

Parvaiz Ahmad
Mohd Rafiq Wani *Editors*

Physiological Mechanisms and Adaptation Strategies in Plants Under Changing Environment

Volume 1

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Parvaiz Ahmad
Department of Botany
Sri Pratap College
Srinagar, Jammu and Kashmir
India

Mohd Rafiq Wani
Department of Botany
Govt. Degree College (Boys)
Anantnag, Jammu and Kashmir
India

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Preface

Food shortage, burgeoning population, and environmental changes have caused grave troubles to mankind globally. Providing food, for the ever-growing population, has become a cumbersome challenge for the governments across the world. On the other hand, changing environment is transforming our cultivated land to wastelands. This adverse impact of climate changes in the form of dwindling rainfall, rising temperatures, increased severity of drought and flooding is bound to threaten the levels of food security and the economy of any nation. Plants on which mankind is directly or indirectly dependent exhibit various mechanisms for their survival. Adaptability of plants, to changing environment, is a matter of colossal concern and almost all the plant biologists worldwide are trying arduously to accomplish the same goal for addressing the key issues vis-à-vis food security. To get more food from the limited resources is rather herculean; however, steady efforts are needed to grow more and more plants in these wastelands to bring them under productive cultivation. To be successful in this campaign of food security, the plant biologists need to be well acquainted with the knowledge of plant adaptability to changing environment. Moreover, consistent research on plant physiological mechanisms under varying and stressed environments will be highly beneficial in the future for reaping out the desired benefits. Therefore, keeping the above facts in mind and problems which are arising out of such environmental stresses every passing day, an endeavour is carried out by the editors to bring out this volume of “Physiological Mechanisms and Adaptation Strategies in Plants Under Changing Environment” *Volume 1* to address these issues and provide some viable solutions in this direction. We hope that our attempt would be a step ahead in generating interest among researchers and students of this field of science worldwide. However, we feel with firm belief that there is no single book which is completely perfect in its contents and matter in the contemporary era because of ultramodern rapid development in the field of science and technology.

The current volume comprises 12 chapters and each chapter has different research dimensions from another having much significance in their respective fields. Chapter 1 deals with the mechanisms and adaptation of plants to environmental stresses: a case of woody species. This chapter throws light on the multiple

responses of plants to stresses and the consequent adaptation mechanisms towards the environmental stress. Chapter 2 addresses the drought tolerance, role of organic osmolytes, growth regulators, and mineral nutrients, wherein the authors have comprehensively put in their efforts in elaborating the role of growth regulators, viz., abscisic acid (ABA), ethylene and salicylic acid (SA), and various organic osmolytes, such as proline, glycine betaine, free sugars and polyols, in increasing the plant tolerance to drought stress. Chapter 3 is concerned with influencing the product quality by applying drought stress during the cultivation of medicinal plants. This chapter highlights the cultivation of medicinal plants under drought stress, besides explaining conspicuously the enhanced synthesis and accumulation of natural products in drought-stressed plants.

Chapter 4 is about the water scarcity and water stress in agriculture. The chapter explicitly discusses the approaches and methods for water balance and potential perspectives for avoiding the water stress in European agriculture. Chapter 5 is regarding the use of biotechnology for drought and salinity tolerance of crops. The chapter covers genetic approaches, RNA interference and its applications, transcriptome analysis, proteomic approaches, etc. Chapter 6 describes the effect of salinity on plants and the role of arbuscular mycorrhizal fungi and plant growth promoting rhizobacteria in alleviation of salt stress. Chapter 7 discusses cash crop halophytes—the ecologically and economically sustainable use of naturally salt-resistant plants in the context of global changes. The chapter encases the most important aspects regarding the sustainable use of halophytes including the general problem of soil salinity, the biology and ecology of halophytes, and the prerequisites and possibilities of halophyte utilization and of saline production systems.

Chapter 8 addresses the effects of heat stress on growth and crop yield of wheat (*Triticum aestivum*). The authors have meticulously explained the effect of high-temperature stresses on various metabolic reactions, photosynthetic processes, and the protective mechanisms in plants. Chapter 9 discusses low-temperature stresses in plants: an overview of roles of cryoprotectants in defense. Here, the authors have discussed in detail the role of cryoprotectants in alleviating the low-temperature stress in plants. Chapter 10 deals with abiotic stress and lignins: an overview. The chapter lays an emphasis on the multiple means of lignin composition, content, accumulation, and rearrangements in response to a number of abiotic stresses in the plant kingdom.

Chapter 11 is about humic substances and plant defense metabolism. The chapter highlights the interactions between plant root systems and humic substances (HS), antioxidative responses to HS and protective effects of HS in plants under stress conditions, besides how HS contribute to improve the plant performance through complex metabolic mechanisms. Chapter 12 is on mitochondrial respiration: involvement of the alternative respiratory pathway and residual respiration in abiotic stress responses. The chapter highlights the structural organizations of eukaryotic mitochondria, mitochondrial genome, and role of AOX in integrating the cell metabolism under stress conditions.

This volume is compiled with wealth of knowledge in the field of physiological responses, adaptability of plants towards drought, salt, temperature, and other

environmental stresses. Chapters contributed in this book have been published keeping intact author's justifications; however, suitable editorial changes were made wherever considered necessary. In spite of our best efforts, there is a possibility of some errors still creeping in the book for which we seek reader's indulgence and feedback. We wish to express our appreciation to the well-versed contributors who readily accepted our invitation to write the chapters. Moreover, we would like to thank Springer Science+Business Media, LLC, New York, particularly Eric Stannard (Editor Botany, Springer), Andy Kwan (Assistant Editor, Springer), Flora Kim (Developmental Editor, Springer), and all the other staff members of Springer, who were directly or indirectly associated with us in this project for their constant help, valuable suggestions, and efforts in bringing out the timely publication of this volume.

Srinagar, Jammu and Kashmir, India
Anantnag, Jammu and Kashmir, India

Parvaiz Ahmad
Mohd Rafiq Wani

About the Editors



Dr. Parvaiz Ahmad (Editor) Dr. Parvaiz is Assistant Professor in Botany at Sri Pratap College, Srinagar, Jammu and Kashmir, India. He has completed his post-graduation in Botany in 2000 from Jamia Hamdard, New Delhi India. After receiving Doctorate degree from Indian Institute of Technology (IIT) Delhi, India, he joined International Centre for Genetic Engineering and Biotechnology, New Delhi in 2007. His main research area is Stress Physiology and Molecular Biology. He has published more than 30 research papers in peer reviewed journals and 19 book chapters. He is also an editor of

6 volumes (5 with Springer NY USA and 1 with Studium Press Pvt. India Ltd., New Delhi, India). He is recipient of Junior Research Fellowship and Senior Research Fellowship by CSIR, New Delhi, India. Dr. Parvaiz has been awarded Young Scientist Award under Fast Track scheme in 2007 by Department of Science and Technology (DST), Govt. of India. Dr. Parvaiz is actively engaged in studying the molecular and physio-biochemical responses of different agricultural and horticultural plants under environmental stress.



Dr. Mohd Rafiq Wani (Co-editor) Dr. Mohd Rafiq Wani is currently Assistant Professor in Botany at Government Degree College (Boys), Anantnag, University of Kashmir, India. Dr. Wani did his Masters in Botany in 2003 with specialization in “Genetics and Plant Breeding” from Aligarh Muslim University (AMU), Aligarh, UP, India. After receiving the Degree of Doctorate in 2008 for his research work on “Chemical Mutagenesis in Mungbean” from the same University, joined Department of Higher Education, Jammu and

Kashmir Govt. in 2009. He teaches a range of bioscience related subjects at undergraduate/post graduate levels. At present, his research interests are mainly focused on the improvement of pulses through induced mutations and exploring the physiological and biochemical responses of crop plants to a range of biotic and abiotic stresses. As a part of his research endeavour, Dr. Wani has extensively researched and written on the issues of induced chemo-mutagenesis among the food crops, with special reference to pulses. He has around twenty eight (28) research publications to his credit, published in various international and national journals of repute. Moreover, he has also submitted several book chapters to various research oriented volumes. Dr. Wani, while constantly working for his academic and research interests, is currently in the process of editing many volumes of books on the subjects of plant stress physiology and induced plant mutagenesis with reputed international publishers. In addition, he is an editorial member and reviewer of few online journals pertaining to plant sciences, besides being the fellow of various scientific societies like Indian Society of Pulses Research and Development and Indian Society of Genetics and Plant Breeding.

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Contributors

Mohammad Abass Ahanger School of Studies in Botany, Jiwaji University, Gwalior, Madhya Pradesh, India

Parvaiz Ahmad Department of Botany, Sri Pratap College, Srinagar, Jammu and Kashmir, India

Ricardo L.L. Berbara Soils Department, Federal Rural University of Rio de Janeiro (Universidade Federal Rural do Rio de Janeiro, UFRRJ), Seropédica, Rio de Janeiro, Brazil

Kalpna Bhandari Department of Botany, Panjab University, Chandigarh, India

Renu Bhardwaj Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Façal Brini Plant Protection and Improvement Laboratory, Centre of Biotechnology of Sfax, (CBS)/University of Sfax, Sfax, Tunisia

Azza Chelli-Chaabouni National Institute of Agronomic Research of Tunisia, Ariana, Tunisia

Silvana Chocobar-Ponce Laboratorio de Fisiología Vegetal, Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Tucumán, Argentina

Andrés C. García Soils Department, Federal Rural University of Rio de Janeiro (Universidade Federal Rural do Rio de Janeiro, UFRRJ), Seropédica, Rio de Janeiro, Brazil

Department of Chemistry, Agricultural University of Havana (Universidad Agraria de La Habana, UNAH), Havana, Cuba

Nicole Geissler Justus Liebig University Giessen, Special Botany, Giessen, Germany

Rosana González Laboratorio de Fisiología Vegetal, Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Tucumán, Argentina

Neha Handa Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Shuijin Hu Laboratory of Soil Ecology, Department of Plant Pathology, North Carolina State University, Raleigh, NC, USA

Anjana Jajoo School of Life Science, Devi Ahilya University, Indore, Madhya Pradesh, India

Harpreet Kaur Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Parminder Kaur Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Kiyoon Kim Department of Agricultural Chemistry, Chungbuk National University, Cheongju, Chungbuk, Republic of Korea

Maik Kleinwächter Institute for Plant Biology, Technische Universität Braunschweig, Braunschweig, Braunschweig, Germany

Sukhmeen Kohli Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Hans-Werner Koyro Institute of Plant Ecology, Justus Liebig University Giessen, Giessen, Germany

Vinod Kumar Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Helmut Lieth Institute of Environmental Systems Research (USF), University of Osnabrück, Osnabrück, Germany

Khaled Masmoudi Plant Protection and Improvement Laboratory, Centre of Biotechnology of Sfax, (CBS)/University of Sfax, Sfax, Tunisia

International Center for Biosaline Agriculture (ICBA), Dubai, United Arab Emirates

Sonal Mathur School of Life Science, Devi Ahilya University, Indore, Madhya Pradesh, India

Harsh Nayyar Department of Botany, Panjab University, Chandigarh, India

Gabrijel Ondrasek Faculty of Agriculture, University of Zagreb, Zagreb, Croatia

Carolina Prado Laboratorio de Fisiología Vegetal, Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Tucumán, Argentina

Fernando E. Prado Laboratorio de Fisiología Vegetal, Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Tucumán, Argentina

Mariana Rosa Laboratorio de Fisiología Vegetal, Facultad de Ciencias Naturales e IML, Universidad Nacional de Tucumán, Tucumán, Argentina

Tongmin Sa Department of Agricultural Chemistry, Chungbuk National University, Cheongju, Chungbuk, Republic of Korea

Dirk Selmar Institute for Plant Biology, Technische Universität Braunschweig, Braunschweig, Braunschweig, Germany

Gopal Selvakumar Department of Agricultural Chemistry, Chungbuk National University, Cheongju, Chungbuk, Republic of Korea

Resham Sharma Department of Botanical and Environmental Sciences, Guru Nanak Dev University, Amritsar, Punjab, India

Shiv Ram Tyagi School of Studies in Botany, Jiwaji University, Gwalior, Madhya Pradesh, India

Mohd Rafiq Wani Department of Botany, Government Degree College (Boys), Anantnag, Jammu and Kashmir, India

Chapter 1

Mechanisms and Adaptation of Plants to Environmental Stress: A Case of Woody Species

Azza Chelli-Chaabouni

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1 Introduction

Environmental stresses affect negatively plant growth, productivity, reproductive capacity, and survival. Their effects are predicted to become more pronounced in both duration and severity in the near future (Osakabe et al. 2012; Stella et al. 2013) partly, due to global climatic changes (Niinemets 2010).

A. Chelli-Chaabouni (✉)
National Institute of Agronomic Research of Tunisia,
Hédi Karray Street, 2049 Ariana, Tunisia
e-mail: a_chellichaabouni@yahoo.fr

Among the total plant kingdom, woody plants and primarily forests greatly contribute to the world carbon biomass stock, biodiversity, and area protection (FAO 2011). Despite afforestation and natural expansion, the world's total forest area that corresponds to 31 % (3.8 billion ha) of the total land area exhibited an increasing reduction—according to the Global Forest Resources Assessment (FAO and JRC 2012) report—due to both anthropogenic and natural actions. The net annual forest loss increased significantly from 1990–2000 to 2000–2005 periods by 3.6 million ha (FAO and JRC 2012).

Environmental stress may result from abiotic factors including drought, salinity, extreme temperature, inadequate or excessive light conditions, ozone, pollution, and radioactivity. It can also be caused by biotic factors resulting from plant interaction with other organisms such as insects, fungi, bacteria, viruses, plant competition, and allelopathy. The occurrence of one abiotic stress may affect the plant functioning mechanisms through the induction of several interrelated changes at the morphological (Karakas et al. 2000; Vollenweider and Günthardt-Goerg 2005), anatomical (Bosabalidis and Kofidis 2002; Chartzoulakis et al. 2002a; Lesniewska et al. 2004; Fortescue and Turner 2005; Junghans et al. 2006; Chelli-Chaabouni et al. 2010; Ennajeh et al. 2010), physiological (Meena et al. 2003; Junghans et al. 2006; Rejsková et al. 2007), and biochemical levels (Kozłowski 1997; Chelli-Chaabouni et al. 2010; Krasensky and Jonak 2012). However, the effect of extra-optimal environmental factors on plant growth and development is not necessarily harmful. Speed at which the stressful factor installs as well as the intensity and duration of stress determines the beneficial or injuring effect of stress. Hence, the gradual physiological adjustments induced by the slow increase of stress may protect plants from inhibition of growth and/or injury resulting from suddenly imposed stress (Kozłowski and Pallardy 2002).

Woody plants are perennial plants (usually trees, shrubs, or lianas) that are predominantly characterized by the production of secondary tissues in stems and roots. In these latter organs, wood is formed, year after year throughout ontogeny, in superposed layers from secondary xylem leading to the reinforcement of the tissue structures. As woody plants have long-lasting biological cycle, they would have to support stress for a long period of time. Therefore, they have evolved specific mechanisms to overcome detrimental injuries resulting from environmental stresses. The situation is more complicated when multiple stresses occur. The mechanisms adopted against one stress factor are not necessarily similar to those evolved to counteract multiple stresses. Plant response may differ when two or more stresses occur successively or simultaneously.

The specificity of woody plants such as longevity and size makes their use in experimental research studies much more complicated and hard but very informative and worthwhile. Most experimental studies on woody plants are performed on seedlings and young trees. However, plant behavior against environmental stresses may significantly differ throughout the successive developmental stages namely germination and both juvenile and adult stages (Ceulemans and Mousseau 1994; Stamp 2003; Boege and Marquis 2005).

As the effects of environmental stresses are well described in the previous sections, this chapter will make only a brief description on the way that various

environmental factors affect woody species. We will emphasize on the specific adaptation and resistance of woody plants to extra-optimal conditions and the current methods adopted to assess stress tolerance/resistance.

2 Plant Responses to Environmental Stresses

When subjected to environmental stresses including drought, salinity, frost, and herbivory attacks, woody plants need to reallocate energy in a way allowing stress adaptation (Skirycz and Inzé 2010) but also to maintain growth and productivity. These latter functions are closely related to water movements within the plant which are supported by vascular tissues (Osakabe et al. 2012). Plant controls gaseous exchanges and water loss mainly by the regulation of stomatal movements (Fini et al. 2013; Sapeta et al. 2013). To reach these vital objectives, plant responds by the activation of many metabolic processes controlling photosynthesis, ion homeostasis, and plant hormone signaling that may alter gene expression. These reactions are usually expressed at both phenotypic and genotypic levels.

2.1 Abiotic Stresses

Abiotic stresses may be defined as nonliving factors affecting growth and productivity of living organisms. They may be divided into two main categories: (1) physical stressful factors including drought, flooding, extreme temperature, and inadequate light quality or intensity; and (2) chemical stressful factors including salinity, ozone, elevated CO₂ level, and heavy metal pollution. Plants respond to abiotic stresses through morphological and anatomical symptoms concerning leaves, stems, and roots.

Drought, salinity, and cold are among the major abiotic stresses that cause serious problems to woody plants (Krasensky and Jonak 2012) including low water and nutrient availability, toxic concentrations of salt ions such as sodium (Na) and chlorides (Cl), and may lead to Ca deficiency (Marschner 1995). Apart from low water availability, an excess of water in the soil induces flooding stress for woody plants. The lack of oxygen resulting from root submersion induces physiological (Polacik and Maricle 2013) and metabolic changes that can be expressed through plant injury, changes of plant anatomy, inhibition of seed germination, decrease of vegetative and reproductive growths, early senescence, and even mortality (Kozłowski 1997; Glenz et al. 2008). Environmental pollution mainly results from widespread urbanization, industrialization, and agriculture intensification increased exponentially in a way making several pollutants reaching toxic levels for vegetation. Investigations on woody plant responses to phytotoxic levels of environmental pollutants have gained an interest since the early seventeenth century. Due to the important extent of forests in space and duration ecosystems, particular interest on the impact of phytotoxic factors on forest trees increased. Short ultraviolet wavelength

radiations (UV-B) increased due to the depletion of stratospheric ozone (O_3) caused by gaseous pollutants, leading, to some extent, to an ecological imbalance and global climatic changes. A 3 years field study on *Pinus taeda* seedlings demonstrated the cumulative inhibitory effect of elevated UV-B on plant growth (Sullivan and Teramura 1992).

Heavy metal concentrations increased at promising toxic levels in the last few years (Sainger et al. 2011). Apart from the direct effect of heavy metals on woody plant growth and survival (Fernández et al. 2013), their effects on soil animals and microorganisms may indirectly decrease organic mineralization (nitrogen and phosphorous mineralization) and subsequently limit nutrient availability to plants (Tyler 1984).

Many morphological and anatomical changes occur in leaves, as they are an important site of photosynthesis and biochemical reactions including defensive mechanisms. Several stresses including drought, salinity, and high light intensity may cause leaf injury varying from chlorosis (Rochdi et al. 2005) to total leaf necrosis (Chelli-Chaabouni et al. 2010). Marginal leaf scorch was associated with sodium accumulation in salt-stressed peach (Karakas et al. 2000). Salt stress may affect cell elongation and expansion inducing a reduction of leaf area (Curtis and Läubli 1987; Abbruzzese et al. 2009). It affects stomatal characteristics such as stomata density and guard cell length which reflects to stomatal conductance and hydraulic status of the plant (Abbruzzese et al. 2009).

Abiotic stresses could cause severe injuries to woody plant stems. Mechanical effects of strong winds may break twigs and provoke flower bud falls. Epidermis of newly formed shoots may be burned by high solar radiations that occur for a relatively long period of time. At an anatomical level, a reduction of xylem differentiation under salt stress leads to a decrease of vessel lamina due to low nutrient supply to the cambium and low potassium ion (K^+) content in the shoots of salt-sensitive poplar species (Escalante-Pérez et al. 2009).

Roots are affected by abiotic stresses in many ways. Drought and salinity induce a reduction of root system biomass through an increase in root length and width. Cotton seedlings growing in hydroponic salt solution produced less and thinner roots with increasing salinity. Root anatomical analysis showed shorter and more nearly iso-diametrical cortical cells than those of control plants (Kurth et al. 1986). Salt stress may lead to root lignifications in pistachio (Walker et al. 1987). Under soil anaerobiosis conditions (waterlogging or flooding), roots suffer from asphyxia before final death (Kozłowski and Pallardy 2002).

Fruits are also affected by many abiotic stresses either directly or indirectly under climatic conditions favoring pathogen proliferation and growth. Strong or sandy winds and hail falling may be harmful to the fruits especially at the maturation stages. In early stages of fruit development, non-optimal temperatures may affect fruit formation and growth. The ovule of banana tree (*Musa* species) affected by sustained low temperature before anthesis showed many changes (size reduction, low growth, and more rounded shape) in comparison with unaffected ones (Fortescue and Turner 2005).

Plant growth and productivity may be affected by abiotic stresses such as drought (Picchioni et al. 1990; Ramoliya et al. 2004), salinity (Chelli-Chaabouni et al. 2010;

Akça and Samsunlu 2012), and flooding (Kozłowski and Pallardy 2002; Capon et al. 2009; Glenz et al. 2008). Growth is either inhibited or stimulated according to the nature, severity, and duration of stress. Environmental stresses that induce water and nutrient deficiency affect leaf regeneration and growth by the reduction of new formed leaves and the decrease of leaf area. Plant increases photosynthate allocation to the roots in expense of shoots.

In mature woody plants, the negative correlation between vegetative and reproductive growths (Kozłowski and Pallardy 2002) plays a major role under moderate stress conditions. The vegetative stage of development at which drought occurs is determinant in further growth response. A short period of water deficit may induce stimulation of reproductive growth through flower bud formation, break of flower bud dormancy, and flowering according to the time at which stress happens (Kozłowski and Pallardy 2002). Stimulation of reproductive growth may occur simultaneously with vegetative growth inhibition.

The disruption of stomatal conductance by stress affects directly gaseous exchanges that are mainly related to photosynthesis (CO_2) and photorespiration (O_2). Various stresses such as drought (Angelopoulos et al. 1996; Flexas and Medrano 2001; Faraloni et al. 2011; Fini et al. 2013), salinity (Walker et al. 1988; Chartzoulakis et al. 2002b; Tabatabaei 2006; Abbruzzese et al. 2009), flooding (Glenz et al. 2006; Polacik and Maricle 2013), and sub- (Costa e Silva et al. 2008) or supraoptimal temperatures (Kozłowski and Pallardy 2002) may affect photosynthesis. Plants control transpiration through early stomatal closure to diminish water loss and enhance water use efficiency. The leaf water status affects photosynthesis through the efficiency of the photosystem II (PSII) activity (Fini et al. 2013). For instance, the olive cultivars that maintained high relative water content (RWC) under water deficit conditions sustained a high chlorophyll fluorescence ratio F_v/F_m and showed less injury to PSII performance (Faraloni et al. 2011). Sublethal high temperatures may inhibit photosynthesis and cause membrane injury and protein aggregation and denaturation (Kozłowski and Pallardy 2002). In leaves of poplar, drought induced changes in photosynthetic reactions through a decrease of rubisco content and the changes of light-related and membrane-related proteins (Durand et al. 2011). The progressive decline of carbon assimilation under stress may result from both stomatal and metabolic limitations (Angelopoulos et al. 1996; Flexas and Medrano 2001). Under severe water stress the decrease of non-stomatal component of photosynthesis in olive trees was thought to be due to light-dependent inactivation of the primary photochemistry related to PSII (Angelopoulos et al. 1996). Photosynthetic metabolisms including ribulose 1,5-biphosphate (RuBP) regeneration capacity, adenosine triphosphate (ATP) synthesis, and ribulose 1,5-biphosphate carboxylase/oxidase (Rubisco) activity could be disturbed (Flexas and Medrano 2001). At the onset of flooding in greenhouse experimental conditions, photosynthesis of *Tamarix ramosissima* decreased by non-stomatal limitations while oxygen stress increased (Polacik and Maricle 2013).

The biochemical and enzymatic activities of woody plants may change under stressful conditions. They include antioxidant activities (Zhang et al. 2013), lipid peroxidation (Fernández et al. 2013), proline and glycine- β -metabolizing system (Ahmad et al. 2010), and cellulose biosynthesis (Zhong and Lauchli 1988; Delmer

and Armor 1995). Low temperatures induce changes in the concentrations of hormones and metabolites such as sugar and protective proteins and cause alterations in gene expression (Zhu et al. 2007).

Stomatal closure due to many abiotic stresses (including drought, salinity, high light, extra-optimal temperatures, and pathogen attacks) leads to a reduction of assimilation rate and the production of reactive oxygen species (ROS) that are responsible of oxidative stress (Osakabe et al. 2012). ROS are highly destructive to lipids, nucleic acids, and proteins (Türkan and Demiral 2009) and have been shown as important second messengers for stress signal transduction pathways. ROS may affect the cellular activity of the plant through molecular, functional, and structural alterations such as protein, DNA, and lipid oxidative damages (Apel and Hirt 2004). Plant exposure to low temperature may cause mild oxidative stress that show many similarities with plant response to water deficits (Costa e Silva et al. 2008).

2.2 *Biotic Stresses*

Many reports describe the close relationship between plant biotic stresses resulting from pests and diseases and abiotic environmental conditions (Shoeneweiss 1981; Luther et al. 1997). The proliferation of insects, bacteria, fungus, and viruses in woody plants depends on climatic and soil conditions in natural habits but also on orchard management systems of cultivated trees and shrubs (Valdés-Gómez et al. 2011) such as a large amount of coarse woody debris in managed forests that may host an important source of pathogens influencing the stability of forest stands (Santini et al. 2008). Apart from their direct effects, the physico-chemical characteristics of the surrounding environment may have an indirect impact on the plant-parasite biological development and proliferation through their interactions with other insects, fungi, or bacteria. The inter- and intraspecific interactions (symbiotic, parasitic, and synergetic) between these organisms determine the level of stress severity.

The severity of pathogen attacks is also associated to host plant physiology and anatomy (Pérez-Contreras et al. 2008; Rieske and Dillaway 2008; Inbar 2011). The host shifting is a specific trait of phytophagous insects such as aphides and lepidoptera. For examples, aphids of *Pistacia* species assess plant chemical, anatomical, physiological, and structural traits before choosing the adequate host plant (Inbar 2011). Herbivore-induced extensive defoliation of oak forests was correlated with depressed C/N ratio and elevated foliar nitrogen (Rieske and Dillaway 2008). Two main hypotheses are suggested to explain herbivore host plant selection strategy. The “plant-stress hypothesis,” mainly adopted by generalist herbivores, states that stressed plants are less able to synthesize defensive chemicals to resist insect attacks and are then more vulnerable (White 1969). The “plant-vigour hypothesis” states that herbivore is indifferent to the level of plant defense and prefers feeding on healthy and vigorous plants (Price 1991). This latter hypothesis is likely preferred by specialist herbivores. However, both main hypotheses may explain plant

selection by herbivores for depositing of eggs namely oviposition (Pérez-Contreras et al. 2008).

Biotic stresses affect plant growth through a reduction of photosynthesis (Christen et al. 2007; Bilgin et al. 2010). Bilgin et al. (2010) attempted to understand how do various biotic stresses (including arthropods, fungi, bacteria, and viruses) affect plant photosynthesis activity at a genetic level. They compared transcriptome data from microarray experiments after 22 different forms of biotic damage on eight plant species. Results revealed that regardless of the nature of biotic factor, transcript levels related to photosynthetic activity decreased. The photosynthetic gene down-regulation was accompanied by an up-regulation of genes coding for synthesis of jasmonic acid and those involved in the responses to salicylic acid and ethylene. Authors suggested that these reactions may be a part of defense mechanism.

In natural ecosystems, woody plants may compete with other woody or herbaceous species for resources in different ways such as the large and deep root invasion of the rhizosphere (Schenk 2006) for water and nutrient uptake, the increase of plant height to enhance light availability (Sterck and Bongers 2001), and the release of chemicals namely allelopathy that inhibit or stimulate growth and survival of the neighboring plant and microorganism species (Maclaren 1983). In some cases, different strategies may explain the inter- and intraspecific plant interactions (Inderjit and Mallik 2002). The plant's release of allelo-chemical products may have several effects on individual neighboring plants and, consequently, on organism ecosystem distribution. At the individual plant level, these products may affect the seed germination ability (Blanco 2007), plant growth (Lodhi 1976), physiology (e.g., respiration, photosynthesis, and hormonal and enzymatic processes), the cellular functioning system (e.g., membrane permeability, chloroplast activity, and chlorophyll concentration), the water and nutrient uptake, and transport.

3 Multiple Stresses: Occurrence and Interaction

The occurrence of only one stress at the same time in the field or in the natural conditions is seldom rare. Often, two or more stresses are simultaneously or successively associated. For example, drought stress is closely related to high temperature and luminosity in hot climate arid and semiarid areas. Plants respond to multiple stresses by the activation of one specific mechanism (Rizhsky et al. 2004) through the activation of numerous biochemical and molecular reactions (Osakabe et al. 2012; Perdiguero et al. 2013). The multiple stress combination may lead to a modification in the plant stress susceptibility. The occurrence of one environmental stress may indispose or predispose plant to a second stress. At the genetic level, the over-expression of genes to adapt to a given stress may incur tradeoffs for acclimation to other stresses (Lynch and St Clair 2004). For example, the increase of plant transpiration resulting from pollutants such as sulfur dioxide (SO₂) may expose plant to drought stress (Shoeneweiss 1981). Inversely, stomatal closure in response to many abiotic stresses including drought, flooding, and low atmospheric

humidity may lead to higher tolerance to air pollutants (Kozłowski and Pallardy 2002). Similarly, elevated atmospheric CO₂ due to global climatic changes may alleviate oxidative stress (drought and salinity) and enhance plant tolerance through the availability of more energy that can be allocated to defensive mechanisms (Kyoro et al. 2012).

In the particular case of biotic and abiotic stresses association, the occurrence of an abiotic stress can enhance or reduce plant resistance to a pest or pathogen and vice versa (Atkinson and Urwin 2012). Abiotic stresses such as water deficit, salinity, freezing, or heavy metal pollution may weaken plants and make them more vulnerable to the attack of some pests and diseases (Shoeneweiss 1981). For forest stands, this vulnerability may be extended to ecosystem level as reported by Luther et al. (1997) in the case of insect defoliation of balsam fir stands. Under abiotic stress, the normal carbon allocation patterns may be deviated in a way making higher carbohydrate allocation to the root and leaves in favor of carbohydrates left for carbon reserve and defense compound biosynthesis (Luther et al. 1997). At a molecular level, the metabolic signaling pathways of such stress combinations can act antagonistically (Anderson et al. 2004). In light of this, studying plant stress tolerance by imposing each stress individually may not reflect the exact plant response in the field (Mittler and Blumwald 2010).

4 Plant Response to Stress Throughout Ontogeny

Several structural (Loney et al. 2006), physiological, and biochemical (Loney et al. 2006; Juvany et al. 2013) changes occur during plant development. As woody plants develop, they show usually an increase in carbon/nutrient balance and carbon storage capacity (Niinemets 2010) as well as greater accessibility to water, nutrients, and sunlight but also a decrease in growth rate, root/shoot ratio, photosynthesis, stomatal conductance, and metabolic activities (Boege 2005). The tree responses to stress vary throughout the ontogeny (Niinemets 2010) in relation with age-related changes of physiological and biochemical processes controlling carbon assimilation and storage, growth rate, and defensive mechanisms. Compared to seedlings and saplings, many reports described greater resistance of large non-senescent trees to abiotic (Kozłowski 1997; Cavender-Bares and Bazzaz 2000; Rozas et al. 2009) and biotic stresses (Basey et al. 1988; Luther et al. 1997). However, regarding plant resistance to herbivore stresses, both positive (Loney et al. 2006) and negative (Schappert and Shore 2000) relationships between ontogeny and resistance were reported for several woody species (Boege and Marquis 2005). During plant development, Boege and Marquis (2005) proposed a pattern of changes in plant defense and tolerance during ontogeny based on the assumption that plant resources may act as a constraining trait of tolerance and resistance of vegetative tissues. Armas and Pugnaire (2009) findings support this statement as the interaction of the two dominant shrub species *Pistacia lentiscus* and *Juniperus phoenicea* did not benefit any species at seedling stage but when plants became progressively mature, *Pistacia* species

gained competitive growth and survival advantage. It should be emphasized that ontogeny has an effect not only on the ability of plant to respond to a given stress but also on the growth recovery after the disappearance of stress (Boege 2005).

At a seedling stage, plants may produce defensive compounds to resist herbivory attacks (Schappert and Shore 2000), but as the plants gain in maturity, the biochemical protective strategy decreases progressively while many protective structural changes (greater leaf thickness, higher lignin and fiber content) occur (Loney et al. 2006). The decrease of plant defensive biochemical synthesis with age was suggested as the result of natural selection based on the reallocation of energy according to the cost/benefit ratio. Plants maximize the production of protective chemicals at developmental stages of great risk of herbivore attack or low tolerance (Schappert and Shore 2000; Stamp 2003).

5 Influence of Biomes on Stress Occurrence and Severity

The severity and timing of stresses vary throughout the growing season according to the nature of a given ecosystem as illustrated by Niinemets (2010). For example, in cool temperate ecosystems, the plant tolerance to frost stress is lower during the early winter period corresponding to the plant dormancy; plants are more susceptible in middle and late winter when temperature becomes progressively warmer (Ögren 1996). In the Mediterranean environments, long-lasting supraoptimal temperatures and light are among the major factors of stress (Angelopoulos et al. 1996). In these areas, plants are exposed to drought and photo-inhibition (Guàrdia et al. 2012) but the severity of stress differs from coastal to high altitudes (Flexas et al. 2001; Yang and Miao 2010). Under progressive drought stress *P. kangdingensis*, originating from higher altitude, displayed superior height growth and leaf development as well as greater increments in soluble proteins, soluble sugars, free proline, and antioxidant enzyme synthesis than *P. cathayana* that grows in lower altitude (Yang and Miao 2010). However, even in Mediterranean areas, woody plants may be subjected to episodic low temperature events (below 0 °C) that limit expansion of species such as *Eucalyptus globulus* (Costa e Silva et al. 2008).

Differing from Mediterranean and cool temperate forest ecosystems, the temperate bogs are subjected to chronic nutrient deficiency and waterlogging (Niinemets 2010).

Climate is an important factor that influences and modulates ecosystem composition and scope. Increasing temperatures may lead some species to move to higher altitudes that are suitable for their growth and development. Increasing plant competition for water and nutrients in arid and semiarid biomes may lead to a dominance of the most adapted species at the expense of species showing lower stress tolerance (Armas and Pugnaire 2009; Eilts and Huxman 2013). Moreover, plant response and susceptibility to various biotic stresses may be affected by the biome (Slippers and Wingfield 2007) as well as by the predicted global climatic changes (Veteli et al. 2002; Allen et al. 2010). Table 1.1 indicates abiotic factors of stress encountered in various temperate climatic conditions.

Table 1.1 Major stress factors encountered in temperate climates

Climate nature	Stress factors	References
Cold and cool temperate climates	Waterlogging and flooding	Kozłowski and Pallardy (2002) and Niinemets (2010)
	Nutrient deficiency	Niinemets (2010)
	Elevated CO ₂	Tjoelker et al. (1998)
Arid and semiarid regions and Mediterranean climates	Drought	Chartzoulakis et al. (2002a) and Guàrdia et al. (2012)
	Salinity	Chartzoulakis et al. (2002b) and Lynch and St Clair (2004)
	Episodic low temperatures (<0 °C)	Costa e Silva et al. (2008)
Tropical and subtropical regions	Soil acidity	Lynch and St Clair (2004)
	Mineral toxicity and deficiency	Lynch and St Clair (2004)
	Light deficiency	Sterck and Bongers (2001)

6 Adaptation and Mechanisms of Stress Tolerance/Resistance

The previous three sections have provided insights into specific responses of woody trees to one or multiple stresses according to many intrinsic or extrinsic factors (multi-stress interactions, response throughout ontogeny, biome influence). Plants may activate different mechanisms at various structural and functional levels to overcome possible injury that may be induced by one stressful condition. These mechanisms act simultaneously or successively in relation with the nature of stress, its duration, and severity. As stated by Glenz et al. (2006) for flooding tolerance, specific biotic factors (developed adaptation and capacity of acclimation) related to the woody species influence the final response of plant to a given stress. As one mechanism may be involved by species under various kinds of environmental stresses (for instance, osmotic adjustment is implicated in both drought and salt stress), we will present the main adaptive strategies adopted by plants at structural (morphology and anatomy) as well as functional (growth, physiology, ionic relations, biochemical and enzymatic activities, and genetics) levels.

6.1 Structural Adaptation

The major feature that determines the plant stress tolerance is concerned with leaf as it is the principal site of gaseous exchange, photosynthesis, and metabolic activities. In many species exposed to various biotic and abiotic forms of stress such as drought, salinity, wounding, and pathogen attacks, an increase in leaf cuticle thickness (Bacelar et al. 2004; Bosabalidis and Kofidis 2002) and epidermis (Kulkarni et al. 2010), a reduction of size and density of epidermal cells (Chartzoulakis et al. 2002a) and xylem (Bosabalidis and Kofidis 2002; Kulkarni et al. 2010), and a

greater cell wall lignification (Niinemets et al. 1999; Osakabe et al. 2011) have been considered as stress-tolerant traits. Drought-stressed olive plants reduced the size of stomata and epidermal and mesophyll cells, increased cell and stomatal density, and reduced the number of nonglandular hairs (Bosabalidis and Kofidis 2002).

These anatomical and morphological modifications reflect a better control of water loss through cuticular transpiration in water deficit conditions. For instance, several olive species tend to diminish leaf area, develop thicker epidermal leaves, and increase trichome density when subjected to drought stress (Ennajeh et al. 2010). The increased leaf fracture toughness seems to be useful in the protection from herbivore damage (Choong et al. 1992) as it improves leaf mechanical properties through the thickening of smaller vein walls forming a venous network (Lucas et al. 1991).

The plant-protective roles of cuticular waxes are widely reported from many species (Shepherd and Griffiths 2006). Cuticular-wax layers are predominately composed from long-chain hydrocarbon compounds, including alkanes, primary alcohols, aldehydes, secondary alcohols, ketones, esters, and other derived compounds (Shepherd and Griffiths 2006). Waxy species are reported to modify reflectance in a way that changes light absorption and consequently photosynthetic activity (Cameron 1970; Holmes and Keiller 2002). The plant reflectance ability plays a major protective role against high radiations in drought conditions and UV-B harmful radiations due to the stratospheric ozone layer damage. Reflectivity is highly influenced by the surface topography of leaves, primary hairs, and cuticular waxes (Shepherd and Griffiths 2006).

The resistance of xylem to cavitation events is an important parameter that determines stress resistance (Tyree and Ewers 1991). The drought-stressed bald cypress plants used their biomass in a way that strengthens the xylem and reduces its vulnerability to cavitation (Stiller 2009). Similarly, woody plants respond to salinity by the reduction of vessel lumina and the increase of wall strength to counteract the reduction of xylem hydraulic conductivity resulting from salt stress. For example, the decrease of the vessel lumina of the salt-resistant poplar species *Populus euphratica* under salt stress conditions was lower than that of the salt-sensitive *Populus × canescens* species (Junghans et al. 2006).

In anoxic conditions such as submersion of the root system, plants develop hypertrophied lenticels that present a pathway for the diffusion of oxygen (O₂) through living bark cells and the release of toxic compounds related to anaerobiosis (Glenz et al. 2006). The presence of lenticels as a morphological adaption to flooding is reported for many Central European trees and shrubs including *Acer campestre*, *Alnus glutinosa*, *Fraxinus excelsior*, *Populus nigra*, and *Salix alba* (Siebel et al. 1998; Hook 1984). In addition of lenticels, aerenchyma tissues are thought to be a morphological adaptation of woody plants to anaerobiosis as they constitute an extensive intercellular air space allowing the diffusion of oxygen from the aerial part of the plant to the roots (Glenz et al. 2006; Wang and Cao 2012).

The variation of cell wall elasticity under stressful conditions was supported as a trait of stress tolerance of some woody species. However, both positive (Chartzoulakis et al. 2002a) and negative (Patakas and Noitsakis 1997) roles of tissue elasticity were suggested as a mechanism of adaptation to stress. As examples of the two

Table 1.2 Morphological and anatomical traits of stress tolerance that have been cited in woody plants

Trait	Stress	Species	References
Increase of leaf cuticle thickness	Drought	<i>Olea europaea</i>	Bacelar et al. (2004) and Bosabalidis and Kofidis (2002)
Increase of leaf epidermis		<i>Ziziphus mauritiana</i> (Lamk.)	Kulkarni et al. (2010)
Increase of thick palissade mesophyll layers	Salinity	<i>Olea europaea</i>	Bacelar et al. (2004)
Reduction of size and density of epidermal cells	Wounding	<i>Olea europaea</i>	Chartzoulakis et al. (2002a)
Reduction of size and density of xylem		<i>Olea europaea</i>	Bosabalidis and Kofidis (2002) and Kulkarni et al. (2010)
Cell wall lignification	Pathogen attacks	<i>Ziziphus mauritiana</i> (Lamk.) Several species	Niinemets et al. (1999) Osakabe et al. (2011)
Great leaf anatomical plasticity	Drought	<i>Quercus</i> species (<i>Q. velutina</i> , <i>Q. coccinea</i> , and <i>Q. rubra</i>)	Ashton and Berlyn (1994)
Increased leaf fracture toughness	Herbivore damage	42 tropical tree species	Choong et al. (1992)
Presence of hair and cuticular waxes	High light intensity	<i>Eucalyptus</i> species 45 species including <i>Citrus</i> , <i>Eucalyptus</i> , <i>Quercus</i> , <i>Prunus</i>	Cameron (1970) Holmes and Keiller (2002)
Chloroplast movements	Light limiting conditions	Woody and non-woody species <i>Tradescantia albiflora</i> <i>Cissus</i> , <i>Eustrephus</i> , <i>Alocasia</i> , <i>Eucalyptus</i>	Shepherd and Griffiths (2006) Park et al. (1996) Williams et al. (2003) and Way and Pearcy (2012)
Lenticels, aerenchyma tissues, and adventitious roots	Flooding	Central European trees and shrub species <i>Taxodium distichum</i> and <i>Sapium sebiferum</i> Woody species (general review)	Glenz et al. (2006) Wang and Cao (2012) Kozlowski and Pallardy (2002)
Resistance to xylem cavitation		Trees and woody plants	Tyree and Ewers (1991)

cases, the reduction of cell wall elasticity was suggested as an efficient mechanism adopted by grapevine to overcome water deficit (Patakas and Noitsakis 1997) and high UV radiation (Lesniewska et al. 2004). Inversely, the increase in tissue elasticity and a decrease of osmotic potential were thought to be likely the two predominant mechanisms of adaptation in avocado (Chartzoulakis et al. 2002a). Table 1.2 shows number of morphological and anatomical traits that have been associated to stress tolerance in woody plants.

6.2 *Physical Movements*

Plants respond to various abiotic (e.g., drought, salinity, UV radiation, high temperature, and heavy metals) and biotic (e.g., herbivores, bacteria, virus, and fungi) stresses by leaf rolling (Bosabalidis and Kofidis 2002; Kadioglu et al. 2012). This physical movement combined with stomata closure plays a key role in the reduction of water loss and the maintenance of cell turgor in plants subjected to osmotic stress conditions. However, stomata closure leads to a reduction of gaseous exchanges through the leaves and a diminution of plant photosynthetic activity due to a reduction of CO₂ entry. In these conditions, plants optimize carbon uptake by different ways such as the modification of crown architecture and leaf angle positioning to adjust within crown irradiance (Egea et al. 2012) and heterogenic stomatal aperture (Guàrdia et al. 2012). At a cellular level, chloroplast movements operate to adjust photon flux density (Park et al. 1996; Way and Pearcy 2012). At low light conditions, chloroplasts move to increase light absorption. The rapidity of chloroplast rearrangements to periclinally or anticlinally position against leaf surface is a viable mechanism for leaves to reduce excess photon flux density interception (Williams et al. 2003; Way and Pearcy 2012). Within chloroplasts, the size and stacking of thylakoid grana may change within 10 min of high light exposure (Rozak et al. 2002).

6.3 *Growth and Physiology*

One of the adaptive responses to stress is the plant growth regulation by modulation of both cell division and expansion (Skirycz and Inzé 2010). Woody plants subjected to nutrient deficiency allocate higher amounts of photosynthate to roots (Kozłowski and Pallardy 2002). Tolerant plants use different ways to reactivate root system functioning and compensate from root alteration and mortalities. Under water deficit conditions, *Fagus* species stimulated fine root growth to compensate from root biomass losses during dry mid-summer (Leuschner et al. 2001). Similarly, plants adapt to flooding conditions by the regeneration and growth of adventitious roots to compensate from the alteration of asphyxiated initial roots. Root initiation takes place on the originated root system and/or submerged portion of the stems (Kozłowski and Pallardy 2002). Flood tolerance in woody plants is positively correlated with the ability of adventitious root regeneration, the conversion of toxins produced in the soil to less toxic compounds by rhizosphere oxidation, and the increase of root-synthesized gibberellins and cytokinins (Kozłowski and Pallardy 2002).

Many reports describe a general close association between morphological and anatomical traits and the efficiency of physiological activity in stressed plants (Ashton and Berlyn 1994; Bacelar et al. 2004; Kulkarni et al. 2010). Ashton and Berlyn (1994) found close correlations between anatomical measures of plasticity and physiological measures of plasticity in *Quercus* species. Stomatal density plasticity was correlated with both net photosynthesis and stomatal conductance plasticity.

The most drought-tolerant and higher light demanding *Q. velutina* species exhibited greater anatomical plasticity and higher net photosynthesis than *Q. coccinea* and *Q. rubra* species. *Quercus ilex* L. adapted to severe drought conditions by patchy stomatal closure leading to heterogenic photosynthesis (Guàrdia et al. 2012). Drought-tolerant *Jatropha curcas* accessions maintained high leaf RWC through water-saving strategy involving strict stomatal regulation and growth reduction (Sapeta et al. 2013).

6.4 Cell Homeostasis and Osmotic Adjustment

Drought and salt stress lead to the increase of osmotic pressure in the cytosol due to water deficiency (drought) or the uptake of large amounts of salts (salt stress). Salt-tolerant species develop different strategies either to exclude salt from the cells or to tolerate it within the cells (Kozłowski 1997; Parida and Das 2005). To maintain cell homeostasis and cell turgor and protect metabolic activities, osmotic adjustment mechanism is adopted by tolerant species through two ways: (1) sequestration of excess of salt ions in the vacuole and (2) biosynthesis of organic osmoprotectant compounds (Munns 2002). Osmoprotectants are named compatible solutes as they do not interfere with plant metabolism even if they accumulate to high concentrations. Main biochemical compounds implicated in osmoregulation are proline (Ahmad et al. 2010), glycine-bétaine, and soluble sugars (Kozłowski 1997; Clifford et al. 2002). The nature of biosynthesized osmoprotectants seems to be species-related (Pallardy 2007). The presence of mucilage and polysaccharides in leaves of drought-tolerant *Ziziphus* species is reported to act in osmotic adjustment by the remobilization of solutes allowing better efficiency in water uptake and translocation to the roots and stems before plant defoliation (Clifford et al. 2002). However, in the special case of salt stress, there is uncertainty with regard to the role of proline in salt tolerance. In fact, both positive (Hokmabadi et al. 2005) and negative (Ashraf 1989) associations of proline accumulation with tolerance to salt stress were reported. Similarly, instances of enhanced (Gucci and Tattini 1997) as well as unchanged and reduced soluble sugar contents were reported (Rejsková et al. 2007).

6.5 Ionic Interactions

Stresses such as drought and salt stress may lead to an ionic imbalance. The disturbance of potassium (K^+) nutrition is a common feature under sodium chloride ($NaCl$) stress conditions and is often associated with potassium deficiency resulting from potassium–sodium interaction (Cramer et al. 1987; Slama 2004; Parida and Das 2005). Thus, the maintenance of normal cellular functions strongly depends on the K^+ nutrient status and K^+ – Na^+ interaction through a selective uptake and transport of K^+ in depend of Na^+ into the shoots (Cramer et al. 1987). A high K^+/Na^+ ratio