

Chapter

Selection of Wheat (*Triticum Aestivum*) Genotypes to Improve Water Use Efficiency for Grain, Biomass Yield, and Carbon Sequestration

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Abstract

Plants can sequester carbon, thereby mitigating climate change and improving soil fertility. Studies have focused on plant carbon (C) storage or on water use efficiency (WUE) for grain and biomass production, while variations between genotypes have been ignored. The objective of this study was to compare WUE for grain yield (GY), plant biomass (PB), and plant carbon stocks (PCs) of selected wheat genotypes under different water regimes. This was done under field and greenhouse conditions using 100 wheat genotypes from CIMMYT, grown at 25% (water-stressed) and 75% (non-stressed) field capacity in an alpha lattice design. Treatments were replicated twice in the field and three times in the glasshouse. Results showed average wheat GY of 326 to 2062 gm^{-2} , shoot biomass of 1873 to 3726 gm^{-2} while average PB was 2992 to 6289 gm^{-2} . Grain carbon stocks averaged 132 and 167 g C m^{-2} in the glasshouse under stressed and non-stressed conditions respectively. The total PC_s ranged from 691 to 3093 gm^{-2} in the glasshouse, and 835 to 4016 gm^{-2} in the field. WUE for grain yield production (WUE-GY) ranged from 0.12 to 2.10 $\text{gm}^{-2}\text{mm}^{-1}$ in the glasshouse, while it was 0.57 to 4.01 $\text{gm}^{-2}\text{mm}^{-1}$ in the field under stress. Varietal performance also varied with LM75 having higher WUE-GY under stress while LM48 and LM47 had lower WUE-GY under non-stressed conditions. LM75 and BW162 were ranked best for WUE- PC_s , while BW162 was best for WUE-root C stocks under water-stress. Variability in storing C under different water availability thus existed among wheat genotypes.

Keywords: agronomic traits, root to shoot ratio, water use efficiency, carbon stocks, wheat genotypes

1. Introduction

The global climate is changing because of natural as well as anthropogenic activities [1]. This causes long-term alterations in temperature and precipitation.

Natural processes, such as solar radiance variations, result in fluctuations in the climate [2]. While anthropogenic activities, e.g., deforestation, agriculture, and others, contribute to carbon dioxide (CO₂) emissions, which result in climate fluctuations since it is considered the primary cause of global warming [3]. According to [4], future projections predict a continual rise in atmospheric carbon dioxide concentration, with the Northern Hemisphere levels expected to reach 450 ppm by 2032, while it will be 438 ppm in the Southern Hemisphere. This continued rise in atmospheric greenhouse gases has caused the average global surface air temperature to rise by just below 1 degree celsius over the past 100 years [3].

According to [5], in South Africa, agriculture is the most vulnerable sector to climate change, since it is affected by a number of factors, including rainfall patterns, temperature, water availability, and evapotranspiration. Carbon dioxide is regarded as the driving force for climate change. However, its direct effect on plants is mostly positive [6], so they could be a potential sink for CO₂. The abundance of CO₂ in the atmosphere can increase photosynthesis in plants [7]. Crops that exhibit positive responses to enhanced CO₂ are characterized as C3 plants [8]. Thus, increased atmospheric CO₂ decreases transpiration in C3 plants as they partially close their stomata, thereby minimizing plant water loss [9]. Wheat, a C3 crop, is the third most produced cereal after maize and rice in the world [10]. In South Africa, it is the second most important grain after maize and is consumed as bread, cakes, cookies, livestock feed, and alcoholic beverages [11]. The South Africa 2022/23 season's wheat production of 2,110,000 tons, which was 8% lower than the previous season but the fourth largest of the last 20 years, was produced on a total area of 566,800 hectares, with an average yield of 3.72 t ha⁻¹ [12]. This decline has been associated with low and unevenly distributed rainfall patterns in South Africa, with an annual average rainfall of 450 mm, which is far below the world's average of 860 mm per year [13]. The decline in wheat production could also be a result of SOC depletion, characteristic of most South African soils [14]. Soil with less organic matter supports poor crop yields as it holds fewer nutrients and is more susceptible to drought [15].

Many studies have focused on the effect of moisture stress on wheat grain yield and measures for improving its WUE [16, 17]. It was found that moisture stress during spike emergence and anthesis reduced wheat grain yield by about 20% through the reduction of individual grain weight [18]. It was also reported that water stress negatively impacted morphological traits of wheat during heading, anthesis, and grain filling. However, conservation practices such as no-till and mulching may increase water storage and wheat yields, enhancing its WUE [19]. Meanwhile, [20] observed that the WUE of wheat grain yield was increased from 9.7 to 11.0 kg ha⁻¹ mm⁻¹ by supplementary irrigation. Studies focusing on WUE for plant carbon stocks production, in order to select crops that are water-use efficient and can sequester more C into the soil, are lacking.

Agricultural soils have significant potential to sequester soil organic carbon (SOC), thereby mitigating climate uncertainties [21]. The actual amount of carbon sequestered depends on management strategies such as residue retention and environmental conditions [22]. Carbon is added to the soil by plants through photosynthesis. This plant carbon then enters the SOC pool through decaying plant litter and/or roots, as well as through root exudates. Different crops exhibit varying abilities for storing carbon in their tissues. According to [23], grasses showed the highest total plant carbon stocks (6.80 ± 0.5 Mg ha⁻¹ yr⁻¹), followed

by maize ($6.30 \pm 0.34 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$), cotton ($4.3 \pm 0.47 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$) and soybean ($3.00 \pm 0.48 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$). Variation in carbon sequestration among crop cultivars also exists. Since wheat is a C3 plant, it has the potential to adapt to increased atmospheric CO₂ and limited water availability. It is also an important crop for South Africa's economy. Therefore, there is a need to select wheat genotypes that produce high plant carbon stocks with less water supply. Thus, this study aimed to select wheat genotypes for improved water use efficiency for grain, biomass yield production, and plant carbon sequestration.

2. Materials and methods

2.1 Plant materials

One hundred genotypes, consisting of 97 drought and heat-tolerant wheat accessions, as well as 2 commercial wheat varieties from France and Triticale, were evaluated. The drought and heat-tolerant genotypes were obtained from CIMMYT. These were used due to their genetic variability in rooting abilities and breeding history for drought tolerance. The French varieties and Triticale were used as comparative controls because they are known for their high rooting capacities. These are winter wheat genotypes with twice the rooting capacity of wheat grown in warmer winters [24], while Triticale has an aggressive root system inherited from rye (*Secale cereale*) [25].

2.2 Growing conditions and trial management

2.2.1 Field experiment

The field experiment was carried out from May to September 2017 at the University of KwaZulu-Natal's Ukulinga Research Farm (LAT: 29.667°, LONG: 30.406°, and ALT: 811 m) using a 10*10 alpha lattice design with two replications. Long-term average temperature and rainfall for Ukulinga are 18°C and 738 mm, respectively. The average temperature during the growing period and soil properties are given in **Table 1**. The field was plowed to a depth of 30 cm, and custom-made plastic mulch was used to exclude rainwater. Three seeds were planted per station at 10 cm intra-row spacing and 30 cm between rows soon after plowing. Each row consisted of 10 genotypes and was treated as an incomplete block. Basal fertilizer was applied at a rate of 120:30:30 kg ha⁻¹ (N:P: K). Other agronomic practices were as per normal wheat production practices in South Africa [11]. Irrigation was applied through drip irrigation to maintain soil water content at 75% field capacity (FC) in the well-watered regime. Under the drought stress treatment, irrigation was withheld 5 weeks after crop emergence until just before signs of wilting were observed, upon which irrigation was reinstated to 25% FC. The level of soil moisture was monitored with hand held digital moisture probes. During the experiment, irrigation was withheld before anthesis to induce drought stress in a way that simulated *in situ* wheat production under field conditions. Due to greater variations among the 100 wheat genotypes, the best 10 genotypes in terms of biomass were selected for the greenhouse experiment.

Property	Greenhouse experiment	Field experiment
Bulk density (g cm^{-3})	0.99	1.04
Phosphorous (mg/L)	29.00	39.00
Potassium (mg/L)	412.00	241.00
Calcium (mg/L)	1386.00	1453.00
Magnesium (mg/L)	504.00	369.00
Electrical Conductivity (cmol/L)	12.24	11.02
pH (KCl)	5.31	4.56
Organic carbon (%)	3.40	2.60
Nitrogen (%)	0.29	0.23
Clay (%)	33.00	28.00
Mean Temperature ($^{\circ}\text{C}$)	20.13	16.63

pH (KCl) is the pH measured in potassium chloride.

Table 1.

Soil properties and mean temperatures for the two environments used in the study.

2.2.2 Greenhouse experiment

A greenhouse experiment was carried out from January to May 2018 at the Controlled Environment Facility of the University of KwaZulu Natal, Pietermaritzburg Campus. This was conducted using a 10×10 alpha lattice design with three replications. Ten seeds were sown in each pot containing soil collected at Ukulinga (properties presented in **Table 1**) and thinned to eight plants per pot three weeks after emergence. Ten pots were allocated per incomplete block, and genotypes were randomly assigned to pots to minimize experimental error. The amount of water required was added manually using a watering can. Fertilizer was applied at a rate of 300 kg N ha^{-1} and $200 \text{ kg P}_2\text{O}_5 \text{ ha}^{-1}$. The different water regimes were initiated six weeks after planting to ensure good establishment and early exposure of all growth stages to drought. In the non-stressed conditions, plants were watered to 75% FC, while in the water-stressed conditions, volumetric soil water content was maintained at 25% FC. The soil water content was monitored using a hand held soil moisture probe and by weighing the pots. The two watering regimes were maintained until maturity (~120 days).

2.3 Data collection

At maturity, which was reached after four months for both experiments, plants were separated into grain, shoot, and root, then oven-dried at 60°C for 72 hours to measure the dry weight. This was then converted to grams per square meter (g m^{-2}) units using a plant population of 128 and 134 plants m^{-2} for the greenhouse and field experiments, respectively. Root:shoot (R:S) ratio and total plant biomass (PB) were computed after determining grain yield (GY), root biomass (RB), and shoot biomass (SB). Grain, shoot, and root samples of the 10 selected wheat genotypes were then ground to $< 0.5 \text{ mm}$ and analyzed for total C and N in triplicates using a LECO CNS-2000 Dumas analyzer [26]. The total carbon contents (TC_C) were then used to estimate the C stocks in the different plant parts as follows:

$$GC_S = GY \times GC_C \times b \quad (1)$$

where GC_S is the grain C stock (kg C m^{-2}), GY is the grain yield, GC_C is the C concentration in the grain (g C kg^{-1}), and b is a constant equal to 0.001.

$$SC_S = SB \times SC_C \times b \quad (2)$$

where SC_S is the shoot C stock (kg C m^{-2}), SB is the shoot biomass, SC_C is the C concentration in the shoots (g C kg^{-1}), and b is a constant equal to 0.001.

$$RC_S = RB \times RC_C \times b \quad (3)$$

where RC_S is the root C stock (kg C m^{-2}), RB is the root biomass, and RC_C is the C concentration in the roots (g C kg^{-1}); and b is a constant equal to 0.001.

The **total plant carbon stocks (PC_S)** corresponded to the sum of C stocks from the different plant parts ($GC_S + SC_S + RC_S$).

Water use efficiency of wheat genotypes was calculated from the ratio of biomass to the total volume of irrigation water applied, using the following formula:

$$\text{WUE} (\text{g m}^{-2} \text{ mm}^{-1}) = \frac{B}{V}$$

Where B is the mass of either grain (GY), shoot biomass (SB), root biomass (RB), total plant biomass (PB), grain carbon stocks (GC_S), shoot carbon stocks (SC_S), root carbon stocks (RC_S) or total plant carbon stocks (PC_S) in g m^{-2} ,

V is the volume of irrigation water applied for the entire season in mm.

The WUE data was normalized by averaging the WUE of wheat genotypes from the field with those from the glasshouse, which resulted in the average WUE of a common genotype across both environments.

2.4 Data analysis

Analysis of variance (ANOVA) was conducted using the lattice procedure with GenStat 18th edition [27]. In addition, the means were separated using the least significant difference (LSD) at 0.05 significance level to quantify the effects of genotype, environment, and water regime on measured variables. A multivariate procedure for hierarchical clustering was performed based on phenotypic data combined across water regimes and sites, in order to group the genotypes according to similarity. A dendrogram was derived from a Euclidean similarity matrix using the unweighted pair group method with arithmetic mean algorithm (UPGMA) (**Figure 1**). Genotypes with high grain yield and biomass production in each cluster were selected (to capture high performance and as much diversity as possible) for further development in the glasshouse.

3. Results

3.1 Variations in agronomic traits among wheat genotypes

The average grain yield (GY) among the initial set of 100 genotypes was $1387 \text{ g m}^{-2} \pm 84 \text{ g m}^{-2}$ (**Table 2**). It varied by a factor of 62-fold, ranging from 75 to 4696 g m^{-2} in the field, and showed a positively skewed distribution (Skew = 1.53, **Table 2**). It was also significantly higher under non-stressed than water-stressed

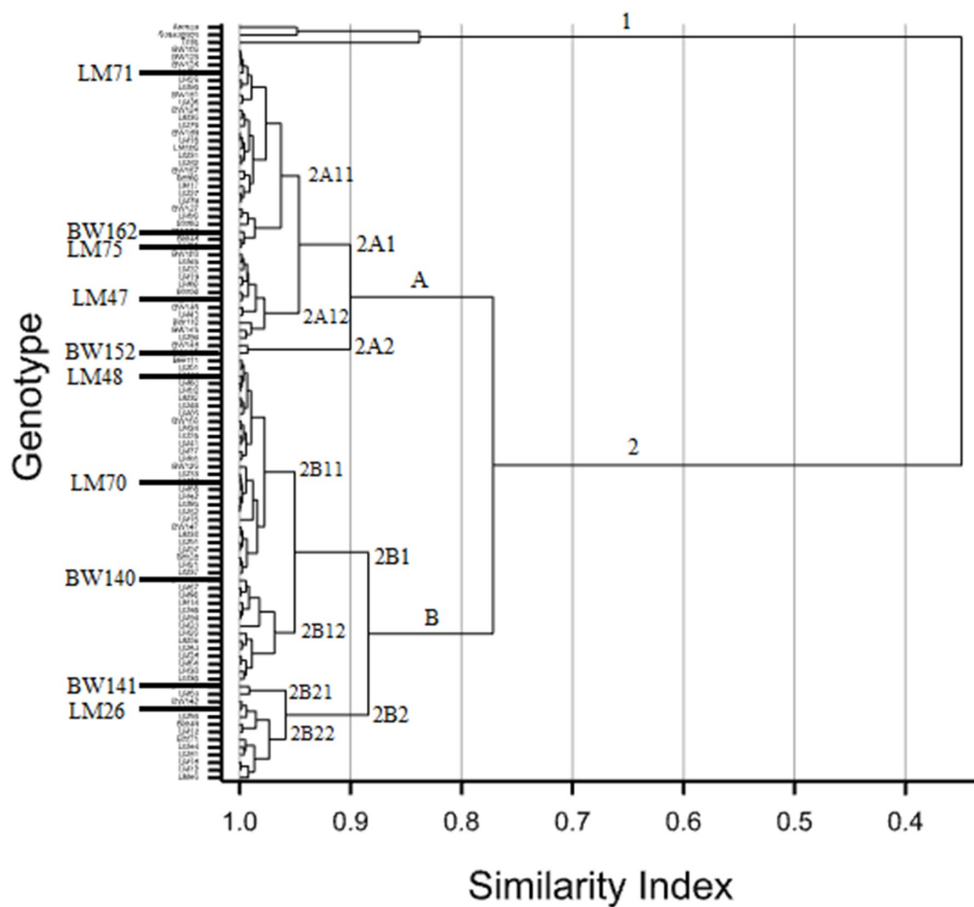


Figure 1.

Dendrogram showing clusters according to phenotypic relatedness of 100 genotypes evaluated.

conditions ($p < 0.001$, **Table 3**). However, total plant biomass (PB) was much less variable than GY, with ranges of 1976 to 13,529 g m⁻², a 6.8-fold difference (**Table 2**), but was also higher under non-stressed compared to stressed conditions ($p < 0.001$, **Table 3**). PB varied among wheat genotypes ($p < 0.001$), as it was lowest in genotype BW142 (1976 g m⁻²) and highest in genotype LM75 (6525 g m⁻²) under stress, while it was lowest in genotype LM32 and highest in LM26 (13529 g m⁻²) under non-stressed conditions. R:S also varied among the 100 wheat genotypes ($p < 0.001$), with an average ratio of 0.12, meaning that they allocated about 12% of their total biomass to their roots (ranges 3 to 38%, **Table 2**), with genotype LM75 exhibiting the lowest (0.03), while *Triticale* had the highest R: S (0.38).

The interaction of the water regime with genotypes for GY or PB of the selected best 10 wheat genotypes in the field was significant ($p < 0.05$). The sub-set of selected 10 genotypes also showed high variations in grain yield, plant total biomass, and biomass allocation, with GY ranging from 621 to 4383 g m⁻² (a 7.0-fold increase) and PB between 2475 and 13529 g m⁻² (5.4-fold increase) (**Tables 2 and 3**). Within this sub-set of 10 genotypes, LM71 exhibited the lowest GY (621 g m⁻²), while LM75

	GY	SB	RB	PB	R:S
-----g m ⁻² -----					
<i>100 genotypes (field)</i>					
Mean	1387	2498	305	4189	0,12
Median	1309	2332	263	3930	0,11
Min	75	1179	65	1976	0,03
Max	4696	8658	1,219	13529	0,38
Q1	959	1827	189	3026	0,09
Q3	1644	2908	365	4893	0,15
CV%	47	37	57	37	41
SEM	84	121	22	200	0,01
Skew	1,53	2,04	2,03	1,82	1,67
Kurt	4,35	7,15	5,76	5,66	4,39
<i>Best 10 selected genotypes (field)</i>					
Mean	1882	3169	356	5408	0,12
Median	1624	2929	326	5214	0,10
Min	621	1598	152	2475	0,06
Max	4383	8658	1,006	13529	0,26
Q1	1349	2317	249	3952	0,09
Q3	2500	3691	427	6140	0,13
CV%	45	44	47	42	35
SEM	109	182	22	290	0,01
Skew	1,05	2,03	1,91	1,65	1,60
Kurt	1,03	6,08	5,89	4,19	3,40

SB – shoot biomass, RB – Root Biomass, PB – Total Plant Biomass and R: S – root to shoot ratio.

SB – shoot biomass, RB – Root Biomass, PB – Total Plant Biomass and R: S – root to shoot ratio.

Table 2.

Summary statistics for grain yield and selected morphological variables for the 100 and the best 10 selected wheat genotypes grown in the field across different water regimes.

(3031 g m⁻²) had the highest under stress. On the other hand, BW140 (1624 g m⁻²) resulted in lower grain yield, while BW141 (4383 g m⁻²) had higher grain yield under non-stressed conditions. In this sub-set, PB was lowest in genotype LM47 (2475 g m⁻²) and highest in genotype LM75 (6525 g m⁻²) under stress; while under non-stressed conditions, it was lowest with BW162 (4971 g m⁻²) and highest in LM26 (13529 g m⁻²) (Table 3).

3.2 Variations in the wheat's ability to store carbon

The average carbon content in the grain, shoots, and roots was not affected by the watering regime ($p > 0.05$) but significantly differed among wheat genotypes ($p < 0.05$) in both the glasshouse and field. It was, on average, 40% in the grain (GC_C), 34% in the shoots (SC_C), and 30% in the roots (RC_C) (Table 3). SC_C ranged from 30% to 37% in the field, while RC_C varied from 21% to 39%, the latter

GY	SB	RB	PB	R:S	GC _C	SC _C	RC _C	GC _S	SC _S	RC _S	PC _S
-----g m ⁻² -----%-----g C m ⁻² -----											
Glasshouse											
25% Field capacity											
Mean	326	1873	792	2992	0,43	40	33	31	132	625	239
Median	266	1826	762	2918	0,44	40	34	31	104	621	225
Min	58	1349	368	2156	0,15	37	25	21	23	409	103
Max	869	2415	1263	3983	0,7	44	37	39	365	805	379
CV%	68	24	36	24	34	18	19	23	69	25	34
SEM	28	57	37	94	0,02	0,96	0,84	0,89	11,77	19,85	10,48
75% Field capacity											
Mean	414	3726	2149	6289	0,57	40	33	31	167	1243	647
Median	397	3440	1823	5508	0,57	40	34	31	150	1186	605
Min	136	2779	1290	4531	0,37	37	25	21	55	851	333
Max	811	5192	3575	9305	0,78	44	37	39	332	1822	1059
CV%	50	26	38	30	26	18	19	23	52	27	35
SEM	27	127	104	247	0,02	0,96	0,84	0,89	11,22	44,05	29,18
Field											
25% Field capacity											
Mean	1700	2507	302	4508	0,12	40	34	30	439	833	89
Median	1401	2534	277	4042	0,12	40	34	30	415	845	76
Min	621	1598	152	2475	0,08	38	30	21	175	534	45
Max	3031	3775	642	6525	0,19	44	37	39	904	1215	214
CV%	53	27	39	34	24	4	6	15	42	28	49

	GY	SB	RB	PB	R:S	GC _G	SC _G	RC _G	GC _S	SC _S	RC _S	PC _S
SEM	116	87	15	199	0,004	0,23	0,27	0,58	24,06	29,70	5,65	45,87
75% Field capacity												
Mean	2062	3714	403	6179	0,12	40	34	30	830	1331	126	2287
Median	1720	3154	382	5462	0,1	40	34	30	714	1211	117	2076
Min	1624	1954	135	4971	0,06	38	30	21	393	811	63	1395
Max	4383	8658	1006	13529	0,26	44	37	37	1843	2869	302	4016
CV%	44	42	44	39	43	5	7	14	49	40	44	36
SEM	117	202	23	313	0,01	0,24	0,29	0,54	52,19	69,50	7,08	10718

Table 3. Summary statistics for grain yield (GY), selected morphological variables (SB: shoot biomass, RB: root biomass, PB: total plant biomass), and plant carbon variables (GCC: grain carbon content, SC_G: shoot carbon content, RCC: root carbon content, GCS: grain carbon stocks, RCS: shoot carbon stocks, and PCS: plant carbon stocks) for selected 10 wheat varieties grown in the field and glasshouse across water regimes.

corresponding to a 90% increase (**Table 3**). Among the 10 selected wheat genotypes, BW141 exhibited the lowest, while LM70 had the highest GC_C , and LM26 gave the lowest, while LM48 had the highest RC_C . Lastly, LM75 had the lowest and LM70 the highest SC_C . There were, however, greater variations in the carbon stocks in shoots, roots, and total plant biomass between environments. For instance, the total PCs had a mean of $996 \pm 31 \text{ g m}^{-2}$ with values ranging from 691 to 1315 g m^{-2} , corresponding to a twofold difference under stress in the glasshouse, but averaged $2058 \pm 78 \text{ g m}^{-2}$ (range 1380 to 3093 g m^{-2}) under non-stressed conditions. In the field, the PCs averaged $1361 \pm 46 \text{ g m}^{-2}$ with ranges of 835 to 1913 g m^{-2} under stress, while under non-stressed conditions, the average PCs was 2287 ± 107 , (range 1395 to 4016 g m^{-2} , **Table 3**).

3.3 Variation of agronomic traits and the wheat genotype's ability to store carbon as influenced by water regimes and the environment

The interaction of watering regime with genotype for grain yield (GY) production in both the field and the glasshouse was significant ($p < 0.05$), with field conditions being more conducive than the glasshouse for grain yield production since the average GY was 1700 and 326 g m^{-2} for field and glasshouse, respectively, under stress (**Table 3**). The same pattern was followed under non-stressed conditions, with GY being lower in the glasshouse (average 414 g m^{-2}) while higher in the field (mean 2062 g m^{-2}). Under stress in the field, GY was lowest in genotype LM71 (621 g m^{-2}) and highest in LM75. While under non-stressed conditions in the field, it was lowest in genotype BW140 and highest in BW141 (4383 g m^{-2}). In the glasshouse under stress, BW162 (58 g m^{-2}) produced the lowest and LM75 produced the highest GY (869 g m^{-2}), while under non-stressed conditions, BW141 (136 g m^{-2}) produced the lowest, with BW162 yielding the highest GY (811 g m^{-2}) (**Table 3**).

The interaction between the watering regime and genotype for total plant biomass (PB) production was significant in both environments ($p < 0.001$). It ranged from 4531 to 9305 g m^{-2} under non-stressed conditions in the glasshouse, while it ranged from 4971 to 13529 g m^{-2} in the field (**Table 3**). Under stress in the glasshouse, BW152 (2156 g m^{-2}) had the lowest PB, and LM75 had the highest (3983 g m^{-2}) PB. Meanwhile, under non-stressed conditions, LM26 (4531 g m^{-2}) had the lowest, with BW140 exhibiting the highest PB (9305 g m^{-2}). In the field, under stress, LM47 (2475 g m^{-2}) had the lowest, while LM75 had the highest PB. Under non-stressed conditions, BW162 had the lowest PB, while LM26 (13529 g m^{-2}) had the highest PB. The watering regime interaction also significantly affected total plant carbon stocks (PCs) of the genotypes in the glasshouse ($p < 0.001$). PCs in the glasshouse under stress were highest (1315 g C m^{-2}) in genotype LM75 and lowest (691 g C m^{-2}) in BW152, while under non-stressed conditions, they were highest in BW140 (3093 g C m^{-2}) and lowest in LM26 (1380 g C m^{-2}). The watering regime also significantly affected the total PCs of the selected 10 wheat genotypes under field conditions ($p < 0.05$). Under stress in the field, PCs were highest for genotype BW152 (1913 g C m^{-2}) while they were lowest for LM70 (835 g C m^{-2}). Under non-stressed conditions, the maximum PCs was 4016 g C m^{-2} for genotype BW141 while the minimum was 1395 g C m^{-2} for BW140 (**Table 3**).

3.4 Water use efficiency for grain, biomass production, and carbon storage of wheat genotypes as influenced by the environment

The interaction between genotype and water regime was significant in the glasshouse ($p < 0.001$), while it was not significant in the field, with only the water regime having a significant effect on WUE for GY in the field ($p = 0.001$). The average WUE-GY was $0.74 \text{ g m}^{-2} \text{ mm}^{-1}$ in the glasshouse under stress, with values ranging from 0.12 to $2.1 \text{ g m}^{-2} \text{ mm}^{-1}$ for BW162 and LM75, respectively (**Table 4**). In the glasshouse under non-stressed conditions, WUE-GY ranged from 0.12 to $0.65 \text{ g m}^{-2} \text{ mm}^{-1}$ for BW141 and BW162 respectively, with an average of $0.33 \pm 0.02 \text{ g m}^{-2} \text{ mm}^{-1}$. Higher WUE-GY was observed in the field than in the glasshouse, since the average was 1.44 and $0.62 \text{ g m}^{-2} \text{ mm}^{-1}$ under stressed and non-stressed conditions, respectively (**Table 4**).

The WUE for total plant biomass (PB) had an average of 6.58 and $5.07 \text{ g m}^{-2} \text{ mm}^{-1}$ in the glasshouse under stressed and non-stressed conditions, respectively (**Table 4**). The watering regime significantly affected WUE-PB in the field ($p < 0.001$). It ranged from 2.19 to $7.24 \text{ g m}^{-2} \text{ mm}^{-1}$ for LM26 and BW152 respectively, under stressed conditions, and was 1.09 to $3.9 \text{ g m}^{-2} \text{ mm}^{-1}$ for LM47 and BW141 respectively, under non-stressed conditions. The WUE of total plant carbon stocks (WUE-PC_S) ranged from 1.16 to $2.68 \text{ g m}^{-2} \text{ mm}^{-1}$ (average $2.12 \text{ g m}^{-2} \text{ mm}^{-1}$) in the glasshouse under stress ($p < 0.001$ for all treatments), while in the field, it averaged 1.12 and $0.65 \text{ g m}^{-2} \text{ mm}^{-1}$ under stressed and non-stressed conditions, respectively (**Table 4**).

3.5 Water use efficiency for grain and biomass production in the field and glasshouse as influenced by the water regime

WUE components were significantly affected by the water regime and differed among the wheat genotypes ($p < 0.05$). On average, the WUE-GY was much higher under stress than under non-stressed conditions, with all the stressed condition values above $0.75 \text{ g m}^{-2} \text{ mm}^{-1}$ and non-stressed condition values below $0.75 \text{ g m}^{-2} \text{ mm}^{-1}$ (**Figure 2A, B**). Under stress, the best two genotypes were LM75 ($1.66 \text{ g m}^{-2} \text{ mm}^{-1}$) followed by LM71 ($1.37 \text{ g m}^{-2} \text{ mm}^{-1}$), while BW141 and BW140 had the lowest WUE-GY of 0.69 and $0.71 \text{ g m}^{-2} \text{ mm}^{-1}$ respectively, which did not significantly differ from genotypes LM70 and LM48 (**Figure 2A**). This corresponded to a maximum 141% difference in WUE for GY under stressed conditions. Under non-stressed conditions, BW162 showed the highest WUE-GY ($0.66 \text{ g m}^{-2} \text{ mm}^{-1}$) of all genotypes, while LM48 and LM47 had the lowest averages of 0.24 and $0.29 \text{ g m}^{-2} \text{ mm}^{-1}$ respectively (**Figure 2B**).

The WUE for total plant biomass (WUE-PB) averaged 6.58 and $5.07 \text{ g m}^{-2} \text{ mm}^{-1}$ in the glasshouse under stressed and non-stressed conditions, respectively (**Table 4**). While in the field, it ranged from 2.19 to $7.24 \text{ g m}^{-2} \text{ mm}^{-1}$ and 1.09 to $3.9 \text{ g m}^{-2} \text{ mm}^{-1}$ for stressed and non-stressed conditions, respectively. It was highest for LM75 ($6.1 \text{ g m}^{-2} \text{ mm}^{-1}$) and lowest for LM48 ($4.2 \text{ g m}^{-2} \text{ mm}^{-1}$) which corresponded to a 45% difference (**Figure 4C**). Meanwhile, BW140 had higher ($4.58 \text{ g m}^{-2} \text{ mm}^{-1}$) and LM47 lower ($1.56 \text{ g m}^{-2} \text{ mm}^{-1}$) WUE-PB under non-stressed conditions (**Figure 4D**).

3.6 Water use efficiency for carbon storage in the field and glasshouse as influenced by the water regime

Analysis of variance showed that WUE for GC_S, SC_S, RC_S, and PC_S significantly differed between water regimes and wheat genotypes ($p < 0.05$). WUE for plant

	WUE- GY	WUE- SB	WUE- RB	WUE- PB	WUE- GCs	WUE- SCs	WUE- RCs	WUE- PCs
-----g m ⁻² mm ⁻¹ -----								
Glasshouse								
<i>Stressed conditions</i>								
Mean	0.74	4.10	1.74	6.58	0,23	1.37	0.52	2.12
Median	0.55	4.16	1.71	6.49	0,18	1.38	0.53	1.76
Min	0.12	2.63	0.89	4.21	0,04	0.80	0.25	1.16
Max	2.10	5.84	3.06	9.63	0,64	1.95	0.77	2.68
CV	75	20	34	22	69	20	28	17
SEM	0.07	0.10	0.08	0.19	0,02	0.04	0.02	0.04
<i>Non-stressed</i>								
Mean	0.33	3.00	1.74	5.07	0,12	1.00	0.52	2.64
Median	0.31	2.73	1.58	4.51	0,11	0.94	0.49	1.31
Min	0.12	2.28	0.94	3.56	0,04	0.64	0.30	1.10
Max	0.65	4.42	3.04	7.92	0,24	1.55	0.90	2.55
CV	51	26	39	31	52	27	36	29
SEM	0.02	0.10	0.09	0.20	0,01	0.04	0.02	0.06
Field								
<i>Stressed conditions</i>								
Mean	1.44	2.11	0.25	3.80	0,34	0.70	0.08	1.12
Median	1.25	2.00	0.23	3.37	0,32	0.69	0.07	1.07
Min	0.57	1.35	0.13	2.19	0,14	0.42	0.04	0.65
Max	4.01	3.49	0.55	7.24	0,70	1.12	0.18	1.45
CV%	55	28	40	36	42	27	48	28
SEM	0.10	0.08	0.01	0.18	0,02	0.02	0.00	0.03
<i>Non-stressed</i>								
Mean	0.62	1.11	0.12	1.84	0,24	0.37	0.04	0.65
Median	0.53	0.94	0.11	1.69	0,20	0.32	0.03	0.59
Min	0.33	0.60	0.04	1.09	0,11	0.21	0.02	0.39
Max	1.26	2.50	0.30	3.90	0,53	0.83	0.09	1.15
CV%	43	40	44	37	49	40	43	37
SEM	0.03	0.06	0.01	0.09	0,01	0.02	0.00	0.02

Table 4.

Summary statistics for crop WUE (WUE-GY: grain yield WUE, WUE-SB: shoot biomass WUE, WUE-RB: root biomass WUE, WUE-PB: plant biomass WUE) and plant carbon WUE (WUE-GCs: grain carbon stocks WUE, WUE-SCs: shoot carbon stocks WUE, WUE-RCs: root carbon stock WUE, and WUE-PCs: total plant carbon stocks WUE) for the 10 selected wheat varieties grown in the field and glasshouse across water regimes (stressed and non-stressed).

carbon stocks (WUE-PCs) also varied within the plant (**Figures 3 and 4**) and was affected by the environment (**Table 4**). WUE-GCs ranged from 0.04 to 0.64 g C m⁻² mm⁻¹ a 16-fold increase in the glasshouse under stress, while it ranged from 0.04 to

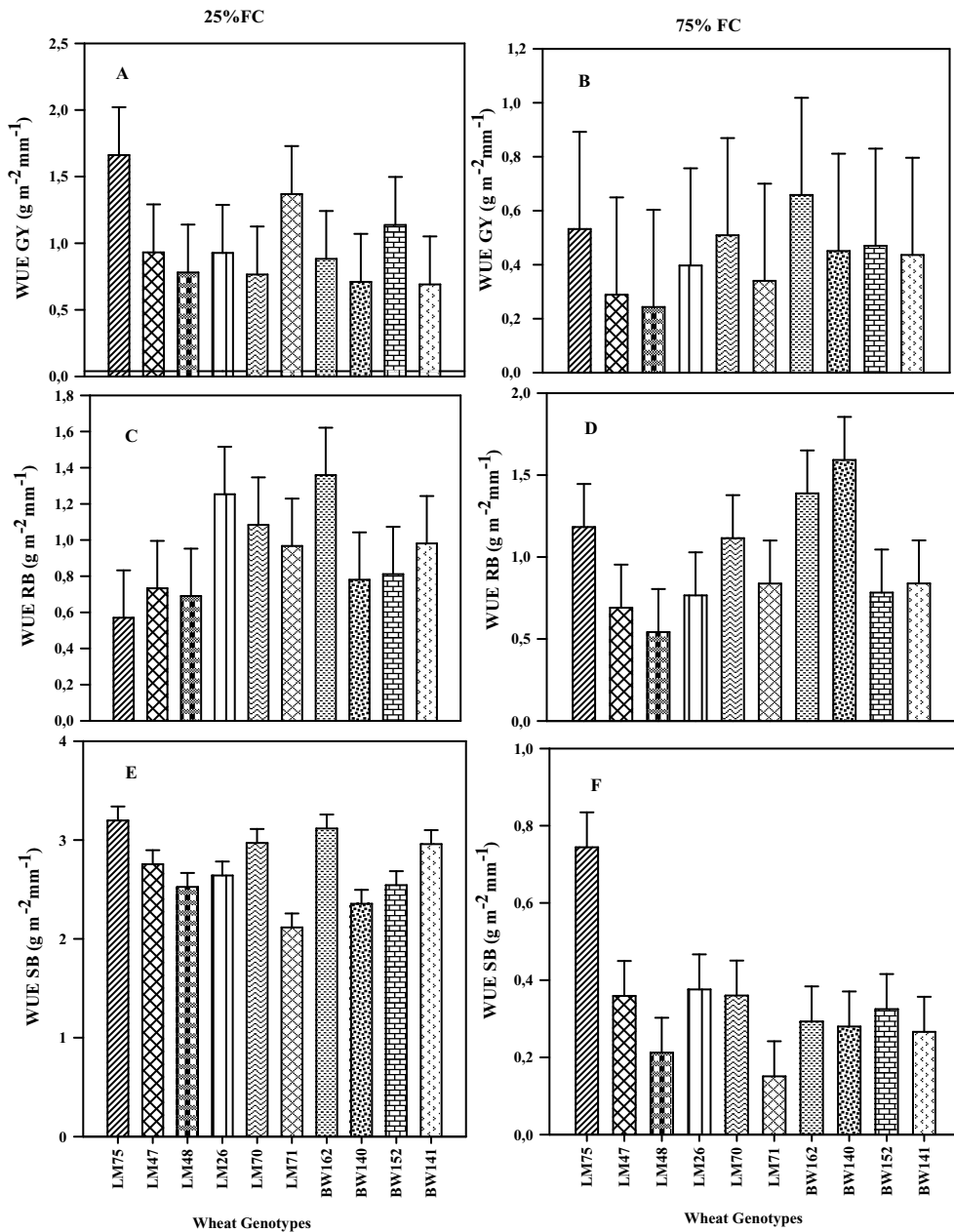


Figure 2. Wheat genotype and soil water availability (25% and 75% field capacity) impacts on WUE for GY (A, B), RB (C, D), and SB (E, F). Bars represent the mean, and error bars indicate LSD ($p < 0.05$) of normalized data across field and glasshouse experiments.

0.24 g C m⁻² mm⁻¹ a 6-fold increase under non-stressed conditions (**Table 4**). The average WUE-PCs was 2.12 ± 0.04 g C m⁻² mm⁻¹ with ranges of 1.16 to 2.68 g C m⁻² mm⁻¹ under stress in the glasshouse, while under non-stressed conditions it averaged 2.64 ± 0.06 g C m⁻² mm⁻¹ with ranges of 1.1 to 2.55 g C m⁻² mm⁻¹. In the field, the WUE-PCs averaged 1.12 ± 0.03 g C m⁻² mm⁻¹ (range 0.65 to 1.45 g C m⁻² mm⁻¹)

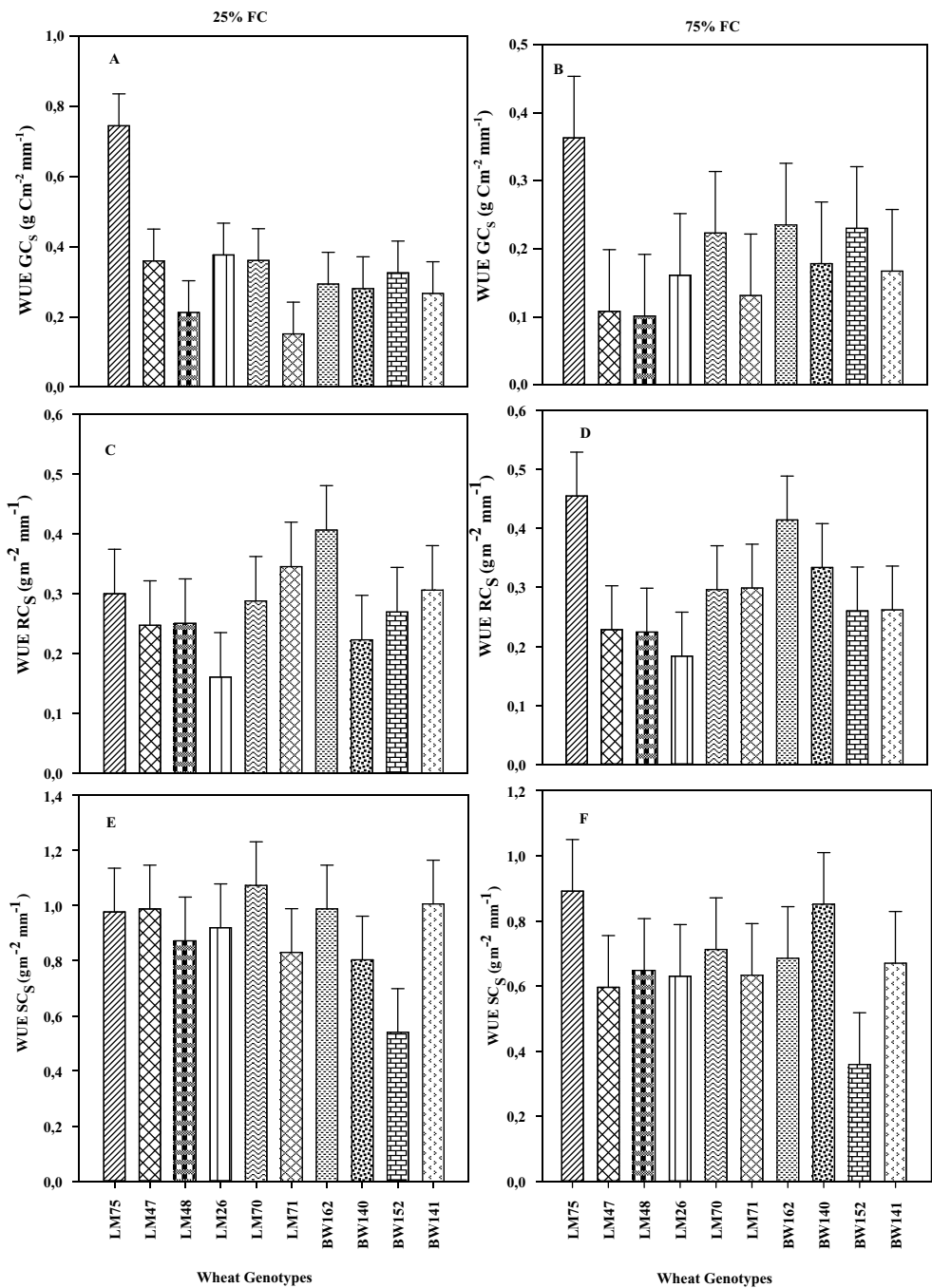


Figure 3. Wheat genotype and soil water availability (25 and 75% field capacity) impacts on WUE for GC_S (A, B), RC_S (C, D), and SC_S (E, F). Bars are mean and error bars are LSD ($p < 0.05$) of normalized data across field and glasshouse experiments.

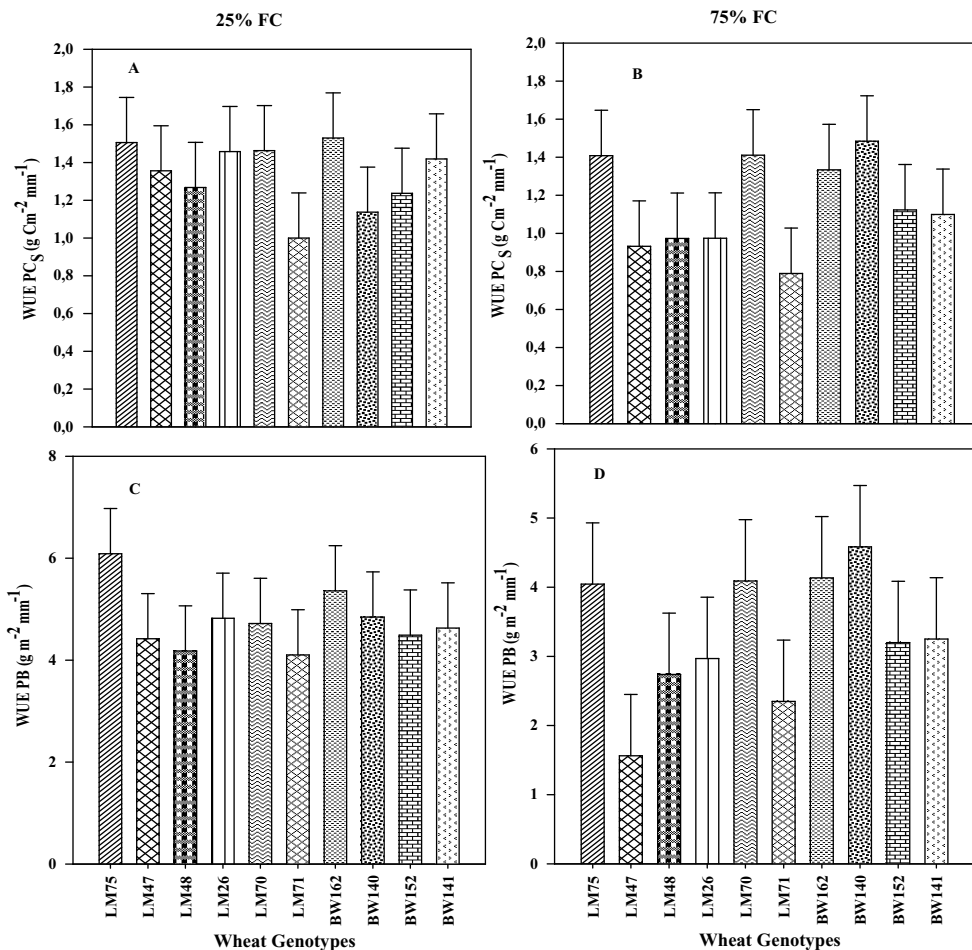


Figure 4. Wheat genotype and soil water availability (25% and 75% field capacity) impacts on WUE for PC_S (A, B) and PB (C, D). Bars represent the mean, and error bars indicate LSD ($p < 0.05$) of normalized data across field and glasshouse experiments.

under stress, while under non-stressed conditions it averaged $0.65 \pm 0.02 \text{ g C m}^{-2} \text{ mm}^{-1}$ (range 0.39 to $1.15 \text{ g C m}^{-2} \text{ mm}^{-1}$, **Table 4**).

In general, the WUE carbon stocks (averaged across all treatments) were higher under stressed (25% FC) than non-stressed conditions (75% FC), except for WUE-RC_S and WUE-RB (**Table 5**). For example, the average WUE-GC_S under stressed conditions was $0.34 \text{ g C m}^{-2} \text{ mm}^{-1}$ while under non-stressed conditions, it was $0.19 \text{ g m}^{-2} \text{ mm}^{-1}$, a 77% difference. The average of WUE-SC_S was $0.9 \text{ g C m}^{-2} \text{ mm}^{-1}$ under stressed conditions, while it was $0.67 \text{ g C m}^{-2} \text{ mm}^{-1}$ under 75%FC, a 35% difference (**Table 5**).

WUE-GC_S under stress ranged from 0.151 to $0.744 \text{ g C m}^{-2} \text{ mm}^{-1}$ for LM71 and LM75 respectively, i.e., a 393% difference (**Figure 3A**). In contrast, under non-stressed conditions, it ranged from 0.101 for LM48 to $0.363 \text{ g C m}^{-2} \text{ mm}^{-1}$ for LM75 which corresponds to a 259% difference (**Figure 3B**). Under stress, BW162 had higher WUE-RC_S ($0.406 \text{ g C m}^{-2} \text{ mm}^{-1}$) with LM26 exhibiting lower WUE-RC_S

Parameters	25%FC	75%FC
GC _s g m ⁻²	327.63	497.95
RC _s g m ⁻²	181.06	436.48
SC _s g m ⁻²	698.77	1229.82
PC _s g m ⁻²	1203.66	2158.22
GY g m ⁻²	810.79	1234.71
RB g m ⁻²	596.13	1450.36
SB g m ⁻²	2156.53	3721.23
PB g m ⁻²	3601.45	6162.31
WUE-GC _s g m ⁻² mm ⁻¹	0.34	0.19
WUE-RC _s g m ⁻² mm ⁻¹	0.28	0.3
WUE-SC _s g m ⁻² mm ⁻¹	0.9	0.67
WUE-PC _s g m ⁻² mm ⁻¹	1.34	1.15
WUE-GY g m ⁻² mm ⁻¹	0.9	0.42
WUE-RB g m ⁻² mm ⁻¹	0.92	0.98
WUE-SB g m ⁻² mm ⁻¹	0.90	0.67
WUE-PB g m ⁻² mm ⁻¹	4.54	3.4

Table 5.

Average variables of parameters as influenced by different water regimes.

(0.16 g C m⁻² mm⁻¹) (**Figure 3C**). While under non-stressed conditions, LM75 had higher WUE-RCS (0.455 g C m⁻² mm⁻¹) with LM26 exhibiting lower WUE-RC_s (0.183 g C m⁻² mm⁻¹) (**Figure 3D**). WUE-SC_s was generally higher than WUE-RC_s both under stressed and non-stressed conditions, with LM70 having higher WUE-SC_s (1.073 g C m⁻² mm⁻¹) and BW152 exhibiting lower WUE-SC_s under stress (**Figure 3E**). While under non-stressed conditions, LM75 had higher WUE-SCS (0.891 g C m⁻² mm⁻¹) and BW152 exhibited lower WUE-SC_s (0.359 g C m⁻² mm⁻¹, **Figure 3F**).

The WUE for total plant carbon stocks (WUE-PC_s) was highest in genotypes BW162 (1.53 g C m⁻² mm⁻¹) and LM75 (1.51 g C m⁻² mm⁻¹) and lowest in LM71 (1 g C m⁻² mm⁻¹) under stress (**Figure 4A**). In contrast, BW140 gave the highest (1.484 g C m⁻² mm⁻¹), while LM71 had the lowest (0.789 g C m⁻² mm⁻¹) WUE-PC_s under non-stressed conditions (**Figure 4B**).

3.7 Associations among agronomic traits and water-use efficiency components across water regimes and environments

There were generally high and significant correlations for most of the genetic traits analyzed. Positive significant correlations were observed between GY and PB ($r = 0.501$), PC_s ($r = 0.533$), SC_s ($r = 0.339$), WUE-GC_s ($r = 0.769$), and WUE-GY ($r = 0.767$, $p < 0.001$). PB also positively correlated with PC_s ($r = 0.987$, $p < 0.001$), RB ($r = 0.309$), RC_s ($r = 0.295$), SB ($r = 0.916$) and SC_s ($r = 0.894$, $p < 0.001$); while root biomass (RB) correlated positively with RC_s ($r = 0.985$), R:S ($r = 0.903$), SB ($r = 0.368$), SC_s ($r = 0.347$), PC_s ($r = 0.24$), WUE-PB ($r = 0.560$), WUE-PC_s

($r = 0.665$), WUE-RB ($r = 0.861$), WUE-RC_S ($r = 0.847$), WUE-SB ($r = 0.542$), and WUE-SC_S ($r = 0.533$). Positive correlations were also observed between PC_S and RC_S ($r = 0.231$), SB ($r = 0.920$), and SC_S ($r = 0.913$, $p < 0.001$); while RCs correlated positively with R:S ($r = 0.895$, $p < 0.001$), SB ($r = 0.346$), SC_S ($r = 0.325$), WUE-PB ($r = 0.545$), WUE-PC_S ($r = 0.650$), WUE-RB ($r = 0.847$), WUE-RC_S ($r = 0.866$), WUE-SB ($r = 0.527$), and WUE-SC_S ($r = 0.528$). The root-to-shoot ratio (R: S) had positive correlations with most of the WUE parameters, such as WUE-GC_S ($r = 0.539$), WUE-PB ($r = 0.570$), WUE-PC_S ($r = 0.644$), WUE-RB ($r = 0.910$, $p < 0.001$), WUE-RC_S ($r = 0.901$), WUE-SB ($r = 0.524$), and WUE-SC_S ($r = 0.527$, $p < 0.001$); while SB correlated positively with SC_S ($r = 0.977$, $p < 0.001$); and WUE-GC_S with WUE-GY ($r = 0.996$, $p < 0.001$).

The WUE parameters also have significant correlations among themselves, as WUE-PB had positive significant correlations with WUE-PC_S ($r = 0.931$, $p < 0.001$), WUE-RB ($r = 0.811$), WUE-RC_S ($r = 0.776$), WUE-SB ($r = 0.958$, $p < 0.001$), and WUE-SC_S ($r = 0.902$, $p < 0.001$); while WUE-PC_S had positive correlations with WUE-RB ($r = 0.841$), WUE-RC_S ($r = 0.817$), WUE-SB ($r = 0.941$, $p < 0.001$), and WUE-SC_S ($r = 0.911$, $p < 0.001$). On the other hand, WUE-RB had positive correlations with WUE-RC_S ($r = 0.973$, $p < 0.001$), WUE-SB ($r = 0.783$, $p < 0.001$), and WUE-SC_S ($r = 0.771$); while WUE-RC_S correlated positively with WUE-SB ($r = 0.756$) and WUE-SC_S ($r = 0.732$); and WUE-SB had positive correlations with WUE-SC_S ($r = 0.966$, $p < 0.001$).

Negative significant correlations also existed between GY and RC_S ($r = -0.590$), RB ($r = -0.579$), WUE-PB ($r = -0.365$), WUE-PC_S ($r = -0.503$), WUE-RB ($r = -0.658$), WUE-RC_S ($r = -0.681$), WUE-SB ($r = -0.484$), and WUE-SC_S ($r = -0.508$, $p < 0.001$). While RB correlated negatively with WUE-GY ($r = -0.563$) and WUE-GC_S ($r = -0.545$), RC_S also had negative correlations with WUE-GY ($r = -0.583$) and WUE-GC_S ($r = -0.569$, $p < 0.001$). The R:S negatively correlated with WUE-GC_S ($r = -0.539$) and WUE-GY ($r = -0.545$). Again, negative significant correlations were observed between WUE-GC_S and WUE-RB ($r = -0.349$) as well as WUE-RC_S ($r = -0.394$, $p < 0.001$), while WUE-GY negatively correlated with WUE-RB ($r = -0.365$) and WUE-RCs ($r = -0.403$).

4. Discussion

4.1 Variations in crop agronomic traits with water regimes and the environment

The agronomic traits (GY, RB, SB, and PB) were significantly affected by the watering regime ($p < 0.05$), being generally lower under water-stressed conditions than under well-watered conditions (**Table 5**). This was because moisture stress is known to reduce biomass and grain yield at any growth stage [28]. Again, under water stress, hastened onset of senescence occurs, which decreases photosynthesis, leading to lower grain and biomass yield [29]. This results in the crop not being able to capture solar radiation for biomass production, which also shortens the time frame for mobilization and translocation of N assimilates from plant tissues to the grain [30]. The lower grain yield under water stress could also be due to limited water availability at the booting stage, which has been reported to reduce grain yield production [29]. Similar results were reported by [31], who found a significant reduction in grain yield under water stress due to the reduction of photo-assimilate production for grain filling.

Under moisture stress, the plant struggles to absorb photo-assimilates, thereby reducing grain filling duration. It has been reported that water stress during the reproductive development stages decreases grain and biomass yield [18]. Furthermore, [29] reported an increase in grain yield when wheat cultivars were irrigated to 100% FC. The increase in grain and biomass yield due to improved water availability has also been demonstrated in many studies [32–34]. Biomass allocation between roots and shoots (R:S ratio) also increased at a higher water regime in the glasshouse (**Table 3**). Similar results of increased R:S ratio of durum wheat with increased irrigation water were reported by [35]. The environment in which the wheat cultivars were grown influenced wheat agronomic traits, with GY in the field being higher than in the glasshouse at both moisture regimes (**Table 3**). Lower GY under glasshouse conditions have been reported by [36–38] and may be due to the fact that, in the greenhouse, temperature may exceed the optimal 21°C, which is likely to result in reduced wheat grain yield. It is necessary for wheat to experience chilling at the early stages of growth for optimal grain filling, which usually does not occur in the glasshouse.

4.2 Variation in water use efficiency for grain and biomass production between genotypes, as influenced by water regimes and the environment

Water use efficiency was generally higher for most of the measured traits under stressed than non-stressed conditions in both environments (**Table 4**). This is in accordance with findings by [39], who reported higher WUE of Bambara groundnut under severely stressed (25% FC) compared to non-stressed (75% FC) conditions. [40] also reported an increase in WUE of wheat with limited water supply. This was attributed to the reduction of stomatal aperture and transpiration rate under moisture stress [41]. Higher WUE could also be attributed to the fact that plant roots extract more soil water from a greater depth under moisture stress compared to when they are irrigated [42]. This means that stored soil water under moisture stress can be used more efficiently.

WUE of wheat genotypes varied under both moisture regimes ($p < 0.05$), with LM75 having the highest WUE-GY, while LM48 was lower under stress (**Figure 2A**). A similar trend was observed for WUE-PB under stress (**Figure 4C**). Similar variation in WUE between cultivars was reported by [43]. This reveals that LM75 is not sensitive to water stress for grain and biomass production, while LM48 is sensitive and therefore not the best genotype for grain and biomass production when water supply is limited. Under non-stressed conditions, BW162 exhibited the highest WUE-GY (**Figure 2B**) while BW140 had higher WUE-PB (**Figure 4D**), but LM47 produced low WUE for both GY and PB (**Figures 2B and 4D**). Therefore, it can be deduced that when water supply is sufficient, BW140 and BW162 could be desirable genotypes for optimal grain and biomass production. [44] pointed out that drought-tolerant wheat cultivars will show increased WUE, while drought-sensitive ones will show decreased WUE when water-stressed. Overall, LM75 was ranked the best genotype for WUE of both GY and PB, while BW162 was ranked the best for WUE of RB production. Thus, these cultivars can be used for wheat production under limited water availability.

4.3 Variation of wheat genotypes in WUE for carbon storage

Annual plant carbon input into the soil is one of the major factors determining the quantity of organic matter in agro-ecosystems. Plant carbon varies between

different crop species, cultivars, and different plant parts of the same species [45]. There was low variation in carbon content between the roots (RCc) and shoots (SCc), with RCc ranging from 21% to 39%, while SCc ranged from 25% to 37% (**Table 3**). This low variability in carbon content is attributed to the similar biophysical microclimate and land management in the study area [46]. However, carbon stocks in the grain (GC_s), shoots (SC_s), roots (RC_s), and total plant biomass (PC_s) showed greater variation. This proved that wheat genotypes can act as storehouses of carbon by stocking it in their tissue, thereby lowering the levels of atmospheric greenhouse gases, as stated by [47]. The variation in carbon stocks also led to variation in WUE for carbon stocks among wheat genotypes.

Generally, WUE for most carbon stocks (WUE-GC_s, WUE-SC_s, and WUE-PC_s) was higher ($p < 0.05$) under water-stressed than non-stressed conditions (**Table 5**). This could be because, under moisture stress, there is a decrease in stomatal conductance and an increase in the photosynthetic rate [48]. Therefore, more carbon is assimilated, and less water is transpired [49]. WUE-RC_s was highest for BW162 under stress and for LM75 under non-stressed conditions (**Figure 3C, D**), while it was lowest for LM26 under both moisture regimes. This suggests that BW162 and LM75 are ideal for improving soil C. The root carbon and soil carbon pool have been reported to have a direct relationship since most soil organic matter is derived from roots [50]. Therefore, the higher WUE-RC_s exhibited by BW162 suggests that growing it will result in higher SOM build-up, thereby improving soil fertility under limited water availability. This also suggests that BW162 can produce below-ground carbon stocks with a lesser amount of water, which aids in carbon sequestration. According to [51], carbon allocated below ground contributes to soil fertility and carbon sequestration.

The positive correlation observed between RC_s with WUE-RC_s and WUE-PC_s suggests that wheat genotypes are ideal for carbon sequestration. WUE-SC_s was highest in genotypes LM70 and BW141 under stress, while it was higher for LM75 under non-stressed conditions (**Figure 3E, F**), suggesting that these genotypes are ideal for the production of shoot carbon stocks. From these findings, it can also be argued that drought-tolerant wheat cultivars will assimilate more carbon with less water. Above-ground biomass has been reported to constitute an important visible carbon pool [52]. Thus, LM75 was ranked the best genotype for WUE-GC_s, WUE-SC_s, and WUE-PC_s, indicating that it has great carbon sequestration potential. However, if its residues are not incorporated into the soil, the C stock could be lost into the atmosphere. Therefore, for optimal soil C sequestration, the biomass for LM75 should be incorporated into the soil after harvest.

5. Conclusions

This study showed that wheat genotypes differ in their response to water availability. When water availability is limited, LM75 is an ideal genotype for grain and total biomass production of wheat since it is tolerant to drought stress. On the other hand, the wheat genotype BW162 is an ideal candidate to build root and plant carbon stocks since it exhibited the highest WUE-PC_s/RC_s under water-stressed conditions. Therefore, these genotypes are recommended to wheat farmers for GY,

PB, and PC_S production under water-stressed conditions. When water is non-limiting, however, BW162 and BW140 have better agronomic performance and carbon sequestration potential. Farmers are advised not to grow LM71 among other genotypes, as it is sensitive to water stress, resulting in poor agronomic performance and low C stocks build-up.

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