Experimentation in Biology of Plant Abiotic Stress Responses

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During the course of growth under natural field conditions, crop plants are exposed to a number of different abiotic stresses (such as water stress, temperature stress, salt stress, flooding stress, chemical stress and oxidative stress). These stresses exert adverse effects on metabolism, growth and yield of the crops. The intensity of the abiotic stresses is on the rise, implying that various possible solutions for mitigating the damage caused by such stresses must be combined for future increase in crop production. At the level of plant genetics, there are indications that it may be possible to improve plants against such stress factors. However, the practical success in this regard depends on how well we understand the biochemistry, physiology and molecular biology of the plant abiotic stress responses. The cellular response of plants to abiotic stresses is of complex nature involving simultaneous interplay of several mechanisms. Although there is a great deal of progress in cataloguing the biochemical reactions that are associated with plant abiotic stress responses, precise understanding of the defense reactions leading to acquisition of stress tolerance remains a challenge. A number of different experimental systems including lower and higher plants as well as microbes have been analyzed for examining the plant abiotic stress responses. The molecular analysis of the stress response has been carried out at the level of stress proteins, stress genes, stress promoters, trans-acting factors that bind to stress promoters and signal transduction components involved in mediation of stress responses. The functional relevance of the stressassociated genes is being tested in different trans-systems including yeast as well as higher plant species. In this article, we discuss selective features of experimentation in biology of plant abiotic stress responses.

Key Words: Abiotic stress response, Biotechnology, Experimentation, Molecular biology

Introduction

Green revolution nearly doubled food production. However, world population will touch the 8 billion mark in about 25 years from now. As per predictions, by 2020 we will need 40% more grains than what we produce today (Chrispeels 2000). That too from the agricultural land that is shrinking every passing day due to increased urbanization and excessive use and abuse. This means it is not just production but production per unit area that must increase. Will we be able to increase the genetic capacity of the crops to yield the desired increased output? But before we ask for the increased future agricultural output, it is rather an uneasy feeling to learn that we harvest only a small proportion of the present-day genetic capacity. Detailed studies have shown that we lose between 10 to 90% of the existing genetic capacity in most of the crops (Boyer 1982, Widawsky & O'Toole 1990).

The tapping of the genetic potential in crops is determined to a large extent on the prevailing environmental factors. The genotype x environment interaction (G x E) is thus a key factor controlling the growth performance of the crops. The term environmental factors in this context includes both the climatic and the soil attributes. The irregularity in circadian and seasonal perturbations of these factors is often a rule and not an exception. When environmental perturbations are rapid and unpredicted, there is hardly an opportunity for plants to adjust to the changed conditions. This causes onset of stress regimes. The abiotic stresses (such as drought stress, water stress or desiccation stress caused by paucity of water for long periods; flooding, waterlogging or hypoxia/anoxia stress caused by excess water; salt stress caused by increased level of salts in the soils; temperature stress which is both due to low

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and high ranges of the ambient temperatures caused due to sudden atmospheric heating or cooling; metal stress caused by excessive levels of heavy metals such as arsenic and cadmium and finally, oxidative stress caused by combination of different stress conditions with high light stress) cause appreciable reduction in biomass production and grain yield in most crops (readers may kindly refer Grime et al. 1989, Jones et al. 1989, Bohnert et al. 1995, Nilsen & Orcutt 1996, Busk & Pages 1998, Khanna-Chopra & Sinha 1998, Lerner 1999 for details on general aspects of plant abiotic stress biology).

Different crop ecosystems are affected by different abiotic stress factors and to a differential extent. Let us consider here an example of rice. This crop species constitutes the most important food crop in the world (Widawsky & O'Toole 1990, Khush & Toenniessen 1991, Khush & Baenziger 1998, Shimomoto 1999). Globally speaking, India is the second largest producer of rice and ranks first in terms of area under rice cultivation (IRRI Rice Alamanac 1993). The world rice-growing areas are divided in four different ecosystems namely irrigated rice, upland rice, lowland rice and deep-water rice. These ecosystems differ appreciably with respect to the grain production levels. The abiotic stresses that prevail in different rice ecosystems are shown in figure 1. These stresses have a large bearing on differential production levels of the different rice ecosystems (Widawsky & O'Toole 1990, Khush & Toenniessen 1991, Khush & Baenziger 1998). The assessment of rice economists is that abiotic stresses affect rice more than the biotic stresses (Hossain 1995). Any improvement made for the tolerance to abiotic stresses in rice would therefore have large economic gains. The abiotic stresses have been reported to cause significant losses in almost all crops including wheat, maize, barley, sorghum, chickpea, pigeonpea and cotton.

The conventional breeding methods such as those based on genetic variations, inter-specific or intergeneric hybridization, induced mutations and somaclonal variations have played a major role in increasing crop production. Systematic screening of plant germplasm has shown that there are excellent stress tolerant types locally available. For instance, rice types "FR13A" and "FR43B" of India, "Kurkaruppan" of Sri Lanka and "Goda Heenati" of Indonesia have notably higher level of flooding

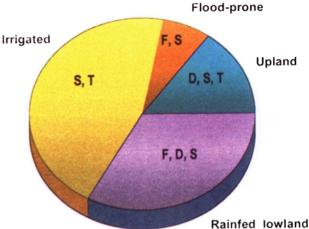


Figure 1 Different world rice ecosystems. The percentage-wise harvested rice area for different ecosystems is as follows: Irrigated-45%, Rainfed lowland-33%, Upland-15% and Flood prone-7%. The major abiotic stress factors that prevail in different rice ecosystems are shown. *D*, drought stress; *F*, flooding stress; *S*, salt stress and *T*, temperature stress.

tolerance (see Mohanty et al. 2000). The geneticallysuperior collection of germplasm has been made for several other abiotic stresses in rice (i.e. "Pokkali" and "Nona bokra" for salt stress response) as well as for different crops (i.e. "Kharchiya" for salt stress in wheat and "Atylosa albicans" for salt stress in pigeonpea). In recent years, the conventional breeding methods have been fortified with the addition of molecular breeding approach which banks on the application of different molecular markers for assisting in the genetic selection process (Mohan et al. 1997, Knapp 1998). Apart from the conventional and molecular breeding methods, production of transgenics has emerged as a powerful approach for altering genetics of crops. Research on production of transgenic plants has made great strides during the past 15 years (Hiatt 1993, Galun & Breiman 1997, Geneve et al. 1997). Tools and techniques for improvement of different crops through genetic engineering approach have been perfected to a great extent in several international as well as national laboratories. There are umpteen reports showing that crops tolerant/ resistant to herbicides, insect pests and viral and bacterial and fungal pathogens have been produced by employing transgenic technology.

In spite of the above progress, stress-tolerant, high-yielding crop cultivars are yet to find place in a common usage in the farmer's field. The success in generation of abiotic stress tolerant crops through the

conventional breeding methods has only been partial (refer Mohanty et al. 2000 for discussion on production of flooding tolerant rice by conventional and unconventional approaches). The application of molecular markers for mapping abiotic stress tolerance is far from fruition. The transgenic approach is yet to produce abiotic stress tolerant plant with high level tolerance that combines well with increased yield (Grover & Minhas 2000). Considering the wide-reaching implications of producing abiotic stress tolerant crops particularly for developing countries which have far-less organized agriculture than the West, incessant research on interactions of abiotic stresses and crops is a must. Our group has discussed the diverse issues that are involved in production of abiotic stress tolerant crops in several recent reviews (Grover et al. 1993, Grover et al. 1995, Singla et al. 1997, Pareek et al. 1997, Grover et al. 1998a, Grover et al. 1998b, Grover 1999, Grover et al. 1999, Minhas & Grover 1999, Katiyar-Agarwal et al. 1999, Grover & Minhas 2000, Grover et al. 2000, Grover 2000, Grover et al. 2001, Katiyar-Agarwal et al. 2001, Dubey & Grover 2001). From these as well as host of other reports published on this theme (Khanna-Chopra & Sinha 1998, Dhaliwal et al. 1998, Bajaj et al. 1999), it can be noted that a number of different biological systems are being employed for the study of abiotic stress responses in crops. These include microbial systems, fish as well as several lower and higher plants for the isolation of requisite genes and yeast and several higher plant systems for testing the relevance of the candidate genes (Grover et al. 1998a, Grover et al. 1999). In this article, we provide details on (i) the experimental systems that have been exploited for understanding the molecular biology and biotechnology of plant abiotic stress responses as well as (ii) the details on molecular parameters that have accrued through the analysis of such systems. It is important to debate on these aspects for making further in-roads into the science of producing abiotic stress tolerant transgenics.

Experimental Systems for Analyzing Molecular Responses of Plants to Different Abiotic Stresses The experimental work on responses of crops to stress has been carried out using stress conditions that prevail in field as well as induced stress conditions in the laboratory set-up. The most favoured approach has been to experimentally subject the control plants to stress conditions simulated in the laboratory (or

greenhouse). This simplified route is practiced to minimize the experimental variations invariably involved in field-conditions. However, the responses of plant to the stress conditions mimicked in the laboratory may not entirely match with those in the field conditions. In natural habitats, onset of stress is often a gradual process. On the other hand, stress imposition is relatively rapid in laboratory-based experiments where small petri dishes or pots are often used. With respect to salt stress, constantly fluctuating positive as well as negative interactions amongst different salts can potentially alter the cell response in natural habitats as against in laboratory-media that have defined and fixed salt compositions. The plant response to stress conditions also shows variations with respect to the degree of stress. Against lethal levels of stress, the metabolic responses mostly represent the events associated with cell senescence or death. On the other hand, the imposition of sublethal stress provides certain beneficial effects in adapting the system to stressful regimes (however, under certain circumstances, even the cell senescence or death associated with lethal or sub-lethal stress levels is the component of the adaptive strategy). Notably, plants exposed to sub-lethal stress prior to lethal stress are often more tolerant to lethal stress than the plants which are directly transferred from control to lethal stress regimes (Lin et al. 1984, Singla et al. 1997). The sub-lethal stress level has therefore emerged as the choicest approach for the analysis of adaptive stress responses. Apart from the sub-lethal stressed systems, there are strong indications that changes that follow in the recovery phase are directly correlated with tolerance mechanisms. The samples harvested at various intervals during recovery from stress have served as useful materials for understanding the tolerance mechanism.

The stress effects have been examined at canopy level, whole-plant level and at the level of organs, tissues and individual cells. At all these levels, plantabiotic stress interactions have been scored using morphological (such as change in growth pattern of the roots etc.), physiological (such as root-shoot partitioning, photosynthesis and nitrogen metabolism) and biochemical (such as enzyme activities and macromolecular changes) parameters (Pareek et al. 1997, Singla et al. 1997, Grover 1999). As the basis of all plant metabolic adaptations are the events that take place at the molecular level (i.e. gene

expression changes in terms of altered patterns of RNA and protein synthesis), molecular events are the targets when aim is to alter the genetics of crops for improved stress tolerance. The understanding of the RNA and protein alterations induced by different stresses has thus turned out to be a key objective in stress-related studies.

The research work on plant-abiotic stress interactive responses has been carried out employing a number of different plant species. This selection is often made on the basis of relative sensitivity/ tolerance as well as economic importance. Rumex has been exploited as a model system to study the relationship between flooding resistance and plant distribution (Arteca 1997). Detailed studies using this genus have provided valuable information on the role of root physiology in determining flooding tolerance. Upon exposure to dehydration stress, Craterostigma plantagineum, a resurrecting moss, is noted to lose almost up to 99% of its total water content and yet upon rehydration revives and turns to the normal growth patterns (Bartels et al. 1990). This system has been intensively analyzed for examining water stress responses. Tortula ruralis has been much-analyzed system for understanding the reasons underlying stability of ribosomes under extreme water stress conditions (Dhindsa & Bewley 1978). Mesembryanthemum crystallinum, the common ice plant, has been studied to a great detail for examining salt stress responses (Cushman et al. 1990). When stressed by addition of salt to the medium, or by drought or cold, Mesembryanthemum plants reproducibly change their primary mode of carbon assimilation from C_3 to CAM (Cushman et al. 1990). The weedy dicotyledonous species Arabidopsis thaliana has been extensively employed for the studies on abiotic stress responses. A large number of mutants have been generated in this species which have proven to be of enormous help in characterization of stress responses (Liu & Zhu 1997, Liu & Zhu 1998, Hong & Vierling 2000). The complete genome of Arabidopsis has recently been sequenced (The Arabidopsis Genome Initiative 2000) and currently there is a great deal of emphasis on the functional genomics of this species (for further details on structural and func-tional genomics, refer Somerville & Somerville 1999, Walbot 1999, Maheshwari et al. 2001, Dubey & Grover 2001). The understanding of the fundamentals of the stress responses from this species will possibly be more

elaborate than any other plant species in times to come. Amongst the crop plants, a great deal of experimental work on flooding stress response has been undertaken on Oryza sativa (Hossain et al. 1994, Hossain et al. 1996, Rivoal et al. 1997) and Zea mays (Wignarajah & Greenway 1976, Laszlo & Lawrence 1983, Kelley 1989, Kelly et al. 1991). Z. mays is a highly-sensitive crop to flooding stress while O. sativa is relatively a floodingtolerant cereal (Perata & Alpi 1993). Hordeum vulgare has turned out to be a favourite material for studies on salt stress. This species is considered to be the most salt-tolerant cereal (Suhayda et al. 1992). O. sativa and Triticum aestivum are reported to be highly-sensitive to salt stress (Maas & Hoffman 1976, Rawson 1986, Maas & Grieve 1990, Bhushan & Grover 1993, Barlow et al. 1977). The effects of water stress have been extensively analyzed using O. sativa and T. aestivum (Mundy & Chua 1988, Claes et al. 1990, Bostock & Quatrano 1992, Kusano et al. 1992, Pareek et al. 1995, Nakagawa et al. 1996, Pareek et al. 1997, Singla et al. 1997). The experimentation in abiotic stresses responses utilizing the above as well as other species have involved high-yielding stress sensitive cultivars, moderately-yielding stress tolerant cultivars and lowyielding stress tolerant wild relatives of the specific plants (figure 2). The wild relatives of crop species are

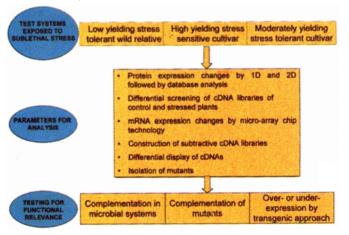


Figure 2 Experimental systems and techniques that have often been employed for the analysis of abiotic stress responses. The experimentation in abiotic stress responses have been undertaken employing highly sensitive and the highly tolerant types as well as the contrasting germplasm. These systems are subjected to sub-lethal stresses in order to evoke the stress responses. The induced responses have subsequently been examined at various hierarchial levels which include molecular, biochemical and physiological changes examined at tissue, organ- as well as organism-based expression. The relevance of the candidate stress responsive genes and proteins towards conferring stress tolerance is examined using different micobial and higher plant systems (see text for details).

extremely useful source for agronomically-important genes. As mentioned above, "Nona bokra" and "Pokkali" are the low-yielding local selections of rice that have proven useful for studying mechanism(s) of salt tolerance in rice (Akbar et al. 1986, Moons et al. 1995). The halophytic wild relative of rice Porteresia coarctata is noted for its salt tolerance (Raychaudhuri & Majumdar 1996). Another wild rice type O. granulata has notable sensitivity to water-logging. The use of breeding lines that have a contrast in their stress responses has also been followed in many instances. In H. vulgare, CM72 and Prato cultivars have a notable contrast with respect to their salt stress responses (Epstein et al. 1980). These contrasting types have been analyzed for RNA and protein expression studies (Ramagopal 1987a, b, c). On the same line, FR13A and FR 43B rice types have been exploited for studies on flooding response (Mohanty et al. 2000). Several national and international breeding programs have been initiated to introgress flooding tolerance from the above sources into high-yielding modern rice cultivars resulting in production of selected tolerant lines which are presently at different stages of testing (Mohanty et al. 2000).

While the use of specific plant species is emphasized in the above account, it must also be appreciated that plant-abiotic stress responses are, by and large, conserved. For instance, the nucleotide sequences of different hsp (heat shock protein) genes is nearly identical in different biological systems (Singla et al. 1997, Katiyar-Agarwal et al. 2001). Therefore, any conclusion made with regard to stress response of a specific plant would be applicable to a wide range of different plant species. This conclusion is further supported by the observed synteny in the genomes of different plant species (Gale & Devos 1998). The use of different species in varied studies is thus hardly a handicap in stress-related literature.

The microbial systems can provide genes for bringing in high-level plant abiotic stress tolerance as well. These organisms are uniquely empowered with the capacities to grow and reproduce under conditions in which the life of higher plants is difficult to even imagine. These organisms are present in snow-capped glaciers, volcanoes, deserts or springs. The natural thermophilic habitats such as sulphur or iron-rich hot springs and geothermal vents allow growth and survival of several microbial populations. Several classes of osmo-tolerant microorganisms are

found in a wide range of environments such as bacteria and algae in salt lakes, several kinds of yeast in syrups and filamentous fungi in saline soils of low water content and stored food. In their natural habitats, microorganisms are frequently exposed to osmotic changes that are not only sensed but converted into an activity change of specific enzymes and transport proteins and/ or their synthesis de novo such that the osmotic imbalance is rapidly restored (Edwards 1990). Selected examples of osmocompatible solutes include glycerol, arabitol, erythritol, mannitol, glycosyl glycerol, sucrose, trehalose, proline, glutamate, glycinebetaine and proline-betaine (Edwards 1990). Bacillus responds to osmotic stress by initially taking up K⁺ ions followed by large amounts of proline by de novo synthesis (Measures 1975, Whatmore et al. 1990, Whatmore & Reed 1990). This bacterium also uses compatible glycinebetaine solute which is accumulated either due to de novo synthesis or direct uptake from the environment. Multiple transport systems are noted to be involved in the uptake of glycinebetaine in Bacillus. It has been observed that the most prominent physiological effect in osmotically-stressed yeast cells is the enhanced production of glycerol to counterbalance the osmotic pressure (Pavlik et al. 1993). Obligate thermophiles are represented by a wide range of species, the best studied of which are Bacillus and Thermus genera. The thermotolerant species of Bacillus such as B. licheniformis and B. subtilis are able to tolerate a temperature of 20-50°C, facultative thermophiles such as B. coagulans tolerate a range of 30-60°C and obligate thermophiles such as B. sterothermophilus and B. acidocaldarius tolerate a range of 40-80°C. Bacillus population is shown to possess well-formed mechanisms for tolerating severe heat stress (Visick & Clarke 1995). Examples of selected genes of microbial origin proven useful for enhancing abiotic stress tolerance of higher plants are mentioned in the subsequent account.

Molecular Parameters for Analyzing Abiotic Stress Responses

Detailed characterization of stress responses has shown that specific proteins accumulate in response to imposition of stress conditions. These proteins are commonly referred to as stress proteins. The classical example of such proteins is the heat shock proteins

(HSPs) that are induced primarily in response to high temperature stress (Vierling 1991, Singla et al. 1997, Katiyar-Agarwal et al. 2001). Specific stress proteins have also been noted to accumulate in response to low temperature stress, water stress, salt stress and oxidative stress (Grover et al. 1998a, Grover et al. 1999, Chang et al. 2000, Grover et al. 2001). The amino acid sequence of the stress proteins has enabled isolation of the specific gene clones (Claes et al. 1990, Moons et al. 1998). The stress genes have also been isolated by differential screening of cDNA libraries constructed from control and stressed tissue mRNAs as well as through use of subtractive cDNA libraries. In recent years, the technique of differential display of cDNA clones has also been successfully employed for isolation of stress-specific clones (Liang & Pardee 1992, Huq & Hodges 1999). Selective examples of genes and proteins induced by heat shock, cold stress, water stress and salt stress are presented in table 1. The stress genes isolated and cloned from microbial systems include mannitol phosphate dehydrogenase gene from E. coli, genes encoding betainealdehyde dehydrogenase, choline dehydrogenase and levan sucrase isolated from B. subtilis and gene encoding choline oxidase from Arthobacter globiformis. The recent progress made in isolation, cloning and characterization of anaerobiosis, low temperature and high temperature-induced stress promoters is among the major developments which have taken place in stress biology in recent years (table 2). Most of the stress promoters contain an array of stressspecific cis-acting elements that are recognized by the requisite transcription factors. Importantly, the knowledge generated from stress promoters is proving useful not only with respect to the fundamental studies on stress-inducibility but also for the regulated expression of stress gene in transgenic systems (for further details see Kativar-Agarwal et al. 1999). The studies on the mechanisms behind switching on and off of the stress genes have placed a great deal of emphasis on transcription factors for the regulation of stress promoters (table 3). The generation of stress tolerance through engineering for over-expression of transcription factor genes is emerging as an attractive possibility in recent years. More details on stress proteins, genes, promoters, transcription factors and signal transduction components can be seen in the recent paper by Grover et al. (2001).

Experimental Systems for Analyzing Functional Relevance of the Stress Genes

The foremost goal of the abiotic stress biology research is to seek understanding of the plant responses at the fundamental level. The question being addressed is how plants sense stresses and how is the defense mounted? The other equally-important goal of stress biology research is to produce plants that have genetically-enhanced capacity to tolerate abiotic stresses. As the output from the first objective is an essential input for the second objective, both basic and applied aspects of abiotic stress molecular biology science have an interwoven relevance.

The term stress genes that includes genes which are up-regulated in response to application of stress treatments is a misnomer. It is possible that a given stress gene may not be primarily related to the events of stress tolerance. Therefore, it is prudent to experimentally work out how the specific stress gene is related to stress tolerance. The methods for genetically introducing the desired gene in the trans-host have fortunately been optimized to a great deal, enabling the use of reverse genetics approach for the same. Further, it is possible now to not only overexpress the gene but to under-express it as well (through antisense technology) so that the consequences of the gene action are proved either way.

In several studies, plant stress genes have been over-expressed in yeast. Yeast is a unique eukaryotic system in terms of its genotypic organization and yet has many of the advantages which are normally seen in the prokaryotes in terms of growth cycle (Bassham & Raikhel 2000). The complete genome of yeast has been sequenced and is noted to encode for nearly 6000 functional proteins (Goffeau et al. 1996). Importantly, attempts are being made to raise knockout mutants of each one of the yeast genes. The availability of this kind of flexibility in the yeast system is of paramount importance. The functional complementation of the higher plant genes with the yeast system has proven a fertile approach. In recent years, a number of different plant genes have been introduced in yeast with this objective. The plant hsp100 genes have been shown to functionally complement hsp104 mutation in yeast (Schirmer et al. 1994, Lee et al. 1994, Wells 1998). On the note of caution, there are several plant

Table 1 Selective examples of genes/ proteins induced by abiotic stresses

Plant Species	Genes/ Proteins Characteristic Feature(S)		Reference	
Heat shock responsive g	gene/ proteins			
Arabidopsis thaliana	HSP81-1	Expression occurs at low level in absence of heat shock (HS) and at high level at 35°C	Takahashi et al. 1992	
	HSP81-2	Constitutively expressed at higher level and is moderately enhanced by elevated temperature; analysis of HSP81-2 genomic and partial cDNA sequence suggests that the coding region is interrupted by two introns of 304 and 106 base pairs	Takahashi et al. 1992	
	hsp70-1	Constitutively expressed, 4-5 fold increase in mRNA levels after HS	Wu et al. 1988	
	AtHSP17.6	Induced by HS; gene encodes 17.6 kDa protein having 157 amino acids	Helm and Vierling 1989	
	HSP18.2 and HSP17.4	Transcript undetectable in control tissues but induced by HS	Takahashi & Komeda 1989	
	AtHSP101	Induced by HS, partially substitutes the function of yeast hsp104	Schirmer et al. 1994	
	A†HSP22	Induced by HS, encodes 22 kDa protein and is localized in the ER during HS	Helm et al. 1995	
Brassica oleracea	90, 88, 86, 74, 69, 66, 47, 43, 42, 27, 23, 21, 19 and 18 kDa proteins	HSPs induced by HS	Fabijanski et al. 1987	
Catharanthus roseus	cDNA for hsp 90 homologue	Protein constitutively expressed in cell cultures grown at 25°C; not detected in young plants at room temperature but seen after a HS at 37°C for several hours	Schroder et al. 1993	
Cucurbita sp.	76 and 73 kDa proteins	HSPs induced by HS	Strzalka et al. 1994	
Daucus carota	pMON 9508	hsp70 genomic clone encoding HSP 70	Rochester et al. 1986	
	Dchsp70	Accumulation of mRNA is heat- inducible and reaches maximum levels at 37°C	Lin et al. 1991	
Glycine max	LMW classI proteins	15-18 kDa, responsible for thermotolerance	Hsieh et al. 1992	
	hsp17.6-L, hsp17.5-M and hsp17.5-E	Code for proteins in molecular weight range of 17.3-17.5 kDa	Nagao et al. 1985	
	hsp22	Induced by HS, encodes 22 kDa protein	Helm et al. 1993	
	hsp101	Induced by HS, encodes 101 kDa protein	Lee et al. 1994	
Helianthus annuus	Tetraubiquitin mRNA known as haUbiS	Induced by HS	Almoguera et al. 1995	

Table 1 (Contd..)

	HSP17.6 and HSP17.9	Induced by HS as well as water stress	Almoguera et al. 1993
Hordeum vulgare	94,85,76,71,39, 32 and 24 kDa proteins	Proteins accumulated in response to HS	Clarke & Critchley 1992
	hsp90 mRNA	Induced by pathogen infection and HS	Walther-Larsen et al. 1993
Lycopersicon peruvianum	Seven LMW HSPs (15- 20 kDa)	Proteins induced by heat stress	Kato et al. 1993
	Polyubiquitin (Ubq1-1)	Induced by HS, 7 ubiquitin units with two additional amino acids	Rollfinke & Pfitzner1994
	25-91 kDa HSPs	Metal ion responsive proteins	Kapoor 1986
Nicotiana tabacum	pTC B48 cDNA clone	Encodes calmodulin-binding HSP	Lu et al. 1995
Oryza satīva	hsp82B	Encodes 82 kDa protein, mRNA accumulates to high levels within 120 min after plants are shifted to 42°C	Breusegem et al. 1994
	33 kDa HSP	Synthesis occurs at high temperature	Fourre & Lhoest 1989
	Oshsp 16.9 A and Oshsp 16.9 B	16.9 kDa HSPs	Tzeng et al. 1992
	110 kDa HSP	Heat and ABA-inducible	Singla & Grover 1993
	pTS1 and pTS3	Encode 16-20 kDa HSPs; also synthesized in response to heavy metal stress	Tseng et al. 1993
	104 kDa HSP	Heat-inducible	Singla & Grover 1994, Pareek et al. 1995
	90 kDa HSP	Heat-inducible	Pareek et al. 1995
Pharbitis nil	hsp83A	DNA sequence homology to members of 83 to 90 kDa hsp gene family; increase in mRNA levels found 2 h after endof-day dark treatment; encodes a protein that exhibits 70% amino acid identity with Drosophila HSP83	Felsheim & Das 1992
Phaseolus aureus	HSP70	70 kDa protein induced under heat stress, also induced due to low temperature	Wu et al. 1993
Phaseolus vulgaris	hsp70	68 kDa protein loosely associated with the mitochondrial envelope	Vidal et al. 1993
Pisum sativum	HSP18.1	18.1 kDa classI protein	Neumann et al. 1989
	HSP62	Etioplast-encoded protein	Necchi et al. 1987
	HSP21	21 kDa nuclear encoded chloroplast-localized HSP	Vierling et al. 1988
	sHSPs	ClassI and classII cytoplasmic HSPs, accumulate in embryo without HS at levels similar as that present in heat-stressed leaves	DeRocher & Vierling 1994

Table 1 (Contd..)

Vigna radiata 114, 79, 73, 70, 60, 56, 51, 46 and 18 kDa proteins		HSPs induced by HS	Collins et al. 1995
Zea mays	60 kDa protein	Protein induced under high temperature	Sinibaldi & Turpen 1985
	108, 89, 84, 76, 73, 30, 23 and 18 kDa proteins	HSPs induced by HS	Atkinson et al. 1989
	hsp70	Low level of expression at normal temperature and it increases 40-60 fold at 42°C, 68% homologous to hsp70 of Drosophila	Rochester et al. 1986
Cold responsive genes	/ proteins		
A. thaliana	corpHH 7.2, 28, 29, 67	Induced by ABA and water stress	Hajela et al. 1990
	skin1	Identical to cor 6.6; ABA and low temperature inducible	Kurkela & Franck 1990
	lti40	Induced by water stress, low temperature and by fluridone treatment	Nordin et al. 1991
	rab18	18.5 kDa glycine rich protein induced by low temperature, water stress and ABA	Lang & Palva 1992
	cor15	Induced by low temperature and drought	Lin & Thomashow 1992
	lti78	Induced by low temperature	Nordin et al. 1993
	lti65	Induced by low temperature, drought and ABA	Nordin et al. 1993
	cor15b	Homologue of cor15a, responsive to low temperature stress and ABA but not to drought stress	Wilhem & Thomashow 1993
	lti30	Belongs to dhn/lea/rab gene family, expressed during cold stress	Welin et al. 1994
	lti45	ABA independent expression	Welin et al. 1994
	cor47	Drought responsive but not responsive to ABA	Welin et al. 1994
Bromus inermis	22 kDa protein	Inhibited by low temperature	Robertson et al. 1987
	pBGA12, 56, 85 and 25	ABA inducble cold responsive genes; implicated in freezing tolerance	Lee & Chen 1993
Brassica napus	22-23 kDa protein	Inhibited by cold stress	Meza-Basso et al. 1986
Cucum is sativus	25, 38, 50, 70 and 80 kDa proteins		
G. max	HSP70 related protein	HSC protein, increased synthesis at low temperature Cabane	
H. vulgare	75 kDa protein	Most abundant cold stress protein	Cattivelli & Bartels 1989

Table 1 (Contd..)

	pAF93, pT59, pAO86 and pAO29	Cold regulated cDNA clones	Cattivelli & Bartels 1990
	45 kDa protein	Protein synthesis in response to cold, drought and ABA	Grossi et al. 1992
	hva1	Group 3 lea gene	Sutton et al. 1992
	bl t 101	Induced by low temperature, ABA and drought	Goddard et al. 1993
Lycopersicon esculentum	27 and 35 kDa proteins	35 kDa protein is synthesized and 27 kDa protein is inhibited by chilling	Cooper & Ort 1988
Medicago sativa	MsaciA clone	Encodes for glycine-rich protein	Laberge et al. 1993
	15 kDa protein	Low temperature responsive protein	Monroy et al. 1993
Nicotiana plumbaginifolia	SOD cDNAs	Transgenic plants overexpressing these cDNAs show freezing tolerance	Bowler et al. 1991
O. sativa	95, 75, 25 and 21 kDa protein	Induced at low temperature	Hahn & Walbot 1989
	rab16A	Induced by low temperature, water stress and ABA	Hahn & Walbot 1989
	psaB, psbB, rbcL and atpE	Chloroplast encoded genes inhibited at low temperature	Hahn & Walbot 1989
	rbcS and cab	Nucleus-encoded genes, reduced expression in response to low temperature	Hahn & Walbot 1989
	lip5, lip9 and lip19	Induced by low temperature; lip5 and lip19 also stimulated by ABA	Aguan et al. 1991
Spinacia oleracea	85 and 160 kDa proteins	Synthesized in response to low temperature and water stress	Guy et al. 1992
	cor85 and cor140	Heat-stable proteins; responsive to low temperature, ABA, drought and wounding	Kazuoka & Oeda 1992
and the state of the	cap 79	79 kDa protein, plays role in renaturation of denatured proteins during cold stress	Neven et al. 1992
Solanum tuberosum	ci13, ci19, ci7 and ci21	Transcript transiently expressed in response to low temperature	Berkel et al. 1994
Triticum aestivum	wcs120	Strongly induced by cold	Houde et al. 1992
	wcs19	Leaf-specific gene stimulated by light during low temperature stress	Chauvin et al. 1993
Z. mays	adh1	Cold inducibility shown; primarily induced by anaerobiosis	Christie et al. 1991

Table 1 (Contd..)

A (1, -1;	14:70 3 10:64	1670 (97 0 LD	N. 1 1
A. thaliana	lti78 and lti64	lti78 (77.8 kDa protein) mainly responsive to low temperature while lti64 (64.5 kDa protein) responsive to drought and ABA	Nordin et al. 1993
	rd 22	ABA mediates the drought induced expression but not the seed-specific expression of rd22	Yamaguchi- Shinozaki & Shinozaki 1993b
	ERD5 cDNA clone	Encodes a precursor of proline dehydrogenase (oxidase) which is regulated at the level of mRNA accumulation during both hydrated and dehydrated plants - homologous to yeast put1 and Drosophila sluggish A genes	Kiyosue et al. 1996
	rd29A and rd29B	Induced by exogenous ABA following 3 h of application	Yamaguchi- Shinozaki & Shinozaki 1993a, 1994
B. napus	bnd 22	Increased by progressive or rapid water stress and salinity and disappeared on rehydration	Reviron et al. 1992
Craterostigma plantagineum	Several in vitro synthesized polypeptides	Synthesized after treatment with ABA; cDNA clones corresponding to mRNA expressed only in desiccation tolerant tissues	Bartels et al. 1990
	Desiccation specific major pcC gene families	Desiccation-related cDNA clones	Piatkowski et al. 1990
	cdeT27- 4 5	Induced by ABA in leaves and callus, promoter active in developing embryos and mature pollen grains in transformed tobacco	Michel et al. 1993
Gossypium hirsutum	6 LEA proteins and genes	Expressed during the maturation and desiccation phases of seed development	Baker et al. 1988
	lea5 and lea14 (27-45 homologue genes)	Highly induced in vegetative tissues; induced in post-abscission stage of embryogenesis and environentally induced in embryo by desiccation or treatment with ABA or high osmoticum	Galau et al. 1993
D. carota	DC8	ABA regulated	Franz et al. 1989
H. annuus	hsp17.6 and hsp17.9 mRNAs	Expressed in response to HS or water stress	Almoguera et al. 1993
L. esculentum	TAS14 and TSW12	Induced by drought stress, also induced by low temperature stress	Godoy et al. 1990, Torres-Schumann et al. 1991, 1992 Hughes et al. 1992
	Genes for proteases and ubiquitin	Induced by water deficit; gene products may be involved in the degradation of proteins that are denatured during cellular water loss	Bray 1993

Table 1 (Contd..)

	le16	Encodes a 12.7 kDa protein, induced by drought stress and regulated by ABA specifically in aerial vegetative tissues; also induced by salt, heat, cold and water stress	Plant et al. 1991
	plc30-15	ABA and drought induced	Chen & Tabaeziadeh 1992, Chen et al. 1993
Mesembryanthemum crystallinum	imt1	Induced by osmotic stress	Vernon & Bohnert 1992
	Two isogenes for PEP carboxylase ppc1 and ppc2	ppc1 shows 30 fold increase in transcription rate in leaves and ppc2 transcripts decrease slightly in leaf tissues; in roots transcripts for both the genes descrease with time of exposure of stress; induced by salt stress also	Cushman et al. 1989
Nicotiana glauca	MIP1	Down regulated under drought stress	Smart et al. (unpublished report)
O. sativa	rab16B, rab16C and rab16D	ABA regulated	Yamaguchi Shinozaki et al. 1990
	23 kDa polypeptide	ABA responsive, not responsive to NaCl and cold treatment, boiling stable and immunologically related to the RAB 16 family of proteins	Rao et al. 1993
	23 kDa polypeptide	Induced in cell suspensions	Reddy et al. 1993
	rab16A	Osmotic stress and ABA responsive, conserved sequence motifs in the <i>rab 16A</i> promoter specifically bind nuclear protein factors	Mundy et al. 1990
	RAB21	RAB21 mRNA and protein (16.5 kDa) accumulate in rice embryos, root, leaves and callus derived suspension cell upon treatment with NaCl or ABA	Mundy & Chua 1988
P. sativum pPsB12 cDNA clone		Encodes a polypeptide of 20.4 kDa; pea dehydrin lacks a stretch of serine residues which is conserved in other dehydrins, ABA induced expression of dehydrins in the unstressed seedlings	Robertson & Chandler 1992
Sorghum bicolor	BADH1 and BADH15 cDNA clones	Encode betaine aldehyde dehydrogenase	Wood et al. 1996
	MIP1	Membrane intrinsic protein and induced by drought stress	Whitsitt et al. (unpublished report)
G. max	p5cs	Encodes 28.6 kDa enzyme that is involved in proline biosynthesis	Delauney & Verma 1990
T. aestivum	em	ABA regulated gene	Marcotte et al. 1989

Table 1 (Contd..)

Vigna radiata	Em like protein clone	Synthesized during early germination of axis and ABA extends its synthesis	Manickam et al. 1996
Z. mays	RAB17	Induced during late embryogenesis when ABA levels are high and it is also ABA and water stress inducible in embryo and vegetative tissues	Vilardell et al. 1990
	rab28	ABA-inducible in embryos and vegetative tissues; also induced by water stress in young leaves	Pla et al. 1993
Salt responsive genes/		<u></u>	*
A. thaliana	Sal1	Induced by salt stress, over expression in Arabidopisis or yeast overcomes Na* and Li* toxicity, homologous to hall of yeast	Quintero et al. 1996
B. napus	bnd 22	22 kDa protein, level increased by progressive or rapid water stress and salinity	Reviron et al. 1992
Citrus sinensis	Salt associated 23-25 kDa protein	Induced by salt stress, ABA and water stress	Ben Hayyim et al. 1993
Dunaliella salina	p150	150 kDa protein, induced by salt stress, de novo synthesized protein	Sadka et al. 1991
H. vulgare	26 kDa and 27 kDa proteins (salt induced poly-peptides SIP S1- S4)	Salt stress induces S ₁ -S ₂ polypetides but water deficit did not induce S ₂ polypeptides	Hurkman & Tanaka 1988
	hva1	Induced by ABA, drought, NaCl, cold and heat treatment	Hong et al. 1992
L. esculentum	TAS-12	Salt and water stress induced lipid transfer protein	Torres-Schumann et al. 1992
	le-16 gene	Induced by drought, PEG, salinity cold and heat stress	Plant et al. 1991
M. crystallinum	ppc-1 and ppc-2 isogenes	Encodes PEP carbroxylase, induced by salt and water stress, exogenous ABA is a poor substitute for NaCl to induce it	Cushman et al. 1989
	lm t1	Encodes myo-insitol o-methyl transferase1; induced by NaCl and osmotic stress	Vernon & Bohnert 1992
	inps1	Encodes myo-inositol 1-phosphate synthase (INPS 1), shows significant homology to corresponding genes in plants and yeast	Ishitani et al. 1996
N. tabacum	26 and 43 kDa polypeptides	Levels increase in both NaCl and PEG induced water stress adapted cells but are not detectable in unadapted cells	Singh et al. 1985
	58, 37, 35.5, 34, 26, 21, 19.5 and 18 kDa polypeptides	Increased levels with increased NaCl tolerance	Singh et al. 1985
	30 kDa polypeptide	Heat shock at 38°C induces cross tolerance to salt stress	Harrington and Alm 1988
	Vitronectin and fibronectin like proteins	Found in membranes and cells wall of NaCl adapted cells	Zhu et al. 1993
	Osmotin	26 kDa protein, protein level enhanced in both NaCl and PEG induced water stress adapted cells but not in unadaptable cells	Singh et al. 1987
O. sativa	RAB21	Induced when plants are subjected to water stress, rab21 mRNA and protein accumulate in rice embryos leaves, roots and callus derived suspension cells upon treatment with NaCl and/or ABA	Mundy & Chua 1988
	salT	mRNA accumulates rapidly in shoots and roots of mature seedlings with ABA salts, PEG, NaCl and KCl; no induction in leaf lamina	Claes et al. 1990
	em	Induced by ABA and salt stress, salt interacts synergistically with ABA	Bostock & Quatrano 1992

^{*}The names of various genes and proteins have been by and large reproduced here as per the original publications of the authors.

Table 2 Selective examples on the stress induced promoters involved in up-regulation of stress-related genes.

Gene'	Source	Trans-Host, If Any	Inducing Stress Type(S)	Reference
Salt, low tempera	ature and abscisic acid			1
bn115	B. napus		Low temperature	Jiang et al. 1996
cat1	Z. mays	Z. mays	ABA and osmotic stress	Guan et al. 2000
cdeT27-45	C. plantagineum	N. tabacum	Desiccation and ABA	Nelson et al. 1994
ci21A	S. tuberosum	S. tuberosum	Low temperature, drought and ABA	Schneider et al. 1997
cor15A	A. thaliana		Low temperature, ABA and drought	Baker et al. 1994
cor6.6	A. thaliana	N. tabacum	Low temperature, osmotic stress and dehydration	Wang et al. 1995
em	T. aestivum	N. tabacum and O. sativa	ABA	Marcotte et al. 1989
hva1	H. vulgare	***************************************	Drought, low temperature, heat, salinity and ABA	Straub et al. 1994, Shen et al. 1996
kin1	A. thaliana	N. tabacum	Low temperature, osmotic stress and dehydration	Wang et al. 1995
osmotin	N. tabacum	N. tabacum	ABA, C ₂ H ₄ and NaCl.	Liu et al.1995, Raghothama et al. 1997
pin2	S. tuberosum	O. sativa	Wounding, ABA and methyl jasmonate	Xu et al. 1993
rab16	O. sativa	O. sativa	Osmotic stress, water stress and ABA	Ono et al. 1996
rab17	Z. mays	A. thaliana	Water stress and osmotic stress	Busk et al. 1997, Vilardell et al. 1994
rab21	O. sativa	O. sativa	Water stress, osmotic stress and ABA	Mundy et al. 1998
rab 28	Z mays	O. sativa	Water stress and ABA	Pla et al. 1993
rd 22	A. thaliana	N. tabacum	Dehydration, salt stress, water deficit and ABA	Yamaguchi- Shinozaki et al. 1993
rd 29	A. thaliana	N. tabacum	Desiccation, cold, high salt conditions and ABA	Yamaguchi- Shinozaki et al. 1993, 1994
β- phaseolin	P. vulgaris	N. tabacum	ABA	Bustos et al. 1998
wcs120	T. aestivum	Several monocots and dicots	Low temperature	Oullet et al. 1998
Anaerobic stress				
adh	A. thaliana	A. thaliana	Dehydration, cold and hypoxia	Dolferus et al. 1994 Kyozuka et al. 1994
	Z. mays	O. sativa	Dehydration, cold and hypoxia	
gapC4	Z. mays	N. tabacum	Anoxia, UV and wounding	Kohler et al. 1996, Geffers et al. 2000
gpc4	Z. mays	Z. mays	Anoxia	Manjunath et al. 1997
High temperatur	e			
gmhsp17.3B	G. max	N. tabacum	High temperature	Rieping et al. 1992
gmhsp17.5E	G. max	H. annuus	High temperature	Gurley et al. 1986, Czarnecka et al. 1992
hahsp17.6G1	H. annuus	N. tabacum	Non-responsive to high temperature	Carranco et al. 1999

"The names of various genes and proteins have been by and large reproduced here as per the original publications of the authors.

Table 3 Selective characteristics of the genes encoding stress-related transcription factors.

Transcription Factor	Plant Species Examined	Binding Site	Characteristics	Reference
alfin1	M. sativa	G- rich triplets	Encodes a novel protein with a Cys4 and His/Cys3 putative zinc-binding domain, may play a role in the regulated expression of MsPRP2 in alfalfa roots contributing to salt tolerance	Bastola et al. 1998
athb-12	A. thaliana	Unknown	These genes contain a conserved sequence motif, the homeobox that encodes a DNA binding domain called as the homeodomain; they also contain a second element that codes for a putative leucine zipper motif; treatment with water stress and ABA resulted in the accumulation of Athb-12	Lee & Chun 1998
athb-7	A. thaliana	Unknown	Homeodomain-leucine zipper proteins; putative transcription factors encoded by a class of homeobox genes and are induced in all the organs by water deficit and osmotic stress	Soderman et al. 1996
AtMYB2	A. thaliana	MYB site	ATMYB2 is drought and ABA inducible and encodes the MYB related protein which functions as transcriptional activator of the rd22 gene along with rd22BP1	Urao et al. 1993
CBF1	A. thaliana	CRT/DRE	CBF1 encodes an AP2 binding domain containing the transcriptional activator that binds to the CRT/DRE sequence in the genes; induced by low temperature	Stockinger et al. 1997, Medina et al. 1999
DREB1A and 2A	A. thaliana	DRE/ CRT	Bind to the DRE sequence in vitro and bring about freezing and dehydration tolerance; deduced amino acid sequence shows similarity in the conserved DNA binding domain found in the ERBP and APETALA2 proteins like that of CBF1	Liu et al. 1998
DREB 2A and 2B	A. thaliana	DRE/ CRT	Induced by dehydration and high salt stress; unlike the DREB1A these are not induced in response to low temperature; contain a conserved Ser/Thr rich region adjacent to the EREBP/ AP2 DNA binding domain which is considered to be phosphorylated	Nakashima et al. 2000
EmBP-1	T. aestivum	ABRE	Interacts specifically with the 8 bp sequence CACGTGGC in the ABRE; deduced amino acid sequence of the EmBP-1 contains some conserved basic and leucine zipper domains found in the transcription factors in the plants, yeast and mammals	Guiltinan et al. 1990
HSF	A. thaliana, L. peruvianum, Z. mays and G. max.	HSE	Despite a considerable variability in size and sequence, their basic structure is similar; there is a highly conserved DNA binding domain near the N-terminus and the oligomerization domain is connected to the DNA binding domain by a flexible linker	Scharf et al. 1993, 1998, Czarnecka- Verner et al. 2000
Rd22BP1	A. thaliana	MYC site	Encodes a 68kDa protein that has a typical DNA binding domain of basic helix loop helix leucine zipper motifs in the MYC related transcription factors; dehydration stress and ABA induce the transcription of the rd22BP1 and its induction precedes that of rd22	Abe et al. 1997.

The names of various genes and proteins have been by and large reproduced here as per the original publications of the authors.

processes that yeast system does not possess and testing relevance of genes associated with such processes in yeast may or may not be a valid approach.

The current success in plant genetic engineering research has been possible due to the development of in vitro techniques for the culture and propaga-tion of cells and tissues. The first method used successfully for the introduction of exogenous DNA into plants employed the soil-borne organism Agrobacterium tumefaciens. Subsequently, several other methods (such as direct DNA transfer through electroporation into protoplasts, particle gun etc.) have been optimized for transferring genes, and this has enabled transformation of a large number of species. As of now, methods for genetic transformation of more than 150 different plant species have been optimized (Birch 1997, Hansen & Wright 1999). Among the plants, the best transformation frequencies have been noted with tobacco and Arabidopsis. Most work on testing of novel transgenes has therefore been carried out using these two species which is fair-enough to make a beginning (Grover & Minhas 2000). However, as the trans-gene for stress tolerance must be introduced in the destined species exhibiting stress sensitivity, optimization of the cultivar-specific methods for the genetic transformation of the crops has emerged as a high-priority objective in recent years (Grover et al. 1999). The production of transgenics involves several steps and techniques such as availability of suitable cloning vectors, promoters and related methods of tissue culture. One of the goals of the future research is to optimize tissue culture and genetic transformation work with more number of crop cultivars so that desired stress genes can be suitably trans-expressed.

Synthesis

Abiotic stresses elicit complex responses. To understand these responses, varied biological parameters have been utilized. From such efforts, we understand that abiotic stress responses are triggered at different levels of hierarchy of the cellular organization. It is shown that a large number of physiological and biochemical attributes of the cell are affected when plants experience abiotic stresses. However, specific biochemical/molecular changes that contribute towards stress

tolerance have only been partially identified thus far. Due to this gap in information, generation of abiotic stress tolerant plants through transgenic technology is proving a handicap. For removing the bottlenecks associated with production of abiotic stress tolerant plants, the detailed understanding of the plant abiotic stress responses is the need of the hour. The plant stress molecular biology and biotechnology research is limited by the non-availability of the stress genes to a large extent. The past attempts on the analysis of stress responses have mostly been made for defining the specific changes in gene expression, biochemical reaction or physiological event. These studies have remained focussed on analysis of single or limited number of genes and proteins at a given time. The present need is to look at stress responses with respect to global changes in different proteins/ genes. Fortunately, the current developments in genomics and proteomics have the potential to present this kind of picture of the global changes in RNA and proteins. The genome-wide analysis of mRNA expression by micro-array chip technology is providing important clues about the expression patterns and the function of gene products while proteomics is turning out to be the major subject of research for defining the gene functions. The enormity of analyzing genomics is such that no laboratory can individually answer all the questions. Therefore, it is important that groups specializing in different aspects of plant biology look at genomics with their own viewpoints. Those who work with abiotic stresses using diverse experimental materials across the globe need to come under an elaborate network so that efforts are co-ordinated amongst different institutions.

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