International Journal of Biotechnology and Bioengineering Research
Volume 1 Number 1 (2010) pp. 11-18

https://dx.doi.org/10.37622/IJBBR/1.1.2010.11-18

Adaptation of Sorghum to Salinity Stress: A Mini Review

H Paramesh, R Vinodh, D Balakrishna* and N Seetharama

Directorate of Sorghum Research (DSR) (Formerly NRCS),
Rajendranagar, Hyderabad – 500030, India

Abstract

Plant salt stress resistance is the inherent ability of plants to withstand the effect of high salt concentrations in the root zone or on the leaves without a significant adverse effect. On the other hand plant salt tolerance is the ability of the plants to grow and complete its life cycle on a substrate that contains high concentrations of soluble salt. The reaction to salt stress varies with the stage of plant development. A given cultivar may be tolerant at one stage, but sensitive to another. Adaptation as a whole is defined as the long-term response during which the plant adjusts its physiology to the environmental conditions. Two types of response coexist in sorghum seedlings after pretreatment with NaCl, an adaptation response in which NaCl tolerance is increased, and a resistance response in which plant copes up with the salinity without modification of its tolerance level. Although salt-adaptation seems to be a widespread property of plants, the adaptive response has been rarely differentiated to the tolerance response. The induction of adaptation in *Sorghum bicolor* was only possible during specific time periods, called developmental windows. The period of exposure of the plants to non-lethal salinity apparently triggered a transient sensitivity to Abscisic acid and coincides with an increase in leaf Phospho Enol Pyruvate carboxylase activity which seems to occur faster if the plants are treated with ABA. The period during which developmentally perturbed leaf occur coincides with the period of induction of adaptation to high salinity suggesting the response may be used as a morphological marker of the adaptation process. The triggering activity of NaCl for adaptation to a whole range of environmental perturbations suggests that adaptation to salinity is not a pre-programmed response of the plants, but relates to learning processes occurring in animals. Adaptive modifications are transmitted to the progeny through maternal imprinting in the absence of natural selection. Adaptive response to salinity in showing variation in large

number of sorghum genotypes reveals the role of change in the level of chromosome endoreduplication and intragenotype variation response.
Keywords: Salinity stress, adaptation, sorghum, reaction types, canalization and endopolyploidy.

Introduction

Sorghum (*Sorghum bicolor* (L.)) Moench is the fifth most important cereal crop after wheat, rice, maize and barley. It is the best suited cereal crop for semiarid environments. It is used for food, feed, fodder and fuel. It is very popular among the farmers due to its high adaptability and various forms of utilization such as green fodder, stover, silage and hay besides its grain. Because of its wide uses and adaptation, Jack Harlan, (1971) remarked that sorghum is one of the really indispensable crops required for the survival of humankind.. It is an annual grass, extremely drought tolerant, making it an excellent choice for arid and dry areas. The origin and early domestication of sorghum took place approximately 5000 years ago in northeastern Africa, north of the Equator and east of 10°E latitude, (Mann *et al*., (1983). It is divided into five major races: *bicolor*, *guinea*, *caudatum*, *kafir* and *durra*. Among these races it is be noted that *bicolor* is the most primitive race and *durra* is the advanced. The sorghum plant is well known for its ability and capacity to tolerate limited moisture conditions and to give yield during the periods of several stresses, in situations where that would impede production in most other grains. Unlike other grain crops, sorghum’s yield under different conditions is not much varied. Under moisture stressed conditions the leaves of the sorghum plants roll along the midrib making the plant more drought resistant than other grain plants. In addition to biotic stresses such as insect pest and disease infestation, the yield loss of the crop is also result of abiotic stresses such as extreme temperatures (cold and heat), drought, soil salinity and heavy metal pollution.

Soil salinity is a major factor in reducing plant productivity and an increasing threat to agriculture; therefore, it is necessary to obtain salinity-tolerant varieties. High salt concentrations in the soil generate a low water potential zone in the soil making it increasingly difficult for the plant to acquire both water as well as nutrients. Therefore, salt stress essentially results in a water deficit condition in the plant and takes the form of a physiological drought. This is the reason for the overlapping in basic physiology of high salt stress and drought tolerance. Unfortunately variation for many of these traits is limited in gene pool and biotechnological tools to improve the crop have been limited. Sorghum is a C_4 species and is recognized as moderately tolerant to soil salinity (Francois *et al.*, 1984), highly water use efficient (Rai *et al.*, 2004), capable of assimilating water from deeper soil layers and tolerating drought (FAO 2002). The response of plants to these environmental changes is through a number of defense mechanisms to maintain the optimal conditions for the growth and development (Bray et al. 2000). Plants respond to stress by altering the expression of many genes, leading to adaptation and survival (Hasegawa *et al.*, 2000). These mechanisms can include several regulatory processes that activate the differential expression of genes responsible for tolerance. It is shown that the role of group 5 chromosomes seem to be central in the defense against abiotic stresses in the species belonging to the tribe *Triticeae*. Some regions in the group 5 chromosomes of the tribe *Triticeae* play a general role in the adaptations to the changing environment, suggesting that they share atleast particularly the same regulatory processes (Cattivelli et al. 2002). The expression of the genes responsible for abiotic stress tolerance may depend upon not only on stress factor, but also possible that in different developmental stages (germination, seedling, growth and maturity stage) different genes can play a role in avoidance of the damage occurred by the stresses. Adaptation to salinity has been studied since long by several researchers in sorghum. Here is an effort to review very briefly on the adaptation of sorghum to salinity.

Adaptation and induction of adaptation in sorghum

Adaptation with special reference to salinity is the process whereby a population becomes better suited to its habitat. It is one of the basic phenomena of biology, important for organism's survival and takes place over many generations. Adaptation to salinity is defined as the development of the ability of the plant to survive, grow, and set seeds upon exposure to a NaCl concentration which is lethal for the unadapted plant. It is characterized by an increase in salinity tolerance, whereas plants rest on their initial level of tolerance throughout the resistance response. The induction of a capacity to survive and tolerate a high NaCl concentration is also considered as an adaptation to salinity. Induction of adaptation to salinity has been tried with exposure to sublethal concentrations of NaCl (Amzallag et al., 1990a), treatment with exogenous abscisic acid (ABA) along with NaCl concentrations (Amzallag et al., 1990b) and addition of exogenous cytokinin (CK) and gibberellic acid (GA) to the medium (Amzallag et al., 1992). An exposure time of 20 days (pretreatment) to 75 or 150 mol m^{-3} of NaCl enabled *Sorghum bicolor* (L.) Moench (S610) plants become capable of growing in medium containing 300 mol m^{-3} NaCl. Unlike, the control sorghum plants without pretreatment or plants pretreated for less than 20 days died within 2 weeks when exposed to 300 mol m^{-3} NaCl (Amzallag et al., 1990a).

Physiological adaptation in sorghum

The exposure of eight-day-old *Sorghum bicolor* for three weeks to sublethal salinity induces an increase in salinity tolerance, called physiological adaptation. The adaptation of sorghum to high salinity is proposed to be a result of modulation of genome expression occurring during extended exposure to non-lethal NaCl concentrations. The adaptation to salinity is more than osmotic adjustment and that it takes longer to develop than osmotic adjustment. Another study with the treatment of *Sorghum bicolor* (L.) Moench, cv. 610, with abscisic acid (ABA) during the first week of salinization with 150 mol m^{-3} NaCl induced enhancement of growth and accelerated adaptation to high salinity (300 mol m^{-3} NaCl) (Amzallag et al., 1990b). Treatment with exogenous abscisic acid (ABA), 40 µM daily sprayed on leaves, during the pretreatment period shortens the time required for adaptation from 20 to 10 days. The exposure of the plants to non-lethal salinity (150 mol m^{-3} NaCl) apparently triggers a transient sensitivity to ABA lasting for about 8 to 10 days following the beginning of salinization. It is shown that the period of ABA treatment coincides with an increase in leaf PEP carboxylase activity which seems to occur faster if the plants are treated with ABA (Amzallag *et al*., 1990b).

Response of adaptation process in sorghum

Adaptation response is induced by exposing to the sublethal level of salinity over 3 weeks, and is limited to a critical stage in the development of a plant (Seligmann et al., 1993). During the 20 day NaC1-pretreatment, the fourth to the ninth leaves develop, and some of these leaves show a perturbed development, referred to as 'DPL' (developmentally perturbed leaf). DPL formation is positively correlated with the mean relative growth rate (RGR) of the plant following exposure to 300 mol m-3 NaC1, which reflects the degree of adaptation to high salinity. Treatments with exogenous phytohormones affect both DPL formation as well as the adaptation response. The period during which DPLs occur coincides with the period of induction of adaptation to high salinity. Thus, suggesting that DPL may be used as a morphological marker of the adaptation process. The intensity of the adaptation response is also genotype dependent (Amzallag and Lerner, 1994). The serial order of appearance of DPL defines categories in a population.

Adaptive determinism

The frequency of a ‘serial DPL group of plants’ defines a level of ‘canalization’ of the adaptation process towards this category. The results on a positive relationship between the frequency of a pattern and its rate of development and similarly the negative relationship between the frequency of a pattern and the rate of senescence reveals the existence of an orientation of the plant response towards the patterns with highest developmental rate and lowest rate of senescence. The property is defined as ‘adaptive determinism’. Studies indicate that the NaCl acts as a trigger for adaptation to a whole range of environmental perturbations. This suggests that adaptation to salinity is not a pre-programmed response of the plants, and may be related to learning processes occurring in animals (Seligmann and Amzallag, 1995). Seligmann and Amzallag (1995) defined adaptive determinism as a negative correlation between Reaction Type frequency and Reaction Type senescence during adaptation. The interpretation of results on variation in adaptive determinism between different samples already indicates that adaptive determinism is observed when the environmental factors to which the plants react during adaptation involve effects above a minimal threshold.

Reaction Types

Even within a sample of plants exposed to homogenous conditions, plants differ in the serial order of development of leaves with a perturbed development, as well as in the total number of DPLs. This serial order defines DPL patterns, which are different reaction types (RT) to salinity. The determinism index is the correlation coefficient between the frequencies of Reaction Types in a sample and an index of salinity tolerance of these plants (senescence of old leaves). The positive inter-genotype correlation between the increase in morphogenic character variation and Adaptability (Amzallag et al., 1995) is a further, independent indication that the adaptive response of *Sorghum bicolor* to salinity is not entirely pre-programmed. Such evidences suggest emergence of information during adaptation (Seligmann, 1997). The results suggest that information relevant to Adaptive Determinism is transmitted to the progeny of adapted plants, and that adaptive information is created during adaptation in plants first exposed to adaptation inducing treatment. In sorghum, the capacity to react as an open system seems limited to the developmental windows for adaptation (Amzallag *et al*., 1993, 1997).

Lamarckian adaptation, Darwinian adaptation and canalization

Two types of adaptations are revealed at the evolutionary level viz., 'Lamarckian' adaptation and 'Darwinian' adaptation. Environmentally induced Lamarckian adaptation, the passage from glycophytic to halophytic *S. bicolor* lasts only one generation and is a process where the organism adapts actively to its environment, as in learning processes. Further specialization to saline conditions after this first step probably will be slow, result of passive, 'Darwinian' adaptations (Seligmann, 1998). Salt-adapted plants displayed many perturbations in reproductive development (Amzallag, 1996, 1998), suggesting that canalization was disrupted by expression of salt adaptation. The response shown with a developmental reversion of the perturbations in reproductive development after salt treatment influencing progeny grown without NaCl may be observed throughout two successive generations is termed as canalization. Canalization, both in its developmental and adaptive dimensions, is not restricted to the expression of a pre-existing program, but is determined by physical considerations governing open systems. During specific periods of transition phases, the possibility of reharmonization exists on all levels, from genome to entire organism (Amzallag, 2000). The different modes of osmoregulations have been interpreted as 'basins of attraction' emerging during a critical phase of self organization in development (Amzallag, 1999a, 1999c).

Maternal imprinting and endopolyploidy

In absence of natural selection a part of the adaptive modifications is transmitted to the progeny through maternal imprinting. In many cases, this persistence is due to maternal-induced changes in repetitive DNA content of the embryo, which might have long-term effects for the next generations (reviewed by Amzallag, 1999b). Moreover, changes in repetitive DNA similar to those induced by exposure to a modified environment are frequently observed during ecotype differentiation and speciation (Miksche & Hotta, 1973; Amzallag, 1999b). This evidence strengthens the link between maternal imprinting and ecotype differentiation. Endopolyploidy may be considered as a part of the adaptive response of *S. bicolor* competent genotypes to salinity. A large variability in the extent of endopolyploidy in the root cells of salt-treated plants carrying the competent sorghum cv. 610 genotype was observed *de novo* in the external layers of the root cortex by using Feulgen cytophotometry (Ceccarelli et al., 2006). Genotypic differences of this kind may exist within lines of *S. bicolor* and might have a role in affecting the level of chromosome endoreduplication and then in determining the within-genotype variation in the adaptive response to salinity (Amzallag 1999).

Conclusion

Adaptation of sorghum to salinity has been studied for long time with the help of several hypothesis, original case studies with evidences and demonstrations. Many workers have reported several important points beginning with the induction of adaptation response to salinity with exposure to sublethal concentrations of NaCl induces increased salinity tolerance, several responses of adaptation process via modifications during different stages of crop growth period, resulting response of their progenies across generations, developmental reversions of the changes during reproductive development after distressing for two generations ending with strengthening the link maternal imprinting and ecotype differentiation with evidence of variability in endopolyploidy in the root cells. Inspite of these many supporting reports on the adaptation of sorghum to salinity stress, with the availability of sequence of the crop and several links from the long time efforts, an in-depth, mere close understanding and deep insight into the mechanism on the topic is required.

Acknowledgements

The financial assistance from University Grants Commission for the Ph.D research work of Mr.Paramesh H is greatfully acknowledged.

References

[1] Harlan, Jack R., 1971, “Agricultural Origins: Centres and Non-Centres. Science”, CLXXIV, pp. 468-474.

[2] Mann JA., Kimber CT., and Miller FR., 1983, “The Origin and Early Cultivation of Sorghums in Africa” Bulletin 1454, Texas Agriculture Experiment Station, College Station, TX, USA.

[3] Francois LE., Donovan T., and Maas EV., 1984, “Salinity effects on seed yield, growth and germination of grain sorghum” Agron J., 76, pp. 741-744.

[4] Rai K N., Reddy BVS., Saxena K B., and Gowda CLL., 2004, “Prospects of breeding sorghum, pearl millet and pigeon pea for high forage yield and quality”. In: new directions for a diverse planet: Proceedings of the 4th international crop science congress Brisbane, Australia, 26 September 2004 to 1 October 2004.

[5] FAO., 2002, “Crop Water management: Sorghum” AGLW water management group.

[6] Bray E., Bailey-Serres, J., and Weretilnyik E., 2000, “Biochemistry and Molecular Biology of Plants” pp. 1158-1203.

[7] Hasegawa P M., Bressan R A., Zhu J K., and Bohnert H J., 2000, “Plant cellular and molecular responses to high salinity” Annu. Rev. Plant Physiol. Plant Mol. Biol., 51, pp. 463-499.

[8] Cattivelli L., Baldi P., Crosatti C., Di Fonzo N., Faccioli P., Grossi M., Mastrangelo A M., Pecchioni N., Stanca A M., 2002, “Chromosome regions and stress-related sequences involved in resistance to abiotic stress in Triticeae” Plant Mol. Biol., 48, pp. 649–665.

[9] Amzallag G N., Lerner H R., and Poljakoff-Mayber A., 1990a, “Induction of increased salt tolerance in *Sorghum bicolor* by NaCl pretreatment”, Journal of Experimental Botany, 41, pp. 29-34.

[10] Amzallag G N., Lerner H R., and Poljakoff-Mayber A., 1990b, “Exogenous ABA as a modulator of the response of Sorghum to high salinity”, Journal of Experimental Botany, 41, pp. 1529-1534.

[11] Amzallag G N., Lerner H R., and Poljakoff-Mayber A., 1992, “Interaction between mineral nutrients, cytokinin and gibberellic acid during growth of Sorghum at high NaCl salinity”, Journal of Experimental Botany, 43, pp. 81-87.

[12] Seligmann H., Amzallag G N., and Lemer H R., 1993, “Perturbed leaf development in *Sorghum bicolor* exposed to salinity: a marker of transition towards adaptation”, Aust. J. Plant Phys., 20, pp. 243-249.

[13] Amzallag G N., and Lerner H R., 1994, “Adaptation versus preexisting resistance: an inter-genotype analysis of the response of *Sorghum bicolor* to salinity”, Israel Journal of Plant Sciences, 42, pp. 125-141.

[14] Seligmann H., and Amzallag G N., 1995, “Adaptive determinism during salt-adaptation in *Sorghum bicolor*”, BioSystems, 36, pp. 71 -77.

[15] Amzallag G N., Seligmann H., and Lerner H R., 1995, “Induced variability during the process of adaptation in *Sorghum bicolor*”, Journal of Experimental Botany, 45, pp. 1017-1024.

[16] Seligmann H., 1997, “Transmission of acquired adjustments to salinity in *Sorghum bicolor*”, BioSystems, 40, pp. 261–275.

[17] Amzallag G N., Seligmann H., and Lerner HR., 1993, “A developmental window for salt-adaptation in *Sorghum bicolor*”, Journal of Experimental Botany, 44, pp. 645-652.

[18] Amzallag G N., Seligmann H., and Lerner HR., 1997, “Leaf malformation during early development in Sorghum: Evidence for an embryonic developmental window”. Physiologia Plantarum, 99, pp. 470-476.

[19] Seligmann H., 1998, “Effect of environmental complexity on salt-adaptation in *Sorghum bicolor*”, BioSystems, 45, pp. 213–220.

[20] Amzallag G N., 1996, “Influence of parental NaCl treatment on salinity tolerance of offspring in *Sorghum bicolor* (L.) Moench” New Phytologist, 128, pp. 715-723.

[21] Amzallag G N., 1998, “Induced modifications in reproductive traits of salt-treated plants of *Sorghum bicolor*”, Israel Journal of Plant Sciences, 46, pp. 1-8.

[22] Amzallag G N., 2000, “Canalization as a non-genetic source of adaptiveness during morphogenesis: experimental evidence from analysis of reproductive development in *Sorghum bicolor*”, BioSystems, 57, pp. 95–107.

[23] Amzallag G N., 1999a, “Individuation in *Sorghum bicolor*: a self organized process involved in physiological adaptation to salinity”, Plant, Cell and Environment, 22, pp. 1389-1399.

[24] Amzallag G N., 1999b, “Plant evolution: towards an adaptive theory”, In: Lerner HR, ed. Plant response to stress: from phytohormones to genome reorganization. New York, USA: Dekker, pp. 171-245.

[25] Amzallag G N., 1999c, “Adaptive nature of the transition phases in development: the case of *Sorghum bicolor*”, Plant, Cell and Environment, 22, pp. 1035-1041.

[26] Miksche J P., and Hotta Y., 1973, “DNA base composition and repetitious DNA in several conifers” Chromosoma, 41, pp. 29-36.

[27] Ceccarelli, M E., Santantonio, F Marmottini., G. N. Amzallag., and P. G. Cionini., 2006, “Chromosome endoreduplication as a factor of salt adaptation in *Sorghum bicolor*”, Protoplasma, 227, pp. 113–118.

[28] Amzallag G N., 1999, “Individuation in *Sorghum bicolor*: A self organized process involved in physiological adaptation to salinity”, Plant Cell Environ., 22, pp. 1389–1399.