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Comparative genetics of drought tolerance

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SUMMARY – This is a review of recent research on drought tolerance among grass species with a comparative genetics perspective. New technologies for evaluating, dissecting, and mapping components of drought tolerance as well as the transfer of this information among species is accelerating the understanding of this phenomenon. In addition, exploitation of the genetic variation and evolutionary advantages of certain species can enhance our knowledge and provide a source of genes for transfer to other species.

Key words: Drought, abiotic stress, osmotic adjustment, candidate genes, comparative genetics.

RESUME – *"Génétique comparative de la résistance a la sécheresse". Cet article passe en revue les recherches récentes sur la tolérance à la sécheresse chez les graminées sous l'angle de la génétique comparative. De nouvelles technologies pour l'évaluation, la dissection, et la cartographie des composantes de la tolérance à la sécheresse ainsi que le transfert de cette information parmi les espèces, permettent d'accélérer la compréhension de ce phénomène. De plus, l'exploitation de la variation génétique et des avantages évolutifs de certaines espèces peuvent augmenter notre connaissance et nous apporter une source de gènes pour les transférer à d'autres espèces.*

Mots-clés : *Sécheresse, stress abiotique, ajustement osmotique, gènes candidats, génétique comparative.*

Introduction

Comparative genetics research has the general goal of estimating similarity at some level of organization. The discovery of structure or patterns in the relationships among species can lead to new knowledge, hypotheses, and predictions about those species. The evolution of comparative genetics research from the whole plant level to the DNA level has greatly expanded our knowledge of genome structure and function because of the diverse approaches scientists take in studying different species. Comparative genetics of drought tolerance will continue to evolve as new technologies, methods, and information become available. Current and future research will emphasize comparisons of genes and their expression under drought conditions across species using sequence and map-based tools that will characterize evolutionary trends in these genes at both the structural and functional levels.

Comparative maps for the gramineae

Comparative maps allow transfer of information about genetic control of traits from species with small diploid genomes, such as rice (*Oryza sativa* L.), to species with more complex genomic structures (increased repetitive DNA, polyploidy) and less economic support. Because of the size and complexity of the genomes, it may not be appropriate to sequence the entire genomes of wheat (*Triticum* ssp.), rye (*Secale cereale* L.), oat (*Avena sativa* L.), or barley (*Hordeum vulgare* L.). However, alternative strategies involving identification of gene-rich regions of the Triticeae genome and comparison of the genome structure and genetic colinearity with rice, maize (*Zea mays* L.), sorghum (*Sorghum vulgare* L.), and other species provide Triticeae researchers with the knowledge and tools necessary for genetic parity with simpler genomes.

The Gramineae family encompasses a diverse group of species that have been classified into two major clades based on molecular phylogenetic studies (Clark *et al.,* 1995; Soreng and Davis, 1998). The Panicoideae subfamily including maize, sugarcane (*Saccharum*), sorghum, and millet (*Pennisetum*) make up one clade while the other clade contains the Pooideae subfamily wheat, barley, rye, and oat. Rice and wild rice, belong to the subfamily Oryzoideae. The genome of cultivated rice is considered to resemble an ancestral grass genome with a high base chromosome number (x=12) and relatively small genome

size of 430MB (Argumuganathan and Earle, 1991). Molecular markers have been used to develop comparative chromosome maps for several members of the Gramineae (for review see Moore *et al.,* 1995; Devos and Gale, 1997) and these have been used to study genes of agronomic importance across species (for review see Snape and Laurie, 1998). Crop species of the Poaceae display a remarkable level of genetic similarity despite their evolutionary divergence 65 million years ago (Bennetzen and Freeling, 1993; Paterson *et al.,* 1995). Large segments of the genomes of maize, sorghum, rice, wheat, and barley conserve gene content and order (Hulbert *et al.,* 1990; Ahn and Tanksley, 1993; Ahn *et al.,* 1993; Kurata *et al.,* 1994; Van Deynze *et al.,* 1995a,b,c; Gale and Devos, 1998), although the correspondence has been modified by chromosome duplications, inversions, and translocations. For the domesticated grasses, the conserved linkage blocks and their relationships with rice linkage groups provides the insight into the basic organization of the ancestral grass genome (Moore *et al.,* 1995; Wilson *et al.,* 1999).

To date, most comparative mapping among the grasses has relied on RFLP probes (cDNAs or genomic clones) to establish gross gene orders and distance in specific chromosome segments. Only to a limited extent have researchers employed cloned genes, ESTs, mutant phenotype loci or QTLs in comparative genomics.

Despite the progress in comparative mapping, the application of this technology, especially for wheat, rye, oat, and barley will not be realized unless scientifically sound strategies for studying drought tolerance are devised that allow researchers to utilize genetic tools and information developed for model species. This will require more detailed comparative genetic analysis from the DNA sequence of genes all the way to comparative analysis of QTL.

Genetics of abiotic stress tolerance

Because the phenotype is the product of genotype and environment, assessment of the desired genotype is highly dependent on the proper environmental conditions. Abiotic stresses such as drought, temperature, salinity, and others generally reduce crop productivity. It has been estimated that crops attain only about 25% of their potential yield because of the detrimental effects of environmental stress (Boyer, 1982). The abiotic stresses are location-specific, exhibiting variation in frequency, intensity, and duration. Stresses can occur at any stage of plant growth and development, thus illustrating the dynamic nature of crop plants and their productivity.

There are several definitions of drought which include precipitation, evapotranspiration, potential evapotranspiration, temperature, humidity and other factors individually or in combination (Renu and Suresh, 1998). Drought is the primary abiotic stress causing not only differences between the mean yield and the potential yield but also causing variation from year to year (yield instability). Although selection for genotypes with increased productivity in drought environments has been an important aspect of many plant breeding programs, the biological basis for drought tolerance is still poorly understood. Also, drought stress is highly heterogeneous in time (over the seasons and years) and space (between and within sites), and is unpredictable. This makes it difficult to identify or simulate a representative drought stress condition.

It has been predicted that in the coming years rainfall patterns might shift due to an increase of the global temperature caused by burning of fossil fuels and the corresponding increase in atmospheric dioxides (Guido and Paul, 1994). Consequently, farming communities in the Northern Hemisphere could become increasingly dependent on drought tolerant varieties. Crop productivity in a water-limited environment derives from mechanisms that either permit tolerance of episodes of cellular dehydration or that minimize water loss and thereby maintain a favorable water status for leaf development.

Different mechanisms may render a plant drought tolerant: (i) the ability of a plant to escape periods of drought, especially during the most sensitive periods of its development; (ii) the ability of a plant to recover from a dry period by producing new leaves from buds that were able to survive the dry spell; commonly considered less interesting from the breeder's point of view; and (iii) the ability of a plant to endure or withstand a dry period by maintaining a favorable internal water balance under drought.

Selection for drought tolerance while maintaining maximum productivity under optimal conditions has been difficult (Rosenow *et al.,* 1983; Clarke *et al.,* 1992; Zavala-Garcia *et al.,* 1992). It has been reported that photosynthesis and several other related physiological traits differed significantly between drought

tolerant and drought susceptible genotypes (Gummuluru *et al.,* 1989). Several characteristics have been considered important in adaptation to stress. For example, osmotic adjustment, in which the plant increases the concentration of organic molecules in the cell water solution to "bind" water is one example of a mechanism that alleviates some of the detrimental effects of water stress by promoting both avoidance and tolerance (Blum, 1989). Instantaneous leaf water efficiency, defined as the ratio of leaf photosynthesis to transpiration measured simultaneously, has also received considerable scrutiny with respect to its postulated adaptive significance for plants growing under drought stress (Morgan and LeCain, 1991). A thicker layer of waxy material at the plant surface and more extensive and deeper rooting are others. Physiological and biochemical traits that might enhance drought tolerance have been proposed, but only a few of these mechanisms have been demonstrated to be causally related to the expression of tolerance under field conditions (Ludlow and Muchow, 1990).

There is a lack of knowledge about the processes between the DNA sequence of a gene, and a trait (the "phenotypic gap"). The analysis and manipulation of complex traits such as drought tolerance and plants grown in stressful and dynamic environments is a challenge. There are several ways to reduce the phenotypic gap. These ways gradually reveal the function(s) of the genes and their connection(s) with the phenotypes. There are many metabolic changes in response to drought stress. One of the most notable changes is the synthesis and accumulation of low-molecular weight, osmotically active compounds such as sugar alcohols, amino acids, organic acids, and glycine betaine (Turner, 1979; Yancy *et al.,* 1982; Morgan, 1984; Good and Zaplachinski, 1994). The accumulation of these compounds leads to osmotic adjustment as indicated by an increase in the intracellular osmotic potential of the cell (Morgan, 1984).

Genetics of drought tolerance in the grasses

Mapping quantitative trait loci associated with drought tolerance

Numerous QTL mapping studies examining drought tolerance and related traits in maize, rice, barley and wheat have demonstrated that this trait is affected by several loci, each of which have relatively small effects (e.g. reviews by McCouch and Doerge, 1995; Quarrie, 1996; CIMMYT conference).

Several studies have mapped loci associated with morphological traits under drought conditions. In maize a reduced anthesis-silking interval (ASI) is one of the traits most commonly associated with drought tolerance (Agrama and Moussa, 1996; Ribaut *et al.,* 1996; Ribaut *et al.,* 1997). Four of the 5 QTL for ASI from Agrama and Moussa (1996) appear to map in the same chromosomal regions (chromosomes 1, 5, 6, 8) as those in Ribaut *et al.* (1996) who identified 6 QTL for this trait. In addition, Ribaut *et al.* (1997) identified two "stable" QTL for grain yield that coincided with QTL for kernel number per plot. Lebreton *et al. (*1995) mapped QTL for physiological traits associated with drought tolerance in maize. They measured stomatal conductance, ABA of different tissues, leaf water relations parameters, fluorescence, root pulling force, and nodal root number. Xylem ABA content and stomatal conductance were associated with root characteristics. They found that xylem and leaf ABA content were positively correlated with nodal root number and root pulling force and negatively correlated with stomatal conductance. This was supported by coincident QTL on chromosome 3 for xylem ABA content and nodal root number; whereas, QTL for stomatal conductance and root pulling force were linked but not overlapping on the same chromosome.

Champoux *et al.* (1995) conducted an early QTL study in rice and found more than 45 QTL associated with leaf-rolling under field drought stress and root-morphology traits. Twelve of the 14 QTL associated with leaf rolling were also associated with root thickness, root/shoot ratio, or root dry weight per tiller. Using the same mapping population, Ray *et al.* (1996) evaluated root penetration. They found that some of these QTL corresponded to QTL for root morphology. Later, Lilley *et al.* (1996) extended the results of those two studies by evaluating osmotic adjustment and relative leaf water content. A single locus on chromosome 8 near RG1 and RZ66 was found to be associated with osmotic adjustment at 70% water potential. Teulat *et al.* (1998) also mapped genes for osmoregulation in barley and one of the QTL on barley chromosome 7H matched the homoelogous chromosome location reported for rice by Lilley *et al.* (1996). For this same chromosome region, Teulat *et al.* (1997) mapped QTL controlling relative water content and number of leaves under water stress. Champoux *et al.* (1995) mapped QTL for root morphology and leaf rolling in the homoeologous rice chromosome region. However a major gene mapped in wheat for osmoregulation (Morgan and Tan, 1996) appears to be distal to this region based

on rice/wheat comparative maps (Van Deynze *et al.,* 1995c). Teulat *et al.* (1998) mapped other osmoregulation genes in barley on 6H near WG286 and on 2H near E9_4 and mwg720. The E9_4 locus also corresponded to a homoeologous rice chromosome segment reported to be associated with lethal osmotic potential in rice (Lilley *et al.,* 1996). Price *et al.* (1997) evaluated several root growth characteristics in rice and in a companion paper (Price and Tomos, 1997) identified several QTL for maximum root length, volume, and thickness. In a comparison with Champoux *et al.* (1995) using a different mapping population, there were 3 QTL in common for maximum root length (chromosomes 2, 11, 9 or 5), 2 for root thickness (chromosomes 2, 3), and 1 for root volume (chromosome 12). The root penetration study by Ray *et al.* (1996) found that the QTL for root penetration on the long arm of chromosome 6 corresponded to root length and the one in the central region of chromosome 11 corresponded to root growth. In a third rice mapping population, Redona and Mackill (1996), identified a root length QTL that corresponded to a QTL in the Ray *et al.* (1996) study for root length at 14 days. Li *et al.* (1999) developed NILs for 4 different rice chromosome regions associated with total root weight, deep root weight, and shallow root weight. Most of the NILs for the target regions did not exhibit the change in the root trait predicted and several of the NILs for the selected allele had increased height and reduced tiller number suggesting linkage drag was a problem.

The stay-green trait has been associated with drought tolerance in sorghum (Borrell *et al.,* 1999). It was found that 3 loci (linkage groups B, G, and I) accounted for 34% of the total variance of stay green under drought stress. These chromosome regions correspond to parts of maize chromosomes 10, 8, and 3, respectively. Yadav *et al.* (1999) reported QTL for drought tolerance and yield components in two mapping populations of pearl millet (*Pennisetumm glaucum* (L.) R. Br.). Grain yield QTL on linkage groups 2, 5, and 6 were identified and QTL for components of yield corresponded to each of them. Homoeology to maize chromosomal regions has not been published.

A more comprehensive approach to studying drought tolerance has been advanced by INRA researchers using proteomics (de Vienne *et al.,* 1999; Prioul *et al.,* 1999). Using large-scale 2-D gel electrophoresis, they quantify protein spot intensities and these are mapped as protein quantity loci (PQL). This approach can aid in the detection of regulatory genes and in identifying candidate genes. This approach was used to evaluate a maize RIL population under mild drought stress. Differentially expressed proteins from leaf tissue were sequenced for identification. One of the proteins was an ABA/water stress/ripening induced protein located on chromosome 10 that had previously been found to be induced by water stress in other species (de Vienne *et al.,* 1999). The location of this candidate gene corresponded with a QTL for xylem sap ABA content, leaf senescence, and anthesis/silking interval. Other PQL reported by Prioul *et al.* (1999) to correspond to QTL for drought responsive traits included those on chromosomes 1 (Sh2 – ADPgulcose pyrophosphorylase), 2 (invertase), 5 (invertase), 6, 8 (sucrose-phospahte synthase), 9 and 10 (Prioul *et al.,* 1999).

Abscisic acid has been demonstrated to play an important role in plant response to water stress. Recent studies have mapped QTL for maize-leaf ABA content under drought stress (Tubersoa *et al.,* 1998; Sanguineti *et al.,* 1999). Sixteen QTL for ABA content corresponded with QTL for at least one of the following traits: stomatal conductance, drought sensitivity index, leaf temperature, leaf relative water content, anthesis-silking interval, and grain yield. An increase in ABA content was generally associated with decreased stomatal conductance and grain yield but increased leaf temperature. However, the opposite effect was observed for a QTL on chromosome 7 that aligned with a QTL from a previous study for root pulling resistance suggesting that elevated ABA stimulated the development of a more extensive root system (Lebreton *et al.,* 1995). In a study of 140 wheat genotypes, associations of yield components, carbon isotope discrimination (CID), ash content in flag leaf and kernels, and canopy temperature,revealed that CID explained approximately 30% of the total variability of dryland grain yield (Nachit, 1998).

Genes with up-regulated expression in response to drought

Plants respond to changing environmental stimuli with the expression of specific sets of genes that allow the plants to adapt to the altered environmental conditions. One of the most common environmental stresses to which plants are exposed is drought stress. The two most productive approaches to establishing the basic responses of plants to drought involve studying candidate genes and differential screening. Comparing the expression of genes thought to be important for drought tolerance, such as the enzymes in drought-induced metabolic pathways under drought versus non-drought conditions can provide useful information. A second approach uses differential screening to isolate up-regulated genes. These experiments have been successful in describing many genes encoding proteins of known function

associated with desiccation (Table 1). While most of these genes are induced by the plant hormone abscisic acid (ABA), several have been shown to be unresponsive to ABA (Guerrero *et al.,* 1990; Nordin *et al.,* 1991; Yamaguchi-Shinozaki *et al.,*1992). These findings suggest the existence of two separate signal transduction pathways responding to intracellular dehydration, an ABA-responsive and an ABA-independent pathway (Nordin *et al.,* 1991). ABA is synthesized through the carotenoid biosynthesis pathway. ABA concentration is altered when there are changes in cellular dehydration. Reduction of turgor results in rapid synthesis of this phytohormone. The synthesis itself requires nuclear gene expression and translation (Quarrie and Lister, 1984; Guerrero and Mullet, 1986). Increased levels of ABA can, in turn, induce changes in gene expression resulting in stomatal closure in leaves, inhibition of photosynthesis and the growth of leaves, stems and hairy roots. When subjected to osmotic stress or abscisic acid, some vascular plants such as barley respond with an increased accumulation of the osmoprotectant, glycine betaine (betaine), being the last step of betaine synthesis catalyzed by betaine aldehyde dehydrogenase (BADH). Manabu *et al. (*1995) have cloned and characterized a BADH cDNA from barley and described the expression pattern of BADH transcript. Two cDNA clones, BADH1 and BADH15, putatively encoding betaine aldehyde dehydrogenase have also been isolated from sorghum and characterized (Andrew *et al.,* 1996).

Table 1. Genes up-regulated by drought stress and encoding polypeptides of known function

cDNA	Plant	Feature	Reference
pSS1; pSS2	*C. plantagineum*	Sucrose synthases	Elster, 1994
PPPC1	*Mesembryanthemum crystallinum*	Phosphoenolpyruvate carboxylase	Vernon *et al.,* 1993
PBAD	*Hordeum vulgare*	Betaine aldehyde dehydrogenase	Ishitani *et al.,* 1995
CAtP5CS	*Arabidopsis thaliana*	Pyrroline-5-carboxylate synthetase	Yoshiba *et al.,* 1995
RD28	*A. thaliana*	Water channel	Yamaguchi-Shinozaki *et al.,* 1992
SAM1; SAM3	*Lycopersicon esculentum*	*S*-adenosyl-L-methionine synthetases	Espartero *et al.,* 1994
rd19A; rd21A	*A. thaliana*	Cysteine proteases	Koizumi *et al.,* 1993
UBQ1	*A. thaliana*	Ubiquitin extension protein	Kiyosue *et al.,* 1994b
PMBM1	*Triticum aestivum*	L-isoaspartyl methyltransferase	Mudgett and Clarke, 1994
SC514	*Glycine max*	Lipoxygenase	Bell and Mullet, 1991
cATCDPK1 and cATCDPK2	*A. thaliana*	Ca^{2+}-dependent, calmodulin-independent protein kinases	Urao *et al.,* 1994
PKABA1	*T. aestivum*	Protein kinase	Anderberg and Walker-Simmons, 1992
CAtPLC1	*A. thaliana*	Phosphatidylinositol-specific phospholipase C	Hirayama *et al.,* 1995
Apx1 gene	*Pisum sativum*	Cytosolic ascorbate peroxidase	Mittler and Zilinskas, 1994
Sod 2 gene	*P. sativum*	Cytosolic copper/zinc superoxide dismutase	White and Zilinskas, 1991
P31	*L. esculentum*	Cytosolic copper/zinc superoxide dismutase	Perl-Treves and Galun, 1991
Pcht28	*L. chilense*	Acidic endochitinase	Chen *et al.,* 1994
Atmyb2	*A. thaliana*	MYB-protein-related transcription factor	Urao *et al.,* 1993
ERD11; ERD13	*A. thaliana*	Glutathione *S*-transferases	Kiyosue *et al.,* 1993
CAtsEH	*A. thaliana*	Soluble epoxide hydrolase	Kiyosue *et al.,* 1994a

Dehydrins [late embryogenesis abundant (LEA) D11 family] are also produced in a wide variety of plant species in response to dehydration, low temperature, osmotic stress, seed drying and exposure to abscisic acid.

Inheritance studies, including QTL analysis, in several crop plants have revealed apparent co-segregation of *Dhn* genes with phenotypes associated with dehydrative stress, such as drought and freezing (Close, 1996). Despite their widespread occurrence and abundance in cells under dehydrative conditions, the biochemical role of dehydrins remains elusive. In some species, dehydrin loci are located within quantitative trait loci (QTL) intervals for important phenotypic traits including winter hardiness in barley and anthesis-silking interval in maize. Lang *et al.* (1998) studied the variation in the dehydrin gene family of barley using 3` fragments of dehydrin cDNA clones (DHN1-4) as hybridization probes. The results of this work indicated that there are two clones (DHN1 and DHN7) that represent allelic alternatives at the *Dhn1* locus. Wheat *Dhn* genes were mapped to 4DS, 5BI, and 6AL, also six maize *Dhn* probes identified eight maize *Dhn* loci on chromosomes 1, 3, 4, 5, 6, and 9 (reviewed by Close, 1996). Some genes are induced by drought, others by low temperature. This variation, together with cross-hybridization between *Dhn* genes highlights the necessity of gene-specific methods to study the *Dhn* multigene family.

Genes that protect plants from drought

There has been substantial progress in identifying genes for resistance to various abiotic stresses such as temperature, salinity, and drought. Table 2 shows some transgenic plants for improved drought tolerance using genes that have been isolated and tested as drought resistance genes. Among these genes, alanine aminotransferease that has been isolated from barley roots (Muench and Good, 1994) and D-myo-inositol methyltransferase from *M. crystallinum* that has been transformed to *Nicotiana tabacum* L.

Table 2. Transgenics produced for improved drought tolerance

Transgenic over-expression	Plant	Reference
alanine aminotransferease	Tobacco	Muench and Good, 1994
D-myo-inositol methyltransferase	Tobacco	Elena *et al.,* 1997
Fructan	Tobacco	Pilon-Smits *et al.,* 1995
HVA1	Rice, wheat	Xu *et al.,* 1996

Plant transformation resulting in stress-inducible, stable solute accumulation appears to provide protection under drought and salt-stress (Elena *et al.,* 1997). Fructans are polyfructose that are produced in only 15% of all flowering plant species, including wheat and barley (reviewed by Renu and Suresh, 1998). It functions mainly as a storage carbohydrate but being soluble may help plants survive periods of osmotic stress induced by drought or cold (Bieleski, 1993). To investigate the possible functional significance of fructans in drought stress, Pilon-Smits *et al.* (1995) have introduced the bacterial gene *SacB* from *Bacillus subtilis* encoding levan sucrose into tobacco, a non fructan-accumulating plant. The transgenic tobacco produced bacterial fructans and was examined for growth performance under PEG-mediated drought stress. The growth of the transgenic plants was higher under drought stress compared to the wild type tobacco.

Xu *et al. (*1996), has adopted the transgenic approach to investigate the function of the *HVA1* protein in stress protection of rice. *HVA1*, is a group 3 LEA protein that is expressed in barley aleurone and embryo during late seed development correlating with the seed desiccation stage (Hong *et al.,* 1988). The transgenic rice plants exhibited constitutive high expression of *HVA1* protein in leaves and roots. The R1 progeny of three transgenic plants was used for evaluation of the growth performance under water deficit and salt stress treatment. The appearance and development of the major damage symptoms such as wilting, dying of old leaves and necrosis of young leaves caused by the stress conditions were delayed in the transgenic plants. The better performance of R1 transgenic lines under stress conditions was correlated with higher level of *HVA1* protein accumulated in their R0 plants.

Regulation of gene expression under drought stress

It has been expected from molecular studies that the basic tools will be provided to modulate stress tolerance. One important component in this tool kit is regulatory elements that are responsive to environmental signals and lead to specific gene expression. The expression of a number of genes from various species has been shown to be induced by drought stress. Responsive to drought or ABA was demonstrated by monitoring steady state transcript levels or by protein analysis. Compared to the number of genes expressed in response to drought stress and/or ABA the number of corresponding promoters analyzed is small. Most of the promoters have been isolated from LEA genes that are abundantly expressed in dehydrated seeds. Table 3 shows activities of some promoters in transgenic plants.

Table 3. Characterization of promoters in transgenic plants

Gene	Isolated from	Reporter gene activity found in	Reference
Rab 16B	Rice embryos	Tobacco embryos	Yamaguchi *et al.,* 1990
Em	Wheat embryos	Tobacco embryos	Marcotte *et al.,* 1989
Rab 17	*Nauze* embryos	Arabidopsis embryos, endosperm	Vilardell *et al.,* 1994
Rd 22	*A. thaliana* dehydrated plants	Tobacco dehydration, ABA	Iwasaki *et al.,* 1995
Rd 29A	*A. thaliana* dehydrated plants	Inducible in almost all vegetative tissue in dehydrated Arabidopsis plants, also cold, ABA, salt inducible tobacco	Yamaguchi-Shinozaki and Shinozaki, 1993, 1994
CdeT27-45	*Craterostigma* dehydrated plants	Tobacco and Arabidopsis embryos, mature pollen	Michel *et al.,* 1993

Conclusions

A thorough analysis of the physiological events during drought stress and their genetic control is essential to define which genes are regulatory, which are primary gene products positively contributing to stress tolerance, which genes may serve as markers for the physiological stage of the plant, and which gene products can be considered as secondary stress-induced metabolites. However, comparative genetic analyses can greatly facilitate the discovery of genes that contribute to this complex trait by allowing scientists to transfer information between species. Furthermore, genetic variation for components of drought tolerance may differ widely among species and this genetic variation is crucial to understanding the underlying mechanisms.

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