Understanding the Physiological processes determining Sorghum Grain Nutritional Quality

A thesis submitted to the Bharathidasan University, Tiruchirappalli-620024
In partial fulfillment for the award of the degree of
Doctor of Philosophy in **Plant Biotechnology**

Submitted by
KEERTHI CHADALAVADA, M.SC.,
(Ref No: 40354/Ph.DK1/Plant Biotechnology/Part Time/April 2017 Dated:27.04.2017)

Under the guidance of
Dr. B. D. Ranjitha Kumari
Professor (Retd.), UGC – BSR Faculty Fellow
Department of Botany, Bharathidasan University,
Tiruchirappalli 620 024, Tamil Nadu, India

Under the co-guidance of

Dr. Jana Kholová, Ph.D.
Senior Scientist, Crops Physiology & Modelling
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT),
Hyderabad 502 324, Telangana, India
&
Dr. T. Senthil Kumar, M.Sc., M.Phil., Ph.D.
Professor, Department of Botany
Bharathidasan University, Tiruchirappalli, Tamil Nadu - 620 024.

Department of Botany
School of Life Sciences
BHARATHIDASAN UNIVERSITY
Tiruchirappalli-620024, Tamil Nadu, India

March 2022

DECLARATION

I hereby declare that the Ph.D. thesis entitled **“Understanding the Physiological processes determining Sorghum Grain Nutritional Quality”** submitted by me for the award of the degree of **DOCTOR OF PHILOSOPHY** in **PLANT BIOTECHNOLOGY**, has been originally carried out by me in the Department of Botany, School of Life Sciences, Bharathidasan University, Tiruchirappalli, under the guidance of **Dr. B.D. Ranjitha Kumari**, Professor (Retd.), UGC-BSR Faculty Fellow, co-guidance of **Dr. T. Senthil Kumar**, Professor, Department of Botany, School of Life Sciences, Bharathidasan University, Tiruchirappalli-620024, Tamil Nadu, India and co-guidance of **Dr. Jana Kholová**, Senior Scientist, Crops Physiology & Modelling, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Hyderabad, India. I, further, assure you that this work has not been submitted either in whole or part for any other degree or diploma at any other university.

(KEERTHI CHADALAVADA)

Tiruchirappalli

Date:

ACKNOWLEDGMENT

I would like to express my deepest gratitude to my supervisor, Dr. B.D. Ranjitha Kumari, Professor (Retd.), UGC-BSR Faculty Fellow, Department of Botany, Bharathidasan University, Tiruchirappalli for her guidance, encouragement, constant support, and valuable advice during my research work. This thesis would not have been possible without her encouragement. I am grateful to her for the time she had devoted to finish this research work.

It is a great privilege to express my gratitude to Dr. Jana Kholová, *co-guide, Senior Scientist, Crops Physiology & Modelling, ICRISAT, Hyderabad, for her valuable guidance, constant encouragement, meticulous suggestions, and productive discussions throughout the research work. Her profound knowledge is a source of inspiration during this journey. I am sincerely thankful for the endless opportunities and experiences she had provided to grow professionally.*

My deepest gratitude to Dr. T. Senthil Kumar, co-guide, Professor, Department of Botany, Bharathidasan University, Tiruchirappalli, for his critical support, guidance, and valuable suggestions to finish my research work.

I am grateful to the doctoral committee members, Dr. A. Lakshmi Prabha, Professor and Head, Dr. M. Sathiyabama, Professor, Department of Botany, Bharathidasan University, Tiruchirappalli, for their scientific discussions and constant feedback.

I sincerely acknowledge the valuable guidance, help, and technical support provided by Dr. Sunita Choudhary, Dr. Krithika Anbazhagan, Dr. Karthika Guna, Dr. Siva Sakthi Kaliamoorthy, Dr. Tharanya Murugesan, Ms. Rekha Baddam, Mr. Srikanth Mallayee, Mr. Subhash, and all the lab members and technical staff at Crop Physiology, ICRISAT.

I sincerely thank all lab members at Bharathidasan University, Dr. Sundararajan, Dr. Anil Kumar Moola, Mr. Thirumurugan, Mr. Prashob, and Ms. Yasotha for their help and co-operation throughout my research work.

I would like to express my deepest gratitude and affection to my parents, aunt, uncle, and my brother for their endless support and sacrifice which helped me to see the best of times. I am truly indebted to my husband, for his constant moral support, guidance, and encouragement to finish the thesis. Lastly, I owe a lot of gratitude to my little son, who needed my constant attention, yet supported me by controlling his emotions throughout this journey. I am extremely thankful to him and it wouldn't have been possible without his love and support.

Lastly, I would like to thank God for giving me the strength to overcome hurdles and to keep my spirits always high through hard times.

Keerthi Chadalavada

ABBREVIATIONS

Kg ha^{-1}	-	Kilograms per hectare
Plants m^{-2}	-	Plants per meter square
cm	-	Centimeter
%	-	Percentage
$g100g^{-1}$	-	grams per 100 grams
R^2	-	R squared
nm	-	nanometer
SD	-	Standard Deviation
SEC	-	Standard error of calibration
SECV	-	Standard error of cross validation
SEP	-	Standard error of prediction
RPDc	-	Ratio of Performance to Deviation for calibration
RPDv	-	Ratio of Performance to Deviation for validation
RMSE	-	Root mean square error
QTL	-	Quantitative trait locus
AFLP	-	Amplified fragment length polymorphism
SSR	-	Simple Sequence Repeats
DArT	-	Diversity Array Technology
stg	-	stay green
RIL	-	Recombinant Inbred Line
m	-	Meter
g	-	Gram
mg kg^{-1}	-	Milligrams per kilogram
g $plant^{-1}$	-	Gram per plant
g kg^{-1}	-	Grams per kilogram
CIM	-	Composite Interval mapping
cM	-	Centi Morgan
p	-	Probability
h^2	-	Heritability
DAS	-	Days to Flowering

WW - Well-watered
WS - Water stress
ANOVA - Analysis of Variance
PCA - Principal Component Analysis
LG - Linkage group
PVE - Phenotypic Variance explained
> - Greater than
< - Less than
SAT - Semi-Arid Tropics
^{o}N - Degree North
^{o}E - Degree East
mm - Millimeter
MJ m^{-2} - Mega Joule per square meter
°C - Degree Centigrade
cm^{2} - Square Centimeter
$m^{2}m^{-2}$ - Square meter per square meter
BPi - Biomass Partitioning Index
IVOMD - Invitro Dry matter Digestibility
w/w% - Percentage of weight per unit of dry weight
N - Normality
H_2SO_4 - Sulphuric Acid
HCl - Hydro Chloric acid
mg - Milligram
ml - Milliliter
PC - Principal Component
p - Pearson’s Correlation coefficient

CONTENTS

Publications

LIST OF TABLES

Table 3.2. Mean values of selected traits for each for seasons, genotypes, water, nitrogen and density . Season, water, nitrogen and density and their interaction (Water x Genotype, Water x Nitrogen, Water x Density, Nitrogen x Density, Nitrogen x Genotype, Density x Genotype) effects (F value and F probability) and LSD at 5% level were generated using ANOVA by taking treatments and their combinations as treatment structure (season+ water+ nitrogen+ density+ genotype+ water x nitrogen + density x nitrogen+ water x density+ water x genotype + density x genotype + nitrogen x genotype). ***, **, * represents significance of the differences (at >0.001; <0.001, 0.01> and <0.01, 0.05> levels) for each treatment and treatment combinations for the estimated characteristics. The letters behind the values represent result of the Tukey-Kramer test and different letters indicate significance of differences between genotypes at 0.05 level. Broad sense heritability (h^2%) was calculated across seasons and treatments by treating genotype as random.

Table 3.3. Mean values of selected traits for water treatment (WW&WS) within each genotype (6008, 6026, K359W, M35-1, R16 and S35) were generated using ANOVA by taking treatments and their combinations as treatment structure (season+ water+ nitrogen+ density+ genotype + water x nitrogen + density x nitrogen+ water x density+ water x genotype + density x genotype + nitrogen x genotype + water x genotype x nitrogen x density). The letters behind the values represent result of the Tukey-Kramer test and different letters indicate significance of differences between genotypes at 0.05 level. values in parenthesis represent proportion of change in measured traits due to water stress treatment for each genotype.

LIST OF FIGURES

GENERAL INTRODUCTION

Worldwide, sorghum grain is used as feed and food and has largely unexplored potential for industrial uses. Apart from this, the livelihood of subsistence farming communities especially in SAT regions of developing countries depends on sorghum grain production. Sorghum is one of the five cereal crops that provide 60% energy intake of the world population (Kane-Potaka et al., 2021). Sorghum production was increased to 60 million tons globally in the year 2020. Improving the agricultural productivity of this crop is a vital issue to feed the expanding population in SAT regions where farming systems are mostly affected by soil infertility and limited water reserves. Along with productivity, improving the nutritional composition of the grain is a key factor to consider for elevating the population living in developing countries from chronic malnutrition. It is estimated that the most fatal form –protein-energy malnutrition affects every fourth child worldwide (McGloughlin and Burke, 2014). Diet including nutritionally improved staple crops, such as sorghum, appears as one of few viable options which can improve the nutritional status of the population in these areas, especially among children. While the research for the improvement of sorghum yields received necessary attention (Vadez et al., 2011a and b, Borrell et al., 2000a, Mace and Jordan 2010, Kholova et al., 2014), the research on sorghum nutrition appears to lag mainly in the understanding of the plant mechanistic leading to variability in grain quality within the complex framework of cropping systems interactions (Betts et al., 2015).

In the last decade, breeding, including selection criteria for various components of stay-green (green shoot until maturity) phenotype (Vadez et al., 2011a, Kholova et al., 2014, Borrell et al., 2013) proved to enhance sorghum adaptation to water-limited cropping systems. Kassahun et al. (2000) developed the plant genetic resources for the characterization of the physiological basis of the stay-green phenotype. Using this material, the physiological processes leading to stay-green phenotype expression underlying the yield improvements under drought have been elucidated (Vadez et al., 2011a, Kholova et al., 2014). This plant material also provided evidence, that the same physiological mechanisms underlying drought adaptations can simultaneously improve the stover quality parameters for livestock production (Blummel et al., 2015). The question persists, whether the plant mechanisms improving sorghum drought adaptation and stover quality could be, in the end, responsible even for the improvement of important grain quality parameters.

In sorghum, a few key indicators reported for grain quality are already defined; Moisture content: (<14.5 %), ash: (<1.5 %), protein: (>7 %), tannins: (<0.5 %) on dry matter basis (FAO/WHO food standards program, Codex Alimentarius Commission, 1995). However, all these physical and chemical grain properties vary significantly due to the influence of genotype, environment, and management (GxExM) (Betts et al., 2015). Understanding the variability of these grain quality determinants due to GxExM is of the utmost importance since the majority of the sorghum is produced under highly variable conditions than most of the other cereals (mostly rain-fed and low-input conditions of semi-arid tropics (SAT)). So, understanding causal plant physiological processes leading to the grain quality fluctuations along with its genetic determination are important to support the breeding programs and increase the potential socio-economic value of sorghum grain for various end-users.

Therefore, the main aim of the study is to understand plant physiological processes leading to the variability in main grain quality characteristics and their interaction with the environment. Planned work will provide the research evidence for setting the sorghum breeding targets in line with a global goal for improvement of the nutritional status of the poverty threatened population in SAT. Generated outputs will be a necessary prerequisite for promoting the sorghum grain value chain.

OBJECTIVES

1. Rapid tools development for nutritional constituents using Near Infrared (NIR) spectroscopic technology

- Development of rapid tools specific to sorghum to estimate main grain nutritional components (Protein, Fat, and moisture) using Near Infra-red Reflectance Spectroscopy (NIRS).
- Collection of various cereals grain material and development of common calibration model for all cereals for respective major macro nutrients (Protein and Fat) which enables to use of single calibration for all cereals used in calibration development.
- Improving common cereal calibration models for major macro nutrients using machine learning algorithms.

2. Genetic determination of the main agronomic and quality indicators

- Screening of the parents of sorghum mapping populations and stay green near-isogenic lines (NILs) for water use traits as well as main nutritional quality indicators

- Selection and screening of suitable mapping population segregating for the main grain quality indicators & QTL (quantitative trait loci) analysis

3. **Understanding the plant physiological mechanisms influencing the main agronomic and grain quality indicators**

   - Assessing the magnitudes of the stay-green QTL effect on main agronomic and grain quality indicators
   - Assessing the Genetic (G) effect), environment (E), and management(M) effect on the agronomic and grain quality indicators
   - Understanding the functional linkages between the agronomic and qualitative traits which affect the grain nutritional quality

CHAPTER 1

Rapid tools development for nutritional constituents using Near Infrared (NIR) spectroscopic technology

1.1 Introduction

Cereal grains are the primary source of nourishment to humans for many decades. Particularly, consumption of coarse grain cereals such as sorghum and millets are more in semi-arid tropics (SAT) of the world where drought stress is the major issue. Thus, these grains are the major contributors to calorie intake in the semi-arid tropics. Particularly, sorghum is one of the staple food grains for the small farming communities in the tropic and semi-arid tropic regions of the world. The food and feed value of sorghum has gained importance as it can sustain well in the water-limiting environments where malnutrition is prevalent. Also, because of its potential health benefits and gluten-free characteristic, sorghum food products gained importance in recent days. It is known that the rheological and sensory properties of millet grains and their end products change based on the parameters like protein and fat. Along with sorghum, other coarse grain cereals such as pearl, foxtail, finger, barnyard, Kodo, porso millets are also typically grown across the semi-arid tropics and became important sources of nutrition for the most vulnerable farming communities in developing countries. All these coarse grain cereals are generally more climate-resilient and nutritionally dense (Diao 2017, Wang et al., 2018) compared to rice and wheat and are slowly gaining interest among governments, public health organizations, and researchers as resources to alleviate malnutrition in SAT regions of developing countries (Mckevith 2004, Girish et al., 2014, Kumar et al., 2018). Despite a reasonably large proportion of the variation of the grain nutritional components for these cereals appears to be genetically controlled (Charmet et al., 2005, Balyan et al., 2013, Mahjourimajd et al., 2016), substantial variation for grain composition might also be driven by environments and crop management practices (Rozbicki et al., 2019). Thus, to further enhance grain nutritional quality, the researchers will have to explore these traits' genetics along with the components linked to environmental variability and this will require rapid and accurate evaluation of germplasm across a range of environments. Nutritionally superior agricultural products also require rapid assessment of grain qualities across the grain-related value-chains to improve the socio-economic potential of these grains.

Assessment of grain quality using traditional laboratory techniques for a large number of samples is cumbersome and time-consuming. Near-Infrared spectroscopy (NIRS) is a rapid tool technique that can assess a large number of samples within no time. The technique is based on the vibrational properties of molecules and their interaction with light. It is an indirect technique that needs accurate chemical analysis of each trait and good variability in the material to develop calibrations. Furthermore, the predictability of the calibration model principally depends on the accuracy of the chemometric method (Estienne et al., 2001, Chang et al., 2016, Levasseur-garcia, 2018) and the algorithms used for the predictions. There have been a lot of methods developed to treat the acquired spectra (Cheewapramong, 2007, Kahriman et al., 2011, Agelet and Hurburgh, 2014). Many statistical [e.g., principal component analysis (PCA), partial least squares regression (PLSR), multiple linear regression (MLR)] and machine learning models [e.g., random forest (RF), support vector machines regression (SVR), artificial neural networks (ANN), ensemble learning techniques and convolutional neural networks (CNN)] have been successfully used for the prediction of grain composition analysis of NIR spectra data.

NIRS is also known to be sensitive to year, location, variety, and time of sowing (Dardenne, 1996). Thus, narrow range-based NIRS calibrations which use only around 50-75 independent samples are useful to test small homogeneous populations. But to increase the preciseness of calibration, a large number of samples (Villamuelas et al., 2017) are required. At the same time, it is essential to include all the possible sample variability to make the calibration suitable for a broad range of situations. But limited sample size and unexplored variability within the species are two major constraints to develop precise calibrations for minor cereals. Even if these were available, developing separate calibrations for the vast number of minor cereals species with limited sample availability might be difficult. Thus, the development of multi-species calibration where the samples from different species with wide variance can be included in a single equation is one of the solutions to use the calibration model for a broad range of situations. Many multi-crop calibrations are reported in the literature, but most of them were focused on forage and feed analysis and less emphasis was given to multi-crop grain calibrations (Garcia and Cozzolino, 2006, Stubbs et al., 2010, Tahir et al., 2012, Black et al., 2009). Hence, we hypothesize, multi-species grain calibrations would be as useful as mono species calibration.

Thus, to start with, our current study aimed

i) To develop and validate single species (sorghum) grain calibration models for basic qualitative traits such as moisture, protein, and fat using sorghum grain samples grown in different environments

ii) ii) to develop and validate multi-species calibration models for protein and fat using sorghum and different millet samples which can be used to predict a wide range of samples within and among different cereal species.

iii) To improve multi-cereals calibration with multivariate algorithms

1.2. Materials and Methods

1.2.1. Plant samples

Grain samples collected for the calibration development consist of samples from different experiments, treatments, genotypes, and species.

Samples for sorghum calibrations were collected from two post rainy seasons, 2013-14 and 2014-15. 2013-14 samples comprise of 12 genotypes which include 8 stay green introgression lines (K359W, K648, 6008, 6026, 6040, and 7001), their senescent parents (R16 and S35), 3 elite lines, and (Phule vasudha, Parbanimoti, CRS1) a local check (M35-1). 2014-15 samples include 8 genotypes which comprise of 5 stay green introgression lines (K359W, 6008, and 6026), their senescent parents (R16 and S35), 2 elite lines (Phule vasudha and REVT 9), and a local check (M35-1). Among these, 6 genotypes were common in both seasons. Experiments were carried out using a completely randomized design with three replications along with factorial treatments of water (well-watered (WW) and water stress (WS)), nitrogen (high Nitrogen (HN): 90 kg ha^{-1} and low nitrogen (LN): 0/30 kg ha^{-1}) and density (high (HD): ~10 plants m^{-2} and low (LD): ~5 plants m^{-2}) for each block, resulting in HNHD, HNLD, LNHD and LNLD in both WW and WS treatments. Each plot contained 8 rows of 4 meters length with 60 cm row to row spacing. Grain samples were collected from 6 rows of each plot by leaving one row on each side. Grains were harvested from each plot at the time of maturity and replicated samples of each treatment combination were mixed to make a single sample that represents the overall variability of the sample.

1.2.2. Samples for cereal calibrations

For cereals calibrations, grains from various species were collected from lysimetric studies conducted in rabi 2016-17. The fertilizer application was the same as the above experiment. Each genotype was grown in 5 replications and irrigated throughout the cropping period. A total of 142 samples of grains from five cereal species were used in the study– sorghum [Sorghum bicolor (L.) Moench], pearl millet [Pennisetum glaucum (L.) R. Br.], foxtail millet [Setariaitalica (L.) P. Beauvois], finger millet (Eleusine coracana Gaertn.) and maize (Zea mays L.). Sixty-two sorghum samples comprising of four races (bicolor, caudatum, durra, and guinea) originating from Burkina Faso, Cameroon, Ethiopia, India, Lesotho, Mali, Nigeria, and the USA were obtained from ICRISAT's sorghum improvement program. This set included released sorghum varieties and BCNAM population lines. Twenty-six pearl millet samples originating from Ghana and India, comprising mostly of private sector-released cultivars were obtained from ICRISAT's pearl millet improvement program. Fourteen maize cultivars were obtained from CIMMYT's maize improvement program. From ICRISAT's gene bank, twenty finger millet samples originating from India, Kenya, Malawi, Senegal, Uganda, and Zimbabwe and twenty foxtail millet samples originating from China, India, Iran, Pakistan, Russia, and the USA were used in the study (Table 1.1).

All the samples were cleaned and dried. The replications of each genotype were mixed to make a single sample and ground to a fine powder using a cemotech sample mill (FOSS technologies). Ground samples were stored in sealed plastic bags and stored at 4°C until the analysis.

The ground grain samples were dried at 130°C for 2 h in the hot air oven before chemometric analyses. Laboratory analysis for each sample was carried out using standard AOAC protocols (Association of Official Analytical Chemists; AOAC, 2000): moisture content (AOAC 925.10); total fat content (AOAC 920.39), and total nitrogen content (Kjeldahl method, AOAC; 2001.11). Crude protein content was estimated by multiplying the nitrogen content with a protein conversion factor of 6.25 (Mulder, 1839). The values were reported on a dry matter basis i.e., weight of the component per total dry weight of the sample (%, [g 100 g^{-1}]).

1.2.3. NIRS analysis

All the milled samples were scanned in the circular ring cups with an inside diameter of 36 mm, with a FOSS XDS NIR spectrometer (FOSS North America, Eden Prairie, MN, USA) before proceeding for chemical analyses. Spectra were collected using ISI scan software, version 4.4. This spectral data was collected as the logarithm of reciprocal of reflectance (1/R) including both visible and NIR range (400-2498 nm wavelength) and stored at 2nm intervals. Then these samples were divided into calibration and validation sets.

1.2.3.1. FOSS inbuilt winISI software

Calibration equations were derived using winISI software, version 4.3. Modified partial least square method (MPLS), which is considered to be a stable and accurate algorithm for agricultural applications (Shenk et al., 1996) was used to get the calibration equation for each variable separately. The internal cross-validation method of groups by cycling was used by the software to validate the calibrations developed. Samples with Mahalanobis distance (H) >3 were considered as outliers and were removed during the calibration process. The scatter correction of standard normal variant and detrend (SNV-D) and mathematical equation of 2,4,4,1 was applied in which the first digit represents the number of derivatives, the second digit represents gap over which derivative is calculated, third is the number of data points used for smoothing and 4th one is second smoothing. This mathematical treatment gave the highest coefficient of variation (R^2) and coefficient of variation for cross-validation (1-VR) and the lowest standard error of cross-validation (SECV) for the calibration equations generated. The ratio of performance to deviation (RPD) (SD÷SECV or SEP) was used to evaluate the quality of calibrations (Williams and Sobering, 1996). Calibrations were validated using validation data set to see the accuracy and predictability of the equations generated. Better prediction performance was identified by the low standard error of prediction (SEP) and the highest coefficient of variation(r^2).

1.3. Results and Discussion

1.3.1. Reference data

Tables 1.2 and 1.3 show minimum and maximum values, range, and standard deviation of datasets used for calibration and validation for sorghum and cereals models respectively. For the sorghum calibration model, ranges were 6.96-13.95 (%) for protein, 1.5-5.41 (%) for fat, and 9.07-10.56 (%) for moisture. For validation, the ranges of samples used were 12.45-15.75 (%) for protein, 2.75-4.78 (%) for fat, and 9.22-10.26 (%) for moisture. For cereals, the calibration data set showed a range of 5.39-15.95 (%) for protein and 1.16-11.36 (%) for fat. The validation set contains a range of 8.73-12.62 (%) for protein and 2.78-4.68 (%) for fat. As expected, the range of protein and fat content for the multi-cereals (6–15 % and 1–10 %, respectively) was higher compared to the individual species. Among the five cereals tested, protein and fat content in pearl millet grains was highest (11 % and 9 %, respectively) and lowest in finger millet grains (8 % and 2 %, respectively).

In addition to that, for all the data sets, median values for each constituent were either left or right-skewed showing non-gaussian distribution of data. When comparing the descriptive statistics between calibration and validation data sets for cereals, mean, standard deviation, and range were within the limits of the calibration data set (tables 1.2 and 1.3) suggesting, developed calibration equations could be applied to validation datasets without any extrapolation. However, in the case of the sorghum calibration model, calibration and validation data sets were different, especially for the protein data set which contains a higher range of values, that gave a chance of extrapolation during validation in the case of the protein model. But due to the availability of a limited number of samples in combination with reliable reference data set, the experiment was progressed as such.

1.3.2. NIR spectra

The overlaid NIR reflectance raw spectra for sorghum and cereal samples were shown in Figures 1.1 and 1.2. The overlaid log 1/R reflectance raw spectra for each crop in the cereal dataset showed peaks and troughs at similar positions, showing they belong to the same population even though they were from different species. 2nd derivative spectra for both the models were calculated from log1/R spectra with a gap of 8 nm (4 data points) and smoothing over 4 data points with no second smoothing (2,4,4,1). The second derivatized spectrum for sorghum and cereal models were shown in Figures 1.3 and 1.4.

The average raw spectrum of sorghum showed NIR absorption bands over different wavelengths such as 984, 1198, 1450, 1934, 2104, 2310 nm. Second derivative spectra showed a trough for each peak in the raw spectra by removing the overlapping peaks and baseline shifts. The important absorption bands observed in the 2nd derivative spectra of sorghum samples were at wavelengths 1390, 1674, 1882, 2014, 2240, and 2294. The average raw spectrum of multi-cereals samples shows absorption bands at nearly the same wavelengths as sorghum samples. 2nd derivative spectrum of cereals shows absorption bands at 1698, 1728,1922, 2052, 2280, and 2332. It shows organic functional groups from different species of cereals show the absorption bands at more or less similar wavelength positions.

Workman and Weyer, (2012) described chemical information with regards to various functional groups responsible for absorption or reflection of NIR spectra at different wavelengths. According to that, in the 2nd derivative spectra of sorghum grain samples, 1390 nm related to C-H methyl C-H, aliphatic hydrocarbons, 1674 nm related to C-H aromatic C-H aryl group, 1882 nm related to O-H hydrogen bonding between water and exposed poly vinyl alcohol (OH), 2014 nm related N-H/C=O combination, poly amides, 2240 nm related to CHO groups and 2294 nm related to C-H aromatic C-H aryl groups. Similar way, in the derivatized spectra of cereal samples, 1698 nm related to CH-methyl -C-H(CH_3), aliphatic hydrocarbons, 1728 nm related to aliphatic hydrocarbons, CH-methylene-(CH_2) and amines, 1922 nm corresponds to amide groups, 2052 nm related to peptide β sheet structures and protein as normalized 2nd derivative spectra of proteins in aqueous solution, 2280 nm related to C-H starch (C-H&CH_2) and 2332 nm related to C-H (C-H &CH_2) polysaccharides (Workman and Weyer, 2012).

1.3.3. Calibration models development

FOSS winISI software: The best equations for all the constituents in both sorghum and cereal calibration models were achieved by modified partial least square regression model using math treatment 2,4,4,1 which gave highest R^2 and lowest SECV.

The accuracy of the calibration model was evaluated from the R^2 value and ratio of performance to deviation of calibration (RPDc: SD of reference values/SECV of calibration). R^2 signifies the variance percentage present in the Y variable that is explained by the X variable (Saha et al., 2017). According to literature (Williams, 2003), R^2 between 0.5-0.65 shows high and low concentrations can be distinguished. A value between 0.66-0.81 shows approximate predictions can be made. A value of R^2 between 0.81-0.9 reveals good predictions can be made and R^2 above 0.91 shows excellent predictions are possible. Calculation of RPD to evaluate the accuracy of the calibration was reported in literature earlier (Saeys et al., 2005, Reeves III. J.B, 2001, Ward et al, 2011, and Williams, 2003). According to William, (2003), calibrations can be distinguished into five groups based on RPD values. RPD value below 1.5 shows calibration is not useful. If the RPD is between 1.5 and 2.0, high and low values can be differentiated. If the value is between 2 and 2.5, predictions can be done approximately. Finally, a value between 2.5 and 3.0 indicates good predictions, and a value above 3 shows excellent predictions are possible.

1.3.3.1.1. Sorghum calibration model

Table 1.4 shows statistics of calibration and validation for sorghum protein, fat, and moisture. The protein equation showed R^2 of 0.94 and SECV of 0.39. Fat equation showed R^2 of 0.94 and SECV of 0.26. Moisture equation showed R^2 of 0.93 and SECV of 0.14. All the constituents in the sorghum calibration model achieved an R^2 value of above 0.91. But the RPDc values were 2.96, 2.5, and 1.75 for protein, fat, and moisture respectively.

When considered RPDc values, it shows calibration equations generated for protein and fat can give good quantitative predictions. Figure 1.6 shows the scatter plots of reference values and NIRS predicted values. Data points near to diagonal 1:1 line show closeness between laboratory analyzed and predicted values. The slopes of the equations slightly deviated from 1 for protein and fat. (Protein: 0.91; fat: 0.95). It shows developed equations may tend to over or under-estimating the constituents. To confirm this, a separate validation set was chosen to validate the accuracy and reliability of these equations.

1.3.3.1.2 Independent validation of calibration models

The prediction ability of calibration models generated was tested using separate validation sets for each equation. Coefficient of determination for validation set (r^2), slope, SEP, RPDv, and RER were used to estimate the reliability and accuracy of calibrations developed. In general, low SEP (bias-corrected SEP), high $r^{2,}$ and slope close to one are considered to be important criteria for calibration reliability and accuracy. Here for sorghum, protein and fat calibration models showed r^2 greater than 0.9 (Protein: 0.93; fat: 0.92) and SEPc as low as 0.44 to 0.29 (Table 1.4). But RPDv (SD of reference values/SEP) values for protein, fat, and moisture were 1.92, 3.52, and 4.07 respectively which shows good prediction ability of fat and moisture equations, but a slight extrapolation given by the protein equation. The protein reference data taken for validation was in a higher range compared to the calibration dataset which contributed to data extrapolation. This shows equation is not good enough for predicting a higher range and this range needs to be included in the calibration to achieve accurate prediction ability.

1.3.3.2.1. Cereal calibration models

Table 1.5 shows the statistics of calibration and validation equations of protein and fat for multi-species cereal dataset which include sorghum, pearl millet, finger millet, maize, and foxtail millet grain flour samples, and figure 1.7 shows measured vs. predicted plots for protein and fat. Around ~15-16 samples from the multi-cereal calibration data set were detected as outliers by winISI software and were removed from the calibration. Protein and fat equations exhibited R^2 of 0.80 and 0.92 respectively along with SEC and SECV values of 0.75 and 0.81 for protein and 0.66 and 0.85 for fat. R^2 values show good predictions can be made for protein and fat constituents, whereas, RPDc calculations of these equations showed fat equation is useful to make good predictions (2.76) and the protein equation is useful only for approximate predictions (2.08).

1.3.3.2.2. Independent validation

Validation of multi-cereal calibrations was done using an independent set of sorghum samples. The accuracy and prediction ability of calibration models for cereals protein and fat were evaluated using this validation set which was not used for calibration. Correlation coefficient (r^2) values for protein and fat were 0.85 and 0.78 respectively (Table 1.5). SEP values were 0.4 and 0.22 respectively for protein and fat. Slope values were 1.3 and 0.88 for protein and fat respectively. RPD values were 2.2 (protein) and 2.08 (fat). These validation statistics revealed, developed calibrations using FOSS built winISI software can make only approximate predictions of given constituents ($0.66<r2<0.8$ and $2<RPDv<2.5$) (Zornoza et al., 2008) but still can be useful for rapid screening of breeding material.

Developed calibration models and independent validation results using winISI software showed it is possible to use a single equation for predicting the grain composition of different cereals. The results revealed many facts which need to be considered while developing either mono-species or multi-species calibration models and analyzing the prediction ability of the equations for accuracy and reliability. Uniform distribution of reference data set is important while developing calibrations. Small concentrations of higher or lower constituent values in the sample set may favor higher correlation coefficients compared to evenly distributed samples. If it is the case, the robustness of equations can be improved by adding additional samples for low-density values (Saha et al., 2017). In the present work, lower concentrations of higher (in case of fat) and lower (protein) values could be seen in the multi-cereal sample set which might have affected the calibration accuracy of the models generated. More samples with reference values closer to the mean could also be affected the calibration accuracy. In addition to that, the type of material used for calibration purposes also affects calibration development. The agricultural products are more complex and heterogeneous material, estimates of which are influenced by many factors such as locations, seasons, and treatments. So, compare to calibrations from more homogeneous samples, less robust calibrations can be expected from agricultural products which is the case here. Even though less robust, these kinds of calibrations are still useful for approximate predictions which in turn allow the rapid screening of breeding material. Previous studies suggested, multi-species calibrations are not necessarily more accurate compared to mono species calibrations and a tradeoff may always exist between the robustness of calibration to predict samples of wide variability and accuracy of those calibrations (SEP) (Villamuelas et al., 2017).

1.3.4. Progress with advanced NIR tools

Recent advance in NIR technology offers a wide range of benchtop (FOSS-DS2500 flour analyzer, Bruker’s Tango FT-NIR spectrometer, Perten-IM9520 as well as mobile sensors (MEMS spectrometer from Fraunhofer and Hone Lab Red from Hone) which are suitable for a wide range of applications and also helpful to use in different environments without any difficulty. ICRISAT in-house laboratory facilities recently acquired a modified version of the FOSS XDS NIR sensor i.e., FOSS DS 2500 and also HLEVT5 (Hone Lab Engineering Validation Test model-5) mobile sensor developed from Hone, Australia. So, it gave the opportunity to treat cereal samples used for multi-cereal calibrations with FOSS DS2500 (range: 400-2498 nm) benchtop sensor and also with mobile HLEVT sensor (range: 1350-2550 nm) in combination with multivariate algorithms offered by Hone Create platform (https://www.honecreate.com) to improve the performance of multi-cereal calibrations.

1.3.4.1. Samples

Additional samples were added to the previous calibration set for multi-cereals which consists of 142 samples collected from sorghum, pearl millet, finger millet, foxtail millet, and maize. So, the total sample size was increased to 328 now. Additional samples were taken from the ICRISAT gene bank. Reference analysis for protein constituents (procedure mentioned in materials and methods) was carried out for all the samples.

1.3.4.2. Collection of spectra

FOSS DS2500 benchtop sensor: Spectra were collected as per the procedure explained for the FOSS XDS sensor explained in the methods and materials section in the wavelength range of 400-2498nm. EVT5 mobile sensor: Each sample was scanned at three different points of the sample spread on the Petri plate. The mobile application was programmed such that to record two scans at each position resulting in a total of six scans per sample. NIR reflectance spectra ranging from 1350–2550 nm with a resolution of 16 nm was subsequently extracted from the Hone Create platform (https://www.honecreate.com)

1.3.4.3. Calibration development

Samples were divided into calibration (80%: 262 samples) and validation sets (20%: 66 samples). This large data set allowed to split samples in such a way, both calibration and validation sets include similar variability to avoid any extrapolation. After feeding the spectral data into FOSS inbuilt winISI software the mathematical treatment 2,4,4,1 was applied and calibration equations were generated for protein constituents (detailed method explained above).

HLEVT 5 generated spectral data was fed into the hone-create platform where it offers a series of pre-processing steps such as derivative, area normalization, baseline shift, standard normal variate to treat the spectra for improved signal. Then the spectral data were processed using a series of multi-variate algorithms available in the hone-create platform such as distributed random forest (DRF), generalized linear model (GLM), gradient boosting machine (GBM), extreme gradient boosting (XGBoost), deep learning, and stacked ensembles. The hone-create platform automatically selected the best calibration model using the metrics, root mean squared error (RMSE), and coefficient of determination (R^2). The same metrics were calculated for FOSS-winISI derived calibration for protein to compare both calibrations. Then both calibrations derived from FOSS DS2500 and HLEVT5 mobile sensors were validated with the validation set with respective algorithms (FOSS- winISI and HLEVT5: multivariate algorithms from Hone) and similar metrics were generated. RPD was also calculated using standard deviation and root mean squared error (RMSE) of calibration and validation data sets.

FOSS winISI software used a modified partial least square algorithm (MPLS) and attained R^2 of 0.90 and RMSE of 0.91 for calibration set and RMSE of 1.09 and R^2 of 0.86 for the validation set (Table 1.6; Figure 1.8). The RPD values for the calibration and validation sets were 3.56 and 3.08 respectively. In the same way, Hone-create platform-selected stacked ensembles as the best calibration algorithm for HLEVT5 generated spectra and achieved R^2 of 0.98 and RMSE of 0.42 for calibration set and R^2 of 0.91 and RMSE of 0.97 for the validation set. (Figure 1.9). The model showed RPD values of 7.79 and 3.48 for calibration and validation set, respectively.

Thus, these results explained the role of advanced NIR tools for achieving better calibrations with improved prediction accuracy. Here, it was demonstrated that handheld mobile sensors are as useful as benchtop NIRS sensors for acquiring spectra from the samples. Also, mobile sensors allow the use of samples in any environment and save time and effort for sample processing. At the same time, these results demonstrated the superiority of multi-variate algorithms for achieving better prediction accuracy compared to classical statistical algorithms such as partial least square and principal component regression. The results obtained for protein constituent using multi-variate algorithms were found to be satisfactory and helped to start similar analyses for other constituents.

1.4. Summary

In the current study, attempts were made to generate NIR calibrations for samples derived from mono-species (sorghum) and multi-species (different cereal samples). The prediction ability of sorghum calibrations was good to estimate protein and fat constituents from grain samples within the calibration range. The inclusion of more variability and range could further improve the calibrations in future studies which will help to test a wide variety of sorghum samples available across different environments. Further, experiments were conducted to develop a single calibration equation to predict grain constituents using different cereal samples. Developed multi-cereal equations for protein and fat are useful to give approximate predictions that help in the rapid screening of breeding material in the agricultural sector. The availability of fewer samples from different species and ununiform distribution of samples within the available range prevented achieving more robust calibrations in this case. These constraints directed to use of advanced benchtop and mobile sensors in combination with multi-variate algorithms for improved calibrations. In the current study, robust calibrations for protein constituent were achieved using these tools compared to classical statistical methods. The generated calibrations can be useful in a wide range of applications and also can replace the time-consuming and laborious reference analysis. In the future, the same kind of robust calibrations can be achieved for various nutritional constituents which help to improve the grain value chain globally.

Table 1.1. **Details of genotypes of five cereal species along with the protein and fat content (%, [g/ 100 g]) estimated by laboratory analysis used as the reference data for the construction of calibration models**

S. No	Crop	Genotypes	Origin	Fat (%, [g/100 g])	Protein (%, [g/100 g])
1	Finger millet	IE 2043	India	1.91	7.21
2	Finger millet	IE 2296	India	1.70	7.65
3	Finger millet	IE 2572	Kenya	1.41	7.37
4	Finger millet	IE 2606	Malawi	3.51	9.59
5	Finger millet	IE 2790	Malawi	1.56	6.76
6	Finger millet	IE 3077	India	1.72	6.76
7	Finger millet	IE 3470	India	1.64	7.61
8	Finger millet	IE 3475	India	1.40	7.54
9	Finger millet	IE 3614	ICRISAT	4.11	5.99
10	Finger millet	IE 3618	India	1.86	7.58
11	Finger millet	IE 4057	Uganda	2.89	8.01
12	Finger millet	IE 4073	Uganda	1.85	7.39
13	Finger millet	IE 4115	Uganda	3.17	7.55
14	Finger millet	IE 4121	Uganda	1.53	8.78
15	Finger millet	IE 4671	India	1.89	9.07
16	Finger millet	IE 5066	Senegal	3.23	9.50
17	Finger millet	IE 5106	Zimbabwe	3.47	8.88
18	Finger millet	IE 5165	India	1.49	8.65
19	Finger millet	IE 518	India	1.59	7.62
20	Finger millet	IE 5367	Kenya	1.63	9.00
21	Foxtail millet	ISe 1251	Russia	4.31	10.96
22	Foxtail millet	ISe 1454	India	4.13	11.08
23	Foxtail millet	ISe 1468	India	4.27	9.06
24	Foxtail millet	ISe 1511	India	4.38	11.13
25	Foxtail millet	ISe 1664	India	5.28	12.39
26	Foxtail millet	ISe 1805	India	4.85	12.45
27	Foxtail millet	ISe 1881	India	4.41	12.66

28	Foxtail millet	ISe 1892	USA	4.78	12.91
29	Foxtail millet	ISe 200	India	5.60	13.18
30	Foxtail millet	ISe 238	India	4.12	11.92
31	Foxtail millet	ISe 289	India	3.89	10.39
32	Foxtail millet	ISe 480	China	3.98	10.86
33	Foxtail millet	ISe 525	Iran	4.09	10.52
34	Foxtail millet	ISe 719	Pakistan	4.74	11.89
35	Foxtail millet	ISe 783	India	5.18	13.42
36	Foxtail millet	ISe 796	India	4.56	11.65
37	Foxtail millet	ISe 827	China	4.75	13.17
38	Foxtail millet	ISe 828	China	4.28	11.40
39	Foxtail millet	ISe 840	India	4.61	9.89
40	Foxtail millet	ISe 869	India	4.76	10.82
41	Maize	783527	CIMMYT	5.64	9.34
42	Maize	4695575	CIMMYT	5.21	9.97
43	Maize	8315622	CIMMYT	5.35	8.68
44	Maize	9424780	CIMMYT	4.72	9.62
45	Maize	14746185	CIMMYT	5.45	8.92
46	Maize	18270413	CIMMYT	5.45	9.04
47	Maize	22525674	CIMMYT	5.11	9.10
48	Maize	30V92	CIMMYT	4.29	9.37
49	Maize	900MG	CIMMYT	4.17	8.98
50	Maize	X35D602	CIMMYT	4.95	8.76
51	Maize	X35D612	CIMMYT	5.05	8.53
52	Maize	X35D620	CIMMYT	4.72	8.81
53	Maize	X35D623	CIMMYT	4.69	8.94
54	Maize	X35F833	CIMMYT	5.02	9.21
55	Pearl millet	9444	India	9.19	12.53
56	Pearl millet	841B	ICRISAT	8.33	10.26
57	Pearl millet	841B x PPMI 301 (Pusa 322)	India	8.81	9.69
58	Pearl millet	86 M 86	India	9.36	14.41

59	Pearl millet	86 M 88	India	8.94	11.42
60	Pearl millet	863B	ICRISAT	7.50	11.65
61	Pearl millet	APH 45	India	8.03	10.45
62	Pearl millet	Bio 451	India	8.66	10.29
63	Pearl millet	Bio 549	India	9.15	10.61
64	Pearl millet	BLMPH 105	India	6.46	10.16
65	Pearl millet	GB8735	Ghana	9.41	10.87
66	Pearl millet	GK 1183	India	6.94	11.75
67	Pearl millet	GK 1207	India	7.55	10.41
68	Pearl millet	GK 1235	India	8.86	11.02
69	Pearl millet	H77/833-2	India	4.12	9.76
70	Pearl millet	HT 416628	India	9.59	12.31
71	Pearl millet	HYMH 5	India	9.16	12.67
72	Pearl millet	HYMH 8	India	7.16	12.24
73	Pearl millet	JKBH 1352	India	8.54	9.72
74	Pearl millet	JKBH 1490	India	8.20	13.44
75	Pearl millet	KH 3022	India	8.52	11.19
76	Pearl millet	NBH 5863	India	8.77	10.48
77	Pearl millet	NU 399	India	9.71	10.62
78	Pearl millet	NU 409	India	10.43	10.65
79	Pearl millet	PRLT	ICRISAT	9.12	10.09
80	Pearl millet	Super Boss	India	9.09	11.91
81	Sorghum	00-CZ-F5P-135	Mali	1.98	12.55
82	Sorghum	01-BE-F5P-15	Mali	1.81	12.07
83	Sorghum	02-SB-F4DT-275	Mali	2.24	13.09
84	Sorghum	296B	India	3.85	10.48
85	Sorghum	98-BE-F5P-84	Mali	3.21	11.67
86	Sorghum	B2-3	Mali	2.10	9.04
87	Sorghum	B2-5	Mali	2.53	10.69
88	Sorghum	B35	USA	5.72	11.07
89	Sorghum	BBISS-08 (vraisauvage No.8)	Mali	3.66	9.46

90	Sorghum	BJV44	India	3.29	9.61
91	Sorghum	BTx623	USA	2.52	10.62
92	Sorghum	CIRAD406	CIRAD/ICRISAT	1.73	12.00
93	Sorghum	CMDT45	Mali	3.98	11.42
94	Sorghum	CRS4	India	2.85	10.42
95	Sorghum	CSH 16 ©	India	3.23	11.25
96	Sorghum	CSM335	Mali	1.40	10.57
97	Sorghum	CSM388	Mali	1.73	14.46
98	Sorghum	CSM63-E	Mali	3.73	11.46
99	Sorghum	DagnaliKossourou	Mali	2.98	10.03
100	Sorghum	Doua-G	Mali	3.82	8.79
101	Sorghum	E36-1	Ethiopia	5.11	10.09
102	Sorghum	E36-1	Ethiopia	1.66	12.04
103	Sorghum	Framida	South Africa	3.15	12.64
104	Sorghum	Gnossiconi	Burkina Faso	5.19	10.74
105	Sorghum	GPN01 267-9-(V1,2,3)-4-2	Mali	3.78	10.56
106	Sorghum	GPN01 S01 266-2-1-6-vr	Mali	3.27	8.68
107	Sorghum	GPN01 S01 266-8-3-3-vr	Mali	2.26	9.70
108	Sorghum	GPN01 S01 267-9-3-1-1	Mali	5.24	10.51
109	Sorghum	GPN01 S01 267-9-3-3-vr	Mali	4.56	9.71
110	Sorghum	GRS1=DSV5	India	2.18	10.58
111	Sorghum	GS15-10	India	2.50	11.21
112	Sorghum	GS23	India	2.63	10.59
113	Sorghum	ICSB 370-2-9	ICRISAT	4.94	10.38
114	Sorghum	ICSV745	ICRISAT	2.24	10.65
115	Sorghum	ICSV93046-P1	ICRISAT	3.18	10.29
116	Sorghum	IS 24887	Nigeria	3.98	11.07

117	Sorghum	IS 41397-3-P6	ICRISAT	2.49	11.02
118	Sorghum	IS 8219-P1	Uganda	4.80	9.34
119	Sorghum	IS10876	Nigeria	2.17	12.45
120	Sorghum	IS14556	Nigeria	2.15	11.82
121	Sorghum	IS15401	Cameroon	2.13	9.65
122	Sorghum	IS18551	Ethiopia	3.93	9.76
123	Sorghum	IS29472	Lesotho	4.38	11.47
124	Sorghum	IS393(411)695	USA	4.72	10.93
125	Sorghum	Keninkeni	Mali	1.02	10.62
126	Sorghum	M35-1	India	4.13	9.69
127	Sorghum	M35-1	India	3.73	10.75
128	Sorghum	N13	India	3.99	10.26
129	Sorghum	Parbahani Moti	India	2.89	10.54
130	Sorghum	Parbhani Jyothi	India	3.07	10.62
131	Sorghum	PB15220-1	ICRISAT	2.58	10.61
132	Sorghum	PB15881-3	ICRISAT	3.14	10.45
133	Sorghum	Phule Maule (RSLG262)	India	3.37	10.48
134	Sorghum	Phule Vasudha	India	3.45	9.97
135	Sorghum	PVK 801-P23	India	2.81	11.75
136	Sorghum	R16	India	4.32	10.87
137	Sorghum	Ribdahu	Nigeria	2.09	10.53
138	Sorghum	S35	Ethiopia	3.59	11.65
139	Sorghum	Sambalma	Nigeria	1.16	9.83
140	Sorghum	SP 2417-P3	India	2.47	10.41
141	Sorghum	SPV2217	India	2.09	10.43
142	Sorghum	SVD806	India	2.90	10.32

Table 1.2. Descriptive statistics (mean, SD and range) of sorghum samples used for calibration development of protein[w/w%], fat[w/w%] and moisture[w/w%]

Trait	Calibration					Validation				
	N	Min	Max	SD	range	N	Min	Max	SD	range
Protein	87	6.96	13.95	1.16	5.12	30	12.45	15.75	0.85	3.3
Fat	92	1.50	5.41	0.65	3.02	28	2.75	4.78	0.56	2.03
Moisture	79	9.07	10.56	0.24	1.48	37	9.22	10.26	0.25	1.021

Table 1.3. Descriptive statistics (Min, Max, SD, and range) of multi-cereal samples (pearl millet, sorghum, maize, finger millet, and foxtail millet), used for calibration development of protein[w/w%] and fat[w/w%]

Trait	Calibration					Validation				
	N	Min	Max	SD	range	N	Min	Max	SD	range
Protein	123	5.55	15.69	1.68	10.2	46	8.73	12.62	0.88	3.89
Fat	127	1.16	11.36	2.36	10.13	45	2.78	4.68	0.46	0.46

Table 1.4. Calibration and validation statistics of moisture[w/w%], protein[w/w] and fat[w/w%] for sorghum grain samples

Trait	Calibration		Cross-Validation			Validation			
	SEC	R^2	SECV	1-VR	RPDc	r^2	SEP	Slope	RPDv
Protein	0.26	0.94	0.39	0.88	2.96	0.93	0.44	0.91	1.92
Fat	0.15	0.94	0.26	0.83	2.5	0.92	0.15	0.95	3.52
Moisture	0.06	0.93	0.14	0.67	1.75	0.94	0.063	1.01	4.07

Table 1.5. **Calibration and validation statistics of protein[w/w] and fat[w/w%] for cereals (pearl millet, sorghum, maize, finger millet, and foxtail millet) grain samples**

Trait	Calibration		Cross-Validation			validation			
	SEC	R^2	SECV	1-VR	RPDc	r^2	SEP	Slope	RPDv
Protein	0.75	0.80	0.81	0.76	2.08	0.85	0.4	1.3	2.2
Fat	0.66	0.92	0.85	0.86	2.76	0.78	0.22	0.88	2.08

Table 1.6. **Calibration and validation metrics of FOSS DS2500 and HLEVT5 mobile sensors treated with winISI (FOSS DS2500) and Hone multivariate (HLEVT5) algorithms for protein constituent**

Sensor	**Model**	**Set**	**Slope**	**Intercept**	**R^2**	**RMSE**	**RPD**
FOSS-DS2500	**WinISI**	Calibration	0.87	1.74	0.9	0.91	3.56
		Validation	0.82	2.38	0.86	1.09	**3.08**
HL-EVT5	**Hone**	Calibration	0.97	0.43	0.98	0.42	7.79
		Validation	0.9	1.35	0.91	0.97	**3.48**

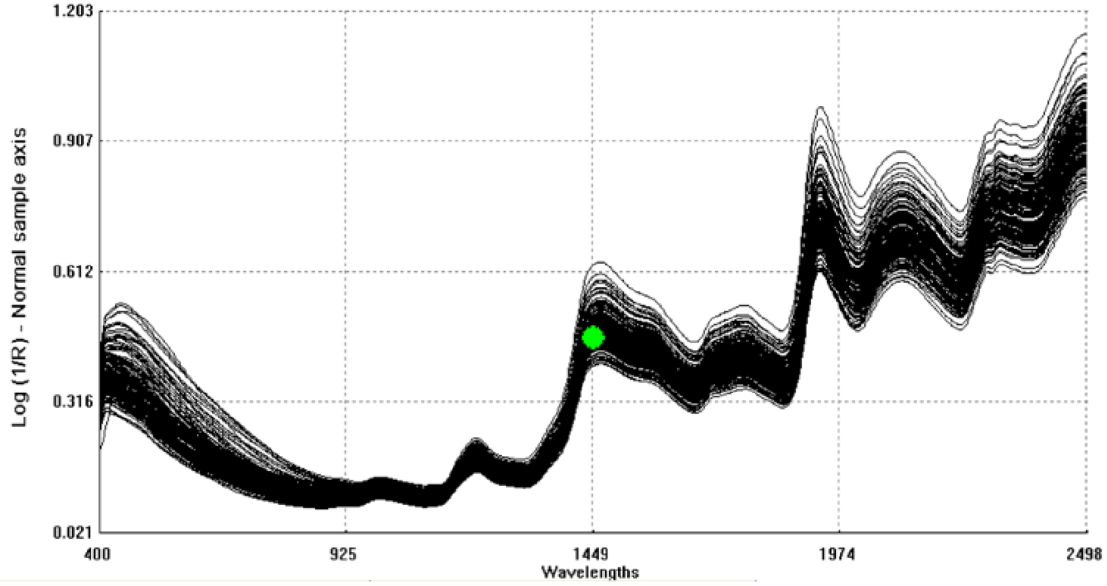


Figure 1.1. Overlaid NIR raw spectra (log1/R) of sorghum grain samples using FOSS ISIscan software

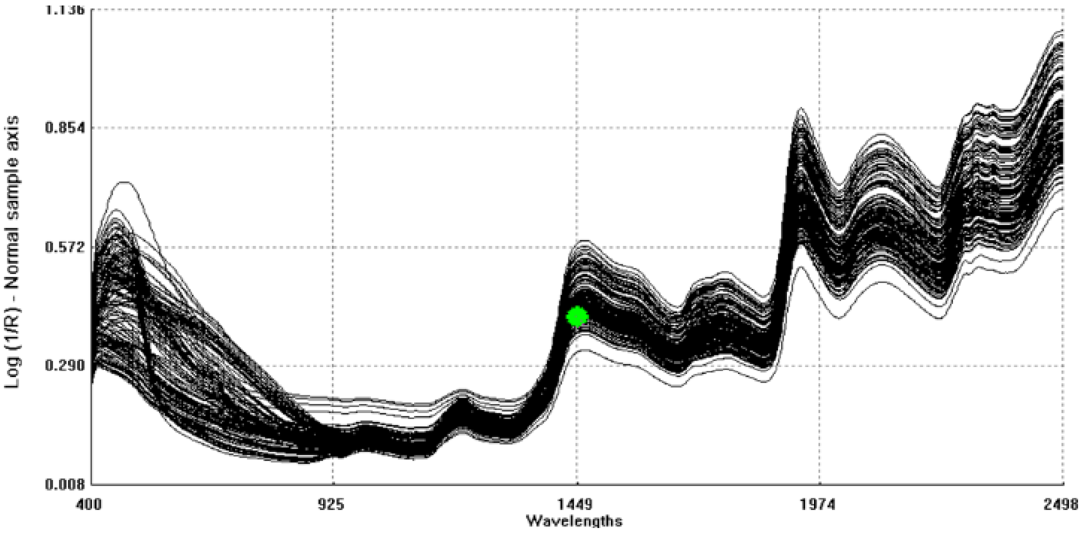


Figure 1.2. Overlaid NIR raw spectra (log1/R) of cereal (pearl millet, sorghum, maize, foxtail millet, and finger millet) grain samples generated using FOSS ISIscan software

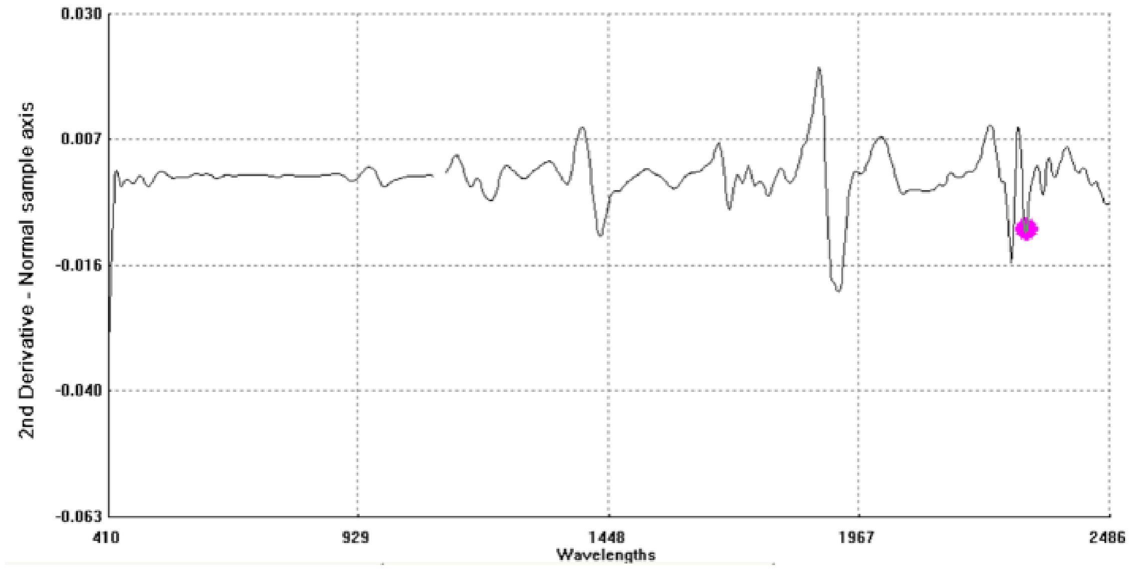


Figure 1.3. 2nd derivative (math treatment 2,4,4,1 &SNVD) spectrum of sorghum

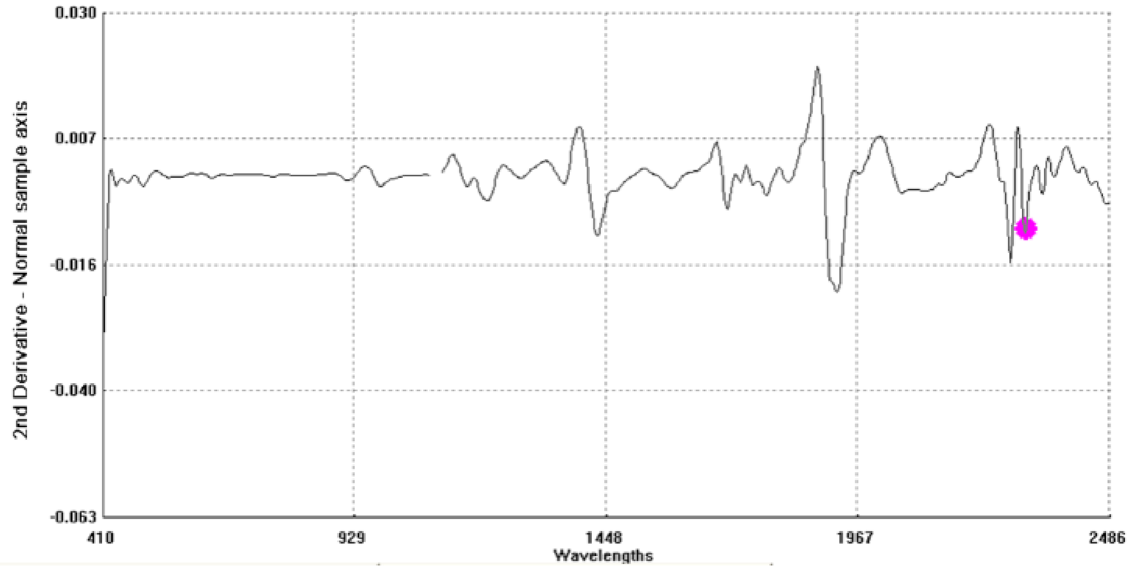


Figure 1.4. 2nd derivative (math treatment 2,4,4,1 &SNVD) spectrum of multi-cereals (pearl millet, sorghum, maize, foxtail millet, and finger millet) grain samples

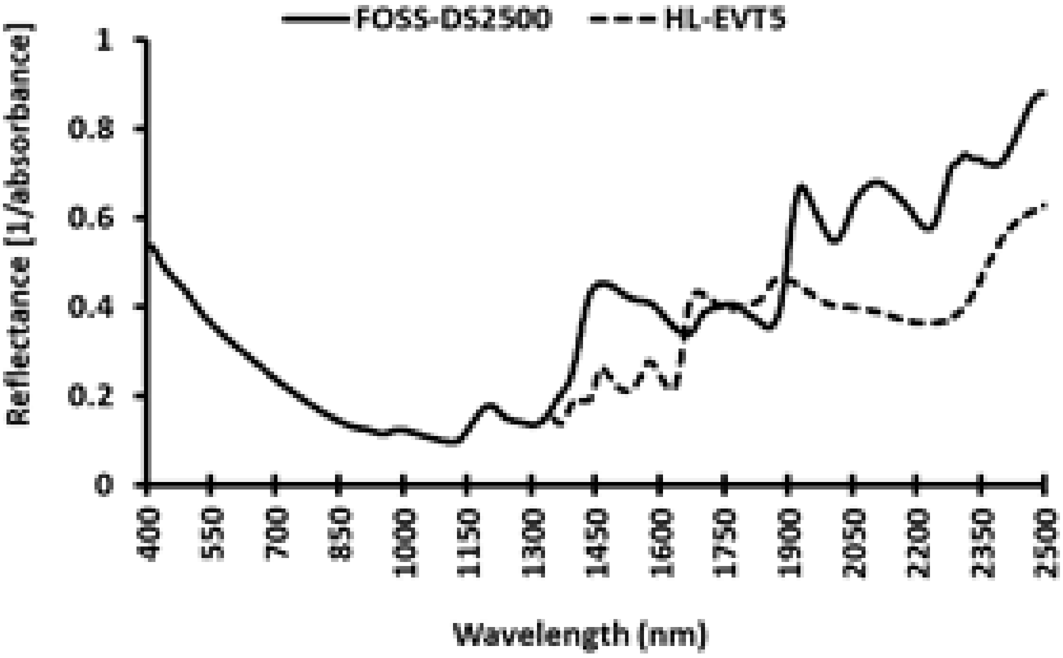


Figure 1.5. **Mean of NIR raw spectra of all grain samples extracted from FOSS DS2500 (400-25498 nm; solid line (–) and handheld HL-EVT5 (1350–2550 nm; dashed line (---) devices**

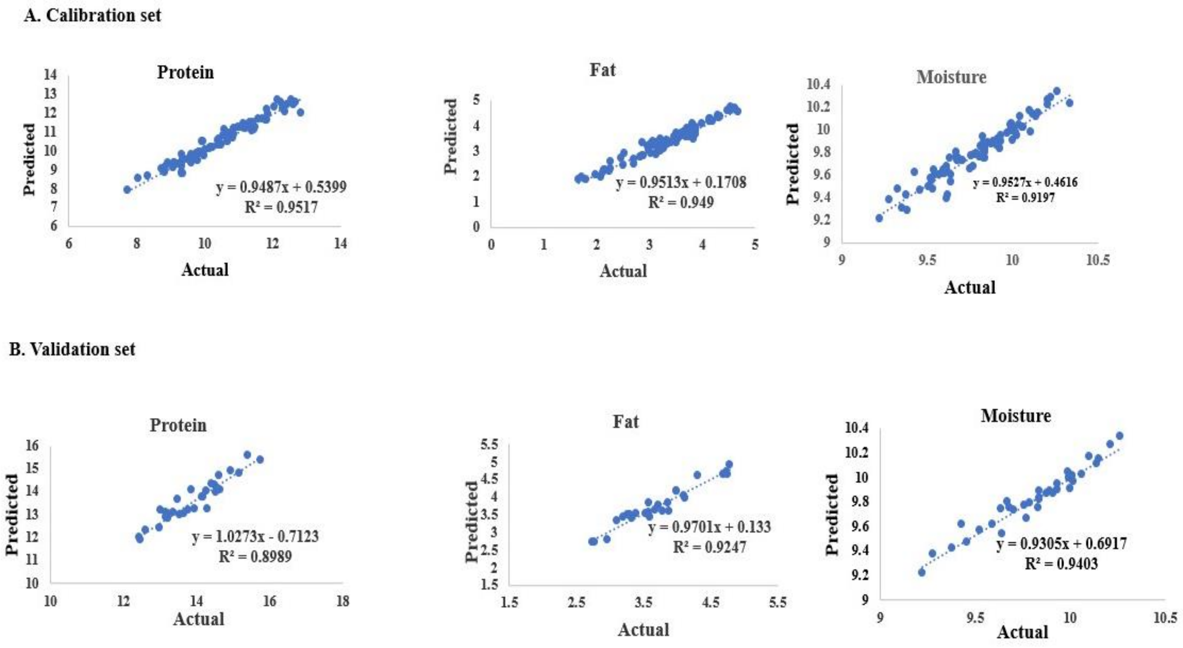


Figure 1.6. Scatter plots showing protein, fat, and moisture NIR predictions against reference values (A) in sorghum calibration data set; (B) in sorghum validation data set by FOSS winISI software

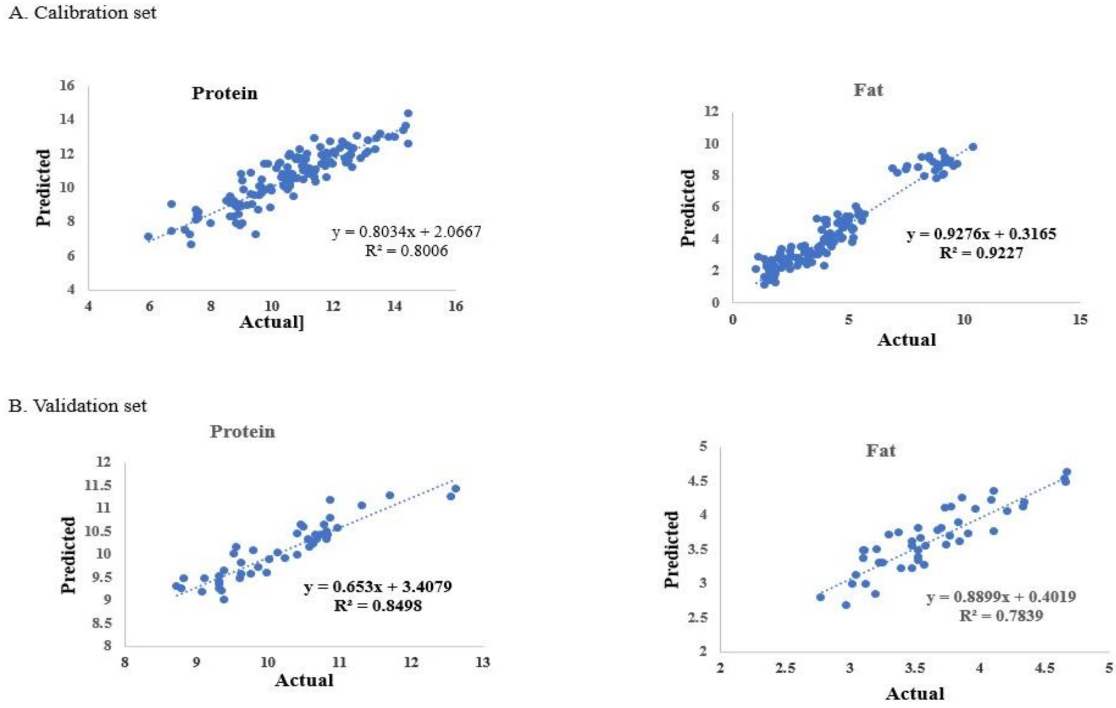


Figure 1.7. Scatter plots showing protein and fat NIR predictions against reference values (A) in multi cereal calibration data set; (B) in multi-cereal validation data set by FOSS winISI software

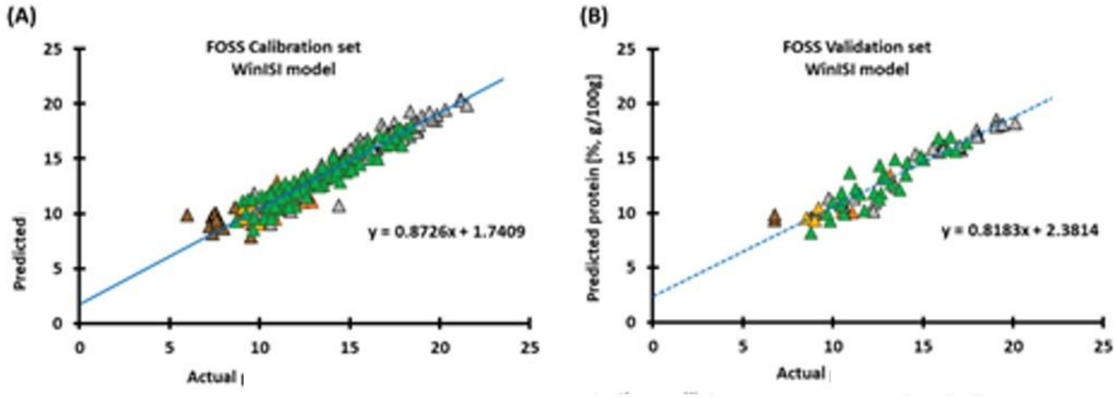


Figure 1.8. Scatter plot showing protein predicted for the (A) calibration set and (B) validation sets of FOSS-DS2500 by WinISI analytical software

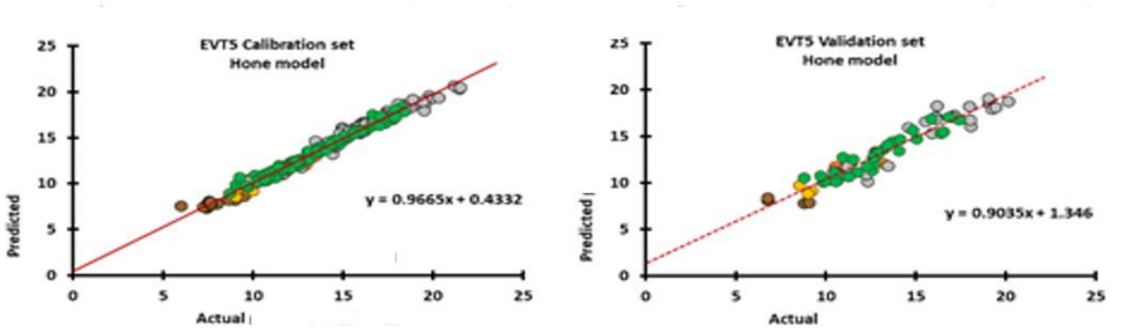


Figure 1.9. Scatter plot showing protein predicted for calibration set and validation sets of HL-EVT5 mobile sensor by Hone Create Software

CHAPTER 2

2. Genetic determination of agronomic and grain quality indicators

2.1. Introduction

Sorghum is one of the important cereal crops in the tropics and semi-tropical regions of the world. It is a staple food grain, especially in SAT (semi-arid tropics) regions, and also nutritionally dense with significant amounts of energy, protein, vitamins, minerals, and antioxidants like phenolics (Taylor et al., 2006). Especially, three macronutrients, starch, protein, and fat are important contributors to grain quality and energy value. Unfortunately, the digestive value of sorghum protein is naturally low due to their binding in tight matrices known as prolamins. Crude fat is mainly stored in the embryo and makes up 2-5 % of all three macronutrients. But its energy density is higher than that of starch and protein. These grain quality traits are indirectly affected by different yield components such as grain size, grain number, grain yield. All these yield attributes are majorly affected by drought in crop plants.

Although sorghum can withstand harsh environments, severe drought stress can still lead to early senescence, stock lodging, and yield reduction in sorghum. In sorghum, two major drought stress responses are pre and post-flowering drought. Pre-flowering drought stress affects mostly panicle differentiation and post-flowering drought stress affects grain developmental stages leading to yield losses. Stay-green is a best-studied trait that contributes to the sorghum adaptation to terminal drought conditions. Several hypotheses have been proposed to explain the expression of a stay-green trait. Studies showed expression of the stay-green trait could be due to plant water management (Hammer et al., 2006). During terminal drought, maintaining green leaf area is a primary requirement to access the available water. It in turn relates to the management of water resources by different genotypes based on their canopy size (Kholova et al., 2010a) or due to deeper root systems (Vadez et al., 2007a). These kinds of water use, as well as canopy-related traits, can be better studied using the lysimetric method (Vadez et al., 2011a and b) and recently developed Leasyscan facility (Vadez et al., 2015). The Leasyscan system is particularly useful to study early vigor traits and the lysimetric facility is useful to study water use-related traits along with yield and quality-related traits.

Breeding for important agronomic, physiological and qualitative traits along with drought-related traits became an important research objective due to changes in climatic scenarios. Though many conventional methods are available to achieve this, QTL (genome) mapping became a popular method to detect complex quantitative traits (Tuberosa et al., 2003). Quantitative trait locus (QTL) mapping mainly focuses on recognizing genetic regions of the genome which are linked to traits of interest. QTL mapping requires a mapping population that is segregating for the trait(s) of interest. Then genetic markers need to be developed which are in linkage disequilibrium (LD) with the gene(s) underlying phenotypic variation. This involves hundreds of genetic markers and this genetic marker data set consists of hundreds of AFLPs and/or SSRs/ DarT markers positioned across the genome (Powell et al., 1996). Then phenotyping of agronomic and qualitative traits allows linkage mapping to identify major QTLs for yield-related traits. Many research groups carried out QTL studies to map stay green QTLs in sorghum (Tuinstra et al., 1997, Crasta et al., 1999, Subudhi et al., 2000, Xu et al., 2000, Kebede et al., 2001, Sanchez et al., 2002, Haussmann et al., 2002, Harris et al., 2007). These studies on the stay-green have shown both dominant and recessive expression (Tunistra et al., 1996). Subudi et al. (2000) studied the consistency of stay-green QTLs in sorghum using recombinant inbred line (RIL) mapping population developed from a cross of B35 and Tx7000. They confirmed four stay green QTLs (*Stg1*, *Stg2*, *Stg3*, and *Stg4*) were consistent across environments. In addition to that, research efforts are going on to discover the genetic basis of grain quality traits, and several QTLs were already reported for grain protein and fat on different chromosomes (Guindo et al., 2019). In addition to that, sorghum mutant lines with high digestibility were developed (Weaver et al., 1998) and QTLs associated with this trait have already been mapped on chromosome 1 (Winn et al., 2009).

The present study aimed at understanding the association between plant vigor traits measured during the early stage of the plant in high throughput phenotyping platform (Leasyscan facility at ICRISAT) and important agronomic and qualitative traits measured under field conditions using the QTL mapping approach. In this study, a lysimetric system was used to identify suitable recombinant inbred populations (RILs) based on water use traits. Then phenotyping for plant vigor traits was conducted in the Leasyscan platform (ICRISAT). This data along with the data collected from the field trial (collected from genomics lab, ICRISAT) was used for QTL mapping studies using available marker data to explore the possible association between vigor traits and grain quality-related traits.

2.2. Materials and methods

2.2.1. Lysimetric studies

Experiment was conducted using 18 sorghum mapping population parents and 6 stay green introgression lines from R16 and S35 background (seeds collected from ICRISAT: 296B, BTx623,E36-1, ICSV74, ICSV93046-P1, M35-1, N13, PB15220-1, PB15881-3, PVK 801-P23, S35, SP2417-P3, IS41397-3-P6, ICSB 370-2-9, IS8219-P1, R16, K359W, K648, S35-6040, S35-6008, S35-7001, S35-6026, Phulevasudha, Parbhani moti). Planting was done in the rabi season of 2015 (28-10-2015) in lysimeters which are PVC tubes with 25 cm diameter and 2 m length, filled with sandy clay loam alfisol. They are kept under natural conditions in rainout shelters (http://gems.icrisat.org/lysimetric-facility/). One plant per lysimeter was maintained after final thinning (12-11-2015). Diammonium phosphate (DAP) and muriate of potash (MOP) were applied at the rate of 200 mg $kg^{-1}$of the soil before sowing. Urea at the rate of 300mg kg^{-1} of soil was applied after two weeks of germination. All genotypes were grown in 5 replications for each water treatment i.e., irrigated, mild stress, and severe stress. For mild water stress, irrigation was stopped at 6 weeks after germination and for severe water stress, irrigation was stopped at 4 weeks after sowing. After 3 weeks of germination, the topsoil of each cylinder was filled with a 2 cm layer of polyethylene beads to prevent soil evaporation and weights of cylinders were measured each week to calculate transpiration at weekly intervals until maturity. Daily transpiration values were calculated for each plant by dividing the transpiration of each time interval between weighing by the number of days in each interval. The pattern of water use by each plant until maturity under each treatment was assessed by following the protocol described by Vadez et al. (2011a) for the lysimetric experiment. The number of days to flowering was noted down for each plant and at the time of harvest, total water use (g plant^{-1}), transpiration efficiency(g kg^{-1}), above-ground dry biomass (g), grain size (100seed weight in g), and grain weight (g) for each plant was calculated. Transpiration efficiency was calculated as the ratio of the total above-ground biomass to the sum of transpiration values between 30 DAS and maturity.

2.2.2. Leasyscan Experiment

A set of 181 recombinant inbred lines derived using the single seed descent method from the cross between N13 and E36-1 was used for this experiment (Haussmann et al., 2002). Line N13 is Indian- origin durra sorghum and known to be resistant to Striga. Line E36-1 is an Ethiopian origin, guinea-caudatum, high yielding hybrid sorghum. It is a drought-tolerant, high yielding breeding line donor of the stay-green gene. The RIL population developed from this cross is segregating for both Striga resistance and the stay-green. This population was selected based on the results obtained from the lysimetric experiment. Both parents belong to the same flowering group (40-50 days) and possess similar water use capacity under irrigated conditions, but at the same time contrasting for grain size and transpiration efficiency.

2.2.2.1. Phenotyping for vigor traits

Plants were phenotyped in the Leasyscan facility (ICRISAT) during the post rainy period of sorghum i.e. October to November in 2014. Pot details and arrangement were in accordance with Vadez et al. ((2015) (LeasyScan facility; http://gems.icrisat.org/leasyscan/) Sowing was carried out with 8 seeds in each pot and two homologous plants were retained per pot during final thinning i.e., 2 weeks after sowing. Diammonium Phosphate (DAP) and Muriate of potash (MOP) were applied at the rate of 200 mg kg^{-1} of soil to each pot at the time of sowing. The alpha lattice design was followed for the experiment with 4 replications of the genotypes. Plants were maintained under irrigated conditions throughout the experimental period. Plants were harvested at the stage of 4 weeks after germination.

2.2.2.1.2. Canopy traits

LeasyScanPlantEye® scanners scanned the plants to analyze plant development-related traits [3D leaf area, projected leaf area (2D-leaf area), and plant height (PH)] on an hourly basis during the entire crop growth period. From these traits, plant growth rate traits were calculated [3D- growth rate (3D-GR), projected leaf area growth rate (2D-GR], based on the average difference in respective leaf area and plant height between successive days during the logarithmic growth phase. Residuals that represent canopy structures were calculated using 3D leaf area and projected leaf area.

2.2.3. Field related traits

The field data for the RIL population of N13 x E 36-1 was taken from the sorghum molecular breeding group from ICRISAT. Experiments were conducted during three consecutive years i.e., post rainy seasons of 2008, 2009, 2010, and agronomic data; days to flowering, plant height and grain size were taken for this QTL mapping studies. At the same time, from the same experiments, data for scoring for Striga resistance, pericarp color (y/w), awns (p/a) were also collected for this study. The same experiment using the N13 x E36-1 RIL population was conducted again in 2017 in three replications under field conditions to collect the grains for measuring grain quality.

Grain quality data: grains of N13 x E36-1 from 3 replications were combined for each genotype and ground to a fine powder using a FOSS-cemotech grinding mill. Near-Infrared spectroscopy was used (NIRS) to measure protein and fat. Briefly, flour of each genotype was scanned using a FOSS-XDS machine, and protein and fat data were extracted using cereal grain calibrations developed earlier (Chapter 1).

2.2.4. QTL mapping

Plant vigor traits from the Leasyscan facility, agronomic and grain quality traits from field data were used to map for any QTLs and possible colocalization. Composite interval mapping (CIM) method in QTL Cartographer version 2.5, was used (window size of 10cM, walking speed of 1cM, control markers = five, and backward regression) for this purpose. LOD threshold was set by using 1000 permutations and p-value $\leq$0.05. QTLs with PVE (phenotypic variation explained) more than 10% were considered as major QTLs and QTLs with PVE less than 10% were considered as minor QTLs.

2.2.5. Statistical Analysis

For the lysimetric experiment, two-way ANOVA was performed to find significant variation for genotype, treatment, and their interactions using GENSTAT 14.0 (VSN International Ltd., Hemel Hempstead, UK). For Leasyscan and field experiments, one-way ANOVA was performed to find genotypic differences among progenies. For both the experiments, mean comparison was done using the Tukey-Kramer test and Least Significant Difference (at $P \leq 0.05$). Principal component analysis (PCA) using R software (R core team, 2018) was performed to find the association between traits. For QTL and PCA analysis, data for Best Linear Unbiased Predictors (BLUPs) were calculated using GENSTAT 14.0. For all the experiments, broad-sense heritability was calculated using genotypic and residuals mean square components obtained from respective ANOVA tables using GENSTAT 14.0. The formula used was $h^2 = \sigma 2 G/ (\sigma 2 G+\sigma 2 E)$ (Kholova et al., 2012, Vadez et al., 2012), where σ 2 G is the genetic variance and σ 2 E is the error variance.

2.3. Results and Discussion

2.3.1. Lysimetric studies

ANOVA results (Table 2.1) showed significant differences for genotype, treatment as well as their interactions. Even though there was a significant genotypic effect on all traits, the effect was high for transpiration efficiency and biomass produced compared to other traits. On the contrary, treatment has less effect on transpiration efficiency compared to other traits. It means genotypes with similar water extraction show different amounts of biomass production per kg of water extracted. It shows genetics of plants play a major role in adaptation to different environments. As mentioned in methods and materials, genotypes used in this experiment consist of parents of different recombinant inbred line (RILs) populations which are contrasting for different traits such as Striga resistance, stay-green, shoot fly resistance, Biological Nitrogen fixation, stem sweetness, stem borer resistance, and grain mold resistance. Along with them, stay-green introgression lines that harbor stay-green gene was also used along with their senescent parents (S35 and R16). All these genetic materials flowered approximately between 40-58 days after sowing (DAS). Based on the days to flowering data, these genotypes were grouped into three groups (40-44, 45-48, and 49-58). Naturally, water use was high (40-44: 29162 g plant^{-1}; 48-58: 38,174 g plant^{-1}) under irrigated conditions in the group with longer flowering time compare to others (Figure 2.1). Contrary to this, more water is extracted under water stress conditions by the genotype in the group with 44-48 DAS flowering time. This genotype which is a stay-green introgression line (S35 6008: 14,196 g plant^{-1} under WS2) also showed higher transpiration efficiency

(TE) under water stress conditions compared to irrigated conditions by retaining more green leaf area under stress conditions which is a phenomenon observed in stay-green phenotype. Differences in TE were mostly observed under irrigated and stress conditions compared to flowering groups (Figure 2.2) and most of the genotypes showed higher TE under stress conditions by efficiently using available water compare to irrigated conditions. The amount of yield components (biomass and grain weight) produced was high for the longer duration group (48-58 DAS) compare to the shorter duration one (40-44 DAS) under irrigated conditions. But genotypes in this group showed higher differences in yield components under irrigated and stress conditions. Grain size which is known to be associated with plant vigor showed differences under irrigated and stress conditions, which was more prominently observed in longer duration genotypes (Figure 2.3). Interestingly, this grain size trait affected the yield components inversely which also shows grain size association with plant vigor. These trait differences among genotypes paved the way to choose a suitable RIL population to study vigor and main grain quality traits and also to analyze possible colocalization of QTLs which will assist in marker-assisted breeding in the future. Based on the data analyzed, the RIL population was chosen in such a way that the parents belong to the same flowering group and have similar water use capacity, but contrasting for grain size and TE which indicates plant vigor indirectly. So, here N13 x E36-1 derived RIL population which met all these criteria was chosen to proceed for Leasyscan studies for vigor traits. Also, the results obtained for stay-green introgression lines and their senescent parents in this study formed a basis to study these lines under different treatments to explore GxExM interactions (chapter 3).

2.3.2.1. Leasyscan studies

Summary statistics: ANOVA results (Table 2.2) showed, there is a significant difference for plant vigor-related traits among the RIL population. Normal frequency distribution was found for many traits under study. The plant vigor traits were grouped into three: early, medium and late vigor traits based on the number of days passed from germination to harvest. Vigor traits in each group, especially, leaf area and growth rates among the RIL population were nearly showed two-fold variation.

Grain size, grain fat and protein content from the samples of field experiment were also showed significant differences among the RIL population through ANOVA results. Figure (2.5) confirmed there was 50 % variability among the population for grain size and plant vigor-related traits.

2.3.2.2. Principle component analysis

Association between the traits and how they formed into groups were analyzed by principal component analysis (PCA) for which BLUPs of phenotypic data were used. The first three components of PCA explained 60.28 % of the total variation shown by the RIL population. PCA showed early vigor traits and grain size exhibited strong positive relation and formed into one group and late vigor traits and phenology traits (flowering time) were closely related and formed into another group. Also, grain size and early plant vigor traits showed a large effect on principal components than qualitative traits (grain fat and protein) and in the other group, late vigor traits have shown a strong effect on principal components than other traits (Figure 2.6).

2.3.3. QTL mapping

2.3.3.1. Linkage map

A total of 82 SSRs and 175 DarT markers were used to construct linkage map (details collected from genomics lab, ICRISAT). The total length of linkage group was 2358.5 centimorgans (cM); LG1a (46.1 cM), LG1b (206.6 cM), LG2 (299.8 cM), LG3 (271.6 cM), LG4 (207.1 cM), LG5a (249.3 cM), LG5b (68.6 cM), LG6 (267.9 cM), LG7 (239.1 cM), LG8 (183.8 cM), LG9 (153.8 cM) and LG10 (164.8 cM). Average interval between the loci was 9.37 cM.

2.3.3.2. QTLs identified in different chromosomes

Total 57 QTLs were identified for 21 traits under study using composite interval mapping in QTL Cartographer. Out of them, 21 QTLs were minor QTLs with PVE% less than 10 and 36 QTLs were major QTLs with PVE% more than 10%. Most of the field related traits (Striga resistance score, Awns, Pericarp color, Plant height, Flowering time, Grain size, Grain fat, and Protein) and a few plant-vigor related traits (2DLA1, 2DLA2, 2DGR1, 3D LA1, and 3DGR1) were collected from Leasyscan platform studies showed higher PVE% (>10%) on linkage groups; LG1b, LG3, LG4, LG5, LG7, LG8, and LG10. QTLs identified for plant vigor traits showed a LOD range of 2.53-4.04 (2D LA1). Whereas among field-related traits, LOD ranged from 2.88 (Striga resistance: LG5a) to 112.58 (Flowering time: LG4). QTL information for important traits used in the study was given in the table (Table 2.3).

2.3.3.3. QTL colocalization

QTL colocalization was found on LG4, LG5a, and LG10. On LG4, late vigor traits were colocalized with grain protein content which was seen between the positions 109 cM and 119.3 cM. On the same LG4, colocalization of QTLs for Striga resistance, pericarp color, flowering time, plant height, and canopy structure was identified between the map positions 94.9 cM to 108.9 cM. In addition to that, QTLs for grain protein and fat were colocalized between 121.2 cM to 126.3 cM. On LG5a, most of the plant vigor traits (2D LA, 2DGR, 3D LA, and 3D GR) were colocalized with QTL identified for grain size between the positions 49.5 cM to 96.1 cM. On LG10, QTLs for Striga resistance, pericarp color, and grain protein were colocalized between 11 cM to 36.2 cM. The phenotypic variation (PVE) explained by most of these traits were high and these details were given in the table (Table 2.3).

All the traits were studied under irrigated conditions in the field and the Leasyscan platform. Most of these traits exhibited high heritability (>60%) (Robinson et al., 1949) indicating the expression of these traits across the environments. Colocalization of flowering time QTL with plant height along with QTL related to canopy structure showed a significant positive association between these traits. Several genes related to flowering have been already reported in sorghum; *Ma1, Ma2, Ma3, Ma4, Ma5, and Ma6* (Childs et al., 1997) confirming its key role in the adaptation of the plant to its environmental conditions. Many QTLs related to flowering time were also reported previously (El Mannai et al., 2012). Recently, Techale et al. (2021) also reported QTL for flowering time and plant height on chromosome 4. Along with chromosome 4, they have also reported QTLs for flowering time and plant height on chromosomes 2,3,5,6, and 9. QTLs for leaf senescence (chromosomes 2,3,5 and 10) and grain yield (chromosomes 2,4 and 6) were also reported by the same group. In support of this, the current study showed colocalization of flowering time, plant height, and Striga resistance which may also be related to the grain yield component. On LG5a, colocalization of grain size and vigor traits suggest plant vigor may influence the grain size. Techale et al. (2021) also reported grain size QTL on the same chromosome along with other chromosomes 2,6,8 and 10. Recently, Tao et al. (2020) conducted GWAS for sorghum grain size and reported 81 QTLs in total. In their study, they reported QTL on chromosome 5 along with other chromosomes. Grain size contribution for reproductive rate, emergence was already established in earlier studies (Westoby et al., 1992, Tao et al., 2017) which confirmed the association of grain size with plant vigor traits in the current study. These results show agronomic traits are complex and their genetic architecture comprises of multiple loci and also possibly multiple alleles in each locus (Yu et al., 2008). Previous studies on grain qualitative traits showed QTLs for protein and fat on chromosome 4 (fat) and 10 (fat and protein) (Murray et al., 2008, Boyles et al., 2017, Patil et al., 2019). The present study showed both the QTLs on chromosome 4 and on the same chromosome, QTL for protein was associated with late vigor traits (LA and GR after 2 weeks of germination). It signifies the relationship between vigor traits and grain quality. Kiranmayee et al. (2020) reported chromosome 10 harbors QTL for stay-green which is colocalized with shoot fly resistance genes in the population of RSG04008-6 x J2614-11. The same study also identified genes for delayed senescence which contributes to the stay-green trait on chromosome10. At the same time, Tao et al. (2020) also reported QTL for grain size on the same chromosome 10. Even though, results were reported in different populations and also in different environments, these types of results suggest the positive association between these traits and are also useful to identify the genomic regions for marker-assisted breeding approach. QTL mapping studies on the same N13 x E36-1 RIL population was first conducted by Haussman et al. (2002 &2004) and showed QTL for stay-green on chromosome 5 (LG5a) (their linkage group E) and also QTLs for Striga resistance on chromosomes (LG) 4 and 10 (their linkage groups D and J). In addition to this, previous studies also confirmed the presence of stay-green QTLs in sorghum on chromosomes 2,3,4,5,6,8 and 10 (Crasta et al., 1999, Subudhi et al., 1999, Subudhi et al., 2000, Xu et al., 2000, Kebede et al., 2001, Sanchez et al., 2002, Sukumaran et al., 2016). Thus, the present study may confirm the association of stay-green trait with genomic regions of co-localized QTLs for different traits under study. Especially, QTLs colocalized for grain size and plant vigor traits on LG5a were present on the same genetic region linked to the stg 4 (associated with leaf size expansion) showing the relationship between stay-green trait and plant vigor which needs further exploration. There is a need to validate these associations in different environments due to QTL x environment interactions. If confirmed, studied genetic regions could be explored for putative candidate genes for simultaneous improvement of these traits through molecular breeding in locally adapted cultivars. Finally, this study suggests the pleiotropic effect of plant vigor traits on different agronomic and qualitative traits and how high trough put technologies help to understand plant functionality at the multi-disciplinary level.

2.3.4. Summary

This study highlighted the importance of genetic determination for grain quality improvement along with the yield traits. Selection of mapping population based on their water use related traits in lysimeters allowed to understand how the parents of mapping populations behave under different environmental conditions and how they contrast to each other for different water use related traits, giving the clue about the behavior of respective mapping population for different traits. The leasyscan platform allowed to study of the plant vigor traits of the entire mapping population vigorously in the first 4 weeks of germination. Colocalization of QTLs identified in this study showed that plant behavior at early stages of development may indicate or determine the size of the source and sink and also grain quality.

Table 2.1. ANOVA table showing genotypic mean across the treatments (mild and severe water stress), F value for genotype (G), treatment (W) and G x W, standard error of difference (SED), Least significant difference (LSD at 5%) and coefficient of variation (CV%) for important water use related traits (Transpiration efficiency (TE), Stover yield, Grain yield, and grain size).

Genotype	TE (g kg^{-1})	Stover yield (g)	Grain yield (g)	Water use (g)	Grain size (g)
296B	3.70	62.42	23.74	10325	1.24
BTx623	3.76	51.19	20.98	8651	1.15
E 36-1	4.90	90.26	39.24	10448	2.72
ICSB 370-2-9	4.17	73.17	38.24	10796	1.96
ICSV745	4.60	82.46	35.57	11985	2.06
ICSV93046-P1	5.92	115.47	15.16	13228	1.57
IS 41397-3-P6	4.49	75.13	29.46	10291	2.01
IS 8219-P1	4.20	53.76	24.52	7051	2.17
K359W	4.76	88.12	21.39	11404	2.23
K648	4.75	89.01	26.45	11360	2.12
M 35-1	5.17	114.37	36.97	13400	2.57
N13	4.58	78.92	23.65	10114	2.38
ParbhaniMoti	5.97	131.38	27.95	14980	2.29
PB15220-1	5.07	81.80	26.43	9990	2.08
PB15881-3	4.12	64.15	17.50	8939	1.87
PhuleVasudha	5.70	127.11	31.91	14897	2.46
PVK 801-P23	4.73	94.31	32.02	13122	2.06
R16	5.41	93.36	33.51	10676	2.40
S35	5.06	90.91	41.94	10253	2.27
S35-6008	5.29	91.95	36.94	10594	1.94
S35-6026	5.42	95.74	35.83	10735	2.82
S35-6040	4.22	65.55	25.36	8848	2.92
S35-7001	5.06	84.53	34.50	9893	2.23
SP 2417-P3	4.47	78.95	27.61	10666	1.87
G	10.11***	11.12***	6.82***	4.67***	7.78***
Water	6.23**	201.95***	225.92***	1512.99***	139.99***
G x W	1.64**	3.84***	3.89***	4.42***	1.67**
LSD	0.55	6.14	9.18	4230.8	0.48
SED	0.28	3.12	4.65	2149.5	0.24
CV%	14.94	26.43	38.45	31.1	25.63

Table 2.2. **ANOVA table showing genotypic mean, F value, standard error of difference (SED), Least significant difference (LSD), and coefficient of variation (CV%) for the measured traits (Leasyscan platform: projected leaf area (2D LA), canopy leaf area (3D LA) and projected and canopy growth rates (2D and 3D GR) at 3 intervals and canopy structure; Field: flowering time, plant height (cm), grain protein (w/w%), grain fat (w/w%)).**

	Genotypic mean	**F value**	**SED**	**LSD**	**CV%**
2D LA-1	307.3	3.63***	37.36	73.39	16.8
2D LA-2	592.1	4.48***	66.85	131.3	15.5
2DLA-3	746	3.15***	84.26	165.5	15.4
2D GR-1	343.1	3.81***	39.76	78.11	16
2D GR-2	630.1	3.57***	76.23	149.8	16.7
2D GR-3	699	1.93***	109.9	215.9	21.6
3D LA-1	38420	3.79***	4788	9407	17.1
3D LA-2	75360	4.45***	8720	17132	15.8
3D LA-3	96397	3.35***	10853	21324	15.2
3D GR-1	43254	3.99***	5126	10071	16.2
3D GR-2	80987	4.15***	9376	18420	15.8
3D GR-3	92151	2.56***	12372	24306	18.3
Canopy structure	1015	1.12	8738	17166	1180.1
Plant height	366.8	2.61***	66.35	33.78	13
Flowering time	75.77	20.21***	0.8808	1.73	2.8
plant height	170.3	24.05***	0.8502	1.66	9.3
grain protein	11.03	44.02***	0.316	0.62	2.5
grain fat	2.813	14.23***	0.1888	0.37	6.6

Table 2.3. **Summary of important QTLs observed for plant vigor-related traits and field-related traits. QTLs were identified using QTL cartographer 2.5 on the RIL population of N13 x E36-1**

Trait	Chromosome	Position (cM)	LOD	PVE%	Position of flanking marker_L (cM)	Position of flanking marker_R (cM)
2D GR1	LG5a	75.71	3.53	7.4	59.4	88.2
2DGR3	LG5a	75.71	2.74	6.1	64.7	96.1
2D LA-1	LG5a	75.71	3.47	7.3	58.3	89.4
2D LA-1	LG5a	185.21	2.50	6.7	179.4	211.3
2D LA-2	LG5a	75.71	2.97	6.1	55.8	90.6
3D GR-1	LG5a	75.71	2.65	5.5	55.8	92.3
3D GR-2	LG4	109.21	3.37	7.1	109	117
3D LA-1	LG5a	75.71	3.29	7	56.4	88.7
3D LA-2	LG4	109.21	2.74	5.6	109	119.3
3D LA-3	LG5a	75.71	3.19	7	68.5	93.1
Striga resistance	LG4	102.01	38.52	66.2	100.3	102.1
Striga resistance	LG10	18.01	27.93	66.2	16	18.2
Striga resistance	LG10	29.91	31.48	66.2	28.9	36.2
Striga resistance	LG4	107.01	5.23	31.7	103.1	108.5
Striga resistance	LG5a	173.31	2.8	10.7	159.9	184.4
Pericarp color	LG4	107.01	3.89	16.7	101.4	108.3
Pericarp color	LG4	87.01	21.64	59.6	85.9	87.1
Pericarp color	LG4	96.01	23.73	59.6	94.9	102.4
Pericarp color	LG4	132.51	6.95	13.8	132.3	138.7
Pericarp color	LG10	15.01	21.88	57.4	11	19
Flowering time	LG4	104.01	112.53	80.5	102.1	104
Plant height	LG4	103.01	48.33	68.2	101.1	103.1
Canopy size	LG4	101.01	23.71	62.9	99.2	101.1
grain size	LG5a	43.51	6.73	13.1	41.2	46.4
grain size	LG5a	61.51	2.93	21.3	49.5	75.6
grain fat	LG4	122.21	13.01	62.8	121.2	126.3
grain protein	LG4	107.01	50.22	70.4	106	119
grain protein	LG4	122.21	41.95	70.4	121.2	125.3
grain protein	LG10	20.01	41.95	72.2	15.8	22.5
grain protein	LG10	30.91	43.47	72.2	27.6	35.2

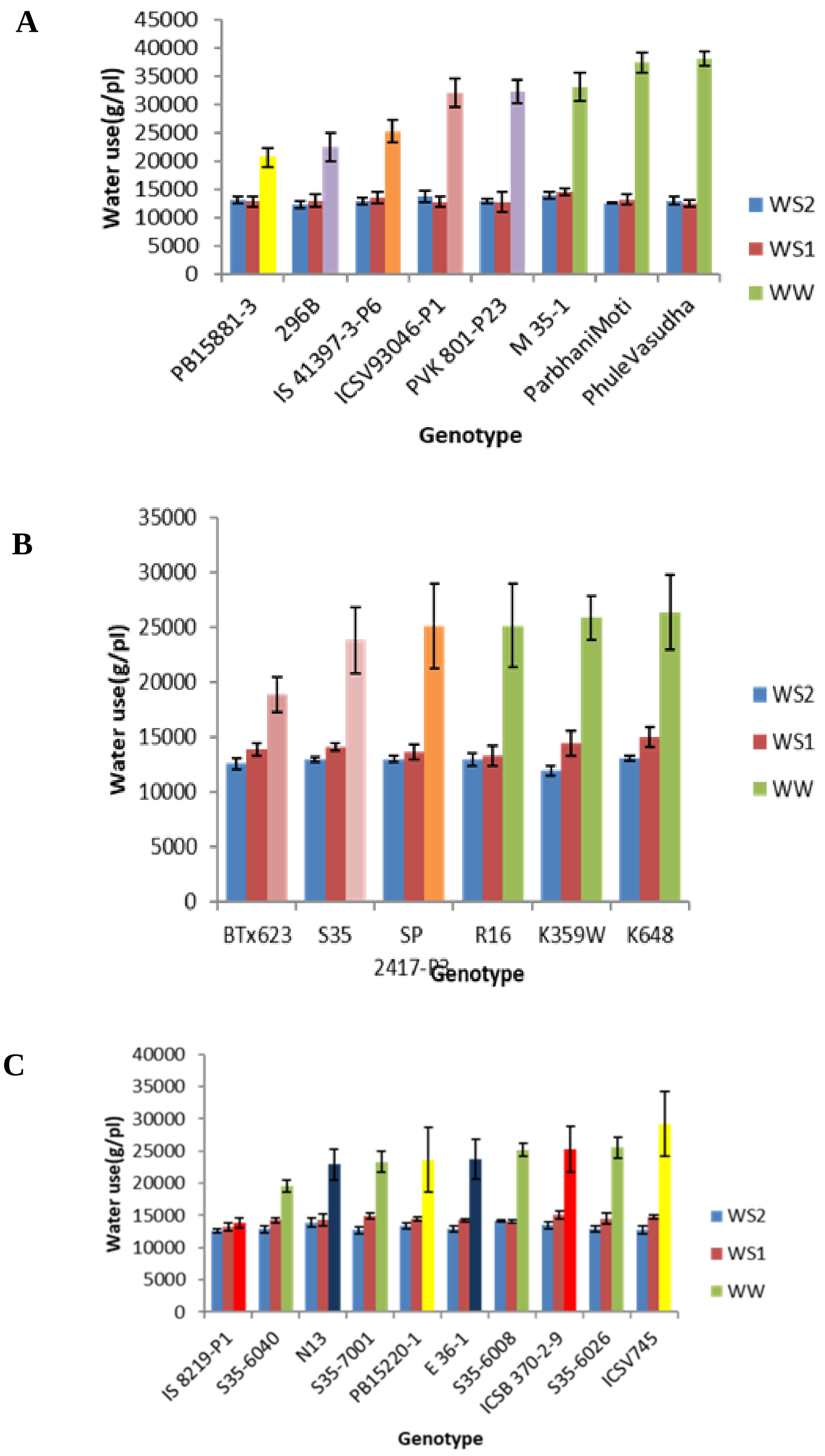


Figure 2.1. Water use pattern of genotypes studied in the lysimetric facility under well-watered (WW), mild water stress (WS1), and severe water stress (WS2) conditions. Genotypes are grouped based on flowering time (days to flowering: 40-44 (A), 45-48 (B), and 49-58 (C))

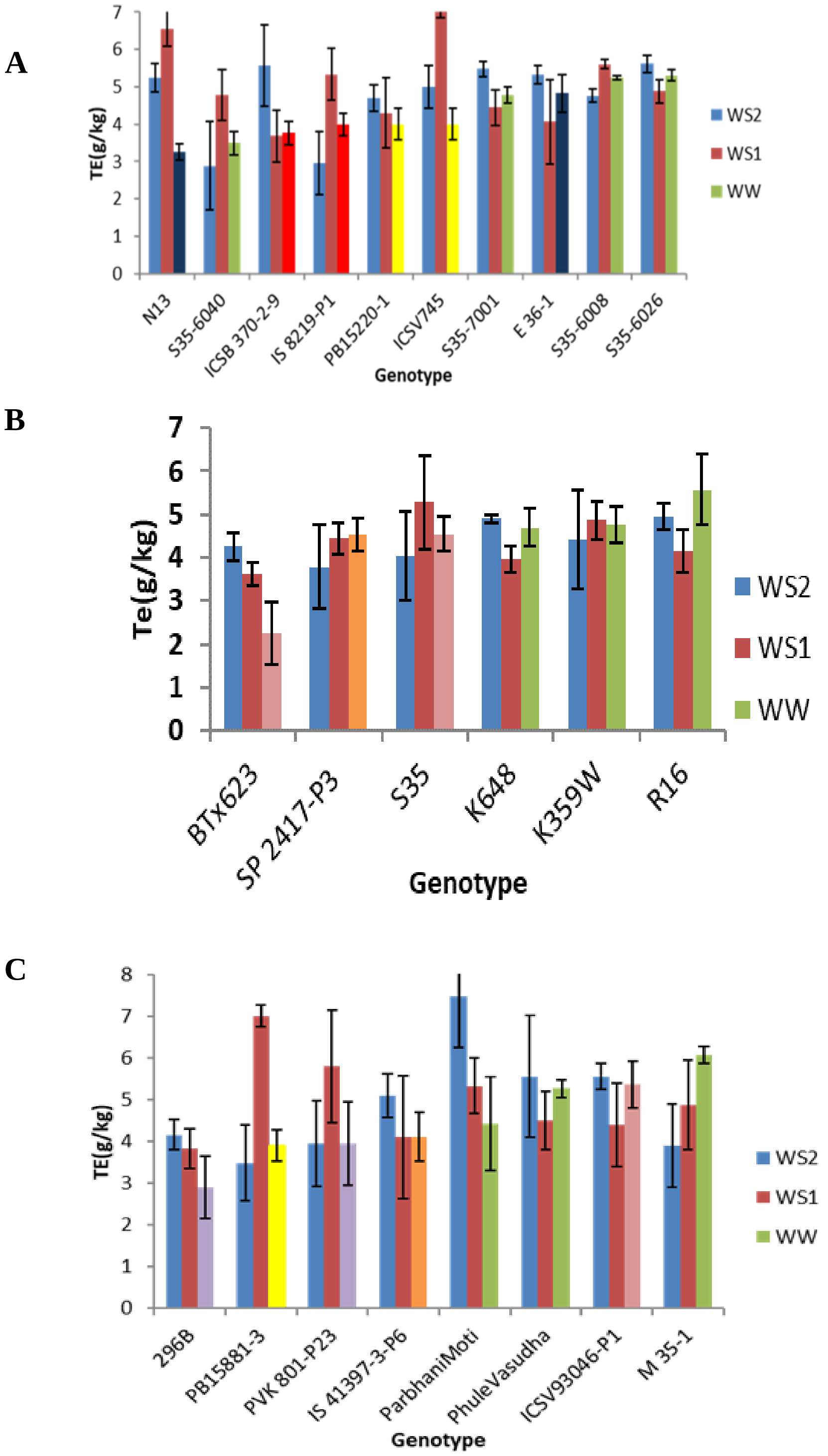


Figure 2.2. **Transpiration efficiency (TE) showed by genotypes studied in lysimetric facilities under well-watered (WW), mild water stress (WS1), and severe water stress (WS2) conditions. Genotypes are grouped based on flowering time (days to flowering: 40-44 (A), 45-48 (B), and 49-58 (C))**

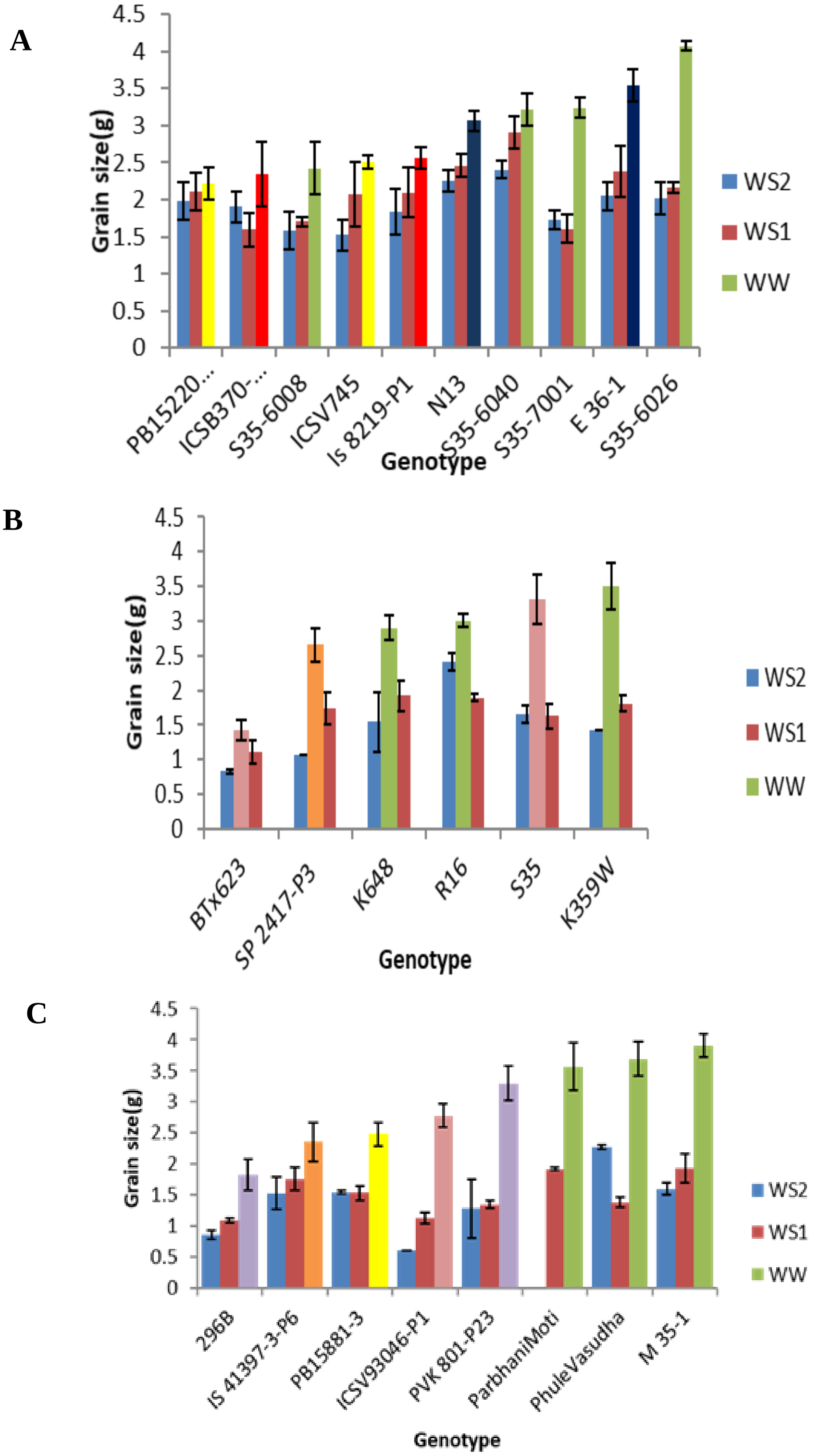


Figure 2. 3. **Grain size differences showed by genotypes studied in the lysimetric facility under well-watered (WW), mild water stress (WS1), and severe water stress (WS2) conditions. Genotypes are grouped based on flowering time (days to flowering: 40-44 (A), 45-48 (B), and 49-58 (C))**

Figure 2.4. Leasyscan facility at ICRISAT

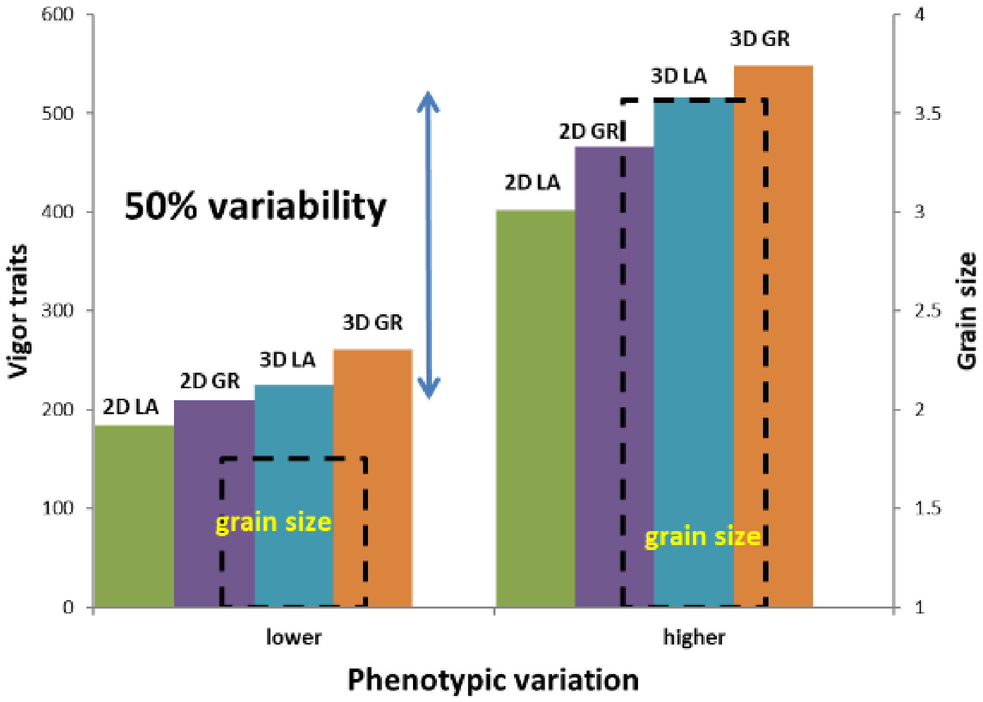


Figure 2.5. Variability for the traits observed (plant vigor traits: projected leaf area [2D LA] and canopy leaf area [3D LA]; 2D growth area [2D GR] and canopy growth rate [3D GR]; Grain size; grouped into low vigor and high vigor lines based on grain size) for the recombinant inbred line [RIL] population derived from the cross between N13 and E36-1.

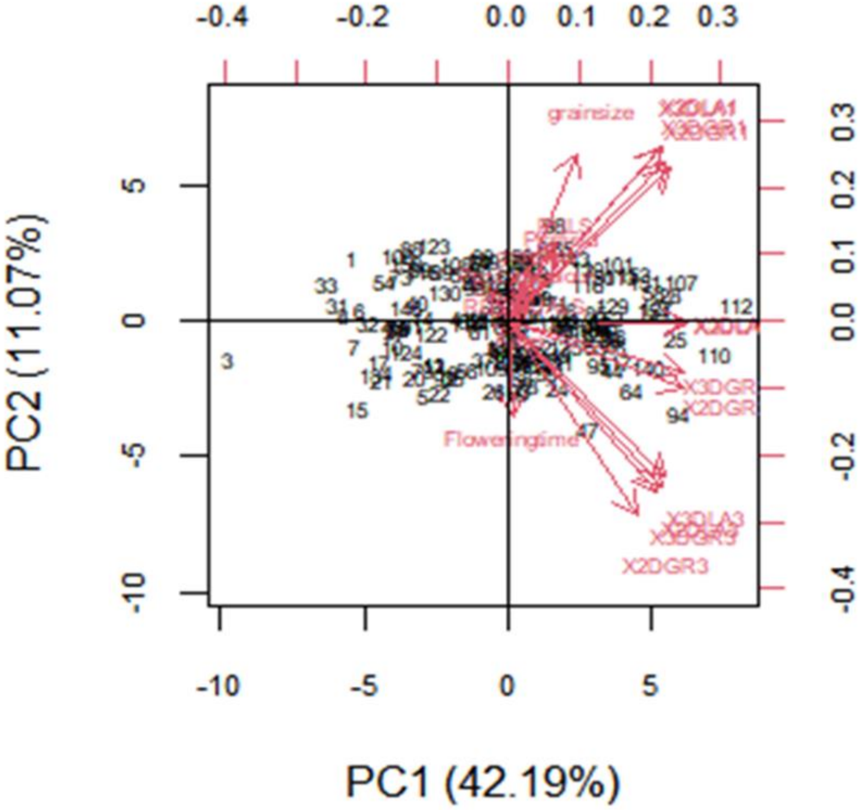
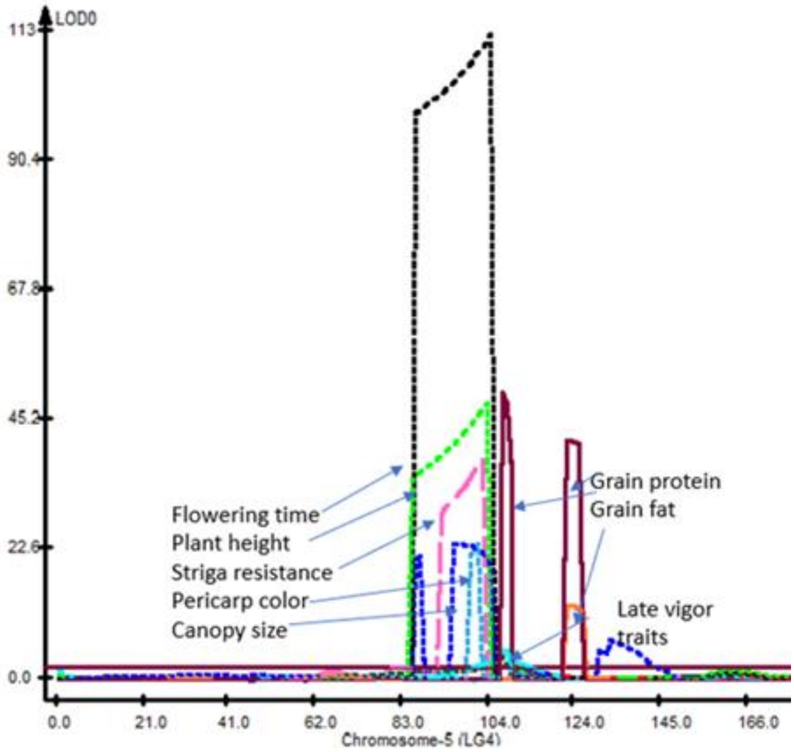
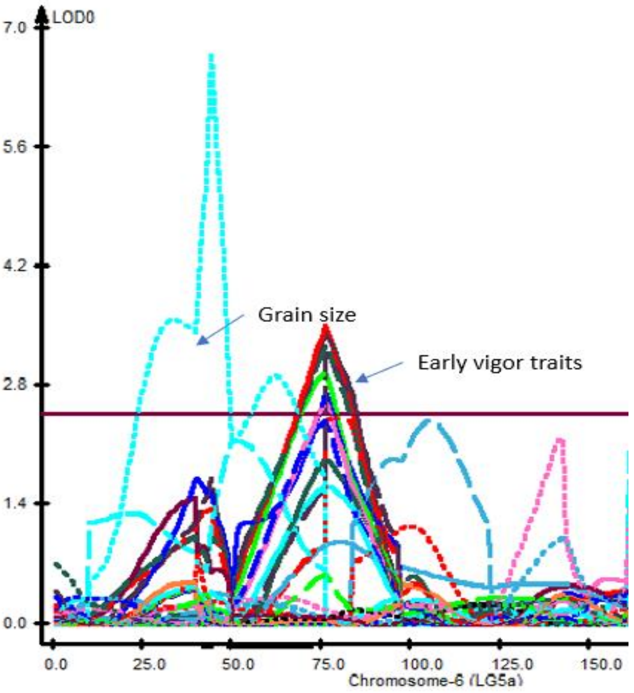


Figure 2.6. Graphical representation of principal component analysis (PCA) for plant vigor traits observed in Leasyscan facility and field-related traits. Numbers represent the recombinant inbred line numbers and trait vectors are represented by red arrows.

A


LOD0
113
90.4
67.8
45.2
22.6
0.0
0.0
21.0
41.0
62.0
83.0
104.0
124.0
145.0
166.0
Chromosome-5 (LG4)
Flowering time
Plant height
Striga resistance
Pericarp color
Canopy size
Grain protein
Grain fat
Late vigor traits

B


LOD0
7.0
5.6
4.2
2.8
1.4
0.0
0.0
25.0
50.0
75.0
100.0
125.0
150.0
Chromosome-6 (LG5a)
Grain size
Early vigor traits

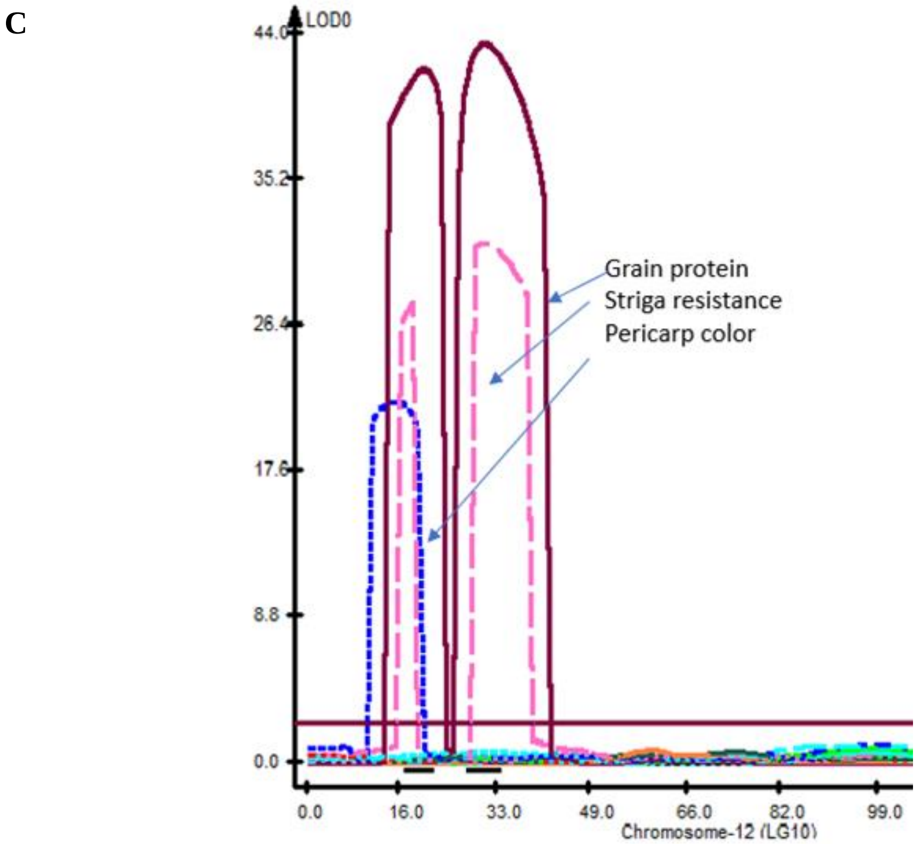


Figure 2.7. Graphical representation of important QTLs identified and their colocalization on different chromosomes (linkage groups). LG4 (A): Colocalization of late vigor traits with phenological traits and trait related to Striga resistance along with grain quality traits (grain protein and fat) on LG4; LG5a (B): Colocalization of grain size QTL with QTLs related to early vigor traits (2D growth rate, 2D leaf area, 3D growth rate, and 3D leaf area) on LG5a which is harboring the previously studied genetic region of stay green 4; LG10 (C): co-localization of grain protein content with Striga resistance trait and pericarp color

CHAPTER 3

Agronomic and qualitative characteristics of sorghum stay-green QTL introgression lines; Effect of GxExM interactions

3.1. Introduction

Sorghum grain is a significant commodity and also serves as an important source of food and fodder for the poorest, malnutrition-threatened, small farming communities in developing countries of the semi-arid tropics (SAT). SAT production systems are already burdened by limited water availability and it is likely to become more severe due to changing climate scenarios which can further suppress the socio-economic development of SAT communities. These communities can substantially benefit from enhanced food productivity and quality.

Genotypes expressing the stay-green trait are characterized by extended maintenance of green leaf area under different environmental circumstances (Thomas and Ougham, 2014). Research on sorghum stay-green phenotype in Australia and the US found that stay-green and grain yield were positively correlated in a range of water-limited environments (Rosenow et al., 1983, Henzell et al., 1992). Detailed physiological studies were undertaken in Australia (Borrell et al., 2000a, and 2000b) and India (van Oosterom et al., 1996, Borrell et al., 1999) to elucidate the plant mechanisms underpinning stay-green. In the initial studies, a cross between B35, donor parent for stay-green, and TX430, a senescent parent was used to produce recombinant inbred line population to map different QTLs (StgA, StgD, StgG, as major QTLs, and StgB, StgI.1, StgI.2 and StgJ, as minor QTLs) (Crasta et al., 1999). Later, the stay-green trait was also identified in four chromosomal regions (quantitative trait loci (QTLs); Stg1, Stg2, Stg3, and Stg4) by many research groups in the US and Australia. In India, four of these stay green QTLs (stg1, stg2, stg3, stg4) along with two additional QTLs identified in India (stgA and stg B; Hash et al., 2003) were transferred into genetically diverse, drought susceptible, elite sorghum varieties by marker-assisted backcrossing (MABC) in different genetic backgrounds (R16, ISIAP Dorado, S35 and ICSV 111) (Hash et al., 2003). These research teams then focused on discovering the physiological and molecular basis of the stay-green mechanisms under-lied by these QTLs and its potential use for the improvement of sorghum drought adaptation in Australia, the United States (Harris et al., 2007, Borrell et al., 2009, Vadez et al., 2013, Borrell et al., 2014a, 2014b), and in India (Vadez et al., 2011a, Kholova et al., 2014). Different stay-green QTLs were found to regulate canopy development before anthesis, such as leaf anatomy, transpiration efficiency, and its components while others were found to influence root morphology and growth and capacity to extract water from the soil profile (Vadez et al., 2011a, Borrell et al., 2014a, 2014b, Kholova et al., 2014). All these studies revealed that these stg-QTLs do influence the plant utilization of soil moisture and, ultimately, grain yield by; (i) reducing water demand before flowering by reducing the size of the canopy, thus, increasing water availability during the post-anthesis period, (ii) increasing access to soil moisture in the soil profile and (iii) regulate plant response to atmospheric drought(vapor pressure deficit; VPD) and consequently transpiration efficiency [TE].

Australian breeding program developed drought-adapted sorghum germplasm carrying various stay-green characters/QTLs and enhancing both grain and fodder yield. Lately, it was also found stay-green characters/QTLs could enhance the fodder quality, particularly in vitro organic matter digestibility and nitrogen content of stover (IVOMD)(Blummel et al., 2015). But this improvement of stover quality along with stover and grain yield depends on genetic background (Blummel et al., 2015). Although grain qualities are very important factors for the development of different end-products and cultivars’ adoption, no study reported the effect of these stay-green mechanisms on the nutritional profile of the sorghum grain and its interaction with different environments (e.g., water stress).

Cereals grain value for food products and feed are generally decided by key indicators such as grain size, grain color, endosperm type and texture, starch, protein content, digestibility, and tannin content. The standards for sorghum grain quality are still under development while some key indicators are already defined; i.e. moisture content (<14.5 %), ash (<1.5 %) protein (>7 %), and tannins (<0.5 %) on dry matter basis (FAO/WHO food standards program, Codex Alimentarius Commission, 1995). However, all these physical and chemical grain properties vary significantly across genotypes, cultivation environment, and management (GxExM)(Betts et al., 2015). In the case of sorghum, very little is known about the variability in grain nutrients (Awika et al., 2018)) and their interactions with the environment.

Therefore, the main objective of the presented study is to understand the effect of stay-green introgression lines and their recurrent parents on important grain constituents, and their interactions with crop environments. Specifically, the main objectives are

i) to investigate whether the stay-green phenotype affects the main nutritional components of the grain

ii) how the nutritional composition of grains and stover (leaf and stem) vary across the range of GxExM combinations

iii) to explore possible functional linkages between different agronomic and stover/grain qualitative traits and possible stay-green mechanisms influencing these relations.

3.2. Materials and Methods

3.2.1. Plant material

Two senescent parent lines S35 and R16 along with three near-isogenic-lines (NILs) derivatives carrying various stay-green quantitative trait loci (stg-QTLs) were tested; S35 is a sweet stemmed, medium duration, dual-purpose senescent variety originated from Ethiopia and R-16 is a highly senescent, post-rainy season adapted cultivar of Indian origin. Stay-green NILs, derivatives of S35 and R16 were developed based on the cross with B35, which is a universal donor of multiple stay green alleles used in prior studies (Tunistra et al., 1996, Crasta et al., 1999), followed by multiple stg-QTLs flanking marker-assisted back-crossing scheme (Kassahun et al., 2010). NILs selected for this study were previously used to describe the stay-green mechanisms (Vadez et al., 2011a, Kholova et al., 2014) and originated from S35: 6008 (stg 3A and C) and 6026 (stg 1 and 2) and from R-16: K359w (stg 3A and 3B) (Figure 3.1). In the experiments, farmer-preferred elite line M35-1 ("Maldandi" type) was included as a check. Yield predictions of this M35-1in post rainy season due to changing climate was also assessed recently using the Crop Environment Resource Synthesis sorghum model (CERES) (Chadalavada et al., 2022). This study suggested increase in the yields in the future due to increase in rainfall and atmospheric CO2 by the end of 21st century, that makes this genotype a feasible option for farmers in India. Thus, taking M35-1 as a check in these experiments was found out to be an appropriate option to assess the production quantity and qualities of stay-green genotypes.

3.2.2. Crop growth conditions in field trials

Trials were planted on 11-12-2013 and 11-04-2014 in post rainy (rabi) seasons "2013-14" and "2014-15" at ICRISAT (Patancheru, Telangana, India, latitude 17.53°N, longitude 78.27°E, altitude: 545m). Crops were raised on ~1m deep vertisols with the water holding capacity between 30% - 51% and plots were organized into hills of 8 rows of 4 m length with 60 cm row-to-row spacing. For these trials, the completely randomized block design with three replications for each block of the factorial treatment combinations was followed. Factorial crop treatments included fully irrigated treatment (WW) and limited water supply (WS), full dose of N-fertilizer (HN), and limited N supply (LN) and two levels of plant populations (HD, LD) in both seasons. Water treatments consisted of fully irrigated control which received four flood irrigations (~50 mm/irrigation) during the crop growth and water-stressed treatment which received two flood irrigations (~ 50 mm after the sowing and at 35 days after sowing). Irrigation treatments were further combined with two levels of nitrogen applications in two doses. A basal dose of diammonium phosphate was applied just before the sowing at the rate of 200 kg ha^{-1} in 2013-14 and 150 kg ha^{-1} in 2014-15. The top dose of urea was applied after a month from crop emergence at the rate of 90 kg ha^{-1} for high nitrogen plots and 30 kg ha^{-1} for low nitrogen plots in 2013-14 and 100 kg ha^{-1} and 0 kg ha^{-1} for high and low nitrogen plots respectively in 2014-15. These were further combined with two levels of plant population densities ("low density" of ~5/8 in 2013-14/2014-15 and "high density" of 14/11.5 plants m^{-2} in 2013-14/2014-15). These resulted in the following treatments combinations replicated in fully irrigated and water-limited conditions; 1) High nitrogen high density-HNHD 2) High nitrogen low density-HNLD 3) Low nitrogen high density-LNHD, 4) Low nitrogen low density-LNLD; therefore, resulted in eight treatments altogether.

3.2.3. Weather details

During the crop cycle, the daily minimum and maximum temperatures, solar radiation, rainfall, and soil evaporation were recorded by the ICRISAT weather station. Minimum and maximum daily temperatures fluctuated between 6.8°C to 38.2°C in 2013-14 and 5.4°C to 35.4°C in 2014-15 (Table 3.1). Average solar radiation in each season was 16.7 MJ m^{-2} and 17.01 MJ m^{-2} and cumulative in-season rainfall were 33.5 mm and 132.6 mm during 2013-14 and 2014-15, respectively. Soil evaporation was 4.7 and 4.8 mm on average in each season respectively. Rainfall was 7 mm before flowering in 2013-14 whereas it was 70 mm before flowering in 2014-15. The weather details and weather summary are shown in Table 3.1 and Fig 3.2. Note: in the 2014-15 season, the night temperatures dropped below 10°C for 3 weeks (Fig. 3.2) which might have resulted in a smaller plant size achieved in this season (Table 3.2).

3.2.4. Agronomic characteristics measured

For evaluation of agronomic traits, inner homogeneous parts of six rows of each 8 rows plot in the field were harvested (i.e., "bulk harvest"). The exact area and plant count were noted in these plots and dry biomass and grain yields were estimated and then converted to the genotype yields per hectare. To evaluate further plant details, in each experimental plot (avoiding the borders) four uniform plants were selected (i.e,.12 plants per each of the genotype-treatment combinations) and evaluated for agronomic traits (plant fractions dry weight, grain number, and size; flowering time) and canopy-related parameters (total leaf area at booting stage [cm^2], leaf are index [m^2m^{-2}], senescence score (0-100%: based on visual senescence scores of the individual plant)). At the time of maturity, leaves, stems were collected separately from the selected plants, and weights of each plant fraction were recorded after drying in a forced-air oven at 60° C for one week. Panicles from individual plants and bulk harvest were weighed, threshed, and dried and grain weight, grain number, and grain size (100-grain weight) were recorded. Biomass partition index (BPi) i.e., amount of above ground stover dry weight accumulated per unit of leaf dry weight which could be considered as a crude proxy for leaf photosynthetic efficiency was calculated as the ratio of dry leaf +stem weight [g] / leaf weight [g] for each plant.

3.2.5. Stover and Grain quality-related characteristics

3.2.5.1. NIRs analyses

Leaf, stem, and grain samples which were harvested from four individual plants in each plot were used for NIRs analysis. Then each of the plant fractions from all the four plants in a plot was mixed to make a single sample that represented the variability of each plant fraction (leaf, stem, and grain) within each of the plots. These samples were homogenized to a fine powder in a Wiley mill (particles size 0.4-0.8mm) to perform near-infrared spectroscopic (NIRs) analysis (Model 5000 Monochromator; FOSS Tecator, Silver Spring, MD, USA).

The qualitative traits estimated for each of the plant fractions by NIRs were: dry and ruminant's in-vitro organic matter digestibility (IVOMD) for leaf, stem, and grain (Blummel et al., 2015). The stover (leaf and stem) IVOMD was approximated by weighting the leaf and stem IVOMD values by their proportional dry weights (Blummel et al., 2009).

3.2.5.2. Wet-lab analyses

The grain quality parameters; protein, fat, and amylose were measured using standard laboratory AOAC (Association of Official Analytical Chemists) methods. Equal quantities of the grain samples (from all the 4 single plants) collected from all three replications of each genotype x treatment combinations were thoroughly mixed, combined into a single sample, and ground to fine powder by Cyclotech sample mill (CT 193, Foss, North America). The analyses quantifying nitrogen, fat, and amylose contents were performed and the qualitative parameters were expressed as a proportional weight of particular components per unit of dry weight [w/w%];

Total nitrogen content was estimated using the Kjeldahl method (AOAC; 2001.11). Briefly, 0.5 g of flour sample was mixed with 3g of catalyst mixture 10 g of potassium sulfate and 1 g of copper sulfate) and 10 ml of conc. H_2SO_4 and subjected to complete digestion at 420°C. After the digestion step, the sample was subjected to alkaline distillation. Finally, distillate which was collected in boric acid was titrated against 0.1 N HCl and nitrogen content was calculated based on the titer value. Protein percentage [w/w %] was approximated by multiplying nitrogen content with the protein conversion factor of 6.25 (Mulder et al., 1839)

Fat percentage was measured using the Soxhlet method (AOAC 920.39). Briefly, 2 g of ground sample was filled into a thimble, placed in an empty beaker and the whole set-up was pre-weighed. 80-100 ml of petroleum ether was added into the set-up and was placed in the Soxhlet unit for boiling. After an hour, the temperature was doubled to collect the solvent in the condenser. Beakers were taken out, dried for 30 minutes, and weighed again. Fat percentage was estimated from the difference between final and initial beaker weights.

Amylose content was measured as per Williams et al. (1970). For this, the first starch was isolated from grain flour samples using the method described in Bangoura et al. (2012). Then, 10 mg of starch sample was taken and 5 ml of 0.5 N KOH was added. The sample was mixed thoroughly and transferred to a 50 ml volumetric flask and made up to the mark with distilled water. 10 ml of an aliquot from this mixture was transferred to another 50 ml volumetric flask and 5 ml of 0.1 N HCl and 0.5 ml of iodine reagent was added and made up to 50 ml mark with distilled water. The absorbance of samples was measured at 625 nm.

3.3. Statistical Analysis

Combined analysis for two seasons was carried out using multiple-way (five-way) ANOVA by keeping season (S), water (W), nitrogen (N), density (D), and genotype (G) as treatment factors and replication as a block (GenStat v. 14.0; Payne et al., 2011) to evaluate the magnitude of the effect of each factor and two-way interactions between treatment factors (W x N, W x D, W x G, N x D, N x G and D x G) and also the effect of season, water, nitrogen and density (S x W x N x D) (Table 3.2). The ANOVA was followed by a Tukey-Kramer test to identify significant differences between genotypes over all the treatments (Table 3.3) and for the different water regimes (WW and WS, Table 3.3).

To investigate the relationship between the measured traits, principal component analysis was performed using the R statistical software version 3.5.1 (R core team, 2018) to find out the relationships between the measured traits. (Figure 3.3-3.7). Based on the PCA results, important correlations between the traits have been plotted separately and Pearson correlation coefficient (*R*) and p values were generated for the same using R statistical software version 3.5.1 (R core team, 2018)

3.4. Results and Discussion

3.4.1. Effect of seasons, treatments, and genotypes on crop agronomic parameters and production qualities

Table 3.2 contains the ANOVA results that showed the effect of season, water regime, nitrogen use, plant density, and genotype on the measured agronomic and quality-related traits. This analysis revealed a large effect of season, water, genotype, and density on most of the measured traits. The effect of fertilizer application was minimal compared to other treatments but showed a significant treatment interaction for traits like BPi and IVOMD.

Although there was a considerable effect of season, some trends showed similarities between both the data sets. Water treatments (W), genotypic (G) differences and planting density (D) had a major influence on the crop productivity whereas the significant effect of treatment interactions for fertilizer (N) input was seen on BPi and quality traits. In this study, the absolute production of stay-green material under WS treatments was not significantly higher compared to recurrent parents and this could have been happened due to less severity of WS (~30%) treatment compared to the majority of previous reports showing the stay-green production benefits (Vadez et al., 2011a, Jordan et al., 2012, Borrell et al., 2014b, Kamal et al., 2017, Sugg et al., 2017).

Stay-green isolines used in this study did not attain higher grain and stover yields, but at the same time significantly improved the grain number (6008) and grain size (K359W) compare to their recurrent parents (Table 3.2). Both of these lines also retained significant canopy greenness (BPi) which is probably reflected in their higher stover IVOMD compared to their respective parental lines. The stay-green lines derived from S35 showed a significantly higher proportion of biomass into the stem (i.e., higher BPi) while the BPi was similar in lines of R16 origin. Across all the treatments, stay-green NILs, K359W and 6008 attained higher content of grain fat compared to their senescent parents. The local check (M35-1) attained significantly higher biomass distribution between stem and leaf (higher BPi) but attained lower fat content compared to stay green lines.

3.4.2 Effect of stay-green technology across seasons, treatments, and genotypes on crop agronomic parameters and production qualities

Across all tested treatments the lines carrying stg C and stg 3A & 3B stay-green QTLs showed less senescence which is in accordance with the previous reports where the association of stay-green technology with canopy greenness that aids in the improvement of crop production in drought-prone environments were reported. (Borrell et al., 2014a, Galyuon et al., 2019). The retention of canopy greenness appeared to be associated with an increase in the stover IVOMD (in-vitro organic matter digestibility for ruminants) and improved grain nutritional composition (fat content). Thus, this study confirmed the positive effect of stay-green technology on fodder qualities (stay-green C and 3A&3B; Blummel et al., 2015) and at the same time showed the stay-green effect on the grain composition - particularly grain fat content. Further, in-depth studies are still required to confirm this effect because some of the grain fatty acids are involved in the milled grains rancidification (Doblado-Maldonado et al., 2012, Čepková, et al., 2014) and might alter the organoleptic qualities of the food products (Heiniö et al., 2002, Osuna et al, 2014).

3.4.3. Genotypic effect on crop agronomic parameters and the grain and stover nutritional composition within the water treatments

The subsequent analysis showed the responsiveness of genotypes to the water treatments (WW, WS; Table 3.3). WS treatments caused a reduction in grain and stover production (~ 30% on average), and also influenced important components of grain yield (grain size reduced: ~ 20% on average, accelerated senescence: ~ 100 % on average). BPi and most of the grain qualities were comparatively less affected by the WS treatments.

When observed the genotypic differences, confirming the ANOVA results (Table 3.2), the differences in grain size were still significant for K359W which produced larger grains (K359W) under both treatments (Table 3.3). In this analysis which considered the water treatments separately, the BPi remained significantly higher for stay-green introgression line 6008 compared to S35 in both treatments as shown by ANOVA results (Table 3.2) and additionally, it was found WS reduced BPi in this line. In general, water stress accelerated senescence, but stay-green variant 6008 remained significantly greener compared to the parental line under WS treatment and the same trend appeared for K359W. The stay-green variants which could maintain greenness (6008 and K359W; Table 3.2, 3.3) also attained significantly higher stover IVOMD compared to the parental lines in both water treatments. Furthermore, the analysis also confirmed these two stay-green variants (6008 and K359W) attained higher grain fat content and this trend was significant for both lines under water stress treatments. Maldandi genotype (M35-1) was distinct from most of the other material mainly with its higher BPi and lower grain fat content and had lower grain protein content compared to lines of S35 origin under both water regimes.

The current study also revealed that different stay-green QTLs might affect different plant processes and their effect would also depend on the genetic background as documented before (Harris et al., 2007, Talwar et al., 2017, Vadez et al., 2011a). Here, it was found that both of the introgression lines of S35 background (6008 and 6026) significantly increased the proportion of stem biomass (increased BPi - probably due to stg C and stg 1&2 introgression) but there was the minimum effect on BPi in R16- 3A & 3B stay-green derivative (K359W).

3.4.4. Relationships between investigated traits

PCA analysis was carried out across and within the water treatments to understand the main relations between the traits in the generated dataset (Figures 3.3-3.7). Analysis results showed a strong link between assimilates source (i.e., biomass accumulation components; stover weight, LA) and sink (i.e., grain yield and its components; grain size) strength. PC1 and PC2 loadings also showed the size of the source and sink tended to be negatively correlated to the senescence scores, and the associations were stronger under WS treatments. (Figure 3.5). PC2 and PC3 components revealed the negative relations between senescence and biomass partitioning index (BPi) i.e. more “leafy” plants were senescing more rapidly. BPi and senescence, in turn, appeared to influence IVOMD of plant parts; i.e. more senescent plants with lower BPi generally attained lower stover, leaf, and stem IVOMD and had lower grain IVOMD and, in some treatments, tended towards lower protein content (Figures 3.3-3.7).

Thus, the main source-sink relations were revealed by PCA analysis. i.e., the plants capable of accumulating more stover biomass across the range of environmental conditions had also enhanced capacity to produce bigger grains and total grain yield. This enhanced production capacity was linked to the maintenance of greenness (lower senescence scores) across the range of studied treatments. Apart from this, this analysis also revealed the relation between BPi and Senescence (Figure 3.8). Lower senescence and higher BPi appeared, in turn, to be associated with grain and stover qualities. Thus, current analysis supports the known functional relationship between the stay-green phenotype and a plant’s capacity to produce grain and stover under water-limited environments. According to previous reports, stay-green phenotypes are associated with higher production in water-limited conditions which links to the increased post-anthesis water availability (Vadez et al., 2011a, Borrell et al., 2014b, Kholova et al., 2014). The increased post-anthesis water use could be attributed to constitutive traits related to canopy features (Vadez et al., 2011a, Borrell et al., 2014a, Kholova et al., 2014) or access of roots to water in deeper soil layers (Borrell et al., 2014a). Supportive evidence for these reports was generated in the current work showing the crop agronomic parameters (grain and stover yield and their components) are likely to be a consequence of the constitutive plant functions.

In addition to that, this study revealed that the altered biomass partitioning (high BPi; more stover biomass per unit of leaf biomass) might be functionally linked to the plant stress-accelerated senescence processes and subsequently reflected into the grain and stover qualities (IVOMD and possibly grain protein content). Also, these high BPi values might be related to higher photosynthetic activity per unit of leaf dry matter, capacity to produce more soluble assimilates per unit of photosynthetically active tissues, and also possibly contribute to higher digestibility (IVOMD) of stover material. This is in accordance with previous reports; Borrell et al. (2015) documented the stay-green technology increased leaf parenchyma layers. Van Oosterom et al. (2010a, 2010b) also found that assimilates re-mobilization during grain filling is linked to leaf senescence processes. In addition to this evidence, the current study also revealed plant photosynthetic efficiency could be related to grain and stover qualities.

3.5. Summary

In this study, we investigated stay-green technology and its effects on sorghum crop quantity and quality across the range of cultivation practices. For this purpose, previously characterized stay-green introgression events, their senescent parental lines, and Maldandi sorghum check were used as study material. The crops were raised in two post-rainy seasons under factorial treatments of irrigation, planting densities, and fertilization, and the crop's grain and stover characteristics were assessed. The study confirmed stay-green technology was associated with enhanced agronomically important traits (grain size and seed number) and stover qualities (IVOMD; across all treatments) and also be associated with altered grain nutritional composition (grain fat content under different environments and protein content under drought). Particularly, the study showed that plant allometry (biomass partitioning index; BPi [stover [leaf+stem] dry weight per unit of leaf dry weight]) could explain a considerable proportion of variation in canopy senescence and stover and grain qualities which has not been described before. If confirmed across a broader range of plant material, BPi might be practically used in crop improvement programs as a proxy of crop propensity to senesce but also an early indicator of grain and stover qualities.

Table 3.1. **Experimental and weather details in experiments conducted during 2013-14 and 2014-15; Crop sowing and maturity Table (average across genotypes) dates, soil type, maximum and minimum temperatures (C°), in-crop rainfall (mm), solar radiation (MJ m^{-2}) and evaporation (mm) are listed for the crop growing period in experiments conducted in seasons 2013-14 and 2014-15.**

Season	Soil	Sowing date	maturity date average	Max. temp (°C°)	Min. temp (°C)	Rainfall (mm)	Solar radiation (MJ m^{-2})	Evaporation (mm)
2013-14	Vertisol	12-11-13	31-03-14	38.2	6.8	33.5	16.7	4.7
2014-15	Vertisol	04-11-14	10-03-15	35.4	5.2	132.6	17	4.8

Table 3.2. **Mean values of selected traits for each for seasons, genotypes, water, nitrogen, and density. Season, water, nitrogen and density and their interaction (Water x Genotype, Water x Nitrogen, Water x Density, Nitrogen x Density, Nitrogen x Genotype, Density x Genotype) effects (F value and F probability) and LSD at 5% level were generated using ANOVA by taking treatments and their combinations as treatment structure (season+ water+ nitrogen+ density+ genotype+ water x nitrogen + density x nitrogen+ water x density+ water x genotype + density x genotype + nitrogen x genotype). ***, **, * represents significance of the differences (at >0.001; <0.001, 0.01> and <0.01, 0.05> levels) for each treatment and treatment combinations for the estimated characteristics. The letters behind the values represent the result of the Tukey-Kramer test and different letters indicate the significance of differences between genotypes at 0.05 level. Broad sense heritability (h^2%) was calculated across seasons and treatments by treating genotype as random.**

Genotype	**Bulk grain yield [kg ha^{-1}]**	**Bulk stover yield [kg ha^{-1}]**	**Grain number [m^2]**	**Grain size (100 grain weight) [g]**	**LAI_max [m^{2}m^{-2}]**	**Senescence [0-100%]**	**BPi**	**Stover IVOMD [%w/w]**	**Grain IVOMD [%w/w]**	**Grain Protein [%w/w]**	**Grain Fat [%w/w]**	**Grain Amylose [%w/w]**
S35	3846bc	4670b	18701bc	2.873ab	2.573b	40.85b	3.684b	49.91b	64.1b	9.401c	3.871c	13.49b
6008	3583ab	4830bc	19226c	2.781a	2.222a	31.64a	4.324d	53.49c	64.26b	9.19bc	4.526d	11.68a
6026	3400a	5524c	15803a	3.061bc	2.531b	42.21bc	4.051c	50.27b	63.58ab	9.653c	3.756bc	12.66ab
R16	3728abc	3173a	16770ab	3.136c	2.231a	49.71c	3.197a	46.55a	63.86b	8.416ab	3.638b	12.87ab
K359W	3827bc	3668a	15046a	3.674d	2.108a	40.22b	3.277a	50.1b	63.58ab	7.834a	3.956c	13.64b
M35-1	4040c	5644c	16005a	3.839d	2.758b	44.82bc	5.012e	50.61b	62.97a	7.496a	3.334a	12.52ab
LSD at 5%level	276.7066	561.343	1675.9	0.1722	0.1899	5.4614	0.1815	0.6828	0.4978	0.6483	0.1526	1.1149
season	53.76***	27.94***	55.88***	39.34***	150.23***	116.7***	195.83***	231.59***	572.03***	140.84***	2.05	3.14
Genotype	5.11***	24.36***	7.78***	49***	13.84***	9.27***	112.07***	81.48***	6.68***	14.55***	52.91***	3.19**
Water	256.2***	106.66***	15.11***	255.17***	3.44	316.34***	66.19***	16.5***	4.4*	0.26	3.42	7.51**
Density	7.4**	24.58***	118.61***	6.28*	290.79***	13.37***	3.04	0.93	5.47*	0.62	0.9	0.41
Nitrogen	0.01	2.48	0.01	1.92	0.11	3.45	1.2	0.92	2.95	0.35	0.71	0.28
Water. Nitrogen	2.16	2.95	0.75	0.71	6.02	0.13	25.57***	0	4.81*	1.52	1.23	0.01
Density. Nitrogen	0.12	0.87	0.1	0.01	0.76	0.57	0.58	4.16*	26.14***	3.18	0	0.18
Water. Density	2.92	2.04	2.8	2.14	2.68	0.31	11.76***	0.1	6.91***	3.88	4.64*	0.64
Water. Genotype	0.98	1.55	0.75	0.71	2.03	0.99	5.66***	5.84***	0.29	0.27	5***	7.71***
Density. Genotype	0.42	0.44	2.6	0.71	1.93	0.54	0.4	0.74	0.25	0.44	2.35*	0.15
Nitrogen. Genotype	0.76	0.42	0.77	0.3	1.43	0.61	0.55	1.8	0.2	0.86	2.61*	5.22***
CV%	18.3	30.2	24.5	13.2	19.5	32.5	11.4	3.4	1.9	14.7	9.1	18.2
h^2(plot based %)	0.17	0.28	0.42	0.75	0.23	0.24	0.72	0.29	0.84	53	30	4

Table 3.3. **Mean values of selected traits for water treatment (WW&WS) within each genotype (6008, 6026, K359W, M35-1, R16 and S35) were generated using ANOVA by taking treatments and their combinations as treatment structure (season+ water+ nitrogen+ density+ genotype + water x nitrogen + density x nitrogen+ water x density+ water x genotype + density x genotype + nitrogen x genotype + water x genotype x nitrogen x density). The letters behind the values represent the result of the Tukey-Kramer test and different letters indicate the significance of differences between genotypes at 0.05 level. values in parenthesis represent the proportion of change in measured traits due to water stress treatment for each genotype.**

Effect	**Bulk grain yield [kg ha^{-1}]**	**bulk stover yield [kg ha^{-1}]**	**Grain number [m^2]**	**Grain size (100 grain weight) [g]**	**LAI_max [m^{2}m^{-2}]**	**Senescence [0-100%]**	**BPi**	**Stover IVOMD [%w/w]**	**Grain IVOMD [%w/w]**	**Grain Protein [%w/w]**	**Grain Fat [%w/w]**	**Grain Amylose [%w/w]**
Water												
S35 WW	4643d	5675ef	18545bcd	3.26d	2.805d	27.6ab	3.99cd	50.47bc	64.17b	9.316de	4.048de	13.29abcde
6008 WW	4181d	5616def	17506abcd	3.191cd	2.187ab	19.4a	4.72ef	54.69e	64.29b	9.156bcde	4.645f	11.03ab
6026 WW	4122cd	6737f	14959abc	3.501d	2.608bcd	29.86ab	4.41de	51.23cd	63.74ab	9.834e	3.625abc	13.65bcde
R16 WW	4377d	3828abc	16156abc	3.465d	2.261ab	32.91bc	3.23a	46.21a	63.98b	8.357abcde	3.747bcd	10.65a
K359W WW	4412d	4168bc	13901a	4.042e	2.066a	25.16ab	3.33ab	50.1bc	63.81ab	7.686abc	3.873cd	12.7abcde
M35-1 WW	4572d	6571f	14737ab	4.316e	2.803d	29.45ab	5.16g	50.7bc	63.26ab	7.352a	3.39ab	12.85abcde
S35 WS	3051ab (-0.34)	3671abc (-0.35)	18894cd (0.02)	2.485ab (-0.24)	2.347abc (-0.16)	54.14de (0.96)	3.38ab (-0.15)	49.34b (-0.02)	64.02b (0)	9.486de (0.02)	3.694bcd (-0.09)	13.69cde (0.03)
6008 WS	3008ab (-0.28)	4070bc (-0.28)	20800d (0.19)	2.388a (-0.25)	2.243ab (0.03)	43.35cd (1.23)	3.94c (-0.17)	52.34d (-0.04)	64.23b (0)	9.225cde (0.01)	4.406ef (-0.05)	12.33abcd (0.12)
6026 WS	2679a (-0.35)	4316bcd (-0.36)	16684abc (0.12)	2.621ab (-0.25)	2.461abcd (-0.06)	54.6de (0.83)	3.69bc (-0.16)	49.31b (-0.04)	63.42ab (-0.01)	9.472de (-0.04)	3.886cd (0.07)	11.66abc (-0.15)
R16 WS	3081ab (-0.3)	2525a (-0.34)	17421abcd (0.08)	2.806bc (-0.19)	2.208ab (-0.02)	66.56e (1.02)	3.16a (-0.02)	46.9a (0.01)	63.74ab (0)	8.476abcde (0.01)	3.529abc (-0.06)	15.08e (0.42)
K359W WS	3215ab (-0.27)	3128ab (-0.25)	16162abc (0.16)	3.293d (-0.19)	2.138a (0.03)	55.8de (1.22)	3.22a (-0.04)	50.09bc (0)	63.34ab (-0.01)	7.983abcd (0.04)	4.04d (0.04)	14.59de (0.15)
M35-1 WS	3510bc (-0.23)	4722cde (-0.28)	17311abcd (0.17)	3.36d (-0.22)	2.72cd (-0.03)	60.22e (1.04)	4.86fg (-0.06)	50.53bc (0)	62.68a (-0.01)	7.641ab (0.04)	3.278a (-0.03)	12.2abcd (-0.05)

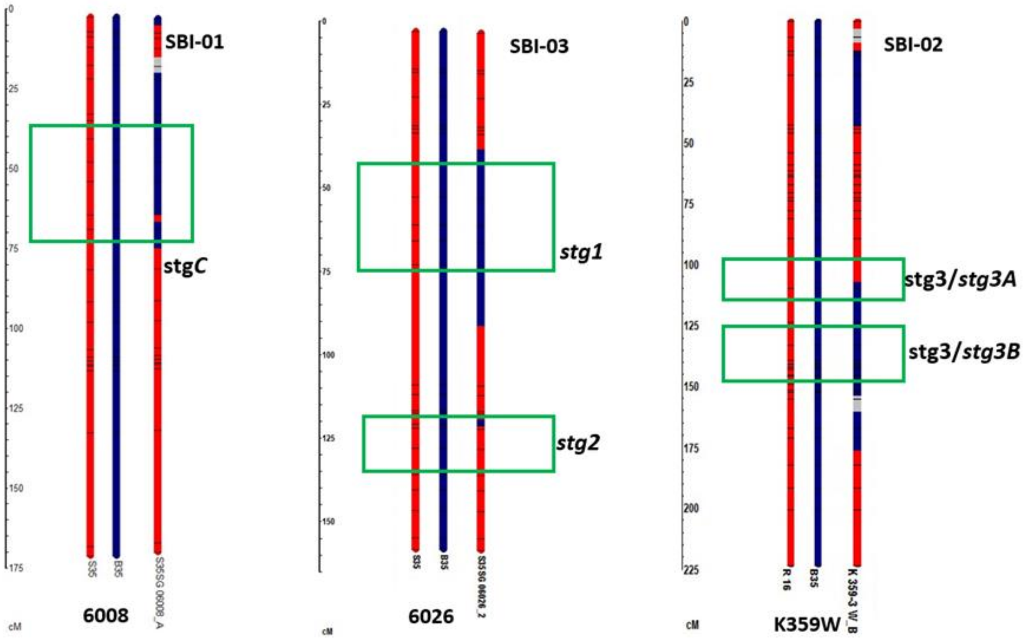


Figure 3.1. Chromosomes showing the stay green QTL introgressions on studied lines; S35 background- 6008 (SBI-01-stg 3A /stgC), 6026 (SBI-03- stg1 &stg2), R16 background- K359W (SBI-02-stg 3A &3B)

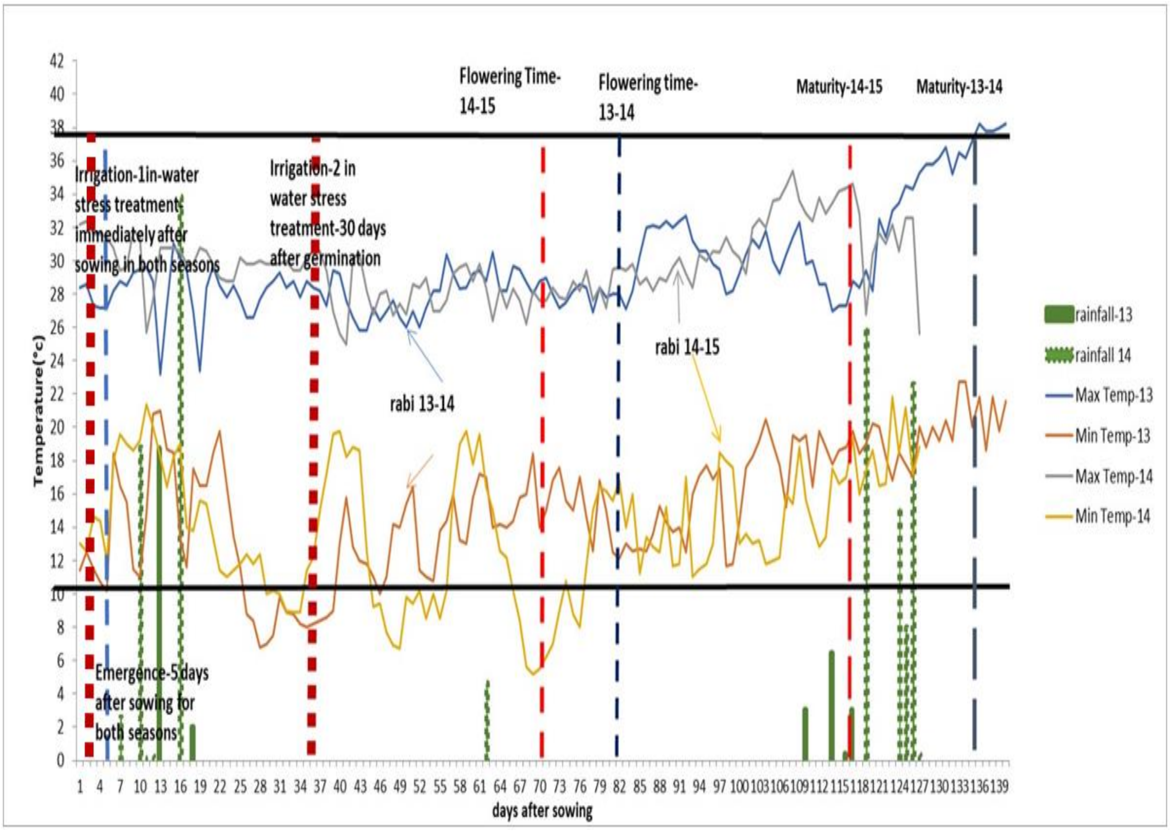


Figure 3.2. Details of crops in 2013-14 and 2014-15; trends in maximum and minimum temperatures[C°] and rainfall [mm] during crop growth period were plotted by keeping days after sowing on X-axis and temperature on Y-axis. The number of days after sowing for crop emergence (~5 days for both seasons), irrigations under water stress treatment (total 2; 1st irrigation- immediately after sowing and 2nd irrigation- at 30 days after emergence for both seasons), flowering time (on an average ~70 days (for 2013-14 and ~80 days for 2014-15 crops) and crop maturity (~115 days for 2013-14 rabi and ~135 days for 2014-15 rabi) were marked on the graph for both 2013-14 and 14-15.

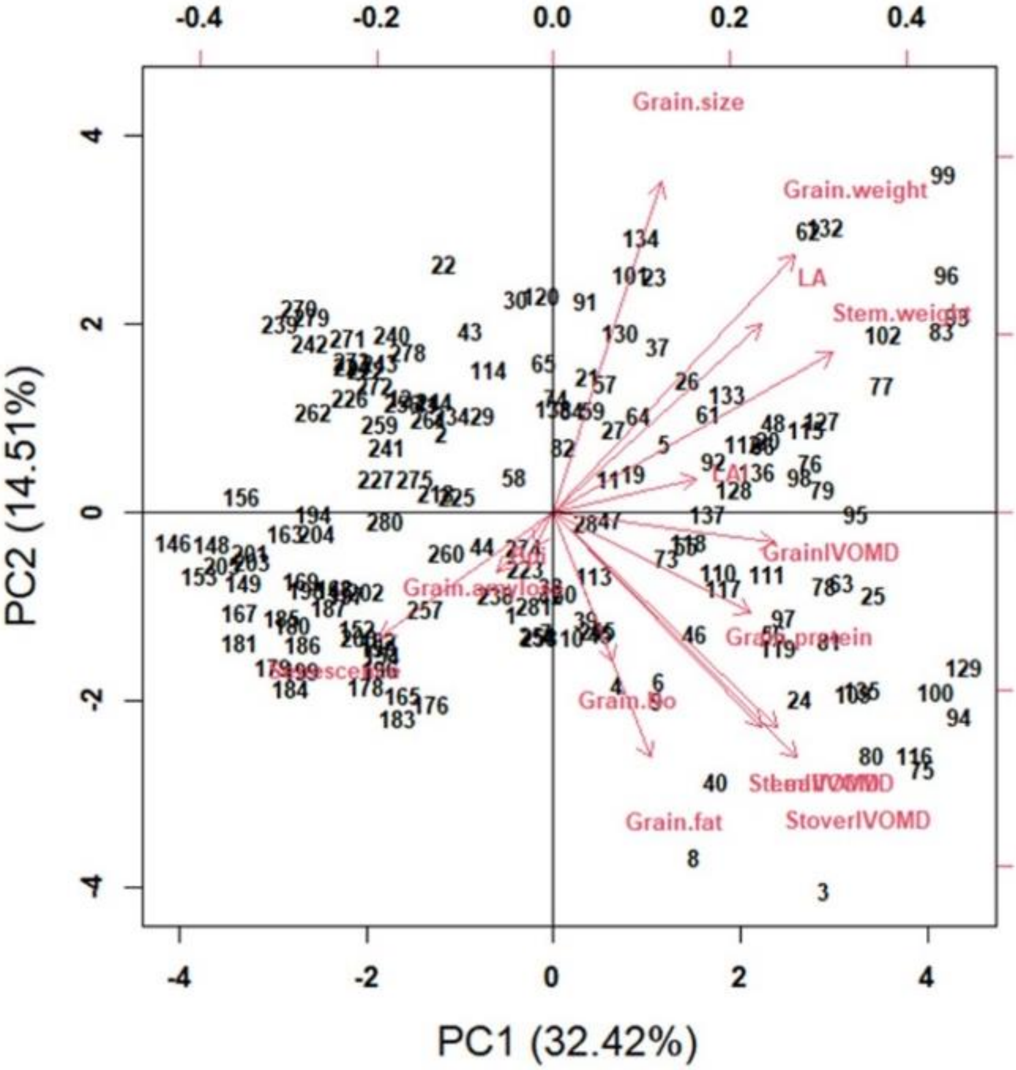


Figure 3.3. Principal component analysis of agronomic, canopy, and qualitative traits measured on studied genotypes- (S35, R16, 6008, 6026 (S35 background), K359W (R16 background), and M35-1) across seasons, water, nitrogen, and density.

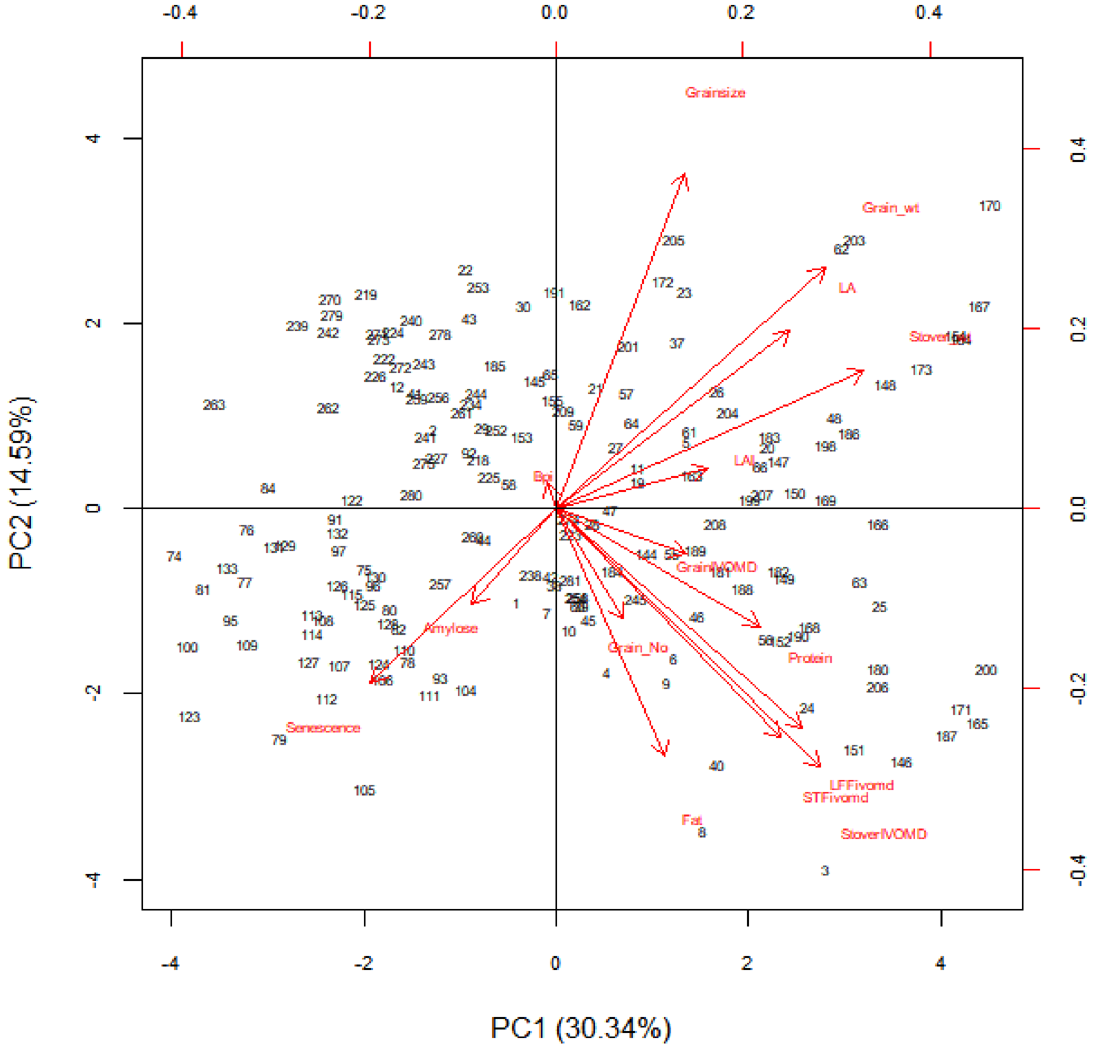


Figure 3.4. **Principal component analysis of agronomic, canopy, and qualitative traits measured on studied genotypes (S35, R16, 6008, 6026 (S35 background), K359W (R16 background), and M35-1) within well-watered (WW) treatment across seasons, density, and nitrogen**

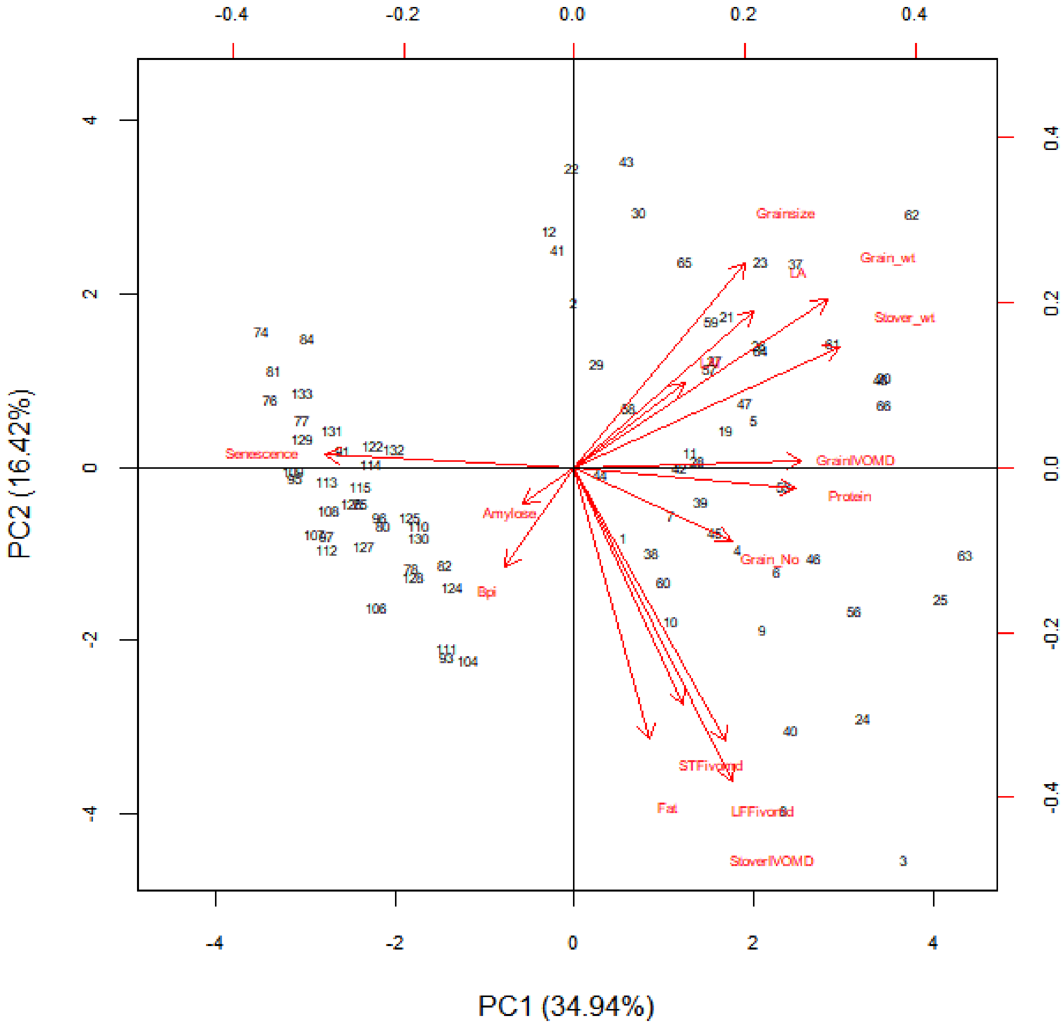


Figure 3.5. **Principal component analysis of agronomic, canopy, and qualitative traits measured on studied genotypes (S35, R16, 6008, 6026 (S35 background), K359W (R16 background), and M35-1) within water stress (WS) treatment across seasons, density, and nitrogen.**

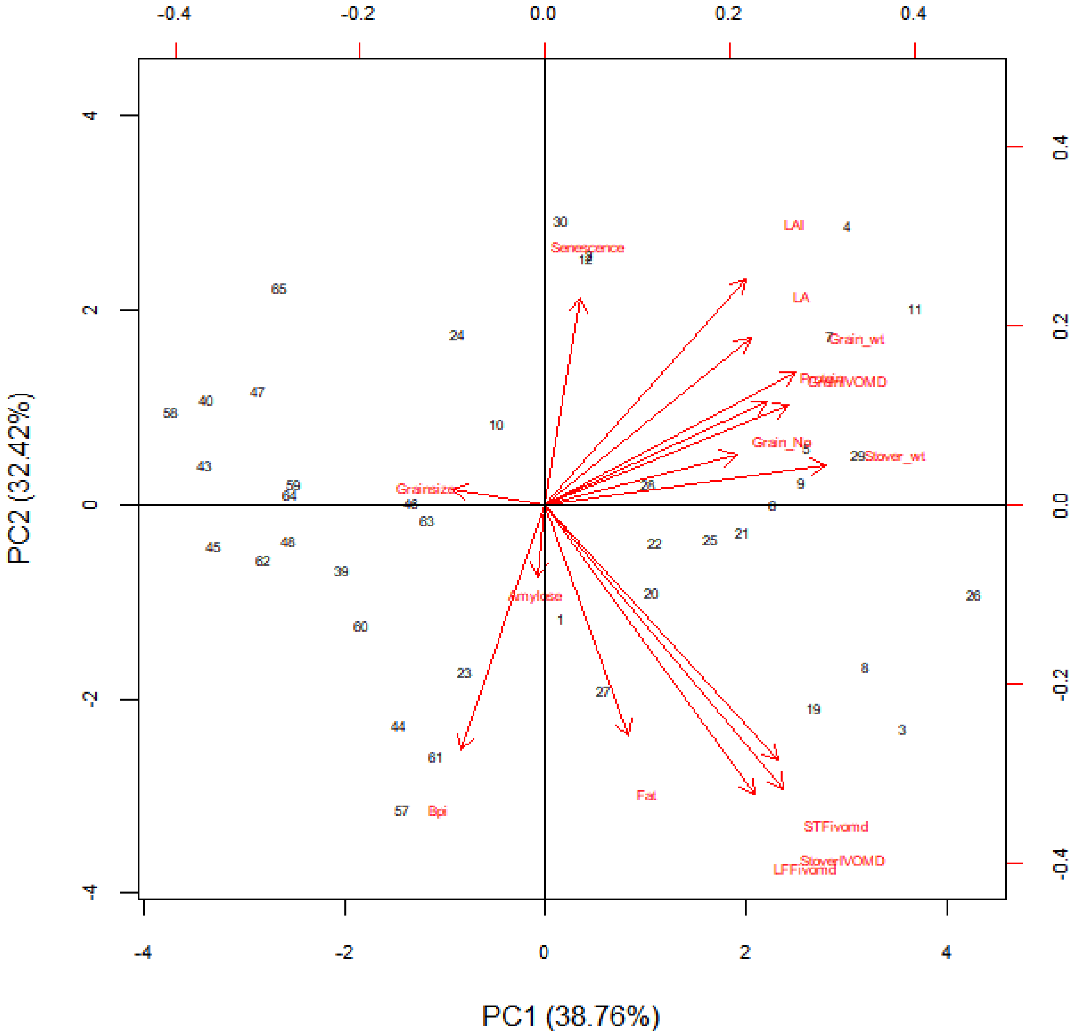


Figure 3.6. **Principal component analysis of agronomic, canopy, and qualitative traits measured on studied genotypes (S35, R16, 6008, 6026 (S35 background), K359W (R16 background), and M35-1) within well-watered (WW), high-density treatment across seasons and nitrogen.**

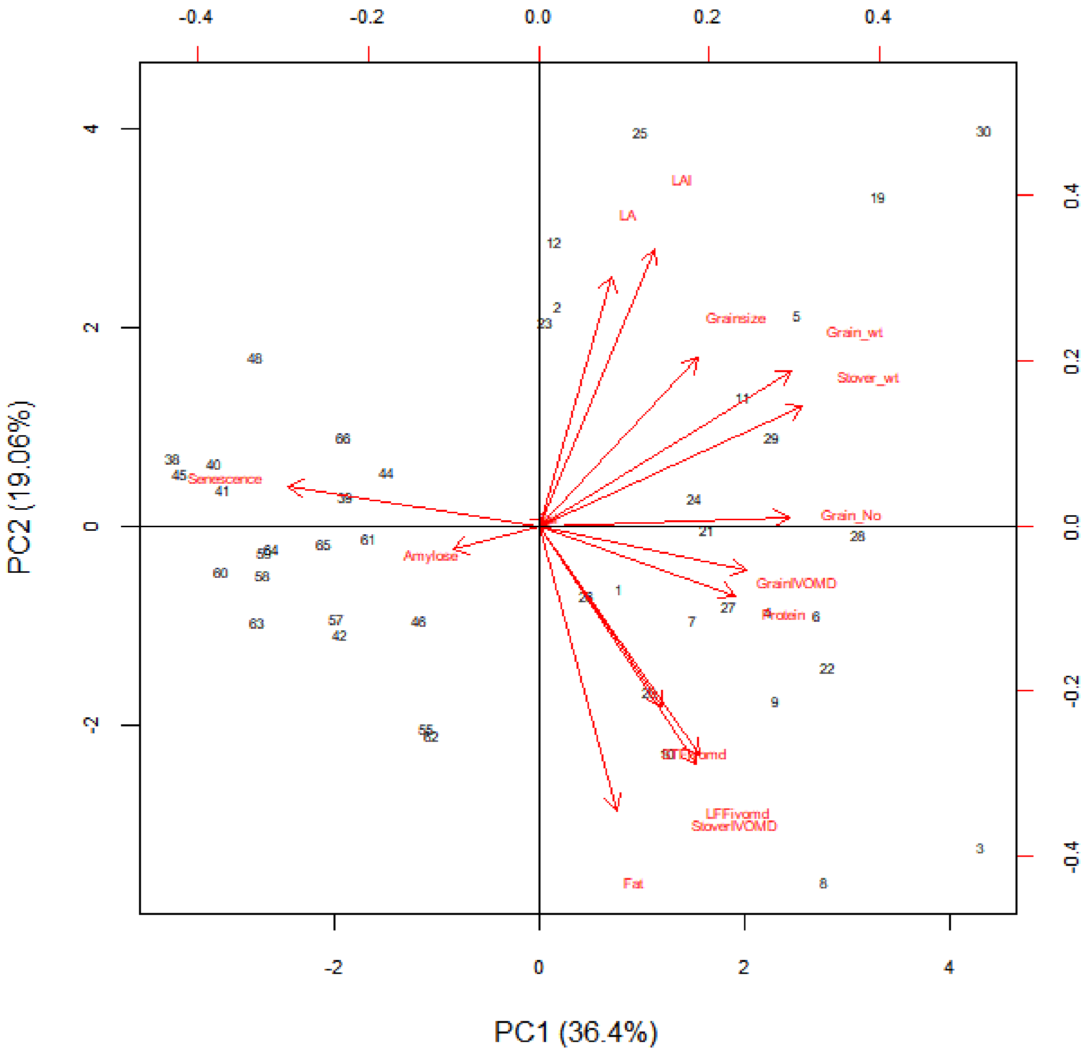


Figure 3.7. **Principal component analysis of agronomic, canopy, and qualitative traits measured on studied genotypes (S35, R16, 6008, 6026 (S35 background), K359W (R16 background), and M35-1) within water stress (WS), high-density treatment across seasons and nitrogen.**

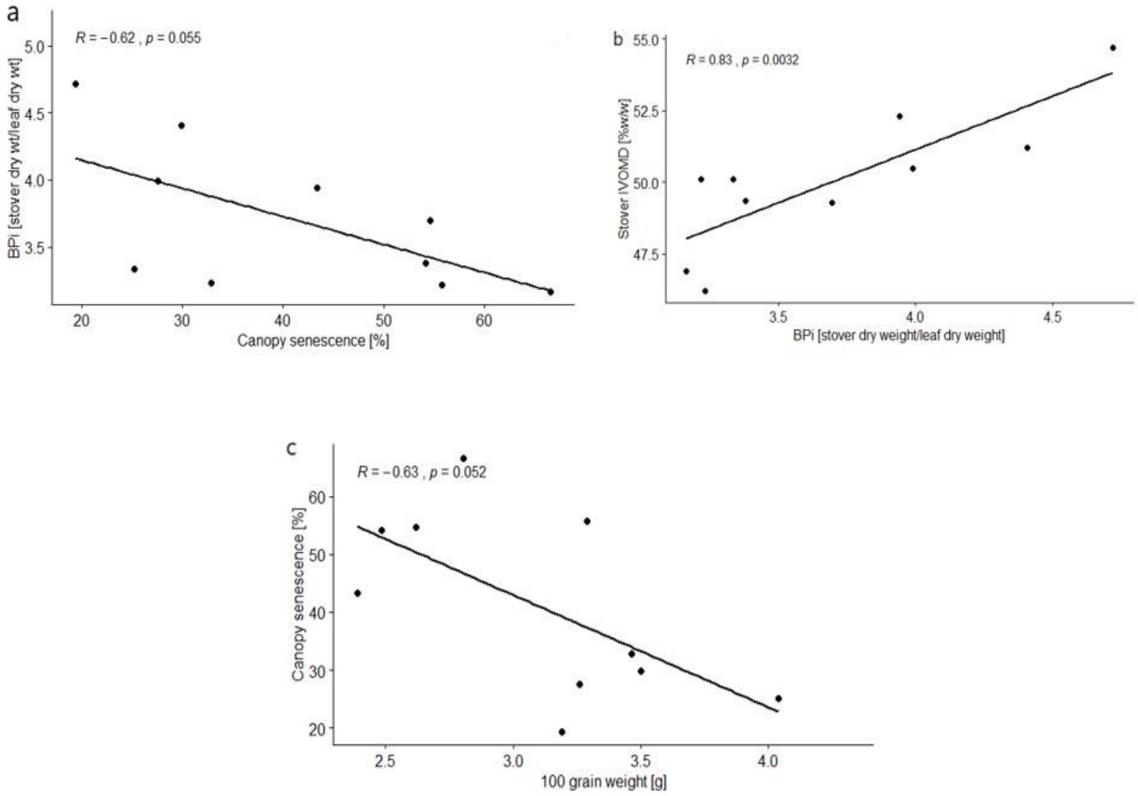


Figure 3.8. Relationships between important agronomic and qualitative traits; a) relationship between Senescence [%] and biomass partitioning index (BPi) b) relationship between BPi and stover in-vitro organic matter digestibility (IVOMD [%w/w]) c) relationship between grain size and canopy senescence [%]. Data points are average values of each genotype across the seasons under well-watered (WW) and water stress (WS) conditions. *R* represents Pearson Correlation and *p*-value represents correlation is significant if it is < 5%.

CONCLUSION

Sorghum is a staple food crop for the population in the semi-arid tropics of the world and is primarily grown by small farming communities in these regions where malnutrition is prevalent. It is a major source of energy, nutritionally dense, and also a valuable source of income that helps to alleviate malnutrition and poverty in developing countries. Sorghum crop is naturally tolerant to harsh environments and primarily cultivated in marginal lands and also in different agro-climatic conditions. But global climate change events led to unreliable sorghum yields, especially in drought-prone environments which directed the global sorghum crop improvement programs to study different sorghum genetic sources available and understand the underlying physiological and molecular processes to improve the sorghum yields in developing countries. Although many research efforts were carried out to improve the sorghum yields, not much research was carried out to enhance the nutritional quality. Due to cultivation in various agro-climatic conditions, improvement of sorghum grain quality mainly depends on the understanding of different genetic, environmental, and management (G x E x M) interactions and physiological and molecular processes involved. Thus, the main aim of the present work is to understand the physiological and genetic determinants influencing sorghum grain quality.

Sorghum stay-green technology involves the expression of stay-green phenotype with extended green leaf area until maturity under water-limited conditions by reducing the pre-anthesis water use and also balancing the nitrogen demand and supply. Many research studies were already carried out to characterize the stay-green phenotype through physiological and molecular studies and provided a lot of genetic material for molecular breeding approaches. Yet, none of the studies focused on the effect of stay-green sorghum on grain quality even though it is proved to enhance fodder quality. So, present research work was carried out to fill this gap by studying the sorghum stay green introgression lines (ILs) and their effect on important agronomic and qualitative traits and genetic (G), environment (€) and management (M) (G x E x M) interactions which influence this effect.

The current research work involved studying a large number of genetic materials for nutritional quality which is time-consuming, laborious, and contra-productive. Thus, rapid tools development is a prerequisite to estimate grain nutritional quality in agricultural as well as industrial sectors. Near infra-red spectroscopic (NIR) technology is already a proven method to analyze grain and stover material by using robust calibrations for different crops. Here, we tried to develop sorghum and multi-cereal grain calibrations for macronutrients (protein and fat) by using classical and multi-variate algorithms. In the current study, sorghum and cereal calibrations which are helpful in rapid screening of breeding material were developed. In addition to that, progress was made to achieve robust multi-cereal calibration (for protein) using mobile sensors in combination with multi-variate algorithms which helps to estimate nutritional quality in different cereal samples using single calibration. Using the same methodology, it is possible to develop robust calibrations for other nutritional constituents that help in a broad range of situations.

To understand the relationship between plant vigor and grain quality traits, a suitable RIL population was selected (N 13 x E36-1) by analyzing the water use traits for different mapping population parents. Then the plant vigor traits (projected and canopy leaf area and growth rate) for the selected mapping population were measured in the Leasyscan platform under irrigated conditions. Different agronomic and grain quality traits were estimated in the field and QTL mapping was carried out to see possible colocalizations. Here, colocalization of plant vigor and grain quality traits (protein and fat), and also colocalization of flowering time, Striga resistance, plant height traits on the chromosome (linkage group LG) 4, colocalization between plant vigor traits and grain size on LG5a and another colocalization on the chromosome (LG) 10 for grain protein and Striga resistance showed the associations between them. If confirmed with further studies, these QTLs can be used as potential target regions for simultaneous improvement of these traits with molecular breeding approaches.

To understand the G x E x M interactions on main agronomic and qualitative traits in stay-green phenotype, stay green introgression lines from a different genetic background (S35:6008 and 6026; and R16: K359W) were selected and grown in the field for two seasons under factorial treatments of water, density, and nitrogen. The results showed, the influence of stay-green phenotype on grain quality, but the extent of this effect depends on genetic background and environment. This study also identified the novel indicator of crop quality i.e., biomass partitioning index (Bpi) which is a crude proxy for photosynthetic efficiency. It emphasizes the need to utilize specific plant materials for different environments to achieve maximum benefits.

Thus, the current study highlighted the importance of rapid tools development for estimation of grain quality that helps in improving the global grain value chain along with the importance of choosing the suitable plant genetic material for various agro-ecological systems by understanding the agronomic, physiological, and molecular aspects which support the socio-economic improvement of sorghum grain, especially in SAT regions.

REFERENCES

Agelet, L.E. and Hurburgh, Jr. CR. (2014). Limitations and current applications of Near Infrared Spectroscopy for single seed analysis. *Talanta*, 121, 288–299.

AOAC. (2000). Official Methods of Analysis, In: Association of Official Analytical Chemists, 17th ed, Gaithersburg, MD, USA.

Awika,. J. (2018). Sorghum bioactives as functional and health promoting food ingredients *Sorghum in 21st Century*, April 9-12, 2018, Cape Town, South Africa

Balyan, H.S., Gupta, P.K., Kumar, S., Dhariwal, R., Jaiswal, V., Tyagi, S., Agarwal, P., Gahlaut, V., Kumari, S. (2013). Genetic improvement of grain protein content and other health-related constituents of wheat grain. Plant Breed. 132(5), 446-57.

Bangoura, M.L., Nsor-Atindana, J., Ming, Z., Wei, P., Mothibe, K.J. and Xue, Z. (2012). Starch functional properties and resistant starch from foxtail millet [Setariaitalica (L.) P. Beauv] species. *Pakistan Journal of Nutrition*, *11*(10), 821-830.

Betts, N.S., Fox, G.P., Kelly, A.M., Cruickshank, A.W., Lahnstein, J., Henderson, M., Jordan, D.R. and Burton, R.A. (2015). Non-cellulosic cell wall polysaccharides are subject to genotype× environment effects in sorghum (Sorghum bicolor) grain. *Journal of Cereal Science*, *63*, 64-71.

Black, J.L., Hughes, R.J., Nielsen, S.G., Tredrea, A.M., Flinn, P.C. (2009). Near infrared reflectance analysis of grains to estimate nutritional value for chickens. In Proceedings of the 20th Australian Poultry Science Symposium, Sydney, New South Wales, Australia, Poultry Research Foundation, 31-34.

Blummel, M., Rao, S.S., Palaniswami, S., Shah, L. and Reddy, B.V. (2009). Evaluation of sweet sorghum (Sorghum bicolor L. Moench) used for bio-ethonol production in the context of optimizing whole plant utilization. *Animal Nutrition and Feed Technology*, *9*(1), 1-10.

Blümmel, M., Deshpande, S., Kholova, J. and Vadez, V. (2015). Introgression of staygreen QLT's for concomitant improvement of food and fodder traits in Sorghum bicolor. *Field Crops Research*, *180*,.228-237.

Borrell, A.K., Bidinger, F.R. and Sunitha, K. (1999). Stay-green trait associated with yield in recombinant inbred sorghum lines varying in rate of leaf senescence. *International Sorghum and Millets Newsletter*, *40*, 31-34.

Borrell, A.K., Hammer, G.L. and Douglas, A.C. (2000a). Does maintaining green leaf area in sorghum improve yield under drought? I. Leaf growth and senescence. *Crop science*, *40*(4), 1026-1037.

Borrell, A.K., Hammer, G.L. and Henzell, R.G. (2000b). Does maintaining green leaf area in sorghum improve yield under drought? II. Dry matter production and yield. *Crop Science*, *40*(4), 1037-1048.

Borrell, A.K., Jordan, D.R., George-Jaeggli, B., Hammer, G.L., Van Oosterom, E., Klein, P., Mullet, J. (2009). Fine-mapping candidate genes for 'stay-green' in sorghum: are we there yet? 3rd International Conference on Integrated Approaches to Improve Crop Production under Drought-Prone Environments (InterDrought-III). Shanghai, China: Shanghai Academy of Agricultural Science. L 5.03.

Borrell, A.K., Mullet, J.E., George-Jaeggli, B., van Oosterom, E.J., Hammer, G.L., Klein, P.E. and Jordan, D.R. (2014a). Drought adaptation of stay-green sorghum is associated with canopy development, leaf anatomy, root growth, and water uptake. *Journal of Experimental Botany*, *65*(21), 6251-6263.

Borrell, A.K., Oosterom, E.J., Mullet, J.E., George-Jaeggli, B., Jordan, D.R., Klein, P.E. and Hammer, G.L. (2014b). Stay-green alleles individually enhance grain yield in sorghum under drought by modifying canopy development and water uptake patterns. *New Phytologist*, *203*(3), 817-830.

Boyles, R.E., Pfeiffer, B.K., Cooper, E.A., Rauh, B.L., Zielinski, K.J., Myers, M.T., Brenton, Z., Rooney, W.L. and Kresovich, S. (2017). Genetic dissection of sorghum grain quality traits using diverse and segregating populations. *Theoretical and applied genetics*, *130*(4), 697-716.

Čepková, P.H., Dvořáková, Z., Janovská, D. and Viehmannová, I. (2014). Rancidity development in millet species stored in different storage conditions and evaluation of free fatty acids content in tested samples. *Journal of Food, Agriculture & Environment*, *12*(2), 101-106.

Chadalavada, K., Gummadi, S., Kundeti, K.R., Kadiyala, D.M., Deevi, K.C., Dakhore, K.K., Bollipo Diana, R.K. and Thiruppathi, S.K. (2021). Simulating Potential Impacts of Future Climate Change on Post-Rainy Season Sorghum Yields in India. *Sustainability*, *14*(1), 334.

Chang, H., Zhu, L., Lou, X., Meng, X., Guo, Y., Wang, Z. (2016). A new local modeling approach based on predicted errors for near-infrared spectral analysis. *J. Anal. Methods Chem*, 5416506. https://doi.org/10.1155/2016/5416506

Charmet, G., Robert, N., Branlard, G., Linossier, L., Martre, P., Triboï, E. (2005). Genetic analysis of dry matter and nitrogen accumulation and protein composition in wheat kernels. *Theor. Appl. Genet.*111(3), 540-50.

Cheewapramong, P. (2007). Use of near-infrared spectroscopy for qualitative and quantitative analyses of grains and cereal products. Ph.D. thesis, University of Nebraska, USA.

Childs, K.L., Miller, F.R., Cordonnier-Pratt, M.M., Pratt, L.H., Morgan, P.W. and Mullet, J.E. (1997). The sorghum photoperiod sensitivity gene, Ma3, encodes a phytochrome B. *Plant Physiology*, *113*(2), 611-619.

Codex standard for sorghum flour.

www.fao.org/input/download/standards/58/CXS_173e.pdf. (Accessed on 24-6-2020)

Crasta, O.R., Xu, W.W., Rosenow, D.T., Mullet, J. and Nguyen, H.T. (1999). Mapping of post-flowering drought resistance traits in grain sorghum: association between QTLs influencing premature senescence and maturity. *Molecular and General Genetics MGG*, *262*(3), 579-588.

Dardenne, P. (1996). Stability of NIR spectroscopy equations. *NIR news*, *7*(5), 8-9.

Diao, X. (2017). Production and genetic improvement of minor cereals in China. *Crop J*, 5(2), 103-14.

Doblado-Maldonado, A.F., Pike, O.A., Sweley, J.C. and Rose, D.J. (2012). Key issues and challenges in whole wheat flour milling and storage. *Journal of cereal science*, *56*(2), 119-126.

El Mannai, Y., Shehzad, T. and Okuno, K. (2012). Mapping of QTLs underlying flowering time in sorghum [Sorghum bicolor (L.) Moench]. *Breeding science*, *62*(2), 151-159.

Estienne, F., Pasti, L., Centner, V., Walczak, B., Despagne, F., Rimbaud, D.J., De Noord, O.E., Massart, D.L. (2001) A comparison of multivariate calibration techniques applied to experimental NIR data sets: Part II. Predictive ability under extrapolation conditions. Chemometrics and Intelligent Laboratory Systems. 58(2), 195-211.

Galyuon, I.K.A., Gay, A., Borrell, A.K. and Howarth, C.J. (2019). Physiological and biochemical basis for stay-green trait in sorghum. *African Crop Science Journal*, *27*(4), 653-677.

García, J., Cozzolino, D. (2006). Use of near infrared reflectance (NIR) spectroscopy to predict chemical composition of forages in broad-based calibration models. Agricultura Técnica (Chile), 66, 41–47.

Girish, C., Meena, R.K., Mahima, D., Mamta, K. (2014). Nutritional properties of minor millets: neglected cereals with potentials to combat malnutrition. *Current Science*, 107(7), 1109-11.

Guindo, D., Teme, N., Vaksmann, M., Doumbia, M., Vilmus, I., Guitton, B., Sissoko, A., Mestres, C., Davrieux, F., Fliedel, G. and Kouressy, M. (2019). Quantitative trait loci for sorghum grain morphology and quality traits: Toward breeding for a traditional food preparation of West-Africa. *Journal of Cereal Science, 85*, 256-272.

Hammer, G. (2006). Drought Adaptation in Sorghum. *Drought Adaptation in Cereals*, p.335.

Harris, K., Subudhi, P.K., Borrell, A., Jordan, D., Rosenow, D., Nguyen, H., Klein, P., Klein, R. and Mullet, J. (2007). Sorghum stay-green QTL individually reduce post-flowering drought-induced leaf senescence. *Journal of experimental botany*, *58*(2), 327-338.

Hash, C.T., Raj, A.B., Lindup, S., Sharma, A., Beniwal, C.R., Folkertsma, R.T., Mahalakshmi, V., Zerbini, E. and Blümmel, M. (2003). Opportunities for marker-assisted selection (MAS) to improve the feed quality of crop residues in pearl millet and sorghum. *Field Crops Research*, *84*(1-2), 79-88.

Haussmann, B., Mahalakshmi, V., Reddy, B., Seetharama, N., Hash, C. and Geiger, H. (2002). QTL mapping of stay-green in two sorghum recombinant inbred populations. *Theoretical and Applied Genetics*, *106*(1), 133-142.

Haussmann, B.I.G., Hess, D.E., Omanya, G.O., Folkertsma, R.T., Reddy, B.V.S., Kayentao, M., Welz, H.G. and Geiger, H.H. (2004). Genomic regions influencing resistance to the parasitic weed Striga hermonthica in two recombinant inbred populations of sorghum. *Theoretical and Applied Genetics*, *109*(5), 1005-1016.

Heiniö, R.L., Lehtinen, P., Oksman-Caldentey, K.M. and Poutanen, K. (2002). Differences between sensory profiles and development of rancidity during long-term storage of native and processed oat. *Cereal Chemistry*, *79*(3), 367-375.

Henzell, R.G. (1992). Grain sorghum breeding in Australia: current status and future prospects. In: Proceedings of the second Australian sorghum conference, Gatton, *Australian Institute of Agricultural Science*, (1), 70-80.

Honecreate; a cloud based chemometric platform. https://www.honecreate.com/ Accessed on 13-03-2022.

Jordan, D.R., Hunt, C.H., Cruickshank, A.W., Borrell, A.K. and Henzell, R.G. (2012). The relationship between the stay-green trait and grain yield in elite sorghum hybrids grown in a range of environments. *Crop Science*, *52*(3), 1153-1161.

Kahriman, F. and Egesel, C.Ö. (2011). Development of a calibration model to estimate quality traits in wheat flour using NIR (Near Infrared Reflectance) spectroscopy. *Research Journal of Agricultural Science, 43*(3), 392-400.

Kamal, N.M., Gorafi, Y.S.A. and Ghanim, A.M.A. (2017). Performance of sorghum stay-green introgression lines under post-flowering drought. *International Journal of Plant Research*, *7*(3), 65-74.

Kane-Potaka, J., Anitha, S., Tsusaka, T., Botha, R., Budumuru, M., Upadhyay, S., Kumar, P., Mallesh, K., Hunasgi, R. and Jalagam, A.K. (2021). Assessing millets and sorghum consumption behavior in urban India: A large-scale survey. *Frontiers in Sustainable Food Systems*, *5*, 260.

Kassahun, B., Bidinger, F.R., Hash, C.T. and Kuruvinashetti, M.S. (2010). Stay-green expression in early generation sorghum [Sorghum bicolor (L.) Moench] QTL introgression lines. *Euphytica, 172*(3), 351-362.

Kebede, H., Subudhi, P.K., Rosenow, D.T. and Nguyen, H.T. (2001). Quantitative trait loci influencing drought tolerance in grain sorghum (Sorghum bicolor L. Moench). *Theoretical and Applied Genetics*, *103*(2), 266-276.

Kholová, J., Hash, C. T., Kumar, P. L., Yadav, R. S., Kocová, M. and Vadez, V. (2010). Terminal drought-tolerant pearl millet [Pennisetum glaucum (L.) R. Br.] have high leaf ABA and limit transpiration at high vapour pressure deficit. *Journal of experimental botany*, *61*(5), 1431–1440. https://doi.org/10.1093/jxb/erq013

Kholová, J., Nepolean, T., Tom Hash, C., Supriya, A., Rajaram, V., Senthilvel, S., Kakkera, A., Yadav, R. and Vadez, V. (2012). Water saving traits co-map with a major terminal drought tolerance quantitative trait locus in pearl millet [Pennisetum glaucum (L.) R. Br.]. *Molecular Breeding, 30*(3), .1337-1353.

Kholová, J., Murugesan, T., Kaliamoorthy, S., Malayee, S., Baddam, R., Hammer, G.L., McLean, G., Deshpande, S., Hash, C.T., Craufurd, P.Q. and Vadez, V. (2014). Modelling the effect of plant water use traits on yield and stay-green expression in sorghum. *Functional Plant Biology, 41*(11), 1019-1034.

Kiranmayee, K.N.S., Hash, C.T., Sivasubramani, S., Ramu, P., Amindala, B.P., Rathore, A., Kishor, P.B., Gupta, R. and Deshpande, S.P. (2020). Fine-mapping of sorghum stay-green QTL on chromosome10 revealed genes associated with delayed senescence. *Genes*, *11*(9), 1026.

Kumar, A., Tomer, V., Kaur, A., Kumar, V., Gupta, K. (2018). Millets: a solution to agrarian and nutritional challenges. *Agric. Food Secur*,7(1), 1-5.

LeasyScan facility, ICRISAT http://gems.icrisat.org/leasyscan/

Levasseur-Garcia, C. (2018). Updated overview of infrared spectroscopy methods for detecting mycotoxins on cereals (corn, wheat, and barley). *Toxins*. 10(1), 38.

Lysimetric facility, ICRISAT http://gems.icrisat.org/lysimetric-facility/

Mahjourimajd, S., Taylor, J., Rengel, Z., Khabaz-Saberi, H., Kuchel, H., Okamoto, M., Langridge, P. (2016). The genetic control of grain protein content under variable nitrogen supply in an Australian wheat mapping population. *PLoS One,* 11(7), e0159371.

Mace, E.S. and Jordan, D.R. (2010). Location of major effect genes in sorghum (Sorghum bicolor (L.) Moench). *Theoretical and Applied Genetics*, *121*(7), 1339-1356.

McKevith, B. (2004). Nutritional aspects of cereals. *Nutr. Bull*,(2), 111-42.

Mekonnen, T.B., Dong, H., Getinet, M., Gabizew, A., Paterson, A. and Bantte, K. (2021). QTL analysis in multiple sorghum mapping populations facilitates dissection of the genetic control of agronomic and yield-related traits in sorghum [Sorghum bicolor (Moench)].

Mulder, G.J. (1839). Ueber die ZusammensetzungeinigerthierischenSubstanzen. *Journal für praktischeChemie*, *16*(1), 129-152.

Murray, S.C., Rooney, W.L., Mitchell, S.E., Sharma, A., Klein, P.E., Mullet, J.E. and Kresovich, S. (2008). Genetic improvement of sorghum as a biofuel feedstock: II. QTL for stem and leaf structural carbohydrates. *Crop science*, *48*(6), 2180-2193.

Newell-McGloughlin, M. and Burke, J. (2014). Biotechnology crop adoption: Potential and challenges of genetically improved crops. In: Encyclopedia of Agriculture and Food Systems. Neal K. Van Alfen (Eds), Academic Press, 69-93.

Osuna, M.B., Judis, M.A., Romero, A.M., Avallone, C.M. and Bertola, N.C. (2014). Improvement of fatty acid profile and studio of rheological and technological characteristics in breads supplemented with flaxseed, soybean, and wheat bran flours. *The Scientific World Journal*

Patil, N.Y., Pugh, N.A., Klein, R.R., Martinez, H.S., Martinez, R.S., Rodriguez-Herrera, R., Rooney, W.L. and Klein, P.E. (2019). Heritability and quantitative trait loci of composition and structural characteristics in sorghum grain. *Journal of crop improvement*, *33*(1), 1-24.

Payne, R.W., Murray, D.A., Harding, S.A., Baird, D.B., Soutar, D.M. (2011). GenStat for windows (14th edition) introduction. VSN International Hemel Hempstead UK

Powell, W., Morgante, M., Andre, C., Hanafey, M., Vogel, J., Tingey, S. and Rafalski, A. (1996) The comparison of RFLP, RAPD, AFLP and SSR (microsatellite) markers for germplasm analysis. Mol. Breed. 2, 225–238.

R Core Team., (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available online at https://www.R-project.org/.

Reeves, J. B. (2001). Near-infrared diffuse reflectance spectroscopy for the analysis of poultry manures. *Journal of Agricultural and Food Chemistry*, *49*(5), 2193-2197.

Robinson, H.F., Comstock, R.E. and Harvey, P.H. (1949). Estimates of heritability and the degree of dominance in corn.

Rosenow, D.T., Quisenberry, J.E., Wendt, C.W. and Clark, L.E. (1983). Drought tolerant sorghum and cotton germplasm. In: *Developments in agricultural and managed forest ecology*,12, 207-222. Elsevier.

Rozbicki, J., Gozdowski, D., Studnicki, M., Mądry, W., Golba, J., Sobczyński, G., Wijata, M. (2019). Management intensity effects on grain yield and its quality traits of winter wheat cultivars in different environments in Poland. Biotechnology. 22(1), 02.

Saeys, W., Mouazen, A. M., & Ramon, H. (2005). Potential for onsite and online analysis of pig manure using visible and near infrared reflectance spectroscopy. *Biosystems engineering*, *91*(4), 393-402.

Saha, U., Endale, D., Tillman, P. G., Johnson, W. C., Gaskin, J., Sonon, L., ... and Yang, Y. (2017). Analysis of various quality attributes of sunflower and soybean plants by near infrared reflectance spectroscopy: development and validation calibration models. *American Journal of Analytical Chemistry*, *8*(07), 462.

Sanchez, A.C., Subudhi, P.K., Rosenow, D.T. and Nguyen, H.T. (2002). Mapping QTLs associated with drought resistance in sorghum (Sorghum bicolor L. Moench). *Plant molecular biology*, *48*(5), 713-726.

Shenk, J. S. and Westerhaus, M. O. (1996). Calibration the ISI way. *Near infrared spectroscopy: The future waves*, 198-202.

Stubbs, T.L., Kennedy, A.C., Fortuna, A.M. (2010). Using NIRS to predict fiber and nutrient content of dryland cereal cultivars. *J. Agric. Food. Chem,* 58(1), 398-403.

Subudhi, P.K., Magpantay, G.B., Rosenow, D.T. and Nguyen, H.T. (1999). Mapping and marker-assisted selection to improve the stay-green trait for drought tolerance in sorghum. In: *Genetic Improvement of Rice for Water Limited Environments*. Los Banõs: International Rice Research Institute.

Subudhi, P.K., Rosenow, D.T. and Nguyen, H.T. (2000). Quantitative trait loci for the stay green trait in sorghum (Sorghum bicolor L. Moench): consistency across genetic backgrounds and environments. *Theoretical and Applied Genetics*, *101*(5), 733-741.

Sugg, J.D., Campanili, P.B., Sarturi, J.O., Ballou, M.A. and Trojan, S.J. (2017). Case Study: Yield and quality of traditional senescent and stay-green sorghum and in situ ruminal disappearance of respective crop residues. *The Professional Animal Scientist*, *33*(6), 748-755.

Sukumaran, S., Li, X., Li, X., Zhu, C., Bai, G., Perumal, R., Tuinstra, M.R., Prasad, P.V., Mitchell, S.E., Tesso, T.T. and Yu, J. (2016). QTL mapping for grain yield, flowering time, and stay-green traits in sorghum with genotyping-by-sequencing markers. *crop science*, *56*(4), 1429-1442.

Tahir, M., Shim, M.Y., Ward, N.E, Smith, C., Foster, E., Guney, A.C., Pesti, G.M. (2012). Phytate and other nutrient components of feed ingredients for poultry. *Poult. Sci*, 91(4), 928-35.

Talwar, H. S., Deshpande, S. P., Madhusudhana, R., Kumar, S.,Vadez, V., Tonapi, V A. (2017). Stay-green QTL Stg3B is the key QTL associated with improved grain and stover yield under post-rainy sorghum growing conditions. In: InterDrought-V, Hyderabad, India.

Tao, Y., Mace, E.S., Tai, S., Cruickshank, A., Campbell, B.C., Zhao, X., Van Oosterom, E.J. *et al.* (2017). Whole-genome analysis of candidate genes associated with seed size and Weight in *Sorghum bicolor* reveals signatures of artificial selection and insights into parallel domestication in cereal crops. Front. Plant Sci. 8, 1–14.

Tao, Y., Zhao, X., Wang, X., Hathorn, A., Hunt, C., Cruickshank, A. W., van Oosterom, E. J., Godwin, I. D., Mace, E. S. and Jordan, D. R. (2020). Large-scale GWAS in sorghum reveals common genetic control of grain size among cereals. *Plant biotechnology journal*, *18*(4), 1093–1105. https://doi.org/10.1111/pbi.13284

Taylor, J.R., Schober, T.J. and Bean, S.R. (2006). Novel food and non-food uses for sorghum and millets. *Journal of cereal science*, *44*(3), 252-271.

Techale, B., Dong, H., Mihrete, G., Aregash, G., Paterson, A.H. and Kassahun, B. (2022). QTL analysis in multiple sorghum mapping populations facilitates dissection of the genetic control of agronomic and yield-related traits in sorghum [Sorghum bicolor (Moench)]. *Euphytica*, *218*(3), 1-22.

Thomas, H. and Ougham, H. (2014). The stay-green trait. *Journal of Experimental Botany*, *65*(14), 3889-3900.

Tuberosa, R., Salvi, S., Sanguineti, M.C., Maccaferri, M., Giuliani, S., Landi, P. (2003). Searching for quantitative trait loci controlling root traits in maize: a critical appraisal. *Plant Soil*, 255, 35–54.

Tuinstra, M.R., Grote, E.M., Goldsbrough, P.B. and Ejeta, G. (1996). Identification of quantitative trait loci associated with pre-flowering drought tolerance in sorghum. *Crop science*, *36*(5), 1337-1344.

Tuinstra, M.R., Grote, E.M., Goldsbrough, P.B. and Ejeta, G. (1997). Genetic analysis of post-flowering drought tolerance and components of grain development in Sorghum bicolor (L.) Moench. *Molecular Breeding*, *3*(6), 439-448.

Vadez, V., Krishnamurthy, L., Kashiwagi, J.W., Kholova, J., Devi, J.M., Sharma, K.K., Bhatnagar-Mathur, P., Hoisington, D.A., Hash, C.T., Bidinger, F.R., Keatinge, J.D.H. (2007a) Exploiting the functionality of root systems for dry, saline, and nutrient deficient environments in a changing climate. *J. SAT Agric Res*, 4, 645-648. (Special 648 Symposium edition) http://www.icrisat.org/journal/specialproject.htm

Vadez, V., Deshpande, S.P., Kholova, J., Hammer, G.L., Borrell, A.K., Talwar, H.S. and Hash, C.T. (2011a). Stay-green quantitative trait loci's effects on water extraction, transpiration efficiency and seed yield depend on recipient parent background. *Functional Plant Biology*, *38*(7), 553-566.

Vadez, V., Krishnamurthy, L., Hash, C.T., Upadhyaya, H.D. and Borrell, A.K. (2011b).Yield, transpiration efficiency, and water-use variations and their interrelationships in the sorghum reference collection. *Crop and Pasture Science*, *62*(8), 645-655.

Vadez, V., Krishnamurthy, L., Thudi, M., Anuradha, C., Colmer, T.D., Turner, N.C., Siddique, K.H., Gaur, P.M. and Varshney, R.K. (2012). Assessment of ICCV 2× JG 62 chickpea progenies shows sensitivity of reproduction to salt stress and reveals QTL for seed yield and yield components. *Molecular Breeding*, *30*(1), 9-21.

Vadez, V., Deshpande, S., Kholova, J., Ramu, P., Hash, C.T., Varshney, R. and Tuberosa, R. (2013). Molecular breeding for stay-green: progress and challenges in sorghum. *Genomic applications to crop breeding, 2,* 125-141.

Vadez, V., Kholová, J., Hummel, G., Zhokhavets, U., Gupta, S. K. and Hash, C. T. (2015). LeasyScan: a novel concept combining 3D imaging and lysimetry for high-throughput phenotyping of traits controlling plant water budget. *Journal of experimental botany*, *66*(18), 5581–5593. https://doi.org/10.1093/jxb/erv251

Van Oosterom, E.J., Borrell, A.K., Chapman, S.C., Broad, I.J. and Hammer, G.L. (2010a). Functional dynamics of the nitrogen balance of sorghum: I. N demand of vegetative plant parts. *Field Crops Research*, *115*(1), 19-28.

Van Oosterom, E. J., et al (2010b) Functional dynamics of the nitrogen balance of sorghum. II. Grain filling period." *Field Crops Research,* 115(1), 29-38.

Villamuelas, M., Serrano, E., Espunyes, J., Fernández, N., López-Olvera, J.R., Garel, M., Santos, J., Parra-Aguado, M.Á., Ramanzin, M., Fernández-Aguilar, X., Colom-Cadena, A. (2017). Predicting herbivore faecal nitrogen using a multispecies near-infrared reflectance spectroscopy calibration. *PLoS One,* 12(4), e0176635.

Wang, J., Vanga, S.K., Saxena, R., Orsat, V., Raghavan, V. (2018). Effect of climate change on the yield of cereal crops: A review. *Climate,* 6(2), 41.

Ward, A., Nielsen, A.L. and Moller, H. (2011) Rapid Assessment of Mineral Concentration in Meadow Grasses by Near Infrared Reflectance Spectroscopy. Sensors, 11, 4830-4839. https://doi.org/10.3390/s110504830

Weaver, C.A., Hamaker, B.R. and Axtell, J.D. (1998). Discovery of grain sorghum germ plasm with high uncooked and cooked in vitro protein digestibilities. *Cereal Chemistry*, *75*(5), 665-670.

Westoby, M., Enrique, J. and Michelle, L. (1992). Comparative evolutionary ecology of seed size. Trends Ecol. Evol. 11, 368–372.

Williams, P.C. (2003). Near-InfraRed Technology-Getting the Best Out of Light. PDK Grain, PDK Project. Inc., 109.

Williams, P. (2014). The RPD statistic: a tutorial note. *NIR news*, *25*(1), 22-26.

Williams, P. C., and Sobering, D. C. (1996). How do we do it: a brief summary of the methods we use in developing near infrared calibrations. *Near infrared spectroscopy: The future waves*, 185-188.

Williams, P.C., Kuzina, F.D. and Hlynka, I. (1970). Rapid colorimetric procedure for estimating the amylose content of starches and flours. *Cereal chemistry*.

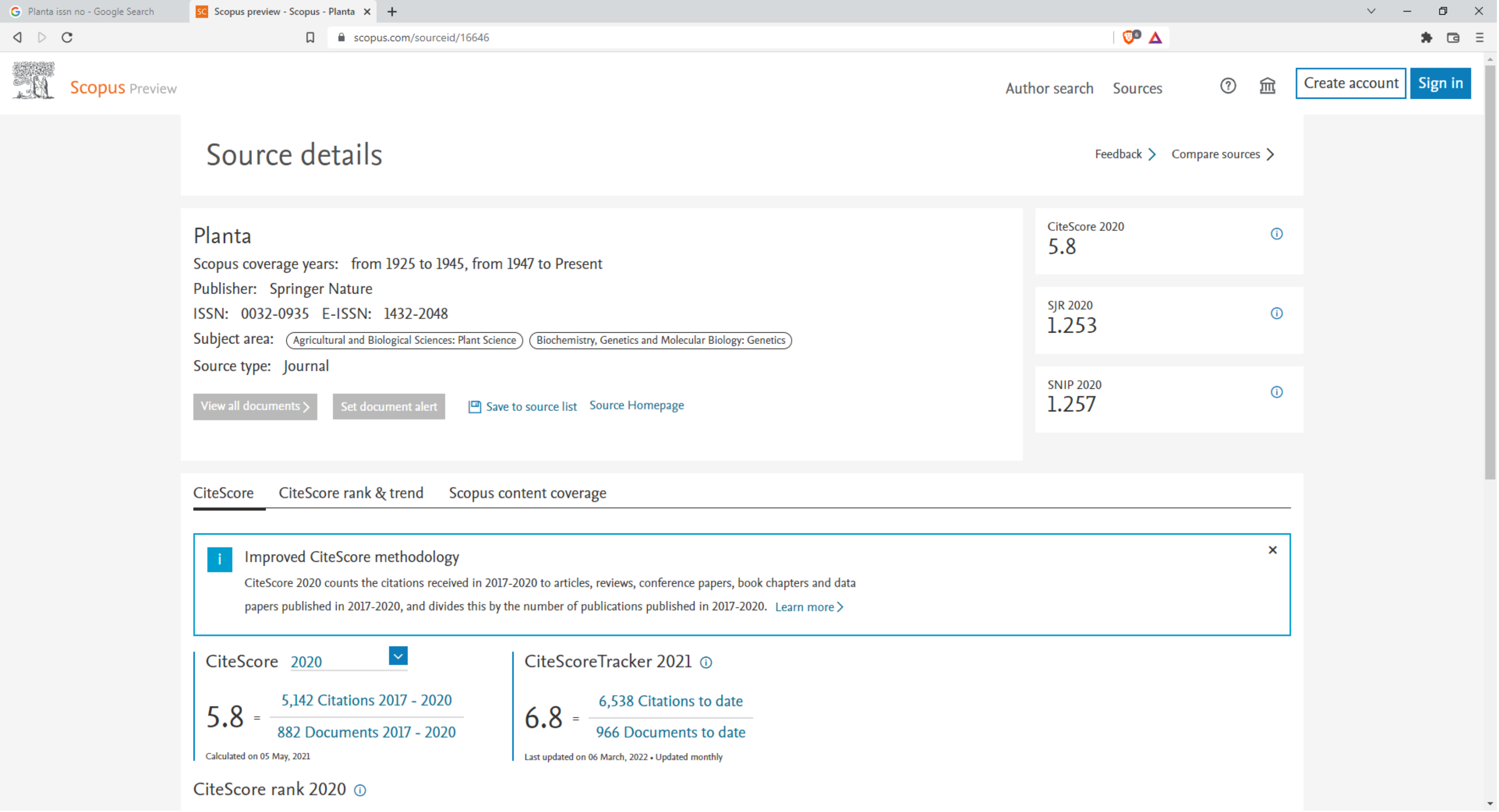
Winn, J.A., Mason, R.E., Robbins, A.L., Rooney, W.L. and Hays, D.B. (2009). QTL mapping of a high protein digestibility trait in Sorghum bicolor. *International journal of plant genomics*.

Workman, Jr. J. and Weyer, L. (2012). Practical guide and spectral atlas for interpretive near-infrared spectroscopy. CRC press.

Xu, W., Subudhi, P.K., Crasta, O.R., Rosenow, D.T., Mullet, J.E. and Nguyen, H.T. (2000). Molecular mapping of QTLs conferring stay-green in grain sorghum (Sorghum bicolor L. Moench). *Genome, 43*(3), 461-469.

Yu, J.B., Bai, G.H., Zhou, W.C., Dong, Y.H. and Kolb, F.L. (2008). Quantitative trait loci for Fusarium head blight resistance in a recombinant inbred population of Wangshuibai/Wheaton. *Phytopathology*, *98*(1), 87-94.

Zornoza, R., Guerrero, C., Mataix-Solera, J., Scow, K. M., Arcenegui, V., and Mataix-Beneyto, J. (2008). Near infrared spectroscopy for determination of various physical, chemical and biochemical properties in Mediterranean soils. *Soil Biology and Biochemistry*, *40*(7), 1923-1930.



Source details

Planta

Scopus coverage years: from 1925 to 1945, from 1947 to Present

Publisher: Springer Nature

ISSN: 0032-0935 E-ISSN: 1432-2048

Subject area: Agricultural and Biological Sciences: Plant Science | Biochemistry, Genetics and Molecular Biology: Genetics

Source type: Journal

CiteScore 2020
5.8

SJR 2020
1.253

SNIP 2020
1.257

Improved CiteScore methodology

CiteScore 2020 counts the citations received in 2017-2020 to articles, reviews, conference papers, book chapters and data papers published in 2017-2020, and divides this by the number of publications published in 2017-2020.

CiteScore 2020

5.8 = 5,142 Citations 2017 - 2020 / 882 Documents 2017 - 2020

Calculated on 05 May, 2021

CiteScoreTracker 2021

6.8 = 6,538 Citations to date / 966 Documents to date

Last updated on 06 March, 2022 • Updated monthly

CiteScore rank 2020

Planta (2021) 253:113
https://doi.org/10.1007/s00425-021-03631-2

REVIEW

Sorghum mitigates climate variability and change on crop yield and quality

Keerthi Chadalavada[1,2] · **B. D. Ranjitha Kumari**[1] · **T. Senthil Kumar**[1]

Received: 23 January 2021 / Accepted: 17 April 2021 / Published online: 29 April 2021

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

[1] Department of Botany, Bharathidasan University, Tiruchirappalli, Tamil Nadu, India

[2] 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_2 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_2 is increased to 400 μmol^{-1}. It is projected to increase up to 800 μmol^{-1} by the end of the century. Elevated CO_2 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_2 on crop plants. Some studies even reported the reduced nutritional quality of crops due to high CO_2 when rising in the nutrient poor soils by reducing the nitrate assimilation (Taub et al. 2008). Elevated CO_2 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_2 conditions, CO_2 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_2, 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 × 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 (Fergason 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_2 and O_3 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).

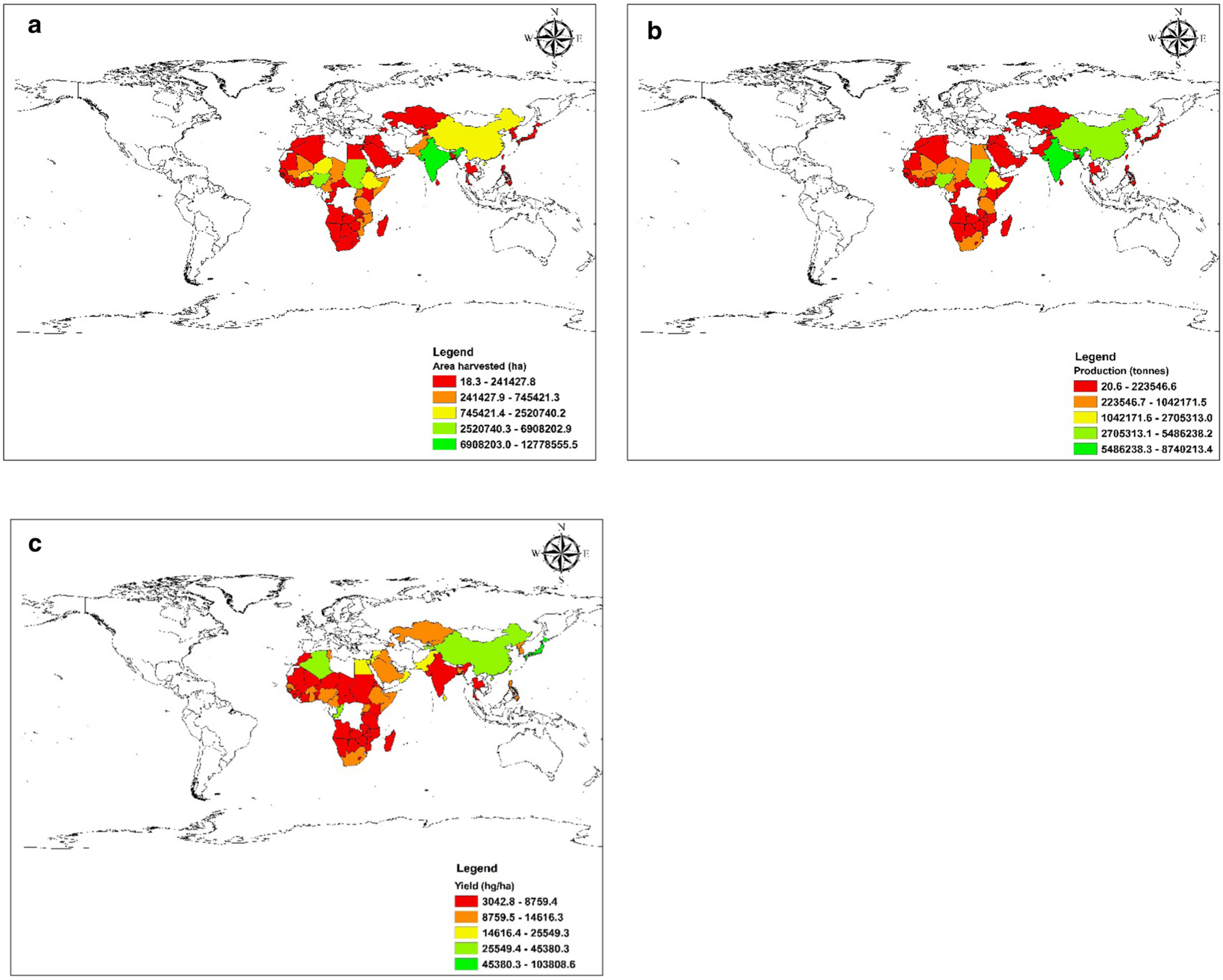


Fig. 1 Spatial distribution of sorghum area (**a**), production (**b**) and productivity (**c**) over Africa and Asia during 1961–2019 based on FAOSTAT 2019. Data source: http://www.fao.org/faostat/en/#data/QC

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

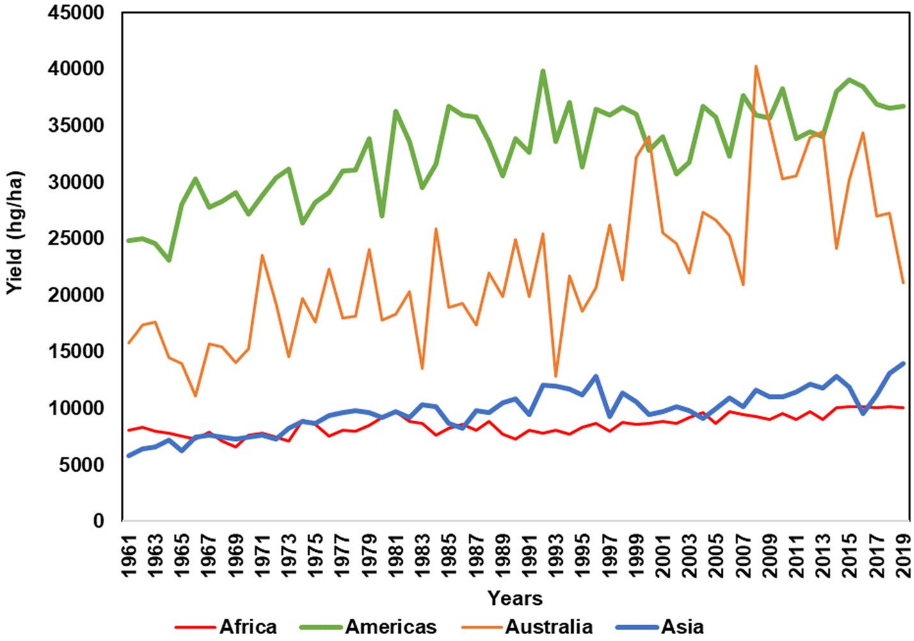


Fig. 2 Trends of sorghum yields over Africa, Asia, Americas and Australia during 1961–2019 based on FAOSTAT data. Data source: http://www.fao.org/faostat/en/#data/QC

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 (Djanaguiraman 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

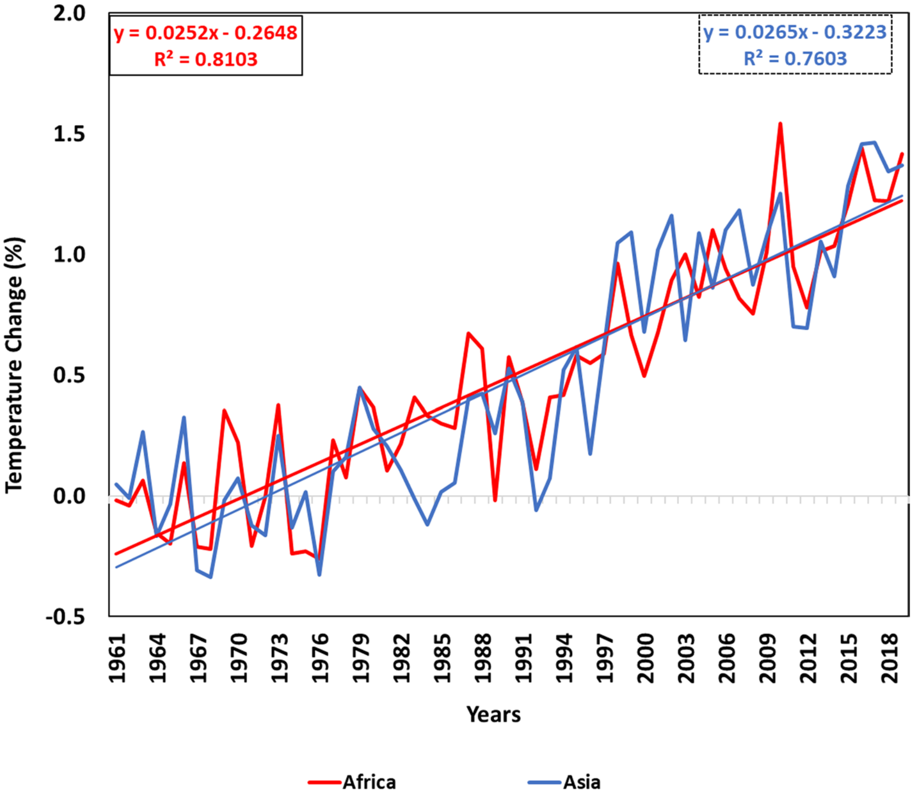


Fig. 3 Percent change in surface temperature during 1961–2019 over Africa and Asia. Temperature change was calculated based on the baseline climatology, corresponding to the period 1951–1980. Data source: http://www.fao.org/faostat/en/#data/ET

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; Chiluwal 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_2

Studies reported sorghum crop shows a significant reduction in transpiration rate due to elevated CO_2 (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_2 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_2 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_2 under drought conditions (Ottman et al. 2001). Torbert et al. (2004) observed around a 30% increase in sorghum biomass production due to elevated CO_2. They noticed a substantial rise in C:N ratio due to CO_2 enrichment.

Very few studies reported grain quality in sorghum with elevated CO_2. De souza et al. (2015) reported there was almost a 60% increase in grain protein content when grown under elevated CO_2 and water deficit conditions. Fatty acids in the grain were slightly increased, but no such increase in starch content was found. Thus, elevated CO_2, 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 osmatic potential. Extensive field trials and data collection help to evaluate the impacts of climate change. Future predictions are possible using remote sensing and crop modelling 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; Chiluwal 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 Burow et al. (2011). Hybrids developed from inbreds were extensively tested and selected for early-stage chilling tolerance (Chiluwal et al. 2018) with high germination and seedling vigor. Ostmeyer 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 α and γ 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, pullulanase 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.

Author contribution statement Keerthi Chadalavada: conducted literature search and drafted the manuscript; Ranjitha Kumari B.D and Senthil Kumar T: conceptualization and draft correction.

Declarations

Conflict of interest The authors have no conflicts of interest to declare that are relevant to the content of this article.

References

Abdelhalim TS, Kamal NM, Hassan AB (2019) Nutritional potential of wild sorghum: grain quality of Sudanese wild sorghum genotypes (*Sorghum bicolor* L. Moench). Food Sci Nutr 7(4):1529–1539

Aboubacar A, Moldenhauer KAK, McClung AM, Beighley DH, Hamaker BR (2006) Effect of growth location in the United States on amylose content, amylopectin fine structure, and thermal properties of starches of long grain rice cultivars. Cereal Chem 83:93–98

Adhikari U, Nejadhashemi AP, Woznicki SA (2015) Climate change and eastern Africa: a review of impact on major crops. Food Energy Secur 4:110–132

Ahmad Z, Anjum S, Waraich EA, Ayub MA, Ahmad T, Tariq RMS, Ahmad R, Iqbal MA (2018) Growth, physiology, and biochemical activities of plant responses with foliar potassium application under drought stress—a review. J Plant Nutr 41:1734–1743

Ahmadi A, Baker DA (2001) The effect of water stress on the activities of key regulatory enzymes of the sucrose to starch pathway in wheat. Plant Growth Regul 35(1):81–91

Ahmed S, Nawata E, Sakuratani T (2002) Effects of waterlogging at vegetative and reproductive growth stages on photosynthesis, leaf water potential and yield in mungbean. Plant Prod Sci 5:117–123

Ali Q, Ashraf M, Anwar F (2010) Seed composition and seed oil antioxidant activity of maize under water stress. J Am Oil Chem Soc 87(10):1179–1187

Allen DJ, Ort DR (2001) Impacts of chilling temperatures on photosynthesis in warm climate plants. Trends Plant Sci 6:36–42

Ananda N, Vadlani PV, Prasad PV (2011) Evaluation of drought and heat stressed grain sorghum (*Sorghum bicolor*) for ethanol production. Ind Crops Prod 33(3):779–782

Arora NK (2019) Impact of climate change on agriculture production and its sustainable solutions. Environ Sustain 2:95–96

Asaoka M, Okuno K, Sugimoto Y, Kawakami J, Fuwa H (1984) Effect of environmental temperature during development of rice plants on some properties of endosperm starch. Starch/Stärke 36:189–193

Assefa Y, Staggenborg SA, Prasad VP (2010) Grain sorghum water requirement and responses to drought stress: a review. Crop Manage 9(1):1–11

Baker JT, Boote KJ, Allen LH Jr (1995) Potential climate change effects on rice: carbon dioxide and temperature. In: Rosenzweig C (ed) Climate change and agriculture: analysis of potential international impacts, ASA Spec. Publ. No. 59. ASA, Madison, WI, pp 31–47

Bekele WA, Fiedler K, Shiringani A, Schnaubelt D, Windpassinger S, Uptmoor R, Friedt W, Snowdon RJ (2014) Unravelling the genetic complexity of sorghum seedling development under low-temperature conditions. Plant, Cell Environ 37(3):707–723

Bidinger FR, Hammer GL, Muchow RC (1996) The physiological basis of genotype by environment interaction in crop adaptation. In: Cooper M, Hammer GL (eds) Plant adaptation and crop improvement. CAB International, Wallingford, UK, pp 329–347

Bing YI, Zhou YF, Gao MY, Zhang Z, Yi HAN, Yang GD, Wenjuan XU, Huang RD (2014) Effect of drought stress during flowering stage on starch accumulation and starch synthesis enzymes in sorghum grains. J Integr Agric 13(11):2399–2406

Blum A (2004) Sorghum physiology. In: Nguyen HT, Blum A (eds) Physiology and biotechnology integration for plant breeding. Marcel Dekker Inc., NY, pp 141–223

Blümmel M, Deshpande S, Kholova J, Vadez V (2015) Introgression of staygreen QLT's for concomitant improvement of food and fodder traits in *Sorghum bicolor*. Field Crops Res 180:228–237

Boote KJ, Allen LH Jr, Prasad PVV, Baker JT, Gesch RW, Synder AM, Pan D, Thomas JMG (2005) Elevated temperature and CO_2 impacts on pollinations, reproductive growth, and yield of several globally important crops. J Agric Meteorol (Tokyo) 60:469–474

Borrell AK, Hammer GL, Henzell RG (2000) Does maintaining green leaf area in sorghum improve yield under drought? II. Dry matter production and yield. Crop Sci 40:1037–1048

Borrell AK, Mullet JE, George-Jaeggli B, van Oosterom EJ, Hammer GL, Klein PE, Jordan DR (2014) Drought adaptation of stay-green sorghum is associated with canopy development, leaf anatomy, root growth, and water uptake. J Exp Bot 65(21):6251–6263

Boyles RE, Brenton Z, Kresovich S (2019) Genetic and genomic resources of sorghum to connect genotype with phenotype in contrasting environments. Plant J 97(1):19–39

Brumm TJ, Hurburgh CR (2006) Changes in long-term soybean compositional patterns. J Am Oil Chem Soc 83:981–983

Burgess MS, Mehuys GR, Madramootoo CA (2002) Nitrogen dynamics of decomposing corn residue components under three tillage systems. Soil Sci Soc Am J 66(4):1350–1358

Burow G, Burke JJ, Xin Z, Franks CD (2011) Genetic dissection of early-season cold tolerance in sorghum (*Sorghum bicolor* (L.) Moench). Mol Breed 28:391–402

Challinor A, Wheeler T, Craufurd P, Ferro C, Stephenson D (2007) Adaptation of crops to climate change through genotypic responses to mean and extreme temperatures. Agric Ecosyst Environ 119:190–204

Chaudhuri UN, Burnett RB, Kirkham MB, Kanemasu ET (1986) Effect of carbon dioxide on sorghum yield, root growth, and water use. Agric For Meteorol 37:109–122

Chen J, Chopra R, Hayes C, Morris G, Marla S, Burke J, Xin Z, Burow G (2017) Genome-wide association study of developing leaves' heat tolerance during vegetative growth stages in a Sorghum Association Panel. Plant Genome 10(2):1–15

Cheng W, Zhang G, Zhao G, Yao H, Xu H (2003) Variation in rice quality of different cultivars and grain positions as affected by water management. Field Crops Res 80:245–252

Chiluwal A (2018) Physiological and genetic characterization of sorghum exposed to early season chilling and terminal heat and drought stress. Doctoral dissertation. Kansas State University

Chiluwal A, Bheemanahalli R, Perumal R, Asebedo AR, Bashi E, Lamsal A, Sebela D, Shetty NJ, Jagadish SVK (2018) Integrated aerial and destructive phenotyping differentiates chilling stress tolerance during early seedling growth in sorghum. Field Crops Res 227:1–10

Cisse N, Ejeta G (2003) Genetic variation and relationships among seedling vigor traits in sorghum. Crop Sci 43:824–828

Cowan MF, Blomstedt CK, Norton SL, Henry RJ, Møller BL, Gleadow R (2020) Crop wild relatives as a genetic resource for generating low-cyanide, drought-tolerant Sorghum. Environ Exp Bot 169:103884

Crafts-Brandner SJ, Salvucci ME (2002) Sensitivity of photosynthesis in a C4 plant, maize, to heat stress. Plant Physiol 129(4):1773–1780

Craufurd PQ, Qi A, Ellis RH, Summerfield RJ, Roberts EH, Mahalakshmi V (1998) Effect of temperature on time to panicle initiation and leaf appearance in sorghum. Crop Sci 38:942–947

Da Silva LS (2012) Transgenic sorghum: effects of altered kafirin synthesis on kafirin polymerisation, protein quality, protein body structure and endosperm texture, Doctoral dissertation, University of Pretoria

Dai Z, Yin Y, Wang Z (2009) Starch granule size distribution from seven wheat cultivars under different water regimes. Cereal Chem 86:82–87

Dang JMC, Copeland L (2004) Genotype and environmental influences on pasting properties of rice flour. Cereal Chem 81:486–489

De Souza AP, Cocuron JC, Garcia AC, Alonso AP, Buckeridge MS (2015) Changes in whole-plant metabolism during the grain-filling stage in sorghum grown under elevated CO_2 and drought. Plant Physiol 169(3):1755–1765

Dennis ES, Dolferus R, Ellis M, Rahman M, Wu Y, Hoeren FU, Grover A, Ismond KP, Good AG, Peacock WJ (2000) Molecular strategies for improving waterlogging tolerance in plants. J Exp Bot 51(342):89–97

Dilley M, Chen RS, Deichmann U, Lerner-Lam AL, Arnold M (2005) Natural disaster hotspots: a global risk analysis. World Bank, Washington

Djanaguiraman M, Prasad PVV, Murugan M, Perumal M, Reddy UK (2014) Physiological differences among sorghum (*Sorghum bicolor* L. Moench) genotypes under high temperature stress. Environ Exp Bot 100:43–54

Djanaguiraman M, Perumal R, Jagadish SVK, Ciampitti IA, Welti R, Prasad PVV (2018) Sensitivity of sorghum pollen and pistil to high-temperature stress. Plant Cell Environ 41:1065–1082

Downes RW (1972) Effect of temperature on the phenology and grain yield of *Sorghum bicolor*. Aust J Agric Res 23:585–594

Duressa D, Weerasoriya D, Bean SR, Tilley M, Tesso T (2018) Genetic basis of protein digestibility in grain sorghum. Crop Sci 58(6):2183–2199

Ebadi MR, Pourreza J, Jamalian J, Edriss MA, Samie AH, Mirhadi SA (2005) Amino acid content and availability in low, medium and high tannin sorghum grain for poultry. Int J Poult Sci 4(1):27–31

Eck HV, Musick JC (1979) Plant water stress effect on irrigated sorghum. I. Effect on yield. Crop Sci 19:586–592

Elkonin LA, Italianskaya JV, Fadeeva IY, Bychkova VV, Kozhemyakin VV (2013) In vitro protein digestibility in grain sorghum: effect of genotype and interaction with starch digestibility. Euphytica 193(3):327–337

Elkonin LA, Italianskaya JV, Domanina IV, Selivanov NY, Rakitin AL, Ravin NV (2016) Transgenic sorghum with improved digestibility of storage proteins obtained by agrobacterium-mediated transformation. Russ J Plant Physiol 63(5):678–689

Eom JS, Chen LQ, Sosso D, Julius BT, Lin IW, Qu XQ, Braun DM, Frommer WB (2015) SWEETs, transporters for intracellular and intercellular sugar translocation. Curr Opin Plant Biol 25:53–62

Ercoli L, Mariotti M, Masoni A, Arduini I (2004) Growth responses of sorghum plants to chilling temperature and duration of exposure. Eur J Agron 2:93–103

Fabian A, Jager K, Rakszegi M, Barnabas B (2011) Embryo and endosperm development in wheat (*Triticum aestivum* L.) kernels subjected to drought stress. Plant Cell Rep 30:551–563

FAO (2002) Crop water management. Online. AGLW Water Management Group, United Nations FAO, Rome, Italy

FAO (2005) Special event on impact of climate change, pests and diseases on food security and poverty reduction. Background document. In: 31st session of the Committee on World Food Security FAO, Rome, Italy. ftp://ftp.fao.org/docrep/fao/meeting/009/j5411e.pdf

FAO (2008) Press release: Agriculture in the near east likely to suffer from climate change. Rome/Cairo, 3 March 2008. http://www.fao.org/newsroom/en/news/2008/1000800/index.html

Fatima Z, Ahmed M, Hussain M, Abbas G, Ul-Allah S, Ahmad S, Ahmed N, Ali MA, Sarwar G, ul Haque E, Iqbal P (2020) The fingerprints of climate warming on cereal crops phenology and adaptation options. Sci Rep 10(1):1–21

Fergason VL, Zuber MS (1962) Influence of environment on amylose content of maize endosperm. Crop Sci 2(3):209–211

Fernandez MGS, Schoenbaum GR, Goggi AS (2015) Novel germplasm and screening methods for early cold tolerance in sorghum. Crop Sci 54:2631–2638

Fischer G, Shah M, Tubiello FN, van Velthuizen H (2005) Socio-economic and climate change impacts on agriculture: an integrated assessment of agriculture, 1990–2080. Phil Trans R Soc B 360:2067–2083

Forbes GA, Ziv O, Frederiksen RA (1987) Resistance in sorghum to seedling disease caused by *Pythium arrhenomanes*. Plant Dis 71:145–148

Fracheboud Y, Haldimann P, Leipner J, Stamp P (1999) Chlorophyll fluorescence as a selection tool for cold tolerance of photosynthesis in maize (*Zea mays* L.). J Exp Bot 50:1533–1540

Franks CD, Burow GB, Burke JJ (2006) A comparison of US and Chinese sorghum germplasm for early season cold tolerance. Crop Sci 46:1371–1376

Garrity D, O'Toole J (1994) Screening rice for drought resistance at the reproductive phase. Field Crops Res 39:99–110

Gibson LR, Mullen RE (1996) Soybean seed quality reductions by high day and night temperature. Crop Sci 36:1615–1619

Gilding E, Frere CH, Cruickshank A, Rada AK, Prentis PJ, Mudge AM, Mace ES, Jordan DR, Godwin ID (2013) Allelic variation at a single gene increases food value in a drought-tolerant staple cereal. Nat Commun 4(1):1–6

Godfray HCJ, Beddington JR, Crute IR, Haddad L, Lawrence D, Muir JF, Pretty J, Robinson S, Thomas SM, Toulmin C (2010) Food security: the challenge of feeding 9 billion people. Science 327(5967):812–818

Gunaratne A, Bentota A, Cai YZ, Collado L, Corke H (2011a) Functional, digestibility, and antioxidant properties of brown and polished rice flour from traditional and new-improved varieties grown in Sri Lanka. Starch/Stärke 63(8):485–492

Gunaratne A, Ratnayaka UK, Sirisena N, Ratnayaka J, Kong X, Arachchi LV, Corke H (2011b) Effect of soil moisture stress from flowering to grain maturity on functional properties of Sri Lankan rice flour. Starch/Stärke 63:283–290

Habyarimana E, Dall'Agata M, De Franceschi P, Baloch FS (2019) Genome-wide association mapping of total antioxidant capacity, phenols, tannins, and flavonoids in a panel of *Sorghum bicolor* and *S. bicolor* × *S. halepense* populations using multi-locus models. PLoS ONE 14(12):e0225979

Hammer GL, Broad IJ (2003) Genotype and environment effects on dynamics of harvest index during grain filling in sorghum. Agron J 95:199–206

Harris K, Subudhi PK, Borrell A, Jordan D, Rosenow D, Nguyen H, Klein P, Klein R, Mullet J (2007) Sorghum stay-green QTL individually reduce post-flowering drought-induced leaf senescence. J Exp Bot 58(2):327–338

Hatfield JL, Boote KJ, Kimball BA, Ziska LH, Izaurralde RC, Ort D, Thomson AM, Wolfe D (2011) Climate impacts on agriculture: implications for crop production. Agron J 103:351–370

Henzell RG, Hare BR, Jordan DR, Fletcher DS, McCosker AN, Bunker G, Persley DS (2010) Sorghum breeding in Australia: public and private endeavours. In: Borrell AK, Henzell RG (eds) Proceedings of the 4th Australian Sorghum Conference. Kooralbyn, Australia

Hicks C, Tuinstra MR, Pedersen JF, Dowell FE, Kofoid KD (2002) Genetic analysis of feed quality and seed weight of sorghum inbred lines and hybrids using analytical methods and NIRS. Euphytica 127(1):31–40

Hurburgh CR, Brumm TJ, Guinn JM, Hartwig RA (1990) Protein and oil patterns in U.S. and world soybean markets. J Am Oil Chem Soc 67:966–973

Hurkman WJ, McCue KF, Altenbach SB, Korn A, Tanaka CK, Kothari KM, Johnson EL, Bechtel DB, Wilson JD, Anderson OD, DuPont FM (2003) Effect of temperature on expression of genes encoding enzymes for starch biosynthesis in developing wheat endosperm. Plant Sci 164:873–881

Impa SM, Perumal R, Bean SR, Sunoj VJ, Jagadish SK (2019) Water deficit and heat stress induced alterations in grain physico-chemical characteristics and micronutrient composition in field grown grain sorghum. J Cereal Sci 86:124–131

International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Food and Agriculture Organization (FAO) of the United Nations (1996) The World Sorghum and Millet Economies: Facts, Trends and Outlook; Food and Agriculture Organization: Rome, Italy. Available online: http://oar.icrisat.org/1024/

Inuyama S, Musick JT, Dusek DA (1976) Effect of plant water deficit at various growth stages on growth, grain yield and leaf water potential of irrigated grain sorghum. Proc Crop Sci Soc Jpn 45:298–307

IPCC-Intergovernmental Panel on Climate Change (2007) Climate change 2007: synthesis report. https://www.ipcc.ch/report/ar4/syr/ Accessed on January 19, 2021

Jain M, Prasad PVV, Boote KJ, Allen LH Jr, Chourey PS (2007) Effect of season-long high temperature growth conditions on sugar-to-starch metabolism in developing microspores of grain sorghum (*Sorghum bicolor* L. Moench). Planta 227:67–79

Jiang W, Zhou H, Bi H, Fromm M, Yang B, Weeks DP (2013) Demonstration of CRISPR/Cas9/sgRNA-mediated targeted gene modification in arabidopsis, tobacco, sorghum and rice. Nucleic Acids Res 41(20):e188. https://doi.org/10.1093/nar/gkt780

Johnson VA, Schmidt JW, Mattern PJ (1968) Cereal breeding for better protein impact. Econ Bot 22:16–25

Johnson WB, Ratnayake WS, Jackson DS, Lee KM, Herrman TJ, Bean SR, Mason SC (2010) Factors affecting the alkaline cooking performance of selected corn and sorghum hybrids. Cereal Chem 87(6):524–531

Johnson SM, Lim FL, Finkler A, Fromm H, Slabas AR, Knight MR (2014) Transcriptomic analysis of Sorghum bicolor responding to combined heat and drought stress. BMC Genomics 15(1):456

Jordan DR, Mace ES, Henzell RG, Klein PE, Klein RR (2010) Molecular mapping and candidate gene identification of the Rf2 gene for pollen fertility restoration in sorghum [*Sorghum bicolor* (L.) Moench]. Theor Appl Genet 120:1279–1287

Jordan DR, Hunt CH, Cruickshank AW, Borrell AK, Henzell RG (2012) The relationship between the stay-green trait and grain yield in elite sorghum hybrids grown in a range of environments. Crop Sci 52(3):1153–1161

Kadam S, Abril A, Dhanapal AP, Koester RP, Vermerris W, Jose S, Fritschi FB (2017) Characterization and regulation of aquaporin genes of sorghum [*Sorghum bicolor* (L.) Moench] in response to waterlogging stress. Front Plant Sci 8:862

Kapanigowda MH, Perumal R, Aiken RM, Herald TJ, Bean SR, Little CR (2013) Analyses of sorghum (*Sorghum bicolor* (L.) Moench) lines and hybrids in response to early-season planting and cool conditions. Can J Plant Sci 93:773–784

Kassahun B, Bidinger FR, Hash CT, Kuruvinashetti MS (2010) Stay-green expression in early generation sorghum [*Sorghum bicolor* (L.) Moench] QTL introgression lines. Euphytica 172(3):351–362

Kaufman RC, Wilson JD, Bean SR, Galant AL, Perumal RR, Tesso T, Herald T, Shi YC (2018) Influence of genotype× location interaction on grain sorghum grain chemistry and digestibility. Agron J 110(5):1681–1688

Kebede H, Subudhi PK, Rosenow DT, Nguyen HT (2001) Quantitative trait loci influencing drought tolerance in grain sorghum (*Sorghum bicolor* L. Moench). Theor Appl Genet 103:266–276

Khizzah BW, Miller FR, Newton RJ (1993) Inheritance and heritability of heat tolerance in several sorghum cultivars during the reproductive phase. Afr Crop Sci J 1(2)

Kimani W, Zhang LM, Wu XY, Hao HQ, Jing HC (2020) Genome-wide association study reveals that different pathways contribute to grain quality variation in sorghum (*Sorghum bicolor*). BMC Genomics 21(1):112

Kiseleva VI, Tester RF, Wasserman LA, Krivandin AV, Popov AA, Yuryev VP (2003) Influence of growth temperature on the structure and thermodynamic parameters of barley starches. Carbohydr Polym 51:407–415

Knoll J, Ejeta G (2008) Marker-assisted selection for early-season cold tolerance in sorghum: QTL validation across populations and environments. Theor Appl Genet 116:541–553

Knoll J, Gunaratna N, Ejeta G (2008) QTL analysis of early-season cold tolerance in sorghum. Theor Appl Genet 116:577–587

Krupa KN, Dalawai N, Shashidhar HE, Harinikumar KM (2017) Mechanisms of drought tolerance in Sorghum: a review. Int J Pure Appl Biosci 5(4):221–237

Kuromori T, Seo M, Shinozaki K (2018) ABA transport and plant water stress responses. Trends Plant Sci 23(6):513–522

Labuschagne MT, Elago O, Koen E (2009) The influence of temperature extremes on some quality and starch characteristics in bread, biscuit and durum wheat. J Cereal Sci 49:184–189

Leakey AD (2009) Rising atmospheric carbon dioxide concentration and the future of C4 crops for food and fuel. Proc R Soc B Biol Sci 276(1666):2333–2343

Li EP, Hasjim J, Singh V, Tizzotti M, Godwin ID, Gilbert RG (2013a) Insights into sorghum starch biosynthesis from structure changes induced by different growth temperatures. Cereal Chem 90:223–230

Li YF, Wu Y, Hernandez-Espinosa N, Peña RJ (2013b) Heat and drought stress on durum wheat: Responses of genotypes, yield, and quality parameters. J Cereal Sci 57(3):398–404

Linkemer G, Board JE, Musgrave ME (1998) Waterlogging effects on growth and yield components in late- planted soybean. Crop Sci 38:1576–1584

Liu P, Guo W, Jiang Z, Pu H et al (2011) Effects of high temperature after anthesis on starch granules in grains of wheat (*Triticum aestivum* L.). J Agric Sci 149:159–169

Liu G, Campbell BC, Godwin ID (2014) Sorghum genetic transformation by particle bombardment. Cereal genomics. Humana Press, Totowa, NJ, pp 219–234

Lobell DB, Burke MB, Tebaldi C, Mastrandrea MD, Falcon WP, Naylor RL (2008) Prioritizing climate change adaptation needs for food security in 2030. Science 319(5863):607–610

Long SP, Ainsworth EA, Leakey ADB, Nosberger J, Ort DR (2006) Food for thought: lower-than-expected crop yield stimulation with rising CO_2 concentrations. Science 312:1918–1921

Lopes MS, El-Basyoni I, Baenziger PS, Singh S, Royo C, Ozbek K, Aktas H, Ozer E, Ozdemir F, Manickavelu A (2015) Exploiting genetic diversity from landraces in wheat breeding for adaptation to climate change. J Exp Bot 66:3477–3486

Lu TJ, Jane JL, Keeling PL, Singletary GW (1996) Maize starch fine structures affected by ear developmental temperature. Carbohydr Res 282:157–170

Mace E, Singh V, Van Oosterom E, Hammer G, Hunt C, Jordan D (2012) QTL for nodal root angle in sorghum (*Sorghum bicolor* L. Moench). co-locate with QTL for traits associated with drought adaptation. Theor Appl Genet 124:97–109

Maiti RK (1996) Sorghum science. Science Publishers, Lebanon, NH

Majora DJ, Hammana WM, Rooda SB (1982) Effects of short-duration chilling temperature exposure on growth and development of sorghum. Field Crops Res 5:129–136

Manjarrez-Sandoval P, Gonzalez-Hernandez AV, Mendoza-Onofret EL, Engleman EM (1989) Drought stress effects on the grain-yield and panicle development of sorghum. Can J Plant Sci 69:631–641

Manolio TA (2010) Genomewide association studies and assessment of the risk of disease. N Engl J Med 363:166–176

Marla SR, Burow G, Chopra R, Hayes C, Olatoye MO, Felderhoff T, Hu Z, Raymundo R, Perumal R, Morris GP (2019) Genetic architecture of chilling tolerance in sorghum dissected with a nested association mapping population. G3 Genes Genomes Genet 9(12):4045–4057

Maulana F (2011) Analysis of cold tolerance in sorghum [*Sorghum bicolor* (L.) Moench]. Doctoral dissertation. Kansas State University

Maulana F, Tesso TT (2013) Cold temperature episode at seedling and flowering stages reduces growth and yield components in sorghum. Crop Sci 53:564–574

McDonald MP, Galwey NW, Colmer TD (2002) Similarity and diversity in adventitious root anatomy as related to root aeration among a range of wetland and dryland grass species. Plant Cell Environ 25:441–451

McWilliams D (2003) Drought strategies for corn and grain sorghum. Coop Ext. Circ. 580. New Mexico State Univ., Las Cruces, NM

Miller FR, Prihoda KL, Rooney LW, Rosenow DT, Waniska RD (1996) Registration of a food quality sorghum restorer parent, Tx2907. Crop Sci 36:479

Mishra AK, Rai R, Agrawal SB (2013) Differential response of dwarf and tall tropical wheat cultivars to elevated ozone with and without carbon dioxide enrichment: growth, yield and grain quality. Field Crops Res 145:21–32

Mitsui T, Shiraya T, Kaneko K, Wada K (2013) Proteomics of rice grain under high temperature stress. Front Plant Sci 4:36

Moritz JS, Parsons AS, Buchanan NP, Calvalcanti WB, Cramer KR, Beyer RS (2005) Effect of gelatinizing dietary starch through feed processing on zero- to three-week broiler performance and metabolism. J Appl Poult Res 14:47–54

Mousavi-Derazmahalleh M, Bayer PE, Hane JK, Babu V, Nguyen HT, Nelson MN, Erskine W, Varshney RK, Papa R, Edwards D (2018) Adapting legume crops to climate change using genomic approaches. Plant Cell Environ 42:6–19

Mudge SR, Campbell BC, Mustapha NB, Godwin ID (2016) Genomic approaches for improving grain quality of sorghum. In: Rakshit S, Wang Y-H (eds) The sorghum genome. Springer, Cham, pp 189–205

Myllarinen P, Schulman AH, Salovaara H, Poutanen K (1998) The effect of growth temperature on gelatinization properties of barley starch. Acta Agric Scand B Soil Plant Sci 48:85–90

Naeve SL, Huerd SC (2008) Year, region, and temperature effects on the quality of Minnesota's soybean crop. Agron J 100:690–695

Nagaraju M, Sudhakar Reddy P, Anil Kumar S, Srivastava RK, Kavi Kishor PB, Rao DM (2015) Genome-wide scanning and characterization of *Sorghum bicolor* L. heat shock transcription factors. Curr Genomics 16(4):279–291

Nguyen CT, Singh V, van Oosterom EJ, Chapman SC, Jordan DR, Hammer GL (2013) Genetic variability in high temperature effects on seed-set in sorghum. Funct Plant Biol 40:439–448

Njuguna VW, Cheruiyot EK, Mwonga S, Rono JK (2018) Effect of genotype and environment on grain quality of sorghum (*Sorghum bicolor* L. Moench) lines evaluated in Kenya. Afr J Plant Sci 12(12):324–330

Orchard PW, Jessop RS (1984) The response of sorghum and sunflower to short-term waterlogging. I. Effects of stage of development and duration of waterlogging on growth and yield. Plant Soil 81:119–132

Orchard PW, Jessop RS (1985) The response of sorghum and sunflower to short-term waterlogging. II. Root growth effects. Plant Soil 88:421–430

Ostmeyer T, Bheemanahalli R, Srikanthan D, Bean S, Peiris KH, Madasamy P, Perumal R, Jagadish SK (2020) Quantifying the agronomic performance of new grain sorghum hybrids for enhanced early-stage chilling tolerance. Field Crops Res 258:107955

Ottman MJ, Kimball BA, Pinter PJ Jr, Wall GW, Vanderlip RL, Leavitt SW, LaMorte RL, Matthias AD, Brooks TJ (2001) Elevated CO_2 effects on sorghum growth and yield at high and low soil water content. New Phytol 150:261–273

Pallas JE Jr (1965) Transpiration and stomatal opening with changes in carbon content of the air. Science 147:171–173

Pang J, Zhou M, Mendham N, Shabala S (2004) Growth and physiological responses of six barley genotypes to waterlogging and subsequent recovery. Aust J Agr Res 55:895–906

Pang B, Zhang K, Kisekka I, Bean S, Zhang M, Wang D (2018) Evaluating effects of deficit irrigation strategies on grain sorghum attributes and biofuel production. J Cereal Sci 79:13–20

Pardales JR Jr, Kono Y, Yamauchi A (1991) Response of the different root system components of sorghum to incidence of waterlogging. Environ Exp Bot 31:107–115

Pazdernik DL, Halgerson PSJ, JL, Orf JH, (1996) Effect of temperature and genotype on the crude glycinin fraction (11S) of soybean and its analysis by near-infrared reflectance spectroscopy (near-IRS). J Agric Food Chem 44:2278–2281

Peacock JM (1982) Response and tolerance of sorghum to temperature stress. Sorghum in the Eighties: Proceedings of the International Symposium on Sorghum. 2-7 Nov 81. International Crops Research lnstltute for the Semi-Arid Tropics, Patancheru, A.P. India

Pedersen JF, Bean SR, Graybosch RA, Park SH, Tilley M (2005) Characterization of waxy grain sorghum lines in relation to granule bound starch synthase. Euphytica 144:51–156

Peleg Z, Saranga Y, Yazici A, Fahima T, Ozturk L, Cakmak I (2008) Grain zinc, iron and protein concentrations and zinc-efficiency in wild emmer wheat under contrasting irrigation regimes. Plant Soil 306(1):57–67

Peng W, Berry EM, Ferranti P, Berry E, Anderson J (2019) The concept of food security. Encycl Food Secur Sustainability 2:1–7

Perry SW, Krieg DR, Hutmacher RB (1983) Photosynthetic rate control in cotton. Plant Physiol 73:662–665

Piikki K, De Temmerman L, Ojanpera K, Danielsson H, Pleijel H (2008) The grain quality of spring wheat (*Triticum aestivum* L.) in relation to elevated ozone uptake and carbon dioxide exposure. Eur J Agron 28:245–254

Polthanee A (1997) Indigenous farming practices and knowledge in Northeast Thailand. Khon Kaen Publishing, Khon Kaen

Prasad PVV, Craufurd PQ, Summerfield RJ, Wheeler TR (2000) Effects of short episodes of heat stress on flower production and fruit-set of groundnut (*Arachis hypogaea* L.). J Exp Bot 51:777–784

Prasad PVV, Boote KJ, Allen LH Jr, Thomas JMG (2003) Supra-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L) reproductive processes and yield at ambient and elevated carbon dioxide. Glob Change Biol 9:1775–1787

Prasad PVV, Boote KJ, Allen LH Jr (2006) Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to higher tissue temperatures. Agric For Meteorol 139:237–251

Prasad PVV, Pisipati SR, Mutava RN, Tuinstra MR (2008) Sensitivity of grain sorghum to high temperature stress during reproductive development. Crop Sci 48:1911–1917

Prasad PVV, Djanaguiraman M, Perumal R, Ciampitti IA (2015) Impact of high temperature stress on floret fertility and individual grain weight of grain sorghum: sensitive stages and thresholds for temperature and duration. Front Plant Sci 6:820

Promkhambut A, Polthanee A, Akkasaeng C, Younger A (2011) Growth, yield and aerenchyma formation of sweet and multipurpose sorghum (*Sorghum bicolor* L. Moench) as affected by flooding at different growth stages. Aust J Crop Sci 5(8):954

Rajkumar BF, Kavil SP, Girma Y, Arun SS, Dadakhalandar D, Gurusiddesh BH, Patil AM, Thudi M, Bhairappanavar SB, Narayana YD, Krishnaraj PU, Khadi BM, Kamatar MY (2013) Molecular mapping of genomic regions harbouring QTLs for root and yield traits in sorghum (*Sorghum bicolor* L. Moench). Physiol Mol Biol Plants 19:409–419

Ram G, Sharma AD (2013) In silico analysis of putative miRNAs and their target genes in sorghum (*Sorghum bicolor*). Int J Bioinf Res Appl 9(4):349–364

Ray SS, Dadhwal VK, Navalgund RR (2002) Performance evaluation of an irrigation command area using remote sensing: a case study of Mahi command, Gujarat, India. Agric Water Manage 56(2):81–91

Raymundo R, Asseng S, Robertson R, Petsakos A, Hoogenboom G, Quiroz R, Hareau G, Wolf J (2018) Climate change impact on global potato production. Eur J Agron 100:87–98

Raza A, Razzaq A, Mehmood SS, Zou X, Zhang X, Lv Y, Xu J (2019) Impact of climate change on crops adaptation and strategies to tackle its outcome: a review. Plants 8(2):34

Reddy BVS, Sharma HC, Thakur RP, Ramesh S, Ashok Kumar A (2007) Characterization of ICRISAT bred sorghum hybrid parents (Set II). Int Sorghum Millets Newslett 48:1–123

Reynolds TW, Waddington SR, Anderson CL, Chew A, True Z, Cullen A (2015) Environmental impacts and constraints associated with the production of major food crops in Sub-Saharan Africa and South Asia. Food Secur 7:795–822

Rhodes DH, Hoffmann L Jr, Rooney WL, Ramu P, Morris GP, Kresovich S (2014) Genome-wide association study of grain polyphenol concentrations in global sorghum [*Sorghum bicolor* (L) Moench] germplasm. J Agric Food Chem 62(45):10916–10927

Rhodes DH, Hoffmann L, Rooney WL, Herald TJ, Bean S, Boyles R, Brenton ZW, Kresovich S (2017) Genetic architecture of kernel composition in global sorghum germplasm. BMC Genomics 18(1):1–8

Richards RA (1996) Defining selection criteria to improve yield under drought. Plant Growth Regul 20:157–166

Rooney WL (2004) Sorghum improvement-integrating traditional and new technology to produce improved genotypes. Adv Agron 83:37–109

Rooney WL, Rooney LW, Awika J, Dykes L (2013) Registration of Tx3362 Sorghum germplasm. J Plant Regist 7:104–107

Rosenow DT, Clark LE (1995) Drought and lodging resistance for a quality sorghum crop. In: Proceedings of the 5th annual corn and sorghum industry research conference (Chicago, IL, 6–7 December 1995). American Seed Trade Association, Chicago, IL, pp 82–97

Rosenzweig C, Iglesius A, Yang XB, Epstein PR, Chivian E (2001) Climate change and extreme weather events—implications for food production, plant diseases, and pests. Global Change Hum Health 2:90–104

Roy SJ, Tucker EJ, Tester M (2011) Genetic analysis of abiotic stress tolerance in crops. Curr Opin Plant Biol 14:232–239

Roy JP, Tschakert H, Waisman S, Abdul Halim P, Antwi-Agyei P, Dasgupta B, Hayward M, Kanninen D, Liverman C, Okereke PF, Pinho K, Riahi AG, Suarez Rodriguez (2018) Sustainable development, poverty eradication and reducing inequalities. In: Masson-Delmotte V, Zhai P, Pörtner H-O, Roberts D, Skea J, Shukla PR, Pirani A, Moufouma-Okia W, Péan C, Pidcock R, Connors S, Matthews JBR, Chen Y, Zhou X, Gomis MI, Lonnoy E, Maycock T, Tignor M, Waterfield T (eds) Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. IPCC, Geneva

Saini HS (1997) Effects of water stress on male gametophyte development in plants. Sex Plant Reprod 10:67–73

Sarshad A, Talei D, Torabi M, Rafiei F, Nejatkhah P (2021) Morphological and biochemical responses of *Sorghum bicolor* (L.) Moench under drought stress. SN Appl Sci 3(1):1–12

Setter T, Belford B (1990) Waterlogging: how it reduces plant growth and how plants can overcome its effects. J Dept Agric Western Austr 31(2):51–55

Shakoor N, Ziegler G, Dilkes BP, Brenton Z, Boyles R, Connolly EL, Kresovich S, Baxter I (2015) Integration of experiments across diverse environments identifies the genetic determinants of variation in *Sorghum bicolor* seed element composition. bioRxiv, p 019083

Siddique KHM, Loss SP, Regan KL, Jettner RL (1999) Adaptation and seed yield of cool season grain legumes in Mediterranean environments of south-western Australia. Aust J Agric Res 50:375–438

Singh S, Singh G, Singh P, Singh N (2008) Effect of water stress at different stages of grain development on the characteristics of starch and protein of different wheat varieties. Food Chem 108:130–139

Singh S, Gupta AK, Gupta SK, Kaur N (2010) Effect of sowing time on protein quality and starch pasting characteristics in wheat (*Triticum aestivum* L.) genotypes grown under irrigated and rain-fed conditions. Food Chem 122:559–565

Singh V, Nguyen CT, van Oosterom EJ, Chapman SC, Jordan DR, Hammer GL (2015) Sorghum genotypes differ in high temperature responses for seed set. Field Crops Res 171:32–40

Singh V, Nguyen CT, Yang Z, Chapman SC, van Oosterom EJ, Hammer GL (2016) Genotypic differences in effects of short episodes of high-temperature stress during reproductive development in sorghum. Crop Sci 56:1561–1572

Sonobe K, Hattori T, An P, Tsuji W, Eneji AE, Kobayashi S, Kawamura Y, Tanaka K, Inanaga S (2010) Effect of silicon application on sorghum root responses to water stress. J Plant Nutr 34(1):71–82

Srivastava A, Kumar SN, Aggarwal PK (2010) Assessment on vulnerability of sorghum to climate change in India. Agric Ecosyst Environ 138(3–4):160–169

Stone LR, Schlegel AJ (2006) Yield-water supply relationship of grain sorghum and winter wheat. Agron J 98:1359–1366

Stone PJ, Wilson DR, Reid JB, Gillespie RN (2001) Water deficit effects on sweet corn. I. Water use, radiation use efficiency, growth, and yield. Austr J Agric Res 52(1):103–113

Sun MM, Abdula SE, Lee HJ, Cho YC, Han LZ, Koh HJ, Cho YG (2011) Molecular aspect of good eating quality formation in Japonica rice. PLoS ONE 6:e18385

Svihus B, Uhlen AK, Harstad OM (2005) Effect of starch granule structure, associated components and processing on nutritive value of cereal starch: a review. Anim Feed Sci Technol 122:303–320

Taleon V, Dykes L, Rooney WL, Rooney LW (2012) Effect of genotype and environment on flavonoid concentration and profile of black sorghum grains. J Cereal Sci 56(2):470–475

Taub DR, Miller B, Allen H (2008) Effects of elevated CO_2 on the protein concentration of food crops: a meta-analysis. Global Change Biol 14(3):565–575

Terbea M, Vranceanu AV, Petcu E, Craiciu DS, Micut G (1995) Physiological response of sunflower plants to drought. Rom Agric Res 3:61–67

Tesso T, Ejeta G, Chandrashekar A, Huang CP, Tandjung A, Lewamy M, Axtell JD, Hamaker BR (2006) A novel modified endosperm texture in a mutant high-protein digestibility/high-lysine grain sorghum (*Sorghum bicolor* (L.) Moench). Cereal Chem J 83:194–201

Tester RF (1997) Influence of growth conditions on barley starch properties. Int J Biol Macromol 21(1–2):37–45

Tester RF, Karkalas J (2001) The effects of environmental conditions on the structural features and physico-chemical properties of starches. Starch/Stärke 53:513–519

Thitisaksakul M, Jimenez RC, Arias MC, Beckles DM (2012) Effects of environmental factors on cereal starch biosynthesis and composition. J Cereal Sci 56:67–80

Thomas H, Howarth CJ (2000) Five ways to stay green. J Exp Bot 51:329–337

Thomas JMG, Boote KJ, Allen LH Jr, Gallo-Meagher M, Davis JM (2003) Elevated temperature and carbon dioxide effects on soybean seed germination and transcript abundance. Crop Sci 43:1548–1557

Tirfessa A, McLean G, Mace E, van Oosterom E, Jordan D, Hammer G (2020) Differences in temperature response of phenological development among diverse Ethiopian sorghum genotypes are linked to racial grouping and agroecological adaptation. Crop Sci 60(2):977–990

Tiryaki I, Andrews DJ (2001) Germination and seedling cold tolerance in sorghum: II. Parental lines and hybrids. Agron J 93:1391–1397

Tolk JA, Howell TA (2001) Measured and simulated evapotranspiration of grain sorghum with full and limited irrigation in three high plains soils. Trans ASAE 44:1553–1558

Torbert HA, Prior SA, Rogers HH, Runion GB (2004) Elevated atmospheric CO_2 effects on N fertilization in grain sorghum and soybean. Field Crops Res 88(1):7–67

Tuinstra MR, Grote EM, Goldsbrough PB, Ejeta G (1996) Identification of quantitative trait loci associated with pre-flowering drought tolerance in sorghum. Crop Sci 36:1337–1344

Tuinstra MR, Grote EM, Goldbrough PM, Ejeta G (1997) Genetic analysis of post-flowering drought tolerance and components of grain development in *Sorghum bicolor* L. Moench. Mol Breed 3:439–448

Tuttle JR, Idris AM, Brown JK, Haigler CH, Robertson D (2008) Geminivirus-mediated gene silencing from cotton leaf crumple virus is enhanced by low temperature in cotton. Plant Physiol 148(1):41–50

Umaharan P, Ariyanayagam RP, Haque SQ (1997) Effect of short-term waterlogging applied at various growth phases on growth, development and yield in Vigna unguiculata. J Agr Sci 128:189–198

UN Report (2019) World population prospects—2019 highlights. https://www.un.org/development/desa/publications/world-population-prospects-2019-highlights.html. Accessed on 23 January 2021

Vadez V, Krishnamurthy L, Hash CT, Upadhyaya HD, Borrell AK (2011) Yield, transpiration efficiency, and water-use variations and their interrelationships in the sorghum reference collection. Crop Pasture Sci 62(8):645–655

Van Bavel CHM (1974) Anti-transpirant action of carbon dioxide on intact sorghum plants. Crop Sci 14:208–212

Vinita J, Bhargava S, Streb P, Feierabend J (1998) Comparative effect of water, heat and light stresses on photosynthetic reactions in *Sorghum bicolor* (L.) Moench. J Exp Bot 49(327):1715–1721

Von Born P, Bernardo-Faura M, Rubio-Somoza I (2018) An artificial miRNA system reveals that relative contribution of translational inhibition to miRNA-mediated regulation depends on environmental and developmental factors in *Arabidopsis thaliana*. PLoS ONE 13(2):e0192984

Wong R, Mufloz OA, Mendoza LE (1983) Water stress effects on vegetative, reproductive and efficiency traits of sorghum varieties I in Spanish. Agrociencia 51:101–114

Wong JH, Marx DB, Wilson JD, Buchanan BB, Lemaux PG, Pedersen JF (2010) Principal component analysis and biochemical characterization of protein and starch reveal primary targets for improving sorghum grain. Plant Sci 179(6):598–611

Wu X, Zhao R, Bean SR, Seib PA, McLaren JS, Madl RL, Tuinstra M, Lenz MC, Wang D (2007) Factors impacting ethanol production from grain sorghum in the dry-grind process. Cereal Chem 84(2):130–136

Wu X, Zhao R, Liu L, Bean S, Seib PA, McLaren J, Madl R, Tuinstra M, Lenz M, Wang D (2008) Effects of growing location and irrigation on attributes and ethanol yields of selected grain sorghums. Cereal Chem 85(4):495–501

Wu G, Johnson SK, Bornman JF, Bennett SJ, Singh V, Simic A, Fang J (2016) Effects of genotype and growth temperature on the contents of tannin, phytate and in vitro iron availability of sorghum grains. PLoS ONE 11:1–12

Xin Z, Aiken R, Burke J (2008) Genetic diversity of transpiration efficiency in sorghum. Field Crops Res 111:74–80

Yu S, Tian L (2018) Breeding major cereal grains through the lens of nutrition sensitivity. Mol Plant 11:23–30

Yu J, Tuinstra MR (2001) Genetic analysis of seedling growth under cold temperature stress in grain sorghum. Crop Sci 41:1438–1443

Yu J, Tuinstra MR, Claassen MM, Gordon WB, Witt MD (2004) Analysis of cold tolerance in sorghum under controlled environment conditions. Field Crops Res 85:21–30

Zaidi PH, Rafique S, Rai PK, Singh NN, Srinivasan G (2004) Tolerance to excess moisture in maize (*Zea mays* L.): susceptible crop growth stage and identification of tolerant genotypes. Field Crops Res 90:189–202

Zeng M, Morris CF, Batey IL, Wrigley CW (1997) Sources of variation for starch gelatinization, pasting, and gelation properties in wheat. Cereal Chem 74:63–71

Zhan X, Wang D, Tuinstra MR, Bean S, Seib PA, Sun XS (2003) Ethanol and lactic acid production as affected by sorghum genotype and location. Ind Crops Prod 18(3):245–255

Zhang F, Wang Y, Yu H, Zhu K, Zhang Z, Zou FLJ (2016) Effect of excessive soil moisture stress on sweet sorghum: physiological changes and productivity. Pak J Bot 48(1):1–9

Zhang R, Zhou Y, Yue Z, Chen X, Cao X, Ai X, Jiang B, Xing Y (2019a) The leaf-air temperature difference reflects the variation in water status and photosynthesis of sorghum under waterlogged conditions. PLoS ONE 14(7):e0219209

Zhang RD, Zhou YF, Yue ZX, Chen XF, Cao X, Xu XX, Xing YF, Jiang B, Ai XY, Huang RD (2019b) Changes in photosynthesis, chloroplast ultrastructure, and antioxidant metabolism in leaves of sorghum under waterlogging stress. Photosynthetica 57(4):1076–1083

Zhuo W, Lin X (1995) Effects of waterlogging at different growth stages on physiological characteristic and seed yield of winter rape (*Brassica napus* L.). Field Crops Res 44:103–110

Terms and Conditions

Springer Nature journal content, brought to you courtesy of Springer Nature Customer Service Center GmbH (“Springer Nature”).

Springer Nature supports a reasonable amount of sharing of research papers by authors, subscribers and authorised users (“Users”), for small-scale personal, non-commercial use provided that all copyright, trade and service marks and other proprietary notices are maintained. By accessing, sharing, receiving or otherwise using the Springer Nature journal content you agree to these terms of use (“Terms”). For these purposes, Springer Nature considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the relevant terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). For Creative Commons-licensed articles, the terms of the Creative Commons license used will apply.

We collect and use personal data to provide access to the Springer Nature journal content. We may also use these personal data internally within ResearchGate and Springer Nature and as agreed share it, in an anonymised way, for purposes of tracking, analysis and reporting. We will not otherwise disclose your personal data outside the ResearchGate or the Springer Nature group of companies unless we have your permission as detailed in the Privacy Policy.

While Users may use the Springer Nature journal content for small scale, personal non-commercial use, it is important to note that Users may not:

1. use such content for the purpose of providing other users with access on a regular or large scale basis or as a means to circumvent access control;
2. use such content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval , sponsorship, or association unless explicitly agreed to by Springer Nature in writing;
4. use bots or other automated methods to access the content or redirect messages
5. override any security feature or exclusionary protocol; or
6. share the content in order to create substitute for Springer Nature products or services or a systematic database of Springer Nature journal content.

In line with the restriction against commercial use, Springer Nature does not permit the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Springer Nature journal content cannot be used for inter-library loans and librarians may not upload Springer Nature journal content on a large scale into their, or any other, institutional repository.

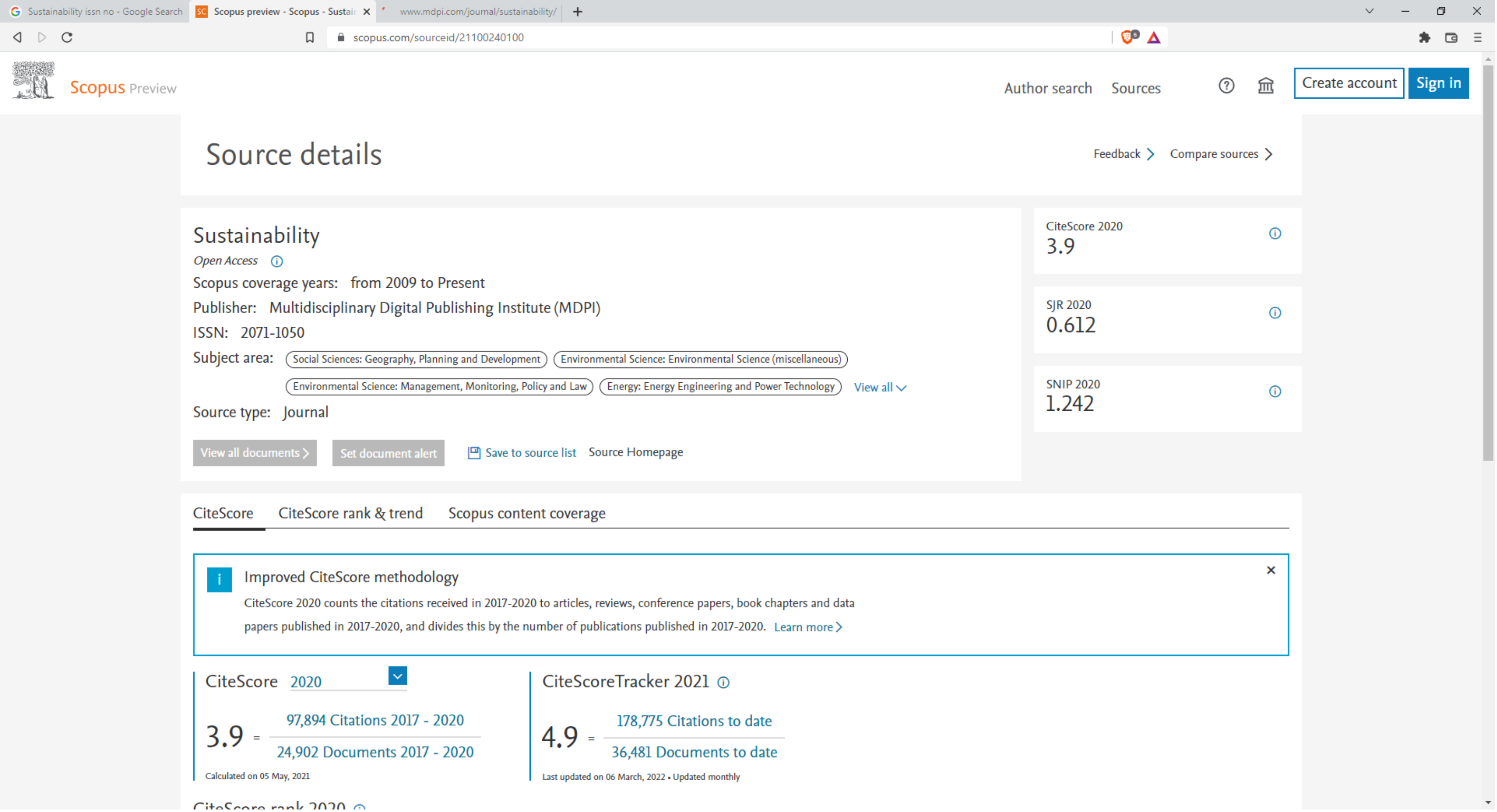
These terms of use are reviewed regularly and may be amended at any time. Springer Nature is not obligated to publish any information or content on this website and may remove it or features or functionality at our sole discretion, at any time with or without notice. Springer Nature may revoke this licence to you at any time and remove access to any copies of the Springer Nature journal content which have been saved.

To the fullest extent permitted by law, Springer Nature makes no warranties, representations or guarantees to Users, either express or implied with respect to the Springer nature journal content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Springer Nature that may be licensed from third parties.

If you would like to use or distribute our Springer Nature journal content to a wider audience or on a regular basis or in any other manner not expressly permitted by these Terms, please contact Springer Nature at

onlineservice@springernature.com



Source details

Sustainability

Open Access

Scopus coverage years: from 2009 to Present

Publisher: Multidisciplinary Digital Publishing Institute (MDPI)

ISSN: 2071-1050

Subject area: Social Sciences: Geography, Planning and Development; Environmental Science: Environmental Science (miscellaneous); Environmental Science: Management, Monitoring, Policy and Law; Energy: Energy Engineering and Power Technology

Source type: Journal

CiteScore 2020
3.9

SJR 2020
0.612

SNIP 2020
1.242

Improved CiteScore methodology

CiteScore 2020 counts the citations received in 2017-2020 to articles, reviews, conference papers, book chapters and data papers published in 2017-2020, and divides this by the number of publications published in 2017-2020.

CiteScore 2020

3.9 = 97,894 Citations 2017 - 2020 / 24,902 Documents 2017 - 2020

Calculated on 05 May, 2021

CiteScoreTracker 2021

4.9 = 178,775 Citations to date / 36,481 Documents to date

Last updated on 06 March, 2022 • Updated monthly

sustainability

Article

Simulating Potential Impacts of Future Climate Change on *Post-Rainy* Season Sorghum Yields in India

Keerthi Chadalavada [1,2], Sridhar Gummadi [3,*], Koteswara Rao Kundeti [4], Dakshina Murthy Kadiyala [5], Kumara Charyulu Deevi [2], Kailas Kamaji Dakhore [6], Ranjitha Kumari Bollipo Diana [1] and Senthil Kumar Thiruppathi [1]

[1] Department of Botany, Bharathidasan University, Tiruchirappalli 620024, India; keerthichadalawada@gmail.com (K.C.); ranjithakumari2004@yahoo.co.in (R.K.B.D.); senthilbdc@bdu.ac.in (S.K.T.)
[2] International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502324, India; d.kumaracharyulu@cgiar.org
[3] CGIAR Research Program for Climate Change, Agriculture and Food Security (CCAFS), International Rice Research Institute (IRRI), IRRI-CCAFS Office, Agricultural Genetics Institute, Hanoi 03000, Vietnam
[4] Center for Climate Change and Sustainability, Azim Premji University, Bengaluru 562125, India; koti.meteo@gmail.com
[5] Department of Agronomy, Acharya NG Ranga Agricultural University, Guntur 522034, India; dakshu2k@gmail.com
[6] All India Coordinated Research Project on Agrometeorology, Vasantrao Naik Marathwada Krishi Vidyapeeth, Parbhani 431402, India; dakhorekk@gmail.com
* Correspondence: sridhar.gummadi@irri.org

Abstract: Given the wide use of the multi-climate model mean (MMM) for impact assessment studies, this work examines the fidelity of Coupled Model Intercomparison Project Phase 5 (CMIP5) in simulating the features of Indian summer monsoons as well as the *post-rainy* seasons for assessing the possible impacts of climate change on post-rainy season sorghum crop yields across India. The MMM simulations captured the spatial patterns and annual cycles of rainfall and surface air temperatures. However, bias was observed in the precipitation amounts and daily rainfall intensity. The trends in the simulations of MMM for both precipitation and temperatures were less satisfactory than the observed climate means. The Crop Environment Resource Synthesis (CERES)-sorghum model was used to estimate the potential impacts of future climate change on post-rainy season sorghum yield values. On average, post-rainy season sorghum yields are projected to vary between −4% and +40% as well as +10% and +59% in the near future (2040–2069) for RCP 4.5 and RCP 8.5, respectively, and between +20% and +70% (RCP 4.5) as well as +38% and +89% (RCP 8.5) in the far future (2070–2099). Even though surface air temperatures are increasing in future climate change projections, the findings suggest that an increase in the post-rainy season sorghum yields was due to an increase in the rainfall amounts up to 23% and an increase in the atmospheric CO_2 levels by the end of the 21st century. The results suggest that the projected climate change during the post-rainy season over India is an opportunity for smallholders to capitalize on the increase in rainfall amounts and further increase sorghum yields with appropriate crop management strategies.

Keywords: *post-rainy* sorghum; crop simulation models; climate change impacts; crop yields

check for updates

Citation: Chadalavada, K.; Gummadi, S.; Kundeti, K.R.; Kadiyala, D.M.; Deevi, K.C.; Dakhore, K.K.; Bollipo Diana, R.K.; Thiruppathi, S.K. Simulating Potential Impacts of Future Climate Change on *Post-Rainy* Season Sorghum Yields in India. *Sustainability* **2022**, *14*, 334. https://doi.org/10.3390/su14010334

Academic Editors: Baojie He, Ayyoob Sharifi, Chi Feng and Jun Yang

Received: 11 November 2021
Accepted: 14 December 2021
Published: 29 December 2021

1. Introduction

Sorghum is an important nutraceutical crop for the small and marginal farmers across the semi-arid tropics (SAT) of the world [1]. Globally, sorghum is the fifth largest cereal preferred in diverse ecologies. Primarily, the crop is cultivated in four (Asia, Africa, the Pacific and the Americas) major regions across the globe. In India, sorghum is the fourth largest cereal crop. In the case of Africa, it is the second most important crop after maize [2]. Sorghum is one of the most preferred climate-smart crops for rainfed farmers under severe moisture stress environments. It can be grown successfully under limited soil moisture availability and with inadequate application of other inputs [3]. At present, the crop is being cultivated in both the monsoon (1.85 m ha) and *post-rainy* (2.89 m ha) seasons [4]. Nearly 1.5 m ha of cropped area is also under use for forage sorghum, which is cultivated during the summer season. More than 90% of the sorghum cropped area in the country is grown under rainfed conditions. Rainy season sorghum is cultivated under both sole (40%) and intercrop (along with pulses and oilseeds) (60%) cropping systems. However, the *post-rainy* sorghum is preferred to cultivate as a sole crop under residual soil moisture conditions.

Sorghum is cultivated for diverse uses, such as food and feed purposes. The forage of the crop is highly nutritious for livestock animals. The crop also has a significant capacity for ethanol production and has been identified as a potential biofuel crop. Sorghum grains are the richest sources of Fe and Zn minerals, apart from starch and protein [5,6]. Since the late 1990s, there has been a remarkable shift in the sorghum cropped area from the monsoon to the *post-rainy* season. The area proportions between monsoon (62%) and *post-rainy* seasons (38%) in the total sorghum cropped area during 1960s has been altered to 39% (monsoon) and 61% (*post-rainy*) by 2020–2021 [4]. The rain that occurs during the rainy season exactly coincides with the time of the rainy season sorghum harvest, resulting in poor quality for the grains due to grain mold attacks and fetching lower market prices. In spite of significant crop improvement exertions by both the public and private sectors [7], the rainy season cropped area has been eroded in the country due to low profitability in its cultivation. The majority of the rainy season's produce is diverted for industrial usage (mainly poultry) rather than human consumption [8,9]. Relatively, the average productivity levels are higher for the monsoon season sorghum because of good access to modern cultivars, including hybrids. The mean productivity levels are lower in the case of the *post-rainy* crops due to the non-availability of improved cultivars and moisture stress conditions. However, the quality of the grain is superior in the *post-rainy* season compared with that of the monsoon season. Grain molds and shoot fly attacks during the rainy season often deteriorate the quality of monsoon production. A major chunk of the *post-rainy* season produce is diverted for human consumption and fetches higher market prices (nearly double) than rainy season grain. In both seasons, stover (straw) forms an important source of crop income as well as animal feed for their livestock. The leading states for growing *post-rainy* season sorghum in India are Maharashtra, Karnataka, Andhra Pradesh, Gujarat and Telangana. It is an important source of food, fodder and livelihood for the sorghum growers in the niche areas located in these states.

Historically, sorghum is a climate resilient crop which developed its drought tolerance traits to withstand and respond to adverse climate conditions. It is a perfect crop for the semi-arid tropics (SAT), which is a permanent home for the poorest of the poor people. Sorghum can thrive well under excessive temperatures, salt and waterlogging situations. It is well-established that sorghum is a good potential crop for promoting household incomes as well as lifting the poor out of poverty [10]. Under the perils of climate change and variability (CCV), the plausible impacts on crop productivity levels across the world, especially in the tropics, are going to be very high. Increasing temperatures coupled with significant deviations in the annual rainfall distribution may exacerbate substantial negative effects in SAT regions [11,12]. *Post-rainy* sorghum is likely to reduce its productivity per ha up to 7% by 2020, up to 11% by 2050 and up to 32% by 2080 due to anticipated climate change projections. The probable impacts will be severe and may vary its intensity across the *post-rainy* sorghum-cultivating agro-ecologies of India [13]. The introduction of climate-smart cultivars and an improved package of practices may compensate for the plausible impacts partially. However, significant crop productivity loss was noticed after a 2 °C rise in temperature and even after providing twice the quantity of rainfall across the major cultivating regions in India [13].

With this background, it is highly important to deeply understand the potential impacts of the future climate on *post-rainy* sorghum crop performance in India. Researchers have attempted to comprehend this with either one or two future climate change scenarios previously [13]. There is scanty information or evidence on plausible climate change impacts on the crop using a whole range (multi-model) of climate change projections. It would be highly interesting to see and understand the entire gamut of those plausible impacts under diverse sorghum agro-ecological conditions in India. This will immensely help us to define and develop location-specific and tailor-made climate change mitigation strategies and management practices well in advance. The present research paper makes robust and systematic efforts to quantify the plausible future climate change impacts on *post-rainy* sorghum performance in India using both crop simulation and multi-model climate scenarios. This exercise will showcase the potential climate change impacts on *post-rainy* sorghum crops across the studied states in India. The findings in this paper will help scientists, agronomists and policymakers in designing suitable climate adaptation strategies and policies for crop improvement. The outcome of this paper will help in protecting the livelihoods of millions of rainfed farmers who are directly or indirectly dependent on *post-rainy* sorghum cultivation in India and their associated livestock population. The lessons learned in India could be scaled up to other similar regions around the world.

2. Materials and Methods

2.1. Climate, Soil and Crop Management Data

The gridded daily data of the rainfall (0.25° latitude × 0.25° longitude) and both the maximum and minimum surface temperatures (0.5° latitude × 0.5° longitude) were obtained from the India Meteorological Department (IMD) for 25 years (1981–2005). Incoming solar radiation (Q) was computed using the Bristow and Campbell (1984) model. The model developed a relationship between the fraction of daily total transmission and the daily time scale air temperature extremes range (D):

$$Q = Q_0\, a(1 - \exp(-bD^c)) \tag{1}$$

The empirical coefficients (a, b and c) for the specific location were determined from the solar radiation data measured for that location. The diurnal range of the surface air temperature (D) was calculated as

$$D = T_{max} - \frac{T_{min}(j) + T_{min}(J+1)}{2} \tag{2}$$

where T_{max} is the daily maximum temperature (°C), T_{min} (j) is the minimum temperature (°C) of the day and T_{min} $(j + 1)$ is the minimum temperature recorded on the next day. The model included an adjustment for the measured D on rainy days, as cloud cover can be another manifestation of rainfall.

Bio-physical crop simulation models require profile-wise soil information, and in this study, we used soil data from SoilGrids1km developed by the International Soil Reference and Information Centre (ISRIC) in collaboration with several international agencies [14]. However, as the rainfall data were available only at a 0.25 × 0.25 degree spatial resolution, we restricted the crop simulations to 0.25 × 0.25 degrees, as simulating 1-km soil grids is computationally every expensive. Soil profiles were overlayed on rainfall grids, and the soil profile that had the maximum area under the rainfall grid was selected. SoilGrids1km offers both the physical and chemical properties of soil profiles at six depth intervals: 0–5, 5–15, 15–30, 30–60, 60–100 and 100–200 cm. The soil properties include sand, silt and clay fractions (%), bulk density (kg m^{-3}), soil organic carbon (g kg^{-1}), pH, cation exchange capacity (cmol kg^{-1}) and coarse fragments (%). To simulate the growth, development and yield of major *post-rainy* season sorghum growing environments in India, we used the Spatial Production Allocation Model (SPAM) of the International Food Policy Research Institute (IFPRI) to identify plausible sorghum crop distribution (IFPRI, 2019) maps in India.

The general recommended package of practices for *post-rainy* season sorghum was presumed to mimic on-farm crop management practices [15–18]. General information on the crop management aspects across *post-rainy* season sorghum growing regions were collected from a literature review. Critical analysis on the information compiled revealed that the crop was usually sown within a short planting window between the end of September and the first half of October. The actual planting date during the sowing window was set based on the criteria of 25 mm of rainfall received in 10 days using a crop simulation model that would facilitate successful emergence and early crop establishment. The cultivar used in this study was M 35-1, and the validated and calibrated DSSAT crop coefficients for M 35-1 were taken from previous studies [19,20] based on long-term All India Coordinated Research Project on Sorghum (AICRPS) trials. In this study, we initialized the simulation start on the first day of August, with sowing performed when the sowing criteria were met. The M 35-1 genotype was sown with a plant density of 12 plants per m^2 along with nitrogen @ 20 kg/ha applied as a basal dose. Furthermore, 30 kg ha^{-1} was applied 30 days after sowing. The simulation was run at a 0.25° × 0.25° resolution scale.

2.2. Climate Scenarios and Bias Correction Technique

The Earth System Models (ESMs) and the General Circulation Models (GSMs) are the most cutting-edge tools currently available to model changes in the global climate to increase in the planet's radiative forcing at large spatial and temporal scales. The impact assessment user community of such projections often needs higher spatial resolutions to understand the impacts of climate change seen at regional and local scales. To accommodate such finer information, the global climate model projections were downscaled through dynamical and statistical approaches, as the GCMs' simulation precisions were poor due to a coarse spatial resolution [11,21]. The Earth Exchange Global Daily Downscaled Projections (NEX-GDDP) datasets of the National Aeronautics and Space Administration (NASA) at high spatial (~25 km × 25 km) and temporal (daily) resolutions were composed of bias-corrected and statistically downscaled climate scenarios derived from 20 GCMs (Table 1) of the coupled model inter-comparison project phase 5 (CMIP5) across two Representative Concentration Pathways (RCPs)—4.5 (mid-range emissions) and 8.5 (high-end emissions)—used in this study. The downscaled climate change projections included the rainfall and maximum and minimum temperatures for the period from 1950 to 2005 (retrospective run) and from 2006 to 2099 (prospective run). The Bias-Corrected Spatial Disaggregation (BCSD) method was used to generate these datasets [22,23]. The NEX-GDDP datasets have been cited as the most promising high-resolution climate change scenarios for carrying out impact studies on the aspects of climate change from the local to regional scales [24]. In the present study, we used the multi-model mean (MMM) approach to evaluate the performance of the NEX-GDDP data (temperature and precipitation) over the historical climate of India with the India Meteorological Department (IMD) (Pune, India) developing daily high-resolution 0.25° × 0.25° gridded rainfall and 0.5° × 0.5° gridded temperature data. The advantage of using the multi-model mean (MMM) was that it performed better than the individual model and averaged out the internal variability when compared with the observations. The current study explores the projected changes in the *post-rainy* season simulated trajectories of sorghum yields over eight states in India in the near future (2040–2069) and far future (2070–2099) with reference to the baseline period (1981–2015). The projected changes in precipitation and temperature were analyzed using these high-resolution datasets.

Table 1. List of GCMs in the NEX-GDDP dataset used in the study.

No.	Organisation	Model Name	Country	Grid Resolution
1	Commonwealth Scientific and Industrial Research Organization (CSIRO) and Bureau of Meteorology (BOM) in Australia	ACCESS1.0	Australia	144 × 192
2	Beijing Climate Center, China Meteorological Administration	BCC-CSM1.1	China	64 ×128
3	Beijing Normal University	BNU-ESM	China	64 ×128
4	Canadian Centre for Climate Modelling and Analysis	CanESM2	Canada	64 ×128
5	National Center for Atmospheric Research	CCSM4	USA	192 × 288
6	National Science Foundation, Department of Energy, NCAR	CESM1-BGC	USA	192 × 288
7	Centre National de Recherches Meteorologiques, Centre Europeen de Recherche et Formation Avancees en Calcul Scientifique	CNRM-CM5	France	128 × 256
8	Commonwealth Scientific and Industrial Research Organization in collaboration with the Queensland Climate Change Centre of Excellence	CSIRO-Mk3.6.0	Australia	96 × 192
9	NOAA Geophysical Fluid Dynamics Laboratory	GFDL-ESM2G GFDL-ESM2M	USA USA	90 × 144 90 × 144
10	Institute for Numerical Mathematics	INM-CM4	Russia	120 × 180
11	Institut Pierre-Simon Laplace	IPSL-CM5A-LR IPSL-CM5A-MR	France France	96 × 96 143 × 144
12	Japan Agency for Marine-Earth Science and Technology, Atmosphere and Ocean Research Institute (The University of Tokyo), and National Institute for Environmental Studies	MIROC-ESM MIROC-ESM-CHEM	Japan Japan	64 × 128 64 × 128
13	Atmosphere and Ocean Research Institute (The University of Tokyo), National Institute for Environmental Studies and Japan Agency for Marine-Earth Science and Technology	MIROC5	Japan	128 × 256
14	Max Planck Institute for Meteorology	MPI-ESM-LR MPI-ESM-MR	Germany Germany	96 × 192 96 × 192
15	Meteorological Research Institute	MRI-CGCM3	Japan	160 × 320
16	Norwegian Climate Centre	NorESM1-M	Norway	96 × 144

2.3. Crop Model Description and Yield Simulations

Crop Environmental Recourse Synthesis (CERES) sorghum modeling under Decision Support System for Agro-Technology Transfer (DSSAT) Version 4.7 [25] is a process-based comprehensive model to simulate the crop growth, development and final grain yield of sorghum. Using a daily time step routine, the model simulates growth and development to the maturity stage based on the complex physiological processes describing crop responses to weather conditions, soil and crop management practices. The cultivar-specific genetic coefficients specify the phenological development and growth based on the thermal time and photo-period conditions defined in the model. The model computes the net photosynthesis based on the light intercepted, and photosynthate is partitioned to different parts of the plant on a given day while constrained by temperature, water deficit, and nutrient stress factors [26,27]. This model can be effectively used for understanding the impacts of climate change on *post-rainy* sorghum growth and yield across dry region tracts of India.

2.4. Crop Model Evaluation Protocols

For evaluation of the simulation’s outputs, we used the mean sorghum yield data product reported at the district level during the *post-rainy* season across the study states in India. The simulated sorghum yield at a 0.25° × 0.25° spatial resolution was subsequently aggregated to the district administrative boundaries. Model performance in reproducing the observed historical yields at the district level was evaluated by calculating the absolute and normalized mean root square error, coefficient of determination (R^2) and the Wilmot d index [28]. The ability of the CERES sorghum model to reproduce historical yields was determined by the values of the RMSE and d index. A good agreement between the observed and simulated yields was represented by a lower root mean square error (*RMSE*) and a d value close to one. The relative difference between the observed and simulated yields was represented by the normalized *RMSE* (%). In the present study, based on [29], the performance of the simulation model was categorized into four categories: excellent, good, fair and poor, depending on the normalized *RMSE* (NRMSE) values of <10%, 10–20%, 20–30% and >30%, respectively. The equations for elevating the model performance were as follows:

$$RMSE = \left[n - 1 \sum_{i=1}^{n} (P_i - O_i)^2\right]^{0.5} \tag{3}$$

where P_i and O_i are the simulated and observed values, respectively, and n is the number of observations:

$$normalised\ RMSE\ (\%) = \left(\frac{absolute\ RMSE}{\overline{O}}\right) \times 100 \tag{4}$$

where O is the average observed yield value [29], and

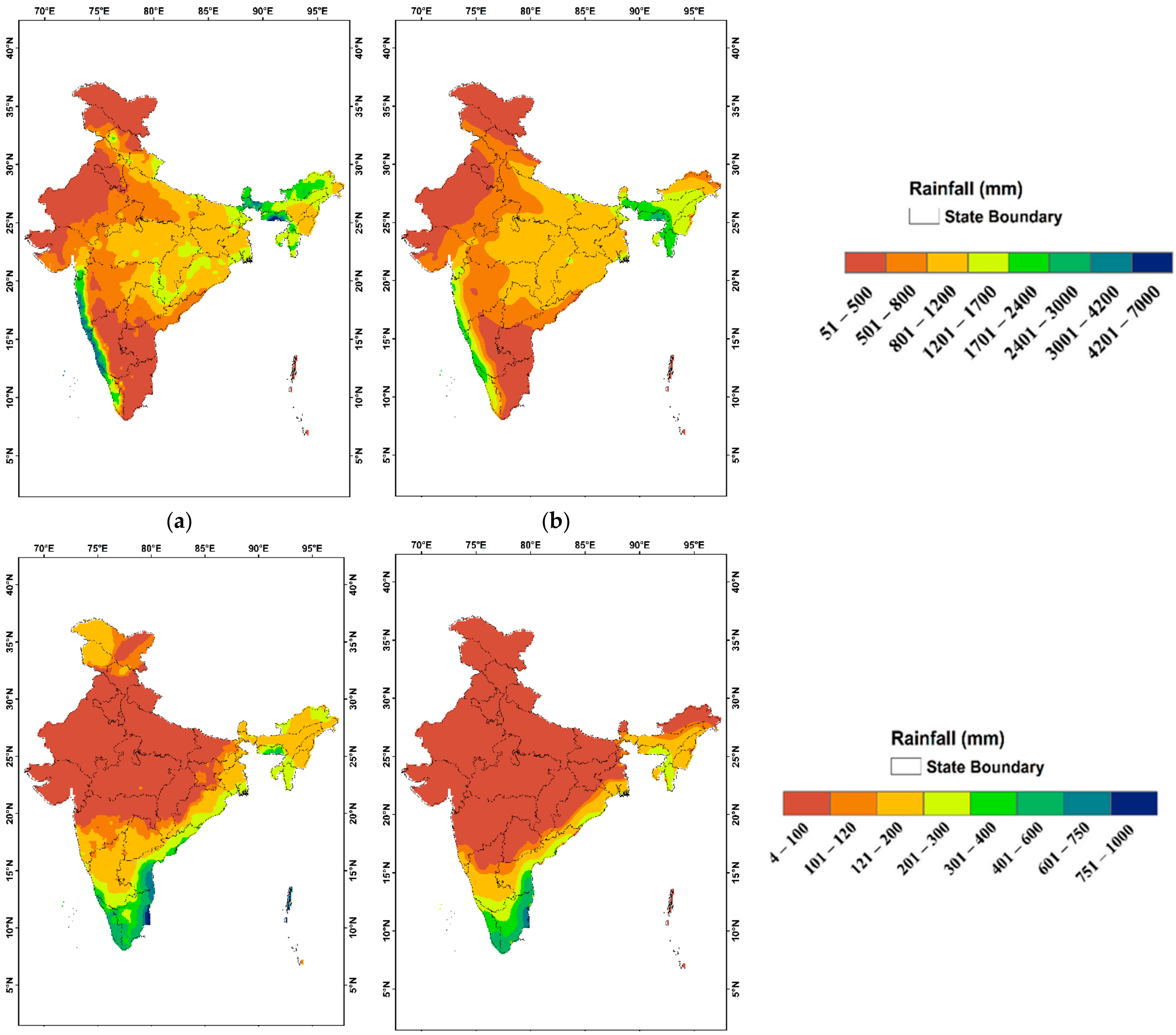
$$d - index = 1 - \left[\frac{\sum_{i=1}^{n} (P_i - O_i)^2}{\sum_{i=1}^{n} \left[P_i' + O_i'\right]^2}\right] \tag{5}$$

where n is the number of observations, P_i is the simulated yield, O_i is the observed yields at the district level and P_i' and O_i' are calculated as $P_i' = P_i - M$ and $O_i' = O_i - M$ (where M is the mean observed yields) [30].

3. Results

3.1. Evaluation of the CMIP5 Multi-Climate Model Mean (MMM)

To understand the spatial distribution of southwest (SW) and northeast (NE) monsoon rainfall, which represent the dominant climatic features, we calculated the mean seasonal rainfall totals of the two seasons for both IMD (1981–2005) and the NEX-GDDP baseline period. The west coast of India and parts of northeast India receive high rainfall amounts (1700–3000 mm). Central India receives about 1000 mm, while southern India receives rainfall ranging from 500 to 800 mm. Figure 1 clearly demonstrates that the multi-model mean (MMM) for the historical NEX-GDDP June through September (JJAS) precipitation mimicked the spatial distribution of IMD rainfall across India. However, the MMM rainfall tended to underestimate the rainfall totals in the western ghats, where average SW rainfall totals varied from 2000 mm to 4300 mm. The low-pressure system and tropical storms originating in the Bay of Bengal or the Arabian Sea and traveling toward the Indian landmass contributed most of the SW monsoon rainfall over India. Southeast India, particularly Tamil Nadu and the bordering regions of other states (Andhra Pradesh, Karnataka and Kerala), received substantial rainfall amounts during the NE season (OND). The MMM of the NEX-GDDP models reasonably simulated the seasonal rainfall totals for both the SW and NE monsoon seasons.



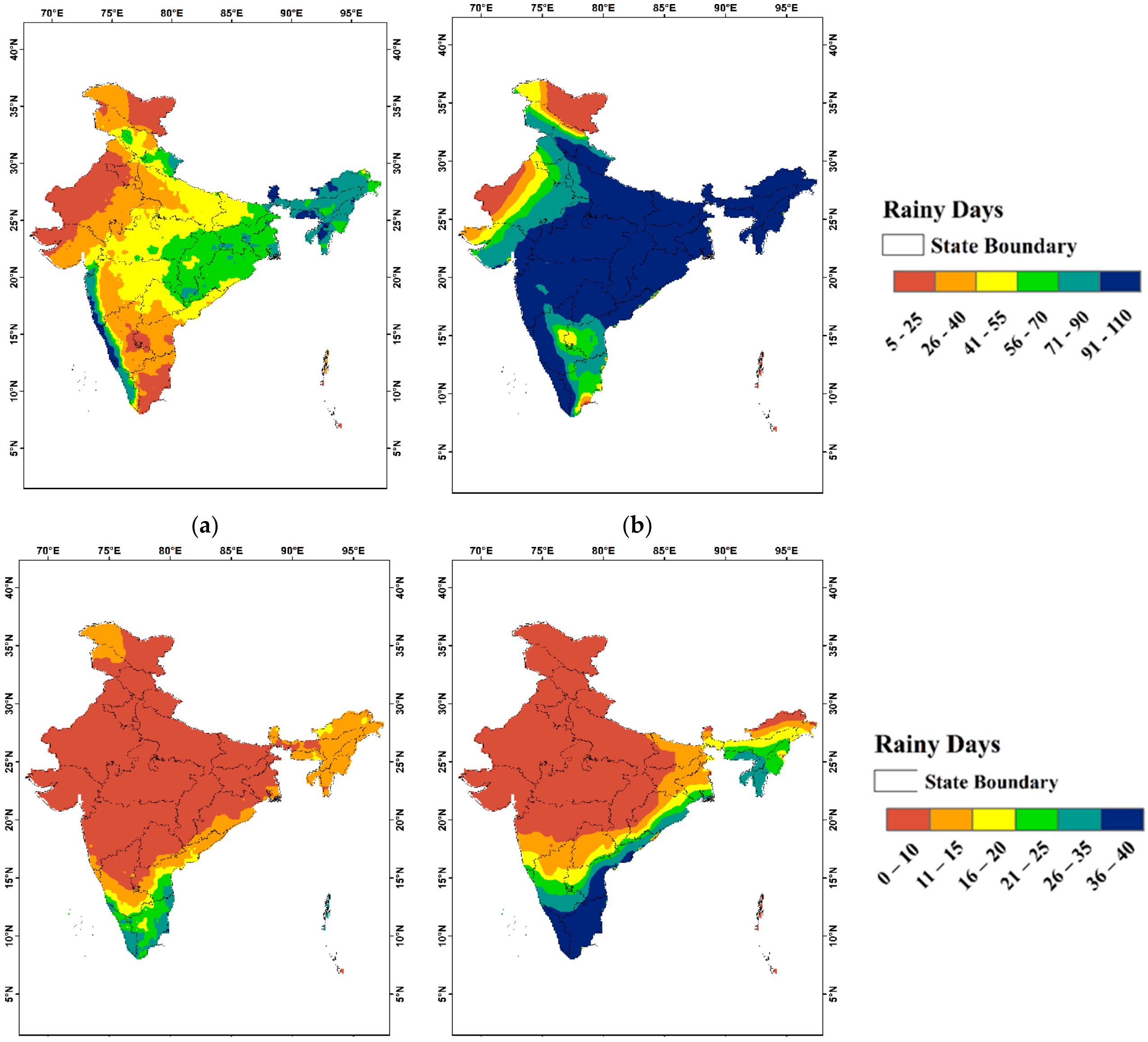
(**a**) (**b**)

(**c**) (**d**)

Figure 1. Comparison of NEX MMM and IMD spatial distribution of the mean SW (JJAS) and NW (OND) rainfall totals over India from 1981 to 2005: (**a**) IMD (JJAS); (**b**) NEX_MMM (JJAS); (**c**) IMD (OND); and (**d**) NEX_MMM (OND).

The NE monsoon rainfall is the primary source of water for crops grown under rained conditions. The interannual variability in NE monsoon rainfall over India (area averaged) is characterized by excesses and deficits in the rainfall totals, and agricultural productivity during the *post-rainy* season is significantly influenced by the NE monsoon rainfall totals. The climatology of NE monsoon rainfall as simulated by the multi-model mean (MMM) of 20 NEX-GDDP models for the baseline period of 1981–2005 is shown in Figure 1. The rainfall over the east coastal belt and the state of Tamil Nadu simulated by the MMM was in good agreement with the IMD climatology. The tropical storms and low-pressure systems over the Bay of Bengal during the OND months were associated with the rainfall received during the NE monsoon over southern India. Most of the region received substantial rainfall due to the formation of these storms. The MMM simulated the NE monsoon reasonably well and provided a realistic representation of the mean NE monsoon pattern.

To assess the ability of the MMM to reproduce SW and NE monsoon rainy days over India, we compared the model's simulated mean rainy days with the observed mean rainy days (Figure 2). The MMM simulated rainfall indicated a daily rainfall amount of 0.1 mm during dry periods. The rainfall series were first subjected to reducing the number of rainy days by using a cut-off (<1 mm) threshold for the rainfall. In both seasons (Figure 2), the MMM simulated rainy days were relatively higher. However, during the NE monsoon season, rainy days represented a similar spatial pattern to that observed in the IMD data.



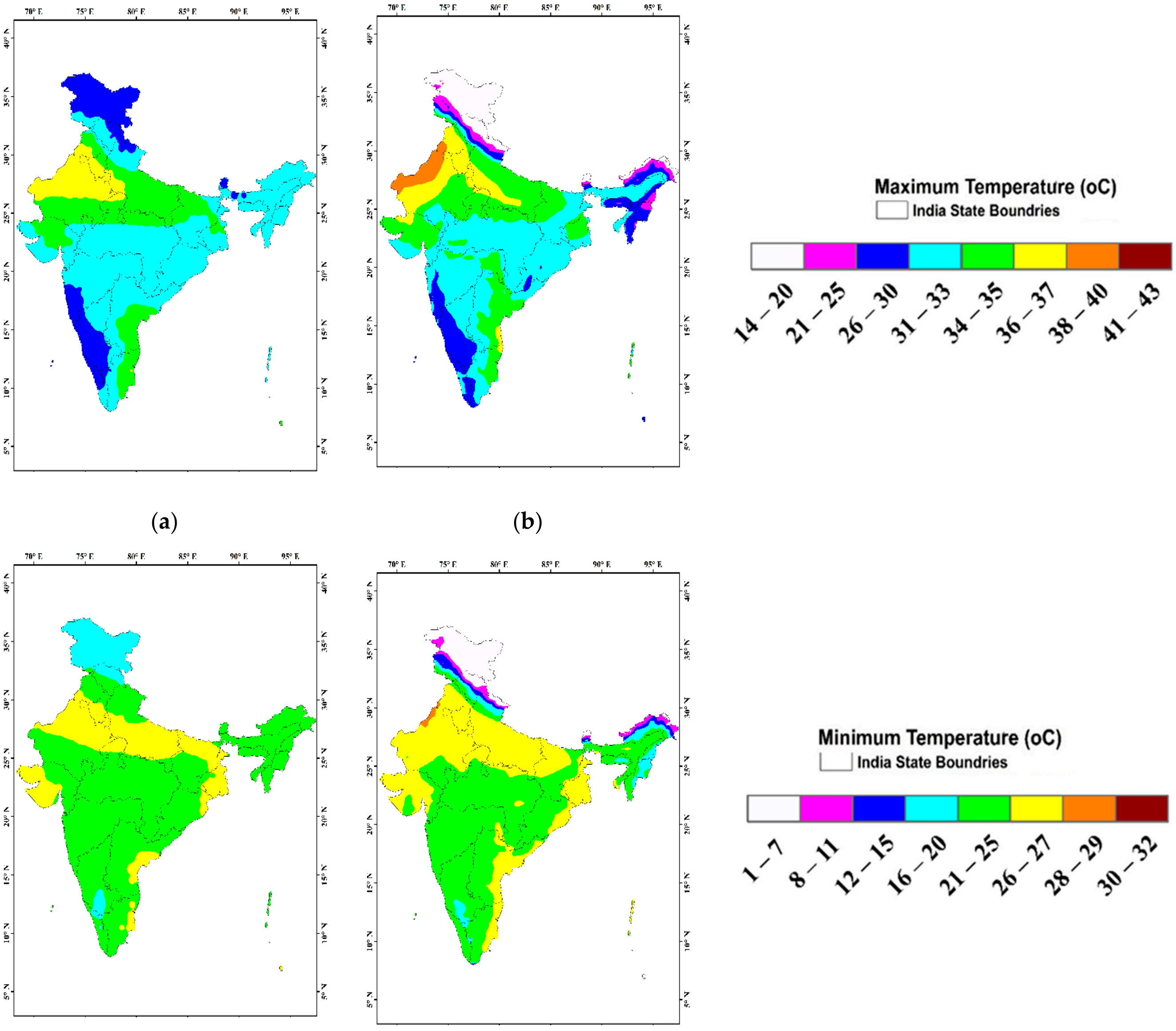
(**a**) (**b**)

(**c**) (**d**)

Figure 2. Comparison of NEX MAM and IMD spatial distributions of the mean SW (JJAS) and NW (OND) rainy days over India from 1981 to 2005: (**a**) IMD (JJAS); (**b**) NEX_MMM (JJAS); (**c**) IMD (OND); and (**d**) NEX_MMM (OND).

The spatial distributions of the climatological mean maximum and minimum temperatures over India are shown in Figures 3 and 4. The MMM of the NEX-GDDP represented good agreement with the mean spatial distributions of the maximum and minimum temperatures over India during the SW monsoon period. The MMM tended to overestimate the maximum and minimum temperatures during the JJAS period over the northwest parts of India, particularly over parts of the Gujarat and Rajasthan states. The MMM simulations during the NE monsoon periods were well-represented spatially over the Indian subcontinent. The MMM captured the spatial distributions of both the maximum and minimum temperatures in the southern and central parts of India, where *post-rainy* season sorghum is predominantly cultivated. It is important to evaluate the performance of the MMM datasets in reproducing the monthly rainfall totals (annual cycle) over India, where both SW and NE monsoons display dominant climatic features.

The annual cycle of rainfall is shown in Figure 5 using a Hovmoller diagram. The figure shows the climatological annual cycle of rainfall over the Indian subcontinent for the IMD and MMM of the NEX-GDDP data. The IMD rainfall showed a clear temporal evolution in the monthly rainfall, with the intense rainfall regions located between 20 and 25° N, and the MMM of the NEX-GDDP reproduced the observed pattern with some difference in rainfall magnitude. Overall, the MMM datasets showed good agreement against the IMD rainfall.



(**a**) (**b**)

(**c**) (**d**)

Figure 3. Comparison of NEX MAM and IMD spatial distributions of mean SW (JJAS) maximum and minimum temperatures over India from 1981 to 2005: (**a**) IMD (JJAS); (**b**) NEX_MMM; (**c**) IMD (JJAS); and (**d**) NEX_MMM (JJAS).

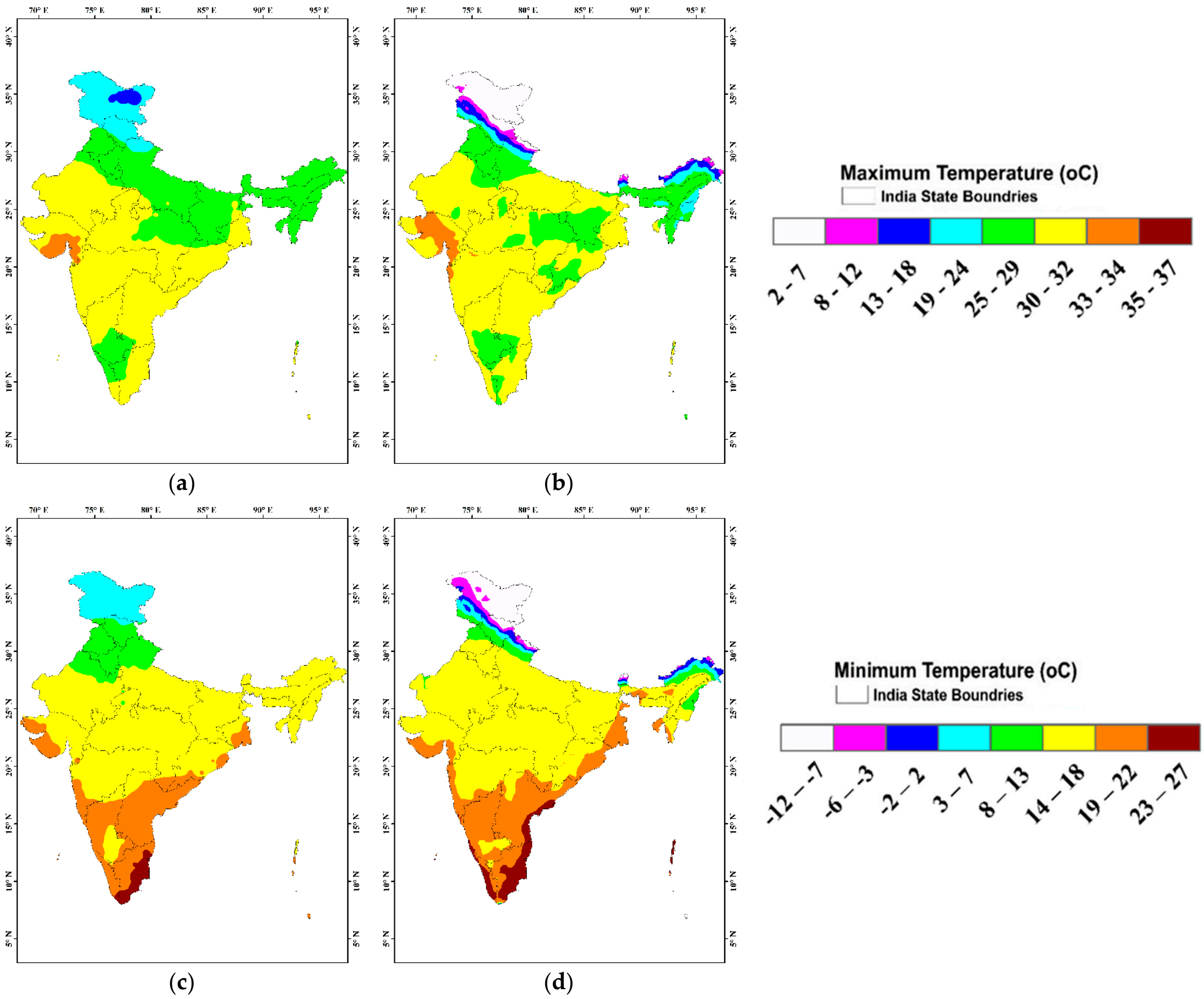


Figure 4. Comparison of NEX MAM and IMD spatial distributions of mean NE (OND) maximum and minimum temperatures over India from 1981 to 2005: (**a**) IMD (OND); (**b**) NEX_MMM (OND); (**c**) IMD (OND); and (**d**) NEX_MMM (OND).

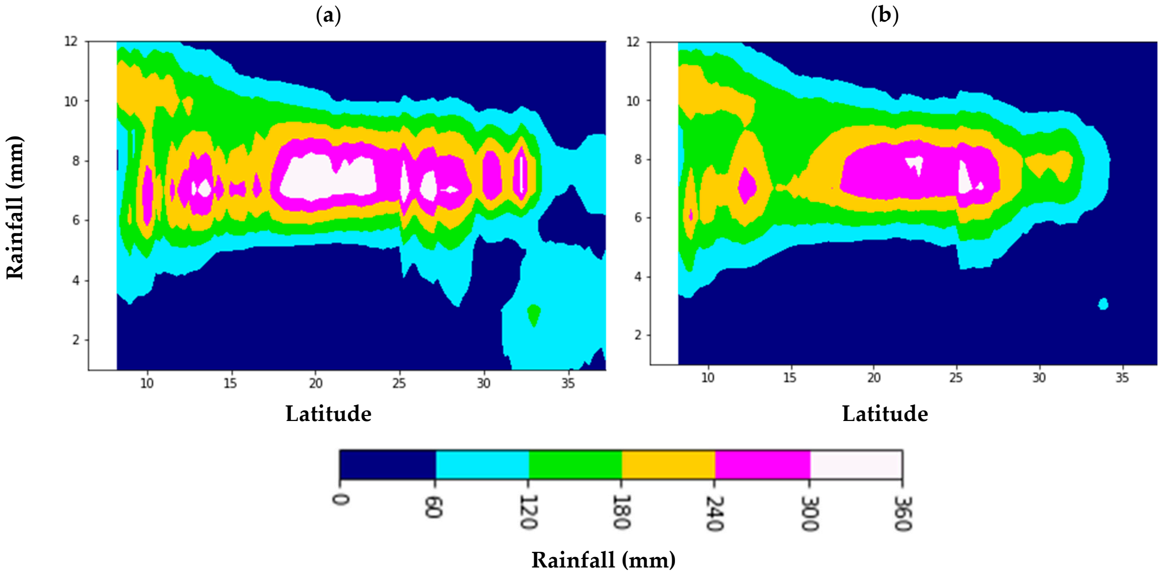


Figure 5. Hovmoller diagram displaying annual cycle of monthly rainfall climatology (mm/month) during 1981–2005 over the Indian subcontinent: (**a**) IMD rainfall and (**b**) MMM of NEX-GDDP.

3.2. Climate Change Scenarios

Global climate change is a long-term phenomenon, with a gradual increase in global temperatures due to enhanced anthropogenic greenhouse gas emissions. Such changes will lead to widespread impacts on natural systems. In this context, we discuss here the projected changes in precipitation and temperatures during the SW and NE monsoon seasons over India. For the SW monsoon period, rainfall amounts are increasing over India. However, the increase in rainfall amounts varies in magnitude both spatially and temporally. RCP 4.5 and RCP 8.5 near future projections indicate that the rainfall amounts are increasing over central India from 90 to 150 mm/season, while in the southwest regions (western ghats) and northeast parts of India, rainfall amounts are increasing from 250 to 450 mm/season. Rainfall amounts are further increasing in the far future in both RCP 4.5 and 8.5, with much of the increase noticed over the central, southwest and northeastern parts of India as displayed in Figure 6. The NE monsoon rainfall amounts are predominantly received over the southern peninsular India (SPI) states, and the MMMs of the NEX-GDDP simulations indicate that rainfall amounts are increasing during the NE monsoon period from 60 to 150 mm/season during the near future for both the RCPs (4.5 and 8.5). By the end of the 21st century, the NE monsoon rainfall amounts are projected to increase from 150 to 300 mm/season over the SPI states.

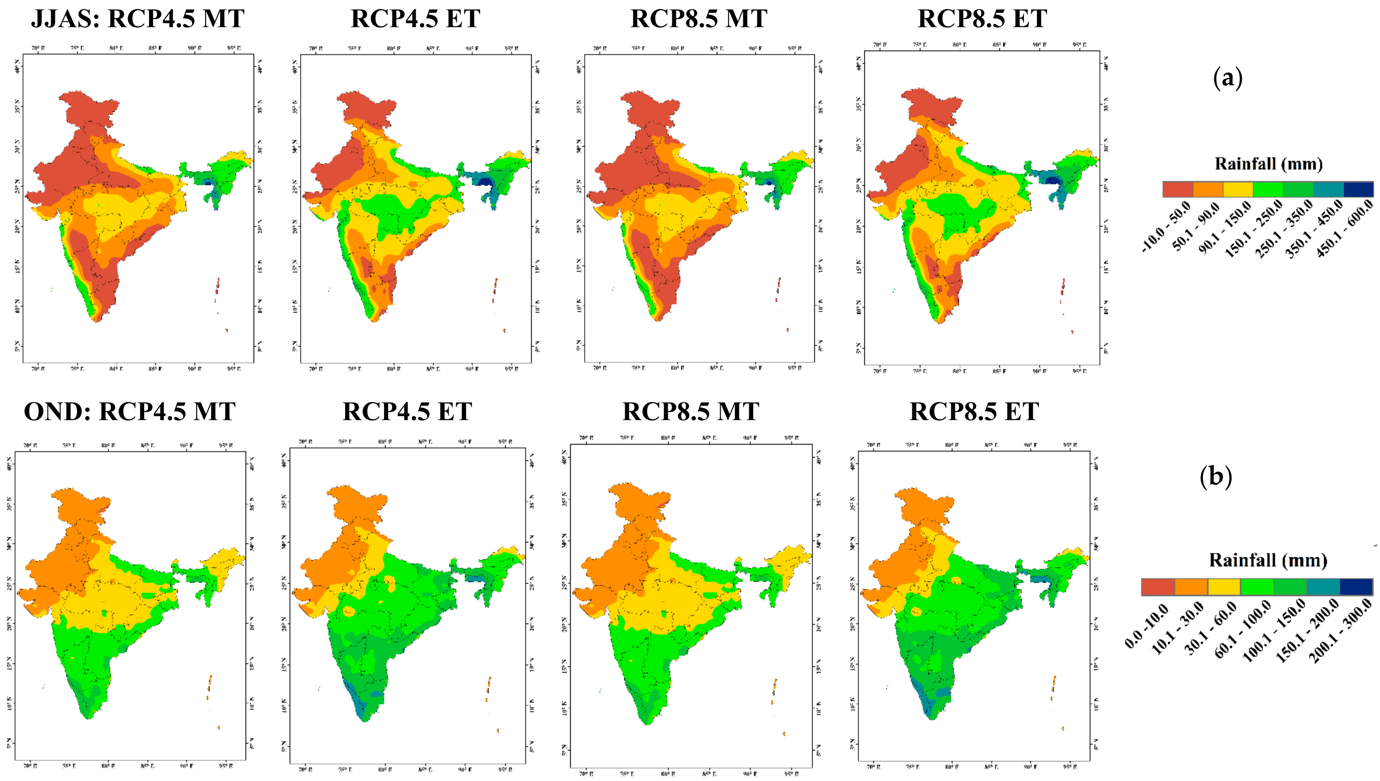
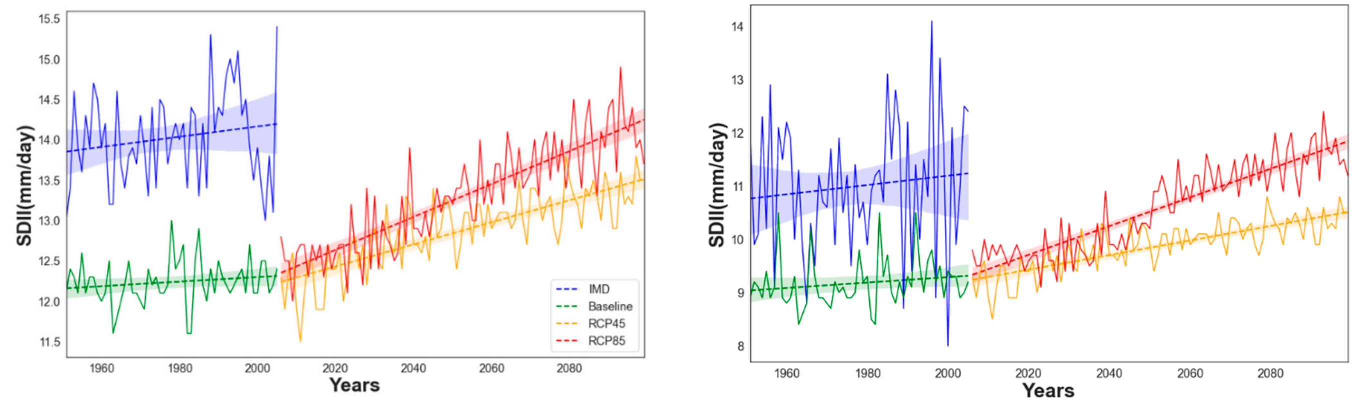


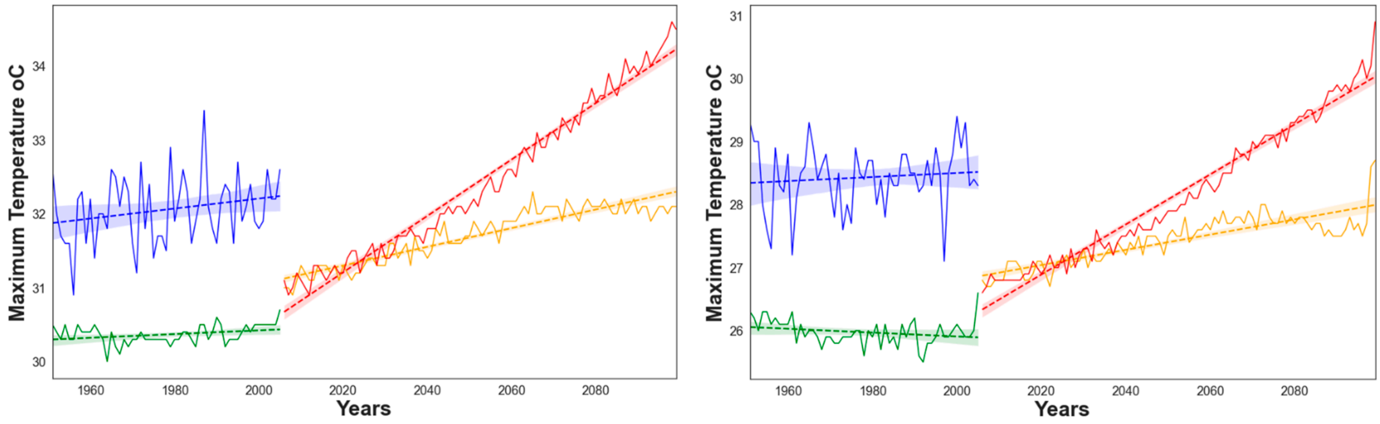
Figure 6. Projected mean changes in seasonal rainfall amounts over India during two time periods (middle and end of century): (**a**) SW and (**b**) NE monsoons.

The past and future trends in the mean maximum, minimum temperatures and precipitation are depicted in Figure 7. The IMD mean's Simple Daily Intensity Index (SDII) exhibited a marginal increasing trend during both the SW and NW monsoon seasons with high interannual variability. The MMMs of the NEX-GDDP baseline datasets presented very low inter-annual variability during the SW monsoon period. However, during the NE monsoon period, the interannual variability was relatively higher compared with the IMD SW monsoon period, and the year-to-year variability of the MMM-generated SDII during the NW season was still underestimated compared with the IMD SDII. The long-term time series of IMD rainfall (1951–2005) indicated a marginal increase in rainfall amounts during the SW and NE monsoon seasons of about 0.04 and 0.07 mm/decade, respectively. Baseline simulations of the MMM of the NEX-GDDP exhibited an increase in rainfall of about 0.03 and 0.04 mm/decade during the SW and NE monsoon periods, respectively. Projected changes in the mean SW and NE monsoon rainfall during the near future (2040–2069) and far future (2071–2099) with respect to the baseline (1976–2005) showed an unswerving increase in the mean rainfall amounts under both RCPs (4.5 and 8.5). The future projections of the MMM rainfall indicated a likely increase in the mean rainfall amounts during the SW monsoon period across India (approximately 2% under RCP 4.5 in the near future and 6% by the far future). The RCP 8.5 projections showed a consistent increase in the mean SW monsoon rainfall over India (around 6% by the near future and 10% by the far future). The projected changes during the NE monsoon period over India indicate a more pronounced increase in rainfall amounts under two emission scenarios: under RCP 4.5 rainfall amounts, which are expected to increase by around 5% during the near future and 20% by the far future, and under the RCP 8.5 emission scenario, where the rainfall amounts are likely to increase up to 8% in the near future and 23% in the far future.

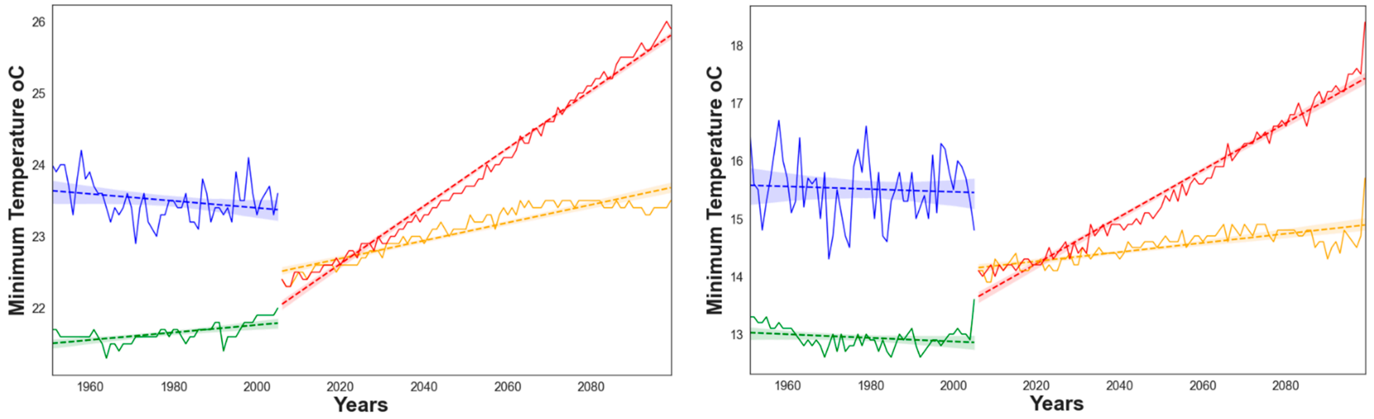
The mean maximum and minimum temperatures were gradually increasing in the future scenarios (RCP 4.5 and 8.5) across India. However, the trend was more prominent under RCP 8.5. This can be noticed through the trajectories of the future projected temperatures, which display a substantial increase under the RCP 8.5 scenario compared with RCP 4.5. The projected changes in air temperatures during the near future and far future under both RCPs relative to the NEX baseline period (1976–2005) indicate a consistent increase in the mean maximum temperature, with RCP 4.5 suggesting a maximum increase of 1.4 °C in the near future to 1.7 °C in the far future over the Indian subcontinent during the SW monsoon period. Meanwhile, during the NE monsoon period, the projected changes in the mean maximum temperature are expected to increase up to 1.6 °C by the near future and 1.8 °C by the far future. The RCP 8.5 scenario projected an increase in the mean maximum temperature during the SW monsoon period of 2.0 °C during the near future and 3.4 °C for the far future. The mean maximum temperature during the NE monsoon period is projected to increase by 2.1 °C and 3.5 °C for the near and far future, respectively. During the SW monsoon period, the mean minimum temperature for the near and far future showed an increase of 1.6 °C and 2.0 °C, respectively, under the RCP 4.5 scenario. Meanwhile, during the NE monsoon period, the increase in the mean minimum temperature was 1.7 °C and 2.0 °C for the near and far future, respectively. Under the RCP 8.5 scenario, the increase in the mean minimum temperature was more pronounced, being 2.3 °C and 3.7 °C for the SW monsoon period for the near and far future, respectively, whereas for the NE monsoon period, the increase was about 2.5 °C and 4.1 °C for the near and far future, respectively. It was noticed that during both of the periods (near and far future), the projected mean minimum temperature was higher than the mean day temperatures.



JJAS SDII **OND**



JJAS Maximum temperature **OND Maximum**



JJAS Minimum temperature **OND Minimum temperature**

Figure 7. Time series of interannual variability of simple daily intensity index of rainfall during SW (JJAS) and NW (OND) monsoon seasons over India (top), as well as the maximum temperature (middle) and minimum temperature (bottom), IMD (blue), baseline (green), RCP34 (orange) and RCP85 (red).

3.3. Evaluation of the Simulated Yields under the Historical Period

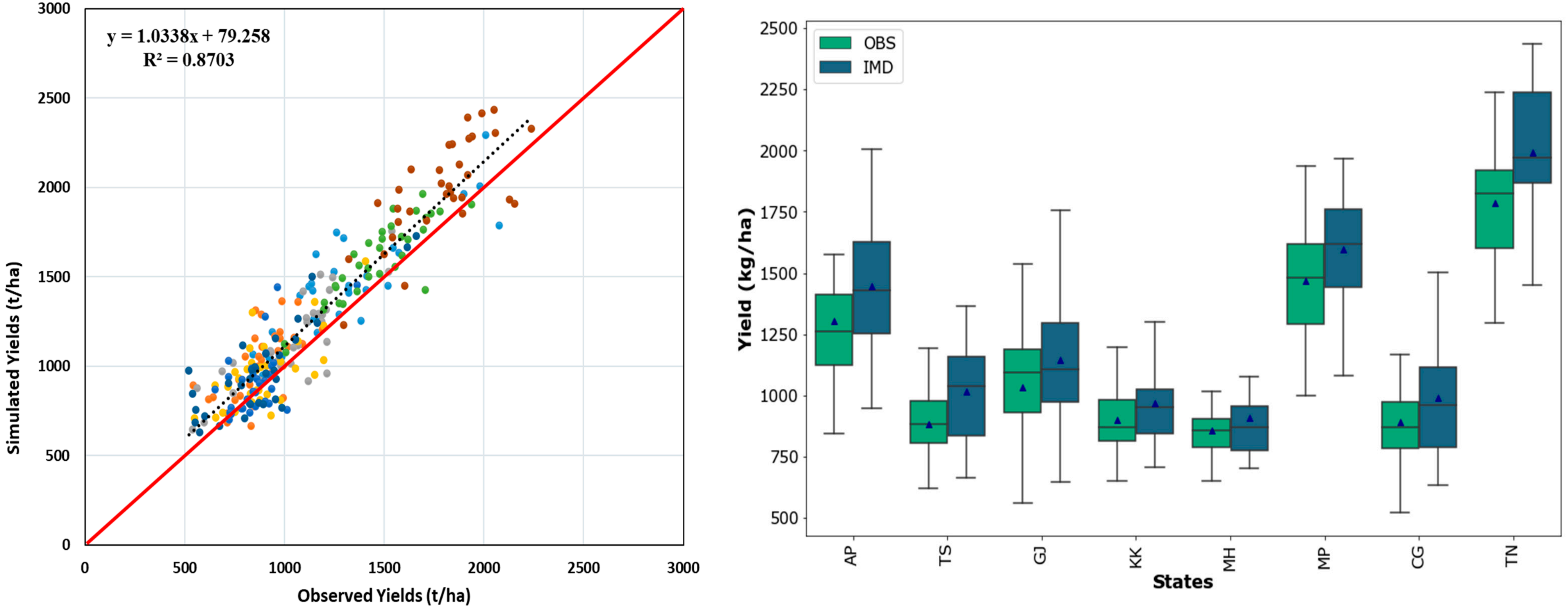
The CERES-sorghum model was configured to be run in a gridded mode at the IMD spatial resolution (approximately 25 km × 25 km). The input requirements of the CERES-sorghum model for each grid were developed spatially at a 25-km resolution. The performance of the CERES-sorghum model, which was driven by the observed climate data for the *post-rainy* season sorghum crop during 1981–2015, was evaluated. The comparison of the observed and simulated sorghum yields for the 64 districts that fell under 8 major *post-*

rainy season sorghum growing states are displayed in Figure 8a,b. The simulated sorghum grain yields showed higher yields compared with the observed yields across the sorghum growing states. The higher simulated sorghum yields perhaps echoed the fact that the crop simulation model was well-fertilized, good crops were established, and it was free from biotic stress conditions. Consequently, similar assumptions at larger geospatial scales, such as districts and states, resulted in higher sorghum yields. The relatively higher interannual variability in the simulated sorghum yields was most likely due to the coarse spatial resolution of the observed climate information. The evaluation statistics for measuring the performance of the CERES-sorghum model for different environmental conditions are presented in Table 1. The coefficient of determination (R^2) between the simulated and the observed sorghum grain yields for the 8 states was 0.87 ($n = 264$, $p < 0.001$), and the root mean square error was 270 kg ha^{-1} (Table 2). The Wilmot d index was 0.82, and the evaluation statistics indicate that the CERES-sorghum crop model was in good agreement with the observed grain yields.

Table 2. Descriptive statistics displaying the capability of CERES-sorghum model in reproducing historic yields.

	Yields (Kg/ha)		**Coefficient of Determination (R2)**	**RMSE**	**NRMSE**	**d Index**
	OBS	**SIM**				
Andhra Pradesh	1305	1447	0.73	217.09	0.17	0.86
Chhattisgarh	892	988	0.72	271.00	0.20	0.88
Gujarat	1034	1144	0.73	270.00	0.14	0.88
Karnataka	898	967	0.48	261.00	0.14	0.86
Maharashtra	858	909	0.36	255.12	0.13	0.82
Madya Pradesh	1467	1597	0.75	300.17	0.13	0.85
Telangana State	881	1017	0.40	301.44	0.23	0.67
Tamil Nadu	1786	1993	0.53	280.48	0.11	0.84

The simulated values of the sorghum grain yields for the period from 1981 to 2015 were significantly correlated with the observed yield data. (For the RMSE, the lowest was observed at Andhra Pradesh (217), and the highest was observed at Telangana and Madhya Pradesh states (301).) The d value, a measure of the model's performance in reproducing historic yields, was also high, varying from 0.67 in Telangana state to 0.88 in Chhattisgarh and Gujarat. These results illustrate that the genetic coefficients of the M 35-1 sorghum cultivar and crop management practices arrayed in the model simulations were presumed to be accurate, and the CERES-sorghum model could be applied to assess the possible potential impacts of climate change on the growth and yields of sorghum crops during the *post-rainy* season. Figure 8b compares the simulated and measured sorghum yield values for the eight states. The 1:1 line plot illustrates that the spread of simulated yields is relatively higher compared with the observed sorghum grain yield values. The statistical indices used to evaluate the performance of the CERES-sorghum model showed good agreement between the observed and modeled yields. The simulated *post-rainy* sorghum yields demonstrated good agreement with the spatial reporting (Figure 9), with the Tamil Nadu state-reported highest sorghum grain yield values ranging from 1200 to 2500 kg ha^{-1} and the CERES-sorghum model simulated yields for the historical period varying from 900 to 3200 kg ha^{-1}. Similarly, parts of Maharashtra, Karnataka, Madhya Pradesh and Gujarat reported that lower yields were spatially captured in the IMD runs.



(**a**) (**b**)

Figure 8. (**a**) Relationship between observed and modeled *post-rainy* sorghum yields during 1981–2015. (**b**) Comparison of observed and modeled sorghum grain yields for the mean and variability across the study area. The eight states used in the study were as follows: AP = Andhra Pradesh; TS = Telangana state; GJ = Gujarat; KK = Karnataka; MH = Maharashtra; MP = Madhya Pradesh; CG = Chhattisgarh; and TN = Tamil Nadu.

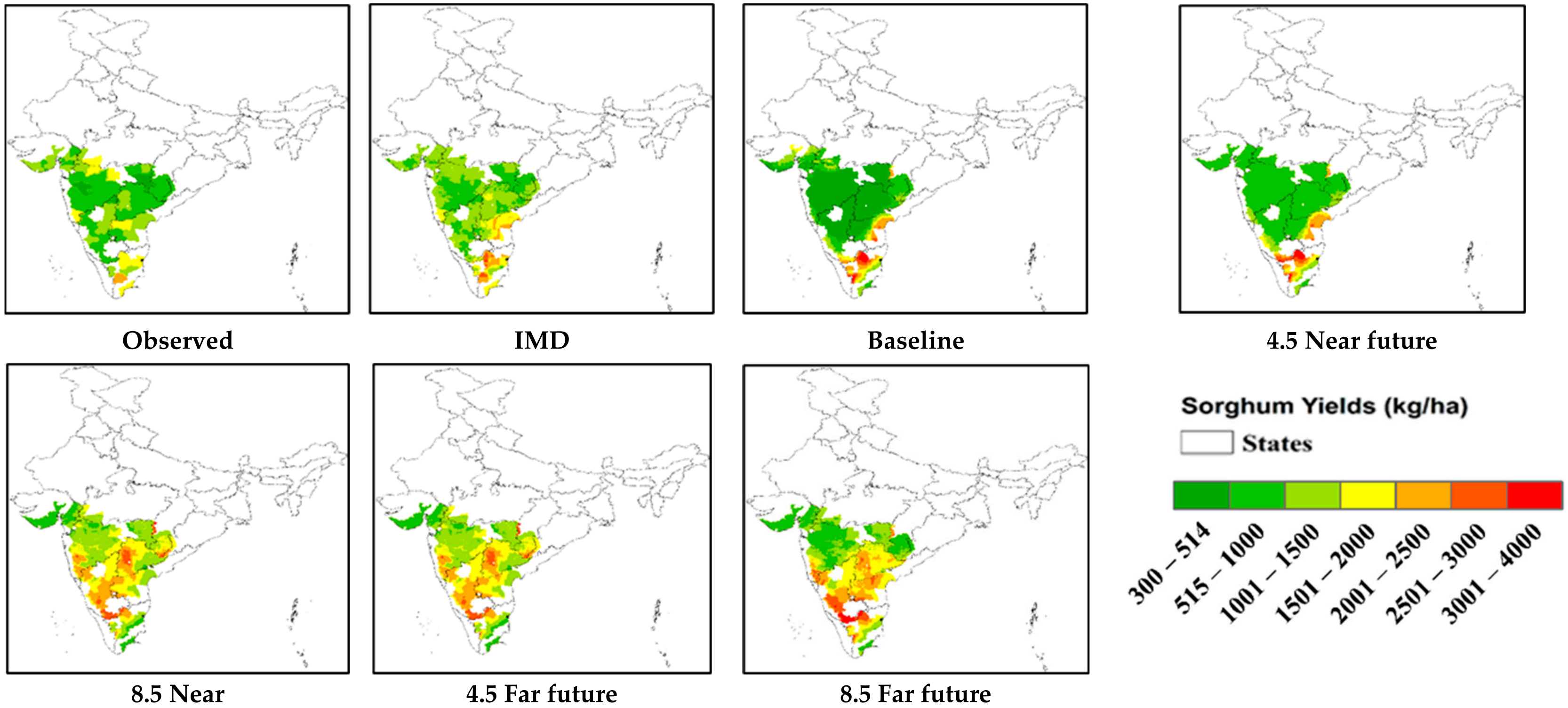


Figure 9. The maps express the spatial patterns of sorghum grain yields during the post-rainy season under each climatic condition. The images shows the reported yields, DSSAT-modeled historic yields using IMD-gridded climate data, simulated sorghum yields for the MMM baseline, RCP 4.5 near future, RCP 8.5 near future, RCP 4.5 far future and RCP 8.5 far future.

3.4. Impacts on Sorghum Yields

The CSM-CERES-sorghum simulation model attached with the seasonal analysis program in DSSAT V4.7 was used to understand the plausible impacts of climate change on sorghum growth and yields under two time periods (near future and far future) and two RCPs (4.5 and 8.5). Simulations were carried out for the baseline, 4.5 near future, 8.5 near future, 4.5 far future and 8.5 far future for each grid that fell within the sorghum growing regions of the selected states. Simulations were initiated on 1 August each year, and the soil profile at the start of the simulation was considered to be at the lower limit of soil water availability. The sowing window assumed was from 25 September to 15 October, and the simulated crop was sown on the day when the accumulated rainfall for 10 consecutive days was $\geq$25 mm.

The simulated sorghum grain yields for the MMM-baseline period across the selected states specified that the sorghum yields were lower compared with the observed and IMD-driven climate, except for Tamil Nadu. In response to climate change, the mean *post-rainy* sorghum yield values were found to be considerably increasing. Yield changes under the future climates (assuming unchanged management) for RCP 4.5 in the near future ranged from -3% (Gujarat) to 40% (Karnataka) on average. Under the climate change scenario, the spatial patterns of the sorghum yields displayed a similar pattern to the IMD-modeled yields (Figure 9). The simulated grain yields for RCP 4.5 in the near future varied from 0.8 t ha^{-1} (Maharashtra) to 2.0 t ha^{-1} (Tamil Nadu), aggregated at the state level. Under RCP 8.5 in the near future, the modeled sorghum grain yields varied from 0.82 t ha^{-1} in Maharashtra to 2.2 t ha^{-1} in Tamil Nadu, and the yields were marginally increasing (approximately 10%) under RCP 8.5 in the near future in Gujarat (6.3%), Tamil Nadu (8.8%) and Madhya Pradesh 11%). The highest increase was noticed in Telangana (59.3%), followed by Karnataka (45.6%), Andhra Pradesh (41.3%), Chhattisgarh (34.3%) and Maharashtra (25%). The projected changes in the far future under RCP 4.5 illustrate that the simulated sorghum yield values were further increasing up to 72% in Madhya Pradesh, and the lowest increase was noticed in Tamil Nadu (20.6%). The aggregated sorghum yields at the state level for RCP 4.5 in the far future varied from 1.0 t ha^{-1} in Maharashtra to 2.5 t ha^{-1} in Tamil Nadu. Similarly, under RCP 8.5 in the far future, the modeled sorghum yields showed that they were slightly higher than RCP 4.5 in the far future. The highest increase in sorghum yields was observed in Madhya Pradesh (89%), followed by Telangana (84%). A comparison of the yield variabilities across different climate scenarios and climate regimes (near future and far future) displayed high interannual variability in the modeled sorghum yields under the climate change scenarios. The modeled sorghum grain yields were relatively stable, with low CV in the reported yields followed by the IMD-simulated yield values. The baseline simulations exhibited high CV across all the states, with the highest interannual variability in the simulated yields noticed in RCP 8.5 in the far future. Both Tamil Nadu and Madhya Pradesh displayed high interannual variability in the simulated yields, followed by, in order, Chhattisgarh, Maharashtra, Karnataka, Andhra Pradesh, Telangana and Gujarat. Furthermore, the higher yields were spatially observed in the southern region of India covering Tamil Nadu, Karnataka, Andhra Pradesh and Telangana (Figure 10).

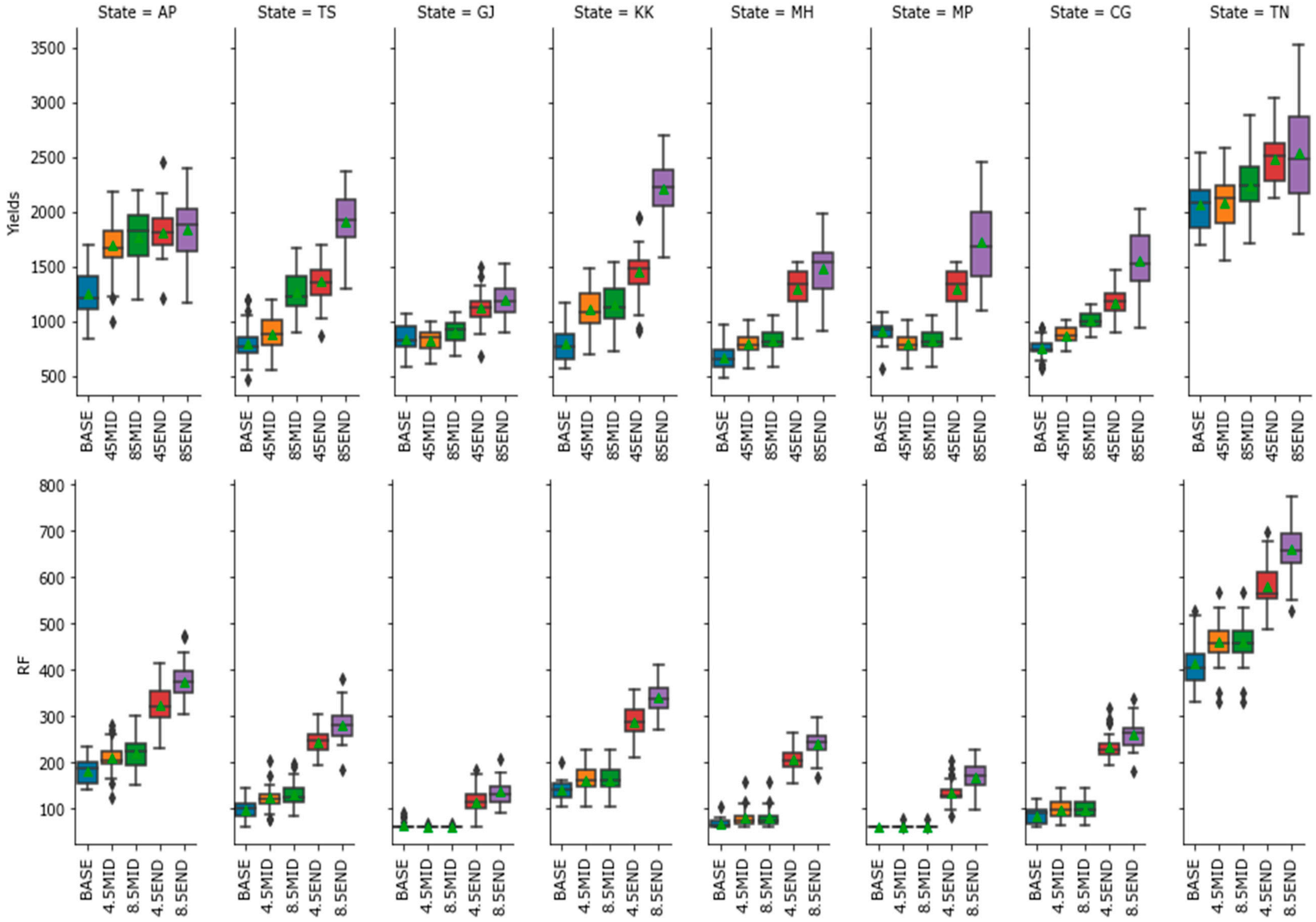


Figure 10. *Cont.*

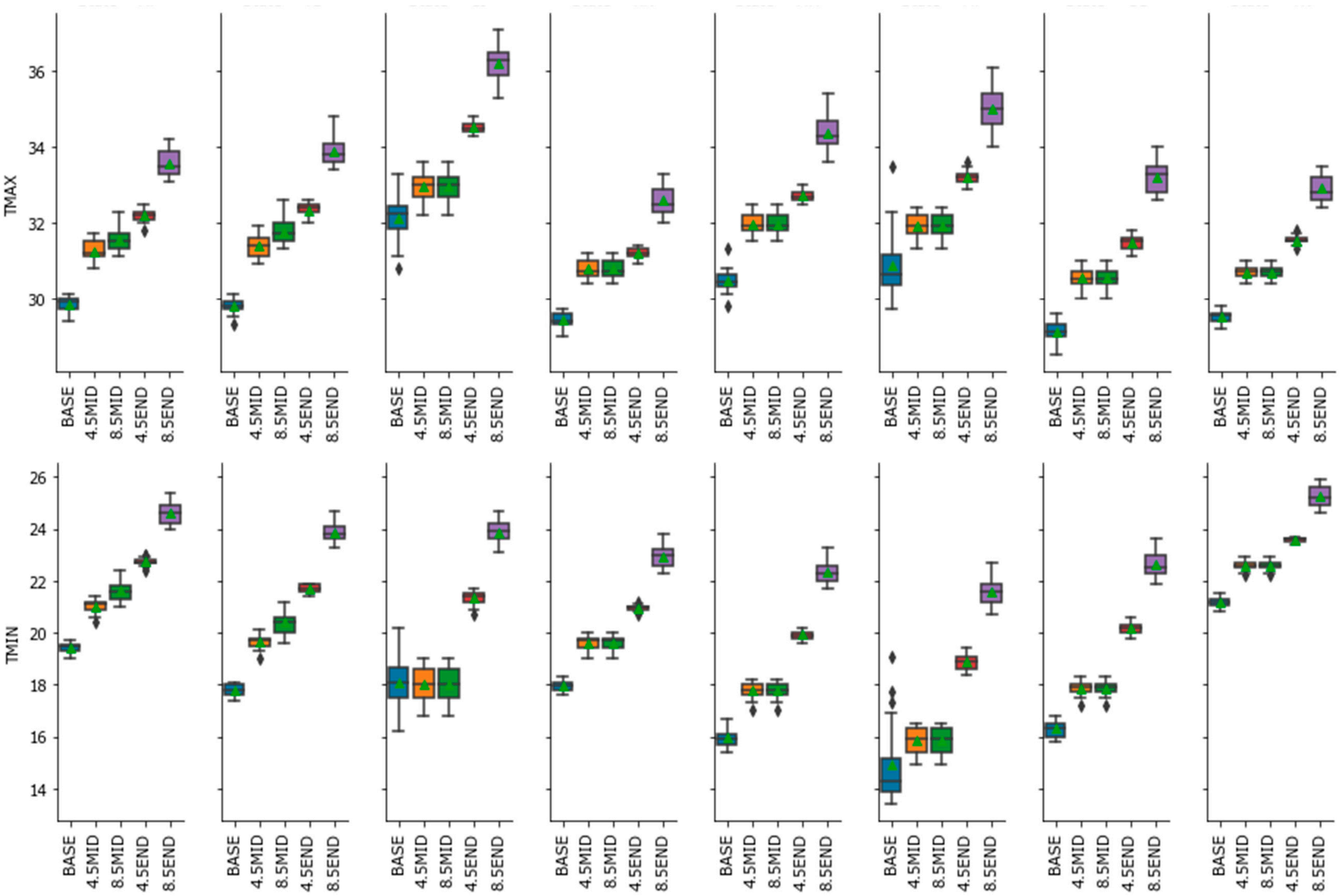


Figure 10. Projected changes in modeled post-rainy season sorghum yields, rainfall amounts, maximum temperatures and minimum temperatures across different time periods and RCPs.

4. Discussion

This paper represents the assessment of future changes in rainfall and temperatures during the northeast monsoon period over the potential sorghum growing regions of India. The statistically downscaled and bias-corrected multi-climate models' projections from the CMIP5 models were used to understand the possible changes in the climate variables and their impacts on *post-rainy* season sorghum growth and yields. The MMM of the NEX-GDDP baseline illustrated the ability of these models to reproduce the historical climate characteristics of the mean and the distribution of rainfall and temperatures. The spatial distribution of the annual, seasonal mean surface temperatures and precipitation distributions agrees well against the IMD gridded data [31,32]. The performance of the MMM-simulated rainfall tended to underestimate the rainfall totals over a complex topography, with the performance of the statistical downscaling largely depending on the historical climate records used. The NEX-GDDP datasets were compared with the Global Meteorological Forcing Dataset (GMFD) for downscaling the near-surface meteorological variables [26]. The fidelity of the MMM simulations over Indian land captured the annual cycle of surface air temperatures, even though there was a cold bias throughout the year. The uncertainties in the NEX-GDDP datasets were due to several factors: (1) the ground-based data (CRU data) could not accurately represent the details of a complex orography due to limited or uneven distribution of the rain gauges; (2) the bias correction was primarily focused on rainy day statistics; and (3) the satellite-estimated datasets such as TRMM (used in bias correction) also contained errors at both the temporal and special scales [33]. Nevertheless, further bias correction using locally relevant datasets (e.g., IMD data) could minimize uncertainties in the current and future ESM and GCM projections.

Projected changes in the mean monsoon rainfall amounts in the near future (2020–2049) and far future (2070–2099) relative to the baseline (1976–2005) indicated an increase of 250–450 mm/season in the SW period and 150–300 mm/season in the NE period. There was a clear consensus among the CMIP5 models about the future projected changes in rainfall amounts over India during the SW and NE monsoon periods. The increase in the rainfall amounts could be attributed to increased intense precipitation events and exaggerated moisture conveyance from the Bay of Bengal into the SPI region, owing to increased warming by the end of the 21st century [34–36]. The MMM of the NEX-GDDP showed around 3.4 degrees of temperature difference by the end of the 21st century during the SW monsoon period and a 3.5-degree increase projected during the NE monsoon period under RCP 8.5.

The CERES-sorghum model was used to simulate the sorghum crops in the Southern Peninsular India (SPI) region using the MMM of the NEX-GDDP climate projections considering two RCPs and periods. The sorghum model performed well in reproducing historic sorghum yields during the *post-rainy* season and matched the reported yields, with R^2 values for the eight states at 0.87 ($n = 264$, $p < 0.001$). The simulated sorghum yields for the current climate indicate that despite slight overestimation of the grain yield values across the study area, the crop model was able to capture the spatial distribution of the sorghum yields, with a close match for the interannual variability in the reported sorghum yield values. In response to climate change, state-level aggregated mean sorghum yields demonstrated an increase in yields across the study area. The increase in yields followed the south-north dipole of projected rainfall changes. An increase in *post-rainy* season sorghum yields could be attributed to several factors, such as an increase in monsoon and *post-rainy* season rainfall totals, elevated atmospheric CO_2 or an increase in surface temperatures. An increase in rainfall amounts during the *post-rainy* season is thought to be beneficial for sorghum plant growth, with more frequent rainy days [37,38]. The projected climate change scenarios indicate an increase in rainfall amounts as well as an increase in rainy days during the *post-rainy* season. Therefore, the increased rainfall frequency would effectively reduce the intervals between soil moisture stress [39].

The elevated concentrations of CO_2 in response differ by crop type, as there are two crop photosynthesis types: C3 (rice and wheat) and C4 (maize and sorghum). Generally, the higher atmospheric CO_2 shows much more response to C3 plants than C4 plants. Elevated CO_2 has generally been established to increase crop growth, and in the CERES-sorghum model, elevated concentrations of CO_2 alter crop growth and yields through radiation use efficiency (RUE) and plant transpiration. Under elevated concentrations of CO_2, the CERES-sorghum model applies a multiplier on the RUE, which increases biomass production [40,41]. The response of the CO_2 has interactions with nitrogen fertilizer, and the response is expected to be small for low nitrogen fertilizer amounts. The lesser response to low nitrogen fertilizer amounts is well documented in experiments on rice crops [42,43]. In this study, the nitrogen fertilizer was based on the recommended practices in the region and ranged from 60 to 80 kg ha^{-1}. Higher CO_2 concentrations in the atmosphere are expected to increase biomass production and yields through a large increase in the utilization of available nitrogen [44,45].

The growing evidence suggests that in the tropics and subtropics, crop yields decreased due to warming associated with future climate change. The direct effects of higher surface air temperatures on sorghum crop growth and yields were negative both in controlled environmental studies [46–49] and custom-designed field-based experiments [50,51], which have documented that those high temperatures lead to heat stress in sorghum crops, and during the critical flowering and grain-filling stages, heat stress substantially decreases crop yields. Recent studies have identified a temperature threshold of 33 °C, beyond which sorghum yields start declining [52]. The projected increasing temperatures increase the rate of crop development as well as transpiration. If rainfall amounts are stable or decreasing, then this could lead to water stress and substantially reduce sorghum yields. However, if the rainfall amounts are projected to increase along with the temperatures, then it may be possible to preserve or increase sorghum grain yields. The authors of [50] demonstrated that sorghum crops exposed to short episodes of high temperatures (40–30 °C) during reproductive development could have a significant effect on sorghum yields. In the current study, the future mean maximum temperatures are expected to increase up to 2.1 °C and 3.5 °C during the *post-rainy* season under the RCP 8.5 scenario. The increase in surface air temperatures under the RCP 8.5 scenarios during the *post-rainy* season was still below the optimum temperature threshold, and the mean maximum temperature across the study area varied from 30 °C to 32 °C. Increasing temperatures under climate change scenarios can affect sorghum yields through their influence on water stress [53]. In the present study, it was observed that the rainfall totals during the post-rainy season were increasing under two time periods and RCPs. The increasing rainfall amounts, along with the elevated CO_2 levels in the atmosphere (499 ppm near century, 532 ppm far future under RCP 4.5 and 571 ppm near future and 801 ppm by the end of the 21st century under RCP 8.5) considered in the simulations, increased the sorghum crop yields during the *post-rainy* season.

5. Conclusions

The MMM is often defined as an "ensemble of opportunity" which solves the problem of uncertainties up to some extent that is embodied in the spectrum of future climate change projections. For decision makers, it is of the utmost importance to understand if the level of uncertainty in the future projections remains unchanged or will be considerably reduced in the coming decades. The multi-model approach used in this study was used to demonstrate that combining multiple climate models' projections increases the skill in accurately representing the historical climate and predicting the plausible changes in future climates. The impact assessment community would benefit from the statistically downscaled GCMs projections and intelligently combining multi-model ensembles that could reduce model uncertainty. Further simulating sorghum yields using these multi-model ensemble climate data suggests that the climate change in the region could be an opportunity for the smallholder to adapt and further improve productivity with proper crop management. Global climate change, particularly increases in rainfall amounts, elevated CO_2 levels and future warming (within the optimum range for crop growth and development), allowed sorghum crops during the post-rainy season to sustain increased production. Sorghum crops are relatively more resilient to harsher environmental conditions, and one reason for this they are often sown under warmer and dry conditions. Our findings suggest that sorghum may indeed be a good crop under climate change in the post-rainy season that is grown under residual soil moisture.

Author Contributions: Conceptualization, K.C. and S.G.; methodology, S.G., K.R.K. and D.M.K.; software, S.G. and K.C.; validation, K.C., K.C.D., K.K.D., R.K.B.D. and S.K.T.; formal analysis, S.G.; investigation, K.C. and S.G.; resources, R.K.B.D. and S.K.T.; data curation, S.G. and D.M.K.; writing—original draft preparation, K.C. and S.G.; writing—review and editing, K.C., S.G., D.M.K., R.K.B.D. and S.K.T.; visualization, S.G.; supervision, S.G.; project administration, S.G.; funding acquisition, S.G. All authors have read and agreed to the published version of the manuscript.

Funding: Authors S Gummadi acknowledges CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS), which is carried out with support from the CGIAR Trust Fund.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Harlan, J.R.; de Wet, J.M.J. Simplified Classification of Cultivated Sorghum A. *Crop. Sci.* **1972**, *12*, 172–176. [CrossRef]
2. Mundia, C.W.; Secchi, S.; Akamani, K.; Wang, G. A Regional Comparison of Factors Affecting Global Sorghum Production: The Case of North America, Asia and Africa's Sahel. *Sustainability* **2019**, *11*, 2135. [CrossRef]
3. Charyulu, K.D.; Cynthia, B.; Bvs, R.; Ashok, K.A.; Moses, S.D. *Development and Diffusion of Sorghum Improved Cultivars in India: Impact on Growth and Stability in Yield*; Working paper series no. 50; International Crops Research Institute for the Semi-Arid Tropics: Patancheru, India, 2014.
4. GOI. Available online: www.agricoop.nic.in (accessed on 7 June 2021).
5. Kumar, A.A.; Reddy, B.V.S.; Ramaiah, B.; Sahrawat, K.L.; Pfeiffer, W.H. Genetic Variability and Character Association for Grain Iron and Zinc Contents in Sorghum Germplasm Accessions and Commercial Cultivars; Hyderabad. *Eur. J. Plant Sci. Biotechnol.* **2012**, *6*, 1–5.
6. Ashok Kumar, A.; Reddy, B.V.S.; Ramaiah, B.; Sahrawat, K.L.; Pfeiffer, W.H. Gene Effects and Heterosis for Grain Iron and Zinc Concentration in Sorghum [*Sorghum Bicolor* (L.) Moench]. *Field Crops Res.* **2013**, *146*, 86–95. [CrossRef]
7. Pray, C.E.; Nagarajan, L. "Improving Crops for arid Lands": Pearl Millet and Sorghum in India. In *Millions Fed: Proven Successes in Agricultural Development*; Spielman, D.J., Pandya-Lorch, R., Eds.; International Food Policy Research Institute: Washington, DC, USA, 2009; Volume 12, pp. 83–88.
8. Gali, B.; Rao, P.P. Regional Analysis of Household Consumption of Sorghum in Major Sorghum-Producing and Sorghum-Consuming States in India. *Food Secur.* **2012**, *4*, 209–217. [CrossRef]
9. Rao, P.P.; Basavaraj, G.; Ahmad, W.; Bhagavatula, S. An Analysis of Availability and Utilization of Sorghum Grain in India. *J. SAT Agri. Res.* **2010**, *8*, 1–8.
10. Talwar, H.S.; Elangovan, M.; Patil, J.V. (Eds.) Sorghum-A Potential Crop to Adapt to Future Climate Change Scenario. In *Managing Intellectual Property under PVP and PGR*; Directorate of Sorghum Research (DSR): Hyderabad, India, 2013; pp. 254–256.
11. Solomon, S.; Qin, D.; Manning, M.; Chen, Z.; Marquis, M.; Averyt, K.B.; Tignor, M.; Miller, H.L. (Eds.) *Climate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*; Cambridge University Press: Cambridge, UK, 2007; ISBN 9780521880091.
12. Cline, W.R. (Ed.) *Global Warming and Agriculture: Impact Estimates by Country*; Peterson Institute for International Economics: Washington, DC, USA, 2007.
13. Srivastava, A.; Naresh Kumar, S.; Aggarwal, P.K. Assessment on Vulnerability of Sorghum to Climate Change in India. *Agric. Ecosyst. Environ.* **2010**, *138*, 160–169. [CrossRef]
14. Hengl, T.; de Jesus, J.M.; MacMillan, R.A.; Batjes, N.H.; Heuvelink, G.B.M.; Ribeiro, E.; Samuel-Rosa, A.; Kempen, B.; Leenaars, J.G.B.; Walsh, M.G.; et al. SoilGrids1km—Global Soil Information Based on Automated Mapping. *PLoS ONE* **2014**, *9*, e105992. [CrossRef] [PubMed]
15. Pagire, G.S.; Gadakh, S.R.; Shinde, M.S.; Dalvi, U.S.; Awari, V.R.; Gadakh, S.S. Seasonal Variation in Sowing and Its Effect on Ethanol and Biomass Yield of Sweet Sorghum. *Energy Sources Part A Recovery Util. Environ. Eff.* **2021**, *43*, 716–726. [CrossRef]
16. Trivedi, T.P. (Ed.) *Handbook of Agriculture*; Directorate of Information and Publications of Agriculture, Indian Council of Agricultural Research: New Delhi, India, 2008.
17. Rana, B.S.; Rao, M.H.; Indira, S.; Singh, B.U. *Technology for Increasing Sorghum Production and Value Addition*; Director and Project Coordinator (AICSIP) National Research Centre for Sorghum: Solapur, India, 1999.

18. Hosmani, M.M.; Chittapur, B.M. *Sorghum Production Technology*; University of Agricultural Sciences: Dharwad, India, 1997.
19. Singh, P.; Nedumaran, S.; Traore, P.C.S.; Boote, K.J.; Rattunde, H.F.W.; Prasad, P.V.V.; Singh, N.P.; Srinivas, K.; Bantilan, M.C.S. Quantifying Potential Benefits of Drought and Heat Tolerance in Rainy Season Sorghum for Adapting to Climate Change. *Agric. For. Meteorol.* **2014**, *185*, 37–48. [CrossRef]
20. Sandeep, V.M.; Rao, U.M.v.; Bapuji Rao, B.; Bharathi, G.; Pramod, V.P.; Santhibhushan Chowdary, P.; Patel, N.R.; Mukesh, P.; Vijaya Kumar, P. Sandeep 2018. *J. Agrometeorol.* **2018**, *20*, 89–96.
21. Rajeevan, M.; Unnikrishnan, C.K.; Preethi, B. Evaluation of the ENSEMBLES Multi-Model Seasonal Forecasts of Indian Summer Monsoon Variability. *Clim. Dyn.* **2012**, *38*, 2257–2274. [CrossRef]
22. Lorenz, C.; Portele, T.C.; Laux, P.; Kunstmann, H. Bias-corrected and spatially disaggregated seasonal forecasts: A long-term reference forecast product for the water sector in semi-arid regions. *Earth Syst. Sci. Data* **2021**, *13*, 2701–2722. [CrossRef]
23. Giorgi, F. Simulation of Regional Climate Using a Limited Area Model Nested in a General Circulation Model. *Am. Meteorol. Soc.* **1990**, *3*, 941–963. [CrossRef]
24. Wood, A.W.; Leung, L.R.; Sridhar, V.; Lettenmaier, D.P. Hydrologic implications of dynamical and statistical approaches to downscaling climate model outputs. *Clim. Chang.* **2004**, *62*, 189–216. [CrossRef]
25. Thrasher, B.; Maurer, E.P.; McKellar, C.; Duffy, P.B. Technical Note: Bias Correcting Climate Model Simulated Daily Temperature Extremes with Quantile Mapping. *Hydrol. Earth Syst. Sci.* **2012**, *16*, 3309–3314. [CrossRef]
26. Bao, Y.; Wen, X. Projection of China's near- and Long-Term Climate in a New High-Resolution Daily Downscaled Dataset NEX-GDDP. *J. Meteorol. Res.* **2017**, *31*, 236–249. [CrossRef]
27. White, J.W.; Hoogenboom, G.; Kimball, B.A.; Wall, G.W. Methodologies for Simulating Impacts of Climate Change on Crop Production. *Field Crop. Res.* **2011**, *124*, 357–368. [CrossRef]
28. Jones, J.W.; Hoogenboom, G.; Porter, C.H.; Boote, K.J.; Batchelor, W.D.; Hunt, L.A.; Wilkens, P.W.; Singh, U.; Gijsman, A.J.; Ritchie, J.T. The DSSAT Cropping System Model. *Eur. J. Agron.* **2003**, *18*, 235–265. [CrossRef]
29. Ritchie, I.T. Soil Water Balance and Plant Water Stress. In *Understanding Options for Agricultural Production*; Tsuji, G.Y., Hoogenboom, G., Thornton, P.K., Eds.; Springer Science and Business Media: Berlin/Heidelberg, Germany, 1998.
30. Willmott, C.J.; Ackleson, S.G.; Davis, R.E.; Feddema, J.J.; Klink, K.M.; Legates, D.R.; O'Donnell, J.; Rowe, C.M. Statistics for the Evaluation and Comparison of Models. *J. Geophys. Res.* **1985**, *90*, 8995. [CrossRef]
31. Garnier, P.; Nell, C.; Mary, B.; Lafolie, F. Evaluation of a Nitrogen Transport and Transformation Model in a Bare Soil. *Eur. J. Soil Sci.* **2001**, *52*, 253–268. [CrossRef]
32. Rao, K.K.; Kulkarni, A.; Patwardhan, S.; Kumar, B.V.; Kumar, T.V.L. Future Changes in Precipitation Extremes during Northeast Monsoon over South Peninsular India. *Theor. Appl. Climatol.* **2020**, *142*, 205–217. [CrossRef]
33. Raghavan, S.v.; Hur, J.; Liong, S.Y. Evaluations of NASA NEX-GDDP Data over Southeast Asia: Present and Future Climates. *Clim. Chang.* **2018**, *148*, 503–518. [CrossRef]
34. Sheffield, J.; Goteti, G.; Wood, E.F. Development of a 50-Year High-Resolution Global Dataset of Meteorological Forcings for Land Surface Modeling. *J. Clim.* **2006**, *19*, 3088–3111. [CrossRef]
35. Kitoh, A.; Endo, H.; Krishna Kumar, K.; Cavalcanti, I.F.A.; Goswami, P.; Zhou, T. Monsoons in a Changing World: A Regional Perspective in a Global Context. *J. Geophys. Res. Atmos.* **2013**, *118*, 3053–3065. [CrossRef]
36. Seth, A.; Rauscher, S.A.; Biasutti, M.; Giannini, A.; Camargo, S.J.; Rojas, M. CMIP5 Projected Changes in the Annual Cycle of Precipitation in Monsoon Regions. *J. Clim.* **2013**, *26*, 7328–7351. [CrossRef]
37. Good, S.P.; Caylor, K.K. Climatological Determinants of Woody Cover in Africa. *Proc. Natl. Acad. Sci. USA* **2011**, *108*, 4902–4907. [CrossRef] [PubMed]
38. Guan, K.; Sultan, B.; Biasutti, M.; Baron, C.; Lobell, D.B. What Aspects of Future Rainfall Changes Matter for Crop Yields in West Africa? *Geophys. Res. Lett.* **2015**, *42*, 8001–8010. [CrossRef]
39. Porporato, A.; Daly, E.; Rodriguez-Iturbe, I. Soil water balance and ecosystem response to climate change. *Am. Nat.* **2004**, *164*, 625–632. [CrossRef] [PubMed]
40. Hatfield, J.L.; Boote, K.J.; Kimball, B.A.; Ziska, L.H.; Izaurralde, R.C.; Ort, D.; Thomson, A.M.; Wolfe, D. Climate Impacts on Agriculture: Implications for Crop Production. *Agron. J.* **2011**, *103*, 351–370. [CrossRef]
41. Boote, K.J.; Prasad, V.; Allen, L.H.; Singh, P.; Jones, J.W. Modeling Sensitivity of Grain Yield to Elevated Temperature in the DSSAT Crop Models for Peanut, Soybean, Dry Bean, Chickpea, Sorghum, and Millet. *Eur. J. Agron.* **2018**, *100*, 99–109. [CrossRef]
42. Ziskaac, L.H.; Weerakoona, W.; Pamplonab, R. The Influence of Nitrogen on the Elevated CO_2 Response in Field-Grown Rice. *Aust. J. Plant Physiol.* **1996**, *23*, 45–52.
43. Poorter, H.; Navas, M.-L. Tansley Review Plant Growth and Competition at Elevated CO_2: On Winners, Losers and Functional Groups. *New Phytol.* **2002**, *157*, 175–198. [CrossRef] [PubMed]
44. Torbert, H.A.; Prior, S.A.; Rogers, H.H.; Runion, G.B. Elevated Atmospheric CO_2 Effects on N Fertilization in Grain Sorghum and Soybean. *Field Crop. Res.* **2004**, *88*, 57–67. [CrossRef]
45. Grant, B.; Smith, W.N.; Desjardins, R.; Lemke, R.; Li, C. Estimated N_2O and CO_2 emissions as influenced by agricultural practices in Canada. *Clim. Chang.* **2004**, *65*, 315–332. [CrossRef]
46. Prasad, P.V.V.; Boote, K.J.; Allen, L.H. Adverse High Temperature Effects on Pollen Viability, Seed-Set, Seed Yield and Harvest Index of Grain-Sorghum [*Sorghum Bicolor* (L.) Moench] Are More Severe at Elevated Carbon Dioxide Due to Higher Tissue Temperatures. *Agric. For. Meteorol.* **2006**, *139*, 237–251. [CrossRef]

47. Prasad, P.V.V.; Pisipati, S.R.; Mutava, R.N.; Tuinstra, M.R. Sensitivity of Grain Sorghum to High Temperature Stress during Reproductive Development. *Crop. Sci.* **2008**, *48*, 1911–1917. [CrossRef]
48. Djanaguiraman, M.; Perumal, R.; Jagadish, S.V.K.; Ciampitti, I.A.; Welti, R.; Prasad, P.V.V. Sensitivity of Sorghum Pollen and Pistil to High-Temperature Stress. *Plant Cell Environ.* **2018**, *41*, 1065–1082. [CrossRef] [PubMed]
49. Singh, V.; Nguyen, C.T.; Yang, Z.; Chapman, S.C.; van Oosterom, E.J.; Hammer, G.L. Genotypic Differences in Effects of Short Episodes of High-Temperature Stress during Reproductive Development in Sorghum. *Crop. Sci.* **2016**, *56*, 1561–1572. [CrossRef]
50. Prasad, P.V.V.; Djanaguiraman, M.; Perumal, R.; Ciampitti, I.A. Impact of High Temperature Stress on Floret Fertility and Individual Grain Weight of Grain Sorghum: Sensitive Stages and Thresholds for Temperature and Duration. *Front. Plant Sci.* **2015**, *6*, 820. [CrossRef] [PubMed]
51. Sunoj, V.S.J.; Somayanda, I.M.; Chiluwal, A.; Perumal, R.; Prasad, P.V.V.; Jagadish, S.V.K. Resilience of Pollen and Post-Flowering Response in Diverse Sorghum Genotypes Exposed to Heat Stress under Field Conditions. *Crop. Sci.* **2017**, *57*, 1658–1669. [CrossRef]
52. Tack, J.; Lingenfelser, J.; Jagadish, S.V.K. Disaggregating Sorghum Yield Reductions under Warming Scenarios Exposes Narrow Genetic Diversity in US Breeding Programs. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 9296–9301. [CrossRef] [PubMed]
53. Lobell, D.B.; Hammer, G.L.; Chenu, K.; Zheng, B.; Mclean, G.; Chapman, S.C. The Shifting Influence of Drought and Heat Stress for Crops in Northeast Australia. *Glob. Chang. Biol.* **2015**, *21*, 4115–4127. [CrossRef] [PubMed]