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Pre-breeding for Silicon-use Efficiency to Enhance Drought Tolerance and Grain Protein Content in Bread Wheat (*Triticum aestivum* L.)

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Pre-breeding for Silicon-use Efficiency to Enhance Drought Tolerance and Grain Protein Content in Bread Wheat (*Triticum aestivum* L.)

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Thesis Abstract

Wheat (*Triticum aestivum* L.; 2n=6x=42, AABBDD) is a key commodity crop globally. Despite its economic importance across diverse value chains, wheat productivity has stagnated in sub-Saharan Africa, particularly in South Africa, due to climate change. Global demand for wheat is increasing due to population growth, climate change, higher input costs, geopolitical factors, and the increased frequency and intensity of biotic and abiotic stresses. Wheat production and quality are limited by abiotic constraints, including drought stress, poor soil nutrition, and management. It is imperative to develop drought-tolerant varieties with high yield potential and enhanced grain protein content for food security. Silicon (Si) has been proven to improve agronomic performance and nutrient uptake under biotic and abiotic stress, in various crops including wheat. Despite the well-researched role of Si in plant nutrition and drought tolerance, genetic variation for Si uptake has not been exploited in breeding programmes, especially those targeting drought tolerance and grain quality improvement. Therefore, the specific objectives of this study were: (1) to evaluate the effects of different Si fertiliser formulations on the agronomic performance of diverse wheat genotypes under drought-stress conditions, (2) to examine the impact of Si fertilisation on agronomic performance and trait associations in wheat under drought stress to identify selection criteria for improving drought tolerance and Si response, (3) to evaluate the effects of two Si fertiliser formulations on the compositions of wheat grain carbon (C), nitrogen (N), sulfur (S) and protein content (GPC) under drought-stress and non-stress conditions to enhance grain yield and end-use quality and (4) to assess the genetic determinants of yield and yield components in newly developed wheat populations under Si fertilisation to guide breeding and select desirable parents and progenies for variety development.

The first study evaluated the influence of different silicon fertiliser formulations on the yield and yield components of diverse wheat genotypes under drought-stress (DS) conditions. Twenty wheat genotypes from the International Maize and Wheat Improvement Centre (CIMMYT) heat and drought tolerance nurseries were evaluated under non-stress (NS) and DS conditions with two Si fertiliser formulations and an untreated control. The four-way interaction involving genotype by environment by water regime by Si formulation was significant ($p < 0.05$) for hundred seed weight (HSW), productive spike number (PS), aboveground biomass (AGB) and grain yield (GY). The best performing genotype was MC18, under DS conditions, which exhibited a mean grain yield of 4.17 t.ha^{-1} with granular Si, 2.56 t.ha^{-1} with liquid Si and 2.18 t.ha^{-1} without Si. Principal component biplot analysis expressed positive yield responses for all test genotypes under DS and NS conditions with both Si fertilisers. Genotype variation reduced with Si fertilisation for agronomic traits and improved its relationships under DS conditions. Si application influenced DS tolerance indices. The effect of Si, both directly and indirectly, influenced

yield and yield components. The study found that Si fertilisation mitigates the adverse effect of DS on wheat.

The second study examined the impact of Si fertilisation on agronomic performance and trait associations in wheat under DS to identify selection criteria for improving drought tolerance and Si response. Twenty genetically diverse wheat genotypes were appraised under DS and NS conditions, with two Si fertiliser formulations across three environments, using a factorial experiment laid out in a randomised complete block design. Both Si formulations enhanced wheat agronomic performance under both DS and NS conditions, compared to the untreated control. The degrees of correlation varied under the two water regimes and Si formulations. GY had positive associations with HSW, when using liquid Si ($r = 0.74$, $p < 0.001$) and granular Si ($r = 0.69$, $p < 0.001$), under NS conditions. Robust trait correlations were identified between productive tiller number (TN) and PS for granular Si ($r = 0.99$, $p < 0.001$), liquid Si ($r = 1.00$, $p < 0.001$) and the untreated control ($r = 0.98$, $p < 0.001$), under DS conditions. There were high trait correlations between spike length (SL) and TN ($r = 0.72$, $p < 0.001$; $r = 0.63$, $p < 0.001$, respectively), and PS ($r = 0.73$, $p < 0.001$; $r = 0.62$, $p < 0.001$), respectively for both Si applications under DS conditions. Under DS, HSW (0.84) and PS (0.64) had higher direct effects on grain yield with granular Si application, while TN and PS (0.94) had higher indirect effects on grain yield under liquid Si application. The study found that the best performing genotypes were MC10, MC6, MC1, MC3 and MC11, with granular Si application. Correlation and path coefficient analyses discerned principal traits TN, PS and HSW as contributors to enhanced GY under DS, elucidating them as vital selection parameters for Si use-efficient breeding lines.

The third study evaluated the effects of two Si fertiliser formulations on wheat grain carbon (C), nitrogen (N), sulfur (S), and protein content (GPC) under DS and NS conditions to improve grain yield and quality. Twenty wheat genotypes were evaluated for C%, N%, S% and GPC% contents under DS and NS conditions with liquid and granular Si formulations. Both liquid and granular Si formulations increased grain C, N, GPC and Si contents under DS conditions. The three-way interaction of genotype by water regime by Si formulation was significant ($p < 0.001$) for Si content. Genotype MC17 (41.17%) under DS conditions, and MC14 (42.19%) under NS conditions had the highest C% with granular Si. Likewise, under DS conditions and with granular Si, genotype MC5 logged the highest grain N (2.88%) and GPC% (16.41%). This study elucidated the positive contribution of granular Si application to enhanced C%, N%, GPC% and Si grain contents in wheat genotypes, particularly under DS conditions.

The fourth study assessed the combining ability effects and gene action conditioning of yield and yield components in newly developed wheat populations under Si fertilisation to identify the best combiner donor parents and progenies for genetic advancement and variety development. Seven genetically diverse wheat parents were selected based on yield and drought tolerance and were crossed using a full diallel mating design. Forty-two full-siblings were generated and assessed alongside the parents under

controlled environment conditions, with and without granular Si application, in three replications for focused phenotyping and selection. The analysis of variance (ANOVA) revealed a significant genotype (G) by Si treatment (T) interaction ($p < 0.05$) influencing the number of kernels per spike (KPS), AGB and GY. Significant maternal effects were observed for plant height (PH), PS and kernels per spike (KPS) with Si application. The general combining ability (GCA) effects significantly ($p < 0.05$) improved for PH, PS, spikelets per spike (SPS), KPS; hundred seed weight (HSW), harvest index (HI) and GY with Si application. Likewise, PH, PS, KPS, HSW and GY with Si application were significant ($p < 0.05$) for the specific combining ability (SCA) effects. Direct crosses MC4 x MC8 (1.57) and MC6 x MC10 (2.68) with Si application had positive and significant SCA effects for GY. The Baker's ratio with Si application was moderately higher (0.77) for KPS, demonstrating the prospect of additive genes. This study determined that Si application supplemented the additive gene effect on yield and yield components in both direct and reciprocal crosses.

The overall study elucidated that Si positively impacts agronomic trait performance, reduces genotypic variation and improves trait correlations. Its level of influence was more evident under DS conditions. Therefore, additional research is vital to investigate the conglomeration of favourable additive genes for the advancement of wheat generations through the breeding populations under Si application.

Declaration

I, **Marylyn Matilda Christian,** declare that:

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other University.
3. This thesis does not contain other person's data, pictures, graphs or information, unless specifically acknowledged as being sourced from other persons.
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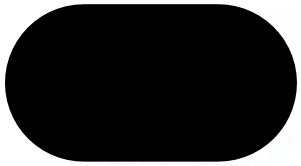

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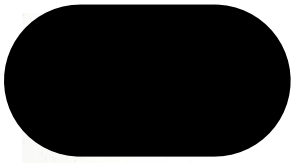
Marylyn Matilda Christian

As the candidate's supervisor, I agree to the submission of this thesis



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Dedication

This thesis is dedicated to:

1. My family and friends who have inspired and supported me. You have taught me that glass ceilings are meant to be shattered.
2. To those who passionately dream of making the world a better place for all.
3. To those who aspire to greatness, it already lives within you; you just need to shine as your glorious self.

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Abbreviations and Acronyms

AGB	Aboveground biomass
ANOVA	Analysis of variance
C	Carbon
CIMMYT	International Maize and Wheat Improvement Centre
CV	Coefficient of variation
DF	Degree of freedom
DS	Drought-stressed
FAO	Food and Agricultural Organization of the United Nations
G	Genotype
GCA	General combining ability
G x E	Genotype x environment interaction
GPC	Grain protein content
GY	Grain yield
H^2	Broad sense heritability
Ha^{-1}	Per hectare
HI	Harvest index
HSW	Hundred seed weight
KPS	Kernels per spike
LSD	Least significant difference
N	Nitrogen
NS	Non-stressed
PCA	Principal component analysis
PH	Plant height
PS	Productive spike number

S	Sulfur
SCA	Specific combining ability
Si	Silicon
+Si	With silicon
-Si	Without silicon
SL	Spike length
SPS	Spikelets per spike
T	Treatment
TN	Productive tiller number
UKZN	University of KwaZulu-Natal
WR	Water regime

Publications Pertaining to this Thesis

Chapter 1

Christian, MM., Shimelis, H., Laing, MD., Tsilo, TJ. and Mathew, I. 2021. Breeding for silicon-use efficiency, protein content and drought tolerance in bread wheat (*Triticum aestivum* L.): a review. Acta Agriculturae Scandinavica, Section B – Soil & Plant Science, 72(1), 17-29. DOI: https://doi.org/10.1080/09064710.2021.1984564

Chapter 2

Christian, MM., Shimelis, H., Laing, MD. and Tsilo, TJ. 2023. The effect of silicon fertilisers on agronomic performance of bread wheat under drought stress and non-stress conditions. Journal of Agronomy and Crop Science, 209(6), 827-840. DOI: https://doi.org/10.1111/jac.12668

Chapter 3

Christian, MM., Shimelis, H., Laing, MD. and Tsilo, TJ. 2025. Association of Yield and Yield Components Among Selected Bread Wheat Genotypes Under Silicon Fertilisation and Drought Conditions. Journal of Agronomy and Crop Science, 211 (1): e70020. DOI: https://doi.org/10.1111/jac.70020.

Chapter 4

Christian, MM., Shimelis, H., Laing MD, Tsilo, TJ. and Burgdorf, R. 2026. Compositions of wheat grain carbon, nitrogen, sulfur and protein under two silicon fertilisers and drought. Journal of Food Composition and Analysis. 156:1009347. DOI: https://doi.org/10.1016/j.jfca.2026.109347.

Chapter 5

Christian, MM., Shimelis, H., Laing, MD., Tsilo, TJ. and Tesfamariam, S. A. Combining ability of bread wheat (Triticum aestivum L.) genotypes for yield and related traits with silicon fertilization Journal of Reproduction and Breeding. 6 (3): 210-222. DOI: https://doi.org/10.1016/j.repbre.2026.06.005.

Introduction to Thesis

Background

Bread wheat (*Triticum aestivum* L., 2n=6x=42; AABBDD) is one of the most economically important crops globally, serving value chains worldwide. It accounts for approximately 35% of food demand globally, providing carbohydrates, proteins, minerals, and vitamins (Igrejas & Branlard, 2020). The global annual wheat production was estimated to be 794.73 million tons (MT) for the 2024/25 season, across 237 million hectares (MHa), with projected production to reach 800.1MT in the 2025/26 season (Collier & Pound, 2024; Feyisa et al., 2024, Collier, 2025). However, wheat consumption outweighs wheat production in both Africa and Asia (Grote et al., 2021). Africa's population continues to grow, increasing at a rate of 2.37% per year, implying an increase of 33.7 million individuals annually, which impacts on food security (Adesina et al., 2024). From 2020 to 2021, Africa imported an estimated 54.8MT of wheat, of which sub-Saharan Africa (SSA) accounted for 26.6 MT (Galal, 2024). As of 2020, SSA became a net importer of wheat to meet the local demand (Glauber et al., 2023). South Africa produced 2.05 MT of wheat during the 2023/24 season, whilst its imports increased by 15% during the same period (Sihlobo, 2024). The forecast wheat production for the 2025 season in South Africa was 2.02 MT, a decline from previous annual estimates (Netshifhefhe, 2025). South Africa imported an estimated 1.82 MT of wheat in 2024/25 to meet domestic demand (Sihlobo, 2025).

Wheat production and productivity in SSA are constrained by many abiotic and biotic factors, notably drought and heat stress (Frija et al., 2021). The mean wheat yield in Africa is < 2.0 tons per hectare ($t.ha^{-1}$) compared to the global mean grain yield of 3.6 to 3.7 $t.ha^{-1}$, and yields of 8 to 16 $t.ha^{-1}$ achieved in high-input production systems (Shewry, 2025). South Africa's wheat yield is estimated at 3.92 $t.ha^{-1}$ (Netshifhefhe, 2025). The above yield and supply gaps in Africa present an opportunity and challenges for the wheat farming sector.

Nutritionally, wheat contains a significant amount of starch (60 to 80%) and protein (8 to15%) required for human well-being (Wieser et al., 2020). The commercial value of wheat is dependent on the grain quality to produce bread and derived products. The grain quality is linked to flour and dough properties, which are conditioned by unique genes (Patel, 2023). Ash content, wet gluten, gluten swelling, falling number and sedimentation index are key parameters used to estimate grain quality, its rheology. Further, the rheological quality of bread is linked with loaf weight, volume, aroma, taste and structure (Gavurníková et al., 2011). Bread wheat has exceptional nutritional value, including essential macronutrients, such as nitrogen (N), sulfur (S), and micronutrients, including iron (Fe) and zinc (Zn) (Adams et al., 2024).

Low soil carbon (C) content affects grain development during crop growth, leading to small, shrivelled grains and diminished rheological quality (Rebetzke et al., 2008). Carbon is critical for the production

of starch and amino acids (Bertoft, 2017). Starch is a key rheological component, accounting for 70-85% of wheat flour's composition, vital for optimal bread dough formation and crumb setting during baking (Onyango, 2016; Khurana & Sharma, 2021). Nitrogen is a key component of amino acids and protein, while S is integral to the formation of some amino acids and disulfide bonds, which increase gluten strength (Roa et al., 2024). The composition of grain N and protein content (GPC) depends on genotype and production environment (e.g., soil fertiliser, biotic and abiotic stresses) and their interaction. Increased N application and crop uptake lead to enhanced GPC and gluten content in grain flour (Mendes et al. 2024). Additionally, high GPC is negatively correlated with grain yield, which is the primary trait in most breeding programs. Breeding for high GPC is challenging due to limited genetic variation in bread wheat, variable crop growing environments and their interactions (Kenzhebayeva et al., 2018).

The potential for wheat production and its economic value is increasingly constrained by the cumulative effects of drought and heat stress. According to climate-change predictions, the global average temperature is projected to increase above 2°C by 2050, along with a rise in drought frequency and severity (Jacob et al., 2024). During 2000 to 2020, there was a 50% increase in global drought occurrences compared to the period 1981 to 2000 (Zeng et al., 2023). Vulnerable regions such as SSA, parts of South America, and South Asia are disproportionately affected by drought stress (OECD, 2025). South Africa is the second-largest wheat-producing country in SSA and is also one of the world's most drought-prone countries, regularly experiencing interconnected climatic events causing severe droughts (Ziervogel et al., 2014; Nxumalo et al., 2022). Elevated temperatures and drought conditions shorten wheat growing seasons by hastening the reproductive processes, leading to reduced yields and ultimately degrading grain quality (Yanagi, 2024).

Historically, drought and heat stress have reduced global wheat production by approximately 35% (Gupta et al., 2020). Drought stress (DS) can reduce wheat production by 50 to 90% and affects global food systems (Awan et al., 2017). The response of wheat plants to drought stress depends on the species, genotype, developmental stage, and the intensity and duration of the stress. The onset of drought leads to severe yield reductions, even after a few successive days of rainfall cessation (Kumar et al., 2008). Drought stress severely impacts yield potential in wheat by inhibiting the biochemical processes, including the reduction of chlorophyll content and photosynthetic efficiency (Khadka et al., 2020). Drought tolerance is governed by the genetic constitution of the genotype, as well as complex morphological, biochemical, and physiological attributes, and their interactions (Grzesiak et al., 2019). Drought tolerance is a polygenic trait, subject to genotype-by-environment interactions and exhibiting low heritability, and thus requires focused genotype screening using morphological, biochemical, and physiological traits (Mwadzingeni et al., 2016; Grzesiak et al., 2019). Drought influences wheat grain quality by restricting enzyme activity, reducing grain starch and protein content (Li et al., 2025).

Therefore, breeding drought-adapted wheat and optimal agronomic management are crucial to boost grain yield and quality, and to maintain food security under future climate change conditions.

Silicon (Si) is classified as a quasi-essential nutrient that has gained popularity for its ability to increase yield and improve nutrient uptake (Kovács et al., 2022). It is the second most abundant mineral element on earth, but its availability to plants in the soil is naturally limited (Paul et al., 2024). As a fertiliser, it has been applied as a foliar spray or directly to the soil, either in liquid, powder or granular form, and with varying chemical formulations (Laane, 2018). Si application has been typically studied as a stress management amendment to improve yields and nutrient uptake (Epstein, 2009). Si also improves hydraulic conductivity, increases aquaporin efficiency, and maintains elevated transpiratory and photosynthetic rates (Avila et al., 2019). It affects other physiological and chemical characteristics, including activating defence-related enzymes and genes, regulating signal pathways and promoting antimicrobial compound production (Basu et al., 2021). Ma et al. (2006) reported that Si uptake is regulated using the Si transporter gene *Lsi*1 and later noted that there are genotypic differences in Si accumulation (Ma et al., 2007). A study by Cen et al. (2022) identified 32 *Lsi* genes from different plant species. Basu et al. (2021) found that under stress conditions, Si modulates gene expression in plants rather than directly signalling or acting as a secondary messenger. This complex mechanism of plant-Si interactions and genes associated with Si transport and utilisation indicates the possibility of selection and breeding for Si-use efficiency, and accumulation of genes through trait introgression. Studies on cultivar development, the combining ability and heterosis analyses for Si-use efficiency have predominantly been reported on rice (Jackson et al., 2019; Keerthiraj et al., 2021), with little research being done on Si and wheat. Therefore, there is a need to investigate the genetic potential of drought-tolerant and Si-use-efficient parents, and new progenies for the genetic management of drought tolerance in wheat through Si application.

Rationale of the study

The wheat sector in South Africa is a 4-billion-Rand industry. Nearly 70-80% of the wheat produced in the country is used for breadmaking. Wheat production and grain quality in South Africa are affected by recurrent droughts, wheat rusts, insect pests, and poor soil fertility. Hence, breeding for abiotic and biotic stress tolerance, grain yield and quality are the major breeding goals. High production input costs, volatile global wheat prices, and adverse climatic factors associated with climate change remain confounding factors, resulting in low grain yields and quality, and economic losses. Developing wheat cultivars that are high-yielding, have enhanced grain nutrient content, and have stable performance under water-stressed conditions will increase economic returns from wheat production. Therefore, there is a need to develop wheat cultivars that can thrive under limited water or supplementary irrigation with judicious crop management practices. However, drought tolerance is a multifaceted genetic trait influenced by numerous minor genes with additive and non-additive effects, and thus, it is a formidable trait to breed

for. There are currently no breeding programs in South Africa targeting Si-use efficiency to concurrently improve drought tolerance and grain nutrient content. Wheat genetic resources with drought and heat stress tolerance are associated with their ability to efficiently take up water and soil nutrients (e.g., Si), with a high conversion efficiency into grain yield and quality. Identification of Si-use-efficient elite parents, through evaluations of various Si formulations and dosages under drought-stress conditions, is crucial to developing new breeding populations for the selection of transgressive segregants. This may deliver new ideotypes with elevated drought tolerance and improved grain nutrient content after Si fertilisation. The selected genotypes should then be advanced for variety development and deployment for commercial wheat production.

Overall Objectives

The overall objective of this study was to improve the production and grain nutrient content of wheat varieties through the development of Si-use efficient, drought-tolerant and high-yielding bread wheat genotypes that incorporate agronomic traits preferred by farmers in drought-prone agroecological areas of South Africa.

The specific objectives of this study were:

i. to evaluate the effects of different Si fertiliser formulations on the agronomic performance of diverse wheat genotypes under drought-stress conditions.

ii. to examine the impact of Si fertilisation on agronomic performance and trait associations in wheat under drought stress to identify selection criteria for improving drought tolerance and Si response.

iii. to evaluate the effects of two Si fertiliser formulations on the compositions of wheat grain carbon (C), nitrogen (N), sulfur (S) and protein content (GPC) under drought-stress and non-stress conditions to enhance grain yield and end-use quality.

iv. to assess the genetic determinants of yield and yield components in newly developed wheat populations under Si fertilisation to guide breeding and select desirable parents and progenies for variety development.

Research hypotheses

i. There is significant genetic variation in bread wheat genotypes for Si-use efficiency and drought tolerance when assessed using various agronomic traits.

ii. Si fertilisation has a beneficial effect on trait associations for selection of wheat genotypes for enhanced yield and drought tolerance.

iii. Si fertilisation positively affects carbon, nitrogen, sulfur, Si and grain protein content of wheat genotypes under both drought-stress and non-stress conditions.

iv. Selected parents and F1 progenies show variable combining ability effects and agronomic trait performance with Si fertilisation.

Thesis Organization

This thesis comprises a total of five chapters as outlined below (Table 0.1). Chapter 1 is written as a separate review paper, whilst Chapters 2 to 5 are written as discrete research chapters, each following the format of a stand-alone research paper, followed by a general overview and the implications of the study's findings. This is the dominant thesis format adopted by the University of KwaZulu-Natal. Due to their interdependence, the chapters may contain unavoidable overlaps in the introduction and reference sections. Chapter 1 was published in the Journal of Acta Agriculturae Scandinavica, Section B – Soil & Plant Science (2021, 72 (1), 17-29, doi: https://doi.org/10.1080/09064710.2021.1984564) and Chapters 2 and 3 in the Journal of Agronomy and Crop Science (2023, 209 (6), doi: https://doi.org/10.1111/jac.12668) and (2025, 211(1), doi: https://doi.org/10.1111/jac.70020), in that order, and Chapter 5 has been accepted with minor revisions in the Journal of Reproduction and Breeding (Manuscript ID: REPBRE-D-25-00054).

Table 0.1. Thesis structure

Chapter	Title
-	Introduction to thesis
1	Breeding for Si-use efficiency, protein content and drought tolerance in bread wheat (*Triticum aestivum* L.): a review
2	The effect of Si fertilisers on agronomic performance of bread wheat under drought stress and non-stress conditions
3	Association of yield and yield components among selected bread wheat genotypes under Si fertilisation and drought conditions
4	Influence of Si fertilisers on the compositions of wheat grain carbon, nitrogen, sulfur and protein contents under drought-stressed and non-stressed conditions
5	Combining ability of bread wheat (*Triticum aestivum* L.) genotypes for yield and related traits with Si fertilisation

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CHAPTER 1

Breeding for Silicon-Use Efficiency, Protein Content and Drought Tolerance in Bread Wheat (*Triticum aestivum* L.): A Review

Abstract

The production and quality of wheat are affected by abiotic constraints including water stress and soil nutrient deficiencies. It is imperative to develop drought-tolerant wheat varieties with high yield potential and enhanced grain protein content for food security. Silicon (Si) is important for plant growth and development but its role in abiotic stress tolerance has been overlooked in breeding programs. Identifying the underlying functional genes controlling drought tolerance, protein content and grain yield is essential for wheat improvement, especially under drought stress. Silicon uptake is conditioned by several Si transporter genes such as *Lsi1*, *Lsi2* and *Lsi6* and aquaporins, which facilitate transport of silicon and water between cells. The objectives of this review are to examine the role of Si in improving plant nutrition and drought tolerance, and to appraise the genetic control of Si uptake and breeding methods for improving Si uptake for drought adaptation and improved grain yield and quality. The review highlights the limited progress made in breeding for drought tolerance in wheat, especially in sub-Sahara Africa where the challenge is prevalent. Limited understanding of the genetic basis for Si uptake and physiology contribute to the limited progress in its exploitation in wheat improvement programs.

Keywords*:* drought-tolerance, genomic selection, protein content, grain yield, phenotypic selection, silicon uptake, silicon-use efficiency, wheat

1.1 Introduction

Bread wheat (*Triticum aestivum* L., 2n=6x=42, AABBDD) is one of the most widely cultivated and traded crops in the world. The global production of wheat is estimated at 215 million hectares with an output of 763 million tonnes of grain (CGIAR, 2017). It accounts for over 35% of the global food demand, providing carbohydrates, proteins, minerals and vitamins (Igrejas and Branlard, 2020). Wheat has a superior nutritional value, containing 60-80% starch and 8-15% protein, compared to maize (60% starch, 9-10% protein) or rice (80% starch, and 7-8% protein) (Nevo et al., 2002, Chaudhari et al., 2018). However, wheat production in most parts of the world is projected to fall short of demand due to several abiotic constraints, including the multiple impacts of climate change, and poor soil fertility.

Water availability and poor soil fertility are particularly important constraints to wheat production in sub-Sahara Africa (SSA) (Fahad et al., 2017). Due to climate change the average rainfall in SSA countries has decreased, and rainfall distribution has become more erratic (Worku et al., 2018). Dryland wheat production is carried out under winter rainfed systems that depend on residual moisture availability. However, low rainfall and erratic rainfall patterns impact on winter rainfed production systems, especially when terminal drought stress occurs post-anthesis (Shavrukov et al., 2017). The progressive decline in rainfall also limits the availability of water for irrigated systems. The widespread distribution of degraded soils with poor mineral content exacerbates the impact of drought stress on wheat production (Assefa et al., 2018). Most soils in SSA are degraded, acidic and highly leached of essential nutrients to support sustainable crop production, including low levels of plant-available Si (Stewart et al., 2020). It is imperative to develop drought tolerant wheat varieties for SSA, coupled with improved nutrient absorption capacity, that can better tolerate production under conditions of drought stress and soils with poor mineral fertility.

Developing drought tolerant varieties has been pursued using various methods, including selection for agronomic traits and grain yield, genetic markers, and genomic selection, with various levels of success. One agronomic trait that has gained recent attention is silicon (Si) uptake. Silicon is a micronutrient that has been shown to improve agronomic performance and nutrient uptake in some plant species under abiotic and biotic stresses. Improved agronomic performance is important for drought tolerance, while enhanced nutrient uptake is vital to ensure high grain quality. Despite information on the role of Si in plant nutrition and drought tolerance, genetic variation for Si uptake has not been exploited in breeding programmes, especially those aiming to improve drought tolerance and grain quality. The hypothesis of this review is that increased Si uptake in wheat will improve nutrition and water uptake, resulting in improved grain yield and quality under a range of stress conditions. Plant breeders have not specifically set a breeding objective to exploit the potential role of Si in improving plant nutrition and drought stress tolerance. The impact of enhanced Si uptake by the plant on grain

quality has also been highlighted as a potential benefit. However, Si uptake efficiency has not been widely studied in wheat breeding, compared to investigations for other agronomic traits. The main reason for the limited exploitation of Si in wheat breeding programs is a lack of knowledge on the role of Si, the nature of the underlying genetics and the development of suitable selection methods. Therefore, the objectives of this review are to examine the role of Si in improving plant nutrition and drought tolerance, and to appraise the current knowledge of genetic control of Si uptake, and breeding methods for improving Si uptake for drought tolerance, and improved grain yield and quality.

1.2 Silicon Uptake Mechanism in Plants

Silicon mostly exists in the soil in solid crystalline forms such as quartz and micas, microcrystalline minerals or as secondary silicate minerals (Cornelius & Delvaux, 2016, Souri et al., 2020). Under aqueous conditions, mineral Si dissolves to form monosilicic and polysilicic acids (H_4SiO_4) (Sauer et al., 2006). Polysilicic acid is predominant at early stages of dissolution, while monosilicic acid is the more abundant at low saturations. Silicic acid is taken up via the primary and secondary root hair of the plant root system (Figure 1.1). From the root hairs, it moves via cortical cells to the xylem using influx and efflux transporter genes (Ma et al., 2011) and into plant tissues using silicon transporters conditioned by a number of genes, such as those denoted as *Lsi1, Lsi2, Lsi3,* and *Lsi6* (Gaur et al., 2020). There are species-specific variations in the uptake, movement and deposition of Si in plant tissues. For instance, species of the family Gramineae tend to deposit Si in endodermal cell walls and stegmata cells of sclerenchyma fibres. Endodermal silicification occurs in a radial pattern, mainly in storage tissues, vascular tissues, sclerenchyma, fibres and epidermal tissue (Mandlik et al., 2020). The specific location of the Si deposits facilitate improved root strength, root length, thickness, volume, biomass, lateral root numbers, nodulation and nitrogen fixation (Lux et al., 2020). These morphological changes allow roots to penetrate enhanced soil depths for effective nutrient and water uptake, and improved plant anchorage. Silicon may also be deposited in cell wall polysaccharides, increasing cell wall strength and protecting against plant pathogens (Guerriero et al., 2016).

Silicon deposits in above ground plants parts has been associated with improved photosynthetic activity, and decreased insect and herbivore damage (Ma & Yamaji, 2008). The Si is deposited to form a silicon bilayer between the cuticle and leaf epidermis of young and mature leaves, which is associated with an increased content of cellulose, fiber and lignin. The Si deposits also enhance physiological activities such as gaseous exchange, maintenance of leaf water potential, enhanced water and nutrient transportation, and improved carbohydrate production, which are critical processes in plant growth and development (Gou et al., 2020).

Silicon uptake by plants is influenced by plant genetics, Si particle size, soil conditions and climatic factors. Previously, it was proposed that Si uptake was achieved through active, passive or rejective uptake (Takahashi et al., 1990, Ma et al., 2001). Active uptake of Si occurs via the root system, whilst passive Si uptake refers to the absorption of Si through stems and leaves (Chiba et al., 2009, Hemmati, 2017). Examples of crop species that actively take up Si are rice and wheat. Solanaceous crops were previously considered to reject Si uptake (Ma, et al., 2001). However, different modes of Si uptake and transport have since been proposed using studies on rice and *Arabidopsis* (Brugiére & Exley, 2017, Putra et al., 2020). Silicon concentration varies from 0.1 to 10% of the plant dry matter in different plant species and genotypes (Epstein, 1999). Broadly, crops can be divided into three categories based on their ability to accumulate Si in their tissue. One category consists of high Si accumulators that have the ability to absorb Si efficiently. High Si accumulators contain >1% Si on a dry weight basis. Moderate or intermediate Si accumulators are categorized as plants with a Si content of between 0.5 and 1% of plant dry weight. Non-Si accumulators are plants with a limited ability to extract Si from the soil, or to deposit the silicon in their tissues. Non-accumulators have Si concentration below 0.5% of plant dry weight (Liang et al., 2007, Meena et al., 2021).

In the soil, the availability of Si depends on the Si particle size, soil pH, soil temperature, concentration of cations such as magnesium, potassium and calcium in the soil, soil organic matter and moisture content. The monosilicic acid molecule is the simplest form, made up of Si bound to four hydroxyl groups in a tetrahedral shape (Alvarez & Sparks, 1985). This is the easiest form of Si for plant uptake. It usually occurs in the soil at low concentrations of below 100 $mg.kg^{-1}$ soil, while soil Si concentrations between 100 and 200 $mg.kg^{-1}$ can cause aggregation of these monomers to form large molecules (Currie & Perry, 2007). The Si uptake by plants decreases when negatively charged polymers larger than 1-3 nm are formed. The formation of these polymers from monosilicic acid depends on soil conditions, especially soil pH (Rashad & Hussein, 2018).

The growth stage at which Si is applied as a fertiliser influences the levels of Si uptake by plants (Maghsoudi et al., 2016). Dorairaj et al. (2020) found that the application method and formulation of Si fertiliser, and the growth stage at which Si fertiliser was applied, had a significant impact on the effectiveness of Si fertiliser on rice growth and development. Application of Si at sowing improved germination (Siddiqui & Al-Whaibi, 2014), while applications at tillering and anthesis provided significant tolerance to drought stress (Maghsoudi, et al., 2016). Split applications of Si at transplanting, tillering and panicle initiation in rice was found to be the most effective approach to improve plant growth (Rehman et al., 2019). The Si application must coincide with important growth stages to improve physiological functions, and to catalyse a range of biological processes, including nutrient uptake and assimilation. In addition, the formulation of Si is also important. In general, soil-applied Si was more effective in improving plant growth than foliar-applied Si (Cacique et al., 2013). Silicon fertilisers are available as granular, powder or liquid formulations. Granules are applied to the soil and

are taken up by the plant through the root system after dissolution. The effectiveness of granular Si is affected by soil conditions that control soil biogeochemical reactions and the root characteristics of the plant. Liquid formulations can be applied as drench or foliar sprays. The effectiveness of foliar applied Si is affected by ambient conditions such as temperature and wind, and plant characteristics (Laane, 2018). Silicon fertilisers have been used to increase Si availability to plants, but effective uptake of Si is affected by the method of Si application, Si formulation, its particle size and concentration, the plant's growth stage at application and genotypic differences. The distribution of foliar-applied Si is limited to plant leaves, whereas soil applied Si is assimilated and distributed throughout the plant (Pilon et al., 2013). In addition, the uptake of foliar-applied Si in plants is lower compared to soil-applied Si (Cacique, et al., 2013). Roots are more effective at assimilating Si due to their specialized role and adaptation to acquire nutrients. It would be valuable to determine the genetic basis of root traits in wheat that result in enhanced Si uptake. There are indications that root traits have been neglected in wheat breeding (White et al., 2015, Fradgley et al., 2020, Svoboda et al., 2020), which could compromise nutrient uptake for improved drought tolerance, grain yield and quality breeding. The factors that affect uptake of Si must be considered to devise suitable strategies for effective selection and breeding of genotypes with an enhanced capacity for Si uptake. For instance, the Si formulation and frequency of application must be consistent to ensure repeatability of phenotyping in multi-environment trials. And these need to relate to the commercial realities of the costs of various formulations of Si fertilisers and their application to a relatively low value field crop such as wheat.

Silicon fertilisation has been used in hydroponic and field systems to boost plant growth (Gerami & Rameeh, 2012). However, very few incidences of Si toxicity have been reported (Kamenidou et al., 2008, Mburu et al., 2016). Mburu et al. (2016) found that weekly applications of between 500 and 1000 mg Si had phytotoxic effects on bananas. Stunting, flower deformation and delayed flowering were observed in sunflowers after application of high concentrations of sodium silicate (Kamenidou, et al., 2008). However, Kamenidou et al. (2010) could not determine whether the stunting in gerbera flowers could be attributed entirely to Si, or to the sodium (Na) effects, which are well known to induce stunting when applied in excess. Excessive application of Si is also discouraged in fodder crop production. Elevated levels of silica and lignin reduce palatability and digestibility of stover used as animal fodder, which would require chemical treatment to improve nutrient availability to livestock (Aquino et al., 2020).

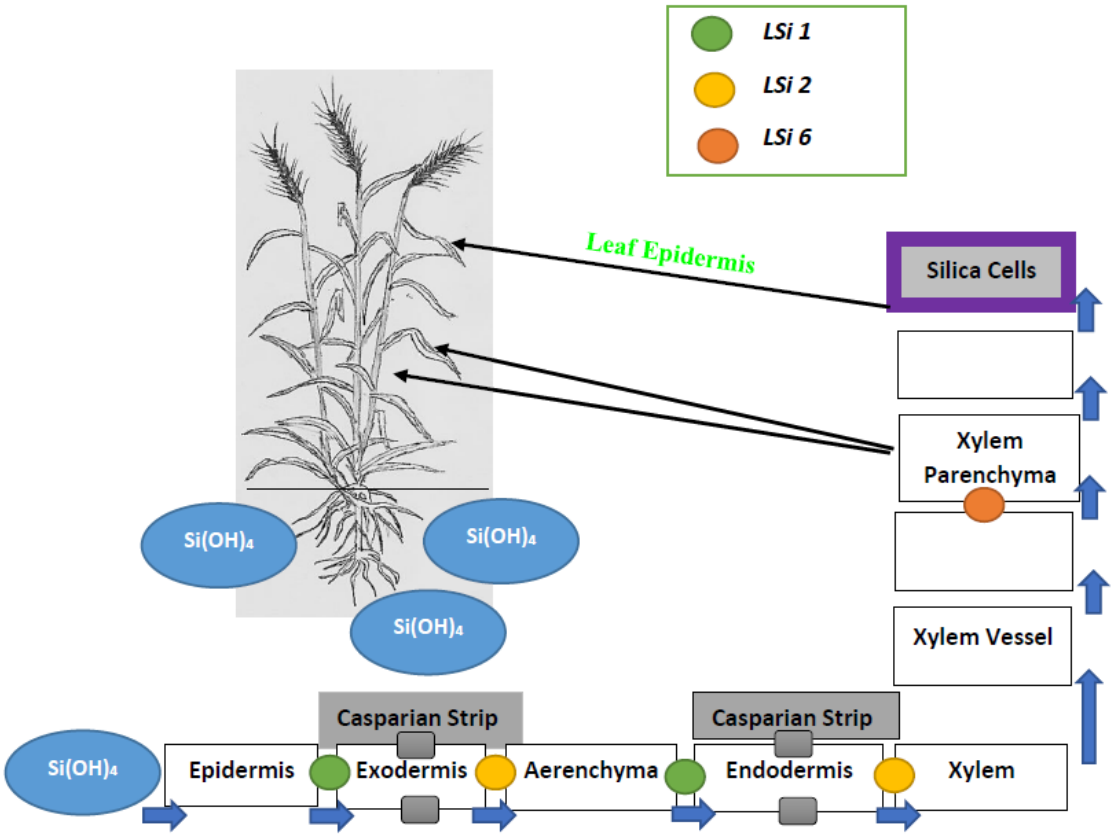

Figure 1.1: The uptake and distribution of Si from soil through to the deposition in silicified cell walls and silica bodies in wheat. *LSi 1*, *LSi 2* and *LSi 6* denote genes that condition Si influx and efflux transporters, $Si(OH)_4$ = orthosilicic acid. Source: Adapted from (Farooq and Dietz, 2015).

1.3 Silicon (Si) Fertilisation and its Role in Improving Drought Tolerance and Grain Quality

Silicon (Si) is the second most abundant element on earth and its role in plant nutrient uptake, nutrient remobilization, and protection against biotic and abiotic stresses has received increased attention. Silicon is involved in physiological activity and structural integrity of higher plants exposed to abiotic and biotic stresses (Liang et al., 2013). A series of biochemical reactions including release of oxidative chemicals are activated in plants under stress. Silicon alleviates stress by altering osmolyte concentrations and enhancing production of anti-oxidant enzymes to break down oxidative chemicals (Sapre & Vakharia, 2016). For instance, germination rate under drought stress conditions can be increased by up to 24% by applying Si as a seed priming agent (Shi et al., 2016, Ayed et al., 2021).

The role of Si in conferring drought tolerance and improving nutrient uptake in plants has been inferred from its role in maintaining plant water balance, photosynthetic activity and the turgidity of leaves and xylem under high transpiration (Melo et al., 2003, Hattori et al., 2005, Ahmad et al., 2007).

Water balance in a plant is important to maintain cell turgidity that drives cell expansion and division for growth. Phenotypic traits such as plant height, dry matter production, leaf area, shoot growth, plant shoot nutrient uptake and thousand grain weight in wheat that are all positively correlated to grain yield depend on cell expansion (Gong et al. (2003). Yield increase due to Si uptake is partially as a result of enhanced chlorophyll concentrations, sustained photosynthetic activity and the maintenance of leaf architecture for effective light interception (Abbas et al., 2017). Si deposits appear to play a role in preventing the collapse of xylem vessels and maintaining stomatal conductance under drought and heat stresses, which is important to sustain water and nutrient transport throughout the plant under stress conditions (Sapre & Vakharia, 2016).

There are indirect effects of Si on yield that accrue through improved accumulation of macro and micro-nutrients in plants with improved Si uptake (Neu et al., 2017). Improved carbon (C) and nitrogen (N) assimilation due to increased Si uptake result in an increased tolerance to both biotic and abiotic stresses in wheat. Improved C sequestration and assimilation in cellulose and carbohydrate production in grass species increases the energy efficiency of Si accumulators (Schoelynck et al., 2010). Most research on Si uptake has focused on improving agronomic yield, mitigating biotic and abiotic stresses, and improving nutrient uptake (Table 1.1). Grain quality improvement is usually inferred as an indirect effect of nutrient uptake and stress alleviation. However, the role of Si uptake in grain quality has not been investigated thoroughly.

The rheological properties of wheat are important indicators of grain quality. These properties include starch, lipids, and protein content, which are the major components of the wheat endosperm, and minerals, vitamins and anti-oxidants (Kumar et al., 2016). Enhanced Si uptake in wheat maintains the balance of nitrogen and carbon, which is important in ensuring high grain quality under stress conditions. The balance of carbon and nitrogen is important in the synthesis of the gliadins and glutenin, which are the main components of protein gluten in wheat. The integrity of the protein gluten is also maintained by disulphide bonds, making sulphur an integral component (Réthoré et al., 2020). Therefore, since Si uptake has cascading effects on carbon, nitrogen, and sulphur uptake, it indirectly affects rheological properties and grain quality of wheat produced under stress conditions. The inclusion of selection for enhanced Si uptake as a breeding objective in wheat will improve plant growth and nutrient acquisition, especially in marginal soils that are highly depleted of micro and macro-nutrients, including Si. Some countries in Asia and the Americas incorporate Si fertilisation as standard practices for sustainable agricultural crop production (Yan et al., 2018). While this is feasible in developed countries, the sub-optimal application of fertilisers in developing countries remains a widespread challenge due to the lack of financial resources and access to agricultural inputs for most of these farmers. The incorporation of Si in inorganic fertiliser could enhance wheat productivity in developing countries but the impact would be limited for smallholder farming communities if they cannot afford the fertilisers. It is thus important to breed for enhanced Si uptake and utilization in wheat cultivars for

deployment among resource poor farming communities, and also for regions where Si is not incorporated into popular fertilisers

Table 1.1: The effect of different Si formulations and concentrations on nutrient uptake, agronomic traits, and abiotic stresses of various crops

Crop species	Si Concentration and formulation	Reported Si effects	Reference
***Avena sativa* L.**	0.8% soluble Silamol	Increased root and seedling length	(Toledo et al., 2012)
***Triticum aestivum* L.**		Enhanced 1000 seed weight	
***Oryza sativa* L.**	0, 100, 200 and 300ppm Calcium silicate	Improved grain and straw weight. Improved P, K, S, Na and Si uptake	(Malav et al., 2015)
***Glycine max* L.**	0.0, 0.5 and 1.0mM $Na_2SiO_3.5H_2O$	Enhanced Zn accumulation and remobilization	(Pascual et al., 2016)
***Gossypium hirsutum* L.**	1.0 mM Na_2SiO_3	Decreased effects of Ni toxicity	(Khaliq et al., 2016)
***Triticum aestivum* L.**	0,1, 10, 50g SiO_2	Improved P and N uptake and aboveground biomass	(Neu, et al., 2017)
***Solanum tuberosum* L. var. Agria**	1000 and 2000ppm nanosilica, sodium silicate, nanoclay, and Bentonite	Improved leaf, root characteristics and mini tuber quality	(Soltani et al., 2018)
***Arachis hypogaea* L.**	150mM sodium metasilicate $Na_2SiO_3.9H_2O$	Improved uptake and distribution of N, P, K, Ca and Mg	(Dong et al., 2018)
***Zea mays* L. cv Reduta**	Soils treated with 0, 80 and 1000kgSi.ha^{-1} $KSiO_3$ and nutrient medium 100, 500, 1000, 5000µM Si $KSiO_3$	Increased Ca, P, S, Mn, Zn, Cu, Mo, Cl and Fe in soils and S, Mg, Ca, B, Fe, Mn in solutions. Translocation of Mg, Ca, S, Mn and Mo increased to shoots.	(Greger and Landberg, 2018)
***Lactuca sativa* L. cv. Amerikanischer brauner**			
***Triticum aestivum* L. cv Tjalve**			
***Daucus carota* L. cv. Nantaise**			
***Pisum sativum* L. cv. Fenom**			
***Triticum durum* Desf.**	150 mg Si L^{-1}sodium silicate ($Na_2SiO_3.H_2O$)	Enhanced drought tolerance by improving chlorophyll content, root and shoot length and relative water capacity	(Othmani et al., 2020)

1.4 Silicon Genes and Aquaporins and Their Potential Use in Marker-Assisted Breeding

The genetic basis of Si uptake and distribution has been investigated most intensively in rice and *Arabidopsis* (Ma et al., 2006), which have less complex and smaller genomes than wheat. The uptake and distribution of Si in plant tissue is controlled by Si transporter genes, namely, low silicon 1 (*Lsi1*) and low silicon 2 (*Lsi2*) (Rao & Sushmitha, 2017). The *Lsi1* belongs to the nodulin 26-like major intrinsic protein (NIP) III subgroup and is a permeable channel, while *Lsi2* is a member of an uncharacterized anion transporter family that acts as an efflux transporter (Ma & Yamaji, 2015). The transporter *Lsi1* belongs to the aquaporin family that controls Si accumulation and is expressed in plant roots (Luu & Maurel, 2005, Ma, et al., 2006). The *Lsi1* and *Lsi2* transporters are situated at different sites on the plasma membrane of root cells and are integral for the effective movement of Si within the exodermis and endodermis or root cells (Ma, et al., 2006, Hernandez-Apaolaza, 2014). Low silicon genes encode for the influx (*Lsi1* and *Lsi6*) and efflux (*Lsi2* and *Lsi3*) transport proteins (Ma, et al., 2006, Ma and Yamaji, 2015). These genes were originally found in rice, but have also been found in other crops, including tomato (*Solanum lycopersicum* L.), sorghum (*Sorghum bicolor* [L.] Moench), grape (*Vitis vinifera* L.) and maize (*Zea mays* L.) (Vatanserver et al., 2017). Aquaporins (membrane water transport proteins) facilitate Si uptake in the root from soil and radial transportation within the root and xylem. These transporter genes and aquaporins have been found in various crops where they facilitate Si uptake and distribution (Table 1.2). The expression of *Lsi1* and *Lsi2* genes varies significantly. The expression levels of Si transporter genes have been correlated with the levels of Si absorption in rice (Ma et al., 2007). Despite the discovery of these genes, their introgression in new breeding populations has not been pursued for improving drought tolerance or grain quality in wheat.

Si-utilization is also facilitated by aquaporins that are responsible for balancing water relations in plant cells during water stress (Zargar et al., 2019). Aquaporins are membrane channels from a family of major intrinsic proteins, approximately 26-30 kDa in size, that facilitate the transport of different substrates, including small neutral solutes such as H_4SiO_4, urea and water across membranes (Xu et al., 2013). Aquaporin expression is influenced by water availability but is generally higher in leaves than in roots and is lowest in shoots (Nada & Abogadallah, 2014, Gambeta et al., 2017). Aquaporins are located in the peribacterioid membrane of N_2 fixing root nodules (NIPs); the cell membrane (plasma membrane intrinsic proteins (PIPs); endoplasmic reticulum (small basic intrinsic membranes (SIPs) and tonoplasts (tonoplast intrinsic proteins (TIPs)) (Nada and Abogadallah, 2014).

The number of aquaporin locations signify their integral role in regulating water movement, even at a cellular level. The aquaporins limit plant water loss to the soil environment by rapidly down-regulating under water stress conditions (Vandeleur et al., 2005), and their expression can be exploited

in marker-assisted breeding for drought stress tolerance (Pandey et al., 2013). Approximately 35 aquaporin genes have been identified in the wheat genome (Huang et al., 2014). Understanding the role of aquaporins in root hydraulic control can contribute to effective genotypic selection (Gambeta, et al., 2017). Although the *Lsi1* gene is associated with aquaporins (NIP III subgroup), the *Lsi2* and *Lsi3* and *Lsi6* genes have not yet been associated with any aquaporins. Establishing whether aquaporins are associated with these genes could potentially facilitate effective selection for Si use efficiency in wheat breeding.

The NIP2 subfamily of aquaporins can be used to predict Si uptake in different plant species using a unique amino acid selective filter (Deshmukh & Bélanger, 2016). Marker-assisted breeding based on the genetic make of the amino acid filter will improve selection efficiency for improving Si uptake in wheat. Ma (2004) mapped the markers RM5303 and EST-PCR marker E60168 on Chromosome 2, which were linked to the Si transporter gene in rice. Identifying similar or related markers in wheat will open opportunities for selection of the transporter genes for improved drought tolerance in wheat, considering that homoeologous relationships exist between rice and wheat (Ahn et al., 1993). Genome-wide analysis studies have shown that aquaporins are important in drought stress management and improving breeding programs (Putpeerawit et al., 2017, Madrid-Espinoza et al., 2018). Genetic sequencing to screen wheat genotypes for silicon genes and aquaporins is a promising approach to accelerate the introgression of genes for enhanced silicon uptake to improve both drought tolerance and grain quality. There is a need for further research to establish whether Si use efficiency would be improved by selecting for Si uptake genes only, or whether they should be selected for in combination with selected aquaporins.

Table 1.2: List of reported aquaporins and transporter genes which facilitate Si uptake and distribution in various crops

Crop species	Crop gene name	Aquaporin/ Transporter gene type	Reference
Solanum lycopersicum L.	*SlPIP1;3,*	Aquaporin	Shi, et al. (2016)
	SlPIP1;5 and SlPIP2;6		
Triticum aestivum L.	*TaPIP1*	Aquaporin	Younis et al. (2020)
	TaNIP2		
***Arabidopsis thaliana* L.**	*TaNIP*	Aquaporin	Monpetit et al. (2012)
***Zea mays* L.**	*ZmLsi1*	*Lsi1*	Bokor et al. (2017)
***Eragrostis tef* (Zucc.) Trotter**	*EtLsi1-1*	*Lsi1*	Ligaba-Osena et al. (2020)
	EtLsi1-2		
***Oryza sativa* L.**	*Lsi1*	*Lsi1*	Ma and Yamaji (2006)
***Hordeum vulgare* L.**	*HvLsi1*	*Lsi1*	Yamaji et al. (2012)
***Arabidopsis thaliana* L.**	*TaLsi1*	*Lsi1*	Monpetit, et al. (2012)
***Fragaria x ananassa* Duchesne**	*Lsi1*	*Lsi1*	Ouellette et al. (2017)
***Oryza sativa* L.**	*OsLsi1*	*Lsi1*	Lin et al. (2019)
***Euphorbia pulcherrima* Willd. ex Klotzsch**	*EpLsi1*	*Lsi1*	Hu et al. (2020)
Oryza sativa* L. subsp. *indica	*Lsi1*	*Lsi1*	Swain & Rout (2020)
***Triticum aestivum* L.**	*Lsi1*	*Lsi1*	Jain et al. (2021)
***Zea mays* L.**	*ZmLsi2*	*Lsi2*	Bokor, et al. (2017)
***Eragrostis tef* (Zucc.) Trotter**	*EtLsi2-1*	*Lsi2*	Ligaba-Osena, et al. (2020)
	EtLsi2-2		
	EtLsi2-3		
	EtLsi2-4		
***Hordeum vulgare* L.**	*HvLsi2*	*Lsi2*	Yamaji, et al. (2012)
***Fragaria x ananassa* Duchesne**	*Lsi2*	*Lsi2*	Ouellette, et al. (2017)
***Festuca arundinacea* Schreb.**	*Lsi1*	*Lsi2*	McLarnon et al. (2017)
***Euphorbia pulcherrima* Willd. ex Klotzsch**	*EpLsi2*	*Lsi2*	Hu, et al. (2020)
Oryza sativa* L. subsp. *indica	*Lsi2*	*Lsi2*	Swain & Rout (2020)
***Hordeum vulgare* L.**	*HvLsi3*	*Lsi3*	Yamaji, et al. (2012)
***Zea mays* L.**	*ZmLsi6*	*Lsi6*	Bokor, et al. (2017)
***Eragrostis tef* (Zucc.) Trotter**	*EtLsi6-1*	*Lsi6*	Ligaba-Osena, et al. (2020)

Abbreviations: Lsi=silicon transporter genes; *NIP*=nodulin-26-like intrinsic proteins; *PIP*=plasma membrane intrinsic proteins; *SIPs*=small basic intrinsic proteins; *TIP*= tonoplast intrinsic proteins. The two-letter prefix in the gene name denotes the crop species.

1.5 Breeding for Drought Tolerance

Breeding for drought tolerance has long been identified as a sustainable and economic strategy to improve wheat production and productivity in marginal regions, especially as farmers try to cope with the impacts of climate change. It has been shown that drought tolerance can be improved by indirectly selecting for traits such as early flowering, plant height, tiller number, thousand kernel weight and grain yield (Mwadzingeni et al., 2016b). Early flowering has been the most exploited trait for drought escape. This allows genotypes to complete their life cycle before the onset of catastrophic drought stress. This strategy is effective in environments such as SSA where terminal drought stress is common due to the farmers' dependence on winter rainfall and residual moisture. The main challenge encountered when breeding for drought tolerance using this strategy is that early flowering can lead to a yield penalty and reduction in other agronomic traits such as plant height and plant biomass, due to the shortened plant life cycle.

Other strategies to manage drought such as slowing biological processes, or by enhancing drought tolerance by accumulating solutes such as proline, have been pursued but with relatively little success (Mwadzingeni, et al., 2016b). High proline accumulation under drought stress has been identified as a proxy trait for drought tolerance but its use has been limited by difficulties encountered in chemical analysis (Maghsoudi et al., 2018). In addition, the genetic basis of these strategies is not well understood. There is a need for innovative approaches to incorporate other traits and strategies to accelerate breeding progress. For instance, Si has been reported to improve growth in drought stressed plants through its role in stabilizing the leaf membrane, maintaining high relative water content, enhancing antioxidant production and reducing oxidative damage (Ahmed et al., 2016). However, Si uptake has not been used as a proxy trait for drought tolerance breeding.

Drought tolerance is a polygenic trait and is subject to genotype by environment interactions, limiting the genotype response to selection efficiency during phenotyping (Souza et al., 2004). The slow progress in developing drought tolerant cultivars has also been attributed to a lack of robust and repeatable methods for screening and maintaining of consistent drought stress conditions (Nhemachena and Kirsten, 2017). As a result, higher genetic gains for yield have been achieved under optimal growing conditions but not as efficiently under drought stress conditions (Ahmed et al., 2007).

Selection of genotypes under both drought and non-stress conditions has the potential to achieve high genetic gains during selection for developing wheat cultivars for the drought prone environments (Trethowan et al., 2002). Screening for drought-tolerant genotypes has been achieved using drought-based grain yield indices under drought conditions in comparison to non-stress conditions. Despite the associated large environmental variances, phenotyping remains fundamental in selecting wheat genotypes that exhibit drought adaptive and constitutive characteristics (Monneveux et

al., 2012, Passioura, 2012, Mwadzingeni et al., 2016a). Evaluating a large panel of genotypes in representative test environments and using robust selection tools has been proposed to counter genotype by environment interactions that confounds phenotypic selection. Multiple environmental trials enable the quantification of genetic and environmental components, and the calculation of yield stability (Mohamed, 2013). Previously, selection for drought tolerance was mainly based on grain yield *per se,* but the inclusion of selection indices has improved selection efficiency (Crespo-Herrera et al., 2018). For instance, indices such as the mean productivity index, stress susceptibility index and stress tolerance index have been developed for improving selection efficiency. These indices have been developed to improve selection efficiency and assist in identifying drought tolerant genotypes (Grzesiak et al., 2019).

Selection for drought tolerance is complex and confounded by environmental variance. Hence, conventional breeding must be complemented with molecular breeding to improve selection efficiency. Natural and controlled environments can be used during phenotypic screening to account for environmental variance (Mwadzingeni, et al., 2016b). Subsequently, molecular data of the genotypes can be generated to identify any markers linked to drought tolerance. The phenotypic and genetic data can then be used in combination to establish marker trait associations for marker-assisted selection (Motawea et al., 2015). The availability of genetic data has improved tremendously in recent years due to the advent of the next generation sequencing (NGS) technologies such as genotyping by sequencing (GBS) for single nucleotide polymorphism (SNP) discovery (Tian et al., 2015). However, the lack of computing capabilities to analyse large-scale data and large panels of individuals remains an obstacle for the full utilization of these technologies in resource-poor countries.

Successful breeding for drought tolerance will depend on the availability of adequate genetic variation for selection. Genetic variation for agronomic traits that could be useful for improving tolerance to drought has been reported previously (Ghaed-Rahimi et al., 2017). World wheat genetic resources are available for improving drought tolerance in locally adapted varieties, including modern and obsolete cultivars, landraces, breeding populations and wild relatives, and are maintained and catalogued by several international and national research programs and genebanks (Mwadzingeni et al., 2017). National research programs should consider assessing the genetic variation for Si uptake and its impact on drought tolerance among the germplasm maintained at these centres to augment other drought tolerance breeding programs. This approach will add a different dimension to the current efforts and will contribute to genetic gains in drought tolerance breeding.

1.6 Integrating Silicon-Use Efficiency in Breeding Programs for Improved Grain Yield and Quality under Stress Conditions

Successful breeding for enhanced Si uptake depends on availability of genetic variation for Si uptake in the breeding population. The effect of Si is most widely studied under stress conditions (Zargar, et al., 2019). Genetic variation for Si-utilization under drought stress conditions has not been widely exploited for improving drought tolerance, despite knowledge of its important role in plant nutrient uptake and remobilization, and protection against biotic and abiotic stresses (Gokulraj et al., 2018, Prasanna et al., 2018). McLarnon et al. (2017) reported significant genotypic variation for Si uptake in grasses. The authors discovered that Si uptake increased under stress, which enhanced drought tolerance. Enhanced Si uptake could be combined with other drought response mechanisms such as drought escape, avoidance, and tolerance to improve wheat productivity in marginal conditions. Efficient Si uptake can be used as a proxy trait for drought tolerance and improved nutritional quality simultaneously. Selecting parental lines with superior Si uptake could provide a basis for developing breeding populations for improved Si uptake. There are indications that Si-use efficiency in wheat is a heritable trait, controlled mostly by additive genes (Jackson et al., 2019), which provide opportunities for early generation selection.

The role of Si in improving drought tolerance in cereal crops and its additive inheritance pattern opens opportunities for exploitation in breeding for drought tolerance and grain quality in wheat. For instance, mandatory incorporation of Si in fertiliser could be encouraged because Si-enhanced fertiliser application could be adopted by farmers as a way to increase yields, grain quality and enhance drought tolerance. However, it would then be imperative for breeders to identify and exploit genetic variation for Si uptake to develop varieties that will efficiently utilise the applied Si for improved drought tolerance, yield and grain quality. This will have positive and cascading effects on wheat productivity, food security and economic gains. Si-use efficiency research has predominantly focused on rice, with recent genome wide studies being carried out on multiple crops (Vatanserver, et al., 2017).

There are efforts to elucidate the genetic basis and inheritance of Si-use efficiency, which will facilitate the establishment of successful breeding programs (Jackson, et al., 2019). However, the large and complex wheat genome could pose a significant challenge in breeding for Si-use efficient wheat. So far, the genetic basis underlying Si uptake and its inheritance have not been established. It is, thus, important to draw insights on the underlying genetics of Si in other crops and infer possible implications for wheat breeding.

Most studies on Si uptake focused on agronomy and physiological responses. However, breeding methods and genetic control of Si uptake in wheat can be improved by adapting knowledge from other related cereal crops, particularly rice. Reportedly, Si uptake is a polygenic trait and its

inheritance is conditioned by many minor genes (Gómez-Merino et al., 2020). Also, the expression of Si uptake is highly affected by genotype by environment interactions, suggesting the need for multi-environmental selection of test genotypes to identify varieties that are efficient in Si uptake, and are high yielding and stable candidates for production or breeding. Due to the additive genetic effect for Si uptake, this review proposes early generation selection of candidate lines after initial crosses are performed. This selection method would enable high genetic gains for superior Si uptake and yield response. Recurrent selection for transgressive segregants would enhance the response to selection for Si uptake. Simultaneous selection for Si uptake, and root biomass and root hairs (which house the Si transporters) would reduce linkage drag of undesirable genes, if any. This may need other complementary breeding tools including mutation induction and molecular marker-assisted breeding. Genetic progress in the breeding for Si uptake is limited by differential responses to different Si formulations, concentrations and rates of Si application, and a lack of knowledge on the genetics of Si-uptake efficiency and genotype by environment interaction effects.

1.7 Conclusions

Drought stress and poor soil fertility are major challenges to crop production in SSA, especially in the context of the growing climate crisis, driving the need for climate smart agriculture and improved varieties. The narrowing crop genetic diversity in modern varieties is likely to hinder progress in breeding for drought tolerance and Si uptake. There is need to harness the genetic diversity of crop species and selection for novel traits such as enhanced Si uptake and improved root systems. Enhancing Si-uptake efficiency in crop species such as wheat is a novel strategy to improve nutrient acquisition and utilization. This is vital in SSA, where inorganic fertiliser use is low. Genetic management of Si uptake in wheat requires greater knowledge of the genes involved, and the nature of gene action for Si uptake, to guide selection. Transgressive selection, marker-assisted and mutation breeding techniques can be used to develop wheat ideotypes with superior Si-uptake efficiency and superior agronomic performance. Gene editing using candidate genes such as the *Lsi1* gene in a reference wheat genome could be a possible strategy to induce elevated Si uptake. Application of Si fertilisers in a range of formulations could be used to improve its availability in SSA soils with low levels of plant-available Si. However, these would need to be affordable and cost-effective Si sources to make this approach viable. Future research direction includes standardizing and developing high throughput phenotyping platforms for Si uptake evaluation, optimizing Si concentration and formulations for the target production environments, identifying QTLs governing Si uptake for marker assisted selection, and developing breeding populations with high Si uptake efficiency, drought tolerance and enhanced grain yield and quality. The above strategies will aid in the development and deployment of silicon-uptake

efficient, drought tolerant and high-quality wheat genotypes to promote sustainable production under drought-prone agro-ecologies.

1.8 References

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CHAPTER 2

The Effect of Silicon Fertilisers on Agronomic Performance of Bread Wheat under Drought Stress and Non-Stress Conditions

Abstract

Drought is one of the major constraints of wheat production, especially in rain-fed wheat production systems. The objective of this study was to evaluate the effects of different silicon fertiliser formulations on the agronomic performance of diverse wheat genotypes under drought-stress conditions. Twenty wheat genotypes were evaluated in field and greenhouse environments under non-stress and drought-stress conditions and two silicon fertiliser formulations (i.e., granular and liquid potassium silicate), and untreated control. The four-way interaction involving genotype, environment, water regime, and silicon formulation had a significant effect ($p < 0.05$) for aboveground biomass, productive spike number, hundred seed weight and grain yield. Granular silicon application was the most effective treatment both under non-stress and drought-stress conditions compared to the liquid and control treatments. Under field and drought conditions, the highest yielding genotype was MC18 which exhibited a mean grain yield of 4.17 $t.ha^{-1}$ with granular silicon, 2.56 $t.ha^{-1}$ with liquid silicon and 2.18 $t.ha^{-1}$ without silicon. The yield of genotype MC18 improved by 91.3% using granular silicon under drought-stress and by 44.6% under non-stress conditions compared with the untreated control. Granular silicon positively affected the drought stress tolerance indices compared to the liquid silicon and untreated control. The principal component biplot analysis revealed that liquid and granular silicon positively impact yield response for all test genotypes under drought-stress and non-stress conditions compared with the control. Silicon application reduced genotype variation for agronomic traits and enhanced agronomic trait relationships under drought-stress conditions. Drought stress tolerance indices are influenced by silicon application. The effect of silicon has a direct and indirect effect on yield and yield components. Silicon fertilisation can be considered as a mitigation measure to cope with the adverse effect of drought stress on wheat.

Keywords: bread wheat, crop management interactions, drought stress, genotype, environment, silicon fertilisation, South Africa, yield components

2.1 Introduction

Bread wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) is a major source of food, feed and industrial raw material with well-defined value chains worldwide (Abou-Elwafa & Shehzad, 2020). Globally, the demand for wheat is increasing due to increased population pressure, climate change, higher input costs, frequency and intensity of biotic and abiotic stresses, and conflict between states (Tadesse et al., 2018). Wheat accounts for 21% of global food production, covering around 250-million hectares of productive agricultural land (Senapati & Semenov, 2020). Consumption of wheat outweighs its production in Africa and Asia (Grote et al., 2021). Africa generates around 25 million tons of wheat grain across 10 million hectares per annum (Tadesse, et al., 2018). However, the regional production is not sufficient to meet demand. Wheat imports in sub-Saharan Africa (SSA) is currently at 26.6 million tonnes per annum. The total wheat production in SSA was 7.5 million tonnes in 2017 from 2.9 million hectares. This accounts for approximately 40% of the potential wheat production in Africa and 1.4% of the global outputs (Tadesse, et al., 2018). Wheat production and productivity in SSA is constrained by many abiotic and biotic factors, notably drought and heat stresses (Frija et al., 2021).

Drought stress associated with climate change limits potential wheat production, especially in rain-fed wheat production systems. Drought limits wheat production by 50 to 90% and affects global food systems (Awan, Ali, & Akmal, 2017). The unpredictability of drought occurrence can lead to severe yield reduction, even after a few consecutive days upon cessation of rain (Kumar et al., 2008). Drought, and heat stress dwindles wheat yields to as low as 2 $t.ha^{-1}$ (Tadesse, et al., 2018). The stage of drought occurrence and severity influence grain development and ultimately yield. Drought stress severely impacts yield gains in wheat by inhibiting the biochemical processes, including chlorophyll and plant water contents and photosynthetic efficiency. Physiological factors such as poor photosynthetic rates and low leaf water potential lead to reduced plant height, spike length, thousand grain weight and grain yield (Khadka et al., 2020). Crop response to drought stress is dependent on the species, genotype, stage of development, intensity and duration of stress. Drought tolerance is governed by the genetic constitution of genotype, the growing environment and crop management options. Complex morphological, biochemical, and physiological attributes are involved in drought tolerance (Grzesiak et al., 2019).

Silicon (Si) is a quasi-essential nutrient, improving nutrient uptake and alleviating various biotic and abiotic stresses in plants, including tolerance to drought, insect damage, fungal infections, salinity, heat and cold temperatures, heavy metal toxicity, soil acidity and nutrient imbalances (Ahanger et al., 2020). Si uptake has been indirectly associated with improved photosynthetic capacity and other biochemical characteristics under biotic and abiotic stresses (Ma & Yamaji, 2006). Si uptake is subject to Si formulation, concentration, volume, plant species and genotypic variations. Most Si-related

research has been focused on the disciplines of pathology and crop science in isolation, but there is a limited effort to integrate this micronutrient into crop improvement programs (Christian et al., 2022).

Silicon is taken up as monosilicic acid via roots and transported through the plant structure using a series of influx and efflux transporters and into cell walls as phytoliths. Phytoliths, which are rigid cell wall structures are made of silica, that improve plant strength and structural support for the above and below ground plant parts leading to increased biomass (Guerriero et al., 2016). Silica deposition in all plant structures facilitates enhanced carbon, nitrogen and phosphorus uptake leading to improved agronomic traits (Li et al., 2018). Influx and efflux transporters are a subgroup of the aquaporin membrane protein family. The efficacy and distribution of Si is dependent on the crop, genotype, the growing environment and their interaction (Ma et al., 2006). The concentrations of Si in soil solution can range between 0.1 to 2 $mM.L^{-1}$. Based on Si utilisation efficiency, crops can be divided into three categories: Si accumulators (Si concentration > 1% and [Si/Ca] ratio > 1); Si excluders (Si concentration < 0.5% and [Si/Ca] ratio < 0.5) and Si intermediates (Si concentration > 0.5 to 1% and [Si/Ca] ratio > 0.5 to 1%) (Guntzer et al., 2012). Wheats are natural silicon uptakers, with optimum Si accumulation occurring twenty days after application (Sapre & Vakharia, 2016). Si dosage rates vary with Si formulations. Ahmad et al. (2016) reported that potassium silicate applied at a rate of 12 $kg.ha^{-1}$ significantly increased plant straw and grain yield in wheat. Whereas Salman et al. (2012) pinpointed that an application of 600 $kg.ha^{-1}$ of calcium silicate had enhanced effects on plant height, panicle length, third internode length and bending moment and stem length. Si formulations play an integral role in efficient uptake in plants. Kowalska et al. (2021) found that the liquid Si formulation applied at 0.3 $L.ha^{-1}$ and powder formulation at 10 $kg.ha^{-1}$, had significant effects on wheat grain yield. However, the authors indicated that on the single wheat cultivar, the soil application was more effective than the foliar application. The objective of this study was to investigate the effects of different silicon fertiliser formulations on the agronomic performance of diverse wheat genotypes under drought-stress conditions.

2.2 Materials and Methods

2.2.1 Plant Materials and Study Sites

The study used 20 wheat genotypes preliminarily selected from the International Maize and Wheat Centre (CIMMYT - Mexico) pre-breeding drought and heat nursery (Table 2.1). The genotypes were previously evaluated for drought tolerance and selected because of higher stress tolerance indices and higher mean grain yields under drought stress (Mwadzingeni et al., 2016). The study was conducted under greenhouse and field conditions. Two greenhouse trials were conducted at the University of

KwaZulu-Natal (UKZN) in Pietermaritzburg (29° 37′ S, 30° 24′ E). Hereafter referred to as E1 (Greenhouse 2017) and E2 (Greenhouse 2018). The greenhouse environment had day and night temperatures of 25°C and 15°C, respectively. Day and night humidity was maintained at between 45 and 55%, respectively. The field experiment was conducted at the Ukulinga Research Farm, [(29° 40' S, 30° 24' E); 806 m above sea level)] during the 2019 cropping season. The weather conditions prevalent at the time of the experiment was recorded (Table 2.2). Weather data was recorded on average maximum and minimum temperatures, average maximum and minimum humidity, average total radiation, and average evapotranspiration.

Table 2.1 List of wheat genotypes and their pedigrees used in this study

Genotype	Pedigree
MC1	QUAIU
MC2	RL6043/4*NAC//PASTOR/3/BAV92/4/ATTILA/BAV92//PASTOR
MC3	PRL/2*PASTOR*2//SKAUZ/BAV92
MC4	MUNAL #1
MC5	CROC_1/AE.SQUARROSA (205)//KAUZ/3/SLVS
MC6	WBLL1//UP2338*2/VIVITSI
MC7	SW94.60002/4/KAUZ*2//DOVE/BUC/3/KAUZ/5/SW91-12331
MC8	ACHTAR/4/MILAN/KAUZ//PRINIA/3/BAV92
MC9	ONIX/4/MILAN/KAUZ//PRINIA/3/BAV92
MC10	FRET2*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/5/ONIX
MC11	CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/2*FRAME
MC12	SOKOLL*2/ROLF07
MC13	PRL/2*PASTOR
MC14	ROLF07/YANAC//TACUPETO F2001/BRAMBLING
MC15	SW89.5277/BORL95//SKAUZ
MC16	BAU/KAUZ//PASTOR
MC17	CNO79//PF70354/MUS/3/PASTOR/4/BAV92/5/FRET2/KUKUNA//FRET2/6/MILAN/KAUZ//PRINIA/3/BAV92
MC18	C80.1/3*BATAVIA//2*WBLL1/3/ATTILA/3*BCN*2//BAV92/4/WBLL1*2/KURUKU
MC19	BABAX/3/PRL/SARA//TSI/VEE#5/4/CROC_1/AE.SQUARROSA (224)//2*OPATA
MC20	JIANG 4/4/DUCULA

Table 2.2 Mean monthly weather data during the 2019 field trial at Ukulinga Research Farm at the University of KwaZulu-Natal

Month	Tmax (°C)	Tmin (°C)	RHmax (%)	RHmin (%)	Rs (MJ/m^2)	ET (mm)
August	24	11.7	86	36	12.2	85
September	25	11.9	89	34	15.7	99
October	27	13.7	90	36	17.7	121
November	25	15.4	94	55	16.2	99

Abbreviations: Tmax: average maximum temperature; Tmin: average minimum temperature; RHmax: average maximum relative humidity; RHmin: average minimum relative humidity; Rs: average total radiation; ET: average evaporation.

2.2.2 Experimental Design and Treatments

Treatments were laid out in a 20 x 3 x 2 factorial experiment using a randomized complete block design with three replications. Treatments comprised of the 20 genotypes, three silicon applications (granular, liquid and control), and two water regimes (drought stress (DS) and non-stress (NS)). The genotypes were subjected to two silicon formulations and untreated control. A slow-release granular potassium silicate ($KSiO_4$) (17mm AgriSil) formulation was applied at planting, and a liquid ($KSiO_4$) (17mm AgriSil) formulation, applied weekly at 150ppm with a drench volume of 500ml/pot until anthesis. The slow-release granulated silicon was applied at planting at 3g per pot and evenly dispersed in the top layer of the growing media. For the field experiment, the liquid Si was applied at 150ppm with a drench volume of 50ml per planting station, and the 1g granular Si application was evenly distributed per plant at planting. Drought-stress was imposed at booting, withholding water up to 35% field capacity until maturity, according to Zadoks et al. (1974). Under non-stress conditions, the plants were well watered throughout the growing period until maturity. A custom-made plastic mulch rain-out system was used to cover the soil to inhibit rainwater infiltration in the experimental area. All other agronomic practices followed the standard guidelines for wheat production in South Africa (DAFF,2016).

2.2.3 Data Collection

Data were collected on the following preharvest and postharvest phenotypic traits. *Preharvest data*: Plant height (PH) measured in centimetres (cm) from the ground to the tip of the spike. The productive tiller number (TN) and the productive spike number (PS) were recorded at physiological maturity. *Postharvest data*: total aboveground biomass (AGB) measured in grams per plant. Spike length (SL) was measured in cm. The number of spikelets per spike (SPS) and the number of kernels per spike (KPS) were recorded from the main tillers of five randomly selected and tagged plants. Hundred seed weight (HSW) was determined by measuring 100 randomly sampled seed after harvesting and reported as g/100 seed, and harvest index per plant (HI) was computed as the (grain yield / biological yield) per plant x 100. Grain yield was measured and converted to tons per hectare ($t.ha^{-1}$) using the plant population of 100 and 134 plants per square meter for greenhouse and field experiments, respectively.

2.2.4 Data Analysis

The quantitative data was subjected to a combined analysis of variance (ANOVA), agronomic means tables, drought-tolerance/susceptibility indices and principal component analysis were deduced for the two different Si formulations and untreated control, under drought-stress and non-stress conditions using Genstat 18th version, VSN, International (Payne & Roger, 2015), and R (R Core Development Team, 2020) to describe the magnitude of the agronomic trait relationships.

Five drought-tolerance/susceptibility indices were calculated based on yield data under drought-stress and non-stress conditions, using the formulae below:

Stress tolerance index $(STI) = \frac{Yp \times Ys}{(\bar{Y}p^2)}$ (Fernandez, 1992)

Stress susceptibility index $(SSI) = \frac{1-\left(Ys/Yp\right)}{1-\left(Ys/\bar{Y}p\right)}$ (Fischer & Maurer, 1978)

Yield index $(YI) = \frac{Ys}{\bar{Y}s}$ (Gavuzzi et al., 1997)

Yield stability index $(YSI) = \frac{Ys}{Yp}$ (Bouslama & Schapouch, 1984)

Tolerance $(TOL) = Yp - Ys$ (Rosielle & Hambelin, 1981)

2.3 Results

2.3.1 Agronomic Performance of Wheat Genotypes under Si Application, Drought, Testing Sites and Their Interactions

The combined analysis of variance (ANOVA) revealing a four-way interaction between genotype, water regime, Si fertiliser application and environment is shown in Table 2.3. Results showed a significant interaction effect of the four factors on the number of productive spikes (PS) and hundred seed weight (HSW) ($p < 0.05$) and aboveground biomass (AGB) and grain yield (GY) ($p < 0.01$). The interactions of genotype, water regime and treatment; genotype, treatment, and environment; and genotype by treatment were significant for PS, AGB and GY.

2.3.2 Mean Genotype Performance for Agronomic Traits

2.3.2a Greenhouse experiments

The mean genotype performance (Table 2.4) for the top five genotypes based on yield under drought stress, shows that MC10 produced the highest yields across the greenhouse environments. The mean data for all the test genotypes are found in Appendices 2.2A-2.2C. Genotype MC10 was the highest yielding under drought stress, across all three Si applications. Under drought stress and greenhouse conditions, granular Si (with grain yield of 9.65t.ha^{-1}) and liquid Si (6.94t.ha^{-1}) improved grain yield for MC10 compared to the control (7.88t.ha^{-1}). Granular Si improved the genotypic performance of MC10 across all agronomic traits tested compared to the untreated control. Genotype MC10, under drought stress and granular Si application, performed better than the untreated control under non-stress conditions, for the following traits, PH, PS, SL, and SPS. Liquid Si application under drought stress rendered better genotype performance than the untreated control under non-stress for the following traits: TN, PS, SL, SPS and KPS. Genotype MC6 is the second-best performing genotype for the granular Si and untreated control treatment. The granular Si enhanced the agronomic performance of MC6 by improving all assessed traits except for HI. Genotype MC6, treated with granular Si under drought stress, had outperformed the MC6 untreated control under non-stress for the following traits: PH, TN, PS, SL, SPS, HI, and AGB. Genotype MC11 was amongst the top 5 high-yielding genotypes under DS. Both granular and liquid Si improved all traits under DS compared to the control. MC11, treated with granular and liquid SI under DS, performed better than the untreated control under NS for PH, TN, PS, SL and SPS. Genotype performance was the best in the following order: granular Si > liquid Si > control. Comparative genotype analysis using data presented in Appendices 2.2A-2.2C, shows that many of the test genotypes improved their agronomic traits in the presence of granular Si compared to the control. The liquid Si did improve the agronomic traits, but the extent of improvement depended on the genotypes and traits involved.

2.3.2b Field experiments

The mean genotypic performance of the top 5 performing genotypes under field conditions is summarised in Table 2.5. The complete mean data for all the test genotypes are presented in Appendices 2.2D-2.2F. Under DS and NS conditions, granular Si induced better genotype performance for all agronomic traits than for untreated control. Genotype MC10 performed better with liquid Si than the untreated control for traits PH, TN, PS, SPS, KPS, HSW, AGB and GY under DS. Under NS conditions, liquid Si improved trait performance for SL, SPS, KPS, AGB and GY, compared to the untreated control. Variation in performance between the liquid and granular Si is genotype dependent. Genotype MC19, had a GY of 1.98t.ha^{-1} under control, 3.17t.ha^{-1} with liquid Si and 2.14t.ha^{-1} with granular Si. Of

all the genotypes tested, 7 genotypes generated grain yields < 2t.ha^{-1}, with the control treatment and under DS. Whereas with liquid Si, only 2 genotypes had grain yields < 2t.ha^{-1} and granular Si had no genotypes with yields < 2t.ha^{-1} under DS. Genotype MC18, treated with granular Si yielded 4.17t.ha^{-1} and was the top yielding genotype under DS compared to the grand mean yield response of 2.13t.ha^{-1} for the control and 2.56t.ha^{-1} for the liquid Si application. Granular Si effectively increased the GY of MC18 by 95.8% over the control treatment under DS, whereas liquid Si application increased GY by 20.2% over the untreated control. Under NS conditions, MC18 generated 5.19t.ha^{-1} with granular Si, 3.59t.ha^{-1} for the control and 4.75t.ha^{-1} for the liquid Si. Granular Si increased the GY by 44.6% and liquid Si by 32.3% over the untreated control, under NS conditions. Genotype MC14 is found amongst the top 5 performing genotypes for the liquid and granular Si. The granular Si formulation performed better for agronomic traits, PH, PS, SL, SPS, HI and GY.

Table 2.3 Combined analysis of variance (ANOVA) and significant tests of wheat genotypes tested against two Si formulations and untreated control, under two water regimes and across three environments.

Source of variation	df	PH	TN	PS	AGB	SL	SPS	KPS	HSW	HI	GY
Genotype (G)	**19**	629.66***	5.90***	6.70***	87.25***	12.27***	24.59**	365.70***	3.31***	119.36***	**14.58*****
Water Regime (WR)	1	5785.11***	26.20***	17.92***	5502.49***	0.18	3.96	6962.97***	479.13***	17968.27***	**7410.64*****
Treatment (T)	2	658.74***	70.83***	115.30***	1593.62***	18.56***	31.00***	661.13***	3.36***	259.82***	**152.18*****
Environment (E)	2	15310.31***	11044.60***	10701.60***	114279.16*	718.68***	792.17***	464149.12***	602.96***	9693.93***	**29.46*****
G x WR	19	33.68	1.75	1.62*	43.64**	0.16	0.78	21.67	0.57***	48.58**	**8.43****
G x T	38	29.25	1.48	1.93***	40.50**	0.20	0.79	26.69	0.21	20.26	**6.13****
WR x T	2	690.02***	1.08	0.89	25.10	0.522	3.31	205.73***	1.45**	45.08	**46.78*****
G x E	38	114.07***	3.45***	3.47***	79.67***	2.14***	4.30***	59.04***	0.87***	73.78***	**10.89*****
WR x E	2	319.04***	23.51***	9.69***	400.33***	5.614***	3.72*	352.22***	135.32***	4885.17***	**280.88*****
T x E	4	53.69	13.31***	29.09***	567.91***	2.50***	6.61***	187.81***	2.65***	68.12*	**99.65*****
G x WR X T	38	22.50	1.51	1.41*	39.66*	0.19	0.65	20.66	0.28	21.01	**5.93***
G X WR X E	38	30.72	1.15	1.08	35.95	0.23	0.88	29.54*	0.37*	31.42	**10.25*****
G x T x E	76	22.70	1.24	1.49**	38.36**	0.25	1.25	19.77	0.23	25.30	**6.86*****
WR X T X E	4	161.49***	3.80**	3.48**	70.87*	1.61***	7.11***	73.86**	1.05**	24.55	**59.43*****
G X WR X T X E	76	21.36	1.30	1.30*	40.33**	0.23	0.96	19.49	0.31*	22.54	**5.68****
Residual	718	25.43	1.11	0.92	25.98	0.24	1.16	20.26	0.24	25.51	**3.68**

Abbreviations: df: degrees of freedom; T: Treatment (untreated control + liquid Si + granular Si); PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; AGB: aboveground biomass dry weight per plant (g); SL: spike length; SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g); HI: harvest index , GY:-Grain yield ($t.ha^{-1}$); *,**,*** Level of significance at 0.05, 0.01 and <0.001 respectively.

Table 2.4 Means for 10 agronomic traits of the top 5 wheat genotypes ranked based on the grain yield for each treatment under drought-stressed and non-stressed conditions across greenhouse environments.

Gen	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
Control																				
MC10	92.4	93.24	2.25	2.64	2.18	2.42	9.77	9.39	19.86	19.17	35.79	36.08	3.66	4.97	5.98	9.33	55.14	53.39	7.88	9.71
MC6	95.82	100.65	2.83	2.47	2.72	2.44	9.54	9.11	21.56	21.58	33.71	39.81	2.62	4.5	7.64	9.78	43.02	61.17	6.93	11.47
MC7	84.89	93.05	2.74	2.61	2.65	2.61	9.29	9.04	19.03	20	35.56	45.14	2.87	4.85	6.61	9.74	51.56	60.70	6.5	12.77
MC11	94.55	99.06	2.75	2.68	2.64	2.61	9.41	8.84	19.19	18.11	31.14	35.69	2.96	5.92	6.38	9.67	42.96	59.39	6.18	13.79
MC16	92.16	97.53	2.86	2.86	2.78	2.69	10	9.67	20.14	19.81	34.83	38.93	3.01	4.66	6.51	8.43	47.00	59.82	6.17	11.02
Liquid Si																				
MC10	88.71	98.37	2.67	2.86	2.64	2.81	10.29	10.15	20.86	21.06	37.58	40.14	3.19	5.08	6.87	10.72	50.88	57.60	6.94	12.27
MC1	90.41	92.61	3.11	3.06	3.03	3.06	9.37	9.35	20.94	21.47	39.61	44.69	2.74	4.21	7.300	11.15	49.48	61.63	6.85	11.42
MC11	103.15	101.9	3.05	2.81	2.97	2.75	9.62	9.90	19.58	20.58	33.47	39.08	3.15	5.46	7.58	10.88	45.20	57.40	6.42	11.96
MC9	96.13	97.32	2.81	3.03	2.88	3.03	10.1	10.29	19.49	20.67	32.65	39.14	2.76	4.67	6.98	9.25	44.13	55.54	6.16	10.09
MC5	89.56	98.74	2.83	2.83	2.75	2.83	8.95	9.11	20.75	21.31	38.03	45.86	2.82	4.68	8.01	10.65	39.61	58.45	5.98	11.36
Granular																				
MC10	95.89	95.18	2.64	3.00	2.61	3.03	10.06	9.89	20.08	20.36	35.97	36.5	3.72	4.99	6.8	9.28	49.86	58.65	9.65	12.05
MC6	102.94	106.49	3.61	3.5	3.53	3.50	9.71	9.32	22.14	21.61	35.44	42.69	3.11	5.14	10.01	13.28	44.13	61.47	8.06	16.32
MC1	89.67	94.56	3.36	3.32	3.36	3.32	9.34	9.25	21.00	20.94	42.21	44.47	2.98	4.75	8.63	12.69	54.64	65.41	7.44	13.41
MC3	89.99	95.94	3.03	3.18	2.92	3.07	9.18	9.46	18.86	19.67	33.61	40.06	3.38	5.44	7.96	11.37	53.32	61.40	6.94	13.97
MC11	102.12	100.83	3.11	3.00	3.08	2.92	9.58	9.69	19.33	19.69	34.14	36.06	3.07	5.53	7.82	9.99	42.96	59.39	6.83	11.7
Mean	**89.94**	**95.51**	**2.91**	**2.94**	**2.79**	**2.89**	**9.79**	**9.71**	**20.27**	**20.43**	**64.98**	**40.97**	**2.86**	**4.86**	**7.17**	**10.56**	**46.5**	**58.45**	**5.85**	**12.06**
SED	**4.660**	**4.660**	**0.365**	**0.365**	**0.363**	**0.363**	**0.374**	**0.374**	**0.973**	**0.973**	**3.474**	**3.474**	**0.447**	**0.447**	**1.467**	**1.467**	**4.61**	**4.61**	**1.70**	**1.70**
LSD (5%)	**9.157**	**9.157**	**0.717**	**0.717**	**0.713**	**0.713**	**0.734**	**0.734**	**1.913**	**1.913**	**6.827**	**6.827**	**0.878**	**0.878**	**2.882**	**2.882**	**9.05**	**9.05**	**3.34**	**3.34**
CV %	**1.1**	**1.1**	**2.5**	**2.5**	**2.5**	**2.5**	**0.3**	**0.3**	**0.3**	**0.3**	**2.5**	**2.5**	**1.4**	**1.4**	**2.4**	**2.4**	**1.7**	**1.7**	**4.5**	**4.5**

Abbreviations: Gen: Genotype; DS: drought stressed; NS: non-drought stressed; PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; AGB: aboveground biomass dry weight per plant (g); SL: spike length; SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g/100 seed); HI: harvest index , GY:-Grain yield ($t.ha^{-1}$). Mean overall mean for the three treatments under drought-stressed and non-stressed conditions.

Table 2.5 Means for 10 agronomic traits of the top 5 wheat genotypes ranked based on the grain yield for each treatment under drought-stressed and non-stressed conditions across field environment.

Gen	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
Control																				
MC2	92.2	94.67	11.5	11.43	9.80	10.57	11.93	12.22	21.22	21.11	48.33	53.7	3.00	2.78	43.17	41.72	55.33	53.86	3.01	4.00
MC9	92.67	97.97	11.23	12.53	11.13	12.00	11.98	12.58	20.56	20.22	45.77	52.9	3.11	3.00	33.11	29.25	48.00	52.33	2.78	3.85
MC6	82.6	92.23	10.77	12.13	10.77	11.19	11.00	12.25	19.44	19.22	44.43	50.03	3.11	3.28	30.5	36.83	49.33	49.00	2.62	3.78
MC10	89.07	99.00	9.98	13.77	8.15	10.65	12.27	12.48	19.89	20.89	42.67	44.66	3.22	3.33	28.61	31.25	53.00	54.41	2.51	3.56
MC1	86.19	94.47	11.84	11.34	10.84	10.8	11.68	11.70	19.67	20.67	44.43	48.23	2.83	2.94	29.06	38.56	49.67	53.00	2.48	4.52
Liquid Si																				
MC14	91.84	94.31	14	13.43	13.2	12.87	12.67	12.92	19.66	18.46	51.84	51.53	3.39	2.78	44.89	50.11	56.33	53.00	3.58	3.63
MC10	93.04	99.00	11.8	12.1	11.57	12	12.22	12.82	20.33	21	44.9	48.66	3.44	3.33	33.61	43.56	55.33	51.33	3.28	5.10
MC3	89.34	93.69	13.35	14.67	14.19	14.67	11.21	11.43	19.78	19.78	51	54.23	3.00	3.11	37.78	47.11	54.67	53.33	3.28	4.06
MC19	89.84	88.9	12.31	13.57	12.31	13.47	11.28	12.04	19	19.56	54	52.66	2.72	2.61	28.5	43.67	53.67	50.33	3.17	3.46
MC15	98	98.67	13.77	12.33	13.67	11.67	12.57	12.83	20.56	20.45	51.33	51.33	2.56	3.11	47.11	46.5	54.00	56.00	3.08	3.70
Granular																				
MC18	90.66	91.35	12.8	14.43	11.8	14.3	12.01	12.02	21.22	20.78	56.00	54.53	3.06	2.94	45.39	47.44	56.67	60.33	4.17	5.19
MC14	92.20	88.50	13.33	14.77	14.10	15.23	12.93	12.7	20.45	19.67	50.33	49.43	2.67	3.33	43.56	47.39	54.00	55.67	3.59	4.10
MC3	93.40	88.31	13.23	13.20	13.10	13.00	13.15	12.08	20.11	20.11	50.70	48.2	2.94	3.00	45.17	38.22	56.67	54.00	3.39	3.85
MC16	93.00	91.84	12.53	14.77	12.53	14.33	11.82	11.69	21.67	20.89	51.33	53.23	2.83	2.67	28.83	46.25	51.33	50.00	3.13	3.43
MC5	96.50	96.66	12.15	14.03	11.67	13.7	11.13	11.73	20.22	20.00	56.10	52.2	2.78	2.56	49.78	52.67	53.67	53.00	3.00	3.26
Mean	**90.10**	**92.83**	**12.07**	**12.95**	**11.99**	**12.56**	**11.72**	**11.96**	**20.42**	**20.46**	**49.56**	**52.8**	**2.94**	**2.93**	**36.25**	**43.02**	**53.43**	**53.92**	**2.59**	**3.69**
SED	**2.477**	**2.477**	**1.361**	**1.361**	**1.230**	**1.230**	**0.451**	**0.451**	**0.641**	**0.641**	**3.752**	**3.752**	**0.269**	**0.269**	**6.68**	**6.68**	**2.78**	**2.78**	**0.41**	**0.41**
LSD 5%	**4.880**	**4.880**	**2.682**	**2.682**	**2.423**	**2.423**	**0.889**	**0.889**	**1.262**	**1.262**	**7.390**	**7.390**	**0.530**	**0.530**	**13.16**	**13.16**	**5.47**	**5.47**	**0.08**	**0.81**
cv%	**0.9**	**0.9**	**4.4**	**4.4**	**3.6**	**3.6**	**0.9**	**0.9**	**0.8**	**0.8**	**3.9**	**3.9**	**3.3**	**3.3**	**7.4**	**7.4**	**1.1**	**1.1**	**1.6**	**1.6**

Abbreviations: Gen: Genotype; DS: drought stressed; NS: non-drought stressed; PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; AGB: aboveground biomass dry weight per plant (g); SL: spike length; SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g/100 seed); HI: harvest index , GY:-Grain yield ($t.ha^{-1}$). Mean overall mean for the three treatments under drought-stressed and non-stressed conditions.

2.3.3 Stress Tolerance Indices

Across all the treatments, the differences in the magnitude of the DS indices varied amongst the genotypes tested (Table 2.6). Under granular Si application, a larger proportion of genotypes showed higher stress tolerance values, across all DS tolerance indices compared to the untreated control. Granular Si improved the Yp and Ys for 17 and 18 of the 20 genotypes tested, respectively, compared to the untreated control. The genotypes, with enhanced Yp and Ys using Granular Si compared to the untreated control are: MC1, MC2, MC3, MC4, MC5, MC6, MC8, MC9, MC10, MC13, MC14, MC15, MC16, MC18 and MC19. These genotypes had improved drought stress tolerance indices for STI, SSI and YI of the granular Si compared to the control treatment. Genotypes MC20 and MC12 had higher Yp for the granular Si but not the Ys compared to the control. The TOL index showed that 6 of the 20 genotypes tested were more tolerant when treated with granular Si in comparison to the untreated control. Liquid Si did not have high drought selection indices compared to the granular Si for both Yp and Ys conditions. Liquid Si did improve the Ys of genotypes MC1, MC3, MC4, MC5, MC8, MC11, MC15, MC17 and MC19, compared to the untreated control. The effect of liquid Si on drought selection indices varied with genotype. For STI: MC1, MC4, MC5, MC10, MC15 and MC19 were higher for liquid Si than the untreated control. Four genotypes; MC1, MC6, MC10 and MC19 had higher SSI when treated with liquid Si than the control. Seven genotypes, namely, MC1, MC3, MC4, MC5, MC8, MC11, MC15, MC17 and MC19 had a higher YI with liquid Si compared to the control. The liquid Si application had a higher tolerance level compared to the untreated control for the following genotypes: MC2, MC3, MC4, MC5, MC7, MC8, MC9, MC11, MC13, MC14, MC15, MC17 and MC20.

Table 2.6 Mean grain yield, under drought-stress and non-stress conditions, and drought selection indices for wheat genotypes without silicon, liquid Si and granular Si application evaluated across three environments.

Genotypes	Treatment	YP	YS	STI	SSI	YI	YSI	TOL
MC1	Control	7.98	4.85	0.45	0.82	1.02	0.61	3.13
	Liquid Si	9.03	5.17	0.54	0.97	1.09	0.57	3.86
	Granular Si	9.91	5.78	0.67	1.11	1.21	0.58	4.13
MC2	Control	9.93	4.35	0.50	1.06	0.91	0.44	5.58
	Liquid Si	7.91	4.09	0.38	0.86	0.86	0.52	3.82
	Granular Si	11.38	5.01	0.66	1.22	1.05	0.44	6.37
MC3	Control	9.86	4.50	0.52	1.06	0.95	0.46	5.36
	Liquid Si	7.60	4.98	0.44	0.74	1.05	0.66	2.62
	Granular Si	10.6	5.75	0.71	1.20	1.21	0.54	4.85
MC4	Control	9.30	3.64	0.39	1.00	0.76	0.39	5.66
	Liquid Si	8.65	4.20	0.42	0.94	0.88	0.49	4.45
	Granular Si	11.23	4.38	0.57	1.16	0.92	0.39	6.85
MC5	Control	9.95	3.91	0.45	1.05	0.82	0.39	6.04
	Liquid Si	8.90	4.96	0.51	0.95	1.04	0.56	3.94
	Granular Si	11.24	4.74	0.62	1.18	1.00	0.42	6.50
MC6	Control	8.91	5.49	0.57	0.94	1.15	0.62	3.42
	Liquid Si	9.28	4.37	0.47	1.00	0.92	0.47	4.91
	Granular Si	11.96	6.31	0.88	1.48	1.33	0.53	5.65
MC7	Control	10.14	5.10	0.60	1.10	1.07	0.50	5.04
	Liquid Si	4.24	4.34	0.21	-0.04	0.91	1.02	-0.10
	Granular Si	9.11	4.96	0.53	0.98	1.04	0.54	4.15
MC8	Control	9.71	4.13	0.47	1.04	0.87	0.43	5.58
	Liquid Si	7.26	4.24	0.36	0.77	0.89	0.58	3.02
	Granular Si	10.27	4.55	0.54	1.09	0.96	0.44	5.72
MC9	Control	10.06	4.90	0.57	1.09	1.03	0.49	5.16
	Liquid Si	8.04	4.90	0.46	0.83	1.03	0.61	3.14
	Granular Si	11.49	5.01	0.67	1.23	1.05	0.44	6.48
MC10	Control	8.30	6.09	0.59	0.78	1.28	0.73	2.21
	Liquid Si	9.88	5.72	0.66	1.10	1.20	0.58	4.16
	Granular Si	9.56	7.39	0.82	1.12	1.55	0.77	2.17
MC11	Control	10.59	4.72	0.58	1.13	0.99	0.45	5.87
	Liquid Si	9.33	5.12	0.56	1.01	1.08	0.55	4.21
	Granular Si	8.96	5.53	0.58	0.95	1.16	0.62	3.43
MC12	Control	7.50	4.55	0.40	0.77	0.96	0.61	2.95
	Liquid Si	7.30	4.23	0.36	0.77	0.89	0.58	3.07
	Granular Si	7.88	4.41	0.40	0.84	0.93	0.56	3.47
MC13	Control	10.52	4.80	0.59	1.13	1.01	0.46	5.72
	Liquid Si	6.73	4.67	0.37	0.62	0.98	0.69	2.06
	Granular Si	10.63	5.19	0.64	1.16	1.09	0.49	5.44

Genotypes	Treatment	YP	YS	STI	SSI	YI	YSI	TOL
MC14	**Control**	8.61	4.61	0.46	0.92	0.97	0.54	4.00
	Liquid Si	7.4	4.45	0.38	0.77	0.93	0.60	2.95
	Granular Si	9.53	5.36	0.59	1.04	1.13	0.56	4.17
MC15	**Control**	9.65	3.9	0.44	1.03	0.82	0.40	5.75
	Liquid Si	9.39	4.77	0.52	1.01	1.00	0.51	4.62
	Granular Si	11.74	4.6	0.63	1.21	0.97	0.39	7.14
MC16	**Control**	8.34	4.82	0.47	0.88	1.01	0.58	3.52
	Liquid Si	7.85	4.07	0.37	0.86	0.86	0.52	3.78
	Granular Si	9.76	5.52	0.63	1.07	1.16	0.57	4.24
MC17	**Control**	9.46	4.74	0.52	1.02	1.00	0.50	4.72
	Liquid Si	8.72	4.95	0.50	0.93	1.04	0.57	3.77
	Granular Si	9.38	5.07	0.55	1.01	1.07	0.54	4.31
MC18	**Control**	9.59	4.5	0.50	1.03	0.95	0.47	5.09
	Liquid Si	8.56	2.98	0.30	0.96	0.63	0.35	5.58
	Granular Si	10.13	4.69	0.55	1.09	0.99	0.46	5.44
MC19	**Control**	8.44	3.67	0.36	0.94	0.77	0.43	4.77
	Liquid Si	9.52	4.35	0.48	1.02	0.91	0.46	5.17
	Granular Si	9.63	4.34	0.49	1.03	0.91	0.45	5.29
MC20	**Control**	8.34	4.6	0.45	0.89	0.97	0.55	3.74
	Liquid Si	7.32	4.54	0.39	0.74	0.95	0.62	2.78
	Granular Si	9.51	4.33	0.48	1.02	0.91	0.46	5.18

Abbreviations: YP: yield under non-stressed conditions; YS: yield under stressed conditions; STI: stress tolerance index; SSI: stress susceptibility index; YI: yield index; YSI: yield stability index and TOL: tolerance.

2.3.4 Principal Component Biplots

The principal components biplots (Figures 2.1A and 2.1B) illustrated the relationships between the agronomic traits and genotypes under DS and NS conditions, respectively, without Si application. The degree of the angle between agronomic trait vector lines indicates the degree of relationship between those traits. Genotypes MC2, MC11, MC16, MC6, MC9, MC13, MC7, MC12, MC1 and MC17 were plotted close to the agronomic vector lines for GY, AGB, HI, SL, SPS and KPS (Figure 2.1A), suggesting these genotypes are highly associated with the above-mentioned traits. In Figure 2.1A, the traits that fall on the positive side of PC1 and PC2 are GY, HSW, SL, PH, AGB, TN and PS. Genotypes which are plotted on the positive side of PC1 include MC13, MC3, MC5, MC11, MC2, MC14, MC19, MC16, MC6, MC9 and MC13, under stress conditions. Under NS conditions (Figure 2.1B), the traits which have positive traits vector lines include GY, AGB, KPS, HI, SL and SPS, under PC1, whilst the traits HSW, AGB and PH are acutely close to the GY and KPS, HI, SL and SPS are closely related. Genotypes which are plotted on the positive side of PC1 include, MC7, MC6, MC12,

MC1, MC2, MC17 and MC18. The majority of the genotypes are clustered close to the point of origin under both drought-stress and non-stress conditions.

In the presence of the liquid Si application, the genotypes are slightly more distributed under both DS and NS conditions (Figures 2.1C and 2.1D), compared to the untreated control. Under drought-stress conditions (Figure 2.1C), the traits which fall on the positive side of PC1 are GY, HI, HSW, AGB, PS, TN, PH and SL. Genotypes which were plotted close to the agronomic trait vector lines are MC12, MC16, MC10, MC20, MC5, MC14 and MC2. HSW and AGB are closely related whilst traits PS, TN and GY are also highly influential on each other. Under NS conditions (Figure 2.1D), the traits which fall on the positive side of PC1 are SPS, HSW, GY, PH, HI, KPS and SL. Genotypes which were plotted on the positive side of PC1 are: MC10, MC11, MC15, MC6, MC12, MC18, MC17, MC9, MC5 and MC10.

In the presence of granular and under DS, several genotypes are clustered near the axis of PC1 and PC2 (Figures 2.1E and 2.1F). With granular Si, the trait associations have shifted more towards the positive side of PC1 compared to the liquid Si and the untreated control (Figure 2.1E). Most of the genotypes are clustered near the point of origin, except for MC10, MC8, MC19, MC20, MC4 and MC6. The genotypes which fall on the positive side of PC1 are MC3, MC16, MC9, MC15, MC6, MC10, MC14, MC1 and MC11. PH and HSW are highly associated with GY under DS conditions. The traits which fall on the positive side of PC1 are PH, SL, HSW, GY, PG, AGB, PS and TN. Under NS conditions (Figure 2.1F), there is a noticeable shift in the agronomic traits and genotypes when compared to the untreated control. Agronomic trait vector lines which fall on the positive side of PC1 are SL, AGB, PS, GY, TN, PH, and HSW. Under NS conditions, the genotypes which fall on the positive side of PC1 are MC5, MC19, MC20, MC6, MC4, MC14, MC16, MC10, MC2, MC3, MC11, MC9 and MC15. PH influences GY and TN influences AGB due to the proximity.

The effect of the silicon treatments under DS and NS are indicated by Figures 2.2 and 2.3, respectively. Under DS (Figure 2.2), the granular silicon treatment cluster is predominantly found on the positive side of PC1 and partly on the negative side of PC1. Liquid Si straddles both sides of PC1 and the untreated control is predominantly on the negative side of PC1. Under both liquid Si and granular Si, the common agronomic trait vectors are PS, TN, SL, KPS, GY, HSW, PH, AGB HI, and SPS. Notably the traits; SPS, KPS and HI; PH and AGB and, SL and GY, are closely associated due to its acute angles, across all three treatments. The untreated control showed only one genotype falls within the lower right quartile and none fall within the upper right quartile of the PCA biplot.

Under non-stress conditions (Figure 2.3), there is a noticeable shift in the treatment clusters compared to its placement under DS. The granular Si applications cluster is larger with majority of the genotypes within the positive side of PC1 and five genotypes located on the negative side of PC1. Many of the genotypes tested under liquid Si, shifted closer to the origin and the positive side of PC1. Majority

of the genotypes under the untreated control, shifted to the left of PC1 with only three genotypes positioned on the lower right quartile of PC1. All the agronomic traits shifted towards the positive side of PC1 and all traits fell within the liquid and granular Si clusters. All agronomic traits have acute angles between them and a higher relatedness between these traits.

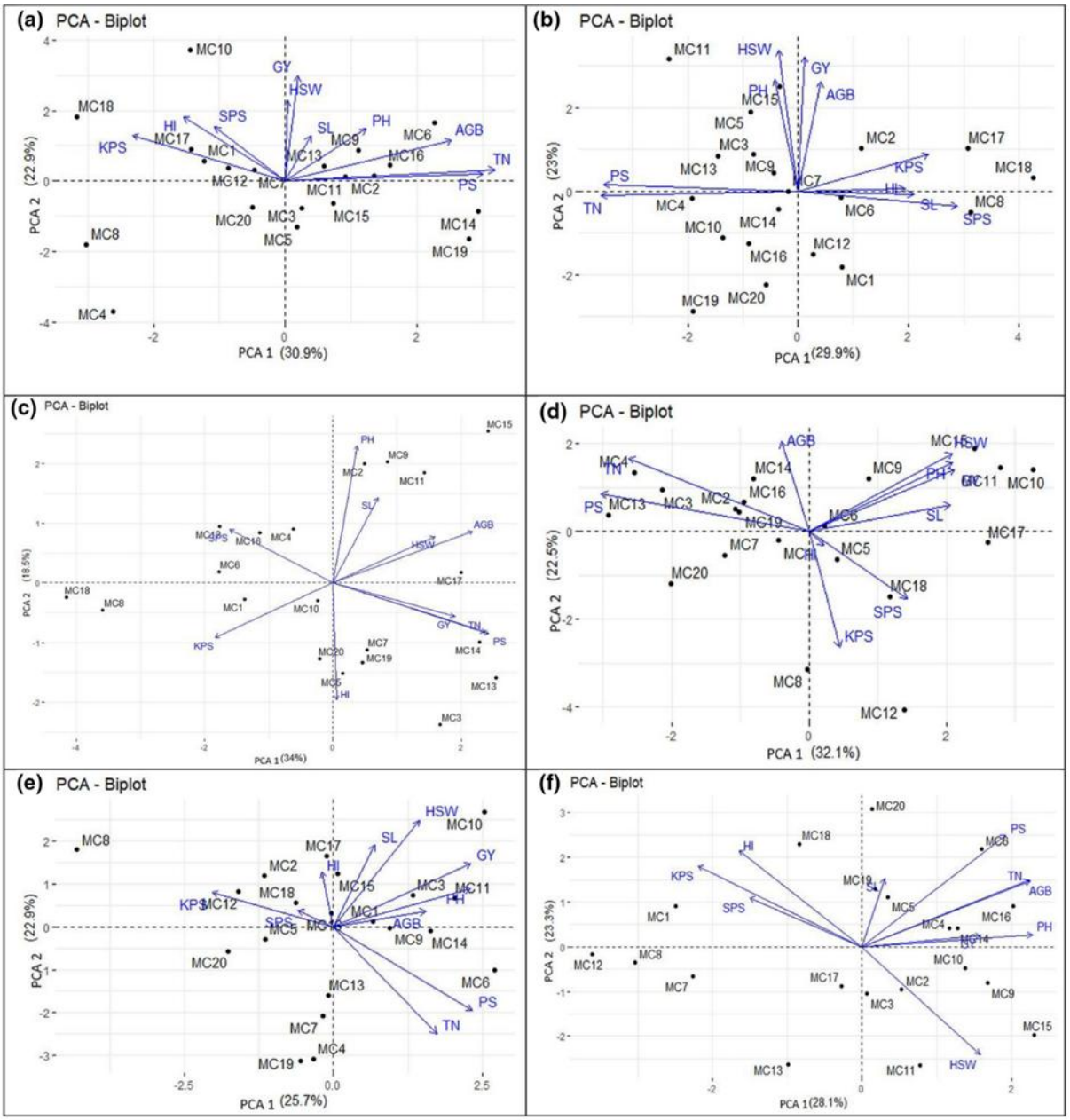

Figure 2.1: Principal component analysis biplots of wheat genotypes: A: without silicon under drought-stress conditions; B: without silicon under non-stress conditions; C: with liquid silicon under drought-stress conditions; D: with liquid silicon under non-stress conditions; E: with granular silicon under drought-stress conditions; F: with granular silicon under non-stress conditions across three environments.

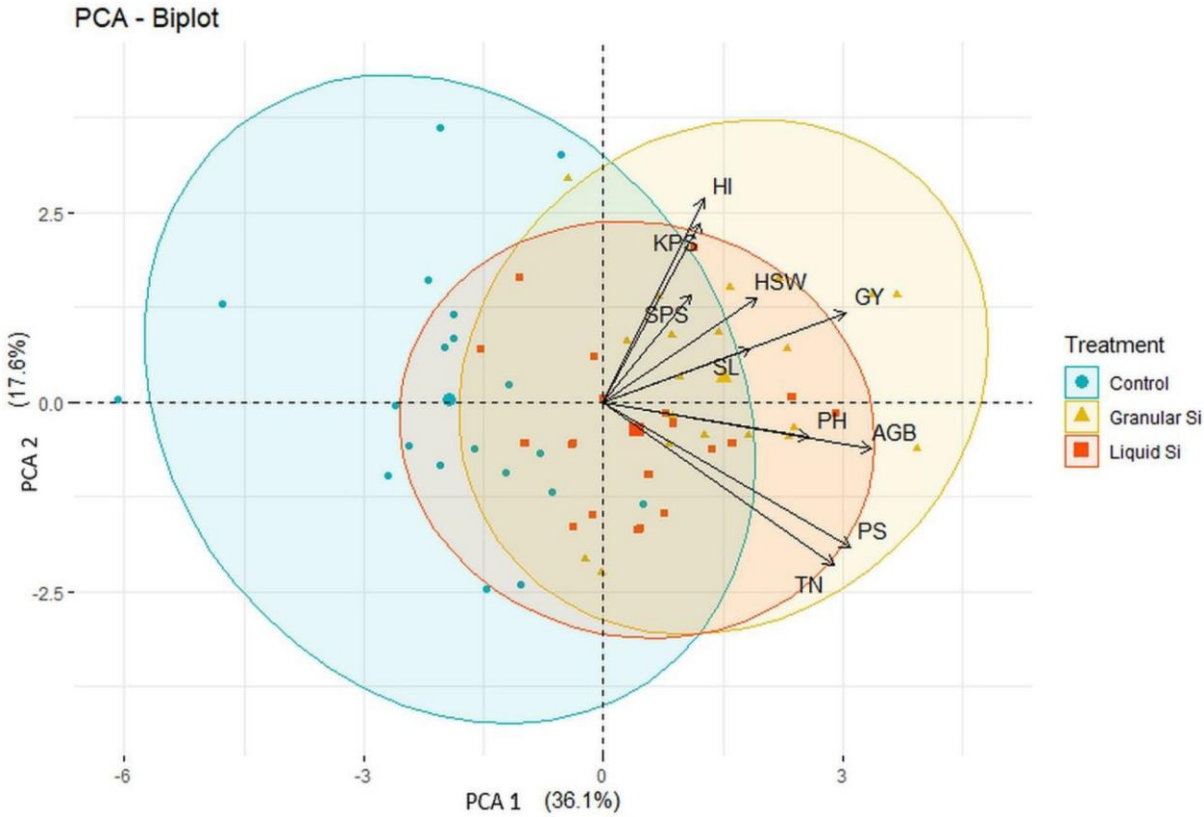

Figure 2.2: Principal component analysis biplot of wheat genotypes of control, liquid Si, and granular Si, under drought-stress conditions across three environments.

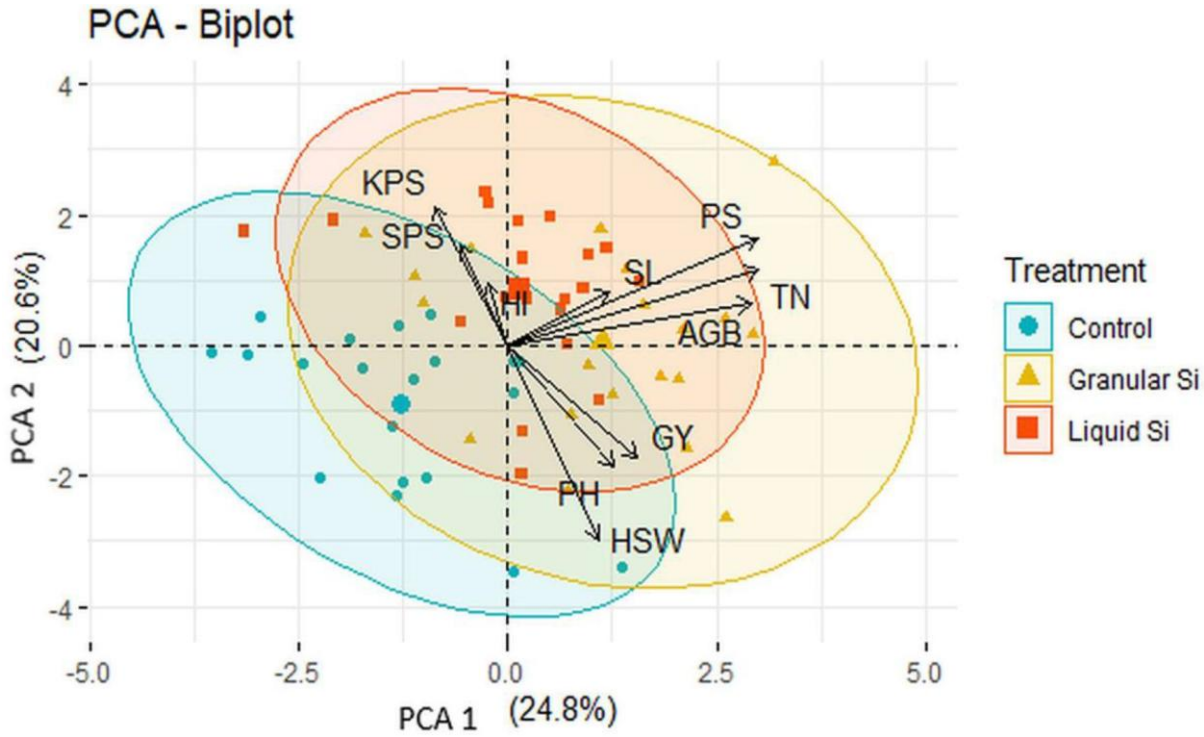

Figure 2.3: Principal component analysis biplot of wheat genotypes of control, liquid Si, and granular Si, under non-drought stress conditions across three environments.

2.4 Discussion

Silicon application enhanced wheat yield and other agronomic traits performance under drought stress conditions. Ahmed et al. (2016), reported that Si improved AGB, HSW and GY of wheat under drought conditions. Silicon application positively affects several agronomic traits measured at maturity stages (Sarma et al., 2017). A study by Thorne et al. (2021), found that Si accumulation increases under drought stress and its accumulation is highly dependent on genotypic variation. Variation in silicon uptake is also affected by silicon formulation, indicating formulation selection as a factor in silicon-use efficiency (Christian et al., 2022).

In the current study, the effectiveness of the two formulations was assessed by the variation in the agronomic trait performance. The granular Si formulation improves most of the assessed agronomic traits compared to the liquid Si (Table 2.5). Kowalska et al. (2021) found that liquid monosilicic acid positively effects agronomic traits, such as productive spikes, plant height and yield compared to the diatomaceous earth powder. Silicon chemical formulation and methods of application will cause variation in silicon uptake and thus have varied effects on agronomic traits (Bukhari et al., 2021; Laane, 2018).

Stress tolerance indices, which are widely used to evaluate genotypes for drought tolerance, have not been widely investigated concerning the effect of silicon. Drought tolerance indices quantify drought tolerance based on yield differences under DS and NS conditions. The NS response is the potential maximum and heritable yield, whilst the DS response is the yield generated under drought stress (Talebi et al., 2009). Several drought stress tolerance indices are used to evaluate genotypic efficacy. For instance, the stress susceptibility index (SSI) > 1 is above-average, and < 1 is below-average susceptibility to DS (Mohammadi et al., 2011). In this study, granular Si increased the SSI of all genotypes tested, with 17 of the 20 genotypes registering an SSI > 1 for granular Si, compared to the 12 genotypes with the untreated control. Higher STI was generated for 17 out of the 20 genotypes when treated with granular Si compared to the untreated control. The liquid formulation varied in stress tolerance levels compared to the other treatments and variation in genotype. Two possible reasons for the liquid Si's inadequate performance compared to the control could be postulated as: Firstly, the liquid Si was discontinued at the beginning of the terminal drought period (anthesis), resulting in limited plant available Si for adequate drought tolerance. Secondly, the concentration and or volume of liquid Si applied may not have been adequate to sustain a drought tolerance response during terminal drought phase (Table 2.6). Si efficacy and performance are formulation dependent (Nikpay 2015). This indicates that Si formulation is highly critical in genotype/cultivar evaluation and ultimately for improved yield gains under drought stress conditions.

Principal component analysis by Biju et al. (2020), found that silicon application shifts drought tolerant and drought-sensitive genotypes into the positive upper right quartile compared to the controls. Based on the principal component analysis biplots (Figure 2.1), there is a noticeable genotypic shift from the untreated control to the granular Si application, under DS conditions. Genotypes are clustered closer together with the granular Si application compared to the control and liquid Si application. Likewise, the agronomic traits also follow the same trend moving towards the upper right quartile. This Si effect is not as prominent under NS conditions. Silicon formulation plays a vital role for its efficient uptake and distribution (Christian et al., 2022). A study by Ma et al. (2007), found that silicon variation occurs even within the shoot. This variation can be a contributing factor in variation amongst Si formulations and can also account for silicon uptake variation amongst agronomic traits.

Trait relationships are strongly correlated with more acute angles notable for the granular Si treated genotypes. Granular Si application decreased the variation between genotypes under drought stress and non-stress conditions. This decrease in variation also allows for agronomic traits to be more strongly correlated and thus influence each other to a higher degree than without silicon application (Figures 2.2 and 2.3). Under stressed conditions, variation amongst the genotypes treated with granular Si is similarly distributed compared to genotypes under non-stress conditions. Genotypes treated with liquid Si has a similar distribution under both stress and non-stress conditions. Many of the agronomic traits tested fall within the Si treated genotypic groupings, indicating that Si application is highly related with agronomic trait performance.

2.5 Conclusion

The use of silicon and the silicon formulation has a significant impact on wheat genotype performance under both drought-stress and non-stress conditions. Silicon application has a significant effect on agronomic trait performance, increasing the influence of trait interactions on each other. It boosts the agronomic performance of wheat under drought-stress conditions. Silicon fertilisation can be considered as one of the mitigation measures to cope with the adverse effects of drought stress on wheat.

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Appendix 2.2A: Means for 10 agronomic traits of the 20 wheat genotypes ranked based on the grain yield without Si, under drought-stress and non-stress conditions across two greenhouse environments.

Gen	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	84.46	88.68	2.15	2.47	2.13	2.36	9.02	8.93	20.92	19.83	40	41.97	2.57	4.07	6.22	8.6	49.97	61.07	6.03	9.71
MC2	86.2	95.76	2.69	2.56	2.58	2.5	9.75	9.82	18.69	19.47	32.72	42.06	2.62	5.1	6.47	9.92	39.78	57.97	5.01	12.9
MC3	89.18	98.79	2.67	2.69	2.39	2.64	9.13	8.94	19.22	19.11	33.81	41.5	2.85	5.03	5.76	9.22	44.61	57.08	5.79	12.7
MC4	90.46	94.39	2.57	2.81	2.43	2.72	9.01	8.71	18.92	19.33	32.39	34.94	2.3	4.86	6.39	9.08	43.65	59.67	4.64	12.34
MC5	84.82	99.17	2.61	2.85	2.19	2.79	8.88	8.7	19.86	20.06	33.86	45.61	2.92	4.75	5.84	8.47	39.61	58.45	4.94	12.57
MC6	95.82	100.65	2.83	2.47	2.72	2.44	9.54	9.11	21.56	21.58	33.71	39.81	2.62	4.5	7.64	9.78	43.02	61.17	6.93	11.47
MC7	84.89	93.05	2.74	2.61	2.65	2.61	9.29	9.04	19.03	20.00	35.56	45.14	2.87	4.85	6.61	9.74	51.56	60.70	6.5	12.77
MC8	79.07	92.88	2.47	2.58	2.42	2.56	9.59	9.79	20.75	21.67	36.61	46.89	2.6	4.89	6.83	10.29	44.09	58.06	5.16	12.76
MC9	93.18	97.46	2.69	2.33	2.56	2.33	9.84	9.51	19.5	19.61	34.83	40.61	2.65	5.29	6.73	9.07	44.13	55.54	5.95	13.16
MC10	92.4	93.24	2.25	2.64	2.18	2.42	9.77	9.39	19.86	19.17	35.79	36.08	3.66	4.97	5.98	9.33	55.14	53.39	7.88	10.67
MC11	94.55	99.06	2.75	2.68	2.64	2.61	9.41	8.84	19.19	18.11	31.14	35.69	2.96	5.92	6.38	9.67	42.96	59.39	6.18	13.79
MC12	88.06	95.25	2.81	2.51	2.64	2.35	9.53	9.5	21.47	21.89	35.58	41.22	2.71	4.33	6.59	7.78	44.82	57.51	5.69	9.46
MC13	82.19	93.01	2.75	2.73	2.63	2.83	9.01	8.86	19.42	20.22	32.64	40.31	3.06	5.19	6.91	9.36	50.46	58.08	6.02	14.00
MC14	85.26	92.62	2.81	2.31	2.69	2.31	9.93	9.69	18.56	18.83	30.47	42.72	3.21	4.85	6.3	10.17	44.63	59.76	6.11	11.03
MC15	86.69	101.14	3.00	2.61	2.44	2.39	10.22	9.59	19.94	19.89	30.97	36.83	2.5	6.04	6.3	12.42	40.63	53.83	4.95	12.69
MC16	92.16	97.53	2.86	2.86	2.78	2.69	10	9.67	20.14	19.81	34.83	38.93	3.01	4.66	6.51	8.43	47.00	59.82	6.17	11.02
MC17	93.31	97.37	2.69	2.56	2.44	2.47	10.57	10.26	20.44	20.44	34.78	41.14	2.94	5.62	7.02	9.38	47.07	66.17	6.05	12.41
MC18	82.2	93.89	2.39	2.28	2.31	2.28	10.34	10.16	21.14	22.11	40.06	45.08	3.06	4.62	9.13	9.42	49.85	58.78	5.68	12.59
MC19	83.6	89.45	3.21	3.00	3.03	3.00	10.14	9.63	19.67	18.89	26.34	34.53	2.51	4.11	5.94	9.54	43.11	59.03	4.51	11.4
MC20	83.85	89.82	2.42	2.28	2.35	2.19	9.06	9.18	19.72	20.33	34.08	39.81	2.69	4.51	5.7	8.93	44.67	58.34	5.83	10.8
Mean	**87.62**	**95.16**	**2.67**	**2.60**	**2.51**	**2.53**	**9.60**	**9.37**	**19.90**	**20.00**	**34.01**	**40.54**	**2.82**	**4.91**	**6.41**	**9.43**	**46.50**	**58.45**	**5.80**	**12.01**
SED	**4.660**	**4.660**	**0.365**	**0.365**	**0.363**	**0.363**	**0.374**	**0.374**	**0.973**	**0.973**	**3.474**	**3.474**	**0.447**	**0.447**	**1.467**	**1.467**	**4.61**	**4.61**	**1.87**	**1.87**
LSD 5%	**9.157**	**9.157**	**0.717**	**0.717**	**0.713**	**0.713**	**0.734**	**0.734**	**1.913**	**1.913**	**6.827**	**6.827**	**0.878**	**0.878**	**2.882**	**2.882**	**9.05**	**9.05**	**3.67**	**3.67**
cv%	**1.1**	**1.1**	**2.5**	**2.5**	**2.5**	**2.5**	**0.3**	**0.3**	**0.3**	**0.3**	**2.5**	**2.5**	**1.4**	**1.4**	**2.4**	**2.4**	**1.7**	**1.7**	**4.5**	**4.5**

Abbreviations: Gen: Genotype; DS: drought stressed; NS: non-drought stressed; PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; AGB: aboveground biomass dry weight per plant (g); SL: spike length; SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g/100 seed); HI: harvest index , GY: Grain yield ($t.ha^{-1}$). Mean overall mean for the three treatments under drought-stressed and non-stressed conditions.

Appendix 2.2B: Means for 10 agronomic traits of the 20 wheat genotypes ranked based on the grain yield without Si, under drought-stress and non-stress conditions across two greenhouse environments.

Gen	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	90.41	92.61	3.11	3.06	3.03	3.06	9.37	9.35	20.94	21.47	39.61	44.69	2.74	4.21	7.30	11.15	49.48	61.63	6.85	11.42
MC2	93.54	94.56	2.83	2.86	2.78	2.86	10.29	10.01	20.36	20.53	32.08	40.58	2.58	4.44	7.70	10.13	41.42	56.96	4.72	10.55
MC3	85.92	95.59	3.06	3.14	2.94	3.11	9.28	9.64	19.53	20.42	34.92	39.03	3.04	4.31	7.62	11.33	48.58	59.58	5.83	9.37
MC4	94.59	94.93	3.39	3.5	3.17	3.44	9.62	9.29	20.83	20.19	32.92	37.5	2.69	4.67	7.38	13.5	41.59	58.47	5.13	11.5
MC5	89.56	98.74	2.83	2.83	2.75	2.83	8.95	9.11	20.75	21.31	38.03	45.86	2.82	4.46	8.01	10.65	46.54	58.43	5.98	11.36
MC6	94.09	103.57	2.92	3.36	2.78	3.31	9.36	9.46	21.81	22.22	33.53	38.36	2.40	4.71	6.36	11.76	43.21	57.37	5.04	12.37
MC7	88.93	93.22	2.89	3.14	2.78	3.14	9.32	9.11	20.06	20.33	35.31	43.89	2.57	4.68	6.86	11.04	47.12	62.96	5.13	11.1
MC8	94.75	89.89	2.83	2.83	2.64	2.83	10.06	10.2	21.92	21.61	37.92	45.39	2.75	4.46	6.84	10.49	43.80	55.25	5.07	9.32
MC9	96.13	97.32	2.81	3.03	2.88	3.03	10.10	10.29	19.49	20.67	32.65	39.14	2.76	4.67	6.98	9.25	43.70	53.76	6.16	10.09
MC10	88.71	98.37	2.67	2.86	2.64	2.81	10.29	10.15	20.86	21.06	37.58	40.14	3.19	5.08	6.87	10.72	50.88	57.60	6.94	12.27
MC11	103.15	101.9	3.05	2.81	2.97	2.75	9.62	9.90	19.57	20.58	33.47	39.08	3.15	5.46	7.58	10.88	45.20	57.40	6.42	11.96
MC12	86.77	91.6	2.78	2.94	2.67	2.94	10.00	10.02	21.89	22.08	38.57	43.31	2.47	4.19	6.08	9.13	46.44	56.69	5.13	9.24
MC13	82.75	89.86	3.25	2.89	3.11	3.01	9.63	9.06	20.14	19.82	32.5	34.76	2.96	4.49	8.58	8.67	45.90	53.25	5.54	8.13
MC14	84.87	90.99	3.06	3.17	3.00	3.14	10.41	10.4	19.08	19.47	33.42	40.78	2.74	4.84	7.34	10.94	46.24	57.47	4.88	9.28
MC15	94.02	102.88	2.92	3.28	2.76	3.06	10.81	10.74	21.58	21.67	32.47	37.47	3.44	4.81	8.82	13.15	42.95	54.07	5.61	12.23
MC16	89.76	98.25	2.64	3.28	2.58	3.28	10.21	10.15	20.22	20.64	32.56	40.53	3.03	4.46	6.47	10.45	47.07	55.07	5.16	9.98
MC17	93.29	94.22	2.99	2.71	2.9	2.74	10.96	10.83	20.4	21	33.08	41.11	3.01	4.98	8.14	10.77	47.25	58.81	5.98	11.33
MC18	90.91	95.94	2.53	2.87	2.50	2.82	10.01	10.63	20.69	22.08	35.11	47.61	2.10	4.47	5.96	11.99	47.32	55.68	3.19	10.47
MC19	88.36	89.49	3.72	3.00	3.58	2.92	10.35	10.16	19.5	19.44	31.25	37.97	2.32	4.42	7.5	10.15	44.64	58.99	4.93	12.55
MC20	86.29	91.13	2.94	3.28	2.86	3.17	9.59	9.7	21.22	21.06	33.78	43.06	2.82	4.54	7.31	9.98	46.37	57.06	5.53	9.44
Mean	**90.34**	**95.25**	**2.96**	**3.04**	**2.87**	**3.01**	**9.91**	**9.91**	**20.54**	**20.88**	**34.54**	**41.01**	**2.78**	**4.62**	**7.28**	**10.81**	**46.50**	**58.45**	**5.46**	**10.70**
SED	**4.660**	**4.660**	**0.365**	**0.365**	**0.363**	**0.363**	**0.374**	**0.374**	**0.973**	**0.973**	**3.474**	**3.474**	**0.447**	**0.447**	**1.467**	**1.467**	**4.61**	**4.61**	**1.87**	**1.87**
LSD 5%	**9.157**	**9.157**	**0.717**	**0.717**	**0.713**	**0.713**	**0.734**	**0.734**	**1.913**	**1.913**	**6.827**	**6.827**	**0.878**	**0.878**	**2.882**	**2.882**	**9.05**	**9.05**	**3.67**	**3.67**
cv%	**1.1**	**1.1**	**2.5**	**2.5**	**2.5**	**2.5**	**0.3**	**0.3**	**0.3**	**0.3**	**2.5**	**2.5**	**1.4**	**1.4**	**2.4**	**2.4**	**1.7**	**1.7**	**4.5**	**4.5**

Abbreviations: Gen: Genotype; DS: drought stressed; NS: non-drought stressed; PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; AGB: aboveground biomass dry weight per plant (g); SL: spike length; SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g/100 seed); HI: harvest index , GY: Grain yield ($t.ha^{-1}$). Mean overall mean for the three treatments under drought-stressed and non-stressed conditions.

Appendix 2.2C: Means for 10 agronomic traits of the 20 wheat genotypes ranked based on the grain yield treated with granular Si under drought-stress and non-stress conditions across two greenhouse environments.

Gen	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	89.67	94.56	3.36	3.32	3.36	3.32	9.34	9.25	21	20.94	42.21	44.47	2.98	4.75	8.63	12.69	54.64	65.41	7.44	13.41
MC2	86.94	93.71	3.03	2.97	2.92	2.97	9.98	10.23	19.92	20.19	36.61	39.47	3.14	5.24	7.43	12.11	46.64	54.94	6.09	14.9
MC3	89.99	95.94	3.03	3.18	2.92	3.07	9.18	9.46	18.86	19.67	33.61	40.06	3.38	5.44	7.96	11.37	53.32	61.40	6.94	13.97
MC4	89.49	98.00	3.68	3.75	3.49	3.64	9.22	9.25	19.72	20.06	32.22	36.75	2.83	5.22	7.79	13.12	45.28	61.42	5.5	15.41
MC5	92.07	95.79	3.00	2.97	2.78	2.89	9.08	9.13	2011	20.25	40.82	48.00	2.72	4.71	8.11	12.47	46.89	59.57	5.61	15.23
MC6	102.94	106.49	3.61	3.50	3.53	3.50	9.71	9.32	22.14	21.61	35.44	42.69	3.11	5.14	10.01	13.28	44.13	61.47	8.06	16.32
MC7	86.89	94.15	3.21	2.89	3.08	2.86	9.24	9.13	19.86	20.19	36.33	43.11	2.82	4.83	7.75	9.46	49.66	61.07	6.00	11.67
MC8	85.1	91.01	2.69	3.31	2.61	3.14	10.19	9.95	21.06	21.36	42.97	47.89	2.90	4.99	9.37	11.08	45.41	58.49	5.47	13.65
MC9	97.09	100.22	3.17	3.18	3.17	3.1	10.17	10.16	20.17	20.22	36.28	40.08	2.85	5.38	7.76	11.67	47.64	56.90	6.25	15.25
MC10	95.89	95.18	2.64	3.00	2.61	3.03	10.06	9.89	20.08	20.36	35.97	36.5	3.72	4.99	6.8	9.28	49.86	58.65	9.65	12.05
MC11	102.12	100.83	3.11	3.00	3.08	2.92	9.58	9.69	19.33	19.69	34.14	36.06	3.07	5.53	7.82	9.99	48.06	56.22	6.83	11.7
MC12	86.89	90.54	2.69	2.94	2.56	2.94	9.76	9.95	20.03	20.11	38.42	43.19	2.79	4.29	6.14	10.08	49.50	59.79	5.16	9.53
MC13	89.81	93.33	3.33	3.31	3.17	3.25	9.63	9.17	20.42	19.72	34.31	39.69	2.90	5.43	7.88	12.28	45.67	58.72	6.39	14.33
MC14	90.21	92.92	3.17	3.25	3.14	3.25	10.19	10.05	18.33	18.53	35.33	40.58	3.27	5.00	8.4	9.74	48.68	59.87	6.24	12.24
MC15	92.98	98.44	2.89	2.96	2.72	2.93	10.26	10.74	20.44	20.5	31.61	36.03	3.62	6.02	8.74	12.73	42.41	58.41	5.74	16.38
MC16	93.06	100.43	3.25	3.64	3.11	3.58	10.24	10.32	20.69	19.83	35.83	42.21	3.01	4.94	7.82	11.96	50.19	56.48	6.72	12.92
MC17	95.09	95.91	3.03	3.03	2.97	3.00	10.72	10.44	20.00	20.61	36.53	41.06	3.29	5.35	7.38	10.21	52.75	46.11	6.32	12.48
MC18	90.49	97.3	3.24	2.92	3.14	2.89	10.54	10.69	21.58	22.17	39.92	48.06	2.56	5.00	7.52	11.14	50.31	62.81	4.96	12.6
MC19	90.71	94.43	3.11	3.5	3.11	3.47	10.24	10.35	19.99	19.22	32.96	38.42	2.08	4.39	6.62	11.4	45.32	59.63	5.44	12.72
MC20	89.68	93.29	2.97	3.22	2.65	3.19	9.82	9.75	21.46	20.89	36.28	43.03	2.83	4.65	6.52	12.81	46.94	59.60	5.13	12.51
Mean	**91.85**	**96.12**	**3.11**	**3.19**	**3.01**	**3.15**	**9.86**	**10.54**	**20.36**	**20.41**	**36.39**	**41.37**	**2.99**	**5.06**	**7.82**	**11.44**	**46.50**	**58.45**	**6.30**	**13.46**
SED	**4.660**	**4.660**	**0.365**	**0.365**	**0.363**	**0.363**	**0.374**	**0.374**	**0.973**	**0.973**	**3.474**	**3.474**	**0.447**	**0.447**	**1.467**	**1.467**	**4.61**	**4.61**	**1.87**	**1.87**
LSD 5%	**9.157**	**9.157**	**0.717**	**0.717**	**0.713**	**0.713**	**0.734**	**0.734**	**1.913**	**1.913**	**6.827**	**6.827**	**0.878**	**0.878**	**2.882**	**2.882**	**9.05**	**9.05**	**3.67**	**3.67**
cv%	**1.1**	**1.1**	**2.5**	**2.5**	**2.5**	**2.5**	**0.3**	**0.3**	**0.3**	**0.3**	**2.5**	**2.5**	**1.4**	**1.4**	**2.4**	**2.4**	**1.7**	**1.7**	**4.5**	**4.5**

Abbreviations: Gen: Genotype; DS: drought stressed; NS: non-drought stressed; PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; AGB: aboveground biomass dry weight per plant (g); SL: spike length; SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g/100 seed); HI: harvest index , GY: Grain yield ($t.ha^{-1}$). Mean overall mean for the three treatments under drought-stressed and non-stressed conditions.

Appendix 2.2D: Means for 10 agronomic traits of the 20 wheat genotypes ranked based on the grain yield without Si, under drought-stress and non-stress conditions across a field environment.

Gen	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	86.19	95.47	11.84	11.34	10.84	10.8	11.68	11.7	19.67	20.67	44.43	48.23	2.83	2.94	29.06	38.56	49.67	53.00	2.48	4.52
MC2	92.2	94.67	11.5	11.43	9.8	10.57	11.93	12.22	21.22	21.11	48.33	53.7	3.00	2.78	43.17	41.72	55.33	53.86	3.01	4.00
MC3	82.6	92.23	10.77	12.13	10.77	11.19	11.0	12.25	19.44	19.22	44.43	50.03	3.11	3.28	30.5	36.83	52.67	53.00	1.93	4.18
MC4	76.53	94.47	6.81	14.10	6.10	13.2	11.01	11.43	20.78	20.89	43.57	55.90	2.39	2.5	14.83	43.33	49.51	54.67	1.63	3.24
MC5	90.4	98.1	10.9	14.57	12.00	11.57	10.63	10.98	19.78	20.67	48.57	59.00	2.94	3.28	30.50	45.67	55.33	53.33	1.84	4.71
MC6	89.7	94.23	13.03	11.53	13.03	11.53	10.78	11.19	21.22	20.78	45.8	50.43	2.50	2.5	39.61	40.28	49.33	49.00	2.62	3.78
MC7	78.57	86.9	11.00	12.43	10.10	13.1	11.14	11.38	20.89	20.78	43.13	51.00	2.61	2.5	29.78	35.44	51.92	53.00	2.32	4.89
MC8	81.5	89.37	7.67	9.87	7.67	8.77	10.86	11.43	18.78	19.89	46.9	58.43	2.67	2.56	16.92	33.72	53.67	55.67	2.05	3.62
MC9	92.67	97.97	11.23	12.53	11.13	12.00	11.98	12.58	20.56	20.22	45.77	52.9	3.11	3.00	33.11	29.25	48.00	52.33	2.78	3.85
MC10	89.07	99.00	9.98	13.77	8.15	10.65	12.27	12.48	19.89	20.89	42.67	44.66	3.22	3.33	28.61	31.25	53.00	54.41	2.51	3.56
MC11	87.07	100.0	10.00	13.33	10.00	13.33	11.87	11.96	20.33	20.78	47.57	50.23	3.00	3.44	35.94	45.28	50.67	51.67	1.81	4.19
MC12	86.67	97.37	9.80	12.77	9.80	11.67	10.94	11.73	19.67	19.22	48.6	47.23	2.78	3.06	29.75	40.11	53.67	54.33	2.27	3.58
MC13	83.47	86.2	11.57	13.3	12.2	12.77	10.97	10.82	19.89	19.33	47.97	53.1	2.72	3.06	36.00	44.33	54.33	56.33	2.36	3.54
MC14	80.03	89.97	14.85	13.43	13.66	12.53	11.94	12.77	19.55	19.11	38.1	47.47	2.83	2.72	29.67	41.61	52.95	54.33	1.62	3.76
MC15	96.13	95.43	10.77	11.33	9.90	11.77	12.5	12.17	20.56	20.78	45.43	48.67	3.22	3.17	31.17	42.00	55.45	52.88	1.82	3.58
MC16	86.83	93.87	13.47	11.77	12.67	13.00	10.67	11.28	20.33	20.78	41.2	46.47	2.67	2.72	27.00	36.72	48.33	52.00	2.11	2.98
MC17	84.03	93.13	8.85	9.77	8.65	9.10	11.87	12.52	20.67	20.67	41.15	48.77	2.83	3.00	18.83	40.78	55.67	54.33	2.13	3.56
MC18	82.27	91.77	8.77	10.10	8.77	8.57	11.72	11.91	20.78	20.78	50.1	54.43	3.06	3.17	27.50	45.5	60.00	58.05	2.18	3.59
MC19	85.00	90.47	13.00	13.22	12.33	12.33	11.48	12.05	19.11	19.89	46.1	47.57	2.56	2.50	39.56	35.22	56.33	53.33	1.98	2.54
MC20	81.47	90.23	11.33	13.1	11.23	11.77	10.51	10.69	20.78	19.56	47.57	48.43	2.89	3.00	28.78	31.94	5467	52.00	2.13	3.44
Mean	**85.62**	**93.54**	**10.86**	**12.29**	**10.44**	**11.51**	**11.39**	**11.78**	**20.19**	**20.30**	**45.37**	**50.83**	**2.85**	**2.93**	**30.01**	**38.98**	**53.43**	**53.92**	**2.18**	**3.75**
SED	**2.477**	**2.477**	**1.361**	**1.361**	**1.230**	**1.230**	**0.451**	**0.451**	**0.641**	**0.641**	**3.752**	**3.752**	**0.269**	**0.269**	**6.680**	**6.680**	**2.78**	**2.78**	**0.41**	**0.41**
LSD 5%	**4.880**	**4.880**	**2.682**	**2.682**	**2.423**	**2.423**	**0.889**	**0.889**	**1.262**	**1.262**	**7.390**	**7.390**	**0.530**	**0.530**	**13.16**	**13.16**	**5.47**	**5.47**	**0.81**	**0.81**
cv%	**0.9**	**0.9**	**4.4**	**4.4**	**3.6**	**3.6**	**0.9**	**0.9**	**0.8**	**0.8**	**3.9**	**3.9**	**3.3**	**3.3**	**7.4**	**7.4**	**1.1**	**1.1**	**1.6**	**1.6**

Abbreviations: Gen: Genotype; DS: drought stressed; NS: non-drought stressed; PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; AGB: aboveground biomass dry weight per plant (g); SL: spike length; SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g/100 seed); HI: harvest index , GY: Grain yield ($t.ha^{-1}$). Mean overall mean for the three treatments under drought-stressed and non-stressed conditions.

Appendix 2.2E: Means for 10 agronomic traits of the 20 wheat genotypes ranked based on the grain yield treated with liquid Si under drought-stress and non-stress conditions across a field environment.

Gen	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	91.13	94.5	10.9	13.67	11.34	13.67	12.23	12.78	19.89	20.89	43.77	51.8	3.06	3.11	35.5	48.94	51.00	50.00	1.83	4.26
MC2	91.81	93.66	12.9	14.23	13	13.84	12.20	12.42	21.11	20.78	47.9	55.66	2.94	2.89	43.61	55.89	51.67	50.33	2.85	2.63
MC3	89.34	93.69	13.35	14.67	14.19	14.67	11.21	11.43	19.78	19.78	51	54.23	3	3.11	37.78	47.11	54.67	53.33	3.28	4.06
MC4	94.5	92.81	12.3	14.67	12.3	14.67	11.24	11.5	20.67	21.55	51.67	49.47	2.56	2.67	34.72	37.67	53.33	52.33	2.33	2.95
MC5	92.67	97.76	13.77	13.57	13.67	13	10.58	10.82	19.89	20.78	54.67	57.23	3	3.28	38.39	44.83	53.33	50.33	2.92	3.98
MC6	91.66	92.1	12.57	13.23	12.57	13.13	10.72	11.28	20.89	22.44	53.9	55.33	2.83	2.67	31.75	39.50	54.33	53.33	3.03	3.11
MC7	88.1	86.5	14.67	13.37	13.57	13.37	11.65	12.04	21.44	21.45	51.9	51.43	2.83	2.61	43.72	47.39	52.67	55.00	2.74	2.9.5
MC8	83.83	90.66	10.5	11.8	10.5	13	11.63	11.12	19.56	19.67	58	61.5	2.89	2.89	34.17	34.28	58.67	55.33	2.58	3.13
MC9	95.2	95.77	12.67	13.1	12.34	12.77	12.4	12.9	20	20.78	46.87	54.57	3	3.56	41.33	52.33	49.00	54.67	2.37	3.94
MC10	93.04	99	11.8	12.1	11.57	12	12.22	12.82	20.33	21	44.9	48.66	3.44	3.33	33.61	43.56	55.33	51.33	3.28	5.10
MC11	92.31	102.84	12.23	13.00	12.23	12.23	11.85	12	20.44	19.56	48.8	52.6	3.56	3.22	42.39	35.61	53.33	58.00	2.57	4.06
MC12	98.16	93	12.13	10.63	12.13	10.97	11.65	11.85	20.55	21.45	48.5	59.84	3.22	2.83	42.5	32.44	49.33	55.00	2.43	3.40
MC13	85.8	56	14.16	14.73	14.16	14.5	11.27	11.48	20	20.11	44.67	55.5	3	3.11	41.22	46.56	55.00	59.00	2.94	3.94
MC14	91.84	94.31	14.00	13.43	13.2	12.87	12.67	12.92	19.66	18.46	51.85	51.53	3.39	2.78	44.89	50.11	56.33	53.00	3.58	3.63
MC15	98	98.67	13.77	12.33	13.67	11.67	12.57	12.83	20.56	20.45	51.33	51.33	3.56	3.11	47.11	46.5	54.00	56.00	3.08	3.70
MC16	91.84	95.23	11.73	12.97	12.5	13.43	11.03	11.8	20.44	19.56	44.9	55.56	3.06	2.61	32.22	51.28	49.33	49.67	1.89	3.60
MC17	95.41	94.66	14.10	11.80	14	11.8	12.78	13.27	20.55	21.11	52.67	55.33	3.06	2.83	38.89	47.83	57.00	55.33	2.91	3.51
MC18	91.34	92.34	11.67	13.23	11.67	13.23	11.99	12.26	21	21.56	61.67	63.1	3.22	2.83	28.83	44.89	55.33	55.67	2.56	4.75
MC19	89.84	88.9	12.31	13.57	12.31	13.47	11.28	12.04	19	19.56	54	52.66	2.72	2.61	28.50	43.67	53.67	50.33	3.17	3.46
MC20	83.5	91.34	13	14	13.13	14	10.69	11.05	19.67	20.22	47.57	56.33	2.89	2.83	34.17	39.5	55.67	57.00	2.57	3.07
Mean	**91.62**	**93.69**	**12.73**	**13.21**	**12.70**	**13.11**	**11.69**	**12.03**	**20.27**	**20.56**	**50.53**	**54.68**	**3.06**	**2.94**	**37.77**	**44.49**	**53.43**	**53.92**	**2.74**	**3.66**
SED	**2.477**	**2.477**	**1.361**	**1.361**	**1.230**	**1.230**	**0.451**	**0.451**	**0.641**	**0.641**	**3.752**	**3.752**	**0.269**	**0.269**	**6.680**	**6.680**	**2.78**	**2.78**	**0.41**	**0.41**
LSD 5%	**4.880**	**4.880**	**2.682**	**2.682**	**2.423**	**2.423**	**0.889**	**0.889**	**1.262**	**1.262**	**7.390**	**7.390**	**0.530**	**0.530**	**13.16**	**13.16**	**5.47**	**5.47**	**0.81**	**0.81**
cv%	**0.9**	**0.9**	**4.4**	**4.4**	**3.6**	**3.6**	**0.9**	**0.9**	**0.8**	**0.8**	**3.9**	**3.9**	**3.3**	**3.3**	**7.4**	**7.4**	**1.1**	**1.1**	**1.6**	**1.6**

Abbreviations: Gen: Genotype; DS: drought stressed; NS: non-drought stressed; PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; AGB: aboveground biomass dry weight per plant (g); SL: spike length; SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g/100 seed); HI: harvest index , GY: Grain yield ($t.ha^{-1}$). Mean overall mean for the three treatments under drought-stressed and non-stressed conditions.

Appendix 2.2F: Means for 10 agronomic traits of the 20 wheat genotypes ranked based on the grain yield treated with granular Si under drought-stress and non-stress conditions across a field environment.

Gen	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	95	91.69	13.23	12.43	13.23	12.33	12.89	12.85	21.67	21.44	51.9	62.5	2.83	2.67	55.42	35.06	54.00	50.00	2.45	2.91
MC2	90.31	92.31	11.03	12.57	11.03	12.57	12.40	12.07	20.78	20.33	54.33	55.7	2.83	2.67	48.58	51.92	56.00	56.00	2.87	4.33
MC3	93.4	88.31	13.23	13.2	13.1	13.00	13.15	12.08	20.11	20.11	50.7	48.2	2.94	3	45.17	38.22	56.67	54.00	3.39	3.85
MC4	90.34	91.34	13	13.53	13.00	13.00	10.81	11.50	21.11	21.11	48.67	51.9	2.67	2.67	32.83	41.58	51.67	55.00	2.13	2.87
MC5	96.5	96.66	12.15	14.03	11.67	13.7	11.13	11.73	20.22	20	56.1	52.2	2.78	2.56	49.78	52.67	53.67	53.00	3.00	3.26
MC6	91.00	89.23	12.53	12.9	15.8	14.43	11.77	11.50	21.89	21	57.67	52	2.61	2.5	46.39	55	50.33	56.00	2.79	3.24
MC7	86.81	83.00	14.57	13.57	13.8	12.67	12.07	11.55	20.56	20	54.87	52	2.5	2.78	42.17	34.42	52.33	54.67	2.90	4.01
MC8	89.9	87.13	10.2	11.67	10.53	11.67	11.37	11.61	20.11	20.33	68.57	58.8	2.83	2.83	28	36.56	59.00	57.00	2.70	3.51
MC9	98.43	96.00	12.8	12.77	12.8	12.43	12.47	12.70	20.78	20.44	46.87	54.23	3.17	3.28	41.28	54.67	51.67	53.00	2.54	3.95
MC10	98.19	96.00	12.8	14.23	13.57	13.67	12.86	12.99	21.45	20.45	48	50.1	3.33	3.28	47.72	54.33	50.00	51.33	2.87	4.57
MC11	98.81	96.7	12.33	13.33	13.00	11.67	12.21	12.56	20.22	20.56	48.43	52.66	3.44	3.39	44.83	43.78	54.00	53.33	2.93	3.49
MC12	100.69	96.5	11.9	11.47	12.33	11.5	12.21	11.71	20.89	21.78	49.33	54.73	3.17	3.28	41.22	43.17	54.67	56.67	2.93	4.59
MC13	86.00	84.84	13.43	12.23	13.23	10.9	11.27	11.24	20.67	20.11	50.87	48.5	2.83	2.83	34.17	31.56	55.00	51.00	2.80	3.23
MC14	92.2	88.5	13.33	14.77	14.1	15.23	12.93	12.70	2045	19.67	50.33	49.43	2.67	3.33	43.56	47.39	54.00	55.67	3.59	4.10
MC15	97.19	92.16	12.00	13.67	11.53	13.43	12.68	12.75	21.22	20.55	49.30	45.23	3.11	3.17	37.67	47.67	52.00	48.00	2.31	2.45
MC16	93.00	91.84	12.53	14.77	12.53	14.33	11.82	11.69	21.67	20.89	51.33	53.23	2.83	2.67	28.83	46.25	51.33	50.00	3.13	3.43
MC17	93.61	91.63	12.34	13.51	12.34	11.84	13.33	13.05	21	20.79	51.43	54.73	2.83	3.28	29.83	52.75	52.67	58.00	2.58	3.17
MC18	90.66	91.35	12.8	14..43	11.8	14.3	12.01	12.02	21.22	20.78	56	54.35	3.06	2.94	45.39	47.44	56.67	30.33	4.17	5.19
MC19	90.68	89.42	14.03	14	14.03	13.87	11.78	11.88	19.56	19.22	53.77	55.43	2.5	2.67	38.11	43.85	51.67	57.33	2.14	3.43
MC20	88.53	90.87	12.37	13.7	13.03	14.57	10.27	11.16	20.22	20.67	57.1	51.77	3	2.83	38.50	53.56	58.00	58.33	2.72	3.53
Mean	**93.06**	**91.27**	**12.63**	**13.34**	**12.82**	**13.06**	**12.07**	**12.07**	**20.79**	**20.51**	**52.78**	**52.89**	**2.90**	**2.93**	**40.97**	**45.59**	**53.43**	**53.92**	**2.84**	**3.66**
SED	**2.477**	**2.477**	**1.361**	**1.361**	**1.230**	**1.230**	**0.451**	**0.451**	**0.641**	**0.641**	**3.752**	**3.752**	**0.269**	**0.269**	**6.680**	**6.680**	**2.78**	**2.78**	**0.41**	**0.41**
LSD 5%	**4.880**	**4.880**	**2.682**	**2.682**	**2.423**	**2.423**	**0.889**	**0.889**	**1.262**	**1.262**	**7.390**	**7.390**	**0.530**	**0.530**	**13.16**	**13.16**	**5.47**	**5.47**	**0.81**	**0.81**
cv%	**0.9**	**0.9**	**4.4**	**4.4**	**3.6**	**3.6**	**0.9**	**0.9**	**0.8**	**0.8**	**3.9**	**3.9**	**3.3**	**3.3**	**7.4**	**7.4**	**1.1**	**1.1**	**1.6**	**1.6**

Abbreviations: Gen: Genotype; DS: drought stressed; NS: non-drought stressed; PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; AGB: aboveground biomass dry weight per plant (g); SL: spike length; SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g/100 seed); HI: harvest index , GY: Grain yield ($t.ha^{-1}$). Mean overall mean for the three treatments under drought-stressed and non-stressed condition

CHAPTER 3

Association of Yield and Yield Components among Selected Bread Wheat Genotypes under Silicon Fertilisation and Drought Conditions

Abstract

Wheat (*Triticum aestivum* L. ($2n = 6x = 42$; AABBDD)) is a commodity crop serving diverse value chains worldwide. However, drought stress and poor soil health are major causes of a yield gap in wheat production. Silicon (Si) fertiliser application with drought-adapted wheat cultivars may enhance wheat productivity. This study aimed to examine the impact of Si fertilisation on agronomic performance and trait associations in wheat under drought stress to identify selection criteria for improving drought tolerance and Si response. Twenty wheat genotypes were evaluated, involving two water regimes and two Si fertiliser formulations in three environments, using a factorial experiment laid out in a randomized complete block design with three replications. Both liquid and granular Si formulations enhanced the agronomic performance of wheat compared to the untreated control, under both drought-stress (DS) and non-stress (NS) conditions. Variable degrees of correlations were recorded under different water regimes and fertiliser formulations. Si fertilisation improved favourable trait correlations compared to the untreated control under DS and NS conditions. Grain yield had positive associations with hundred seed weight (HSW), under NS conditions when using liquid Si ($r = 0.74$, $p < 0.001$) and granular Si ($r = 0.69$, $p < 0.001$). Strong trait correlations were detected between productive tiller number (TN) and productive spike number (PS) for granular Si ($r = 0.99$, $p < 0.001$); liquid Si ($r = 1.00$, $p < 0.001$); and the untreated control ($r = 0.98$, $p < 0.001$), under DS conditions. With both granular and liquid Si applications under DS conditions, there were high trait correlations between spike length (SL) with TN ($r = 0.72$, $p < 0.001$; $r = 0.63$, $p < 0.001$, respectively), and with PS ($r = 0.73$, $p < 0.001$; $r = 0.62$, $p < 0.001$, respectively). Under DS, HSW (0.84) and PS (0.64) had higher direct effects on grain yield with granular Si application, whilst TN and PS (0.94) had higher indirect effects on grain yield under liquid Si application. Under NS, above ground biomass (0.68) had the highest direct effects on grain yield with granular Si compared to the liquid Si formulation and the untreated control. The genotypes MC10, MC6, MC1, MC3, and MC11, with granular Si application, were high yielders in descending order and are recommended for breeding and further wider testing for potential variety release in South Africa. The correlation and path coefficient analyses distinguished TN, PS, and HSW as principal traits contributing to enhanced grain yield under drought stress, making them vital parameters for selecting Si-use efficient breeding lines.

Keywords: bread wheat; correlation analysis; drought tolerance; path coefficient analysis; silicon fertilisation

3.1 Introduction

Bread wheat (*Triticum aestivum* L.; $2n = 6x = 42$) is one of the most important small cereal grains, serving diverse value chains globally. About 24 - 50% of the world's population depends on wheat for daily calories (with a value of 334 kcal/100g) and proteins (12.2 g/100g) (FAO, 2021). Global wheat production is forecasted to reach 800.2 million metric tons (MMT) in 2023/24 (Sowell et al., 2023). Despite the global importance of the crop, its productivity is limited by many production constraints, which include drought, heat stress and poor soil health, some of which are associated with anthropogenic-related climate change (Filho et al., 2022; Senthilkumar, 2022).

The top five wheat-producing countries globally are China, India, Russia, USA and France, with a combined 403 MMT produced in 2021. Africa produces 29 MMT, with the sub-Saharan African (SSA) region accounting for 9.1 MMT. The largest wheat producer in SSA is South Africa, with 2.2 MMT produced in 2021 (FAOSTAT, 2021). Sub-Saharan Africa has the highest number of food-insecure people worldwide. It is estimated that 239 million undernourished people reside in this region. SSA population growth is projected to increase threefold by 2050, which will increase food demand and food insecurity (Kamali et al., 2022). Adding to the complexity of the food insecurity issue in SSA are several biotic, abiotic and socio-economic factors impacting wheat production (Belete et al., 2022). Silva et al. (2023) reported that the major wheat-producing countries in Africa have steadily improved wheat yields from 0.9 tons per hectare (t. ha^{-1}) in 1980 to 4.1 t. ha^{-1} in 2020, increasing by 72 kilograms per hectare per year (kg. $ha^{-1}.year^{-1}$). However, there is a yield gap exceeding 50% of yield potential due to several factors in Africa (Silva et al., 2023). Despite the notable yield increases, the continental supply of wheat at 23 MMT is far less than the demand of 59 MMT for the period 2009-2011 (Negasse et al., 2013). As of 2020, Africa accounts for approximately 25% of global wheat imports. As such, there is a critical need to boost local production to ensure food security and reduce the quantity of wheat being imported.

Drought stress causes yield losses of up to 35% in Africa, which will increase due to climate change (Noort et al., 2022). The adverse effect of drought stress on wheat production occurs across all plant growth stages but is particularly damaging at the flowering, grain filling and maturity stages (Maghsoudi et al., 2019). The combination of drought and heat stress can exacerbate yield losses (Sareen et al., 2023). For instance, crop exposure above 30°C for 24 hours can induce up to 12.5% yield loss (Shew et al., 2020). In addition, poor soil health management, associated with soil nutrient

deficiencies, exacerbates the impact of drought stress, especially in the SSA region. In this region, fertiliser use is limited, and supplementary irrigation is lacking (Assefa et al., 2020).

Under drought stress, crop performance and genotype yield expression depend on drought-adaptive mechanisms, specifically, drought escape, drought avoidance or drought tolerance (Li et al., 2020). Progress in breeding for drought tolerance has been slow due to the polygenic inheritance of the trait, and the interactive effects of genotype (G), environment (E) and management (M) (Mwadzingeni et al., 2016a). The G x E interaction effect reduces selection efficiency given that the genetic potential of the screened genotypes is masked by environmental variance (Mathew et al., 2019; Abou-Elwafa et al., 2020).

Ideotype breeding in wheat depends on selecting vital agronomic traits under optimal or drought-stress conditions and with a range of management practices. Traits such as aboveground plant biomass, plant height and grain yield are used for the selection of drought-tolerant genotypes (Munjal et al., 2016; Sanad et al., 2019). Multivariate analysis is the simultaneous statistical assessment of a collection of correlated metric traits in a population. It is the most common method used in crop improvement programs aiming for the selection of multiple correlated traits (Niazian et al., 2020). Trait associations analysis, such as path coefficient analysis, identifies direct and indirect trait associations. Furthermore, it compares the trait influences and their relative contributions (Patel et al., 2022). Therefore, it is essential to understand the extent of and trend of associations among yield-related traits which are required for simultaneous selection for yield improvement in wheat.

The assessment and classification of genotypes for genetic diversity, biotic and abiotic stress tolerance, yield components, and yield stability is essential in plant breeding programs. Grain yield is a complex trait with several components contributing at various levels to yield expression. Understanding the relative importance of each trait and its contribution to grain yield is vital in genotype selection (Gupta et al., 2019). Correlation, regression, and path coefficient analysis are statistical tools often used to understand the level of variation and relatedness between agronomic traits (Taiwo et al., 2020). Correlation and regression analyses identify the linear relationship between traits, whereas path coefficient analysis creates a causal directional model of effects from several agronomic traits. Path coefficient analysis is a standardized partial regression method for investigating a closed system of linearly connected agronomic traits (Pundir et al., 2022). The complexity of the statistical tools increases with the number of evaluated variables. Path coefficient diagrams are effective for visually interpreting the complex interrelationships of closely interrelated variables (Li, 1975). Several studies have utilized correlations and path analyses to identify direct and indirect trait associations amongst yield and yield components (Sidhu et al., 2018; Shamuyarira et al., 2019; Semnaninejad et al., 2021). The direction and magnitude of these associations determine the selection criteria of a breeding population.

Silicon (Si) application may affect agronomic performance and productivity in wheat under drought stress (Verma et al., 2020). Si is taken up, translocated, and deposited as silica (SiO_2) or phytoliths in some plants such as grasses (Gocke et al., 2013). It also affects abiotic and biotic stress management in many plant species that can take up silicic acid via the roots (Debona et al., 2017). The level of Si accumulation is species and genotype-dependent, and its uptake is conditioned by stress or environmental signals (Putra et al., 2021). Additionally, the uptake of Si affects carbon, nitrogen, and phosphorus ratios in a plant, which is further subject to Si formulation, concentration, application rate and time of application (Neu et al., 2017; Hao et al., 2020; Christian et al., 2022). Trait associations are known to change depending on agronomic management conditions. Si applications combined with drought stress has been shown to cause variations in trait associations in wheat (Christian et al., 2023).

The combination of Si fertiliser and drought-adapted wheat cultivars may enhance wheat production and grain yields (Christian et al., 2023), under drought stress conditions (DS). The combination results in measurable improvements in the performance of several yield-related traits, such as plant biomass, spike weight and plant height (Ahmad et al., 2007); spike length, hundred seed weight and grain yield (Ahmed et al., 2016); and productive tiller number and productive spike number (Christian et al., 2023). However, the extent and trend of agronomic traits association in wheat are yet to be explored where Si fertilisation is combined with DS and NS conditions to guide the breeding and selection of high-performing cultivars. Therefore, this study's objective was to examine the effect of Si fertiliser application on agronomic performance and trait associations in wheat under drought stress to identify criteria for drought stress tolerance selection.

3.2 Materials and Methods

3.2.1 Description of the Study Environments

The study was conducted under field (2019 growing season) and controlled environmental (2017 and 2018 growing seasons) conditions and is briefly described below.

3.2.2 Plant Materials

The study evaluated 20 candidate drought and heat-tolerant bread wheat genotypes. The details of these genotypes along with their pedigrees and the meteorological data were presented in Chapter 2, Section

2.2.1. The genotypes were selected for their genetic variation, high grain yield and drought-tolerance (Mwadzingeni et al., 2016b; Christian et al., 2023).

3.2.3 Greenhouse Experimental Design and Trial Management

A 20 x 3 x 2 factorial experiment was used in a randomized complete block design with three replications. The three factors represent the 20 genotypes, 3 Si treatments and two water regimes (Figure 3.1). Plants were grown in 5 litre (L) plastic pots filled with composted pine bark growing media. This was described in Chapter 2, Section 2.2.2.

3.2.4 Field Experimental Design and Trial Management

The experiment was laid out in a 20 x 3 x 2 randomized complete design with each genotype planted in 6 row plots measuring 9.0m in length, with inter-row spacings of 0.3m and in-row spacing of 0.1m. The experimental design and treatments are described in Chapter 2, Section 2.2.2.

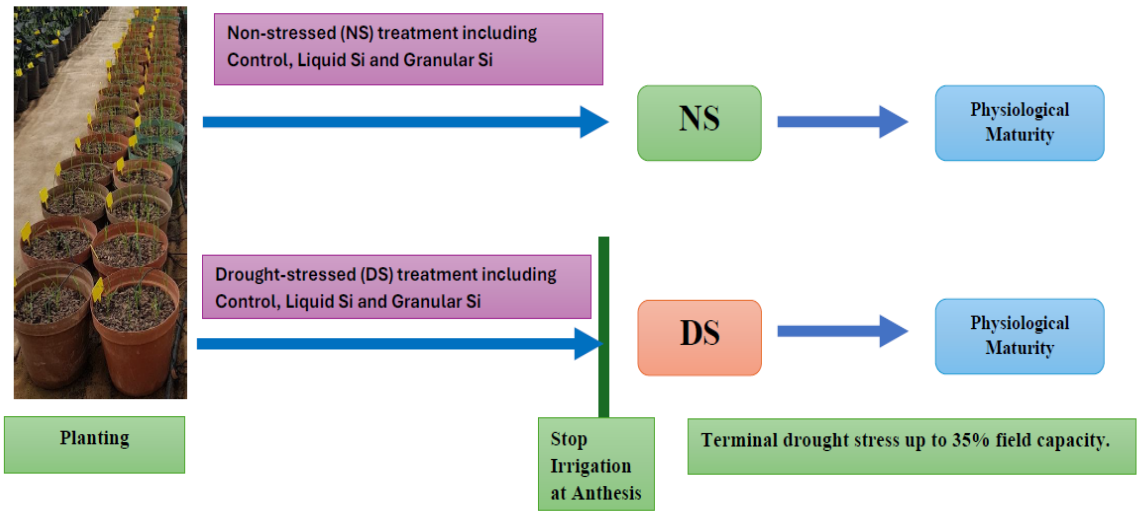

Figure 3.1: Scheme of irrigation water application under non-stress (NS) and drought-stress (DS) conditions

3.2.5 Silicon Formulations

Two Si formulations and an untreated control were applied under DS and NS conditions for both greenhouse and field trials. The treatment application is described in Chapter 2, Section 2.2.2.

3.2.6 Data Collection

Data was collected on 10 agronomic traits under field and greenhouse experiments on a plant and plots basis. Details of the data collection were summarised in Chapter 2, Section 2.2.3

3.2.7 Data Analysis

A combined analysis of variance (ANOVA) was performed on the assessed agronomic traits using Genstat 18th version, VSN, International (Payne et al., 2015). The homogeneity of genotype and environment variances were determined using Bartlett's test (Bartlett, 1937) before a combined analysis of variance. The mean performance of test genotypes was compared at the p-value of 0.05% using Fisher's least significant difference (LSD).

Correlation Analysis

Pearson correlation coefficients were computed for the two different Si formulations and the untreated control under drought-stress and non-stress conditions using the "metan" package in RStudio version 2023.03.0, to discern the magnitude of the agronomic trait relationships (Olivoto and Lúcio, 2020).

Path Coefficient Analysis

Path coefficient analysis was conducted to partition correlation coefficients into direct and indirect effects on grain yield, following Dewey et al. (1959), using "lavaan" and "semPlot" package in RStudio version 2023.03.0 (Epskamp, 2015). The following model was used for path coefficient analysis:

$$r_{ij} = P_{ij} + \sum r_{ik} P_{kj}$$

where r_{ij} = mutual association between the independent variable (i) (yield-related trait) and the dependent variable (j) (yield) as measured by the correlation coefficient P_{ij}. P_{ij} is the components of the direct effect of the independent variable (i) on the dependent variable (j) as measured by the coefficients; $\sum r_{ik} P_{kj}$ is the summation of the indirect effects of a given independent variable (i) on the dependent variable (j) via all the independent variables (k). Path coefficient analysis diagrams were developed using structural equation modelling (SEM) in R (R Core Development Team, 2023).

3.3 Results

3.3.1 Analysis of Variance

The combined analysis of variance revealed significant differences among the test genotypes for all assessed agronomic traits (Table 3.1). There were significant differences for PS, AGB, HSW and GY due to the four-way interaction effect of genotype x water regime x Si treatment x growing environment. Significant differences ($p < 0.05$) were recorded for PS and GY for the three-way interactions of genotype x Si treatment x growing environment, whilst the genotype x water regime x treatment interaction was significant ($p < 0.05$) for PS and AGB only (Table 3.1).

3.3.2 Genotype Performance

Based on grain yield response, the top five (5) best-performing genotypes under drought-stress and non-stress conditions, and treated with either liquid Si, or granular Si and the untreated control are summarized in Table 3.2. The mean data for all the test genotypes are presented in supplemental Tables S3.1 to S3.3.

Under non-stressed and drought-stressed conditions, respectively, the mean grain yields after treatment with granular Si were 12.7 $t.ha^{-1}$ and 6.3 $t.ha^{-1}$, and after treatment with liquid Si were 10.4 $t.ha^{-1}$ and 5.6 $t.ha^{-1}$, compared to the control at 11.5 $t.ha^{-1}$ and 5.7 $t.ha^{-1}$ (Tables S3.1 to S3.3). The highest grain yield was recorded for MC10 genotype across all treatments, which were granular Si (9.2 $t.ha^{-1}$), control (7.6 $t.ha^{-1}$) and liquid Si (7.0 t. ha^{-1}) under DS conditions (Table 3.2). Under NS conditions, MC10 recorded the highest yield of 12.2 $t.ha^{-1}$, 11.8 $t.ha^{-1}$, 10.3 $t.ha^{-1}$ with liquid Si, granular Si and untreated control treatments, respectively. The granular Si application improved the agronomic trait performance of all tested traits under DS conditions for MC10. MC6 was the second highest yielder, with a grain yield of 7.8 $t.ha^{-1}$ and 6.8 $t.ha^{-1}$ with granular Si application and untreated control, respectively, under DS conditions. Under NS conditions, MC6 yielded 15.0 $t.ha^{-1}$ with the granular Si application and 11.0 $t.ha^{-1}$ with the untreated control. The relatively lowest yielding genotypes were MC4 (4.5 $t.ha^{-1}$) and MC19 (4.5 $t.ha^{-1}$) for the untreated control, MC18 (3.6 t. ha^{-1}) with the liquid Si, and MC20 (5.3 $t.ha^{-1}$) with granular Si, under DS conditions (Tables S3.1 to S3.3). The overall mean across agronomic traits improved with granular Si application compared to the untreated control (Tables S3.1 to S3.3). With granular Si application, the agronomic trait performance for all traits were enhanced, particularly under DS compared to NS conditions. The performance of the genotypes with Liquid Si varied with the agronomic traits and genotypes tested.

Table 3.1: Combined analysis of variance (ANOVA) and significant tests for yield components of 20 wheat genotypes treated with two Si formulations and an untreated control under drought-stress and non-stress conditions across three environments

Source of variation	df	PH	TN	PS	SL	SPS	KPS	HSW	AGB	HI	GY
Genotype (G)	19	629.66***	5.90***	6.70***	12.27***	24.59***	365.70***	3.31***	48.03***	0.12***	14.91***
Water Regime (WR)	1	5785.11***	26.20***	17.92***	0.18^{ns}	3.96^{ns}	6962.97***	479.13***	7904.82***	1.79***	7518.20***
Treatment (T)	2	658.74***	70.83***	115.30***	18.56***	31.00***	661.13***	3.36***	847.56***	0.03***	178.80***
Environment (E)	2	15310.31***	11044.60***	10701.60***	718.68***	792.17***	46149.12***	602.96***	12571.94***	0.97***	7756.07***
G x WR	19	33.68^{ns}	1.75^{ns}	1.62*	0.16^{ns}	0.78^{ns}	21.67^{ns}	0.57***	20.83*	0.00*	11.58***
G x T	38	29.25^{ns}	1.48^{ns}	1.93***	0.20^{ns}	0.80^{ns}	26.69^{ns}	0.21^{ns}	18.95*	0.00^{ns}	6.02^{ns}
G x E	38	690.02***	1.08^{ns}	0.89^{ns}	0.52^{ns}	3.31^{ns}	205.73***	1.45**	45.95*	0.00^{ns}	36.59***
WR x T	2	114.07***	3.45***	3.47***	2.14***	4.30***	59.04***	0.87***	34.07***	0.01***	11.30***
WR x E	2	319.04***	23.51***	9.69***	5.62***	3.72*	352.22***	135.32***	1267.17***	0.49***	1178.18***
T x E	4	53.69^{ns}	13.31***	29.09***	2.50***	6.61***	187.81***	2.65***	41.01*	0.01*	118.84***
G x WR x T	38	22.50^{ns}	1.5^{ns}	1.41*	0.19^{ns}	0.65^{ns}	20.66^{ns}	0.28^{ns}	18.73*	0.00^{ns}	5.11^{ns}
G x WR x E	38	30.72^{ns}	1.15^{ns}	1.08^{ns}	0.23^{ns}	0.88^{ns}	29.54*	0.37*	15.61^{ns}	0.00^{ns}	10.52***
G x T x E	76	22.70^{ns}	1.24^{ns}	1.49**	0.25^{ns}	1.25^{ns}	19.77^{ns}	0.23^{ns}	15.63^{ns}	0.00^{ns}	6.17*
WR x T x E	4	161.49***	3.82*	3.48**	1.61***	7.11***	73.86**	1.05**	98.81***	0.00^{ns}	49.26***
G x WR x T x E	76	21.36^{ns}	1.30^{ns}	1.30*	0.23^{ns}	0.97^{ns}	19.49^{ns}	0.31*	21.78***	0.00^{ns}	5.56*
Residual	718	25.43	1.11	0.92	0.24	1.16	20.26	0.24	12.67	0.003	4.38

*Abbreviations:*AGB, above-ground dry biomass weight (t.ha^{-1}); df, degrees of freedom; GY,-Grain yield (t.ha^{-1}); HI, harvest index; HSW, hundred seed weight (g/100 seed); KPS, number of kernels per spike; PH, plant height (cm); PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; T, Treatment (three levels = untreated control, liquid Si and granular Si); TN, number of productive tiller number per plant; *,**,***, ns denote significance differences at $p < 0.05$, $p < 0.01$, $p < 0.001$ and non-significant, respectively.

Table 3.2: Means for 10 agronomic traits of the top 5 wheat genotypes ranked based on the grain yield for each treatment under drought-stress and non-stress conditions across three environments

Genotype	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
Control																				
MC10	91.3	95.2	4.8	6.4	4.2	5.2	10.6	10.4	19.9	19.7	38.1	38.9	3.5	4.4	14.9	16.9	0.5	0.5	7.6	10.3
MC6	93.8	98.5	6.2	5.5	6.2	5.5	10	9.8	21.4	21.3	37.7	43.4	2.6	3.8	15.1	18.4	0.5	0.6	6.8	11.0
MC7	82.8	91	5.5	5.9	5.1	6.1	9.9	9.8	19.7	20.3	38.1	47.1	2.8	4.1	12.6	17.9	0.5	0.6	6.3	12.5
MC9	93	97.6	5.5	5.7	5.4	5.6	10.6	10.5	19.9	19.8	38.5	44.7	2.8	4.5	14.4	16.3	0.5	0.5	6.0	12.5
MC1	85.0	90.9	5.4	5.4	5.0	5.2	9.9	9.9	20.5	20.1	41.5	44.1	2.7	3.7	12.0	16.5	0.5	0.6	6.0	9.8
Liquid Si																				
MC10	90.2	98.6	5.7	5.9	5.6	5.9	10.9	11	20.7	21	40	43	3.3	4.5	13.4	20.1	0.5	0.6	7.0	12.2
MC1	90.7	93.2	5.7	6.6	5.8	6.6	10.3	10.5	20.6	21.3	41	47.1	2.8	3.8	14.4	21.2	0.5	0.6	6.5	11.2
MC11	100.5	102.2	6.1	6.2	6.1	5.9	10.4	10.6	19.9	20.2	38.6	43.6	3.3	4.7	15.3	19.6	0.5	0.6	6.3	11.6
MC5	90.6	98.4	6.5	6.4	6.4	6.2	9.5	9.7	20.5	21.1	43.6	49.7	2.9	4.1	15.5	20.1	0.5	0.6	6.1	11.0
MC17	94.0	94.4	6.7	5.7	6.6	5.8	11.6	11.6	20.5	21.0	39.6	45.9	3.0	4.3	15.8	20.6	0.5	0.6	6.1	10.8
Granular Si																				
MC10	96.7	95.5	6.0	6.7	6.3	6.6	11	10.9	20.5	20.4	40	41	3.6	4.4	15.9	18.9	0.5	0.6	9.2	11.8
MC6	99	100.7	6.6	6.6	7.6	7.1	10.4	10.1	22.1	21.4	42.9	45.8	2.9	4.3	19.3	24.9	0.5	0.6	7.8	15.0
MC1	91.5	93.6	6.7	6.4	6.7	6.3	10.5	10.5	21.2	21.1	45.4	50.5	2.9	4.1	18.1	22.2	0.5	0.6	7.2	12.4
MC3	91.1	93.4	6.4	6.5	6.3	6.4	10.5	10.3	19.3	19.8	39.3	42.8	3.2	4.6	16.1	20.5	0.5	0.6	7.1	13.2
MC11	101	99.5	6.2	6.4	6.4	5.8	10.5	10.6	19.6	20	38.9	41.6	3.2	4.8	15.9	19.0	0.5	0.6	6.8	11.2
Mean	**90.0**	**94.6**	**6.0**	**6.3**	**5.9**	**6.1**	**10.4**	**10.5**	**20.3**	**20.4**	**39.8**	**44.9**	**2.9**	**4.2**	**14.4**	**19.8**	**0.5**	**0.6**	**5.9**	**11.1**
SEM	**0.4**	**0.3**	**0.2**	**0.2**	**0.2**	**0.2**	**0.1**	**0.1**	**0.1**	**0.1**	**0.5**	**0.5**	**0.1**	**0.1**	**2.1**	**2.1**	**0.0**	**0.0**	**1.7**	**1.7**
LSD (5%)	**7.6**	**7.0**	**4.4**	**4.8**	**4.4**	**4.6**	**1.2**	**1.3**	**1.6**	**1.6**	**10.3**	**10.1**	**1.1**	**1.3**	**5.7**	**5.7**	**0.1**	**0.1**	**3.4**	**3.4**
CV (%)	**9.9**	**8.4**	**75.7**	**77.6**	**77.3**	**77.3**	**12.5**	**13.9**	**8.6**	**9.0**	**27.4**	**23.9**	**43.6**	**32.2**	**3.6**	**3.6**	**16.3**	**10.5**	**2.5**	**2.5**

Abbreviations: Overall mean for the three treatments under drought-stressed and non-stressed conditions. AGB, above-ground dry biomass weight ($t.ha^{-1}$); DS, drought-stressed; GY, Grain yield ($t.ha^{-1}$); HI, harvest index; HSW, hundred seed weight (g/100 seed); KPS, number of kernels per spike; NS, non-drought stressed; PH, plant height (cm); PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; TN, number of productive tiller number per plant. SEM: Standard error of the mean; CV: Coefficient of variation; LSD= Least significant difference

3.3.3. Correlations between Agronomic Traits and Grain Yield

Figure 3.2A-F presents Pearson's correlations of agronomic traits under drought-stress and non-stress conditions, with and without liquid and granular silicon, across three environments. A strong positive and significant correlations were recorded between GY and AGB (r = 0.74, p < .001), whilst strong negative and significant correlations were recorded between GY: TN (r = -0.80, p < .001), PS (r = -0.80, p < .001) and SL (r = -0.61, p < 0.001), under DS conditions and without Si fertiliser application (Figure 3.2A). Positive and significant correlations were computed among the following agronomic traits: TN: PS (r = 0.98, p < .001) and KPS with HI (r = 0.71, p < .001). There were strong negative and significant correlations for TN and AGB (r = -0.61, p < .001) and PS with AGB (r = -0.62, p < .001). There were variable associations among the assessed traits. Moderately strong and positive correlations were recorded between SL: TN (r = 0.62, p < .001), PS (r = 0.59, p < .001) and KPS (r = 0.67, p < .001) and HSW: PH (r = 0.65, p < .001); KPS (r = 0.64, p < .001) and HI (r = 0.64, p < .001).

Under NS conditions without Si (Figure 3.2B), there was a strongly positive correlation between HSW with GY (r = 0.72, p < .001) and AGB with GY (r = 0.63, p < .001). There existed strong, positive and significant correlations between PS and TN (r = 0.98, p < .001) and SL and KPS (r = 0.76, p < .001). Moderately high positive correlations were computed for SL and PS (r = 0.69, p < .001) and TN (r = 0.69, p < .001), and KPS with SPS (r = 0.66, p < .001). Three traits were highly and negatively correlated with GY and PS (r = -0.87, p < .001), TN (r = -0.87, p < .001) and SL (r = -0.63, p < .001) (Figure 3.2B). Similar trends were noted under DS conditions without Si fertiliser application (Figure 3.2A). Whilst strong, negative and significant correlations were noted between AGB and PS (r = -0.87, p < .001), and TN (r = -0.87, p < .001). Other trait interactions showed variable associations.

Under DS with liquid Si application (Figure 3.2C) significant associations were discerned among most agronomic traits. The following traits showed strong, negative and significant correlations with GY: TN (r = -0.75, p < .001), PS (r = -0.75, p < .001), whilst the only strong positive and significant correlation with GY was with AGB (r = 0.74, p < .001). Other agronomic traits with high, significant and positive associations were TN with PS (r = 1.00, p < .001), HSW with HI (r = 0.78, p < .001) and KPS with HI (r = 0.79, p < .001). Other positive and relatively strong associations were deduced between HSW with PH (r = 0.61, p < .001), SPS (r = 0.65, p < .001) and KPS (r = 0.62, p < .001); KPS and TN(r = 0.63, p < .001); PS (r = 0.60, p < .001) and SL (r = 0.67, p < .001) and TN with SL (r = 0.63, p < .001).

Under NS conditions and liquid Si treatment (Figure 3.2D), variable trait correlations were discerned. The traits which had strong positive and significant correlations with GY were AGB (r = 0.83, p < .001) and HSW (r = 0.74, p < .001). The traits that had strong, negative, and significant correlations with GY included TN (r = -0.81, p < .001), and PS (r = -0.82, p < .001). Secondary agronomic traits that

showed high and positive correlations were TN and PS (r = 0.99, p < .001); SL and KPS (r = 0.71, p < .001), TN (r = 0.70, p < .001) and PS (r = 0.70, p < .001); PH and SPS (r = 0.60, p < .001) and HSW (r = 0.64, p < .001); and HSW and HI (r = 0.61, p < .001) and AGB (r = 0.80, p < .001).

Under DS conditions with granular Si application conditions assessed agronomic trait associations showed variable degrees of associations (Figure 3.2E). AGB had strong positive and significant correlations with GY (r = 0.63, p < .001). The following traits showed strong, negative and significant correlations with GY: PS (r = -0.78, p < 0.001); TN (r = -0.77, p < 0.001) and SL (r = -0.63, p < .001). Additionally, traits with strong, positive and significant associations included PS: TN (r = 0.99, p < 0.001), SL (r = 0.73, p < 0.001) and KPS (r = 0.63, p < 0.001); SL: TN (r = 0.72, p < 0.001) and KPS (r = 0.72, p < 0.001) ; PH: HSW (r = 0.64, p < 0.001), HI: HSW (r = 0.71, p < 0.001) and KPS (r = 0.69, p < 0.001).

The strong positive and significant correlations with GY were AGB (r = 0.78, p < .001) and HSW (r = 0.69, p < 0.001), under NS conditions with granular Si application (Figure 3.2F). Traits that showed strong negative correlations with GY included TN (r = -0.82, p < 0.001), PS (r = -0.82, p < 0.001), and SL (r = -0.69, p < 0.001). Other strong negative associations were observed between HSW: TN (r = -0.75, p < 0.001) and PS (r = -0.75, p < 0.001). Under the same conditions, several traits exhibited strong positive associations, including TN and PS (r = 0.99, p < 0.001), and SL (r = 0.72, p < 0.001). Secondary agronomic traits with strong, positive and significant associations included PS and SL (r = 0.70, p < 0.001), KPS and SL (r = 0.70, p < 0.001) SPS and KPS (r = 0.64, p < 0.001) and HSW and AGB (r = 0.79, p < 0.001), PH (r = 0.61, p < 0.001).

The association of TN and PS with SL and KPS under DS conditions increased in magnitude in the following order: granular Si > liquid Si > control. Relatively similar pattern was noticed for trait interactions PH with SL, and HI, SL with KPS and PH with HI, under DS conditions. The pattern of liquid Si > granular Si > control occurred for the association of TN with PS under DS conditions. Similar trends in trait interactions were noted for HSW with HI under DS conditions. Under NS conditions, traits TN with PS and SL and, PS with SL, had interactions that showed the granular Si > liquid Si > control. Meanwhile, AGB with GY had the pattern of liquid Si > granular Si > control. It can be inferred that Si application improves the degree of trait associations under both DS and NS conditions. Under DS conditions, both granular Si and liquid Si applications improved trait associations from negative to positive patterns when compared to the untreated control. The magnitude of trait associations under NS conditions, however, is not as substantial as the associations under DS conditions. This suggests that the variation in trait associations necessitates path coefficient analysis to pinpoint the influential traits through their direct and indirect effects.

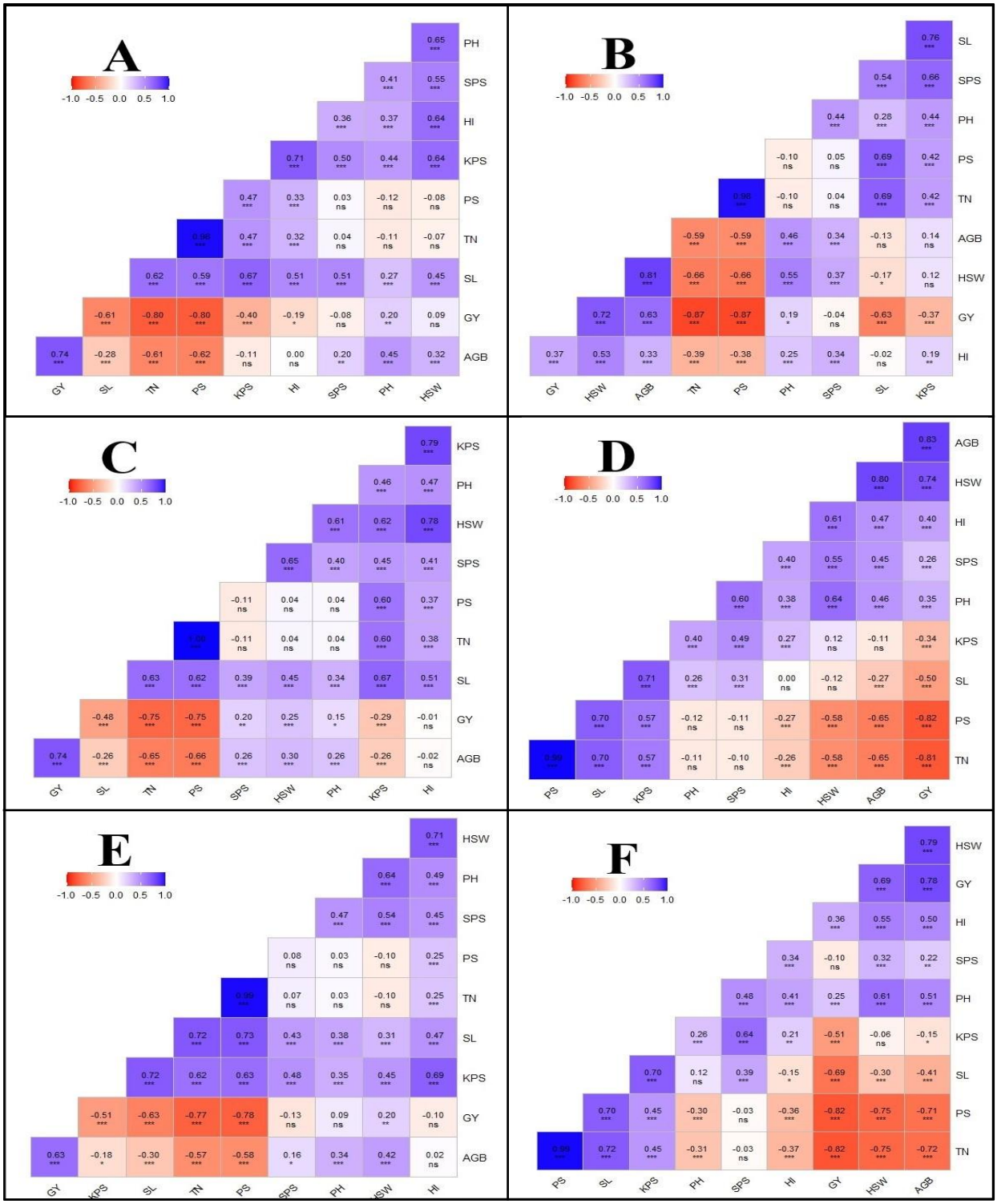

Figure 3.2: Pearson's correlation analysis of agronomic traits in wheat under variable drought stress and Si applications across three testing environments: (A) without Si under drought-stress conditions; (B) without Si under non-stress conditions; (C) with liquid Si under drought-stress conditions; (D) with liquid Si under non-stress conditions; (E) with granular Si under drought-stress conditions; (F) with granular Si under non-stress conditions across three environments. The colour variation indicates the magnitude of correlations, traits with deep blue are strongly and positively correlated, while deep red are strongly negatively correlated. Abbreviations: AGB, above-ground biomass dry weight (t.ha^{-1}); GY, Grain yield (t.ha^{-1}); HI, harvest index; HSW, hundred seed weight (g/100 seed); KPS, number of kernels per spike; PH, plant height (cm); PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; TN, number of productive tiller number per plant. Note: *,** and *** denote the level of significance associations of traits at $p < 0.05$, $p < 0.01$ and $p < 0.001$ probability values, respectively, while ns denotes non-significant associations.

3.3.4 Path Coefficient Analysis of the Effects of Agronomic Traits on Grain Yield of Wheat under Drought Stress and Si Applications

Figures 3.3 to 3.5 depict the direct and indirect effects of agronomic traits on wheat grain yield under drought stress and non-stress conditions, without Si (Figures 3.3A and B), liquid Si (Figures 3.4C and D) and granular Si (Figures 3.5D and E) applications and, across three environments. Under DS conditions and without Si application, the effects of yield components are summarized in Figure 3.3A. The explained GY variation (R^2) of 0.79 is due to yield components. The only traits with high and positive direct effects on GY were TN (0.61) and HI (0.53). Also, higher indirect effects were detected between TN with PS (0.95), PH with AGB (0.59) and HSW with HI (0.52). Under NS conditions and without Si application, the GY response is summarized in Figure 3B. The explained variation in GY (R^2) of 0.83 is attributable to yield components. The direct effects of HSW (0.84), KPS (0.44) and PS (0.48) were the highest and positive on GY. The highest positive indirect effects were between PS with TN (0.78), PH with HSW (0.58), HSW with AGB (0.52), and SPS with KPS (0.49).

With liquid Si treatment and under DS conditions, the response trait GY had an R^2 of 0.75 with the assessed agronomic traits (Figure 3.4C). Direct effects on yield components decreased compared to the untreated control, with the highest effect of AGB (0.61) and HI (0.58). There were marked indirect effects of TN with PS (0.94), TN with AGB (0.67), AGB with PS (0.68) and AGB with HSW (0.57). Under NS conditions and with liquid Si application, the R^2 value of the response trait (GY) explained by the assessed traits was 0.84 (Figure 3.4D). The direct effects on GY were minimal by all yield components. The highest positive direct effect was noted for AGB (0.41). The highest positive indirect effects on GY were recorded for TN with PS (0.92), and PH with AGB (0.43), SPS with KPS (0.47) and PH with HSW (0.58).

Under DS conditions and with granular Si application, the explained variation in GY was 0.73 (Figure 3.5E). Notable direct effects were discerned on GY, including PS (0.64), KPS (0.48) and HSW (0.84). The direct effect of HSW with granular Si application increased compared to the untreated control and liquid Si treatments. PS (with a direct effect of 0.64) improved with granular Si application compared to the untreated control. The only indirect effects on GY were influenced by TN with PS (0.82) and PH with HSW (0.43). Figure 3.5F summarises the grain yield response and path of trait associations under NS conditions and with granular Si application. The R^2 of GY was 0.83 explained by the assessed traits. The only highest positive direct effect was recorded for AGB (0.68). The highest positive indirect effects were between TN with PS (0.83), PH with AGB (0.44), SL with HSW (0.41), KPS with HI (0.49) and SPS with KPS (0.50).

Under both water regimes and Si applications, the indirect influence of the majority of the yield components on GY were low in magnitude. Only a few variables had moderate to high positive indirect

effects on GY. Granular Si application had strong direct effects on PS and HSW traits under DS conditions and improved the trait performances compared to the untreated control and liquid Si application. The R^2 value accounts for the proportion of variance in GY that can be explained by all the measured yield components. The R^2 for the response trait GY across all three treatments under DS conditions were relatively similar. This suggests that, irrespective of the application of silicon, the response by the yield components to GY is homogenous. However, it increased substantially under NS conditions for all treatments. Si application under NS conditions yielded relatively high R^2 values (granular Si at 0.83 and liquid Si at 0.84), suggesting that trait responses impacting GY were magnified compared to under DS conditions.

Granular and liquid Si applications had improved the indirect effects of many trait interactions compared to the untreated control under DS and NS conditions. For instance, the indirect effect of SL with HSW for granular Si (0.38) and liquid Si (0.33) application compared to the untreated control (0.32).

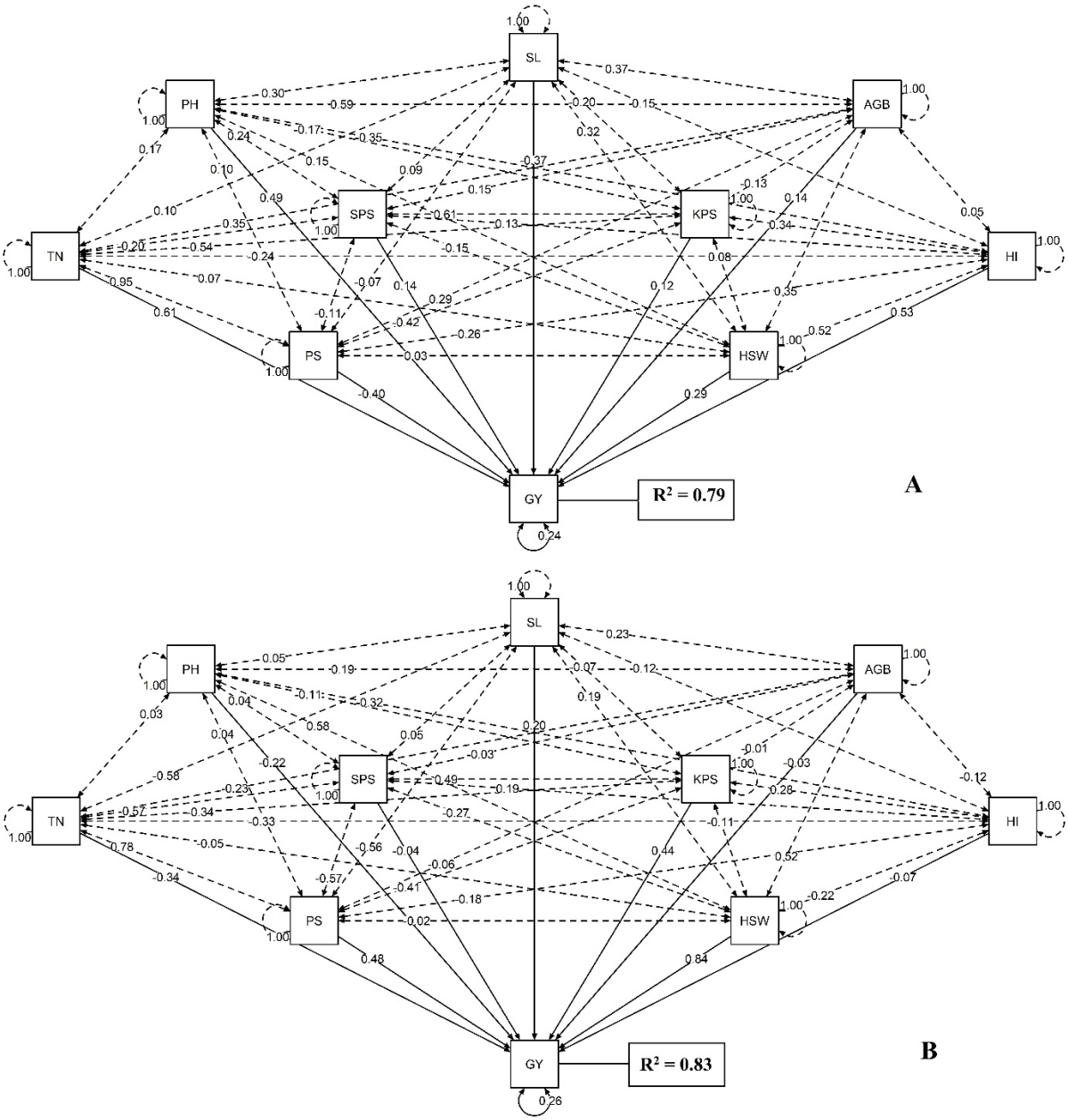

Figure 3.3: Path analysis diagram displaying causal relationships of assessed traits on grain yield in 20 bread wheat lines evaluated under drought-stress conditions (A) and non-stress conditions (B) without silicon. Abbreviations: AGB, above-ground biomass dry weight ($t.ha^{-1}$); GY, Grain yield ($t.ha^{-1}$); HI, harvest index; HSW, hundred seed weight (g/100 seed); KPS, number of kernels per spike; PH, plant height (cm); PS, productive spike number per plant; R^2 = R-squared; SL, spike length (cm); SPS, number of spikelets per spike; TN, number of productive tiller number per plant. Solid lines (—) indicate the direct effects and dotted lines (----) indicate the indirect effects.

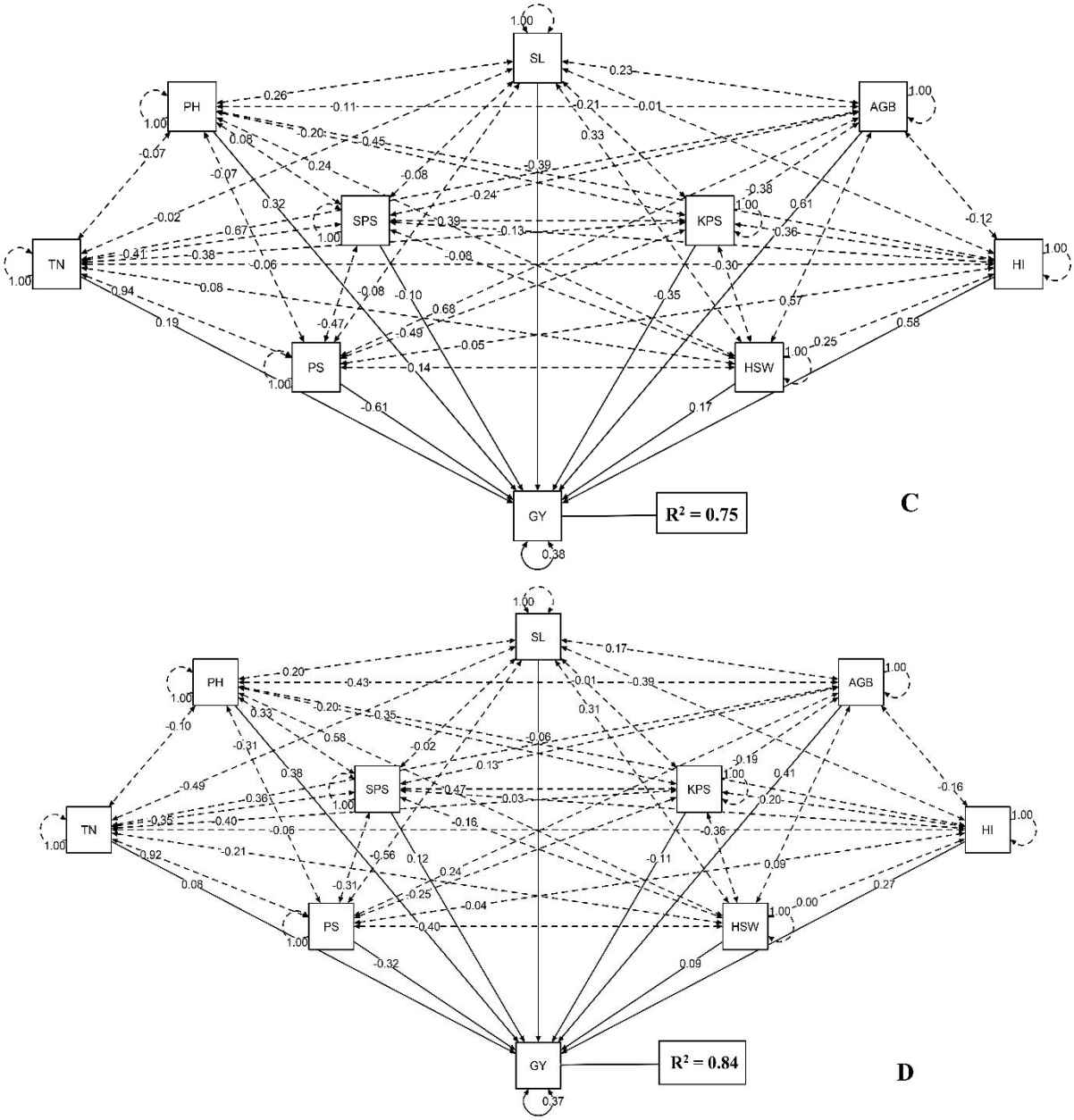

Figure 3.4: Path analysis model diagram displaying causal relationships of assessed traits on grain yield in 20 bread wheat lines assessed under drought-stress (C) and non-stress (D) conditions with liquid silicon. Abbreviations: AGB, above-ground biomass dry weight ($t.ha^{-1}$); GY, Grain yield ($t.ha^{-1}$); HI, harvest index; HSW, hundred seed weight (g/100 seed); KPS, number of kernels per spike; PH, plant height (cm); PS, productive spike number per plant; R^2 = R-squared; SL, spike length (cm); SPS, number of spikelets per spike; TN, number of productive tiller number per plant. Solid lines (—) indicate the direct effects and dotted lines (----) indicate the indirect effects.

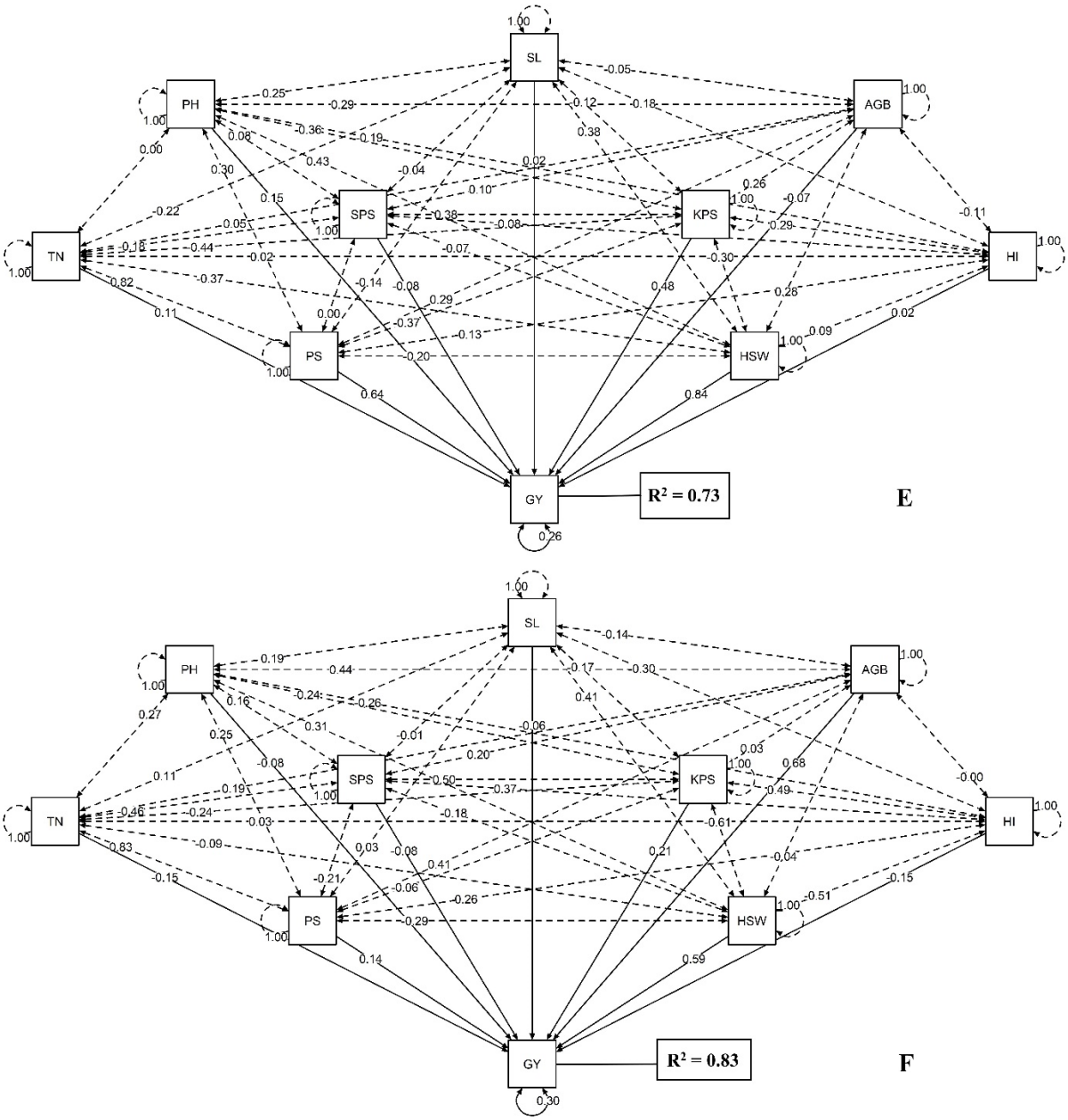

Figure 3.5: Path analysis model diagram displaying causal relationships of assessed traits on grain yield in 20 bread wheat lines assessed under drought-stress (E) and non-stress (F) conditions with granular silicon. Abbreviations: AGB, above-ground biomass dry weight ($t.ha^{-1}$); GY, Grain yield ($t.ha^{-1}$); HI, harvest index; HSW, hundred seed weight (g/100 seed); KPS, number of kernels per spike; PH, plant height (cm); PS, productive spike number per plant; R^2 = R-squared; SL, spike length (cm); SPS, number of spikelets per spike; TN, number of productive tiller number per plant. Solid lines (—) indicate the direct effects and dotted lines (----) indicate the indirect effects.

3.4 Discussion

Low wheat yield is mainly attributable to drought stress and poor soil health (Meza et al., 2021). Drought stress and poor soil health, including poor soil quality and its management, are among the primary abiotic factors limiting crop yield in sub-Saharan Africa (Assefa et al., 2020). Drought stress drastically reduces dry matter accumulation and sink capacity, which ultimately decrease seed set and yield (Tabassum et al., 2018). In the current study, the test genotypes showed significant ($p \leq 0.05$) variation for grain yield and yield components under both DS and NS conditions (Table 3.1). This suggests the presence of considerable genetic variation that could be exploited to improve yield and drought tolerance of the wheat crop through hybridization and selection. The existence of genetic variance among the test genotypes for traits related to stress tolerance is vital for targeted breeding aiming to develop cultivars for a wide range of environments (Asfaw et al., 2014; Semahegn et al., 2020). The interactions between Si treatments and genotypes indicated that there is ample genetic variation that can be utilized for the selection of Si-use efficient genotypes (Table 3.1). Salem et al. (2022) showed that the formulation of Si fertilisers plays a vital role in agronomic performance, with potassium silicate ($KSiO_4$) improving photosynthetic capacity, grain weight per spike, thousand-grain weight, and grain yield more than other silicon formulations. Comparable results were noted for the current study, with significant differences noted for the four-way interaction effect of genotype (G) x water regime (WR) x treatment (T) x environment (E) for PS, AGB, HSW and GY. The difference in the genotypic performance indicated that across both DS and NS conditions, the slow-release, granular Si product outperformed the liquid Si formulation and the control treatments for all agronomic traits. The significance of the four-way interaction, confirms that the genetic variation amongst genotypes, combined with Si fertilisation, can be exploited for the production of wheat in drought-prone environments. The beneficial effects of Si fertilisation were more evident under stress conditions than non-stress conditions (Christian et al., 2023). Genotypes MC10, MC6, MC1, MC3, and MC11, combined well with granular Si application (Table 3.2), and were found to be superior. The selected genotypes should be promoted for further field evaluation and could be utilized in future breeding programs and grain production.

Direct selection for yield is not efficient due to its genetic complexity and the significant impact of the environment. However, selection efficiency can be enhanced by exploiting the interrelationships between grain yield and its components (Yadav et al., 2021). Statistical tools, such as correlations and path coefficient analysis, are used by breeders to select and improve grain yield through direct and indirect selection of proxy traits. Breeders use secondary agronomic traits, related to drought tolerance such as SL, HSW, and KPS, allowing indirect selection for enhanced grain yield (Bänziger et al., 2000). In wheat breeding, the most exploited traits include productive tillers, grain number per spike, spike

length, grain weight per spike, harvest index, grain weight, spike weight and biomass production (Zhou et al., 2007; Zhang et al., 2016; Gao et al., 2017).

Si fertilisation enhances physiological, nutritional and biochemical changes within the plant (Sohail et al., 2019). However, the formulation of Si fertiliser being used may impact on the uptake of Si (Dorairaj et al., 2020). Furthermore, the frequency of application to wheat plants is important, given that Si cannot be stored in monocotyledonous plants. (Kowalska et al., 2021) found that the application of monosilicic acid was more effective than the application of diatomaceous earth as the source of Si in enhancing traits such as PS, PH and GY in wheat. In contrast, in the current study a slow-release granular Si provided an extended period of uptake compared to the weekly liquid Si application. This would have affected the uptake and distribution of Si, directly affecting agronomic trait performances. de Tombeur et al. (2022) reported "Si plasticity" and emphasised the intra- and inter-genotypic differences in Si uptake, which ultimately affect nutrient uptake and agronomic trait performances. Grain yield in wheat has been linked with the nutrient relationship, and may be limited by nutrient availability and accumulation, especially under stress conditions (Aranjuelo et al., 2013). Application of Si has been shown to benefit the source-sink relationship, by maintaining plant assimilate production and partitioning during grain filling (Araújo et al., 2019). Reynolds et al. (2016) noted that active Si uptake within plants varied across plant species. Active plant Si uptake and the metabolic impact of Si can be used as a means of resource-available selection pressure. Si application has been correlated with improved yield and yield components and shows variable correlations under DS and NS conditions with selection responses and yield gains (Ahmed et al., 2016; Neu et al., 2017). Applications of Si fertilisers are more yield-influencing under DS than NS conditions (Christian et al., 2023). This is evident in the current study, where the R-squared values for both liquid Si and granular Si decreased from 0.75 and 0.73 under DS conditions to 0.84 and 0.83 under NS conditions, respectively. This implies that the trait responses impacting GY under NS conditions were maximal compared to DS conditions.

Ahmed et al. (2016) reported that Si fertilisation can be used as a tool to improve yield and drought tolerance in wheat under drought stress. In this study, the effect of Si differed between the two formulations and the untreated control, under DS and NS conditions. Drought-tolerant genotypes tend to take up Si more efficiently than drought-sensitive genotypes and influence the effect of Si on the yield and yield components of wheat (Maghsoudi et al., 2016), implying that selecting for drought tolerance inadvertently selects for Si uptake efficiency. Under DS and NS conditions, the traits directly affecting grain yield were TN, PS, SL, KPS and AGB. Several interactions that indirectly affected grain yield was common across all treatments, and under DS and NS conditions. These included the interactions of TN with PS, AGB, and SL; interactions of AGB with SL and PS and the interaction of KPS with HI (Figure 3.2). In the current study, Si application improved the secondary traits, such as PS, AGB, TN, and KPS, and their interactions. A study by Dorairaj et al. (2020) found that Si application significantly improved the performance of secondary agronomic traits such as spikelets per

panicle in rice. The traits PS and TN are negatively correlated with GY (Figure 3.2). This is conceivably due to multiple interactions and compensation mechanisms between different yield components and is also dependent on genotype by environment by agronomic management interactions (Slafer et al., (2014).

In this study, under DS and NS conditions, the direct and indirect effects varied amongst the three treatments and across the two water regimes (Figures 3.3 to 3.5). Granular Si application had a strong direct effect on HSW and PS under DS (Figure 3.5E) and to a lesser extent under NS conditions (Figure 3.5F). Kumari et al. (2020) found that several traits, including HI, KPS, HSW, AGB and TN, were important as selection indices under NS conditions. In contrast, Fouad (2018) and Tarkeshwar et al. (2020), found that under DS conditions, KPS, SPS, TN, PS and HSW were the traits that should be used to select for drought tolerance. In this study, the interactions of TN with PS were the highest across all the three treatments under DS conditions. The direct and indirect effects of KPS, PS, HSW, SL and AGB all varied in magnitude and direction across DS and NS conditions and treatments.

Data and information describing the direct and indirect effects of Si on agronomic traits under DS conditions for selection programs are limited. Si fertilisation typically improves carbon and nitrogen content in plants (Neu et al., 2017). This would invariably affect the plant biomass and other agronomic traits, particularly yield under DS conditions (Ahanger et al., 2020). However, the use of Si fertilisation to enhance the identification of influential traits for yield in wheat breeding programs is yet to be explored.

3.5 Conclusion

Si application affects agronomic trait responses and enhances drought tolerance in wheat. This implies that the selection for silicon-use efficiency indirectly influences drought tolerance. TN, PS and HSW were found to be the most critical traits that need to be considered for breeding programs for Si-use efficiency to improve drought tolerance, followed by KPS, AGB and SL, especially under DS conditions and with granular Si application. The path coefficient analyses identified HSW had directly, and, PS, and TN indirectly, as the most important contributing traits for improving wheat grain yield and drought tolerance with Si application. In conclusion, Si fertilisation had substantial direct and indirect effects on the agronomic trait performance of wheat, particularly under drought-stressed conditions, which are useful for selection programs.

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Supplemental Table S3.1: Means for 10 agronomic traits of the 20 wheat genotypes ranked based on the grain yield with untreated control, under drought-stress and non-stress conditions across three environments

Genotype	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	85.0	90.9	5.4	5.4	5.0	5.2	9.9	9.9	20.5	20.1	41.5	44.1	2.7	3.7	12.0	16.5	0.5	0.6	6.0	9.8
MC2	88.2	95.4	5.6	5.5	5.0	5.2	10.5	10.6	19.5	20.0	37.9	45.9	2.8	4.3	13.7	18.7	0.5	0.6	5.3	12.3
MC3	87.0	96.6	5.4	5.8	5.2	5.5	9.8	10.1	19.3	19.2	37.4	44.3	2.9	4.4	12.1	17.2	0.5	0.6	5.6	12.2
MC4	85.8	94.4	4.0	6.6	3.7	6.2	9.7	9.6	19.5	19.9	36.1	41.9	2.3	4.1	11.6	17.6	0.5	0.6	4.5	11.6
MC5	86.7	98.8	5.4	6.8	5.5	5.7	9.5	9.5	19.8	20.3	38.8	50.1	2.9	4.3	11.9	16.9	0.5	0.6	4.8	12.3
MC6	93.8	98.5	6.2	5.5	6.2	5.5	10.0	9.8	21.4	21.3	37.7	43.4	2.6	3.8	15.1	18.4	0.5	0.6	6.8	11.1
MC7	82.8	91.0	5.5	5.9	5.1	6.1	9.9	9.8	19.7	20.3	38.1	47.1	2.8	4.1	12.6	17.9	0.5	0.6	6.3	12.5
MC8	79.9	91.7	4.2	5.0	4.2	4.6	10.0	10.3	20.1	21.1	40.0	50.7	2.6	4.1	11.8	18.5	0.5	0.6	5.1	12.1
MC9	93.0	97.6	5.5	5.7	5.4	5.6	10.6	10.5	19.9	19.8	38.5	44.7	2.8	4.5	14.4	16.3	0.5	0.5	6.0	12.5
MC10	91.3	95.2	4.8	6.4	4.2	5.2	10.6	10.4	19.9	19.7	38.1	38.9	3.5	4.4	14.9	16.9	0.5	0.5	7.6	10.3
MC11	92.1	99.4	5.2	6.2	5.1	6.2	10.2	9.9	19.6	19.0	36.6	40.5	3.0	5.1	14.0	18.7	0.5	0.6	5.9	13.2
MC12	87.6	96.0	5.1	5.9	5.0	5.5	10.0	10.2	20.9	21.0	39.9	43.2	2.7	3.9	13.7	15.4	0.5	0.6	5.6	9.3
MC13	82.6	90.7	5.7	6.3	5.8	6.1	9.7	9.5	19.6	19.9	37.8	44.6	2.9	4.5	14.8	18.1	0.5	0.6	5.9	13.1
MC14	83.5	91.7	6.8	6.0	6.4	5.7	10.6	10.7	18.9	18.9	33.0	44.3	3.1	4.1	13.3	19.1	0.5	0.6	5.8	10.7
MC15	89.8	99.2	5.6	5.5	4.9	5.5	11.0	10.5	20.2	20.2	35.8	40.8	2.7	5.1	14.5	22.5	0.5	0.5	4.8	12.0
MC16	90.4	96.3	6.4	5.8	6.1	6.1	10.2	10.2	20.2	20.1	37.0	41.4	2.9	4.0	13.4	16.0	0.5	0.6	6.0	10.4
MC17	90.2	96.0	4.8	5.0	4.5	4.7	11.0	11.0	20.5	20.3	36.9	43.7	2.9	4.8	12.2	17.8	0.5	0.6	5.9	11.8
MC18	82.2	93.2	4.5	4.9	4.5	4.4	10.8	10.8	21.0	21.7	43.4	48.2	3.1	4.1	12.8	18.3	0.5	0.6	5.6	11.9
MC19	84.1	89.8	6.5	6.4	6.1	6.1	10.6	10.4	19.5	19.2	32.9	38.9	2.6	3.6	12.6	17.5	0.5	0.6	4.5	10.6
MC20	83.1	90.0	5.4	5.9	5.3	5.4	9.5	9.7	20.1	20.1	38.6	42.7	2.8	4.0	11.2	16.3	0.5	0.6	5.7	10.4
Mean	**87.0**	**94.6**	**5.4**	**5.8**	**5.2**	**5.5**	**10.2**	**10.2**	**20.0**	**20.1**	**37.8**	**44.0**	**2.8**	**4.3**	**13.1**	**17.7**	**0.5**	**0.6**	**5.7**	**11.5**
SEM	**0.7**	**0.5**	**0.3**	**0.4**	**0.3**	**0.3**	**0.1**	**0.1**	**0.1**	**0.2**	**0.7**	**0.8**	**0.1**	**0.1**	**2.1**	**2.1**	**0.0**	**0.0**	**1.7**	**1.7**
CV%	**10.8**	**7.7**	**76.3**	**81.8**	**77.2**	**80.1**	**12.3**	**15.5**	**7.8**	**10.2**	**25.6**	**24.2**	**41.0**	**32.5**	**5.7**	**5.7**	**17.9**	**11.5**	**3.4**	**3.4**
LSD (5%)	**8.4**	**6.4**	**4.0**	**4.7**	**3.9**	**4.3**	**1.1**	**1.5**	**1.4**	**1.9**	**9.2**	**10.0**	**1.1**	**1.3**	**3.6**	**3.6**	**0.1**	**0.1**	**2.5**	**2.5**

Abbreviations: Overall mean for the three treatments under drought-stressed and non-stressed conditions. AGB, above-ground dry biomass weight ($t.ha^{-1}$); df, degrees of freedom; DS, drought-stressed; GY, Grain yield ($t.ha^{-1}$); HI, harvest index; HSW, hundred seed weight (g/100 seed); KPS, number of kernels per spike; NS, non-drought stressed; PH, plant height (cm); PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; TN, number of productive tiller number per plant. SEM: Standard error of mean; CV: Coefficient of variation; LSD= Least significant difference.

Supplemental Table S3.2: Means for 10 agronomic traits of the 20 wheat genotypes ranked based on the grain yield treated with liquid Si, under drought-stress and non-stress conditions across three environments

Genotype	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	90.7	93.2	5.7	6.6	5.8	6.6	10.3	10.5	20.6	21.3	41.0	47.1	2.8	3.8	14.4	21.2	0.5	0.6	6.5	11.2
MC2	93.0	94.3	6.2	6.7	6.2	6.5	10.9	10.8	20.6	20.6	37.4	45.6	2.7	3.9	15.6	20.3	0.5	0.6	5.0	9.9
MC3	87.1	95.0	6.5	7.0	6.7	7.0	9.9	10.2	19.6	20.2	40.3	44.1	3.0	3.9	14.9	21.3	0.5	0.6	6.1	9.4
MC4	94.6	94.2	6.4	7.2	6.2	7.2	10.2	10.0	20.8	20.7	39.2	41.5	2.7	4.0	14.3	23.7	0.5	0.6	5.2	10.8
MC5	90.6	98.4	6.5	6.4	6.4	6.2	9.5	9.7	20.5	21.1	43.6	49.7	2.9	4.1	15.5	20.1	0.5	0.6	6.1	11.0
MC6	93.3	99.8	6.1	6.7	6.0	6.6	9.8	10.1	21.5	22.3	40.3	44.0	2.6	4.0	12.5	21.3	0.5	0.6	5.3	11.6
MC7	88.7	91.0	6.8	6.6	6.4	6.6	10.1	10.1	20.5	20.7	40.8	46.4	2.7	4.0	14.3	20.9	0.5	0.6	5.3	10.4
MC8	84.4	90.1	5.4	5.8	5.3	6.2	10.6	10.5	21.1	21.0	44.6	50.8	2.8	3.9	13.4	18.9	0.5	0.6	5.2	9.0
MC9	95.8	96.8	6.1	6.4	6.0	6.3	10.9	11.2	19.7	20.7	37.4	44.3	2.8	4.3	14.3	18.7	0.5	0.5	6.1	9.9
MC10	90.2	98.6	5.7	5.9	5.6	5.9	10.9	11.0	20.7	21.0	40.0	43.0	3.3	4.5	13.4	20.1	0.5	0.6	7.0	12.2
MC11	100.5	102.2	6.1	6.2	6.1	5.9	10.4	10.6	19.9	20.2	38.6	43.6	3.3	4.7	15.3	19.6	0.5	0.6	6.3	11.6
MC12	90.6	92.1	5.9	5.5	5.8	5.6	10.6	10.6	21.4	21.9	41.9	48.8	2.7	3.7	13.1	16.7	0.5	0.6	5.2	9.0
MC13	83.8	88.6	6.9	6.8	6.8	6.8	10.2	9.9	20.1	19.9	36.6	41.7	3.0	4.0	16.7	17.3	0.5	0.6	5.7	8.3
MC14	87.2	92.1	6.7	6.6	6.4	6.4	11.2	11.2	19.3	19.1	39.6	44.4	3.0	4.2	15.1	21.0	0.5	0.6	5.4	9.1
MC15	95.3	101.5	6.5	6.3	6.4	5.9	11.4	11.4	21.2	21.3	38.8	42.1	3.5	4.2	17.6	23.9	0.5	0.6	5.8	11.7
MC16	90.5	97.2	5.7	6.5	5.9	6.7	10.5	10.7	20.3	20.3	36.7	45.5	3.0	3.8	12.7	20.4	0.5	0.5	5.0	9.7
MC17	94.0	94.4	6.7	5.7	6.6	5.8	11.6	11.6	20.5	21.0	39.6	45.9	3.0	4.3	15.8	20.6	0.5	0.6	6.1	10.8
MC18	91.1	94.7	5.6	6.3	5.6	6.3	10.7	11.2	20.8	21.9	44.0	52.8	2.5	3.9	11.6	22.1	0.5	0.6	3.6	10.5
MC19	88.9	89.3	6.6	6.5	6.5	6.4	10.7	10.8	19.3	19.5	38.8	42.9	2.5	3.8	13.9	19.2	0.5	0.6	5.3	11.9
MC20	85.4	91.2	6.3	6.9	6.3	6.8	10.0	10.2	20.7	20.8	38.4	47.5	2.8	4.0	14.1	18.6	0.5	0.6	5.6	9.1
Mean	**90.8**	**94.7**	**6.2**	**6.4**	**6.1**	**6.4**	**10.5**	**10.6**	**20.5**	**20.8**	**39.9**	**45.6**	**2.9**	**4.1**	**14.4**	**20.3**	**0.5**	**0.6**	**5.6**	**10.4**
SEM	**0.7**	**0.6**	**0.4**	**0.4**	**0.4**	**0.4**	**0.1**	**0.1**	**0.2**	**0.1**	**0.9**	**0.8**	**0.1**	**0.1**	**2.1**	**2.1**	**0.0**	**0.0**	**1.7**	**1.7**
CV%	**9.6**	**8.8**	**76.1**	**76.6**	**77.3**	**76.6**	**12.1**	**12.8**	**9.9**	**8.3**	**28.8**	**23.8**	**45.5**	**33.4**	**5.7**	**5.7**	**17.9**	**11.5**	**3.4**	**3.4**
LSD (5%)	**7.5**	**7.3**	**4.6**	**4.8**	**4.7**	**4.8**	**1.1**	**1.2**	**1.9**	**1.5**	**11.1**	**10.2**	**1.3**	**1.3**	**3.6**	**3.6**	**0.1**	**0.1**	**2.5**	**2.5**

Abbreviations: Overall mean for the three treatments under drought-stressed and non-stressed conditions. AGB, above-ground dry biomass weight ($t.ha^{-1}$); df, degrees of freedom; DS, drought-stressed; GY, Grain yield ($t.ha^{-1}$); HI, harvest index; HSW, hundred seed weight (g/100 seed); KPS, number of kernels per spike; NS, non-drought stressed; PH, plant height (cm); PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; TN, number of productive tiller number per plant. SEM: Standard error of mean; CV: Coefficient of variation; LSD= Least significant difference.

Supplemental Table S3.3: Means for 10 agronomic traits of the 20 wheat genotypes ranked based on the grain yield treated with granular Si, under drought-stress and non-stress conditions across three environments

Genotype	PH		TN		PS		SL		SPS		KPS		HSW		AGB		HI		GY	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	91.5	93.6	6.7	6.4	6.7	6.3	10.5	10.5	21.2	21.1	45.4	50.5	2.9	4.1	18.1	22.2	0.5	0.6	7.2	12.4
MC2	88.1	93.2	5.7	6.2	5.6	6.2	10.8	10.8	20.2	20.2	42.5	44.9	3.0	4.4	15.6	22.9	0.5	0.6	6.2	14.2
MC3	91.1	93.4	6.4	6.5	6.3	6.4	10.5	10.3	19.3	19.8	39.3	42.8	3.2	4.6	16.1	20.5	0.5	0.6	7.1	13.2
MC4	89.8	95.8	6.8	7.0	6.7	6.8	9.8	10.0	20.2	20.4	37.7	41.8	2.8	4.4	14.7	23.5	0.5	0.6	5.4	14.1
MC5	93.5	96.1	6.1	6.7	5.7	6.5	9.8	10.0	20.2	20.2	45.9	49.4	2.7	4.0	16.8	23.5	0.5	0.6	5.8	14.1
MC6	99.0	100.7	6.6	6.6	7.6	7.1	10.4	10.1	22.1	21.4	42.9	45.8	2.9	4.3	19.3	24.9	0.5	0.6	7.8	15.0
MC7	86.9	90.4	7.0	6.5	6.7	6.1	10.2	9.9	20.1	20.1	42.5	46.1	2.7	4.2	15.5	17.3	0.5	0.6	6.1	11.3
MC8	86.7	89.7	5.2	6.1	5.3	6.0	10.6	10.5	20.7	21.0	51.5	51.5	2.9	4.3	16.6	19.9	0.5	0.6	5.6	12.8
MC9	97.5	98.8	6.4	6.4	6.4	6.2	10.9	11.0	20.4	20.3	39.8	44.8	3.0	4.7	15.4	22.5	0.5	0.6	6.2	14.3
MC10	96.7	95.5	6.0	6.7	6.3	6.6	11.0	10.9	20.5	20.4	40.0	41.0	3.6	4.4	15.9	18.9	0.5	0.6	9.2	11.8
MC11	101.0	99.5	6.2	6.4	6.4	5.8	10.5	10.6	19.6	20.0	38.9	41.6	3.2	4.8	15.9	19.0	0.5	0.6	6.8	11.2
MC12	91.5	92.5	5.8	5.8	5.8	5.8	10.6	10.5	21.7	22.0	42.1	47.0	2.9	4.0	13.0	19.1	0.5	0.6	5.4	9.7
MC13	88.5	90.5	6.7	6.3	6.5	5.8	10.2	9.9	20.5	19.9	39.8	42.6	2.9	4.6	14.9	21.3	0.5	0.6	6.4	13.3
MC14	90.9	91.5	6.6	7.1	6.8	7.2	11.1	10.9	19.0	18.9	40.3	43.5	3.1	4.4	16.6	18.9	0.5	0.6	6.5	11.8
MC15	94.4	96.4	5.9	6.5	5.7	6.4	11.1	11.4	20.7	20.5	37.5	39.1	3.5	5.1	16.6	23.5	0.5	0.6	5.7	14.8
MC16	93.0	97.6	6.3	7.4	6.3	7.2	10.8	10.8	21.0	20.2	41.0	45.9	3.0	4.2	14.4	22.2	0.5	0.5	6.8	12.2
MC17	94.6	94.5	6.1	6.5	6.1	6.0	11.6	11.3	20.3	20.7	41.5	45.6	3.1	4.7	13.8	20.2	0.5	0.6	6.3	11.7
MC18	90.6	95.3	6.4	6.8	6.0	6.7	11.0	11.1	21.5	21.7	45.3	50.2	2.7	4.3	15.5	21.1	0.5	0.6	5.6	12.5
MC19	90.7	92.8	6.8	7.0	6.8	6.9	10.8	10.9	19.8	19.2	39.9	44.1	2.2	3.8	13.4	21.1	0.5	0.6	5.4	12.0
MC20	89.3	92.5	6.1	6.7	6.1	7.0	10.0	10.2	21.1	20.8	43.2	45.9	2.9	4.1	13.3	24.1	0.5	0.6	5.3	11.9
Mean	**92.3**	**94.5**	**6.3**	**6.6**	**6.3**	**6.5**	**10.6**	**10.6**	**20.5**	**20.4**	**41.9**	**45.2**	**3.0**	**4.4**	**15.6**	**21.3**	**0.5**	**0.6**	**6.3**	**12.7**
SEM	**0.6**	**0.6**	**0.4**	**0.4**	**0.4**	**0.4**	**0.1**	**0.1**	**0.1**	**0.1**	**0.8**	**0.8**	**0.1**	**0.1**	**2.1**	**2.1**	**0.0**	**0.0**	**1.7**	**1.7**
CV%	**8.5**	**8.6**	**74.2**	**74.8**	**75.8**	**75.1**	**12.9**	**13.2**	**7.7**	**8.1**	**26.7**	**23.8**	**43.9**	**30.9**	**5.7**	**5.7**	**16.2**	**10.8**	**3.4**	**3.4**
LSD (5%)	**6.7**	**7.5**	**4.6**	**4.8**	**4.7**	**4.7**	**1.3**	**1.3**	**1.4**	**1.4**	**10.5**	**10.1**	**1.3**	**1.3**	**3.6**	**3.6**	**0.1**	**0.1**	**2.5**	**2.5**

Abbreviations: Overall mean for the three treatments under drought-stressed and non-stressed conditions. AGB, above-ground dry biomass weight ($t.ha^{-1}$); df, degrees of freedom; DS, drought-stressed; GY, Grain yield ($t.ha^{-1}$); HI, harvest index; HSW, hundred seed weight (g/100 seed); KPS, number of kernels per spike; NS, non-drought stressed; PH, plant height (cm); PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; TN, number of productive tiller number per plant. SEM: Standard error of the mean; CV: Coefficient of variation; LSD= Least significant difference.

CHAPTER 4

Influence of Silicon Fertilisers on the Compositions of Wheat Grain Carbon, Nitrogen, Sulfur and Protein Contents under Drought-Stress and Non-Stress Conditions

Abstract

Wheat (*Triticum aestivum* L.,$2n = 6x = 42$; AABBDD) is the 3rd leading global commodity cereal crop after rice and maize. The grain yield and quality of wheat are affected by drought stress associated with climate change. Silicon (Si) fertilisation is believed to enhance drought tolerance and improve grain yield and quality compositions. The objective of this study was to evaluate the effects of two Si fertiliser formulations on the compositions of wheat grain carbon (C), nitrogen (N), sulfur (S) and protein content (GPC) under drought-stress and non-stress conditions to enhance grain yield and end-use quality. Twenty preliminary selected bread wheat genotypes were evaluated for their contents of C%, N%, S% and GPC% under drought-stress (DS) and non-stress (NS) conditions with liquid and granular potassium silicate formulations. Both formulations enhanced the contents of grain C, N, GPC and Si, notably under DS conditions. The genotype x water regime x silicon formulation interaction effect was significant ($p<0.001$) for Si content, whilst genotype x water regime x environment was significant for N% and GPC%. The highest C% was achieved with granular Si for genotype MC17 (C content of 41.17%) under DS conditions and MC14 (42.19%) under NS conditions. Genotype MC5 recorded the highest grain N (2.88%) and GPC% (16.41%) under DS conditions and with granular Si. Overall, granular Si application reduced genotypic variation for C, N, S and improved the GPC under DS conditions. The present study revealed that granular Si application positively contributed to higher grain contents of C%, N%, GPC% and Si in the assessed wheat genotypes under DS conditions, implying the contribution of Si to grain quality improvement and drought-stress management.

Keywords: bread wheat; carbon content; drought stress; grain protein content; silicon fertilisers

4.1 Introduction

Bread wheat (*Triticum aestivum* L.; $2n = 6x = 42$, AABBDD) is the 3rd economically important cereal crop after maize and rice. The global annual wheat production is approximately 797.9 million tons (FAO, 2025). In South Africa, wheat is widely cultivated and its annual production ranges from 1.82 to 1.9 million tons (Sihlobo, 2025). Wheat provides approximately 55% of the carbohydrates and 20% of the dietary calories in humans, comprising mainly 54-72% starch, 8-20% protein, and other essential nutrients (Johansson et al., 2020; Khalid et al., 2023). Bread wheat quality is related to flour and dough properties conditioned by polygenes (Patel, 2023). Commercial quality parameters for bread wheat flour include ash content, wet gluten, gluten swelling, falling number and sedimentation index. The rheological quality are related with loaf weight, volume, aroma, taste and structure (Gavurníková et al., 2011).

Bread wheat has a high nutritional value, including essential macronutrients, such as nitrogen (N), sulfur (S), potassium (K), magnesium (Mg), and micronutrients, including iron (Fe), zinc (Zn), copper (Cu) and boron (B) (Adams et al., 2024). Carbon (C), N, and S are building blocks for the formation of grain starch and protein. Carbon forms the carbohydrate backbone of starch and amino acids (Bertoft, 2017), whilst N forms a key component of amino acids and protein; and S is integral to some amino acids and disulfide bonds which increase gluten strength (Roa et al., 2024).

Nitrogen is an essential nutrient for plant growth and protein biosynthesis (Wilson et al., 2020). Improved nitrogen and grain protein content (GPC) are dependent on genotypes' N-use efficiency, -uptake, -translocation, and protein synthesis (Pan et al., 2020). Breeding for high GPC is challenging due to the limited genetic variation amongst genotypes and complex genetic inheritance (Kenzhebayeva et al., 2018). Additionally, high GPC is negatively correlated with grain yield, which is the primary trait in most breeding programs. Peng et al. (2022) highlighted several mechanisms for improving wheat quality, including genetic modification for major genes such as *GluD1* and *GluB1*. Roy et al. (2018); (2019; 2021), reported that the expression of high-molecular-weight subunit (denoted as *Ay*) increases both grain yield and GPC. The N and GPC fluctuate depending on genotype, environment, fertiliser use, biotic and abiotic stresses. Mendes et al. (2024) reported that increased N uptake led to enhanced GPC and gluten content of flour of test genotypes.

Carbon is the building block of living organisms. Approximately 75% of the total C pool found in soil is attributed to the sequestration of atmospheric C, present in the form of carbon dioxide (Elbasiouny et al., 2022). Reduced soil C content affects grain development, leading to small and shrivelled grains, and diminished rheological quality (Rebetzke et al., 2008). Carbon, hydrogen (H) and oxygen (O_2) molecules form carbohydrates that coalesce to form starch (Awuchi & Amagwula, 2021). Starch accumulation occurs from post-anthesis photosynthesis in leaves, spikes and other

tissues as well as the remobilization of pre-anthesis carbohydrates (Uprety et al., 2010; Han et al., 2025). Starch is a key rheological component, accounting for 70-85% of wheat flour's composition (Onyango, 2016; Khurana & Sharma, 2021). Variation in the quality and quantity of starch affects rheological characteristics, which are pasting and dough mixing properties (Jukić et al., 2019; Kim & Kim, 2021). Starch quality is important for optimal bread dough formation and crumb setting during baking (Onyango, 2016).

Sulfur is a secondary macronutrient involved in the functional properties of protein and amino acid assimilation (Wilson et al., 2020). While N plays a vital role in grain yield, S influences grain characteristics and dough properties (Tao et al., 2018). Higher S levels have been linked to improved yields and protein content (Ibrahim et al., 2012). As a result, S has been identified as a key nutrient affecting plant growth and development, grain filling and protein composition. Dawar et al. (2023) reported that 120 $kg.ha^{-1}$ of N and 60 $kg.ha^{-1}$ of S significantly improved wheat grain yields. Similarly, Tao et al. (2018) reported that increases in N and S uptake significantly increased grain protein yield, which is the product of gluten and gliadin. Increased S accumulation led to the enhanced quality of amino acids, such as methionine, cysteine and cystine, which contain disulfide bonds. The proliferation of these sulfide bonds intensifies the gluten network, resulting in increased gluten strength (Mendes et al., 2024).

Drought, elevated carbon dioxide (CO_2), heat, and salinity stress alter wheat grain quality by influencing grain filling and the contents of protein, starch and amino acids (Zahra et al., 2022). Drought stress induces molecular, biochemical, physiological, and morphological changes in plants (Shah & Paulsen, 2003). During grain filling stages, drought stress severely reduces grain yield and quality (El Habti et al., 2020). Under elevated temperatures and during grain filling periods, GPC is increased, whereas its protein functionality is decreased (Silva et al., 2019). With the cumulative effect of drought, including its increasing duration and frequency, the identification of drought-tolerant genotypes is fundamental to improving yield and grain composition (Sallam et al., 2019). The nutritional composition of wheat grain is significantly diminished under drought conditions (Rao et al., 2021). According to Pradhan et al. (2012), drought reduces plant growth, accelerates flowering and diminishes the grain filling stage, leading to limited seed set, size and weight. Drought also affects starch formation by altering starch biosynthetic enzyme activity, impacting the starch biosynthesis pathway (Regina & Guzmán, 2020). Likewise, drought decreases the amylose content, lipid content, and pasting temperature, amongst other rheological properties (Singh et al., 2008). Carbon, N, and S are some of the macro and micronutrients required for the formation of proteins and starches in wheat grain and thus important for bread making quality. Improving grain nutrient composition in wheat potentially improves wheat grain quality (Godfrey et al., 2010).

Silicon (Si) is a quasi-essential nutrient, believed to directly and indirectly improve plant growth and development, grain yield and quality (Chan-in et al., 2024). Si uptake has been linked to improved grain nutrient uptake; however, its effectiveness is determined by crop type, genotype, Si concentration and formulation (Christian et al., 2022). Slow-release Si has been shown to increase wheat yields by approximately 13.8% (Ligaba-Osena et al., 2020). It mediates stress tolerance through mechanical Si deposits, facilitating metabolic changes through biochemical reactions (Bhat et al., 2019; Saitoh et al., 2021). Si fundamentally improves the plant structure and mechanism for increased grain nutrient uptake, relocation and distribution (Neu et al., 2017). Kumar et al. (2022) reported that Si application inhibited degradative enzyme activity and maintained wheat grain quality under stress. Recent studies on maize reported that Si application significantly improved the fat, protein and starch content of the grain (Artyszak et al., 2025). Likewise, Jiang et al. (2023) reported that Si application to rice under dry land cultivation improved grain yield and quality. Singh et al. (2024) reported that Si application increased the wheat grain composition by enhancing both protein and carbohydrate content. The effect of Si on wheat under drought conditions tends to improve agronomic performance compared to NS conditions (Christian et al., 2025). Si plays a multifaceted role in alleviating multiple biotic and abiotic stresses as well as improving nutrient uptake and grain quality (Gill et al., 2024). Earlier studies (Christian et al., 2023, 2025) found that wheat genotypes showed improved agronomic trait performance and drought tolerance when using Si fertilisers under drought conditions. However, there is limited information that examined the effect of Si formulations on grain protein and nutrient composition, using contrasting genotypes to guide production and breeding. Therefore, the objective of this study was to evaluate the effects of two Si fertiliser formulations on the compositions of wheat grain carbon, nitrogen, sulfur and protein content under drought-stress and non-stress conditions to enhance grain yield and end-use quality.

4.2 Materials and Methods

4.2.1 Plant Materials

Twenty preliminarily selected drought and heat-tolerant bread wheat genotypes were used for the study. The pedigree of the genotypes and the meteorological data are presented in Chapter 2, Section 2.2.1.

4.2.2 Study Sites

The study was conducted under two greenhouses and a field trial and is briefly described below.

4.2.3 Field Experiments

The 20 wheat genotypes were field evaluated using a randomized complete block design with three replications. Details pertaining to the experimental design are explained in Chapter 2, Section 2.2.2.

4.2.4 Greenhouse Experiment

The test genotypes were laid out in a factorial randomized complete block design. Description of the experimental design are explained in Chapter 2, Section 2.2.2.

4.2.5 Silicon Formulations

A slow-release granular potassium silicate formulation and a liquid formulation, for this study (Christian et al., 2023). The treatment program is described in Chapter 2, Section 2.2.2.

4.2.6 Data Collection

4.2.6.1 NIR Scanning

The whole grain from all tested genotypes and treatments, across both greenhouse and field experiments, was scanned using a Bruker MPA near-infrared reflectance spectrophotometer (Bruker Optics Co., Ltd., Germany). The NIR spectra were collected by scanning each seed sample in triplicate, with mixing of seed between scans to ensure homogeneous scans for each sample.

4.2.6.2 Analysis of Carbon, Nitrogen, Grain Protein and Sulfur Contents

Fifty randomly sampled whole seed samples were milled using the Retsch (ZM 200) milling machine (Retsch, South Africa). The resulting powder was tested for the contents of C, N, and S, using the Leco Trumac CNS macro analyser (Leco Corp, Michigan, USA). One gram of the powder was loaded onto the ceramic boats for DUMAS testing. Carbon, N and S readings were used for analysis. The resulting N content was converted into grain protein content (GPC), with a wheat protein factor of 5.70 (Mariotti et al., 2008). The whole seed scans together with CNS and protein analysis were done to determine the C, N, S, and GPC content. The C, N, S, Si and GPC assessment was performed using Bruker OPUS Quant II analysis software.

4.2.6.3 Analysis of Foliar Silicon Content

Foliar Si was analysed using the hydrochloric acid digestion process. One hundred leaf samples per genotype and treatment were randomly selected and milled using the Retsch (ZM 200) milling machine. The resulting powder was weighed and placed into an oven for four hours at 105°C. The oven-dried samples were weighed and then placed into the muffle oven at 500°C overnight. The combusted samples were subjected to hydrochloric acid digestion (Kalra & Maynard, 1991). The resulting substrate was measured using the Agilent Microwave Plasma Atomic Emission Spectrometer (MP-AES) analyser (Agilent, U.S.A) to determine silicon content using the spectral line at 288.158 nm. Foliar scans and acid digestion extraction were used to compute silicon uptake and derive the resulting data.

4.2.7 Data Analysis

Data on C, N, S, Si and GPC were subjected to a combined analysis of variance (ANOVA) using the randomized complete block procedure with Genstat 18th version, VSN, International (Payne, 2017). Furthermore, principal component analysis was performed to determine key components affecting genotype performance across treatment combinations. Biplots were constructed to visualize the genotype association for nutrient compositions for the Si formulations under DS and NS conditions, using FactoMiner, Factoextra, Devtools, Tidyverse and Cluster packages in R (R Core Development Team, 2020).

4.3 Results

4.3.1 Grain Nutrient and Protein Contents of Wheat Genotypes under Si Application, Drought, Variable Testing Sites and Their Interactions.

The combined analysis of variance (Table 4.1) revealed a significant ($p < 0.05$) effect of genotype, water regime, location, and their interaction on N% and GPC%. The interactions of genotype × location were significant for N%, S%, and GPC%, while the genotype × water regime effects were significant for N% and GPC%. The genotype x water regime and genotype x Si treatment interaction effects were significant on foliar Si content.

4.3.2 Mean Carbon, Nitrogen, Sulfur, Silicon and Protein Contents of Wheat Genotypes with Varying Si Application, Drought and Test Environments

Tables 4.2 to 4.4 presented the carbon, nitrogen, sulfur, silicon and protein contents of wheat genotypes with varying Si application, drought, and test locations. Genotypic performance varied amongst DS and NS conditions and across the Si treatments. The control treatment (Table 4.2) had few genotypes with better C, N, Si, and GPC%, compared to the liquid Si (Table 4.3) and granular Si (Table 4.4) applications under DS conditions. Fourteen genotypes exhibited increased C% compared to the control under DS conditions following granular Si application. The top five performing genotypes with higher C% content with granular Si were MC17, MC2, MC4, MC14, and MC20, under DS. Similarly, MC19 with liquid Si showed the highest C at 41.32%, under DS conditions. Under NS conditions, liquid Si application improved the C contents of 15 genotypes compared to the control treatment. Genotype MC5 expressed the highest N (2.88%) and GPC (16.41%) with granular Si application, under DS conditions. The top 5 performing genotypes with higher N% with granular Si under DS conditions were MC5, MC18, MC20, MC6 and MC3. Whilst the top 5 best genotypes with higher N% with liquid Si were MC5, MC10, MC1, MC17 and MC6. Fourteen genotypes with granular Si and 12 genotypes with liquid Si had higher GPC% compared to the control, under DS conditions. The genotypes with the highest GPC% were MC5, MC17, MC20, MC6, and MC2, under DS conditions with granular Si. Liquid Si application increased Si content for 17 of the 20 tested genotypes under DS conditions and for 5 genotypes under NS conditions. The granular Si application increased foliar Si content for 18 genotypes under DS conditions and 13 genotypes under NS conditions. Both Si applications increased the overall C, N, GPC and Si contents compared to the control treatment. The effect of Si under NS conditions is not substantially higher compared to DS conditions.

Table 4.1 Combined analysis of variance (ANOVA) and significant tests comparing 20 wheat genotypes tested with two Silicon (Si) formulations and an untreated control, under drought and non-stress conditions across three environments.

Source of variation	df	Carbon%	Nitrogen%	Sulfur%	Silicon (ppm)	Grain protein%
Genotype (G)	19	1.1244***	0.11606***	0.0040971***	2.795.7***	4.2504***
Water Regime (WR)	1	3.8124**	0.80962***	0.0881810***	18984***	25.9301***
Si Treatment (T)	2	0.0791	0.00940	0.0009636*	18353***	0.2259
Location (L)	2	65.1698***	0.00305	0.0025919**	1415	0.6586
G x WR	19	0.3414	0.003104*	0.0004685	13020.2*	1.2553**
G x T	38	0.4326	0.01880	0.0002439	1078.3***	0.5739
WR x T	2	0.2486	0.09116**	0.0003377	4934.3***	2.5619*
G x L	38	0.1886	0.04040***	0.0011955***	140.8	1.2946**
WR x L	2	25.6586***	0.55877***	0.2062227***	185.6	19.1150***
T x L	4	0.6752	0.01187	0.0049037***	427.4	0.6698
G x WR X T	38	0.4436	0.02184	0.0002405	845.1***	0.7488
G X WR X L	38	0.2743	0.04367***	0.0004551	113.8	1.3720***
G x T x L	76	0.4657	0.01776	0.0002743	162.4	0.5273
WR X T X L	4	2.8292***	0.28737***	0.0015808**	0.740	4.8640***
G X WR X T X L	76	0.5071	0.01787	0.0002296	134.8	0.5470
Residual	718	0.3880	0.01664	0.0002929	402.2	0.5508

Abbreviations: df, degrees of freedom; T: Treatment (untreated control + liquid Si + granular Si); WR: Regime (DS, drought stress and NS, non-stressed conditions); environment (2 greenhouse + 1 field); *,**,***, ns denote significance differences at $p < 0.05$, $p < 0.01$, $p < 0.001$, and non-significant, respectively.

Table 4.2: Means for carbon, nitrogen, sulfur, silicon and protein content of 20 wheat genotypes assessed without Si, under drought-stress and non-stress conditions, and across three environments.

Genotype	Carbon %		Nitrogen %		Sulfur %		Silicon (ppm)		Grain protein %	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	40.63	40.57	2.59	2.63	0.20	0.18	234.29	252.40	14.68	14.95
MC2	40.90	40.74	2.74	2.63	0.21	0.19	269.85	284.08	15.83	15.15
MC3	40.58	40.55	2.64	2.65	0.21	0.19	241.63	275.58	15.02	15.10
MC4	40.99	40.81	2.74	2.73	0.20	0.18	248.58	259.10	15.59	15.55
MC5	40.72	40.46	2.85	2.69	0.22	0.18	221.46	267.47	16.22	15.32
MC6	40.68	40.78	2.66	2.67	0.20	0.18	235.83	260.07	15.14	15.02
MC7	40.84	40.64	2.60	2.59	0.20	0.17	237.35	271.61	14.79	14.65
MC8	40.56	40.33	2.76	2.66	0.20	0.18	260.08	276.65	15.71	15.11
MC9	40.74	40.25	2.73	2.59	0.18	0.15	221.06	264.49	15.40	14.71
MC10	41.08	40.88	2.55	2.59	0.20	0.17	235.15	254.47	14.63	14.76
MC11	40.84	40.62	2.58	2.53	0.19	0.16	250.20	245.67	14.71	14.41
MC12	40.69	40.59	2.71	2.64	0.20	0.18	243.90	274.45	15.53	15.05
MC13	40.75	40.16	2.64	2.67	0.20	0.18	253.69	254.68	15.04	15.19
MC14	40.87	40.69	2.67	2.70	0.19	0.17	264.32	258.51	15.16	15.39
MC15	40.56	40.63	2.71	2.60	0.20	0.19	242.95	259.30	15.49	14.79
MC16	40.67	40.56	2.66	2.70	0.19	0.17	247.27	261.72	14.92	15.38
MC17	41.08	41.09	2.57	2.63	0.19	0.17	234.31	261.81	14.79	14.98
MC18	40.98	40.92	2.72	2.69	0.20	0.18	256.94	263.34	15.56	15.33
MC19	41.03	40.72	2.64	2.58	0.20	0.17	229.64	247.60	15.00	14.70
MC20	40.77	40.25	2.67	2.77	0.21	0.19	240.73	279.36	15.18	15.85
Mean	40.80	40.61	2.67	2.65	0.20	0.18	243.46	263.62	15.22	15.07
SED	0.51	0.51	0.11	0.11	0.01	0.01	16.38	16.38	0.61	0.61
LSD 5%	0.999	0.999	0.21	0.21	0.03	0.03	32.18	32.18	1.19	1.19
CV%	1.5	1.5	4.8	4.8	9.1	9.1	1.7	1.7	4.9	4.9

Abbreviations: CV: coefficient of variation DS: drought-stressed, LSD: Least significant difference at 5% level, NS: non-drought-stressed, SED: Standard errors of differences of means, ppm = parts per million.

Table 4.3: Means for carbon, nitrogen, sulfur, silicon and protein content of 20 wheat genotypes assessed with liquid Si, under drought-stress and non-stress conditions and across three environments.

Genotype	Carbon %		Nitrogen %		Sulfur %		Silicon (ppm)		Grain protein %	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	40.64	40.56	2.63	2.68	0.20	0.19	235.28	246.03	14.98	15.32
MC2	40.73	41.37	2.82	2.48	0.22	0.19	257.62	264.37	16.23	14.12
MC3	40.52	40.56	2.63	2.61	0.20	0.19	252.88	272.06	14.97	14.96
MC4	40.68	40.84	2.77	2.68	0.20	0.17	255.56	256.15	15.79	15.25
MC5	40.66	40.74	2.78	2.71	0.20	0.19	255.00	244.58	15.80	15.42
MC6	41.03	40.88	2.67	2.58	0.21	0.18	248.68	257.53	15.19	14.70
MC7	40.51	41.09	2.71	2.49	0.20	0.18	251.52	245.64	15.42	14.02
MC8	40.62	40.72	2.70	2.55	0.20	0.19	258.04	270.73	15.34	14.51
MC9	40.76	40.38	2.69	2.40	0.18	0.14	250.86	245.58	15.28	13.67
MC10	40.91	40.85	2.62	2.58	0.20	0.18	248.25	260.63	14.92	14.70
MC11	41.05	40.91	2.54	2.62	0.18	0.18	240.89	273.26	14.44	14.89
MC12	40.76	39.31	2.70	2.63	0.21	0.19	244.10	239.69	15.34	14.97
MC13	40.73	40.54	2.82	2.69	0.22	0.19	253.52	270.96	16.03	15.31
MC14	40.86	40.74	2.84	2.60	0.19	0.15	268.42	278.82	16.16	14.79
MC15	40.27	40.79	2.66	2.65	0.20	0.21	246.07	253.36	15.15	15.05
MC16	40.72	40.26	2.64	2.60	0.17	0.15	236.14	254.49	15.02	14.78
MC17	40.88	40.64	2.69	2.52	0.19	0.16	272.48	271.69	15.30	14.36
MC18	40.86	40.93	2.84	2.81	0.21	0.18	261.61	276.53	16.14	15.97
MC19	41.32	40.74	2.59	2.56	0.19	0.17	234.54	245.28	14.73	14.58
MC20	40.50	40.83	2.85	2.81	0.21	0.21	245.19	255.52	16.22	15.99
Mean	40.75	40.68	2.71	2.61	0.20	0.18	250.83	259.14	15.42	14.87
SED	0.51	0.51	0.11	0.11	0.01	0.01	16.38	16.38	0.61	0.61
LSD 5%	0.999	0.999	0.21	0.21	0.03	0.03	32.18	32.18	1.19	1.19
CV%	1.5	1.5	4.8	4.8	9.1	9.1	1.7	1.7	4.9	4.9

Abbreviations: CV: coefficient of variation, DS: drought-stressed, LSD: Least significant difference at 5% level, NS: non-drought-stressed, SED: Standard errors of differences of means, ppm = parts per million.

Table 4.4: Means for carbon, nitrogen, sulfur, silicon and protein content of 20 wheat genotypes evaluated with granular Si, under drought-stress and non-stress conditions and across three environments.

Genotype	Carbon %		Nitrogen %		Sulfur %		Silicon (ppm)		Grain protein %	
	DS	NS	DS	NS	DS	NS	DS	NS	DS	NS
MC1	40.70	40.53	2.70	2.59	0.20	0.19	228.19	233.83	15.34	14.90
MC2	41.07	40.69	2.72	2.60	0.21	0.19	263.37	271.87	15.73	14.80
MC3	40.80	40.18	2.73	2.60	0.21	0.19	270.34	261.74	15.33	14.78
MC4	41.05	40.81	2.69	2.64	0.19	0.16	259.69	260.44	15.33	15.04
MC5	40.78	40.70	2.88	2.71	0.21	0.19	258.32	250.57	16.41	15.58
MC6	40.97	40.65	2.81	2.59	0.22	0.17	283.00	264.06	16.02	14.60
MC7	40.99	40.61	2.58	2.63	0.19	0.18	257.71	293.78	14.67	15.02
MC8	40.61	40.47	2.68	2.62	0.20	0.18	260.46	281.63	15.22	15.18
MC9	40.59	40.56	2.71	2.66	0.18	0.15	241.29	255.84	15.42	14.99
MC10	40.40	40.51	2.62	2.64	0.20	0.18	246.45	281.81	14.92	14.97
MC11	40.56	40.47	2.53	2.59	0.18	0.16	297.46	260.62	14.07	14.61
MC12	40.68	40.61	2.71	2.52	0.20	0.16	253.89	251.98	15.39	14.38
MC13	40.81	40.24	2.70	2.65	0.21	0.18	255.63	259.35	15.26	15.25
MC14	41.03	42.19	2.72	2.56	0.19	0.15	283.65	287.46	15.46	14.51
MC15	40.67	40.59	2.73	2.68	0.20	0.18	317.07	275.54	15.54	15.37
MC16	41.01	40.69	2.64	2.68	0.19	0.16	254.50	265.22	15.03	15.43
MC17	41.17	40.88	2.68	2.69	0.19	0.17	270.24	269.69	15.26	15.16
MC18	40.95	40.38	2.86	2.64	0.21	0.18	261.17	240.90	16.27	15.14
MC19	41.02	41.02	2.72	2.59	0.19	0.17	252.00	254.99	15.46	14.50
MC20	41.03	40.25	2.84	2.70	0.21	0.18	261.19	300.09	16.15	15.54
Mean	40.83	40.65	2.71	2.63	0.20	0.17	263.73	266.07	15.41	14.98
SED	0.51	0.51	0.11	0.11	0.01	0.01	16.38	16.38	0.61	0.61
LSD 5%	0.999	0.999	0.21	0.21	0.03	0.03	32.18	32.18	1.19	1.19
CV%	1.5	1.5	4.8	4.8	9.1	9.1	1.7	1.7	4.9	4.9

Abbreviations: CV: coefficient of variation, DS: drought-stressed, LSD: Least significant difference at 5% level, NS: non-drought-stressed, SED: Standard errors of differences of means, ppm = parts per million.

4.3.3 Genotype Association Based on Silicon Treatments under Drought and Non-Stress Conditions

The effects of silicon treatments under DS and NS are illustrated in Figures 4.1 and 4.2, respectively. Under DS conditions and granular Si conditions, genotypes showed variable associations, whilst most of the genotypes with the untreated control are predominantly located in quadrants QIII and QIV (Figure 4.1). The genotype association based on N, S and GPC compositions are closely linked to the acute angles across all Si treatments. Likewise, a similar relationship was noted for C and Si foliar contents. The standard or control genotypes fell within quadrants QII and QIII, whilst the majority of the test genotypes were situated in Q1 for both liquid and granular Si.

Under the NS conditions, genotypes clustered well under the granular Si and the control conditions than the liquid Si treatment (Figure 4.2). The majority of the test genotypes, under granular Si and control, are localised in QI and QII. The extent of genotype distribution for GPC, N and S% had a similar trend as presented in Figure 4.1, where most genotypes were localised in QI and QII. Similarly, based on C and foliar Si contents, genotype relatedness followed the acute angles (Figure 4.1). Genotypic clustering varies under both DS and NS conditions and with the different treatments.

The biplots (Figures 4.3A-F) illustrated the genotypic relationships amongst the tested traits under DS and NS conditions and under Si treatments. Under DS conditions (Figure 4.3A), genotypes for the untreated control are relatively distributed, with the majority of genotypes located in quadrants QII and QIII. Genotypes MC2, MC18 and MC4, are located within quadrant QI. GPC%, N% and S% are closely related traits tended to their acute angles, and these traits are situated in quadrants QI and QII.

Figure 4.3B, PC1 accounted for 47% with the untreated control, under NS conditions. The degree of relatedness is high with the acute angles for GPC%, N% and S%. Whilst C% and Si are indirectly related traits. Notably, there is a genotypic shift towards the PC1 axis with 11 genotypes found in quadrants QI and QII.

The genotypic distribution illustrated in Figure 4.3C indicates that under DS conditions, liquid Si has rendered a relatively distributed pattern of the test genotypes. Genotypes MC6, MC14, MC2 and MC18 are located within quadrant Q1. The majority of the genotypes are located around the PC2 axis in quadrants QII and QIII. The degree of relatedness between GPC%, N% and S% are highly correlated, like Figure 4.3A. The C% and Si% have a closer degree of relatedness in Figure 4.3C compared to Figure 3A and PC1, under DS, and with liquid Si accounting for 54.9% of the total variance.

In Figure 4.3D, under NS conditions, liquid Si had a genotypic cluster close to the x-axis. Genotypes MC11, MC4, MC10, MC15, MC5, MC1, MC20, MC13, MC3 and MC18 are all located

within quadrants QI and QII. The degree of relatedness for N, S, and GPC% is acutely related, and similar to Figures 4.3A and 4.3C. Both C% and Si content are found within quadrant QI. PC1 accounts for 51.3% of the total variation.

Figures 4.3E and 4.3F display a notable genotypic shift towards quadrants QI and QII. Under DS conditions and with granular Si (Figure 4.3E), the C% has shifted with a higher degree of relatedness associated with the acute angle with C%, N%, GPC%, and S%, in comparison to the control and liquid Si treatments under DS conditions. Genotypes MC19, MC2, MC3, MC18, MC20, MC6, MC13, MC15, and MC5 are within the quadrants QI and QII. PC1 accounts for 56.6% of the total variation.

The majority of the test genotypes in Figure 4.3F are located in quadrants QI and QII except for MC14, MC11, MC19, MC12, and MC6. Genotypes MC17, MC16, MC5, MC20, MC15, and MC8 are all within quadrant QI for granular Si under NS conditions. The degree of relatedness is high for N% and GPC%, whereas S% and C% are inversely related. Si is closely related to C% and is similar to the relationships in Figures 4.3A and 4.3C. PC1 accounted for 48.7% of the total variance.

The total percentage of genotype variance explained by PC1 increased under DS Granular Si compared to the control. Likewise, under NS conditions, both Si treatments increased the total percentage of variance of PC1. The trait shift under DS conditions is notable with granular Si compared to the control and liquid Si. Whereas the degree of trait relatedness remained constant with liquid Si across both DS and NS conditions for N%, S% and GPC%. Si application shows a genotypic shift towards the PC1 vertical axis, with clustering more noticeable with granular Si and to a lesser extent liquid Si under DS conditions. Under NS conditions, granular Si showed a genotypic shift towards quadrants QI and QII, whereas with liquid Si and the control, the clustering is within quadrants QII and QIII.

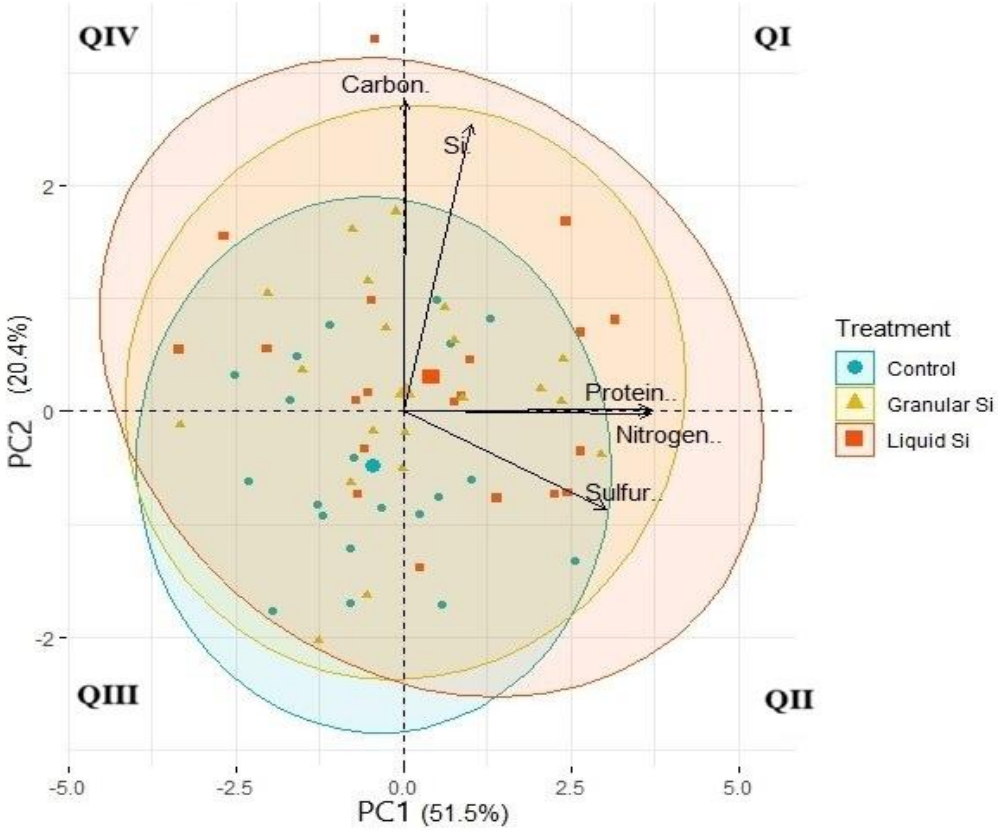

Figure 4.1: Principal component analysis biplot of 20 bread wheat genotypes when evaluated under control, liquid Si, and granular Si, under drought-stress conditions.

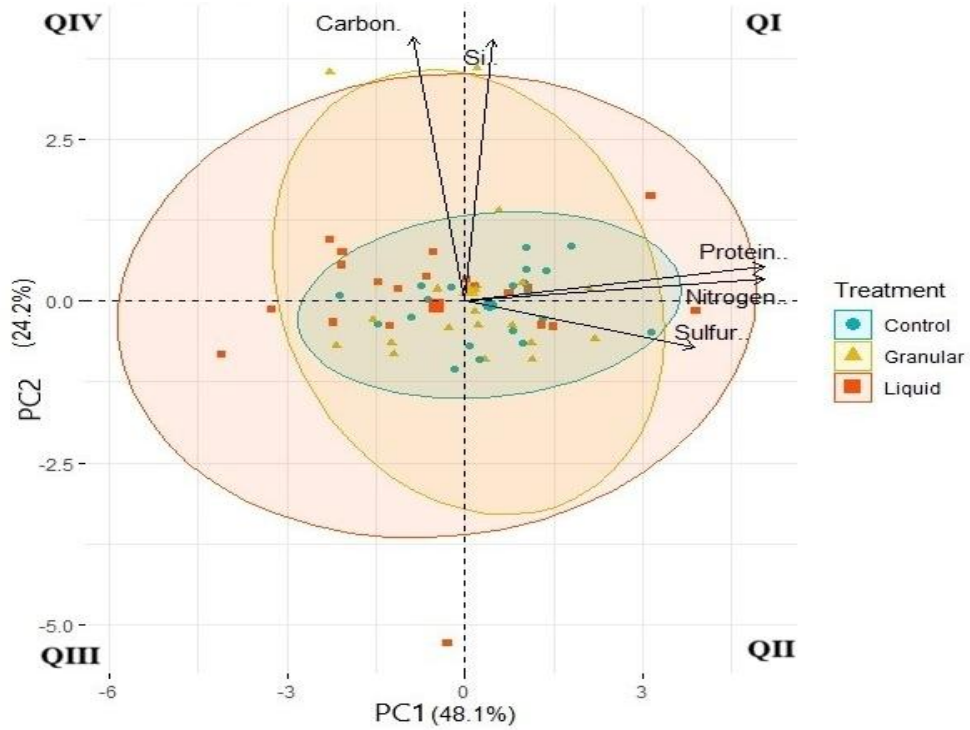

Figure 4.2: Principal component analysis biplot of 20 bread genotypes when evaluated under control, liquid Si, and granular Si, under non-stress conditions.

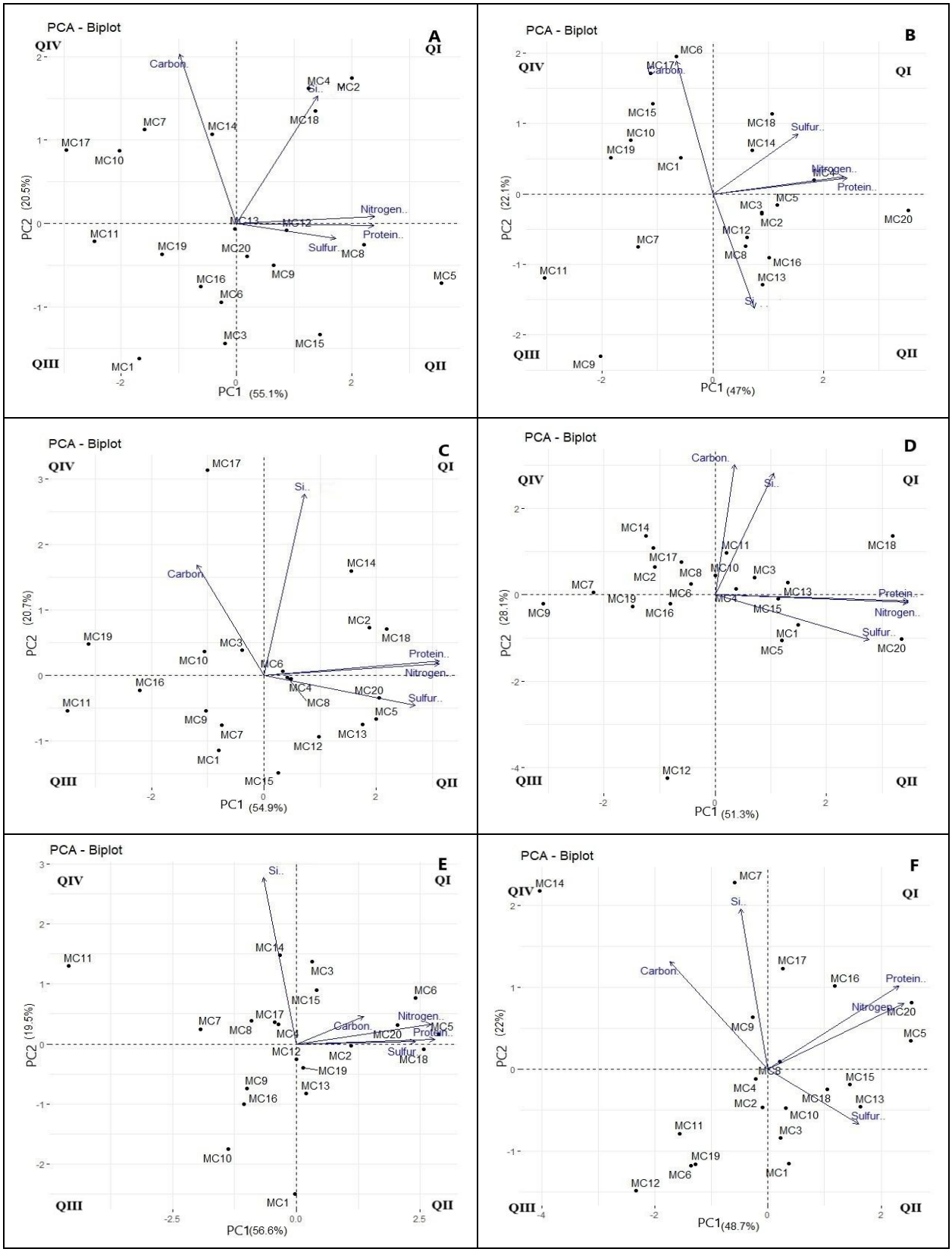

Figure 4.3: Principal component analysis biplots of 20 bread wheat genotypes evaluated without silicon under drought-stress conditions (A); without silicon under non-stress conditions (B); with liquid silicon under drought-stress conditions (C); with liquid silicon under non-stress conditions (D); with granular silicon under drought-stress conditions (E); with granular silicon under non-stress conditions (F) across three environments.

4.4 Discussion

Grain composition and quality are determined through various indicators, including physical, chemical, and biochemical characteristics (Rao et al., 2021). Grain nutrient uptake is a key component of wheat grain quality, affecting grain starch and protein composition. Improving nutrient-use efficiency is essential for grain quality by increasing the uptake, remobilization, utilization, and storage of nutrients (Dawar et al., 2023). Several studies have been carried out to investigate the effect of silicon on yield and yield-related traits (Kheyri et al., 2018; Abd-El-Aty et al., 2024; Ramamoorthy & Porkodi, 2024). However, research into improving wheat grain composition and quality, particularly GPC% using silicon fertilisers is limited. Silicon has mainly been studied in terms of carbon sequestration, macro and micronutrient uptake, improving yields and under various biotic and abiotic stresses (Song et al., 2014; Neu et al., 2017).

In the current study, DS had a significant effect on the genotypic performance under different Si conditions for both nitrogen and grain protein content (Table 4.1). The genotype x water regime x silicon formulation interaction effect was significant ($p < 0.001$) for Si content, whilst genotype x water regime x environment was significant for N% and GPC% (Table 4.1). A study by Neu et al. (2017) found that Si application modifies the nitrogen-use efficiency of wheat, thus altering the levels of N% and GPC%. Although wheat is a natural silicon-uptake crop, its silicon-use efficiency is also genotype dependent (Malik et al., 2023). Si acts both directly and indirectly in influencing agronomic trait performance and dough rheological properties (Dallagnol et al., 2023). Tables 4.2-4.4 showed that with silicon applications, particularly the granular Si formulation, the C %, N%, Si and GPC % increased for tested genotypes under DS conditions. The highest C% was attained for genotype MC17 (C content of 41.17%) under DS conditions whilst under NS conditions the genotype, MC14 had the highest C content (42.19%) with granular Si. The highest recorded grain N (2.88%) and GPC% (16.41%) was genotype MC5 under DS conditions and with granular Si. Similarly, Teixeira et al. (2022), also reported that Si application increased uptake of C and N under DS conditions. Si application is highly dependent on formulation, concentration, and mode of application for effective uptake and utilization (Christian et al., 2022). This is evident in the current study with noticeable differences between the liquid and granular Si treatments. A study by Ligaba-Osena et al. (2020) found that Si uptake significantly improved agronomic trait performance; however, the grain nutrient uptake was not significant. Comparable results were noted for this study, whereby the C%, N%, S% and GPC % were not significant for the four-way interaction of genotype x water regime x treatment x environment.

The biplots (Figures 4.1-3) indicate genotype association regarding the effect of various Si formulations under DS and NS conditions. Genotypic clustering was more evident for granular Si application than the liquid Si application (Figure 4.1). Both Si applications show a shift towards the

positive sides of PC1 and PC2 compared to the control. Related results were noted by Christian et al. (2023), that trait relationships improved and genotypic variation decreased, particularly under DS conditions and Si applications. Si application under NS conditions is less effective in comparison to the control (Figure 4.2). Under DS conditions and with granular Si, there is a notable genotypic shift and increased trait associations with the C%, N%, S%, and GPC % (Figure 4.3). Comparable results were noted by Christian et al. (2023), whilst Tomaz et al. (2022) distinguished that genotypic variation occurs with differences in Si concentration, thus leading to variation in nutrient accumulation. Kumar et al. (2022) established that Si application inhibits the starch-degrading enzyme in grain tissues, thus stabilizing yield and grain quality.

Under DS conditions, Si alters the C/N balance in the plant sink-source relationship, remobilizing amino acids to sustain increased N demand during grain development (Luyckx et al., 2017; Detmann et al., 2012, 2013). Si application also modifies the carbon: nitrogen: phosphorus: silicon stoichiometry favouring grain development (de Carvalho et al., 2022). In the current study, Si formulations enhanced the contents of grain C, N, GPC, and Si, notably under DS conditions. Overall, granular Si application reduced genotypic variation for C, N, S and improved the GPC under DS conditions. The present study revealed that granular Si application positively contributed to higher grain contents of C%, N%, GPC% and Si in the assessed wheat genotypes under DS conditions, implying the contribution of Si to grain quality improvement and drought-stress management.

4.5 Conclusions

In conclusion, granular Si application, although not significant, showed that it positively affects C%, N%, GPC%, and Si uptake on wheat genotypes, under DS conditions. The effectiveness of the Si application on grain nutrient composition is also genotype dependent. The combination of these elemental nutrients invariably affects dough rheological properties. Stankowski et al. (2021) found that Si application played a role in increasing gluten content, sedimentation index, and dough development time. Further research into the effect of granular silicon formulation on the gluten content, sedimentation index, and other dough rheological properties of bread wheat is necessary to fully understand the effect of granular Si application on wheat flour quality, for selection and breeding.

4.6 References

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CHAPTER 5

Combining Ability of Bread Wheat (*Triticum aestivum* L.) Genotypes for Yield and Related Traits with Silicon Fertilisation

Abstract

Silicon (Si), a chemical element, enhances sustainable wheat productivity by improving plant turgidity, nutrient uptake and enhancing beneficial microbial effects. Si uptake improves yield and nutrient uptake under drought conditions. Limited studies explored the gene action and inheritance patterns of yield and yield-related traits in wheat involving direct and reciprocal crosses under Si fertilisation. The objective of this study was to assess the genetic determinants of yield and yield components in newly developed wheat populations under Si fertilisation to guide breeding and select desirable parents and progenies for variety development. Seven wheat parents were selected based on yield and drought tolerance and were crossed using a full diallel mating design. Forty-two full-sibs were generated and evaluated along the parents under controlled environment conditions, without and with granular Si application (3g/pot) for precision phenotyping and selection. The analysis of variance (ANOVA) showed significant genotype (G) by Si treatment (T) interaction ($p < 0.05$) affecting the number of kernels per spike (KPS), aboveground biomass (AGB) and grain yield (GY). Maternal effects were significant for plant height (PH), productive spike number (PS) and kernels per spike (KPS) with Si application. Si application significantly ($p < 0.05$) improved the general combining ability (GCA) effects for PH, PS, spikelets per spike (SPS), KPS; hundred seed weight (HSW), harvest index (HI) and GY. The specific combining ability (SCA) effects were significant ($p < 0.05$) for PH, PS, KPS, HSW and GY with Si application. The following parents, with Si application, had positive and significant ($p < 0.05$) GCA effects: MC17 at 1.07 for GY, MC4 for PS (0.51), MC8 for KPS (5.12), SPS (0.55) and HI (4.56). With Si application, positive and significant SCA effects were recorded for GY for direct crosses MC4 x MC8 (1.57) and MC6 x MC10 (2.68). Other direct crosses with positive and significant ($p < 0.05$) SCA effects, with Si, were MC1 x MC4 (6.60) for productive tiller number (TN), MC1 x MC8 (7.27) for spike length (SL) and MC8 x MC10 (4.26) for KPS. The GCA/SCA ratio was relatively higher (0.77) for KPS, with Si application indicating the preponderance of additive genes. Direct crosses with all traits improved with Si application included MC1 x MC6, MC1 x MC10, MC1 x MC11, MC4 x MC6, MC4 x MC11, MC6 x MC11 and MC8 x MC10 whilst reciprocal crosses MC4 x MC1; MC8 x MC6; MC17 x MC1; MC17 x MC4; MC17 x MC6; MC17 x MC8 and MC17 x MC11 had similar responses for the same traits. These families are selected for genetic advancement and variety development. Overall, the Si application favourably complemented the additive gene effect on yield and yield-related traits of direct and reciprocal crosses. Further research is required to examine the

accumulation of maximum favourable additive genes in advanced generations of wheat through field evaluations of the breeding populations under Si application.

Keywords: additive genetic effect, combining ability, heritability, maternal genetic effects, silicon fertilisation, wheat

5.1 Introduction

Wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) is a crucial commodity crop for the global economy and humankind's daily sustenance. The global annual wheat production is about 787 million tons (MT) across 237 million hectares (MHa) (Mottaleb et al., 2023; Feyisa et al., 2024). Global projections for the 2024/2025 wheat season are estimated to be 794.73 MT produced, which is a 0.8% increase from the 2023/2024 season (Collier et al., 2024). Wheat production for the 2023/2024 season in South Africa is 2 MT, with 1.9MT imported to meet demand (SAGL, 2025). Africa imported an estimated 54.8 MT of wheat from 2020 to 2021, of which imports to SSA account for 26.6 MT (Galal, 2024). As of 2020, SSA is a net importer (80%) of wheat to meet the total domestic wheat supply (Glauber et al., 2023).

Sub-Saharan Africa faces chronic food insufficiency due to low crop production and productivity attributable to drought and heat stress, and poor crop management practices (Dimkpa et al., 2023). Low yields are frequently associated with genetically unimproved genotypes, poor soil fertility and biotic and abiotic stress (Horn et al., 2020). Reportedly, farmers in SSA use a sub-optimal NPK fertiliser exacerbating the yield gaps (Eriksson et al., 2018). In SSA, an average of 8 $kg.ha^{-1}$ NPK fertiliser is used than the optimal and recommended amount of 30 to 120 $kg.ha^{-1}$ (Eriksson et al., 2018). The impact of climate change and its variability severely affects crop growth cycles (Brevik, 2013). The length and frequency of heat and drought stress shorten the cropping seasons, ultimately curtailing yields (Mutegi et al., 2018). There is a need for plant breeding programs in SSA to focus on the screening and development of locally adapted, drought-tolerant genotypes in the face of climate change.

Drought tolerance is a polygenic trait, subject to genotype x environment interaction and low heritability, requiring effective genotype screening using morphological, biochemical and physiological characteristics (Mwadzingeni et al., 2016; Grzesiak et al., 2019). Drought affects wheat's physiological, biochemical, morphological and molecular characteristics (Lan et al., 2022). Drought can lead to severe yield reduction even across a limited timeframe (Kumar et al., 2008), reducing wheat yield between 50% to 90% (Awan et al., 2017). Plant response to drought stress depends on the crop genotype, development stage, duration and intensity (Christian et al., 2023). Significant genetic variation for yield

and yield components in wheat genotypes provides essential genetic resources for drought-tolerance breeding (Semahegn et al., 2020).

Silicon (Si) applications are essential to boost drought-tolerance in wheat genotypes through various mechanisms. Si accumulation improves plant physiological characteristics, alleviating biotic and abiotic stress, by enhancing the leaf thickness of plants through Si deposition in the leaf blades, leaf sheath, hull epidermal and vascular tissue (Meharg et al., 2015). It also affects other physiological and chemical characteristics, including defence mechanisms, by activating defence-related enzymes and genes, regulating signal pathways and promoting antimicrobial compound production (Basu et al., 2021). Si induces systemic acquired resistance (SAR) (Conceicao et al., 2014), leading to a hypersensitive response in plants (Basu & Kumar, 2021). Si application affects plant hormone modulation and gene expression patterns (Shanmugaiah et al., 2023). Wheat is classified as Si accumulator, providing enhanced agronomic trait performance (Kowalska et al., 2020). Variation in Si accumulation is genotype-dependent (Deren, 2001). Ma et al. (2006) reported that Si uptake is regulated using Si transporter gene *Lsi*1. The *Lsi*1 gene is expressed in the root and is predicted to encode membrane protein to the water channel proteins known as aquaporins. High Si accumulators have a highly developed Si transportation mechanism. This mechanism utilizes four *Lsi* genes, namely Low Si 1 (*Lsi*1), Low Si 2 (*Lsi*2), Low Si 3 (*Lsi*3) and Low Si 6 (*Lsi*6), which facilitate the distribution and storage of Si throughout the plant structure (Christian et al., 2022). A study by Cen et al. (2022) identified 32 *Lsi* genes from different plant species. Si is also associated with the mediation of genes (Khan et al., 2023). Basu and Kumar (2021) found that under stressed conditions, Si modulates different plant gene expressions instead of directly signalling or acting as a secondary messenger. This complex mechanism of plant-Si interactions and genes associated with Si transport and utilization indicate the possibility of selection and breeding for Si-use efficiency and accumulation of genes through trait introgression. Studies on the combining ability and heterosis for Si-use efficiency have predominantly been reported on rice under stressed conditions (Jackson et al., 2019; Keerthiraj et al., 2021b), with little emphasis on wheat. Therefore, there is a need to explore the genetic potential of drought-tolerant and Si-use-efficient parents and new progenies for the genetic management of drought tolerance through Si application.

Genetic designs such as the full diallel mating design allow for all possible cross combinations vital to determine the nature and magnitude of gene effects expressed by measured agronomic traits (Jalaj et al., 2021). Diallel analysis has been effectively used for evaluating and interpreting bread wheat genotype combinations for a wide range of qualitative and quantitative traits (Ahmad et al., 2020; Al-Timimi et al., 2020; Maričević et al., 2024). Genotypically diverse parents are essential for critically assessing variability, heritability and the gene action involved in trait expression (Hassan et al., 2007; Dragov et al., 2022). Limited studies explored the gene action and inheritance patterns of yield and yield-related traits in wheat involving direct and reciprocal crosses under Si fertilisation.

Wheat breeders exploit secondary agronomic trait performance to directly select primary traits, such as grain yield. Indirect selection provides information on early-generation breeding cycles with limited seed using highly heritable proxy traits (Sandhu et al., 2021). Combining ability analysis is a powerful tool to postulate gene actions and evaluate both parents and their combinations for yield and yield components (Desale et al., 2014). It confers information about the gene action and inheritance of agronomic traits to select desirable parents and crosses (Olivo et al., 2019). The selection of genotypically diverse parents for hybridization is vital in wheat breeding. Cross performance is correlated with the general combining ability (GCA) of parents and specific combining ability (SCA) of derived families. Promising crosses result from crossing divergent parents with at least one parent having a high GCA (Cruz et al., 1989; Bahari et al., 2012). GCA estimates the relative importance of parents with assessed traits, whereas the SCA evaluates the significance of the combined gene action of the parents in the progeny (Hassan et al., 2020). Keerthiraj et al. (2021b) reported that GCA is attributed to additive gene actions (either additive or additive by additive gene interaction), and SCA is attributable to non-additive gene actions (e.g. dominant, epistasis or both). Additive genetic effects are essential in a synthetic population, whilst more dominant or epistatic effects are important for hybrid breeding or in the selection of novel recombinants (Singh et al., 2021). GCA and SCA effects are integral in selecting and developing breeding populations (Gaballah et al., 2022).

Drought tolerance and grain quality are traits that can both be affected and improved using the Si application (Christian et al., 2022). Diverse drought-tolerant bread wheat breeding lines were acquired from the International Maize and Wheat Improvement Centre (CIMMYT) and exhibited variable agronomic traits. Some 20-bread wheat inbred lines were preliminarily selected owing to their improved drought tolerance. The lines were phenotyped with Si application, and unique parents were identified with drought tolerance using multiple yield and yield-influencing traits and screened for desirable grain quality (Christian et al., 2023). The selected genotypes are useful genetic resources for drought tolerance and improved grain quality with Si application. Nonetheless, the effect of Si on the combining ability effects and the nature of gene action has not been evaluated previously in wheat to guide genotype selection and breeding. The aim of this study was to determine the genetic constituents of yield and yield components of newly established wheat populations with Si fertilisation, for selection, breeding and variety development.

5.2 Materials and Methods

5.2.1 Plant Materials

The study used seven parental bread wheat genotypes of CIMMYT origin (Table 5.1). After extensive phenotyping and Si formulation trials, the parental genotypes were selected based on their divergent agronomic traits, drought tolerance and variable uptake of granular Si. Further, the parents were selected guided by their stress tolerance index (STI) after Si application and grain yield response when compared to the untreated control (Christian et al., 2023). Table 5.1 presents the details of the selected parents, including their STI under the untreated control and granular Si treatments under drought-stressed conditions. The lines had moderate to high STI values, of which MC6 had the highest stress tolerance index (0.88), while MC1 and MC8 had a moderate STI of 0.54 when treated with granular Si.

Table 5.1: **List and pedigree of wheat parents selected for cross-formation.**

Genotype	Pedigree	STI		Grain yield (t.ha^{-1})	
		Without Si	With Granular Si	Without Si	With Granular Si
MC1	QUAIU	0.45	0.54	6.03	7.44
MC4	MUNAL #1	0.39	0.57	4.64	5.5
MC6	WBLL1//UP2338*2/VIVITSI	0.57	0.88	6.93	8.06
MC8	ACHTAR/4/MILAN/KAUZ//PRINIA/3/BAV92	0.47	0.54	5.16	5.47
MC10	FRET2*2/4/SNI/TRAP#1/3/KAUZ*2/TRAP//KAUZ/5/ONIX	0.59	0.82	7.88	9.65
MC11	CNDO/R143//ENTE/MEXI_2/3/AEGILOPS SQUARROSA (TAUS)/4/WEAVER/5/2*FRAME	0.58	0.58	6.18	6.83
MC17	CNO79//PF70354/MUS/3/PASTOR/4/BAV92/5/FRET2/KUKUNA//FRET2/6/MILAN/KAUZ//PRINIA/3/BAV92	0.52	0.55	6.05	6.32

Abbreviations: Si – Silicon, STI – stress tolerance index

5.2.2 Cross Formation

The seven parental lines were established at the University of KwaZulu-Natal (UKZN) in Pietermaritzburg (29° 37′ S, 30° 24′ E), under greenhouse conditions. The lines were crossed using a 7 x 7 full diallel mating design, Method I, Model I, following Griffing (1956) to generate F1 progenies. The parental lines were planted staggered four times at two-week intervals to ensure synchronized

flowering and a continuous pollen supply (Figure 5.1). Hand emasculation and pollination were followed per standard wheat procedures (Curtis et al., 1958). Forty-two F1 crosses were successfully generated and harvested at maturity. The F1 seed was planted for genetic analysis and evaluated for Si uptake and agronomic trait performance.



Figure 5.1: Labels 1-4 represent the four crossing blocks of wheat which were stagger planted to synchronise flower emasculation and pollination.

5.2.3 Si Fertilisation, and Experimental Design

The study was conducted under greenhouse conditions. The seven parental lines and their 42 F1 progenies were established at the University of KwaZulu-Natal (UKZN) in Pietermaritzburg (29° 37′ S, 30° 24′ E). The greenhouse had day and night temperatures of 25 °C and 15 °C, respectively. Day and night humidity was maintained between 45% and 55%, respectively. Plants were grown in plastic pots of 5L capacity filled with composted pine bark growing media. Osmocoat Bloom fertiliser (7.5g) was applied to each pot before planting. The experiment was carried out under two Si regimes, namely, with Si and without Si (control). A slow-release granular potassium silicate ($KSiO_4$) (17mm AgriSil) formulation was applied at planting. The slow-release granulated Si was applied at planting at 3g per pot and evenly dispersed in the top layer of the growing media. All other agronomic practices followed the standard guidelines for wheat production in South Africa (DAFF, 2016). Weed control was done manually, and insecticides (pyridine azomethine) and fungicides (triazole) were used to control aphids and powdery mildew.

5.2.4 Data Collection

Data were collected on the following preharvest and postharvest phenotypic traits. Preharvest data included plant height (PH) measured in centimetres (cm) from the ground to the tip of the spike while productive tiller number (TN) and productive spike number (PS) were recorded at physiological maturity. Postharvest data were total aboveground biomass (AGB) measured in tons per hectare ($t.ha^{-1}$), spike length (SL) was measured in cm; the number of spikelets per spike (SPS) and the number of kernels per spike (KPS) were recorded from the main tillers of all five plants; Hundred seed weight (HSW) was determined by measuring 100 randomly sampled seeds after harvesting and reported as grams per 100 seed (g/100 seed), and harvest index per plant (HI) was computed as the (grain yield/biological yield) per genotype x 100. Grain yield was measured and converted to tons per hectare ($t.ha^{-1}$).

5.2.5. Data Analyses

5.2.5.1 Analysis of Variance (ANOVA), Mean Performances, and Heritability Estimate

The above data was subjected to a two-way analysis of variance (ANOVA) (Table 5.2) (Riyanto et al., 2023) and mean values were deduced for the Si formulation and untreated control using Genstat 18th version, VSN, International (Payne et al., 2015) and using the Plantbreeding package in R (R Core Development Team, 2023). Means were separated by the Fischer's protected Least Significant Difference test at a 5% probability level.

The following statistical model was used for data analysis:

$$Y_{ijk} = \mu + \delta_i + \theta_j + (\delta\theta)_{ij} + e_{ijk}$$

Where Y_{ijk} = the observed measurement for the ith treatment in the jth block in the kth replication; μ = the overall mean, δ_i is the true effect of the ith treatment of factor A, θ_j is the true effect of the jth treatment of factor B, $(\delta\theta)_{ij}$ is the interaction between the ith level of Genotype and the jth level of Treatment and e_{ijk} is the error effect.

Table 5.2: Two way ANOVA with interaction (Isaac et al., 2017).

Source of Variation	df	SS	MS	Expected MS	F-Ratio
Genotype (δ)$_i$	a - 1	$\frac{\sum_{i=1}^{a} T_{i...}^2}{bn} - \frac{T_{...}^2}{abn}$	$Ms_{\delta i}$	$\sigma_{eij}^2 + k\sigma_{(\delta\theta)ij}^2 + \theta_j \times k\sigma_{(\delta)i}^2$	$\frac{SS_\delta}{a-1} / MS_E$
Treatment (θ)$_j$	b - 1	$\frac{\sum_{j=1}^{b} T_{.j.}^2}{an} - \frac{T_{...}^2}{abn}$	$Ms_{\theta j}$	-	$\frac{SS_\theta}{b-1} / MS_E$
Interaction ($\delta\theta$)$_{ij}$	$(a-1)(b-1)$	$\frac{\sum_{i=1}^{a}\sum_{j=1}^{b} T_{ij}^2}{n} - \frac{\sum_{i=1}^{a} T_{i...}^2}{bn} - \frac{\sum_{j=1}^{b} T_{.j.}^2}{an} + \frac{T_{...}^2}{rts}$	$Ms_{(\delta\theta)ij}$	$\sigma_e^2 + k\sigma_{(\delta\theta)ij}^2$	$\frac{SS_{\delta\theta}}{(a-1)(b-1)} / MS_E$
Error (e_{ij})	$ab(n-1)$	$SS_T - SS_\delta - SS_\theta - SS_{\delta\theta}$	$Ms_{(eij)}$	σ_e^2	
Total	abn - 1	$\sum_{i=1}^{a}\sum_{j=1}^{b}\sum_{k=1}^{n} T_{ijk}^2 - \frac{T_{...}^2}{abn}$			

The broad sense heritability (H^2) of recorded traits was estimated using the formula given below (Abraha et al., 2017):

$$H^2 = \frac{\sigma_g^2}{\sigma_p^2}$$

Where, H^2 = broad sense heritability

σ_p^2 = the phenotypic variance for a particular trait = $\sigma^2{}_p = \sigma^2{}_g + \sigma^2{}_{\delta\theta}/k + \sigma^2{}_e/\theta k$

σ_g^2 = the genetic variance for a particular trait $\left(\sigma^2{}_g\right) = \frac{Ms_{\delta i} - \sigma_e^2}{k\theta}$

$\sigma^2{}_{\delta\theta}$ = variance of genotype-by-treatment interaction, θ = treatment, $\sigma^2{}_e$ = error/environmental variance, k = number of replications, $Ms_{\delta i}$ = mean square value of genotypes

5.2.5.2 Estimation of General and Specific Combining Ability Effects and Heterosis

A combining ability analysis of variance was carried out to compute the general combining ability (GCA) and specific combining ability (SCA) effects using AGD-R version 5.0 (Rodríguez et al., 2020) based on the Diallel Method I, Model I (Griffing, 1956). The following statistical model was used:

$$Y_{ijk} = \mu + g_i + g_j + S_{ij} + r_{ij} + b_k + e_{ijk}$$

Where Y_{ij} = the observation of the cross between the parents i^{th} and j^{th} in the kth replication, μ = the general population mean, g_i and g_j = GCA values of the ith and j^{th} parents, respectively, s_{ij} = the SCA effect of a cross between parent i and parent j, r_{ij} = the reciprocal effect for the reciprocal crosses between the ith and j^{th} parents, b_k = the effect of the kth block, e_{ijk} = the residue/experimental error. .

The AGD-R software was used to compute the maternal components.

The relative GCA and SCA ratio was computed to assess the gene action for each trait using the following formula (Baker, 1978).

$$\frac{GCA}{SCA} ratio = \frac{2\sigma^2{}_{gca}}{\left(2\sigma^2{}_{gca} + \sigma^2{}_{sca}\right)}$$

where $\sigma^2{}_{gca}$ = variance due to GCA and $\sigma^2{}_{sca}$ = variance due to SCA

The GCA/SCA ratios indicate if a trait is proportionally governed by additive or non-additive gene action (Fasahat et al., 2016). Traits with a GCA/SCA ratio below 0.5 indicate that the SCA effects are predominant and that a trait is controlled by non-additive gene action, whereas a GCA/SCA ratio > 0.5, indicates that the GCA effect is more important in conditioning the heritability of a trait. Negative GCA/SCA ratios indicate that parents or crosses performed worse than the population average.

5.3 Results

5.3.1 Analysis of Variance and Genotype Performance

Analysis of variance (Table 5.3) showed significant ($p < 0.05$) genotype by treatment interaction effects for GY, KPS and AGB. The genotypic effects were significant for all assessed traits except for SL, whilst the treatment effects were significant for PH, PS, SPS, KPS, HSW, AGB and GY.

The parents, the direct and reciprocal crosses exhibited varying responses with and without Si application, as presented in Tables 5.4 and 5.5. The parental mean for PH was 85.04 cm without Si and 89.01 cm with Si application. The means for PH, TN, PS, SL, SPS, KPS, HSW, HI and AGB were 85.0 cm, 3.51, 3.08, 8.44 cm, 18.36, 39.92, 3.10 g/100 seed, 0.58 and 16.93 $t.ha^{-1}$, respectively, without Si application (Table 5.4). With Si application (Table 5.5), the mean values for PH, TN, PS, SL, SPS, KPS, HSW, HI, and AGB were 89.01 cm, 4.67, 4.54, 8.75 cm, 19.46, 44.44, 3.30 g/100 seed, 0.53 and 20.61 $t.ha^{-1}$, respectively. The mean GY for the parents was 11.59 $t.ha^{-1}$ without Si and 13.02 $t.ha^{-1}$ with Si application. A 12.34% increase in GY was recorded with Si application for the parents than non-Si application. The parents MC1, MC8, MC11 and MC17 had increased GY at 11.82%, 68.05%, 41.12% and 30.00%, respectively, with Si application compared to without Si.

Direct Crosses

Twenty of the 21 direct crosses with Si application had higher GY than the corresponding indirect crosses without Si application. For example, direct crosses MC6 x MC8, MC10 x MC17, MC6 x MC10 and MC4 x MC11 recorded the highest GY with Si application compared to without Si.

Direct crosses, with Si, with all traits improved included: MC1 x MC6, MC1 x MC10, MC1 x MC11, MC4 x MC6, MC4 x MC11, MC6 x MC11 and MC8 x MC10 (Table 5.5), compared to without Si (Table 5.4) application. The direct cross MC6 x MC8, with Si application, had increased GY at 14.25 $t.ha^{-1}$ whilst the same cross without Si had a GY of 6.45 $t.ha^{-1}$. The direct cross MC6 x MC11, had TN of 6.67 with Si application, compared to without Si (TN = 3.50). Likewise, for the direct cross MC1 x MC10, the SL with Si application increased to 10.06 cm compared to the control at 8.28 cm. The cross MC8 x MC10, with Si application, the KPS was 52.44 compared to the same cross without Si, with 35.22. The five best direct crosses for GY are MC6 x MC8, MC10 x MC17, MC4 x MC11, MC6 x MC10 and MC10 x MC11 with Si, compared to without Si application.

Indirect Crosses

Similarly, 20 among the 21 reciprocal crosses with Si applications had higher GY than without Si application. The reciprocal cross MC8 x MC4, had the highest GY of 15.20 $t.ha^{-1}$ with Si application, compared to the same cross with 4.60 $t.ha^{-1}$, without Si application. In comparison, the respective parents, without Si, generated a GY of 9.64 $t.ha^{-1}$ for MC8 and 11.85 $t.ha^{-1}$ for MC4 (Table 5.4) equating to yield increases of 58% and 28%, respectively. With Si application, the GY for the parents MC8 was 16.20 $t.ha^{-1}$ and that of MC4 was 10.80 $t.ha^{-1}$ (Table 5.5). Reciprocal crosses with improved agronomic traits with Si application included: MC4 x MC1; MC8 x MC6; MC17 x MC1; MC17 x MC4; MC17 x MC6; MC17 x MC8 and MC17 x MC11. The top five highest-yielding reciprocal crosses were MC8 x MC4, MC8 x MC6, MC6 x MC4, MC10 x MC6, and MC17 x MC4, with Si application. Genotype responses for agronomic traits varied amongst parents, direct crosses, and reciprocal crosses, with and without Si application.

Table 5.3: Mean squares and significant tests from an analysis of variance of seven bread wheat parental lines, 21 direct crosses and 21 reciprocal crosses for yield and yield components with and without Si application.

Source of variation	df	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
Replications	2	119.00*	60.30	4.95**	27.28	6.07	84.00	2.85***	0.02	3.35	2.00
Genotypes (G)	48	127.70***	98.92**	4.19***	15.13	3.96**	133.90***	1.10***	0.02**	20.22***	17.92***
Treatment (T)	1	1258.40***	3.90	63.99***	41.25	70.69***	894.00***	1.71*	0.00	685.17***	476.99***
G x T	48	48.40	22.35	1.31	12.34	2.02	52.60**	0.37	0.09	11.88*	13.09***
Residual	192	35.00	54.28	0.97	12.88	2.41	30.20	0.30	0.01	7.78	5.04

Abbreviations: T, treatment (two levels = untreated control and granular Si); df, degrees of freedom; PH, plant height (cm); TN, number of productive tiller number per plant; PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; KPS, number of kernels per spike; HSW, hundred seed weight (g/100 seed); HI, harvest index; AGB, above-ground dry biomass weight ($t.ha^{-1}$); GY, grain yield ($t.ha^{-1}$); *,**,***, denote significance differences at $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively.

Table 5.4: Mean values for yield and yield components of seven bread wheat parental lines and direct and reciprocal crosses evaluated without Si application.

Genotypes	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
Parents										
MC1	80.32	3.92	3.11	9.78	19.00	46.83	4.50	0.60	19.65	9.90
MC4	86.22	3.78	3.22	8.61	18.00	38.89	2.44	0.61	15.63	11.85
MC6	89.89	3.56	3.22	7.78	17.67	37.22	2.67	0.51	19.93	13.80
MC8	76.00	3.06	2.11	8.75	18.83	33.17	3.00	0.54	15.67	9.64
MC10	85.22	3.89	3.67	8.33	18.56	42.89	3.39	0.53	18.27	13.40
MC11	96.00	3.44	3.22	9.00	18.11	41.89	3.00	0.63	13.73	9.07
MC17	81.61	2.89	3.00	6.83	18.33	38.56	2.67	0.62	15.60	13.50
Means	**85.04**	**3.51**	**3.08**	**8.44**	**18.36**	**39.92**	**3.10**	**0.58**	**16.93**	**11.59**
Crosses										
MC1 X MC4	83.50	5.83	4.45	8.00	17.78	36.22	3.42	0.50	20.20	12.97
MC1 X MC6	84.33	2.78	2.78	7.72	18.33	35.11	2.89	0.54	16.60	12.30
MC1 X MC8	88.33	3.11	3.00	9.39	17.67	54.00	4.11	0.64	20.87	16.40
MC1 X MC10	84.83	3.92	3.28	8.28	16.78	41.33	2.58	0.63	16.12	11.88
MC1 X MC11	88.89	2.56	2.44	7.58	17.89	32.33	3.28	0.59	13.53	10.96
MC1 X MC17	87.55	3.89	3.89	8.78	19.33	49.33	3.06	0.50	15.56	12.00
MC4 XMC6	90.33	3.56	3.33	8.06	18.33	42.00	3.50	0.57	15.47	13.95
MC4 X MC8	86.72	3.33	3.33	8.83	19.56	53.67	3.78	0.68	20.81	16.43
MC4 X MC10	88.11	2.33	2.55	8.50	18.67	37.11	4.11	0.54	18.73	12.60
MC4 X MC11	93.39	4.06	3.67	7.72	17.78	34.89	3.03	0.60	14.93	6.90
MC4 X MC17	94.34	5.44	5.44	9.33	19.17	45.56	3.67	0.56	19.87	14.40
MC6 x MC8	84.92	2.56	2.67	7.55	17.00	36.56	2.89	0.57	11.20	6.45
MC6 X MC10	86.11	2.11	2.11	8.06	18.22	34.00	2.81	0.48	15.30	9.45
MC6 X MC11	80.83	3.50	3.22	7.33	17.00	35.33	2.89	0.63	16.04	10.65
MC6 X MC17	94.00	2.78	2.78	8.50	17.78	42.00	3.83	0.62	19.27	13.30
MC8 X MC10	81.44	2.22	2.11	7.89	16.89	35.22	3.56	0.61	16.93	10.35
MC8 X MC11	94.38	5.61	3.67	9.28	19.44	48.22	3.72	0.58	19.25	12.10
MC8 X MC17	86.33	2.67	2.89	9.05	19.56	47.78	3.44	0.59	17.67	12.90
MC10 X MC11	93.08	4.50	4.50	9.83	19.83	40.89	4.61	0.57	17.03	10.05
MC10 X MC17	88.46	4.60	3.06	9.67	12.67	32.67	3.94	0.55	15.40	7.30
MC11 X MC17	90.33	2.22	2.22	8.78	17.44	34.00	3.83	0.54	17.60	12.45

Genotypes	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
Reciprocals										
MC4 X MC1	62.55	3.78	3.78	8.72	18.89	42.44	3.50	0.63	18.43	12.30
MC6 X MC1	82.33	5.67	4.44	7.61	19.67	33.56	3.75	0.62	20.65	10.50
MC6 X MC4	88.00	4.50	2.67	8.31	17.89	36.67	2.94	0.66	15.70	7.80
MC8 X MC1	94.17	2.83	2.33	8.67	20.00	42.17	3.08	0.59	16.10	11.10
MC8 XMC4	88.89	3.83	3.11	8.50	18.00	43.67	2.44	0.55	12.00	4.60
MC8 X MC6	79.78	2.89	2.55	8.05	16.89	37.33	2.06	0.77	17.53	7.05
MC10 X MC1	90.08	5.33	5.33	9.50	19.00	43.56	3.67	0.54	18.80	9.80
MC10 X MC4	82.58	5.78	5.67	8.83	20.17	28.00	3.42	0.60	17.25	8.20
MC10 X MC6	86.83	4.45	4.45	8.78	18.33	37.22	3.39	0.55	19.20	10.80
MC10 X MC8	82.67	6.28	5.45	9.17	18.78	45.00	3.56	0.49	20.25	11.00
MC11 X MC1	94.67	3.45	3.00	8.05	17.17	37.44	4.06	0.48	17.87	14.10
MC11 X MC4	87.97	4.56	4.22	8.42	18.33	43.67	3.75	0.55	18.20	11.85
MC11 X MC6	95.17	4.67	4.56	8.72	18.78	40.22	3.61	0.55	19.18	12.50
MC11 X MC8	92.83	3.11	3.00	8.94	19.56	48.00	2.83	0.55	18.87	13.37
MC11 X MC10	93.44	2.44	2.44	8.25	17.67	38.50	3.33	0.41	17.53	10.20
MC17 X MC1	82.78	3.11	2.67	8.17	17.67	38.00	3.00	0.58	15.93	11.40
MC17 X MC4	85.89	3.11	2.55	8.50	18.11	33.89	3.25	0.55	19.73	13.20
MC17 X MC6	87.16	4.72	3.30	8.51	18.31	39.94	3.32	0.57	19.33	13.50
MC17 X MC8	88.33	2.55	2.44	9.17	19.11	47.22	3.28	0.70	19.27	14.55
MC17 X MC10	88.45	2.89	2.78	8.95	19.44	37.44	3.50	0.51	19.80	15.80
MC17 X MC11	93.44	2.22	2.00	8.55	18.89	38.33	3.50	0.54	18.00	12.07
Mean	**87.58**	**3.71**	**3.34**	**8.54**	**18.28**	**40.01**	**3.39**	**0.57**	**17.48**	**11.48**
LSD (5%)	**12.66**	**1.38**	**1.61**	**1.25**	**3.14**	**8.32**	**1.01**	**0.15**	**4.49**	**3.61**
SEM	**4.50**	**5.28**	**0.53**	**0.40**	**1.12**	**2.84**	**0.33**	**0.05**	**2.28**	**1.83**
CV%	**7.75**	**11.57**	**15.42**	**11.10**	**2.58**	**11.03**	**22.34**	**8.46**	**1.0**	**1.1**

Abbreviations: LSD, least significant difference, SEM, standard error of mean, CV, coefficient of variation, PH, plant height (cm); TN, number of productive tiller number per plant; PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; KPS, number of kernels per spike; HSW, hundred seed weight (g/100 seed); HI, harvest index; AGB, above-ground dry biomass weight ($t.ha^{-1}$); GY, grain yield ($t.ha^{-1}$)

Table 5.5: Mean values for yield and yield components of seven bread wheat parental lines and direct and reciprocal crosses evaluated with Si application.

Genotypes	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
Parents										
MC1	88.25	6.11	5.55	9.78	19.00	44.00	3.36	0.48	22.70	11.07
MC4	82.94	6.00	5.89	8.28	18.56	46.33	3.44	0.45	20.23	10.80
MC6	94.72	4.56	4.45	8.45	19.22	45.56	2.83	0.51	20.61	12.30
MC8	81.33	4.33	4.33	9.28	21.11	54.89	3.17	0.68	19.43	16.20
MC10	89.11	3.89	3.66	8.33	19.22	35.89	3.33	0.46	18.80	10.40
MC11	100.05	3.67	3.56	9.06	19.56	40.78	3.11	0.51	18.20	12.80
MC17	86.67	4.11	4.33	8.11	19.56	43.67	3.83	0.60	24.27	17.55
Means	**89.01**	**4.67**	**4.54**	**8.75**	**19.46**	**44.44**	**3.30**	**0.53**	**20.61**	**13.02**
Crosses										
MC1 X MC4	94.11	4.47	5.22	9.83	19.78	46.67	3.67	0.54	23.82	15.45
MC1 X MC6	87.83	3.78	3.67	8.11	18.56	38.44	3.00	0.53	20.70	14.55
MC1 X MC8	88.84	4.11	4.11	9.06	18.89	49.22	4.28	0.63	19.33	12.70
MC1 X MC10	92.50	5.53	4.67	10.06	18.67	48.00	3.50	0.62	18.73	13.55
MC1 X MC11	96.55	3.78	3.66	8.72	18.33	36.78	3.50	0.54	18.17	13.80
MC1 X MC17	88.67	4.67	5.11	9.11	18.33	49.00	3.00	0.50	18.00	15.60
MC4 XMC6	100.78	4.11	4.22	8.89	18.83	42.67	3.06	0.54	18.67	14.00
MC4 X MC8	93.17	4.44	4.44	8.33	19.22	45.33	3.75	0.64	23.43	16.65
MC4 X MC10	93.22	3.89	3.89	9.28	20.33	40.89	3.83	0.63	24.33	15.90
MC4 X MC11	96.42	4.61	4.00	8.22	17.89	36.78	3.36	0.59	17.40	11.20
MC4 X MC17	88.52	5.00	5.00	9.17	19.83	39.33	3.25	0.50	19.37	13.20
MC6 x MC8	84.83	3.55	3.22	7.42	19.11	36.44	2.89	0.68	19.70	14.25
MC6 X MC10	93.33	3.33	3.33	7.83	19.50	37.33	3.72	0.54	20.07	14.70
MC6 X MC11	97.67	6.67	6.67	9.08	19.17	43.56	3.25	0.60	22.87	13.50
MC6 X MC17	96.50	3.44	3.33	8.46	19.78	43.83	3.50	0.56	20.60	14.93
MC8 X MC10	90.22	3.22	3.22	9.00	19.78	52.44	3.50	0.48	20.73	14.00
MC8 X MC11	84.31	6.00	3.89	8.67	18.83	40.22	3.94	0.63	21.33	14.53
MC8 X MC17	87.50	2.89	2.78	6.33	20.22	50.56	2.83	0.62	19.00	13.18
MC10 X MC11	90.00	5.33	5.33	9.84	19.89	42.44	4.50	0.58	23.63	13.65
MC10 X MC17	82.22	3.48	2.78	8.67	17.50	33.67	4.00	0.59	18.60	14.40
MC11 X MC17	98.11	2.78	3.44	9.11	19.00	38.78	4.00	0.55	20.53	15.10

Genotypes	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
Reciprocals										
MC4 X MC1	94.11	5.37	5.22	9.83	19.78	46.67	3.67	0.54	19.80	13.35
MC6 X MC1	100.78	4.11	4.22	8.89	18.83	42.67	3.06	0.54	21.25	13.82
MC6 X MC4	93.17	4.44	4.44	8.33	19.22	45.33	3.75	0.64	18.87	12.90
MC8 X MC1	95.33	5.67	5.11	8.44	19.56	47.33	3.33	0.62	20.53	14.40
MC8 XMC4	87.67	6.67	6.00	9.34	20.33	50.56	3.83	0.66	22.80	15.20
MC8 X MC6	89.17	3.78	3.67	8.61	19.56	47.44	2.83	0.57	20.60	13.95
MC10 X MC1	89.00	5.00	4.89	9.75	20.17	41.33	4.17	0.59	21.80	14.00
MC10 X MC4	87.53	7.05	6.11	8.58	18.33	28.67	3.67	0.55	17.00	11.55
MC10 X MC6	85.61	5.94	5.55	9.06	18.22	38.11	4.00	0.77	22.10	16.97
MC10 X MC8	87.83	6.50	6.00	9.39	19.11	46.56	3.67	0.61	22.53	14.30
MC11 X MC1	98.67	3.89	3.78	8.89	18.89	42.83	3.78	0.54	19.80	13.90
MC11 X MC4	89.50	6.17	4.78	9.34	19.78	45.44	3.67	0.60	21.17	13.77
MC11 X MC6	96.83	4.66	4.55	8.61	19.22	43.67	3.11	0.55	22.95	14.23
MC11 X MC8	95.50	3.56	3.11	8.67	20.11	47.22	2.22	0.49	13.47	8.55
MC11 X MC10	99.89	3.78	3.55	8.94	18.67	38.67	3.78	0.57	19.00	13.10
MC17 X MC1	91.33	5.34	4.56	9.94	19.78	47.33	3.22	0.48	21.50	14.15
MC17 X MC4	94.22	3.89	3.22	9.28	20.00	47.89	4.33	0.55	26.53	19.93
MC17 X MC6	91.36	4.94	4.22	9.27	19.29	43.45	3.49	0.56	16.07	14.02
MC17 X MC8	95.00	2.89	2.89	9.89	20.83	56.67	3.75	0.55	22.47	15.60
MC17 X MC10	89.67	2.89	2.89	9.67	19.67	41.89	3.06	0.41	21.80	16.80
MC17 X MC11	97.95	4.22	4.22	9.06	19.00	44.78	3.33	0.54	20.80	13.00
Mean	**92.27**	**5.00**	**4.26**	**9.40**	**19.28**	**43.50**	**3.53**	**0.57**	**20.53**	**14.03**
LSD (5%)	**5.22**	**1.98**	**1.65**	**8.16**	**1.71**	**9.71**	**0.84**	**0.16**	**4.49**	**3.61**
SEM	**1.79**	**2.84**	**0.59**	**2.91**	**0.60**	**3.43**	**0.30**	**0.06**	**2.28**	**1.83**
CV%	**7.34**	**21.25**	**19.45**	**7.12**	**4.14**	**13.03**	**9.44**	**15.84**	**1.0**	**1.1**

Abbreviations: LSD, least significant difference, SEM, standard error of mean, CV, coefficient of variation, PH, plant height (cm); TN, number of productive tiller number per plant; PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; KPS, number of kernels per spike; HSW, hundred seed weight (g/100 seed); HI, harvest index; AGB, above-ground dry biomass weight ($t.ha^{-1}$); GY, grain yield ($t.ha^{-1}$)

5.3.2 Combining Ability Analysis

The mean squares for GCA and SCA effects and the GCA/SCA ratios for yield and yield components without and with Si application are presented in Table 5.6, respectively. Without Si application, the GCA effects were significant ($p < 0.05$) for PH, TN, PS, SL, KPS, HSW and GY (Table 5.6). The SCA effects were significant ($p < 0.05$) for PH, TN, SL, KPS, HSW, AGB and GY, without Si application. Reciprocal crosses, without Si application, showed significant ($p < 0.05$) on PH, TN, PS, SL, KPS, HSW, AGB and GY. The direct crosses related with the maternal effects were significant for PH, TN, PS, SL, KPS, HSW and GY. Across all the agronomic traits assessed for the GCA/SCA ratio, only SPS had a high ratio of 0.70.

Under Si application, the GCA effects were significant ($p < 0.05$) for PH, PS, SPS, KPS, HSW, HI and GY (Table 5.6). The SCA effects, with Si application, were significant for PH, PS KPS, HSW and GY. Reciprocal crosses with Si application were significant ($p < 0.05$) for PH, PS, SPS and HSW. Maternal effects were significant ($p < 0.05$) for PH, PS and KPS. The GCA/SCA ratio was generally low for most traits across both treatments, except for SPS (0.70 – without Si) and KPS (0.77 – with Si). Si application improved the GCA/SCA ratio for PH, KPS, HSW, HI, AGB and GY compared to without Si application.

Table 5.6: Summary mean squares and significant tests of combining ability and GCA/SCA ratio for yield and yield components for a full diallel crosses evaluated with (+Si) and without (-Si) Si treatment.

Source of variation	df	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
-Si											
Replications	2	25.47	0.81	7.56***	5.84***	3.84	108.86**	3.61***	42.46	10.00*	8.24
Cross	48	67.16***	4.22***	2.66***	1.29***	4.40	96.10***	0.84***	110.45*	15.39***	19.77***
GCA	6	182.41***	7.36***	3.74***	2.33***	1.61	158.20***	1.24***	106.83	5.56	18.39**
SCA Direct	20	59.72***	2.28***	1.31	1.40***	3.53	105.66***	0.73***	114.80	15.19*	14.92***
SCA Reciprocals	20	41.67***	5.26***	3.71***	0.88*	6.05	68.80***	0.83***	107.13	18.40***	25.02***
Maternal	6	46.18*	8.85***	7.83***	1.80***	2.82	99.75***	0.90*	71.37	15.72	45.53***
Residual	96	17.56	1.01	0.85	0.49	3.75	24.64	0.32	70.54	8.14	5.60
GCA/SCA		0.28	0.36	0.45	0.14	0.70	0.12	0.16	0.06	-0.17	0.10
+ Si											
Replications	2	45.28**	45.25	1.31	25.26	2.51	59.44	0.34	211.04	2.01	0.49
Cross	48	72.80***	30.55	2.92***	26.48	1.67*	91.13***	0.64***	134.94	12.31	9.88***
GCA	6	213.40***	46.16	4.19***	26.50	3.02*	312.60***	1.11***	226.19*	9.19	15.33**
SCA Direct	20	48.35***	18.80	2.84***	20.94	1.07	61.24*	0.47*	126.68	11.60	10.67***
SCA Reciprocals	20	57.07***	37.84	2.64***	32.01	1.90*	57.75	0.67***	117.13	13.90	7.54
Maternal	6	83.12***	44.08	4.49***	34.78	2.20	91.55*	0.43	105.01	7.10	3.05
Residual	96	9.64	24.12	1.03	25.34	1.09	35.39	0.27	100.11	9.58	4.71
GCA/SCA		0.38	-0.30	0.12	-0.02	-6.54	0.77	0.30	0.34	-0.01	0.13

Abbreviations: -Si, no silicon; +Si, with silicon; GCA, general combining ability effects; SCA, specific combining ability effects; GCA/SCA, Baker's ratio; df, degrees of freedom; PH, plant height (cm); TN, number of productive tiller number per plant; PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; KPS, number of kernels per spike; HSW, hundred seed weight (g/100 seed); HI, harvest index; AGB, above-ground dry biomass weight ($t.ha^{-1}$); GY, grain yield ($t.ha^{-1}$); *,**,***, denote significance differences at $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively

5.3.3 General Combining Ability of Parents

The parental lines and the test crosses exhibited variable GCA and SCA effects with and without Si (Tables 5.7 and 5.8). Without Si application (Table 5.7), parental line MC8 displayed a negative and significant GCA effect for PH, whilst KPS was positive and significant, in a desirable direction. Parental genotype MC1 had desirable positive and significant GCA effects for TN. Genotype MC4 exhibited desirable positive and significant GCA effects for TN and PS. Genotypes MC4 and MC10 had positive and significant GCA effects for the trait PS. Genotype MC17 was the only parent with a positive and significant GCA effect for GY.

With Si application (Table 5.8), genotype MC8 showed negative and significant GCA effect for PH. It also had positive and significant GCA effects for SPS, KPS, and HI, which was in a desirable direction. Genotype MC4 had positive and significant GCA effects for PS. Parental genotype MC10 had negative and significant GCA effects for PH and positive and significant GCA effects for HSW, in a desirable direction. Similarly, MC17 had positive and significant GCA effects for GY. Genotype MC4 had desirable positive and significant GCA effects for PS.

5.3.4 Specific Combining Ability of Crosses

Without Si

The direct cross MC6 x MC11 had a negative and significant SCA effect for PH in a desirable direction, without Si application (Table 5.7). For the trait TN, direct crosses MC1 x MC10 and MC8 x MC11 had positive and significant SCA effects, without Si application. Direct crosses MC4 x MC17 and MC6 x MC11 had positive and significant SCA effects, without Si, for PS, whilst the cross MC10 x MC17 had positive and significant SCA effects for SL. For the trait KPS, direct crosses MC1 x MC8; MC4 x MC8; MC8 x MC11 and MC8 x MC17 had positive and significant SCA effects without Si application. For HSW, only the direct crosses of MC6 x MC17 had positive and significant effects. Trait HI had positive and significant SCA effects for direct crosses MC1 x MC8, MC4 x MC10 and MC4 x MC17 without Si. Direct crosses MC6 x MC11 and MC8 x MC11 had significant and positive SCA effects for AGB, without Si application. Only two direct crosses, MC1 x MC10 and MC6 x MC11, had positive and significant SCA effects for GY without Si application.

The reciprocal crosses without Si (Table 5.7), including MC8 x MC6, MC10 x MC4, MC11 x MC4, MC17 x MC1, MC17 x MC4 and MC17 x MC6 showed negative and significant SCA effects in a desirable direction for PH. Reciprocal crosses MC4 x MC1; MC11 x MC8; MC11 x MC10; MC17 x MC1; MC17 x MC4 and MC17 x MC10 had positive and significant SCA effects for TN, without Si

application. For the trait PS, without Si, reciprocal crosses MC6 x MC1, MC10 x MC1, MC10 x MC4, MC10 x MC6, MC10 x MC8 and MC11 x MC6 exhibited positive and significant SCA effects. Reciprocal crosses with positive and significant SCA effects for SL, were MC4 x MC1; MC8 x MC6; MC10 x MC1, MC10 x MC6 MC10 x MC8, MC11 x MC4 and MC11 x MC6. Reciprocal crosses MC6 x MC1, MC8 x MC1, MC10 x MC1, MC10 x MC4, MC10 x MC8, MC11 x MC6; MC17 x MC6, MC17 x MC10 and MC17 x MC11 had positive and significant the SCA effects for SPS. For the trait KPS, crosses MC4 x MC1; MC10 x MC8; MC11 x MC1; MC11 x MC4; MC11 x MC6; MC17 x MC10 and MC17 x MC11 had positive and significant SCA effects. Crosses MC6 x MC1; MC10 x MC6; MC11 x MC1; MC11x MC4 and MC11 x MC6 exhibited positive and significant SCA effects for HSW. Reciprocal crosses MC10 x MC6, MC10 x MC8, MC11 x MC1 and MC11 x MC4 expressed positive and significant SCA effects for HI. For AGB, only two reciprocal crosses (MC6 x MC4 and MC10 x MC4) had positive and significant, without Si in a desirable direction. Crosses MC6 x MC4, MC8 x MC1, MC10 x MC1, MC10 x MC4 and MC10 x MC6 had positive and significant SCA effects for GY, without Si.

With Si

The direct crosses (e.g. MC1 x MC6; MC6 x MC8; MC8 x MC11 and MC10 x MC17) with Si had negative and significant SCA effects for PH (Table 5.8). For the trait TN, only the direct cross MC1 x MC4 exhibited positive and significant SCA effects with Si application, whilst MC1 x MC17 and MC6 x MC11 displayed positive and significant effects for PS, with Si. Direct cross MC1 x MC8 had positive and significant effects for SL. For KPS, only the cross MC8 x MC10 had positive and significant SCA effects. Crosses MC6 x MC10 and MC10 x MC11 had positive and significant SCA effects for HSW. One cross (MC6 x MC10) had positive and significant SCA effects for HI. For GY, only the cross MC6 x MC10 expressed positive and significant SCA effects.

The following reciprocal crosses with Si application: including MC4 x MC1, MC6 x MC4, MC8 x MC4, MC10 x MC1, MC10 x MC4, MC10 x MC6, MC10 x MC8, MC11 x MC4 and MC17 x MC6 had negative and significant SCA effects for PH in a desirable direction (Table 5.8). For TN, only the cross MC4 x MC1 had positive and significant SCA effects. Desirable reciprocal crosses with Si application for PS include: MC4 x MC1, MC11 x MC6, MC11 x MC10 and MC17 x MC4. For SPS, the cross MC8 x MC1 had positive and significant SCA effects. Crosses MC4 x MC1, MC10 x MC1, MC10 x MC4, MC10 x MC8 had positive and significant SCA effects for KPS. For HSW, MC8 x MC1, MC11 x MC8, MX11 x MC10, MC17 x MC10 and MC17 x MC11 had positive and significant SCA effects. Crosses MC8 x MC6, MC10 x MC4, MC11 x MC8 and MC17 x MC10 expressed positive and significant SCA effects for HI. The SCA effects for AGB were positive and significant for crosses MC8 x MC4, MC10 x MC4, MC11 x MC6 and MC11 x MC8 in positive direction. Crosses which were positive and significant for GY included MC8 x MC4, MC10 x MC4, MC10 x MC8, MC11 x MC8 and MC17 x MC11, which were selected for genetic advancement.

Table 5.7: Estimates of general combining ability effects of parents and specific combining ability effects of crosses for yield and yield components of bread wheat from a 7 x 7 full diallel evaluated without Si.

Genotypes	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
Parents										
MC1	-1.24	0.50**	0.11	0.06	0.13	1.42	0.19	2.02	0.37	0.31
MC4	0.19	0.46*	0.37*	-0.02	0.17	-0.27	-0.08	-2.01	-0.15	-0.12
MC6	-0.60	-0.18	-0.09	-0.49***	-0.25	-2.66**	-0.27*	-1.76	0.04	-0.38
MC8	-2.02*	-0.35*	-0.38*	0.20	0.27	3.28***	-0.14	-0.58	-0.19	-0.36
MC10	-0.89	0.29	0.36*	0.23	-0.20	-1.61	0.18	0.04	0.30	-0.45
MC11	4.39***	-0.16	-0.05	0.02	-0.02	-0.26	0.12	0.43	-0.65	-0.37
MC17	0.17	-0.56**	-0.32*	0.00	-0.09	0.11	0.00	1.87	0.28	1.38**
Direct crosses										
MC1 X MC4	-0.21	0.54	0.34	-0.19	-0.27	-1.77	0.01	-5.74	1.61	0.98
MC1 X MC6	-2.62	0.19	0.30	-0.42	0.81	-4.37*	0.06	3.61	0.73	-0.32
MC1 X MC8	6.72***	-0.90*	-0.36	0.26	0.12	3.43*	0.21	8.04**	-1.79	-0.09
MC1 X MC10	1.80	0.83*	0.55	0.09	-0.35	2.69	-0.58**	4.47	0.82	2.33**
MC1 X MC11	0.844	-1.06**	-0.63*	-0.77**	-0.89	-6.22***	0.02	-5.98	-0.73	-0.48
MC1 X MC17	-1.55	-0.16	0.20	-0.10	0.15	2.19	-0.50*	-3.97	-2.97**	-3.98***
MC4 XMC6	1.79	0.03	-0.57	0.18	-0.11	2.32	0.22	1.11	-0.69	-0.48
MC4 X MC8	1.84	-0.25	-0.06	-0.03	0.03	5.71***	-0.01	-5.02	0.37	-0.50
MC4 X MC10	-1.74	-0.41	0.09	-0.06	1.14	-5.51**	0.32	6.34*	-0.57	-0.51
MC4 X MC11	-1.68	0.29	0.33	-0.45	-0.40	-0.14	0.01	1.12	1.00	0.01
MC4 X MC17	1.97	0.66	0.66*	0.42	0.25	-0.08	0.19	6.76*	-1.50	1.13
MC6 x MC8	-2.83	-0.46	-0.21	-0.43	-1.38	-3.62*	-0.46*	-2.71	-0.11	-1.60
MC6 X MC10	0.17	-0.54	-0.28	0.17	0.42	-0.06	-0.16	1.17	0.74	0.86
MC6 X MC11	-3.58*	0.71	0.74*	-0.02	-0.14	0.76	0.05	0.50	2.42*	1.99*
MC6 X MC17	3.76*	-0.14	-0.10	0.28	0.54	2.38	0.42*	-0.69	0.16	-0.52
MC8 X MC10	-2.82	0.60	0.51	-0.41	-0.55	-1.50	0.18	-5.48	-2.39*	-1.45
MC8 X MC11	3.45*	1.16***	0.47	0.38	0.94	5.15**	-0.04	0.98	2.19*	1.07
MC8 X MC17	1.40	-0.19	0.78	0.39	0.84	4.16*	0.16	-1.15	1.50	0.94
MC10 X MC11	1.98	-0.37	-0.13	0.28	0.66	1.62	0.33	-0.73	0.90	1.23
MC10 X MC17	1.39	0.30	-0.40	0.57*	-1.96**	-3.39	0.20	-5.01	-0.46	-0.85
MC11 X MC17	-0.45	-0.77*	-0.81*	0.13	-0.29	-3.63*	0.20	2.60	0.69	-0.22

Genotypes	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
Reciprocals										
MC4 X MC1	3.03***	1.45***	-0.34*	0.36**	0.56	3.11***	0.04	-0.10	0.88	0.34
MC6 X MC1	-1.00	-1.45***	0.83***	-0.06	0.67*	-0.78	0.43***	-2.11	-2.03***	0.57
MC6 X MC4	-1.17	-0.47*	-0.33*	0.13	-0.22	-2.67**	-0.28**	-0.33	2.38***	2.65***
MC8 X MC1	2.92***	0.14	-0.34*	-0.36**	1.17**	-5.92***	-0.51***	-4.95**	-1.34*	1.04*
MC8 XMC4	1.09	-0.25	-0.11	-0.17	-0.78*	-5.00***	-0.67***	-4.31**	-2.17***	-1.57***
MC8 X MC6	-2.57*	-0.17	-0.06	0.25*	-0.06	0.39	-0.42***	-0.19	-0.19	0.30
MC10 X MC1	2.63***	0.01	1.03***	0.61***	1.11**	1.11	0.54***	-6.91***	-0.12	3.08***
MC10 X MC4	-2.76***	-1.72***	1.56***	0.17	0.75*	-4.56***	-0.35**	0.48	4.41***	5.92***
MC10 X MC6	0.36	-1.17***	1.17***	0.36**	0.05	1.61	0.29**	9.66***	0.74	2.20***
MC10 X MC8	0.61	-2.03***	1.67***	0.64***	0.94**	4.89***	0.00	8.74***	-1.63**	-2.48***
MC11 X MC1	2.89***	-0.45*	0.28	0.24	-0.36	2.56**	0.39***	6.62***	0.07	0.60
MC11 X MC4	-2.71***	-0.25	0.28	0.35**	0.27	4.39****	0.36***	3.80*	-3.17***	-0.30
MC11 X MC6	7.17***	-0.58**	0.67***	0.70***	0.89*	2.45*	0.36***	2.03	-1.95***	-0.68
MC11 X MC8	-0.77	1.25***	-0.33*	-0.17	0.06	-0.11	-0.44***	-2.36	-1.57**	-0.93*
MC11 X MC10	0.18	1.03***	-1.03***	-0.79***	-1.08**	-1.19	-0.64***	2.83	-0.03	-0.10
MC17 X MC1	-2.39**	0.39*	-0.61***	-0.31*	-0.73*	-5.67***	-0.03	0.24	-1.66**	-0.33
MC17 X MC4	-4.23***	1.17***	-1.45***	-0.42**	-0.53	-5.83***	-0.21*	-0.54	0.19	0.63
MC17 X MC6	-2.89***	-0.06	-0.00	-0.19	0.72*	-2.22*	-0.33**	-3.33*	-0.80	0.83*
MC17 X MC8	1.00	0.06	-0.22	0.06	-0.22	-2.80	-0.09	-3.88*	-0.25	-0.07
MC17 X MC10	-0.01	0.85***	-0.14	-0.36**	3.39***	2.39*	-0.22*	0.92	-2.20***	-4.25***
MC17 X MC11	1.56*	0.00	-0.11	-0.11	0.72*	2.17*	-0.17	2.53	-0.20	0.19

Abbreviations: PH, plant height (cm); TN, number of productive tiller number per plant; PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; KPS, number of kernels per spike; HSW, hundred seed weight (g/100 seed); HI, harvest index; AGB, above-ground dry biomass weight ($t.ha^{-1}$); GY, grain yield ($t.ha^{-1}$); *,**,***, denote significance differences at $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively.

Table 5.8: Estimates of general combining ability effects of parents and specific combining ability effects of crosses for yield and yield components of bread wheat from a 7 x 7 full diallel evaluated with Si.

Genotypes	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
Parents										
MC1	-0.29	1.42	0.26	1.36	-0.13	0.37	0.08	-1.67	0.03	-0.34
MC4	-0.73	1.57	0.51**	-0.43	-0.04	-0.41	0.09	-0.97	0.41	-0.15
MC6	0.95	-0.51	-0.10	-0.84	-0.23	-1.37	-0.28**	1.42	-0.36	-0.16
MC8	-2.66***	-0.51	-0.14	0.86	0.55**	5.12***	-0.13	4.56*	0.20	0.52
MC10	-1.43*	-0.38	0.03	-0.21	-0.13	-3.31**	0.23*	-0.37	0.04	-0.19
MC11	4.45***	-0.45	-0.07	-0.32	-0.16	-1.81	-0.02	-0.71	-0.84	-0.76
MC17	-0.30	1.13	-0.48*	-0.42	0.13	1.42	0.02	-2.27	0.52	1.07**
Direct Crosses										
MC1 X MC4	0.53	6.60***	-0.55	-0.78	0.71	1.05	0.17	-2.27	0.66	1.05
MC1 X MC6	-4.02***	-1.01	-0.94*	-1.62	0.07	-5.16*	0.12	1.67	0.04	0.18
MC1 X MC8	3.66***	-0.95	0.27	7.27***	-0.49	-0.64	0.36	2.80	0.82	1.03
MC1 X MC10	1.09	-0.70	0.26	-0.51	0.38	4.17	0.04	6.13	-1.26	-0.73
MC1 X MC11	2.08	-2.07	-0.69	-1.49	-0.40	-2.19	0.08	0.08	-1.34	0.81
MC1 X MC17	-0.79	-0.22	0.83*	-0.67	-0.23	2.94	-0.48*	-3.64	-1.05	-0.05
MC4 XMC6	3.97***	-1.88	-0.57	0.39	-0.50	1.29	-0.34	-1.38	-1.96	-0.85
MC4 X MC8	2.43*	-0.43	0.63	-0.86	-0.03	-0.20	0.33	4.99	1.88	1.57*
MC4 X MC10	1.16	-0.65	0.24	0.31	0.21	-4.94*	-0.06	4.11	-0.28	0.50
MC4 X MC11	-2.04	-0.66	-0.27	0.26	-0.27	-0.10	-0.05	4.68	0.74	0.57
MC4 X MC17	1.02	-0.93	-0.13	0.81	0.54	-0.84	0.18	-0.78	0.05	0.11
MC6 x MC8	-2.67*	-0.25	-0.53	-1.27	-0.28	-5.24*	-0.23	0.20	-0.76	-0.17
MC6 X MC10	-1.43	0.60	0.29	0.23	-0.07	-1.03	0.42*	7.63*	1.91	2.68***
MC6 X MC11	0.47	1.69	1.56***	0.74	0.29	3.36	-0.02	0.48	1.34	0.21
MC6 X MC17	2.22*	0.21	-0.25	0.67	0.09	1.93	0.15	-0.22	-1.38	-0.63
MC8 X MC10	1.74	0.82	0.50	-0.71	-0.27	4.26*	-0.01	-6.07	1.65	0.00
MC8 X MC11	-3.26**	0.80	-0.51	-1.14	-0.21	-3.02	-0.27	-4.22	-1.91	-2.48***
MC8 X MC17	2.83*	-0.41	-0.76*	-1.59	0.56	3.63	-0.10	-0.44	-0.19	-1.08
MC10 X MC11	0.55	0.45	0.26	0.66	0.27	2.24	0.44*	1.76	0.88	0.57
MC10 X MC17	-3.70**	-0.24	-0.94*	0.54	-0.71	-3.77	-0.21	-3.62	-1.10	0.23
MC11 X MC17	2.51*	0.15	0.17	0.56	-0.26	-1.27	0.17	1.07	0.94	0.05

Genotypes	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
Reciprocals										
MC4 X MC1	-3.22***	10.85***	0.78***	0.42	-0.06	2.22*	-0.17	2.10	1.02	0.05
MC6 X MC1	0.18	-1.05	0.22	-0.05	-0.44*	1.17	-0.42***	-4.91**	0.08	-0.07
MC6 X MC4	-5.21***	0.00	0.17	-0.50	0.31	-0.28	0.08	-1.49	-0.42	0.13
MC8 X MC1	3.25***	-0.78	-0.50**	10.31***	-0.33	0.94	0.47***	0.65	-2.50***	-1.45***
MC8 X MC4	-2.75***	-1.11	-0.78***	-0.50	-0.56**	-2.61*	-0.04	-1.05	2.28***	1.98***
MC8 X MC6	2.17**	-0.11	-0.22	-0.60	-0.22	-5.50***	0.03	5.45**	-0.07	0.18
MC10 X MC1	-1.75**	0.26	-0.11	0.15	-0.75***	3.33**	-0.33***	1.23	-0.37	0.68
MC10 X MC4	-2.85***	-1.58	-1.11***	0.35	1.00***	6.11***	0.08	3.93*	1.97***	1.01*
MC10 X MC6	-3.86***	-1.31	-1.11***	-0.61	0.64**	-0.39	-0.14	-11.57***	-1.12*	-1.47***
MC10 X MC8	-1.20*	-1.64	-1.39***	-0.20	0.33	2.94**	-0.08	-6.49***	-0.08	0.97*
MC11 X MC1	1.06*	-0.06	-0.06	-0.08	-0.28	-3.03**	-0.014	-0.22	-0.57	0.25
MC11 X MC4	-3.46***	-0.78	-0.39*	-0.56	-0.94***	-4.33***	-0.15	-0.07	-3.03***	-0.87*
MC11 X MC6	-0.42	1.00	1.06***	0.24	-0.03	-0.06	0.07	2.53	2.41***	0.70
MC11 X MC8	5.60***	1.22	0.39*	0.00	-0.64**	-3.50**	0.86***	7.21***	2.23***	1.97***
MC11 X MC10	4.95***	0.78	0.89***	0.45	0.61**	1.89	0.36***	0.34	0.60	-0.84*
MC17 X MC1	1.33*	-0.34	0.28	-0.42	-0.72***	0.83	-0.11	0.68	-1.88**	-0.33
MC17 X MC4	2.85***	0.56	0.89***	-0.06	-0.08	-4.28***	-0.54***	-2.50	-1.17*	-1.83***
MC17 X MC6	-2.25***	-0.06	-0.05	-0.21	0.50*	-1.58	0.11	0.87	-0.30	-1.03*
MC17 X MC8	3.75***	0.00	-0.06	-1.78*	-0.31	-3.06**	-0.46***	3.21	-2.22***	-1.85***
MC17 X MC10	3.72***	-0.30	-0.06	-0.50	-1.08***	-4.11***	0.47***	8.86***	0.08	-0.02
MC17 X MC11	-0.08	0.72	-0.39*	0.03	0.00	-3.00**	0.33***	0.37	0.33	1.40***

Abbreviations: PH, plant height (cm); TN, number of productive tiller number per plant; PS, productive spike number per plant; SL, spike length (cm); SPS, number of spikelets per spike; KPS, number of kernels per spike; HSW, hundred seed weight (g/100 seed); HI, harvest index; AGB, above-ground dry biomass weight ($t.ha^{-1}$); GY, grain yield ($t.ha^{-1}$); *,**,***, denote significance differences at $p < 0.05$, $p < 0.01$, $p < 0.001$, respectively.

5.3.5 Genetic Effects and Heritability of Yield and Yield Components in Bread Wheat under Si Application

The additive and dominant genetic effects, genotypic, phenotypic and environmental variances and heritability of yield and yield components of bread wheat under Si application are shown in Table 5.9. Higher additive genetic effects were recorded for PH (7.90), TN (1.30), SL (0.26), SPS (0.09), KPS (12.00), HI (4.77), AGB (-0.11) and GY (0.23) with Si, compared untreated control. Whereas the dominant genetic effects were significantly higher for PS (0.34) and SPS (-0.00) with Si application. The genotypic variance (σ^2_g) for the assessed agronomic traits had marked differences with Si application than without Si application. Low genotypic variances were computed for TN (2.14), KPS (18.58), HSW (0.12), AGB (0.91) and GY (1.73) with Si application compared to without Si. Similarly, the phenotypic variance (σ^2_p) was low with Si application for PH (30.69), TN (26.27), SPS (1.28), HSW (0.39), AGB (10.49) and GY (6.43) compared to without Si. The environmental variance (σ^2_e) had low values with Si application for PH (9.64); TN (24.12), SPS (1.09), HSW (0.27) and GY (4.71) compared to without Si application. The broad-sense heritability (H^2) with Si application were higher for PH (0.69), TN (0.08) and SPS (0.15) compared to without Si application. Medium to high H^2 values were noted without Si application for PS (0.41), KPS (0.50), AGB (0.24) and GY (0.47). Both additive and dominant genetic effects varied with and without Si application.

Table 5.9: Summary of additive and dominant genetic effects and broad-sense heritability values for yield and yield components of bread wheat, with (+Si) and without (-Si) Si application.

Parameters	PH	TN	PS	SL	SPS	KPS	HSW	HI	AGB	GY
-Si										
σ^2A	5.89	0.24	0.17	0.05	-0.09	2.59	0.03	-0.33	-0.45	0.18
σ^2D	8.01	0.24	0.09	0.17	-0.04	15.39	0.08	8.41	1.33	1.77
σ^2_g	14.32	2.44	0.58	0.26	0.17	23.78	0.17	0.00	9.16	4.79
σ^2_p	75.15	86.05	1.44	0.75	3.96	47.96	0.49	0.01	10.50	10.22
σ^2_e	60.83	83.61	0.86	0.49	3.79	24.19	0.32	0.008	7.94	5.43
H^2	0.19	0.03	0.41	0.34	0.04	0.50	0.35	0.12	0.24	0.47
+Si										
σ^2A	7.90	1.30	0.07	0.26	0.09	12.00	0.03	4.77	-0.11	0.23
σ^2D	7.35	-1.01	0.34	-0.84	-0.00	4.90	0.04	5.05	0.38	1.13
σ^2_g	21.05	2.14	0.63	0.38	0.20	18.58	0.12	0.00	0.91	1.73
σ^2_p	30.69	26.27	1.66	25.72	1.28	53.97	0.39	0.01	10.49	6.43
σ^2_e	9.64	24.12	1.03	25.34	1.09	35.39	0.27	0.01	9.58	4.71
H^2	0.69	0.08	0.38	0.01	0.15	0.34	0.32	0.11	0.09	0.27

Abbreviations: -Si: without Si; +Si: with Si; σ^2A: additive genetic effect; σ^2D: dominant genetic effect; σ^2_g: genotypic variance; σ^2_p: phenotypic variance; σ^2_e: environmental variance; H^2: broad sense heritability; PH: plant height (cm); TN: number of productive tiller number; PS: number of productive spike number; SL: spike length (cm); SPS: spikelet per spike; KPS: kernels per spike; HSW: hundred seed weight (g/100 seed); HI: harvest index; AGB: aboveground biomass dry weight per plant ($t.ha^{-1}$); GY: grain yield ($t.ha^{-1}$).

5.4 Discussion

Genetic variability is critical to enhance selection gains and ultimately improve crop yields (Chiipanthenga et al., 2021). Selection response depends on the genetic diversity and complementarity of parental lines involved in the crosses, as well as the combining ability and adaptability of the derived progenies. Silicon (Si) is a quasi-essential nutrient (Manivannan et al., 2023), enhancing cell wall integrity, which improves the resilience of wheat to biotic and abiotic stresses. The significance of Si in improving agronomic traits under both biotic and abiotic stresses in wheat is recognized. However, the combining ability and mode of gene action of yield and yield components under Si fertilisation have not been widely studied. Aurangzaib et al. (2022) reported that Si application improved KPS, AGB and GY, amongst other traits.

In the present study, a highly significant genotype x treatment interaction was recorded for KPS, AGB and GY (Table 5.3), indicating that these traits are crucial for the selection of Si-use efficiency for grain yield and quality. Yield and yield component performance are used to assess genetic variability as part of standard breeding practices. Studies by Ul-Rehman et al. (2022), Yang et al. (2022) and Wu et al. (2006) reported genotypic and phenotypic variation with Si application in wheat . The current study found significant genotype and Si treatment interaction for PH, PS, SPS, KPS, HSW, AGB and GY (Table 5.3). Also, marked genetic variation were recorded amongst the parental lines, direct and reciprocal crosses, which can be exploited for Si-use efficiency breeding in wheat.

In the current study, Si application improved the agronomic trait performance of parents, crosses and reciprocal crosses compared to without Si application (Tables 5.4 and 5.5). PH increased with Si application. However, tall PH is not desirable in wheat breeding for enhanced HI and lodging tolerance. When Si is taken up by plants and deposited into the plant cell wall structures it leads to improved mechanical and structural strength benefiting tall genotypes (Chang et al., 2023). Dorairaj et al. (2020) found that Si application increased lignin content, which improved the hardness, stiffness and brittleness of rice plant stems, thereby decreasing lodging. Si application upregulates genes involved in lignin biosynthesis, leading to increased lignin accumulation and enhanced culm strength (Hussain et al., 2021).

The higher mean yield performance by some direct and reciprocal crosses, with and without Si application (Tables 5.4 and 5.5) indicates possible genetic gain through Si-use efficiency. The mean performance with Si application was higher than without Si, across all agronomic traits tested. This suggests that genetic gain can be realised with increased Si application. Si uptake has been widely linked with improved nutrient uptake, and could attribute to genetic gain (Vatanserver et al., 2017). Direct crosses such as MC1 x MC4, MC4 x MC8 and reciprocal crosses MC17 x MC10 showed higher grain yields without Si application than the parental means. Hence, progenies from these crosses are valuable

transgressive selection. This high relative performance in F1 direct and reciprocal crosses compared to their parents indicates dominance gene actions without Si application. Whereas with Si application, the crosses MC1 x MC4 and MC8 x MC10 and reciprocal crosses MC4 x MC1, MC17 x MC4 and MC17 x MC8 had higher yields than their respective crosses and parentals without Si application. The results imply that the Si application generates an additive gene effect. Jackson et al. (2019) found that additive gene effects contributed more than non-additive effects to the inheritance of Si uptake.

PH, TN, SL, KPS, HSW and GY had significant mean squares for GCA and SCA effects (Table 5.6), without Si application. Similarly, PH, PS, KPS, HSW and GY had significant mean squares for both GCA and SCA effects with Si application (Table 5.6). The GCA mean squares in this study were much higher than the SCA mean squares for PH, TN, PS, SL, KPS and HSW, without Si and PH, TN, PS, SPS, KPS, HSW and HI, with Si. These increases indicate a preponderance of additive gene action affecting the inheritance of the traits mentioned above (Agaba et al., 2017). Yield traits in the F1 are generally biased towards parents with high GCA (Song et al., 2013). The magnitude of the SCA variance compared to the GCA was higher for SPS, HI and AGB, without Si application and only for AGB, with Si application. This indicates a preponderance of dominance and epistatic gene action in the inheritance (Keerthiraj et al., 2021b).

Jia et al. (2022) reported that maternal effects had a marked impact on grain development in wheat hybrids, without Si. Without Si application, the maternal effects were significant for PH, TN, PS, SL, KPS, HSW, and GY. (Table 5.6). In the current study, the maternal effects were significant for PH, PS and KPS with Si application. Research on the effect of Si on maternal effects of wheat on yield and yield components are limited. Wulff et al. (1994) opined that in some instances poor nutritional and environmental conditions in the maternal environment affect progeny trait performance. This is further supported by Naegle et al. (2005), who found seed nutritional content affects the seedling's ability to develop and recover under poor nutritional conditions. Seed development reportedly relies on the contribution by the maternal parent, often linked with mobilization of nutrient resources, hormones and proteins (Donohue, 2009). Silicon application has been shown to improve plant nutrient uptake (Miroshnychenko et al., 2023), hormone production and signalling (Kim et al., 2015), and increases seed germination (El Moukhtari et al., 2023), therefore positively affecting maternal effects. In the current study, the maternal effects mean squares for the PH, TN, PS, SL and HI were higher with Si application, whilst the traits SPS, HI, AGB and GY were lower, compared to the without Si application. Maternal effects are considered to be a transgenerational version of phenotypic plasticity (Vivas et al., 2020). Si application has been shown to improve agronomic trait performance and, to an extent, phenotypic plasticity (Christian et al., 2023). Therefore, it can be deduced that Si has a role in maternal effects, and the degree of the effect is subject to further investigation.

Large GCA/SCA ratio demonstrates the importance of additive genetic effects (Table 5.6), whilst the lower ratio indicate the predominance of dominance and/or epistatic gene effects (Fasahat et al., 2016). In the current study, the GCA/SCA ratio indicated that the additive gene effects were lower except for SPS (0.70 - without Si) and KPS (0.77 - with Si). The negative GCA/SCA ratio for SPS with Si (-6.54), indicated higher contribution of non-additive genetic effects conditioning trait inheritance corroborating with Dholariya et al. (2014).

Both with and without Si application had varying GCA and SCA effects (Tables 5.7 and 5.8). For both treatments, the number of significant reciprocal crosses were higher than the direct crosses. Several reciprocals with Si application had significant SCAs for PH and GY, in a desirable direction. Depending on the genotypes involved, the reciprocal effect can be either positive, negative or statistically non-significant (Kovačević et al., 2022).

The genotypic variance was low with Si application for most assessed agronomic traits (Table 5.9). Reportedly, Si application improved agronomic trait associations, and higher clustering of genotypes was attained under stress compared to non-stress conditions (Christian et al., 2023). The broad sense heritability of assessed agronomic traits varied. Higher heritability (0.69) was recorded for PH, with Si application. Keerthiraj et al. (2021a) reported high heritability for PH, TN, panicles per plant, panicle weight, seeds per panicle, test weight, seed yield per plant and silicon content percentage amongst other tested traits. The study also found high estimates for genetic advance for traits such as: internodal length, culm wall thickness, lodging percentage, silicon and potassium content; all traits effective for improving lodging resistance. Higher additive genetic effects were computed for PH, KPS with Si application. Si is reportedly associated with increased nutrient uptake (Alharbi et al., 2024). Hence, it is plausible that it would have a more significant effect on secondary agronomic traits than yield. The current study showed low genetic and phenotypic variance and broad sense heritability even with Si application. Shamuyarira et al. (2023) also found low broad-sense heritability for bread wheat populations under drought-stress and non-stress conditions. The magnitude of the Si effect has been attributed to stress instead of non-stress conditions (Christian et al., 2023). This indicates that the low heritability, genetic and phenotypic variance in the current study could be attributed to the limited Si effect under non-stress conditions.

Si has a multipronged role to improving stress tolerance through plant structural and nutrient uptake mechanisms. The effect of Si uptake is influenced by stress factors, Si formulation and concentration (Christian et al., 2022). A recent study by Huang et al. (2025), found that Si utilizes both symplastic and apoplastic pathways for Si uptake and distribution. This indicates that Si response is multigenetic (i.e. it involves other plant genes) for effective uptake and mitigation of biotic and abiotic stresses (Khan et al., 2023). This can also explain its low heritability and its low contribution to

improving the phenotypic plasticity for yield and yield components compared to genotypes without Si application (Klotz et al., 2022).The mechanism of heritability of Si genes is yet to be fully understood.

5.5 Conclusion

In conclusion, the current study found variable Si-use response of GY among parents, direct and reciprocal crosses under Si application. Si application improves all agronomic trait performance compared to the control. The following direct and reciprocal crosses: MC6 x MC4; MC6 x MC8; MC6 x MC10; MC8 x MC4; MC8 x MC6; MC10 x MC6; MC10 x MC17 and MC17 X MC4 had increased GY. The identified crosses together with Si application provide a new opportunity for integrated management of drought and to enhance agronomic traits in wheat breeding programs. Yield-related traits, including TN, PS, HSW and KPS, were improved with Si application across direct crosses and reciprocal crosses. The families are selected for genetic advancement and variety development. Overall, the Si application favourably complemented the additive gene effect on yield and yield-related traits of direct and reciprocal crosses. Further research is required to examine the accumulation of maximum favourable additive genes in advanced generations of wheat through field evaluations of the breeding populations under Si application.

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Overview of the Research Findings

Introduction and Objectives of the Study

Bread wheat (*Triticum aestivum* L., 2n = 6x = 42, AABBDD) is an economically vital global commodity crop serving diverse value chains. Drought stress severely affects wheat yield and quality. Recurrent drought together with erratic rainfall due to climate change impede sustainable wheat production. Ideotype wheat breeding depends on selecting vital agronomic traits under optimal and drought-stress conditions. Si application has shown to affect agronomic performance and improve wheat yields under DS conditions. Due to its ability to be taken up via genes and water channels, Si can easily be transported throughout the plant, improving both plant mechanics and structures. The level of Si accumulation is highly dependent on species, genotype and Si formulation. Also, Si uptake has been linked with alleviation of many macro and micronutrient deficiencies, leading to improved plant growth, development and end-use quality. Si applications combined with drought stress have shown variation in trait associations. Identification of parents and progenies which are capable of Si-use efficiency are integral to developing new varieties which have the potential to be high yielding but also improve grain quality. Thus, bridging the negatively correlated and highly economically important traits of grain yield and grain quality.

This chapter summarizes the research objectives and findings of this study and identifies areas for future research. The specific objectives of this study were:

i. to evaluate the effects of different Si fertiliser formulations on the agronomic performance of diverse wheat genotypes under drought-stressed conditions.

ii. to examine the impact of Si fertilisation on agronomic performance and trait associations in wheat under drought stress to identify selection criteria for improving drought tolerance and Si response.

iii. to evaluate the effects of two Si fertiliser formulations on the compositions of wheat grain carbon (C), nitrogen (N), sulfur (S) and protein content (GPC) under drought-stress and non-stressed conditions to enhance grain yield and end-use quality.

iv. to assess the genetic determinants of yield and yield components in newly developed wheat populations under Si fertilisation to guide breeding and select desirable parents and progenies for variety development.

Research Findings in Brief

The effect of silicon fertilisers on agronomic performance of bread wheat under drought stress and non-stress conditions.

Twenty diverse wheat genotypes which were subjected to drought stressed and non-stressed conditions and treated with a control, liquid silicon and a granular silicon formulation, were used in this study. The genotypes were evaluated across three environments, two greenhouse and one field trial using a randomized complete block design with three replications. The main findings were:

- Significant ($p < 0.05$) four-way interactions for genotype x environment x water regime x silicon treatment for aboveground biomass, productive spike number, hundred seed weight and grain yield.
- Granular silicon treatment was the most effective compared to the liquid silicon and control, with genotype MC18 producing a yield of 4.17t.ha^{-1} under field and drought conditions.
- Granular silicon treatment positively affected drought stress tolerance indices compared to the liquid silicon and control treatments.
- Silicon application reduced genotypic variation and enhanced agronomic trait performance, particularly under drought stressed conditions.
- Granular silicon application enhanced wheat yields under both drought and non-stressed conditions.

Association of yield and yield components among selected bread wheat genotypes under silicon fertilisation and drought conditions.

Twenty wheat genotypes were evaluated, involving two water regimes and two Si fertiliser formulations in three environments, using a factorial experiment laid out in a randomised complete block design with three replications. The study examined the influence of silicon fertilisers on the agronomic performance and trait associations to identify selection criteria for improving silicon efficacy and drought tolerance.

The major findings were as follows:

- Grain yield was positively associated with hundred seed weight for liquid Si ($r = 0.74$, $p < 0.001$) and granular Si ($r = 0.69$, $p < 0.001$), under non-stress conditions.

- Under drought stressed conditions, strong trait correlations were noted between productive tiller number and productive spike number for the untreated control (r = 0.98, p < 0.001), liquid silicon (r = 1.00, p < 0.001) and granular silicon (r = 0.99, p < 0.001).
- Granular silicon had higher direct effects on grain yield with HSW (0.84) and PS (0.64), under DS conditions whilst under NS conditions, the aboveground biomass had the highest indirect effect on grain yield.
- Principal traits TN, PS and HSW contribute to enhanced grain yield for selection of Si use-efficient breeding lines under DS.
- The agronomic performance was elevated for both liquid silicon and granular silicon formulations and under drought stressed and non-stressed conditions.

Influence of silicon fertilisers on the compositions of wheat grain carbon, nitrogen, sulfur and protein under drought-stressed and non-stressed conditions.

Twenty preliminary selected bread wheat genotypes were evaluated for their grain contents of C%, N%, S% and GPC% under drought-stressed (DS) and non-stressed (NS) conditions with liquid and granular potassium silicate formulations. The genotypes were profiled for the effects of two Si fertiliser formulations on the grain compositions of carbon (C), nitrogen (N), sulfur (S) and protein content (GPC) under drought-stress and non-stressed conditions to enhance grain yield and end-use quality. The major findings were as follows:

- Both granular Si and liquid Si enhanced to grain C, N, GPC and Si content, particularly under DS conditions.
- The genotype x water regime x environment interaction was significant for N% and GPC% whilst the genotype x water regime x silicon formulation effect was significant ($p<0.001$) for Si content.
- The highest C% was for genotypes MC17 (41.17%) treated with granular Si under DS conditions, and MC14 (42.19%) under NS conditions.
- Granular Si generated the highest grain N% and GPC for genotype MC5 under DS conditions.
- Overall, granular Si positively influences grain C%, N%, GPC and Si compositions under DS conditions. This infers that Si application can improve both grain quality and drought stress tolerance.

Combining ability of bread wheat (*Triticum aestivum* L.) genotypes for yield and related traits with silicon fertilisation.

This study examined the magnitude of genetic determinants of yield and yield components in newly developed wheat populations under granular Si fertilisation to select desirable parents and progenies for variety development and guide breeding. Seven wheat parents were selected based on yield and drought tolerance and were crossed using a full diallel mating design. Forty-two full-sibs were generated and appraised along the parents under controlled environment conditions, without and with granular Si application for selection, breeding and variety development. The research findings are as follows:

- The genotype x Si treatment interaction was significant ($P < 0.05$) for KPS, AGB and GY. The general combining ability for PH, PS, SPS, KPS, HSW, HI and GY were significantly improved with granular Si application. Genotypes with high GCA effects include: MC17 at 1.07 for GY, MC4 for PS (0.51), MC8 for KPS (5.12), SPS (0.55) and HI (4.56).
- The specific combining ability was enhanced with granular Si application for PH, PS, KPS, HSW and GY. High SCA effects were noted for GY for direct crosses MC4 x MC8 (1.57) and MC6 x MC10 (2.68).
- Direct crosses with all traits improved included MC1 x MC6, MC1 x MC10, MC1 x MC11, MC4 x MC6, MC4 x MC11, MC6 x MC11 and MC8 x MC10 whilst reciprocal crosses MC4 x MC1; MC8 x MC6; MC17 x MC1; MC17 x MC4; MC17 x MC6; MC17 x MC8 and MC17 x MC11 had comparable outcomes for the same traits with Si application. These families are selected for genetic advancement and variety development for Si use-efficiency breeding.
- Generally, the Si application favourably complemented the additive gene effect on yield and yield-related traits of direct and reciprocal crosses.

Implications of the Study to Breed for Silicon-Use Efficiency Wheat for Drought Tolerance and Grain Quality.

- This study showed silicon application improved drought stress tolerance indices, reduced variation in agronomic traits, and strengthened relationships between traits under drought conditions. Overall, the use of silicon fertilisation and selection for Si use-efficient genotypes is a promising strategy to mitigate the negative effects of drought stress on wheat production.
- Si application influences agronomic trait responses and enhances drought tolerance in wheat. Agronomic traits HSW, PS and TN were identified as the most important contributing traits for improving wheat grain yield and drought tolerance with Si application. Si fertilisation had

considerable direct and indirect effects on the agronomic trait performance of wheat, particularly under DS conditions, which are useful for selection programmes in breeding.

- The study found that Granular Si application positively influences grain C%, N%, NPC and Si uptake particularly under DS conditions. Genotypic variation is noted in the effectiveness of Si application on grain nutrient composition. Grain composition ultimately affects dough rheological properties. Further research into the full impact of Si fertilisers on the dough rheological properties is necessary for future selection in breeding programmes.

- Si application favourably complemented the additive gene effect on yield and yield-related traits of direct and reciprocal crosses. The study found that several families and progenies have been identified to improve agronomic trait performance with Si application. However, the effect of Si under NS is muted in comparison to under DS conditions. Further research is required to examine the accumulation of most favourable additive genes in advanced generations of wheat through field evaluations of the breeding populations under Si application, and particularly under DS conditions.