Review article

SORGHUM IN CONDITIONS OF ABIOTIC STRESS. STRESS CAUSED BY EXTREME TEMPERATURES AND SOIL REACTION

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SUMMARY

Sorghum is considered as tolerant species toward different environmental conditions. Genetic potential for sorghum yield is being exploited depending on the intensity of production and effect of biotic and abiotic environmental factors. Beside drought, which is the most important abiotic stress factor, extreme temperatures and soil factors can affect sorghum production and yield. This paper gives a summary of previous studies related to the effects of extreme temperatures and unfavorable soil pH on sorghum plants, as well as the plants reaction to such effects. The summary includes studies related to variability analysis of sorghum germplasm and patterns of inheriting tolerance towards stress caused by extremely low or high temperatures and production on acid or alkaline soils.

KEYWORDS: acid soils, alkaline soils, extreme temperatures, sorghum

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INTRODUCTION

Beside pests and diseases that in the conditions optimal for their development represent serious biotic factor for sorghum yield decrease, large reductions in yield are caused by abiotic factors (Boyer, 1982).

The largest areas under sorghum are located in tropic regions, where plants, besides being exposed to high temperatures, experience lack of humidity (Sikora et al., 2013; 2014). Sensitivity to low temperatures is a main factor limiting sorghum distribution, and its cultivation in northern parts of Europe (Reddy et al., 2011). Disorders in mineral nutrition and other physiological processes are the symptoms occurring in unfavorable soil conditions. Since the soils with unfavorable pH occupy significant areas of arable land in the world, selection of cultivars and hybrids tolerant to acid and alkaline soils could enable the cultivation even on marginal terrains (Dalal et al., 2012).

EXTREME TEMPERATURES

Low temperatures

Being a plant species originating from tropic and subtropics regions of Africa, sorghum is well adjusted to warm environmental conditions. Low temperatures are among abiotic factors that significantly affect sorghum production in moderate climate conditions. In this regard sorghum is the most sensitive among all cereals, at all stages of growth and development (Maiti, 1996).

The initial phase of the vegetation that includes germination, emergence, and intensive initial growth of seedlings (seedling vigor) is the period when the plants are the least tolerant to cold. Negative effect of the stress on yield is usually manifested through winter killing and incomplete growth (Tiryaki & Andrews, 2001; Yu et al., 2004; Franks et al., 2006). During cold

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springs, beside low temperatures that directly endanger the plants, seedling diseases caused by Pythium and Fusarium species often occur (Forbes et al., 1987).

In the case of short exposure to low temperatures, plants may survive, but their growth is decreased due to reduction of cellular functions and weakened photosynthetic activity (Brouwer et al., 1973). Decrease in seedling mass ranges from 69% to 92%, whereas reduction of chlorophyll occurs simultaneously, by 16 to 28% in tolerant and sensitive genotypes, respectively (Maulana, 2011). After short exposure to low temperatures and upon returning to more acceptable temperature conditions, plants continue with normal growth. Until the end of vegetation period, they form optimum number of leaves and achieve normal height (Major et al., 1982). Flowering and ripening are postponed in some cases, and it is more noticeable in early-matured lines. Genotypes with longer vegetation recover longer, resulting in shorter postponement of generative phenophases. Postponement is probably caused by reduction of microsporogenesis, macrosporogenesis and photosynthetic activity. Temperatures below 12 °C cause decreased production of pollen, especially in sensitive genotypes (Wang et al., 2000; Osuna-Ortega et al., 2003).

Coldness in later stages of plant growth leaves significant consequences on yield. If low temperatures occur before flowering, all yield components are reduced, including panicle weight, grain number per panicle, grain weight per panicle and 1000-grain weight (Prasad et al., 2008). Reduced pollen quantity results from delayed flowering and significant reduction of anther dehiscence. On the other hand, decreased fertilization because of reduced pistil responsiveness causes lower grain number per panicle (Downes and Marshall, 1971). Low night temperature during flowering favors the occurrence of fungal diseases, such as Sphacelia sorghi McRae (Stack, 2000).

Although majority of available sorghum germplasm originates from tropics and is sensitive to low temperature, group of local populations developed in moderate climate of China shows more uniform emergence and intensive initial growth even in conditions where other sorghums are killed by winter (Singh, 1985; Cisse & Ejeta 2003). These unique local populations called "kaoliang" represent excellent genetic resource for advancement of tolerance toward low temperatures. However, they are with unfavorable agronomic traits: extremely tall (used as construction material or fuel), sensitive toward diseases and with high content of tannin in the grain (Yu & Tuinstra, 2001; Franks et al., 2006).

Yang et al. (1996) tested diversity of a collection consisting of 34 kaoliangs using RAPD, RFLP and ISSR markers, whereby similarity between lines averaged to 70%, based on each of the three marker types. Yu & Tuinstra (2001) recorded good general combinatory traits for seedling tolerance toward low temperatures in kaoliangs, emphasizing the potential of these lines as a source of tolerance gene during hybrid development. It is possible to implement this trait in parent line through multiple backcrossing with a selection of favorable agronomic traits.

In order to more efficiently introduce genes from kaoliangs that are linked to seedling tolerance toward cold to elite high yielding lines using MAS, Cisneros-Lopez et al. (2012) recorded significant divergence in their collection and identified genetic markers related to QTLs for intensive seedling growth in conditions of stress caused by coldness. Knoll et al. (2008) identified two QTLs responsible for germination in lines derived from crossing tolerant (SQR) and sensitive line (SRN39).

Besides kaoliangs, sources of tolerance toward low temperatures were identified in population from higher altitudes of Africa (Singh, 1985). The germplasm was tolerant to low temperatures from flowering to ripening, being useful for development of cultivars and hybrids for highlands of Mexico, East and South Africa (Peacock, 1982).

Introduction of sorghum hybrids tolerant to low temperatures, especially in early stages of growth, would enable its cultivation in regions that are traditionally considered cold for sorghum, as well as early sowing in existing regions of cultivation. That would prolong the period of biomass accumulation and increase grain yield (Cisse & Ejeta, 2003).

High temperatures

Sorghum plants normally develop and grow in temperature range 15-40 °C, however temperatures below and above can affect germination, emergence, flowering and fertilization. According to House (1985), in conditions of sufficient soil moisture, normal flowering and fertilization occur even while temperatures rise to 43 °C. In many regions, temperature stress occurs simultaneously with drought stress, so breeding for heat tolerance includes drought tolerance. Jordan & Sullivan (1982) analyzed a sorghum collection concerning heat and drought tolerance. Although these two phenomena usually occur together, tolerance to heat and drought were not in significant correlation. Therefore, these are separate and independent traits. Concerning high temperatures, the main problem limiting yields and affecting production stability is uneven germination and emergence, and therefore inadequate plant spacing (Peacock, 1982).

Thomas & Miller (1979) found that seedlings of different lines react differently when exposed to high temperatures, with thermal tolerance for emergence of even 55 °C in some lines. Wilson et al. (1982) modified soil temperature in field and controlled conditions of greenhouse by changing the substrate color, showing the variability among genotypes related to germination at high temperatures.

Genetic variability for heat tolerance after seedling stage was investigated in several studies. Sullivan (1972) developed the leaf disc method, which was used to detect positive correlation between heat tolerance and higher yields (Sullivan & Ross, 1979). With the same method, Jordan & Sullivan (1982) screened about 130 sorghum lines and hybrids; confirming significant variation among genotypes and concluding that breeding for heat tolerance is beneficial.

Knowledge on the genetic control of heat tolerance is the basis for defining adequate breeding program. While testing four parent lines, their hybrid and reciprocal combinations, Khizzah et al. (1993) determined that lines were more tolerant than hybrids; and genotypes with higher drought tolerance in later stages of plant development were more heat tolerant. A possible connection of the two traits was suggested. It was assumed that two loci were responsible for the expression of heat tolerance and that there was complete dominance in both pairs of genes. However, when one gene is dominant, it is epistatic to the other. However, Setimela et al. (2007) pointed out higher significance of additive gene activity compared to dominant.

SOIL REACTION

Reaction of soil solution is expressed through pH value which represents activity of H^+ ions in the solution. Acid soil pH is lower than 7, and alkaline is higher than 7. In neutral soil solution, concentration of H^+ and OH^- ions is identical. Availability of mineral nutrients to plants is connected to soil pH value. For majority of plant species, nutrients are most available with pH value within the range of 6-7. Higher and lower pH values cause disorders in plant nutrition and development (Fageria et al., 1990).

Acid soil

Soil acidity is among the most significant problems in many agricultural regions, it is estimated that 50% of arable land in the world is acid (Kochian et al., 2004).

Low pH is manifested on plants through effects on growth and development, i.e. through decrease of mineral nutrients uptake efficiency. Toxicity of H^+, Al^{3+}, and Mn^{2+} affects growth and development of plants. Decrease of solubility and concentration of cations, root system development inhibition and rinsing nutrients into deeper soil layers leads to disorders in mineral nutrition of plants on acidic soils (Marschner, 1991).

Due to the association of pH with the concentration of Al and Mn ions on acidic soils, the direct effect of H ions on plants can be difficult to estimate. More important is the indirect inhibitory effect of a low pH on availability and absorption of nutrients by the plant root (Blamey et al., 1997). The toxicity of Al is manifested through growth reduction of root system and aboveground plant parts. While symptoms of Al toxicity on stem and leaves are difficult to identify and define, the main root is stunted, and the formation of lateral roots occurs. In conditions of Al intoxication, plants uptake limited quantities of nutrients and water, becoming more susceptible to drought stress (Foy, 1984). Toxic effect of Mn on plants occur with pH lower than 6 (Kamprath & Foy, 1985). Harmful physiological and biochemical effects include destruction of auxins, reduction of number and volume of leaf cells, disruption of enzymatic system and reduction of nitrate reductase activity (Heenan & Campbell, 1981). Although substantial production reduction can occur in Mn toxicity, greater importance is given to the effect of Al on plants (Sumner et al., 1991).

High saturation of soil with Al affects the performances of sorghum hybrids in the field and can reduce yields significantly. Yield reduction depends on the level of soil solution saturation with Al ions, accordingly of soil pH. Butchee et al. (2012) stated that critical pH for sorghum is 5.42, below which yield reduction occur. Baligar et al. (1989) determined that Al concentration of 41 and 64% lead to 24 and 54% yield reduction, respectively. Yield reduction of 35% was recorded when pH lowered from 5.1 to 4.8, while decrease from 4.8 to 4.4 led to 92% reduced yield (Duncan, 1988). Despite significant reduction in grain yield on highly acidic soils, the effect of high Al on plant height, vegetation length and harvest index is not significant (Samac and Tesfaye, 2003).

There are several tolerance mechanisms to high soil Al in plants. Đalović et al. (2010) classified in cereals these mechanisms into external, internal and genetic. External mechanisms act preventively against Al penetration and its assimilation in plants, based on Al immobilization in cell walls, secretion through cell membranes, formation of pH barriers in rhizosphere and excretion of organic acids, phosphates and chelate through root. Internal mechanisms activate in case of increased Al concentration in plant cells. Organic acids have the most important role in detoxification. Those form complexes with Al that accumulates in specific cellular organelles, especially vacuoles. Beside variability, knowledge on genetic control of plant reaction to low pH and high Al is the basis for tolerant genotype selection.

Genetic variability for tolerance to low pH and increased Al was documented in a number of plant species (Ryan et al., 2011), including sorghum. Sorghum seedling growth was studied in controlled conditions (Bastos & Gourley, 1982; Furlani et al., 1983; Boye-Goni & Marcarian, 1985) and in field tests (Duncan et al., 1983; Gourley, 1983; Duncan, 1988). Differences among genotypes in tolerance indicate genetic control of this trait.

Pitta et al. (1979) concluded that inheritance of tolerance to acidic soils was controlled by low number of genes with dominant effect, based on the studies of five parent lines and their hybrids in field conditions. According to Bastos (1982), in F2 and F3 populations developed from crossing sensitive and tolerant genotypes, three or more genes are included in tolerance inheritance. While testing combinatory abilities of six parental lines, Boye-Goni & Marcarian (1985) concluded that general combining abilities are more significant than specific ones, which implies additive inheritance. Borgonovi et al. (1987) found dominant specific combining abilities effect, indicating complex quantitative method of tolerance inheritance. According to Gourley et al. (1990), sorghum tolerance to Al toxicity is dominant over sensitivity and includes additive and non-additive gene activity. Mode of gene action depends on stress intensity and genetic constitution of the tested material. Based on the extensive study of tolerance to Al in Poaceae family, Magalhaes et al. (2004) concluded this sorghum trait was encoded in a semi dominant major locus (AltSB) located on chromosome 3. The locus was identified in SC283 line, which is considered standard for the trait, as well as in SC566 line. Tolerance degree is due to mutations in one or more genes in the locus. Because of this mode of inheritance, the authors suggest intraspecific gene "accumulation" is not the most effective strategy for increasing tolerance to Al toxicity.

Alkaline soil

Basic characteristic of alkaline soils is high saturation of soil solution with soluble salts, which is why such soils are often called "salty". Alkaline level is estimated based on total quantity of exchangeable cations that the soil can retain. Soluble cations characteristic for these soils are Na^+, K^+, Ca^{2+}, Mg^{2+}, and predominant anions occurring with them are Cl^-, SO_4^{2-}, NO_3^- i HCO_3^- (Tanji, 1990). It is estimated that alkaline soils occupy 5-10% of arable worldwide areas (Szabolcs, 1994). Due to inadequate irrigation, areas under alkalization increase (Ghassemi et al., 1995).

Increased soil salt concentration affects plants complexly. The plants are exposed to osmotic stress, ion toxicity, water stress and mineral nutrition disorders (Neumann, 1997; Yeo, 1998; Hasegawa et al., 2000; Munns, 2002). The metabolism disorders occur due to osmotic stress in the first several days of the exposure to high salt. There is direct toxic activity on plant tissue after prolonged exposure; first visible effect is water stress (Pardossi et al., 1998). In case of longer exposure, disruption in water and mineral nutrients supply occurs, leading to plant growth and development inhibition (Hu & Schmidhalter, 1998).

The effect of salt on plant growth and development is the most apparent on leaves. The increased concentration of salts, primarily NaCl, acts inhibitive, associated with reduction of leaf turgor and carbon dioxide assimilation, increased accumulation of toxic ions and disturbance in mineral nutrition (Bernstein et al., 1993).

Plants developed mechanisms to maintain low level of ions such as Cl^- and Na^+ in tissues, such as the ability to reduce salt intake through root cell membranes, and the ability to translate already received salt ions from leaves into the root, from where they are directly secreted (Koyro, 1997). At the cellular level, the salt is stored in vacuoles (Ashraf et al., 2001).

Sorghum is defined as a species moderately tolerant to alkaline soils (Francois et al., 1984), more tolerant than e.g. maize. Therefore, sorghum's place in field production systems is, inter alia, on the soils subjected to alkalization (Igartua et al., 1994). Tolerance to increased salt is mostly expressed in initial growth and development stages. In addition, the effect of salt is more pronounced on the reduction of grain yield than to the reduction of vegetative growth (Francois et al., 1984). Other authors (Wolf et al., 1990; Bernstein et al., 1995; Hu & Schimidhalter, 1998) stated that inhibition of leaf growth in sorghum occurs because of accumulation of toxic ions and the disturbance of mineral nutrition.

Sorghum plants are capable to reduce Na^+ and Cl^- transport from root to aboveground plant parts, or to store them partially to specific places in stem, root and leaves (Lacerda et al., 2001).

Wide genetic variability for tolerance to alkaline soils, i.e. increased concentration of salts in soils was recorded (Azhar & McNeilly, 1987; 1988; Maiti et al., 1994). Significant potential for selection is intraspecific variability for tolerance at the stage of germination and emergence (Padoley, 1984; Taylor et al., 1975). There is also an important interspecific variability in sorghums, where S. *halepense* has more expressed tolerance than S. *bicolor* (Yang et al., 1990).

Tolerance to alkaline soils is inherited quantitatively with moderate to high heritability in wider sense (Ratanadilok et al., 1978). Azhar & McNeilly (1988) determined that additive and dominant gene activity plays an important role in tolerance in young sorghum seedlings. They determined narrow sense heritability for low (0.51%) and high (0.19%) salt soil concentration.

CONCLUSION

Plant production increased in second half of twentieth century due to breeding for yield and resistance to diseases, whereas breeding for tolerance to abiotic stresses received little attention. With the decrease in yield improvements per selection cycle, knowledge on tolerance mechanisms to abiotic stress gained in importance.

Although several sources of tolerance to extreme temperatures were identified, selection depends on methodology of analysis in laboratory that may not be compatible with field. On the other hand, there is a minimal possibility of controlling field conditions.

Concerning tolerance to low soil pH and Al toxicity, positive correlation between the results obtained in laboratory and in the field was recorded in several studies, but in this respect, field trials were limited due to the lack of uniform experimental parcels with targeted land performances.

Studies on sorghum tolerance to abiotic environmental factors indicate the usefulness of the initial germplasm screening in laboratory conditions. Thus the genotypes with tolerance genes to abiotic stress were identified. However, the evaluation of tolerant lines and hybrids can be completed only in multi-year field trials that include various environmental conditions.

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SAŽETAK

SIRAK U USLOVIMA ABIOTIČKOG STRESA. STRES IZAZVAN EKSTREMNIM TEMPERATURAMA I REAKCIJOM ZEMLJIŠTA

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Sirak se smatra za biljnu vrstu tolerantnu prema različitim uslovima spoljne sredine. Genetički potencijal za prinos sirka se eksploatiše u različitoj meri u zavisnosti od intenziteta proizvodnje i delovanja biotičkih i abiotičkih faktora sredine. Pored suše kao najznačajnijeg abiotičkog faktora sredine, na proizvodnju sirka u znatnoj meri utiču ekstremne temperature i faktori zemljišta čijim delovanjem dolazi do redukcije prinosa. U radu je dat pregled dosadašnjih istraživanja koja se odnose na delovanje ekstremnih temperatura i nepovoljne reakcije zemljišta na biljke sirka i njihovu reakciju na ovo delovanje. Pregled obuhvata i istraživanja vezana za analizu varijabilnosti germplazme i načina nasleđivanja toterantnosti sirka prema stresu izazvanom ekstremno niskim odnosno visokim temperaturama i proizvodnjom na kiselim ili alkalnim zemljištima.
KLJUČNE REČI: sirak, kisela zemljišta, alkalna zemljišta, ekstremne temperature