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Sharda Rani Gupta
Ashwani Kumar *Editors*

Halophytes vis-à-vis Saline Agriculture

Perspectives and Opportunities for Food Security

Springer

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Foreword

भारत सरकार
कृषि अनुसंधान और शिक्षा विभाग एवं
भारतीय कृषि अनुसंधान परिषद
कृषि एवं किसान कल्याण मंत्रालय, कृषि भवन, नई दिल्ली–110 001

GOVERNMENT OF INDIA
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AND
INDIAN COUNCIL OF AGRICULTURAL RESEARCH (ICAR)
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डॉ. हिमांशु पाठक
DR. HIMANSHU PATHAK
सचिव (डेयर) एवं महानिदेशक (आईसीएआर)
Secretary (DARE) &
Director General (ICAR)

The global population is growing rapidly, necessitating food production to combat climate change and conserve biodiversity. The cultivable land resources are finite rather than declining due to developmental works, faulty methods of cultivation, over-exploitation of resources, and urban pressure on arable land; therefore, every piece of land available including degraded saltlands and salt marshes needs to be utilized for food production. As good-quality water per capita is declining, poor-quality water including sea water will become inevitable for irrigation in agriculture. Saline agriculture offers an alternative to increasing productivity in this situation. During the last two decades or so, the attention of global researchers and policymakers has been focused on identifying, evaluating, domesticating and developing new crops of potential halophytes. These are plants which can thrive in high-salinity environments, making them a promising solution for addressing food security challenges in regions with limited freshwater resources. Halophytes are diverse trees, shrubs, forbs, and grasses that can adapt to various environments, including xerophytic and wet conditions under salt stress. They fill crucial ecological niches in various ecosystems and are classified by ecologists based on their habitats, life forms, and adaptation strategies. They can be improved into salt-resistant crops or used as genes for conventional crop species. With 2600 known species, only a few have been extensively studied for their agricultural, food, oil, and pharmaceutical applications. Efforts have been made to understand their genetic makeup, adaptability, and potential for sustainable agriculture.

Keeping in view the availability of more than a billion hectares of saltlands (otherwise lying almost barren) including salt marshes and degraded mangrove areas and the rich biodiversity of halophytes, there is a wide scope of saline agriculture and its role in the food industry, phytoremediation, as well as a source of bioactive compounds including modern drugs. The new technologies for the cultivation of halophytes help to utilize saline and arid wastelands and waterlogged areas sustainably for humans and livestock. Having the above-mentioned facts in mind the present book "Halophytes vis-à-vis Saline Agriculture: Perspectives and Opportunities for Food Security" is conceptualized. The book, has been edited by JC Dagar, SR Gupta, and Ashwani Kumar, who have made a significant contribution to the field.

The wide-ranging research explores the emerging area of ecology, physiology and genetics of halophytes, which have evolved specifically to survive in salty conditions. This book is an innovative effort which provides optimism for a future that may change how we grow and protect our food supply under resource-limited conditions, climate change and land degradation. This book covers 20 chapters on halophytes, including their evolution, classification, historical perspectives, and potential for saline agriculture in the 21st century. It also provides an ecological overview of plant communities, focusing on salt marshes and mangroves and their role in agriculture and environmental services. It includes chapters on reproductive physiology, seed germination, seed banks, and endangered halophytes and their conservation methods. Additionally, using the unique characteristics of halophytes might help conserve biodiversity and restore degraded ecosystems.

The adaptation mechanism is very important to understand the reasons for their survival, optimal growth and productivity, hence the aspect is discussed in detail along with their morphological, anatomical, eco-physiological and biochemical adjustments to salinity tolerance, which involve controlling ion balance and segregation, bolstering antioxidant systems, and synthesizing osmoprotective compounds and plant hormones, collectively empower them to flourish in saline ecology. Chapters on recent studies on genetic engineering and mining of genes for crop production and to enhance stress tolerance in crops to increase agricultural production from degraded saline lands have been included. Further, the contribution of molecular approaches (omics) in understanding the mechanism of salinity tolerance in halophytes has been added. There is a significant role of microbes in nutrient cycling and enriching organic matter into the soil. Many microbial organisms inhabit the soil under halophytes including mangroves which play different roles through enzymes in saline environments. This biota may play a significant role in evolving transgenic crops tolerant to salinity. The role of halophytic microbiomes in ameliorating stressed ecosystems has been discussed. The potential of halophytes in saline agriculture is the main theme of the book, therefore, chapters such as halophytes as potential food and cash crops of the future; halophytic crops- a resource to reduce water crisis in future; restoration of saline and waterlogged soils; and halophytes as a source of therapeutic medicinal and secondary metabolites; domestication of wild halophytes and harnessing their potential for enhanced resilience in arid agroecosystems have been included.

The book is a valuable resource for researchers interested in innovative farming methods and improving food security. I would like to express sincere appreciation to all the contributors for their hard work and highlighting the significance of halophytes in saline agriculture. I trust and believe that this book would be an invaluable resource for helping researchers, policy makers, academician, students, as well as farmers to develop strategic action plans for sustainable food production in harsh environments. This book is an outcome of sincere efforts of authors who deserve great appreciation.

5th January, 2024
New Delhi

(Himanshu Pathak)

Preface

Food production and other agricultural commodities throughout the world are seriously threatened by salinity and waterlogging. Salts affect more than one billion hectares of land, and one-third of all agricultural fields are saline. Crop production under saline conditions must be significantly increased due to the ever-increasing population's rapidly growing demand for more food, fibre, fuel, and pharmaceutical drugs. As good-quality water per capita is declining at a pace, poor-quality water including sea water will become inevitable for irrigation in agriculture. Saline agriculture offers a potential solution to increase production by domestication of halophytes in degraded ecosystems like salty deserts, salt-affected soils, and salt marshes. Seawater can be used as an irrigation source, making it suitable for desert regions with water shortages along the coast. Saline aquifers can be utilized in arid and semi-arid locations for cultivation of halophytes which also provide a significant source of biomass.

Recent research on ecology, physiology, and genetics of halophytes has greatly enhanced our understanding of their survival in salty conditions. Saline agriculture has many applications in the food industry, phytoremediation, as well as a source of bioactive compounds including modern drugs, and with the availability of over a billion hectares of salt lands (which would otherwise be nearly barren), including salt marshes and degraded mangrove areas, it can be handy in contributing towards the livelihood security to some extent. The utilization of salty water for a sustainable irrigation supply in waterlogged areas and saline and desert wastelands is possible with the application of new technologies for growing halophytes. This compilation on *Halophytes vis-à-vis Saline Agriculture: Perspectives and Opportunities for Food Security* aims to provide a comprehensive understanding of the potential of halophytes in addressing food security challenges. It explores the various perspectives and opportunities that arise from integrating saline agriculture practices into existing farming systems. This book offers optimism for a future that may alter food production and protection under natural resource-limited conditions, climate change, and environmental degradation.

The book covers the vegetation ecology of halophytes including their evolution, classification, historical perspectives, and potential for saline agriculture in the next century. It also provides an ecological overview of plant communities, focusing on salt-affected areas of arid and semi-arid regions, salt marshes and mangroves and their role in agriculture and the provision of environmental services. There are chapters on reproductive eco-physiology, seed germination ecology, seed banks, and endangered halophytes and their conservation strategies. The adaptation mechanism is very important to understand the reasons for their survival, optimal growth, and productivity. This aspect is discussed in detail, covering the morphological, anatomical, eco-physiological, and biochemical adjustments to salinity tolerance. The role of microbial populations inhabiting the rhizosphere of salt-tolerant plants, in enhancing plant growth and productivity in saline environments, has been discussed. Recent studies on genetic engineering and the mining of genes for crop production and to enhance stress tolerance in crops to increase agricultural production from degraded saline lands have been discussed. By exploring the mining of genes for crop improvement, researchers aim to develop crops that can thrive in saline soils, ultimately contributing to sustainable agricultural practices.

Further, the contribution of molecular approaches (omics) in understanding the mechanism of salinity tolerance in halophytes has been added. The potential of halophytes in saline agriculture is the main theme of the book; therefore, substantial information has been incorporated on halophytes as potential food and cash crops of the future, halophytic crops—a resource to reduce water crisis in future, restoration of saline and waterlogged soils using suitable species of halophytes, halophytes as a source of therapeutic medicinal and secondary metabolites, and domestication of wild halophytes and harnessing their potential for enhanced resilience in arid agroecosystems.

The book is a valuable resource for academics aiming to enhance food security and explore innovative farming techniques. It highlights the importance of halophytes in combating climate change and land degradation. The authors hope that this comprehensive compilation will prove useful to researchers, students, policymakers, and farmers alike and inspire new ideas for sustainable food production in saline environments. The editors thank all the authors for their contributions that have greatly advanced our understanding of halophytes and highlighted their importance in saline agriculture. They are pleased to express their gratitude to the chapter contributors for their commitment and insightful contributions to halophyte research. We deeply appreciate the support of several anonymous reviewers who devoted a great deal of time to meticulously review and assess the chapters that were sent to them. Their dedication and expertise greatly contributed to the overall quality of the chapters. The editors owe their gratitude to Professor (Dr) Himanshu Pathak, Secretary, Department of Agricultural Research & Education (DARE), and Director General, Indian Council of Agricultural Research (ICAR), New Delhi, for graciously agreeing to write the Foreword for this book.

New Delhi, India — Jagdish Chander Dagar
Kurukshetra, India — Sharda Rani Gupta
Karnal, India — Ashwani Kumar

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Editors and Contributors

About the Editors

Jagdish Chander Dagar Former Assistant Director General and Emeritus Scientist in ICAR, has been well recognized both nationally and internationally and grown professionally through strong pursuit in agricultural, ecological, and agroforestry research which is evident from his more than 300 research papers published in peer-reviewed journals, book chapters, and in proceedings of conferences/symposia and 13 books authored/edited. He has guided many research students for their project work and obtaining Ph.D. degrees. His research interest has been in the areas of agroforestry, management of natural resources, biosaline agriculture, rehabilitation of degraded lands including salt-affected and waterlogged soils, biodrainage, ethnobotany, plant ecology, environmental sciences, biodiversity, halophytes, climate change, sustainable agriculture and policy. Recognizing the research contributions, he was conferred with several awards and honours: Sajjad Memorial Gold Medal, Hari Om Asharam Trust Award of ICAR, Swami Pranavananda Saraswati National Award of UGC, CSSRI Excellence Award on Soil Salinity & Water Management, Dr KG Tejwani Award for Excellence in Agroforestry Research & Development, and Life Time Achievement Award for outstanding work in Agroforestry Research & Development. Further, he is a Fellow of National Academy of Agricultural Sciences, International Society of Tropical Ecology, Indian Botanical Society, National Institute of Ecology, Range Management Society of India, National Environmental Science Academy, Andaman Science Association, Indian Society of Soil Salinity & Water Quality, and Honorary Fellow Indian Society of Agroforestry. He is a Life Member of these societies and the Indian Society of Coastal Agricultural Research. He has also been a consultant for several national and international agencies such as FAO of UN, CIMMYT, and Haryana Forest Department. Dr Dagar is Chief Editor of the *Journal of Soil Salinity and Water Quality* and active in social services.

Sharda Rani Gupta Former Professor of Botany, Dean Life Sciences, and Emeritus Fellow of UGC, is a well-known ecologist nationally and internationally, who has served in the Department of Botany, and the Institute of Environmental Studies at Kurukshetra University, Kurukshetra, India. Dr Gupta has made significant contribution towards better understanding biodiversity and ecosystem functioning of grassland and forest ecosystems, soil biodiversity, and ecological rehabilitation of salt-affected soils, carbon sequestration in agroforestry systems, and the sustainability of conservation agricultural systems. Her work concerns standardizing methods for studying decomposition processes, soil respiration, and soil microbial biomass in tropical systems. She has published 98 research papers in national and international journals, successfully completed several funded research projects, and guided the project work of 20 research students for their Ph.D. degrees. She has been associated with the Soil Science Department, Rothamsted Experimental Station, Harpenden, and Herts, UK, on Commission of European Communities Fellowship (1990–1991). For significant contributions to the fields of ecology, environment sciences, and agroforestry, she has been elected as the Fellow of the National Institute of Ecology, India; and is listed in Asia's Who's Who of the Men and Women of Achievement. She is now associated with the Institute of Environmental Studies and actively participates in socially relevant programmes and activities.

Ashwani Kumar Senior Scientist (Plant Physiology), has been working on various aspects of Crop Improvement for salt- affected areas through institutional and externally funded research projects at ICAR-CSSRI, Karnal. He has made significant contributions for studying the physiological and biochemical mechanisms of different crop plants in varying environments of salinity or drought. His scientific efficiency is evident from his participation in inter-divisional/inter-institutional research programmes with over 3 crores in funding from different agencies. His Google Scholar Citation of 803, with an h-index of 15, reflects his scientific output, including more than 50 peer-reviewed research papers, 15 book chapters, 15 popular articles, 4 technical bulletins, 9 training manuals, success stories, etc. He has over 10 years of teaching experience and has guided 08 research students for their Ph.D. degrees.

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Introduction: Definition, Evolutionary Trends, Classification, Historical Background, and Prospects of Halophytes in Agriculture

1

Jagdish Chander Dagar and Sharda Rani Gupta

Abstract

Halophytes have a phenomenal ability to complete their life cycle with optimal growth under saline conditions and represent about 1% of the total flora of flowering plants. During their evolution, various structural and functional adaptive mechanisms have appeared which enabled these plants to tolerate the saline environment. About 1 billion ha of land in the world is salt-affected and about 32,000 km stretches of coastal sands lie unutilised for agriculture. Most of the deserts and arid regions possess saline aquifers. Though there is a long history of using seawater for irrigation in coastal areas, the main attention was paid only after the 1960s when experimentations were initiated on the use of seawater for the irrigation of crops. Now, when the world's population has crossed the eight-billion mark and is expected to reach nine billion in 2037, the arable land is shrinking fast, and the availability of good-quality water for irrigation is reduced; hence the use of poor-quality water in irrigation is inevitable; the potential of bio-saline agriculture is being recognised globally. During the last two decades or so, the attraction of global researchers and policymakers across the globe has been focused on identifying, evaluating, domesticating, and developing new crops of potential halophytes. Therefore, the present publication has been planned, and introductory information about the halophytes and the publication has been included in this chapter. A brief account of the concept, evolutionary trends, classification, historical background, and potentials of halophytes in agriculture has been given.

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Keywords

Halophytes · Classification · Evolutionary trends · Saline agriculture · Potential halophytes · Mangroves · Biodiversity · Adaptation mechanism

1.1 Introduction

The word 'halophyte' is derived from Ancient Greek ἅλας (halas) 'salt' and φυτόν (phyton) 'plant', that is, 'salt-loving plant'. The term 'halophyte' was first applied to that class of higher plants early in the nineteenth century by Pallas (Schrader 1809) because of their extraordinary capacity to complete their life cycles in salty environments. The term 'halophytes' was first used over a century ago to refer to plants that have evolved to survive in permanently salty environments (von Marilaun 1896; cited by Cheeseman (2015)). Several scientists have defined them according to differing standards. Halophytes were first described by Schimper (1891, 1903) as plants that could grow normally in saltwater environments as well as on 'ordinary' soil. According to Stocker (1928), these plants can withstand salt concentrations above 0.5% at any point in their lifespan. According to Dansereau (1957), halophytes are plants that only thrive in saline soil. According to Flowers et al. (1977), halophytes are plants that can complete their life cycles at 300 mM NaCl. However, some researchers have set the cut-off at 85 mM (Glenn et al. 1999) or as low as 70 mM (Greenway and Munns 1980). Afterwards, Xu et al. (2016) defined halophytes as plants that can complete their life cycle in a living environment with a salt concentration greater than 0.5% NaCl, contrary to Flowers and Colmer (2008) who believed that halophytes are plants that naturally survive in salt-affected environments and can tolerate salinity concentrations as high as 1 M NaCl. They added that they can withstand salt stress and can endure for at least one life cycle in an environment that would be fatal to many types of plants. As a result, different researchers have different numbers of halophytes in saline environments. While the eHALOPH Halophyte Database (Flowers 2014) lists about 1500 species as salt tolerant—though without naming them 'halophytes'—Glenn et al. (1999) proposed as many as 6000 species.

The term 'halophytes' was used by Saslis-Lagoudakis et al. (2014) to refer to a somewhat higher number, that is, 1653. Halophytic plants, which comprise around 1% of the world's total flora (including dicots and monocots), are mostly found in high-salinity wetlands along tropical and subtropical coasts, as well as arid and semi-arid inlands (Etesami and Beattie 2018). To mitigate the negative effects of salinity, halophytes possess genes and proteins which help adapt to salt (Askari et al. 2006; Yu et al. 2011). These plants have evolved a variety of structural and functional mechanisms of adaptation that have enabled them to withstand the salinity of the environment. Whether they thrive in the salty environment or just tolerate, it is open to discussion. Understanding the interrelationships between these plants and the environment from the climatic, edaphic, and biotic points of view is of interest to ecologists, geographers, and environmentalists. This is considering these plants can be used as crops to meet the needs of a growing population, including food, fodder, fuel, and fibre, and for the rehabilitation of degraded saline landscapes. Therefore, to understand their ecology and potential in the scenario of a changing environment, the present publication has been planned so that a strategy can be developed by ecologists, agriculturists, and planners at the global level for the sustainable utilisation of these valuable resources particularly as crops.

1.2 Evolutionary Trends in Halophytes

The effective development of salt-tolerant crops requires an understanding that the evolution of halophytes, glycophytes, and our major grain crops has involved significantly different processes. Cheeseman (2015) has summarised the process of evolution among halophytes, glycophytes, and crops and its implications on food security under saline conditions. Contrary to the explanations given by many others (Flowers et al. 2010; Saslis-Lagoudakis et al. 2014), he is of the opinion that halophytes (and other edaphic endemics) generally arose through colonisation of habitats in severe disequilibrium by pre-adapted individuals, rather than by gradual adaptation from populations of 'glycophytes'. Dörken et al. (2017) while studying evolutionary and ecological implications of foliage in *Myricaria germanica* (Tamaricaceae) mentioned that it is a species of montane to sub-alpine-flooded riverine areas on non-saline limestone and dolomite soils. The leaves show strong leaf reduction but no other significant xeromorphic or scleromorphic features. While the salt glands of most Tamaricaceae secrete NaCl, *M. germanica* secretes large amounts of Ca and Mg, as $CaSO_4$ and as Mg-containing $CaCO_3$, rather than NaCl. This suggests that the evolution of salt glands in a halophytic ancestor may have been an enabling trait that facilitated the adaptation of this plant to non-saline Ca-rich soils. The deciduous nature of leaves may be an adaptation to reduce NaCl contents in plant. Similarly, leaf reduction can evolve as a response to osmotic stress in saline areas while the same may no longer have any adaptational significance in *M. germanica*. Thus, their work emphasises the dichotomy of the stress-tolerant family Tamaricaceae into two types of stressful habitats, one lowland (e.g. *Tamarix*) and one montane to alpine (*Myricaria*). Similar range fragmentation is known in Mediterranean taxa like *Armeria* and *Astragalus.*

The latter occurs under low salinity; hence it has a better chance of survival in favourable situations. For the domestication/evolution of crop plants, the selective pressure was human-imposed and involved humans co-opting functions of defence and in the process might have lost the genetic variability. The need to comprehend, fuse, and adjust the three modes of evolution has been stressed. This is especially true for generating salt-tolerant crops that would provide food security in underdeveloped nations with scant infrastructure and little financial resources. To achieve these goals, it will be necessary to make use of the genetic architecture of newly evolved halophytes, the genetic diversity of model plants, endemic halophytes, and currently existing 'minor' crops (Cheeseman 2015). The interesting fact is that among halophytes, there are not many taxonomical similarities among individuals.

For example, many species of Asteraceae and Poaceae are glycophytes or crops while some are halophytes. The only exceptions are families Rhizophoraceae (mangroves) and Chenopodiaceae where a majority of the plant species are halophytes. To understand the clear picture, we need to develop a separate chapter on this aspect.

1.3 Classification

Halophytes are a diverse group of hundreds of species of trees, shrubs, forbs, and grasses that can adapt to a broad variety of harsh environments, from xerophytic to wet conditions of salty and alkaline ecosystems. As a result, they lack a single taxonomic identity. These species fill important ecological niches in several ecosystems. Halophytes have been categorised in a variety of ways by several ecologists based on their habitats, life forms, and strategies for adapting to the salinity of their surroundings. Braun-Blanquet (1932) classified halophytes into facultative and obligatory categories based on their salt requirements. While facultative halophytes may develop in soil free of salt and can also withstand saline conditions, obligatory halophytes require salt for their growth.

A long time back, during his ecological studies in Rumania, Tsopa (1939) classified halophytes into *obligate halophytes*, *preferential halophytes* (not linked fully with salinity but show better development in saline conditions, for example, species of *Atriplex*, *Salvadora*, *Maireana*, *Tamarix*, *Populus euphratica*, *Elaeagnus angustifolia*, *Hedysarum cornosum*, etc.), *enduring halophytes* (capable of surviving in saline conditions but can grow better in non-saline or low saline conditions, for example, species of *Cyprus*, *Scirpus*, *Carex*, *Juncus*, *Phragmites*, etc), *occasional halophytes* (which normally behave as glycophytes but occasionally grow in low saline conditions), and *accidental halophytes* (glycophytes occurring in the saline environment by chance, for example, during flooding salts leach down and some species of glycophytes appear there).

From an ecological standpoint, one may take into account the following categories, regardless of the salt tolerance mechanism involved (Stocker 1928; Iversen 1936; Waisel 1972; Chapman 1974):

1. *Hypohalophytes*—tolerant to salt at ECe 4–10 dS m^{-1} in the soil, which is a comparatively low level. These include numerous natural species as well as crops that can tolerate salts, such as barley, asparagus, beetroot, alfalfa, date palms, pomegranates, Rhodes grass, clover, and wheat grass (Mass 1990). They were sometimes referred to as miohalophytes (Chapman 1974) or oligohalophytes (Iversen 1936).
2. *Euhalophytes*—Tolerate salt concentrations of 10–50 dS m^{-1} in irrigation water (ECiw) or soil (ECe), which is equal to or more than seawater concentration. For instance, the majority of the mangroves, the *Tamarix*, *Atriplex*, *Maireana*, *Spartina*, and other species.
3. *Hyperhalophytes*—which can tolerate salt concentrations above that of seawater, for example, species of *Arthrocnemum*, *Halopeplis*, *Halosarcia*, *Salicornia*,

Suaeda, *Atriplex*, *Salsola*, *Halocharis*, *Halostachys*, *Sarcocornia*, *Gamanthus*, *Aellenia*, *Mesembryanthemum*, *Distichlis*, *Halimione*, *Limonium*, *Leptochloa*, *Spartina*, etc.

Many of these species can accumulate up to 25–50% (sometimes more) of salts in their living dry matter (Flowers et al. 1986).

While studying the vegetation and flora of the salt basins in Northwest India, Sen and Rajpurohit (1978) classified halophytes into five categories, namely, (1) **true halophytes**, plants growing in saline soil; (2) f**acultative halophytes**, plants growing in saline as well as in non-saline soils; (3) **transitional halophytes**, plants growing only at the transitional margin of saline and non-saline areas; (4) **marshy halophytes**, plants growing in high salinity soil; and (5) **true glycophytes**, plants growing in non-saline soil. They were then divided into three categories by Rajpurohit (1980) and Sen and Rajpurohit (1982):

1. True halophytes can only grow to their full potential in saline soil (above a 0.5% NaCl level).
2. Facultative halophytes can grow exceptionally well in saline soil (above a 0.5% NaCl level).
3. Glycophytes can only develop to their full potential in non-saline environment.

Based on salt absorption and adaptation to salinity, while describing vegetation of Egypt, Zahran (1982) classified 38 dominating halophytic communities into succulent types (e.g. *Halocnemum strobilaceum*, *Arthrocnemum glaucum*, *Salicornia fruticosa*, S*uaeda monoica*, *S. fruticosa*, *S. pruinosa*, *S. vermiculata*, *Halopeplis perfoliata*, and *Salsola tetrandra*, all belonging to Chenopodiaceae (*Inula crithmoides* and *Zygophyllum album*), excretive type (*Avicennia marina*, *Limonium pruinosum*, *Limoniastrum monopetalum*, *Aeluropus* spp., *Sporobolus spicatus*, *S. virginicus*, *Nitraria retusa*, *Tamarix mannifera*, *T. passerinoides*, *Frankenia revoluta*, *Cressa cretica*, *Halimione portulacoides*), and cumulative types (*Rhizophora mucronata*, *Typha elephantina*, *T. domingensis*, *Phragmites australis*, *Imperata cylindrica*, *Lygeum spartum*, *Halopyrum mucronatum*, *Juncus rigidus*, *J. acutus*, *Cladium mariscus*, *Cyperus laevigatus*, *Schoenus nigricans*, *Scirpus litoralis*, and *Alhagi maurorum*). This classification has been widely used in vegetation ecology with some modifications.

From the perspective of salt tolerance, some eco-physiologists (e.g. Breckle (1983, 1986)) divided halophytes into halophytes (which accumulate salts becoming leaf or stem succulent, for example, *Suaeda*, *Arthrocnemum*, etc.) and pseudohalophytes (which avoid salinity or excrete salts via various mechanisms; Chapman (1974) called these crinohalophytes, for example, *Tamarix*).

Based on the criteria of availability of water in the environment (habitat), Le Houerou (1993) classified halophytes into *xerohalophytes* (highly tolerant to drought and salinity, for example, species of *Atriplex* and *Haloxylon*), *mesohalophytes* (moderately tolerant to drought, such as *Salsola*, *Atriplex*, *Suaeda*, *Salsola*, and *Chloris gayana*), *hygrohalophytes* (which do not tolerate any soil dryness such as species of salt marshes—*Distichlis*, *Halimione*, and *Triglochin*), *phreatohalophytes* (which grow on saline water table or seepage areas, for example, *Eucalyptus*, *Populus euphratica*, *Tamarix*, *Haloxylon aphyllum*, *H. persicum*, *Salvadora persica*, *Phoenix dactylifera*, *Hyphaene thebaica*, *Salix babylonica*, *Atriplex* spp., *Prosopis* spp., *Acacia* spp., etc.), *spray halophytes* (which are tied to seaside where seawater spray occurs), and *dust halophytes* (linked with desert habitats affected by salt dust from nearby salt lakes, sebkhas, etc. and taxonomically not different from other dry saline habitats; examples are *Atriplex*, *Suaeda*, *Frankenia*, *Tamarix*, S*alsola*, etc.).

Based on the behaviour of halophytes with different soil texture and its nature, some salt-tolerant species prefer sandy soils, and some are found growing in clay soils or on the rocky substratum. Accordingly, these may be classified (Le Houerou 1993) as *psammohalophytes* (sand-loving), *siltohalophytes* (linked to medium-textured saline soils), *pelohalophytes* (tied to saline clay soils and often found in saline and sodic soils), *petrohalophytes* (tied to rocky saline substrates along sea shores or saline rocks geological outcrops such as salt mounts), *chasmohalophytes* (in cracks of rocky substratum), and *sodic halophytes* (extensively on high pH soils).

Jaradat (2003) reporting halophytes from the Middle East, classified halophytes into salt-requiring *obligatory* (dependent on salt for survival, for example, species of *Salicornia*), *preferential* (growth and development are improved in the presence of salt, for example, species of *Arthrocnemum*, *Salicornia*, and *Suaeda*), *salt-enduring* (enduring a high protoplasmic salt content, for example, *Suaeda monoica*), *salt-resisting* or *salt-excluding* (accumulating salts in special hairs or glands, for example, *Atriplex* and *Zoysia*, or secreting salts from their shoots, for example, *Aeluropus*, *Limonium*, and *Tamari*x, and transport salts from shoots into the roots, for example, *Salicornia*), *salt-evading* (evading salt uptake, for example, *Rhizophora* or evading salt transport into the leaves, for example, *Prosopis farcta*), and *salt-avoiding* or *pseudo-halophytes* (ephemerals and niche plants). This classification with minor modifications has been generally followed widely. Another classification of halophytes separates them into mesophytes, which can develop in large quantities in a saline environment and reversible and irreversible extremophytes. Another division of halophytes, as previously mentioned, includes hydro-halophytes and xero-halophytes. Xero-halophytes can grow in situations where the soil is constantly salted and dry, while hydro-halophytes can grow in aquatic environments or on wet soil (Kumari et al. 2015). The majority of herbal species in arid climates are xero-halophytes, many of which are succulents. Halophytes are regarded as extremophiles since they thrive in high-salinity environments (Kosová et al. 2013).

1.4 Halophytes in Agriculture: A Historical Perspective

Since the dawn of agriculture, salinity has been a part of human existence. However, its detrimental effects were not fully understood until it affected people's access to food and nourishment. It is well known that there previously was a stretch of rich soils between the Tigris and Euphrates rivers in ancient Mesopotamia, which produced enough grain to sustain a significant population. Today, however, the area is known only as a bare desert. When tracing the history of salinity in this area, Jacobsen and Adams (1958) presented information from historical records indicating that the Nahrwan area east of Baghdad only became salinised after 1200 AD due to improper irrigation techniques and that salinity affected Southern Iraq from 2400 BC to at least 1700 BC. According to Jacob (1982), salinity has played a significant part in agricultural history since ancient Babylonia, when humans may have attributed cosmic importance to saline water.

It is also commonly known that large areas of ancient China, the Indus Valley, and South America became deserts due to salt issues brought on by improper irrigation practices by those societies (Dregne 1967). For instance, irrigation was used in the arid Nile Valley for thousands of years without causing secondary salinisation. However, the Nile Delta became salinised when permanent irrigation was introduced into Egypt in the nineteenth century, leading to the construction of an artificial drainage system to remove excess salts (El-Gabaly 1972). Hence, in arid and semi-arid regions, the absence of artificial drainage results in secondary salinisation, and up to half of the world's irrigation systems are impacted by secondary salinisation, alkalisation, and waterlogging, with the lack of good natural drainage, which are relatively uncommon (Szabolcs 1989; Dagar et al. 2019).

Due to salinity or a lack of water, around one billion hectares of the world's dry and semi-arid regions are damaged by salt and remain uninhabitable. According to Pessarakli and Szabolcs (1999), irrigation has damaged around 100 million hectares of land, and 11% of the world's irrigated land has already seen some degree of salinisation (FAO 2012). The issue is especially serious in places where there is low-quality groundwater. The groundwater aquifers are saline in the majority of arid and semi-arid regions. Traditionally, saltwater irrigation has not been a sustainable method of growing typical arable crops. Furthermore, one of the largest obstacles facing farmers and plant scientists—whose primary focus is on finding solutions to salinity-related issues—has been irrigating crops with seawater. Hugo Boyko and Elisabeth Boyko, a geophysicist and plant ecologists, were motivated by the desire to increase the use of natural resources. They showed that it was possible to cultivate crops with full-strength seawater and opened the way for groundbreaking research on seawater agriculture (Boyko and Boyko 1964). They were able to successfully cultivate *Agropyrum junceum* and *Juncus arabicus* for the production of fibre as well as certain varieties of barley on sand dunes using seawater dilution.

Furthermore, since most agricultural crops are sensitive to even trace levels of sodium chloride, the primary goal of individuals involved in saline agriculture has been to find more crop species that can grow economically in saline environments. According to Ventura et al. (2014), the scientific community as a whole began working in two directions: domesticating naturally occurring wild salt-tolerant plants and developing salt-tolerant lines using standard breeding techniques such as crossing salt-tolerant lines with sensitive crops that generate high yields. Because this is a multigenetic characteristic, the breeding technique did not provide the desired results (Flowers et al. 2010). Despite several attempts, only a small number of salt-tolerant lines of a limited number of crops were produced.

Finding possible salt-tolerant species that are appropriate for a given area is the first step in domesticating salt-tolerant plants. The initial stage was the creation of an ecological desert garden in 1962, where xerophytes and halophytes with potential for commercial gain were established (Boyko 1964, 1966, 1968). A systematic investigation for the collection and assessment of halophytes for the production of fodder under saltwater irrigation followed this approach (Pasternak 1987, 1990).

A list of over 140 halophytic plants that grew well even when watered with 100% saltwater and an additional 22 species that produced well at 15% seawater were compiled after the species were assessed in an extensive experimental plot on the Mediterranean coast. This list served as the foundation for the HALOPH database, which was later expanded and published by Aronson (1989). It contained information on approximately 1560 plant species that could flourish under conditions of 7–8 dS m^{-1} saline soil (ECe) or electrical conductivity of irrigation water (ECiw) for significant periods of their life cycles. Since then, Menzel and Lieth (2003), Dagar (2003), and Dagar and Singh (2007) have added to Aronson's data. Yensen created a second version of the information on halophytes and their applications (http://www.ussl.ars.usda.gov/pls/caliche/Halophyte.query). The eHALOPH database is an interactive version that was most recently assembled (accessible at http://www.sussex.ac.uk/affiliates/halophytes).

In the past, many interesting publications regarding the distribution of halophytes and their vegetation ecology (Blasko 1974; Chapman 1976; Sen and Rajpurohit 1982; Dagar 1982; Saenger et al. 1983; Hamilton and Snedaker 1984; Vannucci 1989; Lieth and Al Masoom 2003; Dagar et al. 1991, 1993; Barrett-Lennard 2003; Hari-Bhagwab and Dagar 2004; Dagar 1995, 2003, 2018; Tomlinson 2016; Leal and Spalding 2022); adaptations of halophytes (Khan and Weber 2008; Flowers and Colmer 2008; Flowers et al. 2010, 2015; Manousaki and Kalogerakis 2011; Etesami and Beattie 2018; Hasanuzzaman et al. 2019; Zhao et al. 2020) and potential uses of halophytes as plants/crops, rehabilitation of degraded lands, and genetic resources (Glenn et al. 1992, 1998; Masters et al. 2007; Toderich et al. 2009; Ladeiro 2012; Mishra and Tanna 2017; Dagar 2018; Dagar et al. 2016a, b) have been brought out, but only recently much emphasis is being given regarding their potential as crops.

For the last two decades, successful attempts have been made to evaluate several tree species, fodder grasses, and food and other economic crops and medicinal plants to rehabilitate the salt-affected soils (Barrett-Lennard 2003; Dagar 2014; Singh and Dagar 2005; Gururaja-Rao et al. 2004; Gururaja-Rao and Dagar 2020; Dagar et al. 2022a, b, 2023) and also use saline water for irrigation (Ventura et al. 2014; Dagar 2012, 2014, 2018; Dagar et al. 2013, 2019a, b, 2023) and also developed sustainable and profitable farming systems for saline conditions (Dagar et al. 2014, 2016a, b, 2022a, b, 2023).

1.5 Prospects for Using Halophytes in Saline Agriculture

During the last couple of decades, the potentiality of halophytes in saline agriculture has been explored, but their use in commercial exploitations is limited. These can be improved into new salt-resistant crops of high value or used as a source of genes to be mined into conventional crop species. About 2600 halophytic species are known, but only a limited number of those have extensively been studied for their potential as agricultural crops for food, oils, fibers, gums, flavours, and pharmaceuticals or environmental services for the protection and conservation of ecosystems (Galvani 2007; Masters et al. 2007; Zhang et al. 2007; Ladeiro 2012; Dagar 2018).

Species such as *Distichlis palmeri*, *Zostera marina*, *Chenopodium quinoa*, *C. album*, *Salicornia bigelovii*, *Diplotaxis tenuifolia*, and many others have been established as food crops and can be explored commercially using seawater for irrigation. The Palmer salt grass (*Distichlis palmeri*) used as food by natives in Australia (which contains protein contents 8.7% and fibre higher than wheat) has been used to develop grain crops by NyPa, Inc., having well-balanced amino acid composition (Leal and Spalding 2022).

Halophytes have been used as forage in arid and semi-arid parts of the world for millennia. A large number of salt-tolerant species have been incorporated into pasture improvement programmes across the globe. For cooking and heating, over a billion people in poor nations rely on wood (Ladeiro 2012). Many salt-tolerant shrubs and trees are the source of fuelwood. The majority of the species also make fine lumber.

Mangrove species are frequently investigated for their use as fuel wood for charcoal production in coastal settings. Globally, a lot of arid regions are being investigated for the production of biofuel. Among potential source of liquid fuel-bearing salt-tolerant species include tree-borne oil seeds (TBOS) *Pongamia pinnata* (36% seed oil), *Jatropha curcas* (37%), *J. gossypifolia* (40%), *J. podagrica* (35%), *Aphanamixis polystachya* (38%), *Calophyllum inophyllum* (51%), *Sapium baccatum* (49%), and *Simarouba glauca* (53%) which are potential coastal plants (Velmurugan et al. 2016). *Ricinus communis* produces seed oil used as fuel and medicine; *Pongamia pinnata*, a tree along coasts which tolerates high salinity, bears seeds yielding oil; and *Euphorbia antisyphilitica*, which produces biomass used as liquid fuel extraction, are potential petro-crops for sandy soils irrigated with saline water of ECiw 8–10 dS m^{-1} (Dagar et al. 2012, 2019c).

A number of salt-tolerant species are frequently used as sources of pulp and fibre. These include species of *Pandanus*, *Hibiscus* (*cannabinus*, *tiliaceous*), *Phragmites* (*australis*, *karka*), *Juncus* (*rigidus*, *acutus*), *Typha domingensis*, and grass *Urochondra setulosa*. Many other grasses and sedges are contributing to pulp resources. Many tree species such as *Casuarina*, *Tamarix*, and *Eucalyptus* contribute to pulp wood.

Valuable extracts from seeds, leaves, and bark of a number of halophytes have been used in the health industry. For example, *Catharanthus roseus* withstands ECiw of 12 dS m^{-1} and produces an alkaloid used in the treatment of leukaemia (Dagar et al. 2005), and various parts are used in many Ayurvedic drugs. Many attractive halophytes are used as ornamental and landscape plants. These may be trees, shrubs, succulents and semi-succulents, biennial and perennial ground cover, and lawn grasses. Among them, there are some useful ornamental plants which may find a place in landscaping (Khan et al. 2006; Dagar 2018).

Protecting the shoreline and restoring the coastal ecology are major goals for the majority of mangroves and their associates. Mangroves have an aerial root net that shields their habitats in coastal regions from cyclonic tidal surges. Additionally, they give other creatures, particularly coastal animals, a life support system via the food web. One of the main carbon sinks on the planet is the mangrove forests.

1.6 Saline Agriculture in the Twenty-First Century and Policy Thrusts

The human population has exceeded eight thousand million in March 2023 and reach nine thousand million by 2037 at the present rate of growth of 67 million people annually (https://worldmeters.info/world-population). One of the main issues facing agriculture in the twenty-first century is how to feed the growing population while also providing for their other farm-related requirements. Future generations will thus undoubtedly face tremendous population and economic strain, which will increase the need for agricultural output from all available land, even degraded salt-affected and waterlogged areas. Additionally, there will not be as much clean water available for farming; therefore using brackish and saltwater irrigation including with seawater will become necessary. The situation of ongoing land and water degradation brought on by human activity and climate change will make the issue worse by increasing the frequency of natural disasters including cyclones, floods, droughts, and outbreaks similar to the corona virus. As a result, it has been recognised that the world's food needs are growing more rapidly than crop yields, and scientists, policymakers, and other stakeholders are working and would have to work harder to discover new and innovative approaches to agriculture in order to meet the challenges of the twenty-first century.

It is estimated that developing nations would require 202 million hectares of arable land to boost agricultural production, while only around 93 million ha appear to be accessible (Khan and Duke 2001; Ladeiro 2012). Millions of hectares of agricultural land are also lost annually as a result of development and other factors including unsustainable irrigation methods, overuse of fertilisers, contaminated soil, urban pressure, and climate change. According to estimates from the US Department of Agriculture, ten million hectares of arable soils are lost per year due to salinisation (http://www.usda.gov/).

In light of the aforementioned information, an innovative approach for improving the availability of land and water is necessary for further exploration of salted lands and water in a strategy known as 'saline agriculture', which entails profitable and improved agricultural practices using saline lands and saline irrigation water to achieve better production through integrated and sustainable use of genetic resources (plants, animals, fish, insects, and microorganisms) while avoiding costly soil recovery measures (Aslam et al. 2009; Ladeiro 2012). To boost the income of farmers and other stakeholders, halophytes have thus been investigated as viable crops for saline agriculture during the past few decades (Dagar 2018). However, further research is required to determine if halophytes can be grown commercially. To create new salt-resistant crops and domesticate high-value halophytes, research is required. Halophytes can be used as a source of genes for transgenic crops, which are crops that would not survive or would significantly reduce yields when grown in a saline environment.

An effective way to address environmental problems is through the introduction of herbaceous halophytes and salt-tolerant trees in an agroforestry system. From a financial standpoint, tree plantations provide a sustainable supply of raw materials needed for many different industries, including paper and pulp production, sports goods, furniture manufacturing, plywood, fuel wood, and in certain cases pharmaceuticals (Ladeiro 2012; Dagar 2018). Trees especially in silvopastoral mode help in ameliorating saltlands by decreasing salt load in the upper layer, adding organic carbon through litter and root decomposition increasing the infiltration rate and reducing the capillary rise of water (Dagar et al. 2022a, b). With this approach, farmers get instant economic returns and sustain their livelihood instead of following engineering-based costly technologies. The vital impacts of trees on microclimate, soil erosion, floods, and carbon sequestration are well known (Fedoroff et al. 2010). Dagar (2014, 2018) has thoroughly examined a number of agroforestry systems involving halophytes. To promote saline agriculture in the twenty-first century, given the current edaphic and hydrological circumstances, as well as the economic, climatic, and social factors at play, we thus need a clear and long-term plan.

Research on regulatory and policy mechanisms related to salt-affected lands will be essential. This includes understanding the impact of policies on land management, water usage, and incentives for adopting salt-tolerant crops. Collaborative studies may investigate the socio-economic implications of sustainable salt-affected agriculture (Arora et al. 2018). The future of research in the field of salt tolerance in plants will encompass a multidisciplinary approach, combining cutting-edge technologies and a deeper understanding of genetic, molecular, and environmental factors. The ultimate goal is to develop innovative strategies and technologies that enable sustainable agriculture in the face of increasing salinity challenges.

Governments and organisations will need to develop and implement policies and regulations that address the effects of climate change on salinity stress. This may involve sustainable land management practices, the protection of natural salt-tolerant ecosystems, and the promotion of climate-resilient crops. Many halophytic species have tremendous potential to meet the sustainable livelihood if cultivated in saline including hypersaline arid deserts, salt marshes and coastal swamps. For this we need proper policy initiatives at administrative level.

1.7 About the Book

In this era of global population increase and environmental change, there is a need to provide food to the ever-growing population, combating climate change and conserving biodiversity. The cultivable land resources are finite rather than declining due to developmental works, faulty methods of cultivation, over-exploitation of resources, and urban pressure on arable land; therefore, every piece of land available including degraded saltlands and salt marshes needs to be utilised for food production. At the same time, the availability of good-quality water per capita is declining at a fast rate, and in times to come, there will be limited availability of good-quality water for irrigation; hence the use of poor-quality water in agriculture will be inevitable. Hence, saline agriculture has a stake as an alternative way of increasing productivity.

Keeping in view the availability of more than a billion hectares of saltlands (otherwise lying almost barren) and the rich biodiversity of halophytes, there is a wide scope of saline agriculture and its role in the food industry, phytoremediation, as well as a source of bioactive compounds including modern drugs. The new technologies for the cultivation of halophytes help to utilise saline and arid wastelands and waterlogged areas sustainably for humans and livestock. Having the above-mentioned facts in mind, the present book is conceptualised.

This book contains 20 chapters dealing with a variety of topics related to different aspects of halophytes. It starts with the present introductory chapter dealing with the concepts of halophytes, their evolutionary trends, classification, historical prospectives vis-à-vis agriculture, and main potentials and scopes of saline agriculture in the twenty-first century to play a role in meeting the food requirement of an ever-increasing population. To understand the structure of halophytic communities, two chapters have been planned on ecological overview explaining different formations of plant communities in different ecological regions of the world, one exclusively on mangroves and their associate flora with emphasis on their role in agriculture and environmental services. To understand the initial phase of life of halophytic plants, a chapter on reproductive eco-physiology including seed germination, seed banks, heteromorphism, and flower-ecology has been included along with another on endangered halophytes and means of their conservation.

The adaptation mechanism is very important to understand the reasons for their survival, optimal growth, and productivity; hence the aspect is discussed in detail along with their morphological, anatomical, eco-physiological, and biochemical adjustments to salinity tolerance, which involves controlling ion balance and segregation, bolstering antioxidant systems, and synthesising osmoprotective compounds and plant hormones, collectively empowering them to flourish in saline ecology. These insights are invaluable for comprehending plant responses to stress and exploring potential applications in agriculture and ecology. Understanding these adaptations is crucial for advancing our knowledge of plant biology and for harnessing the potential of halophytes in sustainable agriculture and land reclamation efforts. Chapters on recent studies on genetic engineering and mining of genes for crop production and to enhance stress tolerance in crops to increase agricultural production from degraded saline lands have been included. Further, the contribution of molecular approaches (omics) in understanding the mechanism of salinity tolerance in halophytes has been further added. The role of halophytes in the rehabilitation of unproductive salty lands is very important and has been discussed in detail by competent authors in the field.

There is a significant role of micro-biology in nutrient cycling and enriching organic matter into the soil. Many microbial organisms inhabit the soil under halophytes which play different roles through their enzymes in saline environments. This biota may play a significant role in evolving transgenic crops tolerant to salinity. Therefore, a chapter has been included on halophytic microbiomes and their role in ameliorating stressed ecosystems. The potential of halophytes in saline agriculture is the main theme of the book; therefore, a couple of chapters have been planned which include halophytes as potential food and cash crops of the future; halophytic crops, a resource to reduce water crisis in future; developing bio-saline pastures to enhance agricultural production and restoration of saline and water-logged soils; halophytes as a source of therapeutic medicinal and secondary metabolites; domestication of wild halophytes for high economic gains, some success stories; and harnessing the potential of halophytes for enhanced resilience in arid agroecosystems. In the end, the entire content of the book has been synthesised in the form of a chapter which also includes the policy initiatives.

The book provides a better insight into the basic concepts of the classification, distribution, diversity, and ecology of halophytes. It emphasises applied aspects of the restoration of degraded saline environments, bio-saline agriculture, phytoremediation strategies, and the development of new industrial crops. The contents establish the linkages between ecology, environment, and sustainable development goals.

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