



# Sorghum mitigates climate variability and change on crop yield and quality

Keerthi Chadalavada<sup>1,2</sup> · B. D. Ranjitha Kumari<sup>1</sup> · T. Senthil Kumar<sup>1</sup>

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## Abstract

**Main conclusion** Global food insecurity concerns due to climate change, emphasizes the need to focus on the sensitivity of sorghum to climate change and potential crop improvement strategies available, which is discussed in the current review to promote climate-smart agriculture.

**Abstract** Climate change effects immensely disturb the global agricultural systems by reducing crop production. Changes in extreme weather and climate events such as high-temperature episodes and extreme rainfalls events, droughts, flooding adversely affect the production of staple food crops, posing threat to ecosystem resilience. The resulting crop losses lead to food insecurity and poverty and question the sustainable livelihoods of small farmer communities, particularly in developing countries. In view of this, it is essential to focus and adapt climate-resilient food crops which need lower inputs and produce sustainable yields through various biotic and abiotic stress-tolerant traits. Sorghum, “the camel of cereals”, is one such climate-resilient food crop that is less sensitive to climate change vulnerabilities and also an important staple food in many parts of Asia and Africa. It is a rainfed crop and provides many essential nutrients. Understanding sorghum’s sensitivity to climate change provides scope for improvement of the crop both in terms of quantity and quality and alleviates food and feed security in future climate change scenarios. Thus, the current review focused on understanding the sensitivity of sorghum crop to various stress events due to climate change and throws light on different crop improvement strategies available to pave the way for climate-smart agriculture.

**Keywords** Climate change · Food security · Sorghum · Crop improvement

## Introduction

Climate change is a serious and growing threat to global food security. The major effects of climate change are increased frequency and magnitude of extreme climate events such as extreme rainfall events, increased dry spells, droughts, water shortages, land degradations, and rise in sea levels. All these effects could negatively impact the global agricultural system which in turn leads to food insecurity in all its dimensions—availability, stability, access, and utilization (Peng et al. 2019). Global atmospheric temperature is

predicted to rise by 2–4.5 °C by the end of the twenty-first century with increased concentrations of greenhouse gases (Raza et al. 2019). This global warming leads to increased interannual rainfall variability, reduced precipitation during monsoon season, and an increase in unseasonal rainfall activity which poses a severe threat to agriculture’s ability to deal with the world’s hunger, poverty, and malnutrition. According to IPCC report (Roy et al. 2018), global warming could drive 122 million more people into extreme poverty by 2030. The world population is expected to reach 9.7 billion by 2050 (UN 2019), which furthermore increases pressure on the agriculture sector for growing food requirements. Climate change negatively influences crop yields globally, moreover, extreme temperatures and variable rainfall prevent the growth of crops completely. Especially in tropical regions, extreme weather and droughts are two major hazards for rainfed agriculture (Dilley et al. 2005). In the long term, these extreme events adversely affect the

✉ Keerthi Chadalavada  
keerthichadalawada@gmail.com

<sup>1</sup> Department of Botany, Bharathidasan University, Tiruchirappalli, Tamil Nadu, India

<sup>2</sup> International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Telangana, India

agroecological systems and social resilience (Rosenzweig et al. 2001). Likewise, climate variability has a great impact on global food production in the arid and semi-arid tropical (SAT) regions of the world which account for 30% of the world's total area and approximately 20% of the world's population (Lobell et al. 2008). Lobell et al. (2008) reported that increasing temperatures and declining precipitation over semi-arid regions are likely to reduce crop yields due to climate change and variability, particularly rural households which are extremely dependent on agriculture and farming systems are overwhelmed. Thus, it is important to develop and adapt the strategies for changing climate in the SAT regions due to already warmer climates, but also subsistence farmers in the SAT regions will have far fewer options in their agricultural systems to cope with changes in climate.

Cereal grains such as wheat, maize, and paddy are the primary staple food crops across the globe. By 2050, a 70–100% increase in the cereal food supply is desirable for the projected world population (Godfray et al. 2010). But due to a global decrease in fertile and arable lands, it is almost impossible to meet the global food demand with current agricultural practices under climate change scenario. A more hazardous situation could be possible in the SAT regions of the world due to the adverse effects of climate change in these regions. So, it is important to focus on the alternative crops which could adapt to climate change, and could sufficiently fulfill the nutritional needs of the undernourished people across the globe. Sorghum is one such hardy crop that can grow on marginal lands and tolerant to climatic change in different agroecological regions. Sorghum acts as a staple diet for millions of people in the SAT regions of Asia and Africa. It is the major source of food and fodder and is primarily consumed by the producers. Apart from it, sorghum is one of the staple foods for the population in semi-arid and arid regions of the developing countries where malnourishment and poverty are more prevalent. It is a major source of energy and contains many essential nutrients which are necessary to meet the daily nutritional demand of an individual. Thus, it became an important crop for the sustainable livelihood of poor farmers in arid and semi-arid regions. Sorghum can grow in marginal lands with low input and is a predominately rainfed crop in these regions. Although a hardy crop, rainfall variability and heat stress due to changing climate could reduce crop yields substantially in many regions of the world. According to studies, due to climate change, yields of post rainy sorghum likely to reduce 7% by 2020, 11% by 2050 and 32% by 2080 (Srivastava et al. 2010). Climate change variability mostly affects sorghum during reproductive and grain-filling stages and leads to loss of crop. Not only the yield, but the nutritional quality of the crop could also suffer the impacts of climate change by decreasing the major and essential nutritional components in the grain. So, it is essential to improve

crop yields without compromising quality. Implementing strategic adaptation approaches like varietal selection and sowing dates could benefit the crop yield to some extent, but the complete loss cannot be prevented if the severity of global warming continues to increase in near future. With the availability of a wide array of new technologies in plant breeding and molecular studies, strategies for climate change adaptation should focus on improving crop yields as well as grain quality. There is no recent assessment of climate variability and change affecting sorghum production at a regional or global scale. The last assessment conducted by the International Crops Research Institute for the Semi-arid Tropics (ICRISAT) and Food and Agriculture Organization (FAO) dated 1996 (ICRISAT and FAO, 1996). There are other studies particularly focused on regional challenges in Sub-Saharan Africa and arid and semi-arid regions of South Asia (Adhikari et al. 2015; Reynolds et al. 2015). Similarly, recent work showed potential impacts of climate change on sorghum crop production (Raymundo et al. 2018). Thus, in the current review, we examine the existing literature to identify the most potential climate change impacts on crop yields and grain quality and adaptation strategies available were discussed with the major emphasis on the sorghum crop.

## Crop response to climate change

### Crop yields

During the last several years, global warming has a serious impact on cereal cropping regions in many parts of the world. Rapid changes in climatic conditions resulted in increased incidences of various abiotic stresses, thus causing an adverse effect on plant productivity. With a temperature increase of 3–4 °C, 15–35% loss in crop yields in Africa and West Asia and 25–35% yield loss in the Middle East could be expected (FAO 2008). There is a risk of losing around 280 million tons of cereal production potentially among Asian and African countries (FAO 2005). It is projected that agricultural production could decline by 4–10% in developing countries of Asia due to climate change (Fischer et al. 2005).

Climate change effects are generally assessed by the number of stress events and their effect on day-to-day life and loss of agricultural productivity. Climate change severely disrupts plant development by causing several morphological, physiological, biochemical, and molecular changes which ultimately lead to yield loss (Raza et al. 2019). Predominant yield losses and resulting food insecurity in developing countries show the impact of climate change in these regions.

Water stress and extreme temperature are two major forces that impact the reproductive phase in plants. In cereals, water stress shows a negative effect on flower initiation and inflorescence, which leads to a decrease in grain set and thus reducing the harvest index by 60% (Garrity and O'Toole 1994). At the same time, high-temperature episodes, above 30 °C during the flowering stage lead to sterility in cereals, affecting the grain yields. Also, several crop models predicted high rates of evapotranspiration and less soil moisture in drier regions due to high temperatures. It leads to a loss in crop growing area in these regions (IPCC 2007). Various other stresses such as salinity, drought, and chemical effluence damage plant tissues and organs which results in the production of stress responsive proteins, solutes, and elevated antioxidant ratios. They in turn lead to oxidative and osmotic stress in plants.

Crops, in general, adapt to higher temperatures by reducing the crop cycle, which affects yields substantially. This reduced crop yield is due to a decrease in the rate of photosynthesis, respiration, and grain filling. Although C4 crops have a better photosynthetic capacity, higher temperatures cause a decline in photosynthesis rate, which in turn affects crop yields (Crafts-Brandner and Salvucci 2002). Warming causes an increase in vapour-pressure deficit (VPD) which results in reduced water use efficiency of plants due to loss of more water per unit of carbon gain (Ray et al. 2002). Temperature instability will also provide more favourable environmental conditions for insects and pests of crops to boost their capacity to stay alive in cold temperatures and emerge during critical crop stages. An increase in temperature leads to a reduced grain-filling stage which is the primary cause of reduced crop productivity during climate change scenario (Challinor et al. 2007). Heat stress normally is a function of the intensity of temperature, duration, and rate of increase. When it occurs before anthesis, it causes sterility of florets (Prasad et al. 2000, 2008). If exposed to long-term heat stress, reproductive processes impair significantly which was noticed in rice (Baker et al. 1995), soybean (Boote et al. 2005), peanut (Prasad et al. 2003) and sorghum (Prasad et al. 2006). Heat stress accelerates the overall female development which reduces the duration of their receptiveness to pollen and pollen tubules. When exposed to high temperatures during seed filling, it reduces the seed set and seed weight and decreases the overall yield by reducing the seed filling rate and duration (Siddique et al. 1999). This process is similar to drought stress, however, in heat stress, seed filling duration decreases severely compare to seed filling rate. Thus, heat stress along with drought is a major constraint during grain filling for many cereal crops.

Climate change increases the frequency and magnitude of droughts, thus intensifying the crop water stress. In general, crops can tolerate water stress to some extent by closing stomates. However, an increase in potential heat related

impact results in more pronounced water stress which could lead to loss of crops. Particularly, in the tropics, the chances of experiencing drought are high during the start and end of the season, resulting in significant crop losses (Krupa et al. 2017). In general, pre-anthesis water stress affects stand count, tillering capacity, number of panicles and seeds per panicle while post-anthesis water stress affects transpiration efficiency, CO<sub>2</sub> fixation, and carbohydrate translocation. These changes ultimately lead to premature plant senescence and yield losses (Thomas and Howarth 2000; Xin et al. 2008). In cereals, water stress during the reproductive phase (Stone et al. 2001; Hatfield et al. 2011) is especially harmful and reduces the yields substantially. Not only the droughts, more intense rainfall in some regions lead to flooding and waterlogged soils that could damage the crop yields. Waterlogging due to floods/extreme rainfall events affect the soil physical, chemical and biological properties which eventually affect the crop water and nutrient uptake from soil. Due to the closure of stomata (Ahmed et al. 2002), photosynthetic rate and net carbon assimilation decrease under excess soil moisture. Thus, resulting events lead to a reduction in yields (Zhuo and Lin 1995; Ahmed et al. 2002). However, these effects vary from species to species and between genotypes within species (Orchard and Jessop 1984; Umaharan et al. 1997; Pang et al. 2004).

Due to deforestation and fossil fuel utilization, currently atmospheric CO<sub>2</sub> is increased to 400 μmol<sup>-1</sup>. It is projected to increase up to 800 μmol<sup>-1</sup> by the end of the century. Elevated CO<sub>2</sub> was found to reduce the stomatal conductance, thus increasing the water use efficiency of both C3 and C4 plants. But there are contradictory studies (Long et al. 2006) which reported the effect of elevated CO<sub>2</sub> on crop plants. Some studies even reported the reduced nutritional quality of crops due to high CO<sub>2</sub> when rising in the nutrient poor soils by reducing the nitrate assimilation (Taub et al. 2008). Elevated CO<sub>2</sub> during drought could lead to the induction of reactive oxygen species (ROS) which disturb photosynthesis and respiration. ROS can cause disturbance in the synthesis of carbohydrates, protein, lipids, nucleic acids which are building blocks for plant growth (Ahmad et al. 2018). Leakey (2009) reported, under elevated CO<sub>2</sub> conditions, CO<sub>2</sub> concentration increases in the bundle sheet cells which lead to reduced photorespiration in the case of C4 plants. However, like C3 plants, C4 plants also exhibit high photosynthetic rates, water use efficiency by reducing stomatal conductance due to elevated CO<sub>2</sub>, and reduce the effects of drought.

During climate change, phytohormones also play a major role by inducing stress responsive signal transduction mechanisms. For example, ethylene is found to act as signalling pathway among plant growth and environmental variations. During abiotic stress conditions, it controls seed germination, leaf growth, senescence, and ripening. Abscisic

acid also induces several physiological mechanisms during drought stress by producing stress responsive genes and controlling transpiration and stomata closure and opening (Kuromori et al. 2018).

### Grain quality

The growth environment plays important role in all aspects of seed quality—seed size, seed composition, and germination ability. Several studies showed the effect of environment on grain composition and many of them reported year to year variability and region  $\times$  year interactions for grain quality traits such as protein and oil concentrations (Hurburgh et al. 1990; Brumm and Hurburgh 2006; Naeve and Huerd 2008;). Drought and heat stress are the two major stresses which affect the size and composition of matured seed both in cereals and legumes due to their negative impact on nutrient uptake, assimilate supply, and remobilization of nutrients (Prasad et al. 2008). In addition to that, these stresses negatively affect the viability of harvested seeds. Seed filling is the most crucial stage and temperature influence the various processes involved in seed filling, ultimately affecting seed quality. The optimum temperature for normal grain filling varies from species to species (Hatfield et al. 2011). Due to high temperature, there will be a decrease in seed size, glucose concentration, and at the same time increase in sucrose and raffinose concentrations in grain. Studies also showed decrease in oil concentration and protein percentage with an increase in temperature (Gibson and Mullen 1996; Pazdernik et al. 1996; Thomas et al. 2003; Naeve and Huerd 2008).

Changes in the environment also has a significant impact on starch biosynthesis and properties (Tester and Karkalas 2001; Thitisaksakul et al. 2012). Changes in planting seasons, higher night temperatures, decreased water availability, and soil quality could significantly affect the starch accumulation and physical properties which in turn affect the downstream uses (Hatfield et al. 2011). The structure and composition of starch are important indicators for quality and nutritive value of cereal products as animal feed and suitability as feedstock for biofuels (Dang and Copeland 2004; Moritz et al. 2005; Svihus et al. 2005; Sun et al. 2011). In addition to the genotypic effect, starch functionality also varies with increasing air and soil temperatures, rainfall pattern, growing locations and environmental stresses (Dang and Copeland 2004). In addition to total starch concentration, minor changes in amylose concentrations could seriously alter the starch gelatinization and pasting properties (Zeng et al. 1997; Hurkman et al. 2003). These changes in amylose concentrations due to high temperatures are more evident in maize, rice, and wheat compare to barley and sorghum (Tester 1997; Tester and Karkalas 2001; Kiseleva et al. 2003; Li et al. 2013a, b). Time and severity of heat stress can also alter the starch granule size, shape, and structure (Liu et al.

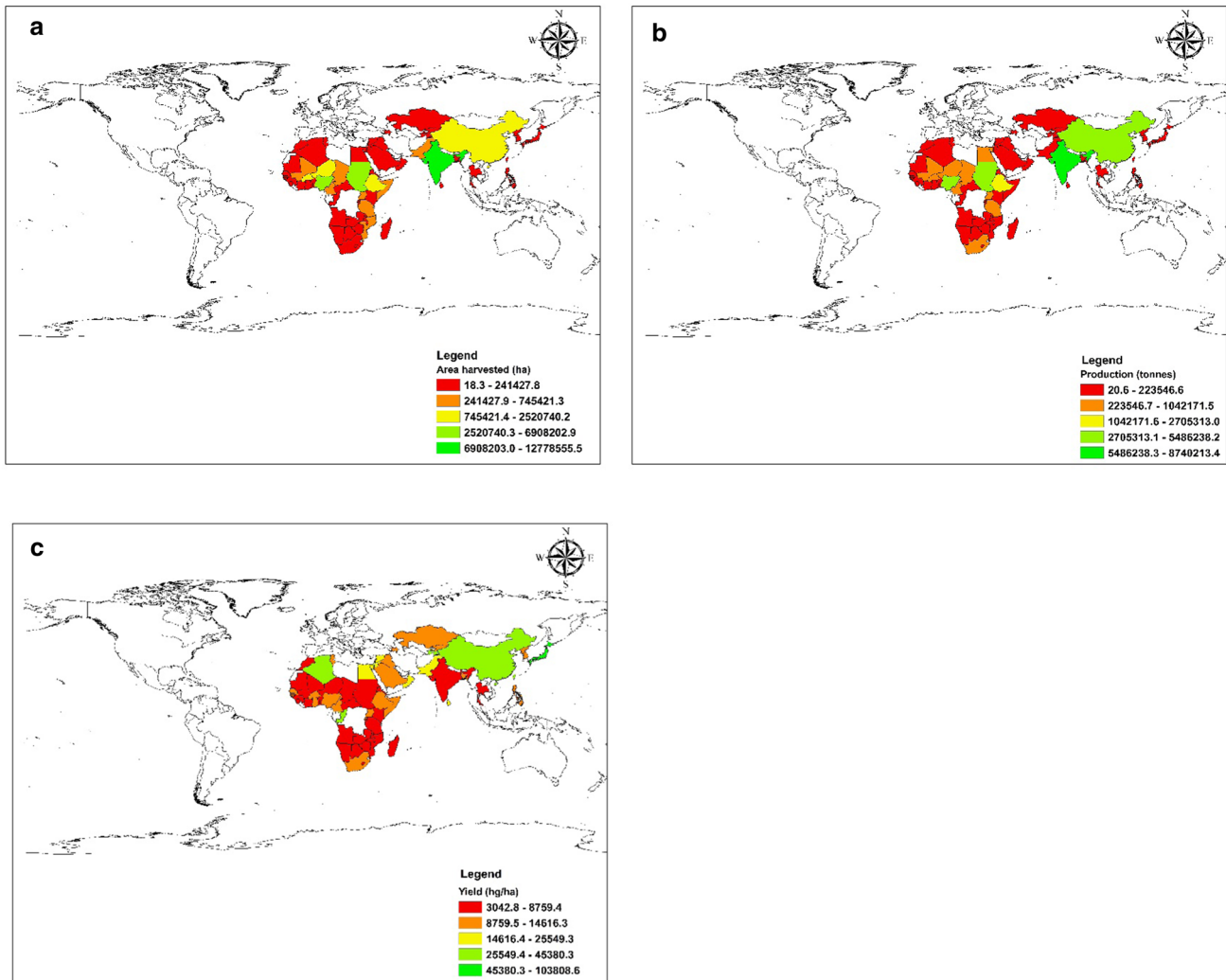
2011). For example, when applied before anthesis, the size of wheat A granules were affected disproportionately (Liu et al. 2011). Reduction in granule size was also observed in sorghum, rice, and maize (Lu et al. 1996; Li et al. 2013a, b; Mitsui et al. 2013). On the contrary, low temperatures and cold seasons increase the ratio of amylose to amylopectin in cereals such as rice, maize and wheat (Ferguson and Zuber 1962; Asaoka et al. 1984; Dang and Copeland 2004; Labuschagne et al. 2009; Singh et al. 2010). Studies showed starch gelatinization and pasting temperatures also decreased in cold treated cereals (Myllarinen et al. 1998; Aboubacar et al. 2006).

Water stress negatively affects grain physical attributes. Reduced grain weight and grain size and increase in grain hardness was reported under water stress (Pang et al. 2018; Impa et al. 2019). Water stress also affects starch accumulation, leading to changes in starch composition, structure, and functionality (Thitisaksakul et al. 2012). Water stress also decreases the amylose content in wheat, rice, and barley (Cheng et al. 2003; Dai et al. 2009; Singh et al. 2010; Gunaratne et al. 2011a, b). Increased flour swelling power, viscosity, gel hardness, and granular breakdown could also be seen due to water stress (Gunaratne et al. 2011a, b). In addition to flour properties, an increase in grain chalkiness and milling properties can also be seen during water stress. Ali et al. (2010) reported grain oil content was reduced up to 40% in maize due to drought stress, at the same time it increased the oleic acid content by > 25% and reduced the linoleic acid content. Reduced grain starch-lipid content was seen in wheat studies due to water deficit (Singh et al. 2008; Fabian et al. 2011). In addition to heat and water stresses, elevated CO<sub>2</sub> and O<sub>3</sub> also have a significant impact on grain productivity which in turn affects the starch composition and functionality (Mishra et al. 2013; Piikki et al. 2008).

## Sorghum

### Production

Sorghum is the fifth most important cereal crop in the world. Due to its high photosynthetic efficiency, sorghum can grow both in temperate and tropical regions. It has a short maturity period and can grow both in irrigated and rainfed conditions, thus suitable for subsistence as well as commercial farming. Developing countries, mostly, Africa and Asia account for nearly 90% of sorghum production area. Production-wise, 38.6% was from the Americas, 38.5% from Africa, 18.6% from Asia and remaining 4.3% of sorghum production was from Europe and Oceania (FAOSTAT). Sorghum crop was harvested in nearly 40 million hectares of the world's area and the total sorghum production in this area was around 57.9 million tonnes in 2019 (Fig. 1).



**Fig. 1** Spatial distribution of sorghum area (a), production (b) and productivity (c) over Africa and Asia during 1961–2019 based on FAOSTAT 2019. Data source: <http://www.fao.org/faostat/en/#data/QC>

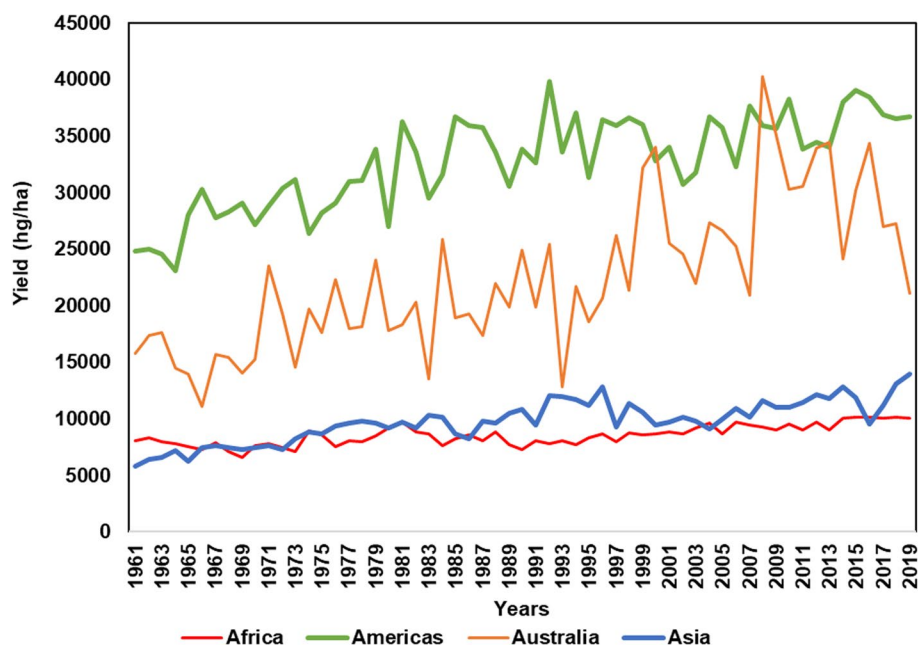
In the past two decades, sorghum production (~1%) and production area (2%) was decreased slightly. Over the last decade, sorghum production area and yields increased in Africa (area: 27.5–28.4 M hectares; Yield: 25.6–28.6 M tonnes), whereas it was reduced significantly in Asia (area: 9.3–5.6 M hectares; yield: 10.9–7.8 M tonnes) and Americas (area: 7–5.1 M hectares; yield: 25.1–18.8 M tonnes) (FAOSTAT). Overall productivity is high in commercial systems where sorghum production area is roughly 15%, but produce 40% of global sorghum yields. In contrast, most of the developing world including Africa and Asia grow sorghum extensively, but in low input systems and average yields in these areas remained 0.5–1 tonne per hectare. More than 70% of the sorghum grown in these areas is consumed as food. Especially in Africa, cropping area has increased significantly, but productivity remained

low due to the use of marginal, drought-prone lands and poor soils (ICRISAT and FAO 1996). Figure 2 depicts a change in the sorghum production trends over the past few decades in predominantly sorghum growing regions.

**Growth conditions**

Sorghum is mainly cultivated in drier environments on shallow and deep clay soils. It is more tolerant to alkaline soils and can be grown on soils with a pH between 5.5 and 8.5. The minimum temperature requirement for germination is 7–10 °C. More than 80% of the seeds germinate at 15 °C. The optimum temperature requirement for growth and development is 27–30 °C. Growth and yields can be affected beyond 35 °C. It is a short-day plant with a photoperiod requirement of 10–11 h to induce flower formation. Tropical

**Fig. 2** Trends of sorghum yields over Africa, Asia, Americas and Australia during 1961–2019 based on FAOSTAT data. Data source: <http://www.fao.org/faostat/en/#data/QC>



varieties are more sensitive to photoperiod than short-season varieties. It has a growing season of 115–140 days. Water requirement mainly depends upon growth and environment. Typically, medium to late maturing grain sorghum cultivar requires 450–650 mm of water during growing season (Assefa et al. 2010). Water use is less during the early stages of development and then maximum water use occurs from booting stage to anthesis. Then it gradually decreases during the grain-filling stage. Along with these critical requirements, the production potential of sorghum also depends upon plant population, cultivar choice, fertilizer input, and pest and insect control.

## Potential impacts of climate variability and change

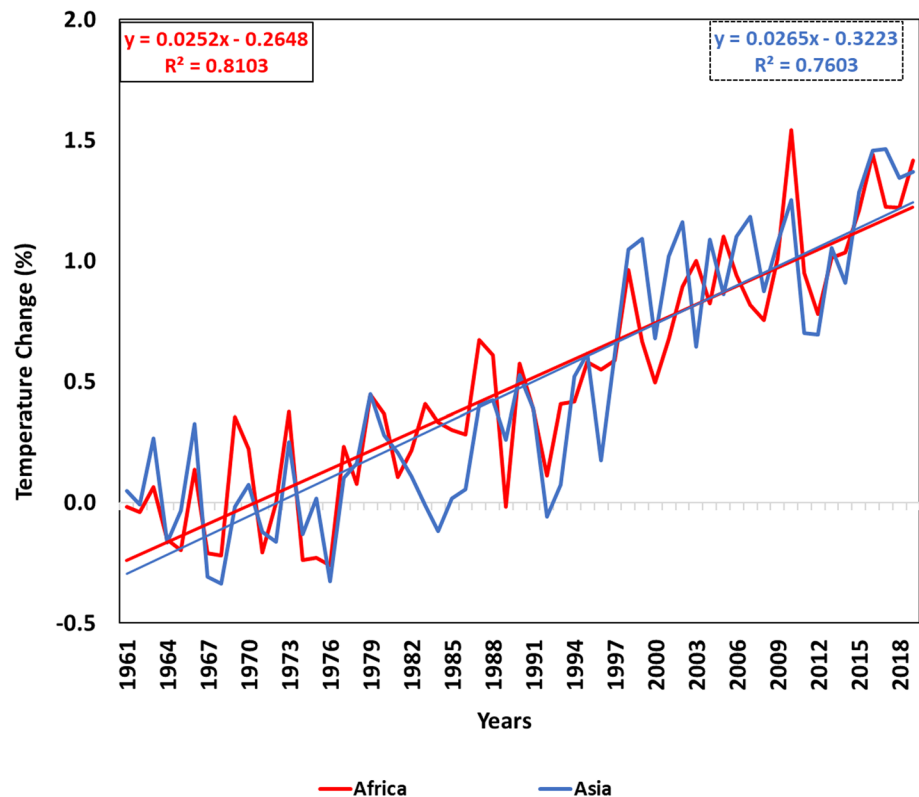
### Heat stress

Human activities already had a significant impact on global and regional climate, it is evident from Fig. 3 there was approximately 1 °C increase in the surface temperatures across Africa and Asia over the past decade 2009–2019.

Gradual change in surface temperatures also negatively affects the sorghum crop and reduces the yield potential. Generally, the optimum temperature requirement for sorghum crop is 21–35 °C for germination, 26–34 °C for vegetative growth and 21–35 °C for reproductive growth (Maiti 1996). Maximum yields and dry matter can be obtained at 27/22 °C (day/night temperatures). Temperatures above 33/28 °C during panicle development results in floret and embryo abortion (Downes 1972). In general, reproductive

stages (panicle initiation, grain filling and grain size) are more sensitive to heat stress compare to the vegetative stage (leaf growth, photosynthesis) (Downes 1972; Craufurd et al. 1998; Hammer and Broad 2003; Prasad et al. 2006). Prasad et al. (2008) found the most sensitive stages for heat stress in grain sorghum were flowering and 10 days before flowering which results in reduced seed set, seed number and yields. In grain sorghum, these most sensitive stages to high temperatures are characterized by a maximum decrease in floret fertility. Meiosis, anthesis, fertilization and embryo formation occur during these periods. As a result, negative impacts like pollen sterility, decreased seed set (Djanaguira-man et al. 2014) and changes in concentration and composition of carbohydrates and starch deficiency (Jain et al. 2007) could be seen during heat stress. Prasad et al. (2008) showed continuous exposure to high temperature (40/30 °C) leads to a delay in panicle emergence by 28 days and flowering by 20 days. Heat stress significantly decreases the plant height at maturity, seed set, seed number and size, but does not have a significant impact on leaf area and leaf dry weight. Maximum seed set decrease was observed when heat stress occurred at the flowering stage (54%) (Prasad et al. 2008). Short periods of heat stress in sorghum during panicle emergence result in a decreased grain-filling rate and duration which in turn leads to smaller seed size. At the same time, an increase in heat stress at the beginning of grain-filling stage leads to a decrease in individual grain weight which was observed both in controlled as well as field grown sorghum. Thus, short periods of heat stress in sorghum significantly affect seed set (Singh et al. 2015) and seed number, whereas season long heat stress has a negative impact on individual seed weight (Prasad et al. 2006) due to reduced grain-filling

**Fig. 3** Percent change in surface temperature during 1961–2019 over Africa and Asia. Temperature change was calculated based on the baseline climatology, corresponding to the period 1951–1980. Data source: <http://www.fao.org/faostat/en/#data/ET>



period (Prasad et al. 2015). However, different genotypes exhibit different responses to heat stress (Nguyen et al. 2013; Djanaguiraman et al. 2014; Singh et al. 2015) and also severity of impact on floret fertility and grain weight varies between tolerant and susceptible sorghum hybrids (Prasad et al. 2015).

The impact of heat stress on sorghum grain quality traits was reported only by a few researchers so far (Wu et al. 2016; Impa et al. 2019) and still needs further investigations. It is speculated, like other cereals, accumulation of starch decreases under heat stress in sorghum. Decrease in activities of different enzymes (Ahmadi and Baker 2001; Hurkman et al. 2003; Li et al. 2013a, b) contribute to reduction in starch synthesis and altered amylose to amylopectin ratio. Li et al. (2013a, b) also reported lower starch weight per grain and smaller starch granules under elevated temperatures. Lower starch concentrations under heat stress in grain samples was also found by Johnson et al. (2010) while working on corn and sorghum. Effect of heat stress on starch accumulation also negatively affects the biofuel industry. Heat stressed grain sorghum samples release less sugars due to altered starch accumulation and composition, ultimately causing reduced ethanol production compare to non-stressed sorghum grains (Ananada et al. 2011). However, Impa et al. (2019) reported there was no significant effect of heat stress on starch content, but grain protein decreased under stress with a significant reduction in protein digestibility. The same

study reported increase in grain hardness and diameter and a reduction in grain micronutrients under heat stress. Wu et al. (2016) reported a decrease in tannin content under high temperatures, whereas phytates and mineral contents were highly influenced by genotypes compare to growth temperature. Taleon et al. (2012) found a strong effect of abiotic stress factors such as light and temperature on the flavonoid content of black sorghum.

### Cold stress

As a tropical crop, sorghum is highly sensitive to chilling stress (Peacock 1982; Rooney 2004). It is sensitive to cold stress than any other cereal. Sorghum production in most of the temperate regions affects by cold temperature stress. Chilling stress can affect the sorghum both in pre- and post-flowering stages thus mitigating the vegetative growth as well as grain-filling period. When planted early in the season with low soil temperatures, sorghum suffers from poor seedling emergence and seedling vigor which results in yield losses (Yu and Tuinstra 2001; Cisse and Ejeta 2003; Burow et al. 2011; Kapanigowda et al. 2013; Maulana and Tesso 2013; Chilual 2018). Not only this, emerging seedlings are more prone to soil-borne pathogens such as *Pythium* and *Fusarium* spp. (Forbes et al. 1987). As a result, plant population reduce significantly, although this effect varies from genotype to genotype (Tiryaki and Andrews 2001; Franks

et al. 2006). Cold stress affects the development and function of chloroplasts (Fracheboud et al. 1999; Allen and Ort 2001), thus reducing photosynthetic capacity and respiration. But in sorghum, Ercoli et al. (2004) found, the photosynthetic rate was severely affected compare to respiration which resulted in reduced leaf area due to loss in leaf turgor. Early season cold stress in sorghum also delays panicle emergence and heading in sorghum (Majora et al. 1982) along with maturity time (Maulana 2011). Moreover, Ercoli et al. (2004) showed N fertilized plants are more sensitive to cold stress than non-fertilized crops. Mid-season cold stress which coincides with the reproductive stage negatively affects the yield components. Cold temperatures at flowering significantly reduce the mean panicle weight, number of seeds per panicle and thousand seed weight (Maulana 2011). These effects are primarily due to the impact of stress on flowering, pollination and fertilization. However, these negative effects depend on genotype and degree of sensitivity to cold stress.

Cold stress in sorghum not only affects the yield but also impacts the grain nutritional quality. Cold stress reduced the grain protein and starch compositions (Ostmeyer et al. 2020). High tannin contents also observed in sorghum genotypes under cold stress. Although grain protein and starch composition differ in genotype to genotype, there was a significant genotype by environment interaction observed in recent studies (Ostmeyer et al. 2020). Ostmeyer et al. (2020) also reported that not only chemical composition, physical traits such as reduction in kernel hardness and diameter also reduced due to chilling stress. Development of early chilling tolerance hybrids found to improve the nutritional quality along with yields. Also, tannin free chilling tolerant hybrids were identified (Chiluwal et al. 2018) which improves the grain quality by enhancing protein digestibility.

## Drought stress

With current global climate change trends, there is an increasing frequency of droughts, particularly in arid and semi-arid regions of the world. Although a stress-tolerant crop, sorghum is usually affected by water stress experienced due to drought during pre-and post-flowering stages. Drought stress occurs at these stages results in substantial yield loss in sorghum (Tuinstra et al. 1997; Kebede et al. 2001; Blum 2004). Drought stress at post-flowering stage affects the seed size and number per plant (Rosenow and Clark 1995) by 55 and 36%, respectively, ultimately reducing the grain yield (Assefa et al. 2010).

Generally, a medium to late maturing sorghum cultivar requires 450–650 mm of water during the growing season (Tolk and Howell 2001; FAO 2002), although daily requirements depend on the growth stage. Roughly 1–2.5 mm of water is sufficient for sorghum at the early growth stage to avoid water stress. Later water requirement increases up to

7–10 mm and then it is maximum from booting stage to anthesis (Assefa et al. 2010). Thus, reduced soil moisture below this minimum requirement results in developing water stress. A further study on water use of sorghum reported the addition of every mm of water above 100 mm results in an additional 16.6 kg of grain (Stone, and Schlegel, 2006). Water deficit at certain growth stages results in yield loss in sorghum. So, a well-distributed water supply based on the growth stage is necessary for good grain yield, rather than the amount of total water available throughout the cropping season. Majorly, sorghum is vulnerable to long periods of water stress and susceptible to yield losses. For example, Eck and Musick (1979) showed water stress for 35–42 days from the beginning of boot stage resulted in yield loss of 43 and 54%, respectively. Likewise, Inuyama et al. (1976) reported, 16 and 28 days of water stress during the vegetative stage resulted in 16 and 36% of yield reduction. It shows water stress at the reproductive stage is more sensitive than vegetative stage. Water deficit at this stage prevents the development of pollen and ovules, fertilization and premature abortion of fertilized ovules (Saini 1997; McWilliams 2003). As a result, a number of panicles, seeds per panicle, and individual grain size decrease with drought. Precisely, if the drought stress occurs at the early boot stage, yield loss would be due to reduced seed size and number, but if the stress occurs at later stages, yield loss would be only due to reduced seed size (Eck and Musick 1979). Severe water stress at pre-flowering stage lowers the net photosynthetic rate by reducing PSII and PEPcase activities and by closing stomata (Vinita et al. 1998). Thus, water stress ultimately increases photorespiration and internal oxygen concentration. The resulting formation of reactive oxygen spp. leads to cellular death, thus reducing total dry matter production under drought conditions (Perry et al. 1983; Terbea et al. 1995). Wong et al. (1983) found drought at the vegetative stage accelerates flowering but does not affect the grain-filling period. Manjarrez-Sandoval et al. (1989) reported, microsporogenesis is the most susceptible stage to drought stress in sorghum by causing panicle loss and resulting yield loss. The same study also reported severe drought stress at the microsporogenesis stage does not affect grain yields, because of compensated yields by tillers produced at later stage, especially in long maturity sorghums (Manjarrez-Sandoval et al. 1989).

Impa et al. (2019) showed that terminal water stress decreased the individual grain size and diameter, but increased the grain hardness. This reduced grain size and number might be attributed to decreased grain-filling duration under drought stress which terminates the grain-filling period early (Impa et al. 2019). Pang et al. (2018) also reported, reduced test weight, grain size, and grain hardness in sorghum under low soil moisture. Drought stress, depending on the severity reduces various enzyme



activities involved in starch biosynthesis and accumulation (Ahmadi and Baker 2001; Hurkman et al. 2003; Pang et al. 2018), thus reducing the total starch content in the grain. Bing et al. (2014) reported, drought stress at the flowering stage shows a reduction in activities of granular bound starch synthase which is responsible for amylose synthesis, starch branching enzyme activity, that is responsible for amylopectin formation and also starch debranching enzyme activity. However, many studies reported an increase in grain protein content under drought stress (De Souza et al. 2015; Impa et al. 2019; Sarshad et al. 2021), but decrease in protein digestibility, one of the important factors which determine the quality of sorghum feed. On the contrary, a few researchers noticed increased kernel hardness and protein content in irrigated sorghum grain samples (Wu et al. 2008; Njuguna et al. 2018). Zhan et al. (2003) and Wu et al. (2007) showed protein content is inversely proportional to starch content, a property that negatively affects the biofuel industry by reducing ethanol production from sorghum grain samples. Increased protein content may contribute to more starch–protein complexes which in turn results in less starch availability to hydrolytic enzymes to release glucose and less fermentation efficiency for ethanol production (Wu et al. 2007). Ananda et al. (2011) confirmed the same by showing increased ethanol yields from drought stressed grain samples compare to controls, whereas Pang et al. (2018) showed irrigation capacity has a positive impact on final bioethanol yields although less fermentation efficiency was observed for the irrigated grain samples during the first 48 h of fermentation. Thus, these contradictory results support the fact that grain quality not only depends on climate but also on genotype and location and their interactions (Ebadi et al. 2005). Wu et al. (2007) found reduced crude fiber content in drylands grown sorghum compare to irrigated lands. The same study reported there was no significant reduction in mineral content (ash) under drylands, at the same time noticed, location specific increase in mineral content. On the contrary, Impa et al. (2019) showed reduced micronutrient concentration under moisture stress except for grain Fe content. An increase in tannin content was noticed by Njuguna et al. (2018) under less soil moisture compare to higher moisture soils.

### Waterlogging (excess moisture)

Waterlogging that occurs mainly due to flash and heavy floods is a major constraint for crop growth and yield due to current management practices and changes in precipitation levels (Polthanee 1997). Many studies (Orchard and Jessop 1984, 1985; Pardales et al. 1991; McDonald et al. 2002) reported the effect of waterlogging on growth and yields in sorghum. Adverse effects of flooding depend on the crop growth stage. The early growth stage was found

to be more susceptible compare to the early and late reproductive stages (Orchard and Jessop 1984; Umaharan et al. 1997; Linkemer et al. 1998). Promkhambut et al. (2011) showed flooding applied for 20 days at the early growth stage severely impaired the primary root and shoot growths in sorghum. Moreover, root growth was severely affected than shoot growth. Low radial oxygen loss in sorghum in response to flooding was also observed by McDonald et al. (2002). Due to this oxygen deficit, sorghum experience anaerobic conditions when exposed to prolonged excess moisture stress (Pardales et al. 1991). Promkhambut et al. (2011) observed aerenchyma development on nodal and lateral roots in response to early vegetative and reproductive stage flood conditions, which is an adaptive response to flooding stress (Zaidi et al. 2004). Root aerenchyma development in response to flooding stress, which is high at the vegetative stage than late growth stage in grain sorghum was also reported by Orchard and Jessop (1985). Pardales et al. (1991) observed nodal root development in a few sorghum genotypes under flooding stress, which is an important trait for waterlogging tolerance. This increase in nodal root number was also observed in sweet sorghum genotypes (Promkhambut et al. 2011) with an increase in the duration of flooding. Excess moisture conditions at the vegetative stage led to a reduction in net photosynthetic rate, transpiration, and stomatal conductance in sweet sorghum genotypes as observed by Zhang et al. (2016). Resulting in poor panicle differentiation and seed setting rate showed reduced grain yields in sorghum (Zhang et al. 2019a, b). Thus, excess moisture in soil due to flooding at early vegetative and reproductive stages leads to a reduction in stalk and grain yields due to stunted root and shoot growths (Promkhambut et al. 2011).

Sorghum grain quality due to excess moisture in the soil is not reported much due to limited literature. Studies conducted on sweet sorghum (Promkhambut et al. 2011; Zhang et al. 2016) showed crops experience anaerobic conditions due to oxygen depletion in the soil. As a result, nutrient uptake decreases (Setter and Belford 1990). Limited N supply causes stunted growth. Overall, photosynthetic efficiency decreases due to a reduction in chlorophyll content. The resulting senescence conditions impair the relocation of photoassimilates. It impacts carbohydrate accumulation, grain size, and grain nutrient composition along with the yields due to nutrient deficiency experienced by the crop.

### Effect of elevated CO<sub>2</sub>

Studies reported sorghum crop shows a significant reduction in transpiration rate due to elevated CO<sub>2</sub> (Pallas 1965; van Bavel 1974) under irrigated conditions like C3 cereals. An increase in stomatal resistance results in reduced water use increased nutrient and water uptake from deeper soils due

to increased root mass at every growth phase (Chaudhuri et al. 1986). This allows optimum growth and development in case of sorghum. This characteristic indeed benefits the crop during drought conditions. Elevated CO<sub>2</sub> was found to reduce the water use under drought stress, resulting in the availability of soil water for a long time during dehydrated periods. It was found, elevated CO<sub>2</sub> increased the growth during the grain-filling period under drought, but decreased the vegetative growth (Ottman et al. 2001). Thus, with continuous carbon gain, an increase in yields was observed for sorghum due to elevated CO<sub>2</sub> under drought conditions (Ottman et al. 2001). Torbert et al. (2004) observed around a 30% increase in sorghum biomass production due to elevated CO<sub>2</sub>. They noticed a substantial rise in C:N ratio due to CO<sub>2</sub> enrichment.

Very few studies reported grain quality in sorghum with elevated CO<sub>2</sub>. De souza et al. (2015) reported there was almost a 60% increase in grain protein content when grown under elevated CO<sub>2</sub> and water deficit conditions. Fatty acids in the grain were slightly increased, but no such increase in starch content was found. Thus, elevated CO<sub>2</sub>, in the case of sorghum was found to be beneficial to mitigate the drought conditions as well as enhanced grain quality.

### Potential sorghum adaptation strategies for climate change effects

Sorghum crop improvement programs along with strategic crop adaptation approaches are designed to cope with the negative impacts of climate change and further maintaining the production and income of smallholders. Different adaptation approaches like crop management practices, breeding, and biotechnological approaches could enhance the sorghum grain productivity and quality under extreme climatic scenarios to a great extent. Understanding genetic variation and the development of climate-resilient sorghum genotypes broaden its adaptation and enhance the production in different agroclimatic zones. The following adaptation strategies could benefit the sorghum crop from climate change impacts.

#### Crop management practices

Better crop management practices are the first step to be taken to improve the sorghum yields under different stress conditions. Generally, yield potential can be enhanced by adapting changes in sowing time, crop cultivars and mixed cropping systems, alteration of planting, and harvesting time, short life cycle cultivars, use of drought and heat-resistant cultivars and implementing different irrigation techniques to tolerate abiotic stresses (Fatima et al. 2020). Adoption of suitable soil, water, and pest management

practices maintains crop production under climate change situations. Choosing commercial sorghum hybrids, which possess different stability components (drought, disease and heat tolerance, photosynthetic efficiency, nutrient use efficiency) enhances yield stability across a wide range of environments compared to inbred lines (Boyles et al. 2019). Management of planting geometry such as decreased planting density, increased plant or row to row spacing and skip row configurations helps to better utilize soil moisture in dryland areas (Fatima et al. 2020). It enhances the dry matter accumulation and grain yields with an increase in photo assimilates available. Delay in sowing time helps the crop to escape from heat stress at critical stages of development like flowering and grain filling. The use of genetically pure and quality seed reduces the negative effects of climate change to some extent and provides scope for sustainable nutritional security (Yu and Tian 2018). Making use of agricultural biodiversity is another promising option to reduce future climate change effects. Crop rotation and multi-cropping systems such as combining deep-rooted with shallow-rooted, C3 crops with C4 crops, combining different varieties of crop in the same field may enhance productivity by reducing the adverse effects of climate change (Fatima et al. 2020). Optimum use of fertilizers is also vital for crop growth and productivity as it provides sufficient nutrients to plants and also enhances the fertility of soil (Raza et al. 2019). Sonobe et al. (2010) found the application of silica fertilizer for sorghum crop improved growth under water stress conditions by increasing the root water uptake and reducing the root osmotic potential. Extensive field trials and data collection help to evaluate the impacts of climate change. Future predictions are possible using remote sensing and crop modeling strategies which helps to apply corrective measures to improve the yields for different agroecological zones (Arora 2019).

#### Breeding and genetic modifications strategies

Plant breeding gives ample opportunities to develop stress-tolerant cultivars that escape extreme weather changes and gain yield benefits. Landraces are a significant source for genetic studies as they contain broad genetic variation. The genetic divergent analysis is an important tool to develop new cultivars with stress resistance (Lopes et al. 2015; Raza et al. 2019). Molecular breeding is a powerful technique which couples breeding with genomic approaches to screening elite germplasms. QTL studies, genomics, and transcriptomic analyses enable to identify the molecular mechanisms responsible for stress tolerance. All these techniques help to develop new cultivars with improved production potential under different climatic change effects (Roy et al. 2011). Genome wide association studies (GWAS) is a powerful tool to identify allelic variants linked with any specific trait

(Manolio 2010). GWAS has been extensively used for many crops to exploit the genetic basis for stress resistance under climate change (Mousavi-Derazmahalleh et al. 2018). High throughput phenotyping is extensively used to screen germplasm for various traits of interest. The biotechnological approach uses genetic engineering techniques to develop transgenic plants with different biotic and abiotic stress tolerance. Herewith, important molecular and high throughput approaches used for sorghum crop improvement under different stress scenarios were discussed further.

### Heat tolerance

Sorghum, naturally, a heat-tolerant crop, experience heat stress at critical stages which result in reduced yields. At the vegetative stage, it decreases the photosynthetic rate (Djanaguiraman et al. 2014) and when it occurs at the reproductive stage, it reduces pollen viability and impacts fertilization (Djanaguiraman et al. 2014, 2018; Prasad et al. 2015). Genetic variation is available in sorghum to develop heat-tolerant cultivars (Singh et al. 2015, 2016). BTx 623 is one of the heat-resistant cultivars that is being used (Singh et al. 2015). Understanding the genetic control of heat tolerance is a basic requirement for developing the appropriate breeding program. Khizzah et al. (1993) studied sorghum lines and reported heat tolerance is associated with two genes with a simple additive model. GWAS was applied for sorghum by Chen et al. (2017) to identify loci for heat tolerance during the vegetative stage.

14 SNPs that are associated with leaf firing and blotching in sorghum were identified in their study which could serve as candidate gene markers in molecular breeding for heat tolerance under the vegetative stage. Another genome-wide analysis (Nagaraju et al. 2015) of sorghum reported 25 heat shock transcription factors expressed under different abiotic stress conditions. Out of them, Hsf1 was expressed under high-temperature stress and Hsf 5, 6, 10, 13, 19, 23 and 25 expressed under drought stress. These genes provide insights into abiotic stress-tolerance mechanisms under different conditions. Transcriptomic analysis of sorghum under drought and heat stress revealed (Johnson et al. 2014) 4% of genes were differentially expressed for drought and 17% for heat stress. Also, a 7% of unique genes were identified for combined stress response. Identification of these differentially expressed genes could be targeted for improvement of sorghum for heat as well as drought stress tolerance under changing climatic conditions.

### Cold tolerance

Improvement of early-stage chilling tolerance hybrids is an important breeding target for improved sorghum productivity (Knoll et al. 2008; Knoll and Ejeta 2008; Fernandez et al.

2015; Chilual et al. 2018). Currently, cold tolerant sorghum hybrids are limited compare to other cereals (Yu et al. 2004). Many sorghums originated from semi-arid tropics are sensitive to low temperatures. Detailed physiological studies help to understand the effect of chilling stress on root conductance, shoot growth, and seedling development. Franks et al. (2006) identified Chinese kaoliangs as cold tolerant landraces with improved seedling vigor and emergence under cold stress. Another germplasm from Ethiopian highlands found to retain the growth below base temperature of 10 °C, indicating adaptation to chilling conditions (Tirfessa et al. 2020). Simple sequence repeat markers associated with traits for early season chilling tolerance were identified by Buraw et al. (2011). Hybrids developed from inbreds were extensively tested and selected for early-stage chilling tolerance (Chilual et al. 2018) with high germination and seedling vigor. Ostmeier et al. (2020) reported, a promising tannin free hybrid (ARCH11192A/ARCH12012R) with early-stage chilling tolerance significantly enhanced the yields without affecting the grain quality during early-stage chilling stress. These tolerant hybrids found to take a longer duration for flowering and extended grain-filling period which enhances the grain yields without impacting quality.

Bekele et al. (2014) screened a sorghum RIL population by phenotyping to select the traits useful in breeding for chilling tolerance. They also identified potential QTL regions on chromosomes 1,2,3,4 and 6 responsible for cold tolerance, which can be further used for fine mapping and candidate gene identification for early-stage chilling tolerance. Interestingly, QTLs identified in their study corresponds to the QTLs for stay-green which was identified earlier (Harris et al. 2007; Mace et al. 2012). Thus, these QTL hotspots facilitate the development of sorghum varieties with broad abiotic stress tolerance. Marla et al. (2019) studied sorghum NAM population developed from sensitive BTx 623 and three chilling tolerant Chinese lines (Niu Sheng Zui (NSZ; PI 568016), Hong Ke Zi (HKZ; PI 567946), and Kaoliang (Kao; PI 562744)). They found chilling tolerant QTLs were co-mapped with tannin and dwarfing genes. So, it is essential to carefully understand the genetic tradeoff to go for further genomic selection for chilling tolerance as it can negatively affect the grain quality.

### Drought resistance

As sorghum is majorly grown in arid and semi-arid environments, breeding for drought-resilient cultivars requires an understanding of environmental control over crop growth (Bidinger et al. 1996). The development of drought-tolerant cultivars with the help of genetic improvement not only stabilizes productivity but also provide sustainable production systems. Screening and selection under optimal as well as stress conditions is necessary to select for yield stability,

drought tolerance, and expression of drought-tolerant related traits (Richards 1996; Tuinstra et al. 1997). Tuinstra et al. (1997) identified 13 genomic regions related to the post-anthesis drought tolerance in sorghum. Out of them, four QTLs were identified for yield and yield stability, seven for grain weight and development and two for stay-green trait. In the past decade, several post-flowering drought-resistance cultivars were developed in sorghum. Drought-resistant cultivars showed high chlorophyll and photosynthetic efficiency and also stay-green phenotype. These stay-green phenotypes found to improve the grain yields significantly under drought conditions. BTx 642 has been a primary source to stay-green. This stay-green source was widely tested and also used to develop new hybrids with drought resistance (Borrell et al. 2000; Henzell et al. 2010; Jordan et al. 2010). Kassahun et al. (2010) identified similar stay-green loci an important for early-stage drought. Sta-green phenotype found to reduce water uptake and vegetative biomass during pre-flowering growth stages and uses the soil moisture during grain filling for yield benefits (Borrell et al. 2014). Reddy et al. (2007) showed genotypes with stay-green trait also exhibit resistance to lodging and charcoal rot. In addition to that, several QTLs for nodal root angle, root volume, dry weight, fresh weight were identified in past few years (Mace et al. 2012; Rajkumar et al. 2013). Mace et al. (2012) found root angle QTL was co-located with stay-green QTL and linked with grain yield. Jiang et al. (2013) reported reverse genetic approaches such as RNAi / type II CRISPR/CAS systems help to characterize the individual gene functions when expressed under stress conditions. In addition to that, miRNA expression studies (Ram and Sharma 2013) in sorghum reported mi169 is an excellent source to improve drought tolerance in sweet sorghum through genetic engineering.

### Waterlogging

Enhancement of hypoxia tolerance is a convincing route to mitigate the waterlogging stress in crop plants. Understanding of molecular and physiological basis for this tolerance plays a key role to breed for waterlogging tolerance by expression of fermentation pathway genes (Dennis et al. 2000). Literature available on this is still inadequate for sorghum. Formation of root aerenchyma (Promkhambut et al. 2011), nodal root development (Pardales et al. 1991), maintaining high leaf air temperature difference (Zhang et al. 2019a), maintaining high antioxidant activity (Zhang et al. 2019b) are some of the waterlogging tolerance mechanisms observed in sorghum. Breeding for the varieties which express these tolerance mechanisms is prerequisite to improve the cultivation of sorghum under waterlogging conditions. Kadam et al. (2017) worked on the transcriptional profiling of aquaporin genes expressed under waterlogging

conditions. They noticed tissue-specific, differential expression of AQP genes (*PIP2-6*, *PIP2-7*, *TIP2-2*, *TIP4-4*, and *TIP5-1*) under waterlogging conditions. The genetic variation observed in these AQP genes may play important role in breeding for waterlogging stress tolerance.

### Improvement of grain quality

Stay-green phenotype was found to maintain higher stem carbohydrates, in addition to higher photosynthetic efficiency, grain yields, and resistance for lodging under drought conditions (Borrell et al. 2000; Burgess et al. 2002; Jordan et al. 2012). Also, leaves of stay-green phenotype found to have high N and nutritional quality (Borrell et al. 2000; Jordan et al. 2012) and predicted to contain high sugar concentrations in leaves and stem. Thus, breeding for stay-green trait also help to improve the nutritional quality of sweet sorghum cultivars along with drought resistance. Moreover, Blümmel et al. (2015) found stay-green sorghum contains higher In vitro organic matter digestibility (IVOMD) and use as animal feed. In addition to that, unpublished results from ICRISAT also showed stay-green trait could also enhance grain major nutritional components (protein, fat, and starch), but this capacity is highly dependent on genotype and genetic background.

Apart from stay-green, many studies have been attempted to improve the grain quality by developing new cultivars (Miller et al. 1996; Rooney et al. 2013) or identifying mutants with unique grain composition (Pedersen et al. 2005; Tesso et al. 2006). One such most popular mutant line is P721Q with high protein digestibility and high lysine content but with agronomically undesirable floury endosperm texture. However, Tesso et al. (2006) reported the possibility of developing sorghum with near-normal endosperm along with high digestibility through traditional breeding approaches. But still, limited breeding efforts were carried out till now to develop agronomically adapted, high protein digestible sorghum cultivars (Duressa et al. 2018). In addition to mutant lines, large genetic variability for protein digestibility (Hicks et al. 2002; Wong et al. 2010; Elkonin et al. 2013) and protein content (Rhodes et al. 2017) were observed by many researchers. This genetic variability could be a potential source to breed cultivars for high protein digestibility and high protein content. Especially, Durra and Durra-bicolor races which were known to contain higher protein levels (Johnson et al. 1968; Rhodes et al. 2017) in their grains are potential breeding targets to develop cultivars with high protein content. Specifically, the durra race was found to have higher water extraction capacity under terminal water stress which gives yield advantage (Vadez et al. 2011). Therefore, this race is possibly useful to maintain yield and quality under a drought stress scenario.

A few researchers (da Silva 2012; Elkonin et al. 2016) reported work on transgenic sorghum where they used RNA silencing technology to silence  $\alpha$  and  $\gamma$  kaffirins synthesis to improve protein digestibility along with desirable vitreous endosperm). However, gene silencing was found to be sensitive to environmental conditions (Tuttle et al. 2008; Von Born et al. 2018), making it unsuitable for a wide range of environments. Another efficient transformation system was developed for sorghum by Liu et al. (2014) that allowed the development of transgenic sorghum for improved starch content. Particularly, overexpression of two potential target genes, sucrose synthase (Su Sy) and SWEET sugar transporters from maize and Rice (Eom et al. 2015) leads to improved starch content in the grain. Thus, upregulation of these homologous in sorghum may not only improve the starch content but also improves kernel size (Mudge et al. 2016). Nevertheless, these transgenic sorghum lines can serve as donors to transfer these traits into locally adapted cultivars through breeding. Same way, Gilding et al. (2013) identified a mutant allele in the starch metabolic gene, pululanase with increased digestibility and without any yield tradeoff. Introgressions of this mutant allele into elite sorghum lines through breeding may increase the yields as well as nutritional quality in adapted environments.

Exploitation of genetic variability in sorghum wild relatives is also an important strategy to improve the crop nutritional quality. Abdelhalim et al. (2019) found genetic variability and elevated microelements, protein content, digestibility and lower tannins in their study using Sudanese wild sorghum genotypes. Similar results were also shown by Peleg et al. (2008) in wheat wild genotypes. Recently, Cowan et al. (2019) demonstrated several sorghum wild relatives were less affected by severe drought compare to cultivated sorghums. Thus, introgressions of useful genes from wild sorghum to cultivated sorghum may improve the nutritional quality without compensating agronomical adaptability. Moreover, a wide genetic variability and a few GxE interaction for grain chemical attributes allow the ability to select desirable traits for particular environment (Kaufman et al. 2018). However, grain physical traits such as kernel weight, hardness, and diameter were found to be more prone to GxE interactions (Kaufman et al. 2018) which need to be taken into account while improving the quality under stress conditions.

GWAS is another promising tool to dissect genomic regions for several qualitative traits. In sorghum, GWAS has been used to identify several QTLs for protein, fat (Rhodes et al. 2017), starch (Boyles et al. 2019), minerals (Shakoor et al. 2015) and polyphenols (Rhodes et al. 2014). Recently, Kimani et al. (2020) used GWAS to identify 14 loci for starch content, 492 loci for 17 amino acids and 8 candidate genes for BCAA (branched chain amino acid) biosynthetic pathway. Other than macronutrients, sorghum

polyphenols are of major interest recently owing to their importance as healthy antioxidants. A few recent studies on GWAS for polyphenols reported several small and major effect markers as well as many QTLs for variation in tannin levels (Rhodes et al. 2017; Habyarimana et al. 2019). Two novel functional markers for antioxidant activity, identified on chromosome 9 and 10 could be directly used in breeding programs to improve the antioxidant levels in sorghum (Habyarimana et al. 2019). Identified candidate genes could be exploited in molecular breeding programs to improve the grain quality. However, while employing these tools to improve the grain quality under stress scenarios, it is necessary to study the stability of end-use quality traits across different environments.

## Conclusion

Climate change is a serious threat to the world agriculture and food production. Climate change affects agroecological systems and crops are more prone to abiotic stresses which results in substantial yield losses. Especially food crops in the arid and semi-arid regions of the world suffer from climate changes tremendously, affecting millions of people in those regions to suffer from malnutrition and hunger. In this scenario, it is essential to focus on climate-resilient crops to minimize the negative effects of climate change. Sorghum is one such climate-resilient crop which is naturally tolerant to abiotic stresses and can grow on marginal lands with minimum input. Also, it is one of the staple foods for people in the arid and semi-arid regions of the world where food security is at greater risk due to climate variability. It is also used as feed, fodder, bioenergy feedstock, and also gained recent popularity as healthy alternative food grain due to its nutritional quality and health benefits. Understanding sorghum sensitivity to different abiotic stresses allows breeding for improved cultivars for climate change vulnerabilities through conventional and molecular approaches. Advanced NGS technologies, high throughput GWAS and genetic engineering approaches identified several candidate genes/QTLs/alleles which would benefit the crop improvement programs under changing climate. So far, tremendous progress has been made to improve sorghum crop yields under stress scenarios. Although several efforts were made to improve the grain quality at the genetic level, maintaining and improving the quality under different stress scenarios is still challenging as grain physical and chemical attributes are prone to environmental changes and to some extent GxE interactions. Thus, further research efforts are still required to enhance the nutritional quality under changing climate. Moreover, in context to climate change, it is also essential for the research community as well as growers to diversify the strategies based on the local environments.

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## Declarations

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