



SALINITY STRESS

1 Responses of Sorghum to Abiotic Stresses: A Review

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Abstract

Sorghum (*Sorghum bicolor* L. Moench) is a highly productive crop plant, which can be used for alternative energy resource, human food, livestock feed or industrial purposes. The biomass of sorghum can be utilized as solid fuel via thermochemical routes or as a carbohydrate substrate via fermentation processes. The plant has a great adaptation potential to drought, high salinity and high temperature, which are important characteristics of genotypes growing in extreme environments. However, the climate change in the 21st century may bring about new challenges in the cultivated areas. In this review, we summarize the most recent literature about the responses of sorghum to the most important abiotic stresses: nutrient deficiency, aluminium stress, drought, high salinity, waterlogging or temperature stress the plants have to cope with during cultivation. The advanced molecular and system biological tools provide new opportunities for breeders to select stress-tolerant and high-yielding cultivars.

Introduction

Sorghum (*Sorghum bicolor* L. Moench) is a multipurpose crop belonging to the Poaceae family, which are C4 carbon cycle plants with high photosynthetic efficiency and productivity. Sorghum is one of the five major cultivated species in the world because it has several economically important potential uses such as food (grain), feed (grain and biomass), fuel (ethanol production), fibre (paper), fermentation (methane production) and fertilizer (utilization of organic by-products) (ICRISAT 2009). Sorghum originates from Africa, from the southern region of the Sahara Desert, where several closely related wild species are found (Legwaila et al. 2003). The cultivated genotypes and hybrids are very diverse. In the European Union and in the USA, sweet sorghum has been bred as a promising energy crop (Berenji and Dahlberg 2004), and it is also suggested as a candidate for biofuel production in hot and dry (arid) countries, such as Nigeria, India, Australia or Mexico (Almodares and Hadi 2009). It is an important cereal in Africa, the Middle East, Asia and Central America and is a principal source of food for millions of people. The purpose of breeders in China is to develop genotypes of both high grain yield and high sugar content in the stem juice.

Germplasm resources of sorghum show that a competition exists between grain yield and stem biomass production, and the task of the breeders is to find the optimum conditions for the different productivities in the plants. Breeding strategies for adaptation of sorghum to climatic variability have been excellently reviewed by Hausmann et al. (2012).

Morphological and Physiological Characteristics of Sorghum

The plant is native in tropical areas and is also well adapted to temperate climate. It is highly resistant to drought (Steduto et al. 1997), salinity (Almodares et al. 2008a,b) as well as water logging (Promkhambut et al. 2010), and it can be grown and can maintain remarkable yield potential in environments that are normally too extreme for other C4 plants. Some of its morphological features are advantageous for the acclimation to specific abiotic stresses.

The height of the plants ranges from 1.5 to 3.0 m, depending on the number and length of the internodes as well as on the length of the peduncle and the panicle. Tillers may develop from the lower nodes, while lateral branching may occur higher up on the stem. In adult plants, lateral branches usually develop when a significant amount of

1 moisture is available in the soil and more extensive tiller
2 production can be observed during and after the anthesis
3 of the main shoot (Isbell and Morgan 1982).

4 Primary roots have a limited growth, and their function
5 is taken over by the secondary root system, developing
6 from the root crowns. The roots of an adult sorghum plant
7 are all secondary adventitious roots with numerous lateral
8 roots penetrating the soil in all directions. The difference in
9 total water use due to changes in root morphology and bio-
10 mass was responsible for an increased yield of newly
11 released hybrids under rain-fed conditions (Assefa and
12 Staggenborg 2011); likewise, the structure of the root sys-
13 tem plays an important role in the drought stress tolerance
14 of the respective cultivars (Salih et al. 1999).

15 Sweet sorghum is a short-day plant, but large genotypic
16 differences exist in the photoperiodic requirement for the
17 transition from the vegetative to the generative phase.
18 There are varieties in Australia, which are insensitive to
19 photoperiods but late sorghum varieties are known to be
20 highly photoperiod sensitive. The choice of cultivar and
21 sowing date should be combined in order that the plants
22 flower during the last 20 days of rainy seasons ensuring an
23 unperturbed grain-filling process. Experiments were con-
24 ducted in three representative sites along a latitudinal gra-
25 dient in Mali with seven sorghum cultivars (Abdulai et al.
26 2012). Although the largest difference in day length was
27 8 min between the experimental areas, even these relatively
28 small differences caused variations in the duration of
29 vegetative phase of up to 3 weeks.

30 The appearance of the panicle determines the distribu-
31 tion of assimilates because it is a better sink than the leaf,
32 leaf sheath and stalk. Before stem elongation, the photosyn-
33 thates accumulate mainly in the leaves, but after elonga-
34 tion, the sugars begin to accumulate in the stalk and
35 inflorescence. The dry matter distribution and sugar con-
36 tent vary along the stalk. The central part of the stalk con-
37 tains the most of soluble sugars, especially that of sucrose
38 (Coleman 1970, Eastin 1972). More glucose can be detected
39 in the lower part of the stem, while the upper part contains
40 more sucrose and starch (Ventre et al. 1939).

41 **Effects of Appropriate Nutrient Supply and** 42 **Nutrient Deficiency**

43 The early and late application of fertilizers can promote
44 growth and biomass production of sweet sorghum, and the
45 plants respond with higher yield to both organic and inor-
46 ganic fertilizers (Amuyojegbe et al. 2007). However, the
47 effect of nitrogen fertilizers proved to be contradictory.
48 Increasing N supply in the form of composted bio-solids
49 was expected to contribute to plant growth and nutrition;
50 thus, a mixed compost was prepared using (15)N-labelled
51 materials. It was found that the compost enhanced the fibre
52
53

sorghum biomass at midgrowth. N concentration in plant
tissues followed a common dilution curve, indicating that
fertilized sorghum efficiently utilized the supplied N, avoid-
ing luxury consumption (Barbanti et al. 2011). However,
nitrogen fertilization increased the stem dry matter without
enhancing the sugar content of the tissues (Ferraris 1981).
It was an interesting finding that the expression of the stay-
green phenotype in sorghum exhibited higher use and
uptake of nitrogen (Addy et al. 2010).

The form of inorganic N also determines the dry matter
accumulation of the plants. The tolerance of ammonium
nutrition depends on the ammonium detoxification capac-
ity of the root tissues via the cytosolic form of glutamine
synthetase, GS1 (GS, EC 6.3.1.2). It was shown that sor-
ghum-sudan grass (*S. bicolor* L. × *S. bicolor* var. sudan-
ense) hybrids exhibited enhanced biomass production and
increased capacity for N assimilation at increasing NO₃⁻
and NH₄⁺ supplies. In sorghum, the two distinct cytoplas-
mic forms of GS were found to be the expression products
of the *SbGln1.2* and *SbGln1.3* genes. The expression of the
SbGln1.3 gene was up-regulated by high levels of inorganic
N, with a maximal abundance of transcripts after NH₄⁺
treatment (El Omari et al. 2010).

The different N forms supplied in the root medium
affected the uptake of K⁺ from low-K⁺ solutions. NH₄⁺ in
full nutrient solution increased the depletion of K⁺ from
the incubation medium, which correlated with an
enhanced activity of the plasma membrane H⁺-ATPase in
sorghum roots, while NO₃⁻ was not very effective (Alvarez-
Pizarro et al. 2011).

The interaction between K and Zn supply was studied on
growth, yield and quality of forage sorghum grown in
loamy sand soil (Moinuddin 2010). Increasing K levels sig-
nificantly improved the yield and quality attributes, and
the beneficial effects of Zn application increased progres-
sively with increased K supply.

The uptake of the other macroelement, phosphorus, by
sorghum depended on the concentration of the P forms
available to plants in the soil (Khorasgani et al. 2009).
Phosphorus supply affects photosynthetic performance,
starch synthesis and transport of sugars across the chloro-
plast membrane and hence also plant growth and yield. P
deficiency seriously reduced the biomass production of
grain sorghum plants, decreased the performance of PSII,
the photosynthetic rate under light saturation, the effi-
ciency of carboxylation, ATP production and the rate of
ribulose-1,5-biphosphate regeneration (Ripley et al. 2004).

Photosynthetic activity of plants is determined not only
by the availability of macroelements but also by that of
microelements. Critical Mn levels are needed for water
splitting in C3 and C4 plants and malate decarboxylation
for CO₂ release in C4 plants. NADP-malic enzyme (NADP-
ME) C4 plants, such as sorghum, reached maximum

1 biomass production and photosynthetic rate at 2–5 μM Mn
 2 in the nutrient solution (Kering et al. 2009). Increasing Cu
 3 supply for sweet sorghum in combination with ethylen-
 4 ediaminetetraacetic acid (EDTA) in hydroponic culture led
 5 to increased biomass production (Székely et al. 2011) and
 6 increased the elongation growth of plants.

7 Plants cannot easily acquire iron from the soil, so iron
 8 deficiency is one of the major limiting factors affecting crop
 9 yield. Gramineous species can enhance iron uptake from
 10 inorganic Fe(III) derivatives by releasing phytosiderophores
 11 (PS), the Fe-chelating compounds. The PS release by roots
 12 and the uptake of Fe(III)PS by root cells increase by a factor
 13 of about five under Fe deficiency. Sorghum is susceptible to
 14 Fe deficiency, and therefore an increase in its resistance to Fe
 15 deficiency (to 'lime chlorosis') can be achieved by breeding
 16 the cultivars with high rates of PS release (Römheld and
 17 Marschner 1990). Several simple and effective soil manage-
 18 ment practices, such as root feeding and bag fertilization,
 19 were developed to improve the Fe nutrition of plants (Zuo
 20 6 and Zhang 2011). Singh et al. (2011) investigated the trans-
 21 location of radiolabelled iron (^{59}Fe) supplied through the
 22 root system to non-chlorotic and chlorotic sorghum. They
 23 also treated the leaves with foliar spray of FeSO_4 solution
 24 combined with various chelating compounds and found
 25 that under iron deficiency the differential uptake of labelled
 26 Fe was markedly increased in the leaves and stems of chloro-
 27 tic plants as compared to non-chlorotic ones, and the
 28 foliar spray with FeSO_4 + thiourea increased the (^{59}Fe)
 29 uptake through the roots. In contrast to the Fe-efficient barley,
 30 where iron was allocated preferentially to the thylakoid
 31 membranes during Fe deficiency, in the Fe-deficient sorghum,
 32 the photosynthetic apparatus was seriously damaged,
 33 and the proportion of leaf Fe allocated to the thylakoids was
 34 not altered (Mikami et al. 2011).

35 Aluminium Stress

36 The rhizotoxicity of Al^{3+} is the major limitation to plant
 37 production in acidic soils, a problem which is exacerbated
 38 by the use of ammonium fertilizers and acid rain (von
 39 Uexkull and Murtert 1995). Higher concentrations of Al^{3+}
 40 were found in the soil solution at pH 3.7 than at pH 5.8 or
 41 6.3 (Miller et al. 2009).

42 The resistance mechanism of plants to Al^{3+} toxicity can
 43 be classified into two main groups: (i) the external toler-
 44 ance, the chelation of the metal ion by organic acids in the
 45 rhizosphere, or (ii) the chelation of Al^{3+} inside the cells
 46 7 (Inostrosa-Blancheteau et al. 2008). The main mechanism
 47 for the alleviation of Al^{3+} toxicity relies on the release of
 48 organic anions from the root cells to the apoplast, which
 49 may bind and detoxify the harmful Al^{3+} cations extracellu-
 50 larly. *Sorghum bicolor* belongs to the first group and uses
 51 the exclusion mechanism through organic acid exudation
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(Magalhaes et al. 2004, Caniato et al. 2007). In two sorghum cultivars, Magalhaes et al. (2004) found a major locus (Alt_{sb}) for Al^{3+} tolerance, which might be associated with citrate exudation from root apices. Most recently, a gene encoding a member of the multidrug and toxic compound extrusion (MATE) family, an aluminium-activated citrate transporter has been identified in sorghum plants (Magalhaes et al. 2007). Genes controlling Al^{3+} resistance have already been cloned from various crop plants including sorghum (Ryan and Delhaize 2010).

Drought Stress

The scarcity of water may exert an adverse effect upon seed germination and embryo growth rate in the field, but several sorghum cultivars adapted well to semi-arid areas (Patanè et al. 2012). Although water-use efficiency and 8 other physiological characteristics of sweet sorghum indicate that this species can successfully adapt to drought, the research so far has mainly focused on biomass yield and sugar content under unfavourable conditions.

Sorghum developed two important strategies for adaptation to water deficit. The primary way is the tolerance of water potential decrease, while the second mechanism is the escape from water stress due to deep and extensive root formation.

Drought resistance of sorghum has been attributed to morphological and physiological factors such as the dense roots system (Mayaki et al. 1976, Jordan and Miller 1980), the ability to maintain stomatal opening and photosynthesis at low water potentials, and the ability for osmotic adjustment (Ludlow et al. 1990). Sometimes, late-flowering cultivars can tolerate water deficit more effectively (Hsiao et al. 1976).

It was reported that the high drought tolerance of sweet sorghum cv. Gadambalia was associated with high water extraction efficiency from the soil, fewer nodal roots per plants and fewer metaxylem vessels in nodal roots. The plants had a smaller leaf area and well-developed sclerenchyma in their leaf tissues (Salih et al. 1999).

Drought-tolerant genotypes can be characterized by high epicuticular wax deposition on the leaf surface, which increases leaf reflectance in the visible and near-infrared radiation and contributes to decreased transpiration (Surenwishi et al. 2010). Another important function of the leaf epicuticular wax is to reduce the cuticular conductance to water vapour and thus to increase water-use efficiency (WUE).

As a positive correlation was found between leaf photosynthesis, total biomass and grain production, the effects of drought stress on photosynthetic activity, stomatal conductance and transpiration have been investigated by several authors (Younis et al. 2000).

Drought stress decreased the transpiration rate and stomatal conductance (Premachandra et al. 1994, Massacci et al. 1996), and these parameters varied among cultivars. Tsuji et al. (2003) characterized the physiological responses of an isohydric cultivar, which was able to maintain the water potential (cv. Gadambalia), and a desiccation-tolerant one, which reduced the water potential under drought stress (cv. Tabat). Drought tolerance of Gadambalia was associated with high leaf water potential and relative water content, while the reduction in net photosynthetic rate, stomatal conductance and transpiration rate was low in Gadambalia and high in cv. Tabat.

The effect of moderate and serious drought stress on the diurnal changes of photosynthetic parameters as well as on their variation in various developmental phases has been investigated in the sweet sorghum hybrid BJ0601. Photosynthesis declined in most plants around mid-day, which was a combined consequence of high irradiation and water deficit. This hybrid displayed a significantly lower water potential, the net photosynthetic rate (Pn) exhibited a depression under serious water stress and it was closely correlated with stomatal conductance. With increasing drought stress, the light compensation point increased, whereas the light saturation point, the apparent quantum yield and dark respiration declined. The stem fresh biomass was the highest under moderate drought stress (Xie et al. 2010).

Net CO₂ assimilation rate (NAR), leaf area index (LAI), which is a measure of the total one-sided area of photosynthetic leaf surface per unit ground surface area, and relative growth rate (RGR) are good indicators of the effectiveness of solar radiation capture (Patterson 1982). Comparing five sweet sorghum cultivars and four lines, it was found that except at post-grain maturity stage, the correlations of LAI, NAR and RGR with sucrose and total sugar contents were positive, whereas with glucose, fructose, maltose and xylose contents, they were negative (Almodares et al. 2007a). This means that as plants grow, LAI, NAR and RGR increase in parallel with sucrose accumulation and with the reduction in invert sugars. Allen et al. (2011) found that canopy net photosynthesis of grain sorghum was only 9 % lower at ambient (360 μmol mol⁻¹) and 7 % lower at elevated (720 μmol mol⁻¹) CO₂ concentration under water-limited conditions than in well-watered plants. This suggests that effect of drought stress in C4 crop plants can be slightly ameliorated at elevated CO₂ levels.

The sensitivity of sweet sorghum to water shortage depended on the developmental stage. The plants were very sensitive to drought in the vegetative and early reproductive stages. In the late reproductive phase, their water requirement was lower, but the yield decreased due to terminal drought (Younis et al. 2000, Xie et al. 2010). In contrast, Oliveira Neto et al. (2009) found that the plants were

the most sensitive to drought in the maturation stage, which was probably due to their higher transpiration rates. They found accumulation of soluble carbohydrates, sucrose, glucose and fructose in the leaf tissues during the vegetative and reproductive stages under water stress. However, at maturation, significant decreases were observed. This suggests that the plants were able to adapt osmotically due to the accelerated degradation of starch and formation of soluble sugars during the vegetative and early reproductive stages. Both unstressed and drought-stressed plants accumulated sucrose and starch after the anthesis in the stem. In the course of panicle maturation, sucrose and starch contents were higher in drought-stressed than in unstressed stems (Massacci et al. 1996).

It was also found that a silicon (Si) fertilizer improved the growth of sorghum under water stress, increased the root water uptake and decreased the osmotic potential in the root cells indicating an osmotic adjustment. Under drought stress, silica is deposited in the endodermis of the root to avoid tissue collapse. An analysis of root solutes showed that soluble sugars and amino acids (alanine and glutamic acid) were accumulated as compatible osmolytes in root tissues after Si application (Sonobe et al. 2010). Moreover, under water stress, silicon-treated seedlings exhibited higher stomatal conductance and photosynthetic rate than untreated ones (Sonobe et al. 2009).

Proline also acts as a compatible osmolyte and accumulates during abiotic stresses. Δ1-Pyrroline-5-carboxylate synthetase (P5CS, EC 2.7.2.11) is a key regulatory enzyme of proline biosynthesis. Two closely related *P5CS* genes, *SbP5CS1* and *SbP5CS2*, were isolated from sweet sorghum, which were located on chromosomes 3 and 9. Promoter analysis of the two *P5CS* genes uncovered several stress-responsive *cis*-acting elements. The expression analysis revealed that the genes were up-regulated when the plants were exposed to drought stress and that proline concentration was in correlation with the expression of *SbP5CS* genes (Su et al. 2011).

Molecular variation within the defined genes underlying specific biochemical and physiological functions provides candidate gene-based markers, which show very close association with the trait of interest. Srinivas et al. (2009) presented a microsatellite linkage map containing 128 microsatellite loci from subtracted drought stress ESTs in *S. bicolor* (L.) Moench. The developed EST markers include genes coding for important regulatory proteins and enzymes that are related to drought stress.

The transcriptome of sorghum shoot and root tissues exposed to polyethylene glycol (PEG)-induced osmotic stress or to exogenous abscisic acid (ABA) was studied using next-generation sequencing (NGS) technology to reveal the specific genes and gene networks that contribute to the drought tolerance of this crop (Dugas et al. 2011).

The authors found more than 28 000 unique genes that showed transcriptional activities during osmotic stress or ABA treatment. Expression analysis revealed 5156 unique genes expressed differentially (DE genes) in treated and control samples. The genes coding for the late embryogenesis abundant (LEA) proteins, WSI18, a water stress-induced protein and dehydrins were found in the top five genes up-regulated in response to both PEG and ABA. In contrast, a gene coding for peroxidase 6 and a gene similar to OSIG-Ba010B08.10 coding for a sugar substrate transporter domain-containing protein were down-regulated. Genes enriched in gene ontology (GO) categories, such as response to drought, osmotic stress, cold and heat stress, were up-regulated in the roots and shoots after ABA and PEG treatments, and only a small number of genes were down-regulated in these categories. The pathway enrichment analysis revealed that both choline and the proline biosynthesis pathways contained DE genes in both shoots and roots, but the authors did not observe enrichment for the glycine betaine biosynthesis pathway after ABA and osmotic stress treatments. ABA and osmotic stress affected the biosynthetic pathways of other hormones, such as ethylene, gibberellins, jasmonic acid and brassinosteroids; some of them also showing enrichment while cytokinin and indoleacetic acid conjugation pathways, which render these hormones biologically inactive, also contained DE genes. In PEG-treated roots, the up-regulated genes were enriched in the GO categories such as nodulation and epidermal cell differentiation, while the genes coding for an auxin efflux carrier and a phosphate transporter as well as the genes involved in lateral root development were down-regulated. Promoter analysis of the DE genes up-regulated in the shoots due to ABA treatment revealed ABA-responsive (ABRE) and dehydration-responsive (DRE) *cis*-acting elements, and the members of the AP2-ERE BP transcription factor family, which can bind these *cis*-acting elements, were also over-represented within the DE genes.

Waterlogging

In tropical and sub-tropical regions, the crops may suffer intermittent or long-term waterlogging due to heavy rains, storms, excess irrigation or flooding. In these areas, waterlogging has a particularly deleterious effect on the crop, because it does not only influence plant metabolism but also induces unfavourable changes in the soil texture. The harmful effects of flooding depend on the age of the seedlings (Orchard and Jessop 1984). The plants were most sensitive to flooding and responded with the highest reduction in growth and dry mass at the early vegetative and early reproductive stages (Promkhambut et al. 2011a). Flooding later than 30 days after emergence did not significantly affect shoot growth. However, there were genetic variations

in the response of the root system to waterlogging, and several genotypes responded with aerenchyma formation from the roots to the stalk base in flooded soils (Promkhambut et al. 2011b). Development of new nodal roots appeared to be also an adaptive response of sorghum to waterlogging (Pardales et al. 1991). The responses of three sweet sorghums and a forage cultivar were compared after twenty days of waterlogging (Promkhambut et al. 2010). This long-term flooding caused significant reduction in biomass production, increased the allocation of biomass to the roots and reduced the leaf area, and in the sweet cultivars, it significantly reduced photosynthetic rate, stomatal conductance and transpiration. The ability to extend the youngest leaves, to produce new leaves, to increase the root length and nodal root development indicated the high tolerance of a sweet cultivar, Wray, to waterlogging. The biochemical mechanisms underlying the adaptation of plants to O₂ deficiency are based on the ability of a genotype to maintain active fermentative metabolism under anaerobiosis. The roots of a flood-tolerant sorghum cv. SSG-59-3 exhibited a constant increase in alcohol dehydrogenase (EC 1.1.1.1) and lactate dehydrogenase (EC 1.1.1.27) activities and higher ethanol concentration than the sensitive variety S-308, suggesting that the flood-tolerant variety tends to attain greater capacity for various fermentative pathways as alternative means to sustain production of ATP under flooded conditions (Jain et al. 2010).

Salt Stress

Although sorghum is a moderately salt-tolerant crop, genotypic differences exist among cultivars. High salinity is a consequence of the excess accumulation of various ions, first of all sodium, calcium, magnesium, chloride and sulphate in the soil, and among them, sodium chloride is the most harmful for plant growth and development. There are several classical methods for screening salt tolerance of plants because the majority of the physiological processes, for example, germination, K⁺ uptake, photosynthesis, biomass production and biochemical parameters, such as electrolyte leakage or chlorophyll content, are all highly sensitive to salt stress. The resistance of plants to salinity is based on three strategies: (i) exclusion of Na⁺ from the cytoplasm due to low uptake, or pumping out of the ion from the cell by active mechanisms, (ii) sequestration of Na⁺ into the vacuole and (iii) preferential accumulation in the leaf tissues. However, the genotypes with high leaf Na contents proved to be generally salt sensitive and only those can tolerate high tissue concentrations, which can sequester Na⁺ into the vacuoles of leaf cells. The essential processes leading to plant adaptation to high salinity include ionic, metabolic and osmotic adjustments. The salt-resistant genotypes can successfully cope with osmotic and ionic

stresses caused by the excess of NaCl; they can effectively reduce the oxidative damage and are able to detoxify the harmful metabolites (Zhu 2001).

The two-phase model of growth reduction caused by salt stress divides the response of plants into two distinct periods (Munns 1993). The retardation of growth in the first phase was shown to be due to osmotic stress and in the second phase to ion-related effects caused by high NaCl concentrations. It was observed by several authors that long-term salt stress led to chlorosis and impaired photosynthesis in older leaves (Munns 1993, 2002). In sorghum plants, a notable salt-stress phenotype was observed after 4 days of growth in 200 mM NaCl (Swami et al. 2011).

Salt stress decreased the percentage (Almodares et al. 2007b) and increased the duration of germination (Gill et al. 2003) in sweet sorghum. Significant differences can be detected in the sensitivity of germination to high salinity among cultivars (Samadani et al. 1994).

The accumulation of toxic ions (Na^+ and Cl^-) causes disturbances in ion uptake and K^+ status of tissues; thus, it is the high K^+/Na^+ discrimination and the maintenance of low Na^+/K^+ ratio in tissues, which characterize the salt-tolerant genotypes (Amtmann and Sanders 1999, Hasegawa et al. 2000). The Na^+ content of tissues in sorghum increased with increasing external sodium concentrations (Lacerda et al. 2003), and there were significant differences in root and shoot Na^+ contents among genotypes (Bavei et al. 2011a). Lower accumulation of sodium in the shoot results from either lower Na^+ uptake by the root or from the differences in the rate of Na^+ transfer to the shoot. It was found that the salt-tolerant sorghum variety, Jambo, accumulated less Na^+ in the root and shoot tissues than the salt-sensitive genotypes and maintained lower Na^+/K^+ ratios both in the root and shoot (Bavei et al. 2011a). Preferential deposition of Na^+ ions in the shoot occurred in the leaf base (Lacerda et al. 2003), and increasing levels of Ca^{2+} in the culture solution enhanced growth and lowered sodium uptake of sorghum plants (Asghar et al. 2009). It was also observed that the salt-tolerant genotype Jambo accumulated more Ca^{2+} both in the leaf and root tissues than the sensitive varieties, Kimia and Payam (Bavei et al. 2011b).

The control of the excess accumulation of reactive oxygen species (ROS) generated as a secondary stress under high salinity is also an essential component of salt tolerance. Many studies attributed the salt tolerance to an increase in the activity of antioxidant enzymes. However, salt tolerance did not consistently depend on higher antioxidant activities, and a fine tuning of both enzymatic and non-enzymatic ROS-scavenging components can contribute to successful acclimation. Application of silicon to soil alleviated salinity stress in two sorghum cultivars and caused an increase in the activities of ascorbate peroxidase

(APX, EC 1.11.1.11), catalase (CAT, 1.11.1.6), superoxide dismutase (SOD, EC 1.15.1.1), peroxidase (POX, EC 1.11.1.7), glutathione reductase (GR, EC 1.6.4.2) and total antioxidant and phenol contents of tissues, suggesting that the alleviation of salinity stress was associated with enhanced antioxidant activity. Moreover, the plants accumulated compatible osmolytes, soluble sugars and proline and exhibited higher osmotic adaptation after the application of silicon (Kafi et al. 2011). Increasing salinity levels decreased the stem yield and soluble carbohydrate levels in two sweet sorghums (cvs Keller and Sofra) and in one grain sorghum cultivar (Kimia), but at the higher salinity level the cv. Keller had the highest stem yield and sucrose content (Almodares et al. 2008b).

Although the analyses of transcriptomes in response to abiotic stresses have already been published by several authors (see in Dugas et al. 2011), studies on cellular proteome in sorghum are limited. Swami et al. (2011) investigated overall changes in the protein complement of sorghum leaves after 96-h exposure to 200 mM NaCl. They found 21 spots with altered expressions on 2-DE gels, and after tryptic digestion of the excised spots, they identified them by MALDI-TOF/TOF mass spectrometer. One protein, the ATP synthase α -subunit, showed enhanced abundance, which points to an impact of salt stress on the photosynthetic machinery. Eight of the up-regulated proteins were involved in scavenging of ROS (POX and APX) or in the detoxification of reactive electrophilic compounds (glutathione S-transferase, EC 2.5.1.18). Other proteins, such as lectin-like protein kinase, salt-inducible protein kinase, serine/threonine protein kinase, may be putative components of the Na^+ -induced signal transduction. GS was also an overexpressed protein in sorghum under salt stress, which corresponds to the findings of Pang et al. (2010) in salt-stressed *Thellungiella*. This suggests that re-assimilation of ammonia is a crucial process under high salinity in sorghum.

Low and High Temperature Stresses

The planting date determines the total sugar content and biomass production of sweet sorghum: the later is the planting, the lower are the yields of the stalk in arid environments (Almodares and Mostafi Darany 2006). The shortage in soil water and the heat stress sensitivity of cultivars are the primary factors for deciding the date of planting in hot and dry climate zones (Teetor et al. 2011). In these areas such as Arizona (USA), the growing season is over 6 months long and sunlight is not limited. It was found by several researchers that the amounts of non-structural carbohydrates increased from pre-boot stage to anthesis (McBee and Miller 1982) and sucrose accumulation reached the highest value at the 'soft dough' stage (Lingle

1987). During a delayed harvest period, the main carbohydrate components in the stems in decreasing order were sugar > cellulose > hemicellulose > starch in Chinese sweet sorghum cultivars (Zhao et al. 2012).

In temperate zones, the optimal growth can be constrained by chilling stress in early spring and it determines the planting date in these areas.

Sweet sorghum is a cold-sensitive crop, and the seed germination, seedling emergence and the growth of plants are all sensitive to low temperatures (Alegre De La Soujeole and Miller 1984). The seeds cannot germinate below a soil temperature of 10 °C (Anda and Pintér 1994). Generally, stand establishment and early-season vigour are adversely affected by air and soil temperatures below 15 °C (Yu and Tuinstra 2001). It was found that chilling stress caused a significant decline in photosynthetic capacity (Taylor and Rowley 1971) and photosynthetic rate was more severely affected than respiratory rate (Ercoli et al. 2004). After a prolonged exposure to low temperature (8 °C), the plants were able to adapt by restoring photosynthesis, but at lower temperatures the growth ceased. After screening for the chilling tolerance of sweet sorghum genotypes, it was found that chilling temperatures drastically inhibited the photochemical quenching of chlorophyll *a* fluorescence. This effect characterized the chilling-susceptible genotypes, and it was not observed in chilling-tolerant plants (Havaux 1989).

Chinese landraces 'kaoliangs' were found to show higher seedling emergence and improved seedling vigour under cool conditions (Franks et al. 2006), but unfortunately these landraces also harbour poor and undesirable agronomic traits. To produce elite sorghum lines with stable and good early-season cold tolerance, Burow et al. (2011) identified simple sequence repeat (SSR) molecular markers associated with various traits for early-season cold tolerance. The mapping population consisting of 171 F₇-F₈ recombinant inbred lines (RILs) derived from the cross between RTX430 (cold-sensitive) and PI610727 (cold-tolerant) lines. PI610727 is also known as Gaigao Liang, a landrace from a Chinese germplasm selected for early-season cold tolerance. The RILs were evaluated for cold and optimal temperature germinability in the laboratory, field emergence and seedling vigour in two locations during early-season planting. Two or more quantitative trait loci (QTLs) were detected for all traits, except for seedling vigour; here, only one QTL was found. Using a new source of cold tolerance, PI610727, the authors tagged the genome regions of sorghum that have significant contributions to traits for early-season cold tolerance.

High temperature stress may also result in the reduction in biomass and sugar yield. Photosynthetic activity, the light reactions and the activity of Calvin cycle enzymes are highly sensitive to heat stress (Yan et al. 2011, 2012). It has

recently been found that the photosynthetic activity does not depend only on the day temperature but also on the temperature detected in the night period (Prasad Vara and Djanaguiraman 2011a). The authors compared the effect of an optimal day/night temperature combination (32/22 °C, respectively) with an optimal day temperature (32 °C)/high night temperature (HNT) (28 °C) combination and found that HNT adversely affected the photosynthetic activity of plants. Exposure to HNT increased thylakoid membrane damage and non-photochemical quenching but decreased the chlorophyll content of the tissues, the photochemical quenching parameter, the electron transport rate and the photosynthetic activity of the leaves. The other interesting finding was that HNT increased ROS production in leaves and pollen grains. The latter led to decreased pollen germination and lower seed set. It is in agreement with the results of Prasad et al. (2011b) who found that grain sorghum pollen had shorter lifespan and exhibited much lower germination percentage on artificial growth medium at high temperatures.

High temperature stress (40/30 °C day/night temperatures) in grain sorghum decreased the chlorophyll content, photosynthetic rate and antioxidant enzyme activities but increased oxidant production and membrane damage as compared to the control plants growing at optimal temperatures (32/22 °C). This oxidative stress can be mitigated by sodium selenate sprayed onto the plant leaves, indicating that selenium can play a protective role during high temperature stress by enhancing the antioxidant defence system (Djanaguiraman et al. 2010).

Heat shock proteins (HSPs) are synthesized in response to high temperature or other abiotic stresses, and as molecular chaperones, they can protect proteins from the harmful effects of the stressors. The expression of *hsp90* was compared in various types of sorghum (in grain and forage sorghum hybrids and in a sweet sorghum cultivar) after various durations of heat stress (Pavli et al. 2011). The accumulation of *hsp90* transcripts was determined by means of RT-qPCR analysis, and it was found that the levels of gene expression were significantly different in the investigated genotypes.

The complete genome sequence for sorghum has been recently released (Paterson et al. 2009). This, in parallel with the analysis of abiotic stress-induced transcriptomes, proteomes and metabolomes, provides an excellent tool for breeders to improve stress tolerance of this important energy crop.

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