NO_3, PO_4^-, etc.) which have consequential effects on enzyme activity, senescence, and photosynthesis (Zörb et al. 2019). Läuchli and Grattan (2007) ascribed that accumulation of Na and Cl ions usually occurs in older leaves which formidably reduces the rate of photosynthesis and causes abnormalities in transpiration. Greater accumulation of these ions in leaves also results in leaf death and senescence. Like other stressful conditions such as drought, flooding, heat stress, and pathogenic interactions, salinity is also known to cause production of reactive oxygen species (ROS) in plants through a variety of mechanisms which lead to suffocation of enzymes, DNA and protein damages, cell membrane injury, disturbance of pigment systems, and lipid peroxidation (Bose et al. 2014). The net results of salinity stress are reduced growth and production output of challenged crop plants (Plett and Møller 2010).

1.4 Effect of Salinity on Crop Plants

Crop plants are variable in their response to salinity stress. Crops on the basis of their tolerance to salinity may be halophytes or glycophytes. Halophytes are salt-tolerant while glycophytes do not exhibit tolerance to salinity beyond a certain level. Even some crops may show extreme sensitivity to salinity and are unable to survive at salt concentration beyond the threshold level. Generally, most of the cultivated crops which cannot tolerate salinity beyond threshold levels are glycophytes although some authors describe them as moderately salt-tolerant. Important cereals such as maize, rice, and wheat, most of the vegetables, ornamentals, and other domestic crops are glycophytes which exhibit salinity tolerance at variable ranges, e.g., 1–8 dS m^{-1} (Kataria and Verma 2018). Among cereals, wheat and barley are regarded as comparatively salt-tolerant while rice is a sensitive glycophyte (Munns and Tester 2008). Salinity level of 100–200 mM has been described as formidable for most of the domestic crops which retards their growth and productivity or even their survival (Kataria and Verma 2018).

Glycophyte crop plants like other non-cultivated plants show similar responses to salinity stress. In the first instance, the higher salt concentration in soil decreases water availability causing osmotic stress. Under osmotic stress, crop glycophytes either cannot absorb water or they take up a very little amount of water resulting in wilting or even death of the challenged crop plants. Surviving glycophytes under osmotic stress exhibit further abnormalities in their growth and physiology due to several secondary effects such as alteration in transpiration and photosynthetic processes. Salinity-induced osmotic stress can significantly alter the concentration of carbohydrates and their metabolism which essentially affect processes such as photosynthesis, respiration, and translocation (Kerepesi and Galiba 2000). Deficiency in water status directly disturbs photosynthesis because of disturbance in cellular turgidity and availability of CO_2 to Rubisco—a key enzyme in photosynthesis (Chaves et al. 2009).

Besides osmotic problems, salinity also induces imbalance in nutrients both in the soil and in plant tissue. Depending on the types of salts, available nutrients in the soil may experience imbalance due to competitive interactions between anions and cations present in salts and in nutrients. Hu and Schmidhalter (2005) suggested the interaction of salt ions with several nutrients present in soil which leads to deficient availability and uptake of N, Ca, K^+, P, Zn, Mn, etc. by crop plants. These and several other minerals are crucial for vital processes and for overall growth and development of crops. Several enzymes and metabolic processes work properly in the presence of important minerals whose deficiency leads to severe abnormalities in enzymes and metabolic events. Respiration, photosynthesis, and transpiration under imbalanced nutritional distributions in plant tissues are affected to drastic extents. Zörb et al. (2019) outlined that higher concentration of Na and Cl ions in plant tissues is toxic to the cytosol and cellular components besides their role in preventing the uptake and distribution of beneficial minerals such as K^+, Ca^{2+}, and Mg^{2+}. Finally, specific ion effect or ionic toxicity induced by salinity stress in crop plants corresponds directly to cellular, membranal, and molecular damages or indirectly by causing oxidative stress in crop plants. The production of ROS as a result of salinity stress creates oxidative stress which is lethal for cells as well as for their components including membranes, DNA, proteins, and lipids (Rivera-Ingraham et al. 2016). Osmotic stress, nutritional imbalance, and ionic toxicity either alone or in combination make it hard for glycophyte crops to grow and develop normally; consequently retarded growth and production occur.

1.5 Agronomic Practices for Salinity Stress Management

The problem of salinity corresponds to substantial yield losses of major crops, and some studies estimate that yield losses of important crops and vegetables may reach 50% (Shrivastava and Kumar 2015). To attain maximum yields of crop plants and make the available maximum of the cultivated land, dedicated efforts are needed to manage soil salinity. The success of salinity management depends on (1) the site where salinity is prevailing, (2) the crop species, (3) the concentration of salinity, and (4) other prevailing stresses. Salinity management approaches should be multifaceted, and only employment of a single remediating approach seems less effective particularly in the current scenario of climate change (Fig. 1.2).

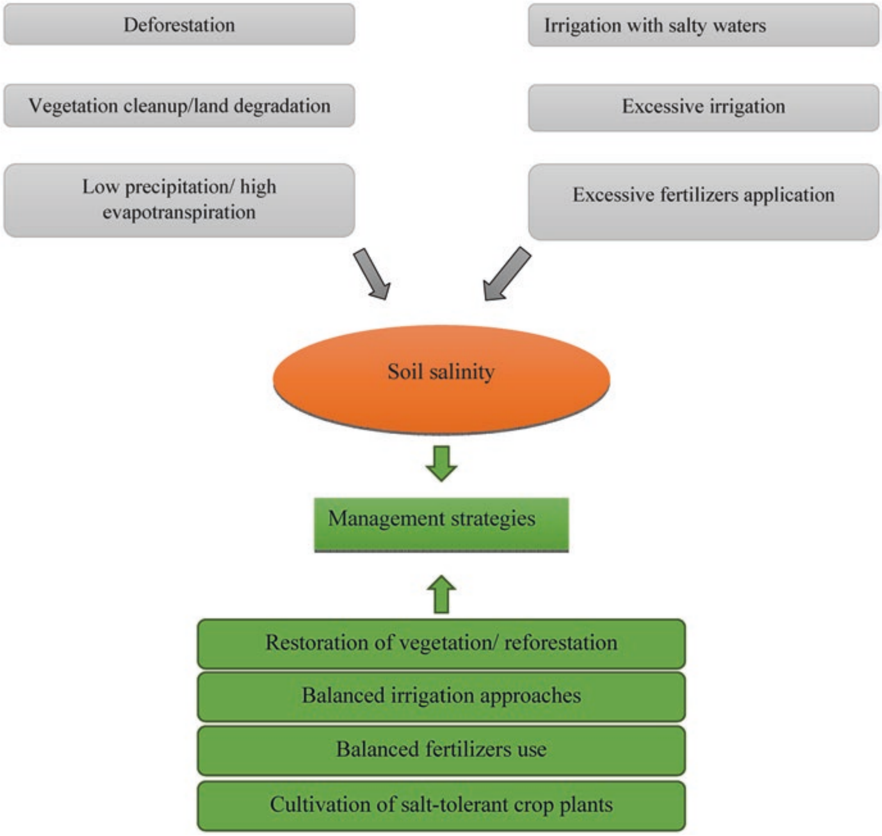

Fig. 1.2 Causes of agricultural salinity and mitigation methods employing agronomic practices

1.5.1 Changes in Irrigation Pattern

Excessive irrigation of soil and irrigation with substandard water are the leading causes of salinity in cultivated lands. In areas where natural precipitation is not adequate, crops are watered with extensive irrigation both from natural (rivers, water bodies, etc.) and built resources (streams, canals, wells, ponds, etc.). Water used for irrigation from such sources is regarded as freshwater if it does not contain any appreciable amount of salts or other pollutants. Balanced and well-designed irrigation with freshwater does not pose a significant threat of salinity to irrigated land. However, when proper scientific approaches are not observed in irrigation or water containing salt is used for irrigation purposes, lands become salinized. Irrigation practices cause salinization by introducing salts to irrigated water (if a sufficient concentration of salts is present in irrigated water) directly or by raising the water table which communicates with root zone and brings with it salts from mineral deposits (Hillel 2000).

The problem of irrigated salinity is prominent in developing countries because of the scarcity of freshwater and lack of well-suited irrigated systems there (Umali 1993). A technical report compiled by the author described that rise in groundwater and irrigation with saline water promoted soil salinity in arid regions in the developing countries. In arid and semi-arid areas, the rate of evapotranspiration is higher which leads to water evaporation leaving salts behind in the cultivated zone of soil (Kirzhner et al. 2008). In most of the developing countries, irrigation water flows through simple streams and canals which are not lined thus resulting in substantial leaching of water that leads to the rise of water table. Moreover, water flowing through saline areas may dissolve salts in it, and when such water is served for irrigation, soil will become salinized. Although, in such areas, excessive irrigation seems to lower the water evaporation rate and consequently reduce salinity, however, in practice, without adopting suitable measures, the salinization problem will worsen.

In order to minimize or prevent irrigation-induced salinity, sustainable measures in arid and semi-arid lands are necessary to be practiced. These include the use of freshwater sources not contaminated with salts, provision of proper drainage and lining of streams and canals, and frequency of irrigation strictly focusing on soil's conditions and prevailing climate. The lining of canals and streams prevents seepage of water and minimizes the chances of water table rise. Discouraging the use of heavy machinery for irrigation in soils is a helpful technique because it would reduce poor drainage and leaching. Groundwater may be balanced by lining water canals, by improving percolation, and by installing pump wells (Smedema 1990). Fayrap and Koç (2012) proposed the use of drip irrigation as an efficient way to decrease irrigation-induced salinity and waterlogging in irrigated systems. Machado and Serralheiro (2017) also favored the use of surface drip, subsurface drip, and furrow irrigation in soils where potent salinization as a result of salinity is evident. Improvements in irrigation system by canal lining and installation of tube wells are ideally approached to prevent irrigation-induced salinity; the processes, however, require huge financial resources and technical expertise which without the help of governments and other financial institutions are not possible.

1.5.2 Restoration of Vegetation Cover and Reforestation

In tropical, arid, and semi-arid regions, the evaporation rate is higher in warmer seasons which causes reduced water availability in soils. The problem becomes worst when rainfall is infrequent. Rich vegetation in those areas can be a check for water loss because plants hold water as well as recycle water by transpiration process. In recent years, diversification and increase in human needs have resulted in substantial deforestation activities. Trees and other plants including herbs and shrubs are removed for domestic burning, commercial, and medicinal purposes. The large-scale removal of plantation leaves the land barren making it prone to accelerated evapotranspiration. Moreover, cleaning up vegetation for building houses,