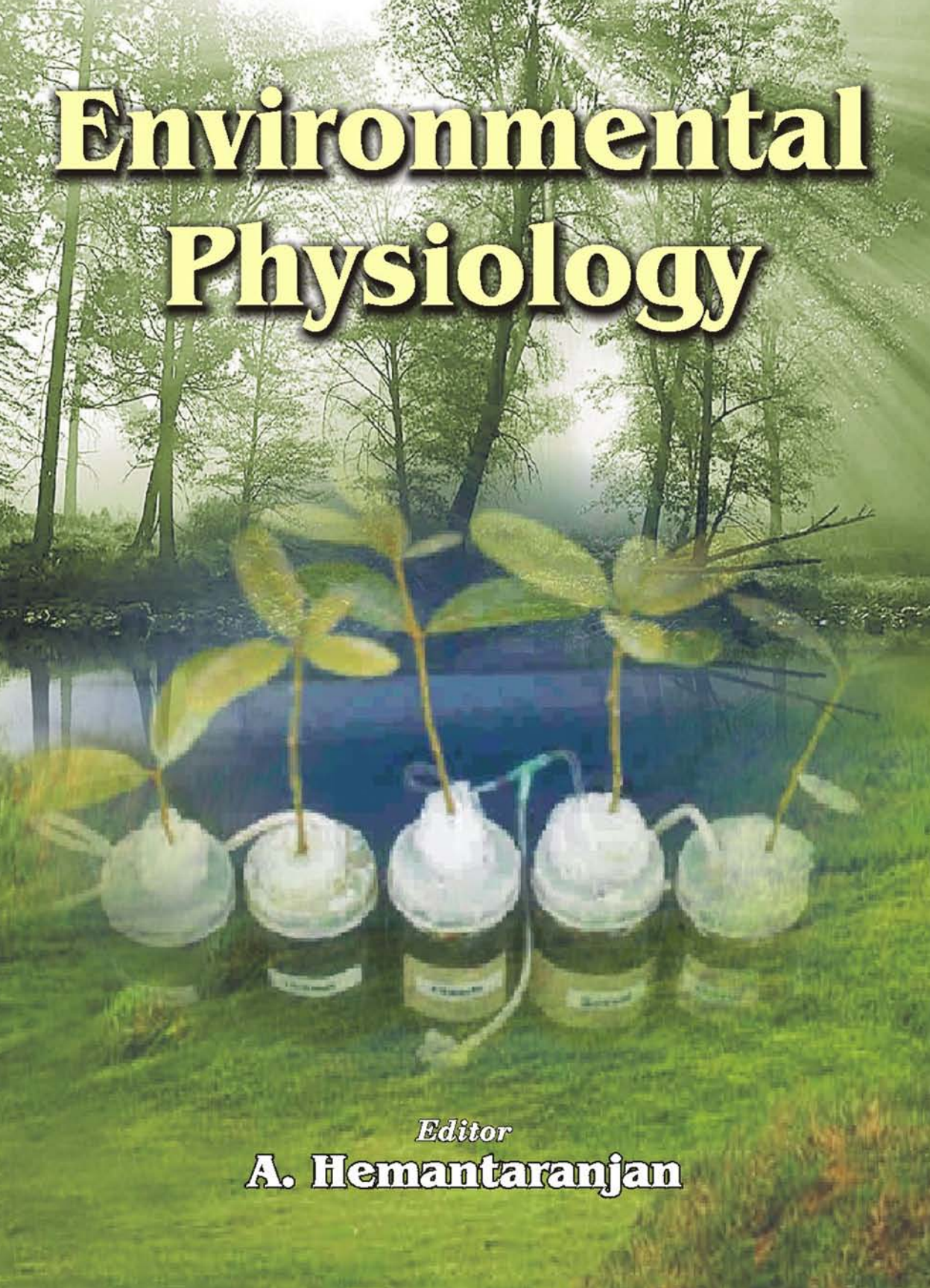


Environmental Physiology



Editor

A. Hemantaranjan

ENVIRONMENTAL PHYSIOLOGY

ENVIRONMENTAL PHYSIOLOGY

Editor

A. Hemantaranjan

Department of Plant Physiology,
Institute of Agricultural Sciences,
Banaras Hindu University,
Varanasi 221 005, INDIA



SCIENTIFIC PUBLISHERS (INDIA)

P.O. BOX 91

JODHPUR

Published by:

Pawan Kumar

Scientific Publishers (India)

5-A, New Pali Road, P.O. Box 91

JODHPUR - 342 001

Tel.: +91-291-2433323

Fax.: +91-291-2512580

E-mail: info@scientificpub.com

www.scientificpub.com

© Hemantaranjan, A., 2007

ISBN: 978-81-7233-720-9 (PB)

EISBN: 978-93-87307-52-0

Lasertype set: Rajesh Ojha

Printed in India

PREFACE

The innovative theme of the book entitled “*Environmental Physiology*” has been especially edited for realistic and rational utilization by planners, scientists, investigators, academicians and postgraduate students. This book is an exceptional assimilation of well-timed, crucial and comprehensive ***twenty-one worthy reviews*** of diverse significance contributed by sincere dedication of experienced, laudable and well-known scientists/ stalwarts all over the world. Almost certainly, the worthy theme of this book has been well justified and elucidated primarily in the section “***From Editor’s Desk***”, nevertheless, in this segment, necessarily the major relevant topics of all the twenty-one reviews have been introduced. I am ecstatic to mention the genuineness that due to incredible harmony with the world scientists of various disciplines developed in the last eight years, over nineteen Indian and twenty-nine foreign intellectuals enthusiastically came forward and associated in this extensive project of pragmatic importance. In fact, this kind of momentous work cannot be accomplished effectively and productively by a single person belonging principally to a specific field of specialization. This is also strongly realized that there is progressively more a need of united effort of experts in the ground-breaking work of precise importance above all in the agricultural sciences, which absolutely depends on environmental situations.

The intricacies of abiotic and biotic stresses on growth and development of plants have been understood in the last few decades. This is the right time to apply the knowledge acquired in this direction, out of exhaustive research throughout the globe, in anyhow enhancing yield of crop plants cultivated under a variety of environmental stresses, in general, and extending basic research, in particular, for having more insight in establishing new cultivars under higher intensities of abiotic stresses like drought, high and low temperature, salinity, sodicity, flooding, mineral, oxidative, heavy metals, etc. This book too is an endeavour to make aware the young workers with allied techniques comprising destructive and non-destructive methods for extending relevant research incessantly in the years to come to gain further information of both basic and applied significance for sustainability of agriculture under environmental stresses. The manifold ideas on basic problems of the present and the future as well as resolutions have been

consolidated through precious reviews by distinguished personnel of plant sciences in twenty-one chapters as follows:

The first three chapters are mainly devoted to techniques for physiology of plants under stress including the recent ones. In *Chapter 1* three eminent scientists from Belgium have well explained extensively that imaging techniques are an ideal method to visualise the evolution of patterns of plant physiological parameters and by using imaging techniques, plant physiological parameters can be assessed *in vivo* without contact with the plant and in a non-destructive way, from a microscopic to a remote sensing scale. In *Chapter 2*, distinguished Indian workers have discussed at length various techniques available for monitoring abiotic stresses. Besides these, in *Chapter 3*, illustrious Australian scientists have exclusively detailed the application of the chlorophyll fluorescence technique to assess plant responses to high and low temperatures, drought stress, waterlogging, salinity and nutritional disorders. They also briefly review a theory of chlorophyll fluorescence and give a physiological background for its application as a screening tool. In *Chapter 4*, scientists from Bulgaria have very well discussed the influence of high temperature on the photosynthetic apparatus. Later, the function of antioxidants in stressed plants is diverse and complex, and studies on their function should be considered within the whole physiology of the plant, so in *Chapter 5*, the veteran Spanish workers have described meticulously the function of plant hormones and antioxidants in the regulation of plant responses to drought. Subsequently, in *Chapter 6*, photosynthetic responses of C₃ plants to drought have been comprehensively reviewed by two Spanish scientists. In *Chapter 7*, the renowned Brazilian scientist has painstakingly reviewed some recent advances in drought effects on photosynthesis of tropical tree crops, which may serve as a stimulus for additional effort in this important demanding field of research. Next to this, scientists from Argentina have wonderfully reported in *Chapter 8* the effects of defoliation under water stress on several physiological, morphological and demographic factors which may be important in determining plant and community productivities.

In *Chapter 9*, an illustrated account of biological role and regulation of heat shock proteins has been given by two prominent Indian workers. Review in *Chapter 10* by two reputed scientists from Portugal focuses on molecular and biochemical changes triggered in plants by UV-B exposure. Leaves are the main target of PAR and UV-B radiation and as UV-B light is potentially deleterious, knowledge of the ultrastructural alterations are of paramount importance because photosynthetic performance of the plants is dependent upon the integrity of the mesophyll cells. Afterwards, an eminent Australian Scientist in *Chapter 11* has given an account of the increasing understanding of the Ca²⁺ signatures which are proposed to encode the specificity of the

ozone-induced response, and in so doing, lead to the appropriate downstream response. Besides this, the chemistry behind the "natural" production of reactive oxygen species during "normal" photosynthetic and respiratory processes has been briefly summarised and the various mitigating defence mechanisms of the plant outlined. Next to this, oxidative stresses in plants with reference to glutathione have been substantially described in *Chapter 12* by a brilliant Indian scholar. In addition, in *Chapter 13*, very dedicated workers from Portugal have thoroughly reviewed Ca^{2+} signaling systems in plants. One of our present challenges is to map the spatial distribution of Ca^{2+} regulated downstream proteins and to understand their role in the network control. Furthermore, the *Chapter 14* concisely and precisely reviews the response of N_2 fixation to some of the environmental factors such as salinity, drought, water-logging, temperature, acidity, elevated atmospheric CO_2 and agrochemicals.

The *Chapter 15* reviews the recent findings on the Al stress and necessary steps to obtain the transgenic crops, which can grow in acidic soil. This is followed by another interesting article in *Chapter 16* on aluminum tolerance in *Glycine max* illuminating the physiological mechanism behind this, as this is a crucial problem of acid soils. Remarkably both the reviews have been contributed by the outstanding team of Japanese scientists. Accordingly, the next review article by another group of intellectuals from Morocco and India in *Chapter 17* provide sufficient information to determine what acid and alkaline soils are as well as to allow a best understanding of the performance of plants in these soils and the strategies developed by these species to attain the necessary metabolic activity required for their normal growth.

The book, in addition, is found enriched in true sense by having two important review articles on the whole on salt stress, which is indeed the most critical abiotic stress problem throughout the world. In this regard the *Chapter 18* deals methodically with the cellular and molecular responses to salt stress tolerance mechanisms, whereas the *Chapter 19* presents the indispensable crisis of *rhizobium* – legume symbiosis especially under salt stress. This book makes it pioneer in adding another requisite research on coconut palm, which responds to the stress conditions at morphological, anatomical, physiological and biochemical levels. The atmospheric stress influences the photosynthetic rates and if prolonged with soil moisture stress, dry matter production and its partitioning are influenced. Consequently, a very demanding review on adaptive strategies of coconut palm under stressful conditions has been extensively written in *Chapter 20* where experienced authors from the Central Plantation Crops Research Institute, Kasaragod have suggested that to develop the molecular markers linked to desirable traits and to understand the inheritance patterns of these traits.

The genotypes with desirable traits for tolerance to stress conditions can be used in breeding strategies for abiotic stress tolerance in future crop improvement strategies. Last but not the least, to feel a sense of completion, it was thought worthwhile to include at least one significant review reflecting biotic stress amidst the theme of abiotic stress. Hence, the last *Chapter 21*, unfolding mechanisms involved in establishment of pathogen to their host. After considering possible signaling mechanisms and systemic acquired resistance (SAR), the biotechnological approaches which are currently used to defend plants from pathogens have been reviewed meticulously by BHU scientists.

In this enthusiastic and forceful enterprise, I am elated to state my real appreciation to all notable and brilliant authors, for bringing up most needed unrivalled, pragmatic, thoughtful and comprehensive reviews of international standard on physiology of plants and their responses under wide-ranging environmental stresses. My esteem is very much due to the Honourable Vice-Chancellor Prof. Panjab Singh, Banaras Hindu University, the Director, Institute of Agricultural Sciences Prof. Shiv Raj Singh, the Dean, Faculty of Agriculture Prof. Janardan Singh, and my admired colleagues of this and other universities/institutes of the world for their steady moral support in this constructive vast task. Nevertheless, for this conquest, I candidly accept that I have been ever imbibing perpetual force from the ***Fellow Members of the Indian Society for Plant Physiology, New Delhi*** and for this reason; my gratefulness is due to all of them for their trustworthy moral support and valued suggestions from time to time. Besides these, I have my sincere thanks to Mr. A. Ishan Rahul, N.T.S.E. *Fellow* (Govt. of India) and student of National Institute of Technology, for his great thoroughness in the origin of the very perceptible and exceptional cover page of this book.

Last but not the least, I am beholden to my affectionate mother and my all family members for their blessings and good wishes in this vital project. I have my profound esteem to all of them. Above and beyond, I am very much thankful to the excellent team members of the Scientific Publishers (India), Jodhpur, India, for their genuine competence in the perfect printing and worldwide circulation of this specific book.

December 12, 2006

Dr. A. Hemantaranjan
EDITOR

Department of Plant Physiology
Institute of Agricultural Sciences
Banaras Hindu University
Varanasi 221 005
INDIA

FROM EDITOR'S DESK

While editing the *International Treatise Series on **Advances in Plant Physiology***, I was amazed to find significant developments in the field of environmental stresses. The similar ideas were already dwelling in the core steadily to come forward with prosperous scientific literature not only inspiring for materializing the theme but to meet the challenges of food problem with innovative applied research, existing at present as well as gravely assumed in future. Therefore, it was thought worthwhile to present before you the long awaited needful book on the vital theme entitled “**ENVIRONMENTAL PHYSIOLOGY**” is basically the compilation of outstanding research in the area of the ***Molecular Physiology of Abiotic Stress Response in Plants*** has been duly edited for practical use by planners, researchers, teachers and postgraduate students. This book is certainly only one of its kinds for a rare integration of most timely and indispensable ***twenty-one worthy reviews*** of manifold significance contributed by sincere dedication of experienced, laudable and well-known scientists/stalwarts all over the world. They are all devotedly engaged in research and with due concern shared their precious time to draw attention upon the relevance of the very useful topic crucial for promoting investigations in right direction in the years to come.

Doubtless, we all are some way or other, deeply involved with the present situation with regard to gross damages in the growth and development of economic plants caused due to environmental stresses either by abiotic or biotic means, which is quite alarming in view of the shrinking agricultural land area and the recurrently expanding population on the earth. Now it's a right time to be strategic by first understanding the reasons fundamental to complex in yield reductions so that precise research planning could be brought about to alleviate problems with plants under stress. In nature, plants are exposed to ever changing environmental conditions or stresses, which are broadly, put under two groups – biotic and abiotic stresses. Abiotic stresses include water deficit, water logging, salinity and alkalinity, heavy metals, low and high temperature, ozone, UV radiations etc. To survive these challenges, plants have developed adaptive mechanisms that manifest themselves in morphological, physiological, developmental and molecular changes.

During **Conventional Breeding**, it was found that when crop was exposed to sub lethal levels of stress, it could induce stress tolerance to that particular type of stress. Increased tolerance was due to synthesis of some metabolites (sugars, proline and glycinebetaine, proteins etc.). Transgenic approaches offer powerful means to gain valuable information towards a better understanding of mechanism that govern stress tolerance. However, it has paved the way for the new opportunities to improve tolerance by incorporating a gene involved in stress protection from any source into agriculturally important crops. The genetic makeup of the plant comprises a finely balanced system of specialized cells programmed to carry out complex functions in response to developmental as well as situational conditions. Addition of new genes can disrupt these higher functions even though the critical functions necessary for cell metabolism may remain intact. The genetically engineered plant must not only have its full functional complement of capabilities, but must also be capable of performing well under the wide variety of circumstances that typically accompany the field environment. The transformation of genes into the plant system has been through *Agrobacterium tumefaciens* a soil bacterium 'the gene ferry' in the hands of plant genetic engineers. In recent years, methods such as particle gun, electroporation, particle bombardment (biolistics) and microinjections have been cultivated for gene transfer. Further a host of DNA sequences called promoters (e.g. active promoter) are available for regulation of these genes and expression can be obtained either in constitutive (with out any external or internal factor) or the inducible (in response to inducers) mode.

Response to abiotic stresses has always been complex at genetic level as the expression of large number of genes is altered at the same time. This statement has been proved by the molecular biologists, as the expression of more than 100 transcripts was affected, when the plants faced osmotic stress. RNA analysis had revealed the existing physiological/biochemical knowledge of plant responses is scanty & several mechanisms are yet to be understood.

Some of the major abiotic stress responses, which need to be illustrated extensively up to the molecular level in a variety of plant species inhabit diverse climatic conditions with a view to purposely find out the remaining areas of relevant research in overcoming stress problems coming on way of especially the food grain production. Indeed, for doing untiring indispensable work in this direction, it is essential now for all the agricultural scientists to be first familiar with different components and kinds of abiotic stresses, which originate a number of terminologies. Some vital areas in different captions, as given below, could be captured in gist in unimaginable vastness of one's mind prior to read the plentiful critical and extensive twenty-one reviews assembled in this exceptional book, which is the immense need of time.

Drought Stress

Drought stress can limit plant growth, resulting in reduced crop yields. **Drought stress** has been correlated with expression changes in many plant genes. These include the heat shock proteins (HSPs), late embryogenic-abundant proteins (LEAs) and aquaporins. Some of the more well-characterized responses include genes whose products regulate expression of **drought** responsive genes, the dehydration-responsive element-binding proteins, and abscisic acid-responsive element-binding proteins. Other genes involved in **drought stress** are those associated with lipid signaling such as the phospholipase gene families and those associated with detoxification of reactive oxygen species.

Plant tolerance to drought results from both morphological adaptation and responses at the biochemical and genetic levels. Among the various mechanisms developed by plants to resist drought, tolerance at the cellular level is essential since it allows tolerant plants to maintain cellular homeostasis. In contrast, sensitive plants suffer rapid irreversible cell damage essentially due to degradation of their membranes. Membranes are main targets of degradative processes induced by drought and it has been shown that, under water stress, a decrease in membrane lipid content is correlated to an inhibition of lipid biosynthesis and a stimulation of lipolytic and peroxidative activities. Water stress may conceivably arise either from an insufficient or from an excessive water activity in the plant's environment. In case of terrestrial plant in nature, the former occurs as a result of a water deficit or drought and therefore is called a water deficit stress (shortened to water stress) or drought stress. Drought is a meteorological term, and is commonly defined as a ***period without significant rainfall***.

A reduction in mesophyll water potential (with or without a reduction in turgor pressure) can affect the physiology of cells in several ways, viz., (i) Reduced water potential reduces the chemical activity of water and thereby modifies the structure of water in the cell; (ii) a lower chemical activity of water can cause a change in the structure of the sheath of hydration around proteins and thereby reduces their efficacy; (iii) the relationship among intracellular membranes of chloroplast, nucleus, mitochondria, endoplasmic reticulum, tonoplast, plasmalemma and others will change because the cellular position of these membranes will change; (iv) a loss of turgor may cause a change in the spatial position of transport channels and membrane enzymes and decrease membrane thickness; (v) a change in cell pressure and the resultant cell wall shrinkage may constrict the entrance to plasmodesmata; (vi) the concentration of molecules in specific regions may change due to the loss of water in some sub cellular locations.

Drought is an example of an abiotic stress in which components of the antioxidative system are perturbed or up-regulated. Responses are associated with oxidative stress. It can therefore be inferred that enhanced production of **active oxygen species** (AOS), a compromised capacity to remove AOS or both, elicits acclimatory events during drought. Most discussion has centered on accelerated AOS production through side-reactions in the chloroplast, in particular the formation of superoxide and H_2O_2 linked to auto-oxidation of components associated with photosystem I (PSI; Mehler reaction). Less attention has been paid to the influence of photorespiration. Both AOS and soluble antioxidants are involved in signaling processes in plants: the picture that is emerging suggests that relatively stable oxidants (H_2O_2) and antioxidants act as sensors of the 'oxidative load' on the cell. According to this view, mild increases in oxidative load trigger events that lead to acclimation and enhanced resistance, while more severely increased and sustained loads tilt the developmental balance towards senescence and death. Most studies suggest that drought-induced decreases in net CO_2 uptake are due to stomatal limitations.

Genes of the flavonoid pathway are specifically up-regulated during mild **drought stress** and, thus, are associated with photosynthetic acclimation. Furthermore, regulation of genes encoding polyamine biosynthesis is indicative of senescence and dormancy in response to severe **drought stress**. **Drought stress** has been correlated with expression changes in many plant genes. These include the heat shock proteins, late embryogenic-abundant proteins (LEAs), and aquaporins. Some of the more well-characterized responses include genes whose products regulate expression of **drought** responsive genes, the dehydration-responsive element-binding proteins, and abscisic acid-responsive element-binding proteins. Other genes involved in **drought stress** are those associated with lipid signaling such as the phospholipase gene families and those associated with detoxification of reactive oxygen species. Although these studies relate the expression of specific genes to **drought** imposition, no one has defined the role of **stress**-related genes in acclimation to the **stress**. The plant is able to sense the degree of **stress** and may activate different response pathways accordingly. It also delineates among the LEAs in terms of those that are expressed to allow acclimation to occur. Changes in transcript levels of genes encoding enzymes of core carbon metabolism are also reflective of acclimation during mild **drought stress**. This suggests that alteration of core metabolism can play a significant role in the **stress** response, perhaps in directing carbon or energy into pathways necessary for acclimation. Moreover, drought interacts with other stresses like high temperature, provided that the drought-induced decrease in transpiration did modify the leaf energy balance, so the leaf temperature usually increases during drought.

Temperature Stress

High temperature is one of the main stress factors, which in association with other stresses like drought, salinity, and high irradiance, can limit the productivity of plants. Understanding the mechanisms of heat damage and tolerance is, therefore, important if we are to improve the crop yield under stress conditions. The temperature sensitivity of photosynthesis is dependent upon plant species and intensity and time of exposure to the new temperature regime. A long period at a moderately high temperature may be as injurious as a brief exposure to an extreme temperature. High temperature affects photosynthesis by changing the structural organisation of the thylakoids and thus altering the excitation energy distribution, changing the activity of Calvin cycle and other metabolic processes such as photorespiration and product synthesis. However, plants have evolved a number of adaptive mechanisms allowing the photosynthetic apparatus to cope with changes in temperature. These mechanisms may involve changes in membrane fluidity and lipid composition, increased thermal energy dissipation, decreased absorption cross-section, synthesis of heat-shock proteins.

When temperatures exceed a plant's normal growing range, heat injury may occur. Most crop plants generally grow in the 15-30°C temperature range. However, long day periods with air temperature above 35°C are relatively common in tropical areas. High air temperatures may steeply increase the leaf-to-air temperature difference to values above 5 to 10°C or more. Plants of the same genotype grown at different temperatures and then, tested for their photosynthetic response show temperature optima that correlate with the temperature at which they were grown and are typically reflective of the plant's native climate. For every 5°C change in growth temperature between 10°C and 35°C, the temperature optima for photosynthesis shift approximately 2 to 3 °C.

The widespread occurrence of the nucleic acid-binding cold shock domain (CSD) in plants and identification of the first eukaryotic homologs that are nearly identical to bacterial cold shock proteins (CSP) have been reported in the recent years. Using *Arabidopsis* as a model system, it was determined that its four unique CSD genes are differentially regulated in response to low temperature. The CSD is proposed to be an ancient structure that was present before the divergence of prokaryotes and eukaryotes

Further, low-temperature (LT) tolerance is a complex quantitative character that is expressed following exposure of plants to temperatures that approach freezing. The biochemical, physiological and morphological changes associated with LT tolerance clearly affect active growth and development and, as a result, a plant must be programmed to recognize and respond to temperatures that are favourable for growth and

Cold Shock Proteins

Many prokaryotes respond to low temperature by markedly up-regulating the synthesis of cold-shock proteins (CSPs). In *Escherichia coli*, for example, CspA, the most prominent of the nine-member family, constitutes about 10% of the bacteria's total protein during cold stress. The three-dimensional structure of *E. coli* CspA forms a five-stranded β -barrel structure that contains two RNA-binding motifs that facilitate nucleic acid recognition/binding. Thus, it has been hypothesized that CspA may serve to prevent RNA secondary structure formation, thereby enhancing translation at low temperature. The nucleic acid-binding cold shock domain (CSD) found in most bacterial CSPs is the most conserved nucleic acid-binding domain and is capable of binding single-stranded DNA/RNA and double-stranded DNA.

Heat Shock Proteins

Heat shock proteins are defined as the polypeptides whose synthesis is dramatically increased at elevated growth temperatures, usually 10-15°C above the optimum for plants. HSPs are a family of proteins that are constitutively expressed at a high level e.g. HSPs account for 5-10% of the total protein content in all cell types under normal growth conditions; their level is significantly increased when a cell is subjected to stress conditions, including heat shock or a change in ambient temperatures. Heat shock proteins, the “molecular chaperones”, stabilize proteins and are involved in the folding of denatured proteins. High temperatures and other stresses; such as altered pH and oxygen deprivation make it more difficult for proteins to form their proper structures and cause some already structured proteins to unfold. Left uncorrected, mis-folded proteins form aggregates that may ultimately kill the cell. Heat shock proteins form aggregates that are induced rapidly at high levels to deal with this problem. HSPs are generally divided into two classes: high-molecular-mass HSPs (60-110 kDa) and low-molecular-mass HSPs (15-30 kDa). The low-molecular-mass HSPs, which are encoded by a large gene family, are the most abundant HSP class found in plants. HSPs of the family of 60, 70 and 90 kDa are known as “molecular chaperones”. Molecular chaperones are proteins that bind to partially fold or denaturised substrate proteins and thereby prevent irreversible aggregation or promote correct folding of the substrate.

Excessive Water (Flooding) Stress

Flooding of agricultural and natural ecosystems has a dramatic impact on the growth and occurrence of terrestrial plants in these systems. The negative effects of flooding are strongly related to severely hampered diffusion of gases in water, which is 10,000 times slower than in air.

Transient flooding with fresh water is a world-wide phenomenon in river floodplains and wetlands as well as other terrestrial ecosystems. It frequently results in complete submergence of plants. In general, this excess of water has a negative impact on growth and survival of most terrestrial plants, especially when flooding occurs during the growing season. Well-adapted plants may overcome the effects of submergence by adopting an avoidance strategy in which individual leaves grow differentially to a more vertical position followed by enhanced elongation. Analysis of these processes at the molecular level will generate new insights into the complexity of plant–environment interactions and potentially help to improve submergence tolerance of agricultural crops.

The most important detrimental characteristic of the flooded ecosystem for plant is the resulting oxygen partial pressure in the root zone. This is important because (1) roots are particularly sensitive to anaerobic conditions, and (2) anaerobic conditions support a unique microbial community compared with aerobic conditions, and this severely affect the nutrient relations of the soil. The particular end product of anaerobic respiration is partly dependent on pH. At a pH above neutrality, lactate fermentation is dominant, and as pH decreases (due to partially lactate fermentation), ethanol fermentation is induced. Rapid drop in cytosolic pH, called *acidosis*, is thought to be one of the main reasons why cells die in response to flood. In flood-tolerant plants the pH drop may be counteracted by an alkalization process.

Salinity Stress

Salt affected soils have commonly been grouped into saline soils and alkali / sodic soils. Saline soils contain soluble salts mostly chlorides and sulphates of sodium, calcium and magnesium in quantities enough to interfere with growth of most crop plants. The meaning of soil salinity for agricultural yields is vast. The agricultural problem of salinity tolerance is in all probability best undertaken by either changing farming practices to prevent soil salinization occurring in the first place, or by implementing schemes to try to remediate salinized soils. The soil pH of saturated paste (pH 2) under these soils is less than 8.5, Electrical Conductance (EC 2) more than 4 deci-Siemens/m (dS/m) and exchangeable sodium percentage (ESP) less than 15. On the other hand, alkali/sodic soils contains salts dominated by bicarbonates, carbonates and silicates of sodium, capable of alkaline hydrolysis or have sufficient exchangeable sodium to interfere with the growth of most crops. The soil pH 2 is greater than 8.5, EC 2 of saturation extract less than 4 dS/m and ESP of 15 or more

High concentrations of salts in soils account for large decreases in the yield of a wide variety of crops all over the world. The problem is huge; almost 1000 million ha of land is affected by soil salinity, 7 % of all land area. Of the

1.5 billion ha that is cultivated, about 5 % (77 million ha) is affected by salt. Critically, the problem of salinization is increasing, often due to bad agricultural practices. Irrigated land is particularly at risk with approx. one-third being significantly affected by salinity. However, dryland salinity is also an important, and increasing, problem, at least in some areas of the world.

All salts can affect plant growth, but not all inhibit growth. In addition, salts do not act alone in the soil, but interact in their effects on plants; some of these interactions are simple (e.g. interactions between Na^+ and Ca^{2+}), whereas some are complex (e.g. carbonates, and their effects via increased soil pH). Among the most common effects of soil salinity is growth inhibition by Na^+ and Cl^- .

Saline solutions impose both ionic and osmotic stresses on plants. These stresses can be distinguished at several levels. In salt-sensitive plants, shoot and to a lesser extent root growth is permanently reduced within hours of salt stress and this effect does not appear to depend on Na^+ concentrations in the growing tissues, but rather is a response to the osmolarity of the external solution.

Salt stress is also known to depress greatly the growth and symbiotic performance of nodulated legumes and soil salinity is one of the major evil constraints on agriculture in many regions of the world. Localised application of some phytohormones under such environmental stresses is reported to exert profound effects on assimilation and transport which in some instances resulted in enhanced productivity.

Plants adapt to osmotic stress/salt stress by accumulating physiologically compatible solutes (osmolytes) like sugars, proline and glycinebetaine or by excluding Na^+ or K^+ ions from the roots at the expense of metabolic energy. Due to similarities in the physiological mechanism of acclimation to these stresses, some common genes such as dehydrins, LEA, *Atbi*, RAB etc. are expressed under stress conditions.

Oxidative Stress

Chemical activation of molecular oxygen has shaped the biochemistry of life. The formation of reactive oxygen species (ROS) accompanies every normal metabolic process in all aerobic organisms. The association of oxygen in respiratory processes and the production of oxygen during photosynthesis results in the generation of ROS. It is generally accepted that stress-induced deregulation of plant metabolism leads to the enhanced production of active oxygen species (AOS), the cellular titre of which is policed by the antioxidant system. Both AOS and soluble antioxidants are involved in signaling processes in plants : the picture that is emerging suggests that relatively stable oxidants (H_2O_2) and antioxidants act as sensors of the 'oxidative load'

on the cell. According to this view, mild increases in oxidative load trigger events that lead to acclimation and enhanced resistance, while more severely increased and sustained loads tip the developmental balance towards senescence and death. Most studies suggest that drought-induced decreases in net CO₂ uptake are due to stomatal limitations. The tripeptide glutathione (GSH; γ Glu-Cys-Gly) is the major non-protein thiol in most plants, prokaryotes and animals. GSH is a versatile antioxidant and is involved in the enzymatic detoxification of activated oxygen species (AOS) and participate in the ascorbate -GSH cycle for peroxide removal in the chloroplasts of plants.

The participation of calcium signaling in oxidative stress is widely acknowledged. However, how these signals are generated and how the "message" is encoded by the calcium signal is still not fully understood. Numerous plant signal transduction pathways have been shown to use Ca²⁺ as an integral signaling component. At their simplest, Ca²⁺ based signaling systems are composed of a receptor, a system for generating the increase in [Ca²⁺]_{cyt}, downstream components that are capable of reacting to the increase [Ca²⁺]_{cyt} and other cellular systems responsible for returning [Ca²⁺]_{cyt} back to its pre-stimulus level. Downstream from the stimulus-induced [Ca²⁺]_{cyt} increase, or "Ca²⁺ signal", the cell possesses an array of proteins that can respond to the message, such as calmodulin (CaM), Ca²⁺-dependent protein kinases and CaM binding proteins.

Soil Acidification

Risks arising from soil acidification have environmental, social and economic implications. In many rural regions, acidification can be considered as major constraint to sustained productivity. For example, soil acidification can be a more serious agricultural problem than salinity in terms of area affected and cost to the economy. On the other hand, calcareous soils that cover more than 30% of earth's surface may cause serious problems to non-adapted plants. Several soil factors influence plant success; these include soil type, texture, pH, and nutrient content. The makeup of a soil (soil texture) and its acidity (pH) determine the extent to which nutrients are available to plants. So, plants that permanently face nutritional limiting situations (alkaline or acidic) may use certain efficient strategies to overcome nutrient shortage.

In acidic soil with a pH lower than 5, the phytotoxic species of Al which is octahedral hexahydrate [Al(H₂O)₆³⁺], often abbreviated as Al³⁺, is solubilized to the levels that inhibit root growth and in turn decrease crop production. Therefore, the adverse effect of acidic soil on plant growth is strongly related to the toxicity of the solubilized Al ion.

Excess of Heavy Metals

Heavy metals are a group of metals with density higher than 5.0 g cm^{-3} . When heavy metal (HM) levels increase in the environment, they reach concentrations that plants can no longer tolerate, their ions being highly toxic to plant growth and metabolism. Plants in areas of industrial pollution frequently encounter heavy metal stress. The plant and soil scientists have been studying HM toxicity in plants vis-à-vis soil properties and plant response to metal accumulation for several decades. Frequently, the HMs, causing toxicity in plants, are biologically non-essential. These include cadmium (Cd), lead (Pb), chromium (Cr) and mercury (Hg). However, even the biologically essential heavy metals, such as manganese (Mn), iron (Fe), zinc (Zn), copper (Cu), and molybdenum (Mo) or those which are essential only to a limited number of species [such as nickel (Ni) and cobalt (Co)] can be toxic when they accumulate in plants in relatively high concentrations. The essential HMs are required in small quantities (micronutrients) for normal metabolism and growth of the plants, and their deficiency or excess can impair these phenomena, rendering the plants with low yield and quality. However, the non-essential heavy metals could be immensely harmful for plants even in very small amounts. Heavy metals are being drawn into the soil-plant-animal continuum progressively. Once inside, they cannot be removed easily from the system. Hence, important preventive as well as curative measures must be taken regarding HM hazards and special attention is needed to be paid by soil and plant scientist in this regard. In several cases, increased use of municipal sewage sludge on soils has resulted in increased HM content of soils and crops grown thereon. HM toxicity varies greatly with element, element concentration and plant species. HM become toxic because they have no free specific sites for them and bind to any molecule that cannot chemically refuse them, modifying the functional properties of the host molecule. Consequently, the general cell metabolism is modified. The roots are damaged first and most severely in many cases. The HMs that is translocated slowly accumulates in the roots, affecting the overall plant growth primarily through root damage. The most common symptoms of slight HM stress are leaf chlorosis, similar to that induced by iron deficiency. Excess of Zn in soil has recently been reported to decrease nitrate reductase activity in sorghum leaves. Heavy metals often compete with essential elements for active site of the enzymes. As a result, enzyme reactions are blocked, disturbing the normal plant metabolism. Besides these, harmful activated oxygen species such as hydroxyl radicals and hydrogen peroxide are triggered in the presence of excess HMs in plants such as Fe^{2+} , Cd^{2+} and Cu^{2+} . The mechanisms of HM tolerance are heritable attributes of tolerant mutants and genotypes. However, laboratory studies, employing suspension culture techniques, have also shown inducible HM tolerance in

plants due, primarily, to the production of metal-complexing compounds such as organic acids and phytochelatins. Thus, HM tolerance is controlled partially by metal-induced changes in plant physiological traits.

Systemic Acquired Resistance

Plant disease resistance to pathogens often depends on whether the plant is able to recognize the pathogen early in the infection process. Recognition of pathogens triggers a large range of inducible defense mechanisms that are believed to contribute to overall resistance in the plant. Systemic acquired resistance of plants against pathogenic organisms probably constitutes a naturally occurring defense strategy that contributes to limiting the damage caused by virulent pathogens. Many of these responses are due to transcriptional activation of specific genes that are collectively known as plant defense or defense-related genes.

UV-B Radiation

UV-B radiation may affect plant life directly or indirectly. Enhanced UV-B radiation leads to a multitude of morphological and physiological effects on plants. UV-B has the potential to damage macromolecules such as DNA and proteins and cell structures particularly at the high doses currently used in laboratory experiments, consequently it is difficult to separate the specific UV-B response from the secondary consequences of generalized damage caused under such harsh conditions. A variety of protective mechanisms have been considered important to avoid the deleterious effects of UV-B radiation such as leaf surface reflectance capability and the concentration of UV-B absorbing compounds. Knowledge of the ultrastructural alterations is of paramount importance because photosynthetic performance of the plants is dependent upon the integrity of the mesophyll cells.

Global Warming

The burning of fossil fuels, the large-scale clearing of forests, and other human activities are altering global climates at an alarming rate. The continued consumption of fossil fuels is expected to result in a doubling of the current $[\text{CO}_2]$ by sometime in this century. These increases in CO_2 as well as other "greenhouse gasses" are expected to raise world temperatures by 0.03°C per year in the 21st century. Global warming and increased atmospheric $[\text{CO}_2]$ are already having a major impact on plant distributions. Plants, in general, benefit from slightly warmer temperatures and higher $[\text{CO}_2]$, but not all plants will benefit equally from these conditions, and some may even be harmed. Global warming during this century will favor C_3 vegetation because the increase in C_3 photosynthetic efficiency that occurs under higher

atmospheric [CO₂] conditions will outweigh the reduction of photosynthesis that is attributable to higher temperatures.

The phenology or time of flowering of a plant is one such seasonal event that is critical for its sexual reproduction. Although the initiation of flowering is typically mediated by changes in daylength and, as such, is independent of temperature, the time required for flowers to develop to maturity, like most growth processes, is strongly dependent upon temperature. Annuals were more likely to flower earlier than perennials, and insect-pollinated species more than wind-pollinated. Accelerated phenologies may alter patterns of resource allocation, may affect interactions with pollinators, and could alter the size, species richness, and intraspecific genetic diversity of the soil seed bank.

Stress Adaptation Effectors

Stress adaptation effectors are categorized as those that mediate ion homeostasis, osmolyte biosynthesis, toxic radical scavenging, water transport, and transducers of long-distance response coordination. Some of the relevant terminologies are illustrated below:

Ion Homeostasis

A hypersaline environment, most commonly mediated by high NaCl, results in perturbation of ionic steady state not only for Na⁺ and Cl⁻ but also for K⁺ and Ca²⁺. External Na⁺ negatively impacts intercellular K⁺ influxes, attenuating acquisition of this essential nutrient by cells. High NaCl causes cytosolic accumulation of Ca²⁺ and this; apparently, signals stress responses that are either adaptive or pathological. Ion homeostasis in saline environments is dependent on transmembrane transport proteins that mediate ion fluxes, including H⁺ translocating ATPases and pyrophosphates, Ca²⁺-ATPases, secondary active transporters (SAT) and channels. A role for ATP-binding cassette (ABC) transporters in plant salt tolerance has not been elucidated, but ABC transporters regulate cation homeostasis in yeast.

Aquaporins

The hydrophobic nature of lipid bilayer presents a considerable barrier to the free movement of water into the cell and between intracellular compartments. However, plasma membranes and tonoplasts can be rendered more permeable to water by proteinaceous transmembrane water channels called aquaporins. Water movement through aquaporins can be modulated rapidly. Evidences suggest that these channels may facilitate water movement in drought stressed tissues and promote the rapid recovery of turgor on watering. The aquaporin RD28 is located in the plasma membrane.

Genes encoding MIP-related proteins have been identified in *M. crystallinum* and *Arabidopsis*. The abundance of mRNA transcripts of RD28 genes correlates with the turgor changes in leaves of plants subjected to a 400 mM NaCl shock treatment. The amount of transcript first decreases after the initial shock, as does turgor. Transcript concentrations then increase as turgor is restored. Greater transcript concentrations, enhanced translocation, and activation of existing proteins each may constitute a mechanism for regulating aquaporin abundance and activity in response to water stress. Expression studies in *Xenopus oocytes* link α -TIP phosphorylation with increased permeability of cell membrane to water.

Osmoprotectants

Transgenic plants with improved tolerance to stress have been produced using various genes encoding enzymes that synthesize osmoprotectants. Principle behind the engineering is identifying the enzyme regulating the biosynthetic pathway of the metabolite and then putting the promoter to increase the expression of that particular protein.

Proline (Pro)

During periods of drought or NaCl stress plants increase their pools of free Pro far in excess of the demands of protein synthesis. They do this by inducing Pro biosynthetic enzymes while repressing further synthesis of catabolic enzymes. Under dehydration conditions, when expression of the gene for P5CS is strongly induced, expression of the gene for ProDH is inhibited. By contrast, under rehydration conditions, when the expression of the gene for ProDH is strongly induced, the expression of the gene for P5CS is inhibited. Thus, P5CS, which acts during the biosynthesis of Pro, and ProDH, which acts during the metabolism of Pro, appear to be the rate-limiting factors under water stress. Therefore, it is suggested that levels of Pro are regulated at the level of transcription the genes of these two enzymes during dehydration and rehydration. Moreover, it has been demonstrated that Pro acts as an osmoprotectant and that overproduction of Pro results in increased tolerance to osmotic stress of transgenic tobacco plants. Genetically engineered crop plants that overproduce Pro might, thus, acquire osmotolerance, namely, the ability to tolerate environmental stresses such as drought and high salinity.

Very recent reports indicate that the transgenic plant lines tolerated 14 d of drought stress, which confirms that both P5CS transgenes had full functionality. Exogenous L-Pro treatment caused the plants to accumulate Pro; plants treated with 5 mM L-Pro accumulated up to 18 times more free Pro than untreated plants. Exogenous L-Pro restricted the growth of wild-

type petunias more than that of *Arabidopsis* plants. The capacity for free Pro accumulation might depend on the plant species. The growth of petunia plants was influenced not only by the Pro concentration in the plants, but by the ratio of the Pro content to the total amino acids, because the growth of the transgenic petunia plants appeared normal. The enzyme Δ -pyrroline-5-carboxylate synthetase (P5CS) catalyzes the conversion of glutamate to Δ -pyrroline-5-carboxylate, which is then reduced to proline. Over expression of a gene encoding for moth bean P5CS in transgenic tobacco plants resulted in accumulation of proline upto 10 to 18 fold over controls. This group also showed that transgenic plants demonstrated enhanced production and flower development under salt stress conditions, as determined by increased root length, root dry weight, capsule number and seed number per capsule. The same gene was introduced in rice under control of an ABA/stress inducible promoter and it accumulated up to 2.5 fold more proline than control plants under stress conditions. Preliminary results showed that under stress, individual expression of P5CS transgene in second generation of transgenic rice plants showed an increase in biomass as reflected by higher fresh shoot weight under salt and water stress conditions compared with untransformed control plants. The extent of salt tolerance could be correlated with the levels of proline accumulated. Pro may interact with enzymes to preserve protein structure and activity within the cell. *In vitro* studies have shown that high concentrations of Pro reduce enzyme denaturation attributable to heat, freeze-thaw cycles, and high NaCl. Alternatively, Pro may protect proteins and membranes from damage by inactivating hydroxyl radicals or other highly reactive chemical species that accumulate when stress inhibits electron-transfer processes. Pro catabolism is capable of a high-energy output and has been proposed to donate electrons to the respiratory electron transport chain. Each molecule of Pro, when oxidized, can yield 30 ATP equivalents and has been considered a primary fuel in energy-intensive processes, such as insect flight or pollen germination.

The role of Pro catabolism has been highlighted in the field of **nitrogen fixation**. Plants such as soybean (*Glycine max*) synthesize high levels of Pro in the host cells of nodules, and bacteroids are capable of high Pro-oxidizing activity, suggesting that free Pro entering the bacteroids from host cells might be an important energy source for nitrogen fixation. Nodulation tests with a bacteroid PDH-deficient mutant revealed that PDH activity is essential for nodulation efficiency. Thus, increased oxidative flux of Pro in bacteroids might provide an agronomically significant yield advantage

Mannitol

Mannitol, the sugar alcohol, is largely dispersed among plants and mannitol concentration increases in response to osmotic stress. In sharp

contrast to glycine betaine, mannitol accumulation appears to be regulated by inhibition of competitive pathways and by decreased rates of mannitol consumption and catabolism. In celery, salt stress inhibits sucrose synthesis, but does not seem to affect the enzymes that synthesize mannitol. It is basically found in microbes as an osmoprotectant.

Glycine betaine

It is synthesized and accumulated by many algae and higher plants and its presence is cosmopolitan. Its accumulation in osmotically stressed plants results from the increased rates of its synthesis. The glycine betaine does not show the degradative pathway, but its concentration is controlled by its biosynthesis and its transport through phloem to growing tissues. The two key enzymes in the biosynthetic pathway of glycine betaine from choline in two step pathway are choline monooxygenase and betaine aldehyde dehydrogenase. Both the enzymes have been purified and their cDNA's are available. Activities of these enzymes have been increased several folds under osmotic stress.

D-ononitol

Expression of a cDNA encoding myo-inositol O-methyl transferase (IMT1) in tobacco during salt and drought stress resulted in the accumulation of methylated inositol (D-ononitol), which in turn conferred tolerance for both stresses. Since the level of D-ononitol reached upto 600 mM in the cytosol and it did not enter the vacuole, its accumulation provided an osmolyte for osmotically balancing Na⁺.

Polyamines

Polyamines are minute, ever-present, nitrogenous cellular compounds that have been concerned in a variety of stress responses in plants. Polyamines assemble under quite a few abiotic stress conditions including salt and drought. Cultivars demonstrating a higher degree of salt tolerance contained higher levels of polyamines. Since most of the osmolytes did not accumulate in amounts large enough to play a role in osmotic adjustments, it is not clear how they provide protection against dehydration stress. Alternatively, they may act as scavengers of reactive oxygen species.

Late Embryogenesis Abundant (LEA) Proteins

The *LEA* genes were first identified as genes induced in seeds during maturation and desiccation. The amount of some lea gene products are now known to increase in the vegetative tissues of plants exposed to stresses that

include water deficit component. Over expression of lea proteins in rice and yeast have been shown to enhance the resistance to specific water deficit stresses. The lea genes have been divided into five groups namely group 1, 2, 3, 4 and 5.

Future Strategies

Much more work is needed to gain a better understanding of the biochemical and physiological basis of stress tolerance. Crops, in general, during their ontogeny faces a number of abiotic stresses, *viz.*, soil water deficit stress, soil salinity stress, high as well as low temperature stress, and excessive soil moisture stress. No effective field screening technique is available so far to study variation in yield due to abiotic stresses. Transgenic approaches for increasing plant tolerance to dehydration stresses are experimentally feasible. Preliminary results are encountered for enabling scientists to better understand the effects of single-gene transfers to plants. However, it should be emphasized that success to date represents only a beginning. Once it is better understood how different single genes work, it is likely that several genes will need to be simultaneously transferred into plants to produce high levels of stress tolerance. This may more closely resemble what occurs in nature where stress tolerance is the cumulative effect of several genes. Recent advances in transformation of agronomically important crops and the development of better expression systems in terms of using stress-inducible promoters and adding MAR sequences hold much promise in this direction. These and other advances are needed to produce stress-tolerant transgenic crop plants that give significantly higher productivity under field conditions.

Drought stress can limit plant growth, resulting in reduced crop yields. Many attempts to analyze plant responses to **drought** have focused on single genes. However, the product of a single gene can function in or act upon multiple response pathways, influencing many aspects of plant growth and development. Therefore, it is necessary to understand how gene products act in concert and upon each other to effect adaptive changes to **stressful** conditions.

Growth and productivity of coconut palms also cannot be overshadowed as this is influenced by the external factors such as rain fall, temperature, sun shine duration and relative humidity. The coconut palm experiences atmospheric and edaphic moisture stress. Coconut palm responds to the stress conditions at morphological, anatomical, physiological and biochemical levels. The atmospheric stress influences the photosynthetic rates and if prolonged with soil moisture stress, dry matter production and its partitioning are influenced. Additional studies should be focused to develop the molecular markers linked to desirable traits and to understand the

inheritance patterns of these traits. The genotypes with desirable traits for tolerance to stress conditions can be used in breeding strategies for abiotic stress tolerance in future crop improvement strategies.

Hopefully, the wonderful multifaceted reviews selected and compiled very systematically in this exclusive book for the first time in over twenty-one extensive chapters by genuine experts and distinguished scientists of international stature all over the globe, would enable to plan meaningful advanced research and profuse consequential teaching on the extremely crucial theme of abiotic stress responses in plants. Being the University Teacher I firmly consider this unique collection to be of enormous help for post-graduate studies and higher research in all universities and research institutes of the world.

December 12, 2006

Dr. A. Hemantaranjan

EDITOR

Department of Plant Physiology
Institute of Agricultural Sciences
Banaras Hindu University
Varanasi 221 005
INDIA

CONTRIBUTORS

- A. Alem**, UFR Ecophysiology of Forest Trees, Laboratory of Plant Physiology, Department of Biology, University Mohammed V, Rabat, MOROCCO.
- A. Bhattacharya** Division of Physiology, Biochemistry & Microbiology, Indian Institute of Pulses Research, Kanpur – 208 024, INDIA
- A. Hemantaranjan**, Department of Plant Physiology, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi 221.005, INDIA. E-mail: hemantaranja@satyam.net.in
- A.C. Flemmer**, Departamento de Agronomía y CERZOS (CONICET), Universidad Nacional del Sur, 8000 - Bahía Blanca, ARGENTINA.
- A.I. Bolletta**, Departamento de Agronomía y CERZOS (CONICET), Universidad Nacional del Sur, 8000 - Bahía Blanca, ARGENTINA.
- Anu**, Department of Botany, Panjab University, Chandigarh-160014. INDIA.
- B. Ezaki**, Research Institute for Bioresources, Okayama University, Chuo, Kurashiki, Okayama 710-0046, JAPAN.
- B. K. Singh**, Department of Botany, Banaras Hindu University, Varanasi 221005, INDIA.
- C.A. Busso**, Departamento de Agronomía y CERZOS (CONICET), Universidad Nacional del Sur, 8000 - Bahía Blanca, ARGENTINA.
- D. Van Der Straeten**, Department of Molecular Genetics, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, BELGIUM. E-mail: dostr@gengenp.rug.ac.be
- E. Brugnoli**, CNR, Istituto per l'Agroselvicultura, via Marconi 2, 05010 Porano (Tr), ITALY. E-mail: brugnoli@ias.tr.cnr.it
- F. M. DaMatta**, Departamento de Biologia Vegetal, Universidade Federal de Viçosa, 36571-000 Viçosa, MG, BRASIL. E-mail: fdamatta@mail.ufv.br
- G. Kaur**, Department of Botany, Panjab University, Chandigarh 160014, INDIA.
- Geetanjali**, Department of Botany, Panjab University, Chandigarh-160014. INDIA.
- H. Matsumoto**, Research Institute for Bioresources, Okayama University, Chuo, Kurashiki, Okayama 710-0046, JAPAN.
- H. Medrano**, Laboratori de Fisiologia Vegetal, Departament de Biologia Carretera de Valldemossa Km 7.5, 07071. Universitat de les Illes Balears – Instituto Mediterráneo de Estudios Avanzados Palma de Mallorca, Balears, SPAIN.
- H. Nian**, Department of Agronomy, South China Agricultural University, Guangzhou 510642, P.R. CHINA.

- H. Zaïd**, UFR Ecophysiology of Forest Trees, Laboratory of Plant Physiology, Department of Biology, University Mohammed V, Rabat, MOROCCO. E-mail: zaid@fsr.ac.ma
- I. Santos**, Department of Botany and Institute for Molecular and Cell Biology (IBMC), University of Porto, Rua do Campo Alegre, 823, 4150-180, Porto, PORTUGAL; E-mail: isantos@ibmc.up.pt
- J. F. You**, Department of Agronomy, Changchun University of Agriculture and Animal Sciences, Changchun 130062, P.R. CHINA.
- J. Flexas**, Laboratori de Fisiologia Vegetal, Departament de Biologia Carretera de Valldemossa Km 7.5, 07071. Universitat de les Illes Balears – Instituto Mediterráneo de Estudios Avanzados Palma de Mallorca, Balears, SPAIN. E-mail: dbajfs4@ps.uib.es
- J. M. Almeida**, Department of Botany and Institute for Molecular and Cell Biology (IBMC), University of Porto, Rua do Campo Alegre, 823, 4150-180, Porto, PORTUGAL.
- J. Pang**, School of Agricultural Science, University of Tasmania, GPO Box 252-54, Hobart, Tas 7001, AUSTRALIA.
- J.D.S. Panwar**, Division of Physiology, Biochemistry & Microbiology, Indian Institute of Pulses Research, Kanpur – 208 024, INDIA.
- K. Georgieva**, Institute of Plant Physiology, Bulgarian Academy of Sciences, Acad. G. Bonchev Street, Bl. 21, 1113 Sofia, BULGARIA. E-mail: katyamg@yahoo.com
- K.V. Kasturi Bai**, Central Plantation Crops Research Institute, Kasaragod, 671 124, INDIA.
- L. A. Batlle**, Departament de Biologia Vegetal. Facultat de Biologia. Universitat de Barcelona. Av. Diagonal, 645. 08028-Barcelona, SPAIN. E-mail: leonor@porthos.bio.ub.es
- L. Camacho**, Departamento de Biologia Vegetal, Faculdade de Ciências de Lisboa, Bloco C2, 1749-016 Lisboa, PORTUGAL
- L. Chaerle**, ¹Department of Molecular Genetics, Ghent University, K.L. Ledeganckstraat 35, B-9000 Ghent, BELGIUM.
- M. Singhi**, Department of Botany, Panjab University, Chandigarh-160014. INDIA.
- N. Garg**, Department of Botany, Panjab University, Chandigarh-160014. INDIA.
- R. Layachi** UFR Ecophysiology of Forest Trees, Laboratory of Plant Physiology, Department of Biology, University Mohammed V, Rabat, MOROCCO.
- R. Malhó**, Departamento de Biologia Vegetal, Faculdade de Ciências de Lisboa, Bloco C2, 1749-016 Lisboa, PORTUGAL. E-mail: r.malho@fc.ul.pt
- R. S. Upadhyay**, Department of Botany, Banaras Hindu University, Varanasi 221005, INDIA.
- R. Valcke**, Limburgs Universitair Centrum, Universitaire Campus, Dept. SBG, B-3590 Diepenbeek, BELGIUM.

-
- R.E. Brevedan**, Departamento de Agronomía y CERZOS (CONICET), Universidad Nacional del Sur, 8000 - Bahía Blanca, ARGENTINA.
- S. Agarwal**, Department of Botany, Stress Physiology Laboratory, J.N.V. University, Jodhpur 342001, (Rajasthan), INDIA.
- S. Dua**, Department of Botany, Panjab University, Chandigarh 160014, INDIA.
- S. Munné-Bosch**, Departament de Biologia Vegetal. Facultat de Biología. Universitat de Barcelona. Av. Diagonal, 645. 08028-Barcelona, SPAIN. E-mail.: smunne@porthos.bio.ub.es
- S. Naresh Kumar**, Central Plantation Crops Research Institute, Kasaragod, 671 124, INDIA. Email: nareshkumar.soora@gmail.com
- S. Shabala**, School of Agricultural Science, University of Tasmania, GPO Box 252-54, Hobart, Tas 7001, AUSTRALIA;. E-mail: Sergey.Shabala@utas.edu.au
- S.P. Saikia**, C/o J.D.S. Panwar, Division of Physiology, Biochemistry & Microbiology, Indian Institute of Pulses Research, Kanpur – 208 024, INDIA.
- Tracey Ann Cuin**, School of Agricultural Science, University of Tasmania, Private Bag 54, Hobart, Tasmania, 7001, AUSTRALIA. E-mail: Tracey.Cuin@utas.edu.au
- V. Rajagopal**, Central Plantation Crops Research Institute, Kasaragod, 671 124, INDIA.
- V.S.G.R. Naidu**, C/o J.D.S. Panwar, Division of Physiology, Biochemistry & Microbiology, Indian Institute of Pulses Research, Kanpur – 208 024, INDIA.
- Vijaylaxmi**, Division of Physiology, Biochemistry & Microbiology, Indian Institute of Pulses Research, Kanpur – 208 024, INDIA
- Vini Arora**, Department of Botany, Panjab University, Chandigarh-160014. INDIA.
- Y. Yamamoto**, Research Institute for Bioresources, Okayama University, Chuo, Kurashiki, Okayama 710-0046, JAPAN.
- Z.M. Yang**, Research Institute for Bioresources, Okayama University, Chuo, Kurashiki, Okayama 710-0046, JAPAN.

CONTENTS

<i>Preface</i>	<i>v</i>
<i>From Editor's Desk</i>	<i>ix</i>
<i>Contributors</i>	<i>xxvii</i>
1. Imaging techniques for physiology of plants under stress	1
— <i>L. Chaerle, R. Valcke, and D. Van Der Straeten</i>	
2. Abiotic Stresses and Different Techniques	29
— <i>Vijaylaxmi, A. Bhattacharya and J.D.S. Panwar</i>	
3. Chlorophyll Fluorescence as a Screening Tool in Plant Breeding	95
— <i>Sergey Shabala and Jiayin Pang</i>	
4. Influence of High Temperature on the Photosynthetic Apparatus	185
— <i>Katya Georgieva and Enrico Brugnoli</i>	
5. Function of plant hormones and antioxidants in the regulation of plant responses to drought	209
— <i>Leonor Alegre Batlle and Sergi Munné-Bosch</i>	
6. Photosynthetic Responses of C ₃ Plants to Drought	231
— <i>J. Flexas and H. Medrano</i>	
7. Drought as a Multidimensional Stress Affecting Photosynthesis in Tropical Tree Crops	307
— <i>Fábio M. DaMatta</i>	
8. Responses to Defoliation of Perennial Grasses under Water Stress	357
— <i>C.A. Busso, R.E. Brevedan, A.C. Flemmer and A.I. Bolletta</i>	
9. Biological Role and Regulation of Heat Shock Proteins	419
— <i>Saroj Dua and Gurpreet Kaur</i>	

10. Molecular, Biochemical and Ultrastructural Responses of Plants to UV-B Radiation	439
— <i>Isabel Santos and José Manuel Almeida</i>	
11. Calcium Signalling in oxidative stress	471
— <i>Tracey Ann Cuin</i>	
12. Oxidative Stresses in Plants and Glutathione	503
— <i>Sheela Agarwal</i>	
13. Ca ²⁺ signalling systems in plants. The cell as the minimum unity for complexity	541
— <i>Rui Malhó and Luísa Camacho</i>	
14. Abiotic Stress Response to Symbiotic Nitrogen Fixation	573
— <i>V.S.G.R. Naidu, J.D.S. Panwar and S.P. Saikia</i>	
15. Recent advances in the physiological and molecular mechanism of Al toxicity and tolerance in higher plants	587
— <i>H. Matsumoto, Y. Yamamoto and B. Ezaki</i>	
16. Aluminum tolerance in <i>Glycine max</i> L.: The physiological mechanism	645
— <i>Hideaki Matsumoto, Zhen Ming Yang, Jiang Feng You and Hai Nian</i>	
17. Soil acidity and alkalinity: two main constraints influencing plant performance	675
— <i>H. Zaïd, A. Hemantaranjan, R. Layachi and A. Alem</i>	
18. Salt stress tolerance mechanisms - cellular and molecular responses	711
— <i>Neera Garg and Monika Singhi</i>	
19. <i>Rhizobium</i> – legume symbiosis under salt stress: effects, adaptations and amelioration	739
— <i>Neera Garg, Anu, Geetanjali and Vini Arora</i>	
20. Adaptive strategies For coconut palm under stressful conditions	769
— <i>S. Naresh Kumar, V. Rajagopal and K.V. Kasturi Bai</i>	
21. Fungal Host – Pathogen Interaction: Attack and Defense Mechanisms – A Biotechnological Approach	785
— <i>Balwant Kumar Singh and R.S. Upadhyay</i>	
Subject Index	815