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RECEIVED 28 January 2026

REVISED 25 March 2026

ACCEPTED 13 April 2026

PUBLISHED 30 April 2026

CITATION

Mutanda M, Figlan S, Ngidi A,
Tsfamariam SA, Chaplot V and
Shimelis H (2026) Evaluation of maize
(*Zea mays* L.) genotypes for yield and
yield components and carbon storage.
Front. Agron. 8:1798511.
doi: 10.3389/fagro.2026.1798511

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Evaluation of maize (*Zea mays* L.) genotypes for yield and yield components and carbon storage

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Introduction: Maize is a global commodity crop cultivated under monocropping systems and diverse environmental conditions. While different genotypes exist with various abilities to store carbon into tissues and into the soil to mitigate against climate change and soil degradation, the links with grain yield remains uncertain.

Methods: Therefore, the present study aimed to screen a series of maize germplasm planted in southern Africa for carbon storage and agronomic performance to assess the link between these and identify superior genotypes. We evaluated as a first attempt, forty-five genotypes using a 5 x 9 alpha lattice design across two South African sites during the 2022/23 growing season. The recorded agronomic traits include plant height (PH), grain yield (GY), total plant biomass (PB), shoot biomass (SB) and root biomass (RB) together with total plant carbon stocks (PCs), shoot carbon stock (SCs), root carbon stock (RCs), root to shoot carbon stock ratio (RCs/SCs), and grain carbon stock (GCs).

Results: Significant ($p < 0.05$) genetic variations were recorded for all the assessed agronomic traits. The high yielding maize genotypes were TZECOMP3DT-C2, TZE(OMP3DT/WHITEDTSTRSYN)CZ and DT-STR-Y-SYN14. The maize genotypes which sequestered more carbon were TZE(OMP3DT/WHITEDTSTRSYN)CZ, 9022-13 and ZDIPLOBC4-C3-W. High phenotypic and genotypic coefficient of variations were recorded for PB and GY, respectively. The GY showed significant positive correlation with PH, SB, RB and PB. The principal component analysis highlighted that RCs, RCs/SCs, PCs, SCs, and GCs as key contributors to carbon sequestration.

Discussion: Genotypes TZECOMP3DT-C2, TZE(OMP3DT/WHITEDTSTRSYN)CZ, TZECOMP5C7/ TZECOMP39TCZ and 9022-13 were selected for their high GY production and carbon storage capacity. The selected genotypes are recommended for production and future breeding.

KEYWORDS

biomass production, carbon sequestration, climate change, grain yield, total plant carbon stocks

Highlights

- High carbon storage genotypes have high grain yield potential.
- Biomass production and grain conversion efficiency are vital in maize production and carbon sequestration.
- Genetic composition and growing environment affect carbon storage traits in maize.

1 Introduction

Maize (*Zea mays* L., $2n = 2x = 20$) is the world's third mostly widely produced cereal crop after rice and wheat, mainly cultivated under monocropping systems and across diverse agro-ecological zones (Nzuve et al., 2014; Alam et al., 2022). The crop plays a central role in global food systems by providing food, feed and industrial raw materials. It contributes substantially to caloric intake in many developing regions and provides essential nutrients such as starch (65–75%), proteins (8–11%), fiber (7%) and fat (4%) (Erenstein et al., 2022; Gunundu et al., 2023). Maize is highly versatile and adaptable to a wide range of soils and environmental conditions which allows cultivation from lowland tropical regions to temperate highlands, contributing to both food security, income generation and supporting rural livelihoods. Global maize production exceeds one billion metric tons annually, highlighting its economic and agricultural significance. Despite its importance, improving both productivity and environmental sustainability remains a major challenge in maize-based systems.

South Africa is the leading maize producer in Africa, with an annual production of eight million tons from an estimated area of 3.1 million hectares of land (Kotze, 2020). The major maize-producing provinces in South Africa are the Free State (contributing to 44% of the national annual output), followed by Mpumalanga (25%) and North-West (17%) (FAOSTAT, 2022). Despite the socio-economic significance of maize in SSA, maize yields are stagnant and low ($< 2 \text{ t ha}^{-1}$) compared to the global average of 6 t ha^{-1} . The low productivity is attributable to a range of established and climate-change-induced biotic stresses (e.g. insect pests, diseases, and parasitic weeds) and abiotic factors (e.g. drought, heat, flooding, soil erosion and poor soil fertility) (Cairns et al., 2013; Rane et al., 2021; El-Sappah et al., 2022). In addition, increasing climate variability during the growing season has been shown to significantly influence maize yield through the interaction of temperature, rainfall distribution and soil conditions, thereby affecting yield stability across environments (Božović et al., 2022; Šimon et al., 2023; Mazibuko et al., 2024; Rajičić et al., 2025; Stojiljković et al., 2025). There is a burgeoning demand for maize products for food and energy due to population pressure, urbanization, and climate change. Hence, it is critical to develop and deploy locally adapted, high-yielding and nutrient- and water-use efficient maize varieties. Achieving this requires integrating genetic improvement with a better understanding of genotype $\times$ environment interactions influencing both productivity and resource-use efficiency. Such integration should incorporate novel genetic resources with efficient

and strategic breeding technologies and innovations to accelerate the development and release of resilient and productive cultivars (Gunundu et al., 2023), especially under different environmental conditions.

Compared to other crops of C_4 photosynthetic pathway, maize is known for its high biomass production (Saenz et al., 2025). This efficient photosynthetic mechanism enables maize to effectively capture sunlight, water, and nutrients, leading to high productivity even under suboptimal conditions. With an estimated biomass production of $11.2 \text{ Mg ha}^{-1} \text{ yr}^{-1}$, maize outperforms other cereals such as wheat, rice, and sorghum and serves as an important crop for carbon (C) sequestration (Mathew et al., 2017). However, most studies have primarily focused on yield and biomass independently, with limited emphasis on genotype-specific carbon allocation patterns and their interaction with environmental conditions, particularly in Southern Africa. In agricultural systems, carbon losses due to unsustainable land management practices contribute to declining soil fertility and increased greenhouse gas emissions. Enhancing carbon storage through crop genetic improvement, particularly by selecting genotypes with efficient biomass production and root carbon allocation, offers a promising pathway to improve soil health and mitigate climate change. Improving genetic resources for traits related to carbon allocation into biomass and roots offers a promising approach to mitigating carbon loss. Soil carbon sequestration through maize thus plays a vital role in promoting sustainable agriculture and climate change adaptation (Roohi et al., 2022). Soil carbon storage and retrieval by maize can be enhanced by selecting novel genetic resources that can capture and transfer C into agricultural soils (Roohi et al., 2022).

Carbon sequestration in cropping systems contributes to increased soil organic carbon (SOC), improved soil structure, and reduced atmospheric carbon dioxide (CO_2) levels (Srivastava et al., 2012; Kumar et al., 2020). Agricultural soils have been seen as having an estimated C sequestration potential of 0.4 to $1.2 \text{ Gt C year}^{-1}$ (Meena et al., 2020) through improved land management practices including conservation tillage and cover cropping. But recently the potential of these practices to sequester atmospheric C has been challenged (Chaplot et al., 2023). This highlights the need to complement agronomic practices with genetic strategies aimed at improving plant carbon capture and allocation efficiency. Growing improved crop varieties with increased biomass production and C sequestration potential is increasingly seen as a credible alternative to sequester C into soils while enhancing soil health, fertility, and crop production (Mathew et al., 2017; Ngidi et al., 2024a).

Biomass accumulation and allocation across different plant parts are critical strategies for adapting to various environmental conditions. Studies have shown that under sub-optimal production conditions, such as limited water availability, maize plants may prioritize increasing biomass allocation to their roots rather than their shoots (Yan et al., 2023). This adaptation enhances water absorption while reducing transpiration and water loss. Significant variation in biomass allocation has been reported across different maize genotypes and environmental conditions. For instance, Ordóñez et al. (2020) demonstrated that root biomass in maize varied significantly, ranging from 1.2 to 2.8 Mg ha^{-1} across different maize genotypes. Korsa et al. (2024) observed notable variations in

yield and yield-related traits among the evaluated maize genotypes in the Central Highlands of Ethiopia. The authors reported that aboveground biomass yield ranged from 414.94 to 893.82 g per plant, with the maize line AMH169–87 producing higher aboveground biomass than all other lines evaluated. A study conducted in the Highveld of Zimbabwe revealed significant variation in shoot biomass ranging from 0.1 to 0.8 g per plant among maize genotypes (Mwafurirwa et al., 2021). Similarly, studies in sub-Saharan Africa have reported significant genotype $\times$ environment interactions influencing both biomass production and yield stability, reinforcing the importance of multi-environment evaluation of germplasm (Mazibuko et al., 2024; Mullualem et al., 2024). Therefore, genetic variability exists among maize genotypes for strategic genetic enhancement, selection, and breeding.

Variations in biomass production among maize genotypes and environmental conditions led to variable carbon sequestration (Mathew et al., 2017). For instance, a study by Joshi et al. (2023) reported carbon sequestration rates ranging from 2.6%–9.8% in cold climates, 2.7%–16.1% in temperate regions, and 4.1%–11.2% in tropical climates of maize production. Environmental variability could be attributable to the differences in temperature, soil characteristics, moisture availability, and agricultural practices. (Arellano Vazquez et al., 2024) highlighted carbon sequestration rates in selected major staple crops including maize (genotypes), ranging from (0–0.5 Mg/ha/yr) to medium values (1–5 Mg/ha/yr). Similarly, Biswas et al. (2022) reported that net CO₂ sequestration rates ranged from 984.3 to 5757.4 kg ha^{−1} in the wet season and from 1188.62 to 5757.39 kg ha^{−1} in the dry season in maize major production regions in Bangladesh. Additionally, a study on Ferric Lixisols soils in southern Malawi by Makumba et al. (2007) found that carbon sequestration in maize ranged between 0.4 and 1.0 Mg C ha^{−1}. These results highlight substantial variation in carbon sequestration across environments and genotypes, indicating that both genetic and management factors influence outcomes (Zhang et al., 2024). Accordingly, combining high-biomass genotypes with targeted soil and crop management practices, such as residue retention, crop rotations, and amendments like biochar, can enhance soil organic carbon stocks while also improving crop productivity, thereby supporting both carbon sequestration and yield goals in agroecosystems (Xu et al., 2021; Jayara et al., 2022).

There is limited information documenting maize genotypes with balanced biomass allocation and carbon sequestration in the Southern African region. Most existing studies have focused on yield or biomass traits in isolation, with minimal evaluation of genotype $\times$ environment interactions across diverse field conditions. In addition, assessments involving diverse tropical germplasm under Southern African conditions remain scarce. Consequently, there is a need for integrated studies that simultaneously evaluate agronomic performance and carbon storage potential of maize genotypes in this region. This knowledge gap limits the identification of genotypes that can combine high productivity with enhanced carbon sequestration, which is critical for sustainable maize production and climate-smart agriculture. To address these gaps, 45 genetically diverse maize genotypes were sourced from key producing countries such as Nigeria, Zimbabwe and South Africa for evaluation under South African conditions. The selections were

made based on their high grain yield, drought tolerance, and *Striga* resistance (Dossa et al., 2024). The selected genotypes need to be field evaluated across selected environments to identify best-performing genotypes with higher carbon storage capacity. Integrating carbon storage traits with yield-related traits provides an opportunity to identify dual-purpose genotypes suitable for productivity and environmental sustainability. Therefore, the aim of this study was to screen genetically diverse tropical maize germplasm for agronomic performance and carbon storage capacity to identify unique genotypes for sustainable production and breeding programs.

2 Materials and methods

2.1 Plant materials

Forty-five genetically diverse maize genotypes, consisting of 19 genotypes from the International Institute of Tropical Agriculture/Nigeria, five inbred lines from the International Maize and Wheat Improvement Center/Zimbabwe, 10 genotypes from South Africa and 11 inbred lines originated from Selian Agricultural Research Institute in Arusha, Tanzania (Ritte et al., 2017). The genotypes were selected for their high grain yield and *Striga* resistance (Dossa et al., 2024). A detailed description of the genotypes is presented in Table 1.

2.2 Study site description and experimental design

Field experiments were conducted in the 2022/23 growing season at two locations (Ukulinga Research Farm and Bethlehem) in South Africa. The Ukulinga Research Farm (latitude: 30°24' S, longitude: 29°24' E) is situated at the University of KwaZulu-Natal in Pietermaritzburg. The long-term average temperature and rainfall for Ukulinga are 16.7 °C and 966 mm, respectively. The Bethlehem site is situated at the Agricultural Research Council–Small Grain Institute (latitude: 28°09' S, longitude: 28°18' E). The long-term mean annual temperature and rainfall at Bethlehem site were 14.4 °C and 702 mm, respectively. The soils at Ukulinga and Bethlehem are clay loam and sandy clay loam, respectively, with moderate fertility based on historical surveys. Compound fertilizer (15-15-15) was applied before planting at a rate of 750 kg/ha. Subsequently, 80 and 120 kg/ha of N fertilizer were applied during the elongation and tasselling stages, respectively. Mean monthly weather data of the two locations during the growing period is presented in Table 2. The soil properties of the experimental area are given in Table 3.

2.3 Field establishment

The field trials were laid out using a 5 $\times$ 9 alpha lattice design with two replications. Each genotype was planted on a two-meter-long row with inter-row spacing of 90 cm and intra-row spacing of 40 cm, and the number of rows per genotype within each plot was kept consistent across the trial to reduce intra-genotype variation.

TABLE 1 List, source and description of maize genotypes evaluated in this study.

Genotype designation/ pedigree	Origin/ Source	Genotype description
8338-I	ITA/Nigeria	OPV
9022-13	ITA/Nigeria	OPV
A21/DT-STR	Unknown south Africa	OPV
CKDHL0378	CIMMYT/ Zimbabwe	inbred line
CLHP0343	CIMMYT/ Zimbabwe	inbred line
CML393	CIMMYT/ Zimbabwe	inbred line
CML510	CIMMYT/ Zimbabwe	inbred line
CML540	CIMMYT/ Zimbabwe	inbred line
DT-STR-W-SYN11	IITA/Nigeria	OPV
DT-STR-W-SYN12	IITA/Nigeria	OPV
DT-STR-W-SYN13	IITA/Nigeria	OPV
DT-STR-Y-SYN14	IITA/Nigeria	OPV
IWDC3 SYN Z1 WHITable DT STR SYN-DTC1	IITA/Nigeria	OPV
PAN6326R	South Africa	Hybrid (GMO)
PAN6823	South Africa	Hybrid (GMO)
SAMMAZ-16	IITA/Nigeria	OPV
STR SYN-WI	IITA/Nigeria	OPV
STR-SYN-YZ	IITA/Nigeria	OPV
SYN-12	IITA/Nigeria	OPV
T81	Unknown/South Africa	inbred line
TZ COM1/ZDP	IITA/Nigeria	OPV
TZ-21	SARIA/ Tanzania	inbred line
TZ-22	SARIA/ Tanzania	inbred line
TZ-3	SARIA/ Tanzania	inbred line
TZ-30	SARIA/ Tanzania	inbred line
TZ-35	SARIA/ Tanzania	inbred line
TZ-38	SARIA/ Tanzania	inbred line
TZ-41	SARIA/ Tanzania	inbred line
TZ-44	SARIA/ Tanzania	inbred line
TZ-46	SARIA/ Tanzania	inbred line
TZ-5	SARIA/ Tanzania	inbred line

(Continued)

TABLE 1 Continued

Genotype designation/ pedigree	Origin/ Source	Genotype description
TZ-50	SARIA/ Tanzania	inbred line
TZE (OMP3DT/WHITable DT STRSYN)CZ	IITA/Nigeria	OPV
TZE COMP5C7/TZE COMP39TCZ	IITA/Nigeria	OPV
TZECOMP	IITA/Nigeria	OPV
TZECOMP3 DT-C2	IITA/Nigeria	OPV
TZL (OMP1-WCB2 WHITEDT STR SYN)D1C1	IITA/Nigeria	OPV
UK1-2-2	Unknown/South Africa	OPV
UK1-3	Unknown/South Africa	OPV
UK1-33	Unknown/South Africa	OPV
UK1-4	Unknown/South Africa	OPV
UK1-55	Unknown/South Africa	OPV
UK1-6	Unknown/South Africa	OPV
ZDIPLOC4-C3-W	IITA/Nigeria	OPV
Z-DIPLO-BC4-C3-W-DTC1	IITA/Nigeria	IITA/Nigeria

CIMMYT, International Maize and Wheat Improvement Centre/Zimbabwe; IITable, International Institute of Tropical Agriculture/Nigeria; OPV, open-pollinated variety, SARIA, Selian Agricultural Research Institute in Arusha/Tanzania.

While the inter-row spacing aligns with common maize production practices in South Africa, the wider intra-row spacing resulted in a lower plant population than typically recommended for Southern Sub-Saharan Africa. This spacing was intentionally adopted to reduce inter-plant competition and allow clearer expression of genotypic differences in carbon-related traits. Standard agronomic practices were used in the two locations according to maize production guidelines in South Africa (Du Plessis, 2003). Supplementary irrigation was applied based on soil moisture measurements using water sensors (HOBO UX120, Onset, Bourne, MA, USA). Water was applied in the morning to maintain optimal soil moisture without waterlogging, ensuring uniform growth conditions for all genotypes.

2.4 Data collection

2.4.1 Agronomic traits

The following agronomic data were collected: days to 50% flowering (DTF) recorded as the number of days from planting to when 50% of the genotypes in each plot had fully exerted panicles; days to 50% maturity (DTM) were recorded as the number of days from planting to when 50% of the genotypes in each plot reaches physiological maturity. Plant height (PH) was recorded in centimeters (cm) as an average measurement of three randomly selected plants from the soil surface to the tip of the tassel after the plants

TABLE 2 Monthly weather data during the field trials at Silverton, Ukulinga and Bethlehem, South Africa, during 2022/2023 growing seasons.

Location	Month	Year	Rainfall (mm)	Tmax (°C)	Tmin (°C)	RH (%)
Ukulinga	November	2022	121	23	14	79
	December	2022	137	25	15	81
	January	2023	140	25	16	83
	February	2023	118	26	17	82
	March	2023	106	25	16	80
	April	2023	62	23	13	77
	May	2023	32	22	9	70
Bethlehem	November	2022	109	25	11	56
	December	2022	150	25	13	63
	January	2023	148	25	14	68
	February	2023	102	25	14	67
	March	2023	97	24	12	65
	April	2023	55	21	9	62
	May	2023	27	18	5	56

Tmax, average maximum temperature; Tmin, average minimum temperature; RH, relative humidity.

reached physiological maturity. Shoot biomass (SB) was recorded as the total mass of the above-ground biomass cut from the base to the tip of the plant, excluding the grain. The shoots were oven-dried at 70 °C for 48 hours, weighed and expressed in g plant⁻¹. Root biomass (RB) was recorded as the total root dry matter harvested per genotype per plot, with roots collected up to a depth of 50 cm. This depth was

chosen because over 80% of maize root biomass is typically concentrated in the top 50 cm of soil (Wang et al., 2018), which captures the majority of root carbon and nutrient acquisition (Zhang et al., 2018). The roots were separated from the soil by hand and washed under running water to remove all soil particles. The remaining soil was mixed with water, and the suspension was sieved through a 2 mm sieve. Fine roots were collected from the sieve residue and added to the large roots. The roots were oven-dried at 60 °C for 72 hours. The dried roots were weighed on a balance to get the RB was adjusted to t ha⁻¹. Total plant biomass (PB) was the sum of all dry plant material for each genotype including RB and SB harvested from the test plots and recorded in t ha⁻¹. Root-to-shoot biomass ratio (RS) was recorded as the ratio of the root biomass produced per plant to shoot biomass produced. Grain yield (GY) was recorded as the weight of harvested grain at 12.5% moisture content per genotype per plot and expressed in t ha⁻¹. Harvest index (HI) was computed as the ratio of grain production to total above-ground plant biomass.

2.4.2 Carbon stocks parameters

Twenty-five maize genotypes, comprising 10 high-yielding, 10 low-yielding, and five other genotypes chosen randomly from a pool of 45 genotypes, were used for carbon analysis, conducted with two replications. This selection provided a representative range of biomass and yield potential while remaining cost-effective. Grain, shoot and root samples were collected to measure the carbon contents of grain (GCc), shoot (SCc) and root (RCc), respectively. These samples were oven-dried at 70 °C for 48 hours and grounded into a fine powder, each weighing five grams, using a ZM 200 ultra-centrifugal mill. The total carbon content of shoot, root, and grain samples was determined by combustion using a LECO TruMac CNS Analyzer (Rayment and Lyons, 2011). The grain (GCs), shoot (SCs) and root (RCs) carbon stocks were computed as the total amount of C measured in the respective plant parts according to Grever et al. (2018). These C stocks in the two parts (SCs and RCs) were summed up to derive total plant carbon stocks (PCs).

TABLE 3 Soil properties for the environments used in the present study.

Location	Soil properties	Field conditions
Ukulinga	Bulk density (g cm ⁻³)	1.04
	Phosphorus (mg/l)	39
	Potassium (mg/l)	241
	Nitrogen (%)	0.23
	Calcium (mg/l)	1453
	Magnesium (mg/l)	369
	pH	4.56
	Clay (%)	28
	Organic carbon (%)	2.6
	Carbon-to-nitrogen ratio	7.67
	Electrical Conductivity	11.02
Bethlehem	Bulk density (g cm ⁻³)	1.34
	Phosphorus (mg/l)	2.7
	Potassium (mg/l)	206
	Nitrogen (%)	0.36
	Calcium (mg/l)	848
	Magnesium (mg/l)	197
	pH	5.8
	Clay (%)	15
	Organic carbon (%)	1.49
	Carbon-to-nitrogen ratio	6.33
	Electrical Conductivity	10.56

2.5 Data analysis

Data were subjected to analysis of variance using the Statistical Analysis System (SAS) software version 9.4 program with the lattice procedure (Guide, 2014). A combined analysis of variance was conducted after testing the homogeneity of variance using Levene's test procedure (Levene, 1960). Variance components for agronomic and carbon storage traits were estimated based on combined and single environment analyses, respectively. Pearson's correlation coefficients were calculated separately to examine the magnitude and trend of the relationship between agronomic traits using R statistical software. Pearson's correlation coefficients were performed on R statistical software to explore the magnitude of relationship between carbon storage traits.

2.5.1 Estimation of phenotypic and genotypic variance

Phenotypic and genotypic variance for agronomic traits were calculated from the results of a combined analysis of variance according to Rahimi and Hernandez (2022):

$$\begin{aligned}\sigma_p^2 &= \sigma_g^2 + \sigma_{ge}^2 + \sigma_e^2 \\ \sigma_g^2 &= \left(\frac{MSg - MSge}{r * e} \right) \\ \sigma_{ge}^2 &= \left(\frac{MSge - MSe}{r} \right) \\ \sigma_e^2 &= MSe\end{aligned}$$

Where; σ_e^2 is the environmental variance; σ_{ge}^2 is the genotype x environment interaction variance; σ_g^2 is the genotypic variance; σ_p^2 is the phenotypic variance; MS_e is the mean square of the environment; MS_{ge} is the mean square of genotype x environment; MS_g is the mean square of genotype; r = number of replications; and e = number of locations/environments.

Phenotypic and genotypic variance for carbon storage traits were calculated from the results of a single environment analysis of variance, as suggested by Burton and DeVane (1953).

$$\begin{aligned}\Sigma_p^2 &= \sigma_g^2 + \sigma_e^2 \\ \sigma_g^2 &= \frac{MSg - MSE}{r} \\ \sigma_e^2 &= MSE\end{aligned}$$

Where MSE is the mean square error and σ_e^2 is the error variance component.

2.5.2 Estimation of coefficient of variability

Phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) expressed in percent were computed according to Burton and DeVane (1953):

$$PCV = \left(\frac{\sigma_p}{\bar{x}} \right) * 100$$

$$GCV = \left(\frac{\sigma_g}{\bar{x}} \right) * 100$$

Where σ_g is the genotypic standard deviation; σ_p is the phenotypic standard deviation, and $\bar{x}$ is the mean.

2.5.3 Heritability and genetic advance

The broad-sense heritability of a given trait in a single environment was calculated according to Alvarado et al. (2020):

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2/r}$$

Where σ_g^2 is the genotypic variance; σ_e^2 is the error variance component, and r is the number of replications, whereas regarding combined analyses, broad-sense heritability was calculated as:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_{ge}^2/e + \sigma_e^2/(r * e)}$$

Where σ_{ge}^2 is the genotype x environment interaction and e is the number of sites (environments).

Genetic advance (GA) and the genetic advance as a percent of the mean (GAM) were computed using the following formulae (Allard, 1999):

$GA = K \quad H^2 \sigma_p \quad GAM = \left(\frac{GA}{\bar{x}} \right) * 100$ Where K is 2.06 at 5% selection intensity.

3 Results

3.1 Analysis of variance

3.1.1 Agronomic traits

The analysis of variance showed significant ($p < 0.05$) differences among the maize genotypes for all the assessed agronomic traits (Table 4). The genotype x location interaction was significant ($p < 0.05$) for all the traits except DTF, DTM and PH (Table 4).

3.1.2 Carbon storage traits

Table 3 presented mean square values and significant tests of 25 tested maize genotypes. There was a significant genetic variation in maize for all the carbon variables ($P < 0.05$) except for RCc, and GCc (Table 5).

3.2 Performance of maize genotypes for agronomic traits and carbon allocation

3.2.1 Agronomic performance

The mean agronomic performances of the top 10 and bottom 5 performing maize genotypes across the two environmental

TABLE 4 A combined analysis of variance and significance tests for agronomic traits of 45 diverse maize genotypes across two locations in South Africa.

SOV	df	DTF	DTM	PH	GY	SB	RB	HI	RS	PB
Replication in locations	1	13.34	25.69	2317.9	0.047	3.84	9.826	0.552	0.001766	1.38
Block	4	102.67**	59.10	544.8	183.956***	649.30***	362.722***	32.499**	0.009390	1963.17***
Genotype	44	58.69***	61.23*	3613.5***	499.608***	1416.03***	358.701***	201.302***	0.014701***	3075.89***
Location	1	0.05	25.69	2782.7	702.228***	20176.93***	4574.674***	1752.025***	0.008109	43966.49***
Genotype x location	44	26.67	39.28	768.6	159.719***	976.71***	340.550***	167.045***	0.010326***	2397.40***
Residual	89	21.17	35.46	850.9	8.977	31.90	7.100	7.615	0.004345	50.73
Trial statistics										
CV (%)		7.83	5.37	14.94	8.72	9.60	9.10	7.27	13.03	8.08
LSD (5%)		9.14	1.79	8.76	0.89	1.69	0.80	0.83	0.02	2.13

* Significant at $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; SOV, source of variation; df, degrees of freedom; CV, coefficient of variation; DTF, days to 50% flowering; DTM, days to 50% maturity; PH, plant height (cm); PB, total plant biomass (g plant^{-1}); SB, shoot biomass (g plant^{-1}); RB, root biomass (g plant^{-1}); RS, root to shoot biomass ratio; GY, grain yield (g plant^{-1}); HI, harvest index (%); LSD, least significant difference.

conditions are presented in Table 6. The mean DTF and DTM were 58.79 and 110.64 days, respectively. Genotypes, TZE (OMP3DT/WHITE DT STRSYN)CZ (51 days) and TZ-38 (53 days) were recorded as the earliest flowering genotypes. The earliest maturing genotypes were ZDIPLOBC4-C3-W, UK1-6 and UK1-33, which reached 50% maturity at 101, 103 and 104 days, respectively (Supplementary Table 1). Plant height of the evaluated maize genotypes varied from 131.42 cm, observed in genotype UK1-6 to 252.25 cm, recorded in genotype ZDIPLOBC4-C3-W. The mean plant height for the evaluated genotypes was 195.28 cm across the two locations. The evaluated maize genotypes' mean grain yield (GY) was 1.87 t ha^{-1} (Supplementary Table 1).

Grain yield varied from 0.92 to 3.30 t ha^{-1} , with genotypes TZE COMP3 DT-C2, TZE (OMP3DT/WHITE DT STRSYN)CZ and DT-STR-Y-SYN14 recording the highest grain yield of 3.30 t ha^{-1} , 3.10 t ha^{-1} and 2.91 t ha^{-1} , respectively. The mean shoot biomass across the two locations ranged from 1.72 to 5.42 t ha^{-1} . The highest shoot biomass production was recorded for TZE (OMP3DT/WHITE DT STRSYN)CZ, 9022-13 and TZL (OMP1-WCB2 WHITEDT STR SYN)D1C1 with mean values of 5.42 , 5.21 and 5.09 t ha^{-1} , respectively (Supplementary Table 1). The mean root biomass for all the 45 maize genotypes was 1.56 t ha^{-1} , with a minimum of 0.88 t ha^{-1} recorded in TZ-5 and a maximum of 3.12 t ha^{-1} observed in genotype TZL (OMP1-WCB2 WHITEDT STR SYN)D1C1. The total plant biomass varied between 3.72 and 11.47 t ha^{-1} (Supplementary Table 1), with

genotypes TZE (OMP3DT/WHITE DT STRSYN)CZ, TZL (OMP1-WCB2 WHITEDT STR SYN)D1C1 and 9022-13 recording the highest total plant biomass production of 11.47 , 10.33 and 10.17 t ha^{-1} , respectively (Supplementary Table 1).

3.2.2 Carbon storage traits

The mean performance of the top 10 and bottom 5 maize genotypes for carbon storage (SCc, RCc, GCc, PCs, SCs, RCs, RCs/SCs, and GCc) is presented in Table 7. The grain carbon ranged from 43.83 for TZ-5 to 45.37% for UK1-6, with a mean of 44.55% (Supplementary Table 2). The highest root carbon content was observed for CML540, UK1-6 and ZDIPLO-BC4-C3-W-DTC1, with mean values of 47.18 , 47.02 and 46.65% , respectively, whilst the lowest root carbon content was recorded for DT-STR-Y-SYN14 (40.41%), TZ COM1/ZDP (36.76%) and 9022-13 (35.58%) (Supplementary Table 2).

The grain carbon stocks varied from 0.43 t ha^{-1} for genotype CKDHL0378 to 1.47 t ha^{-1} for genotype TZE COMP3 DT-C2, with a mean of 0.68 t ha^{-1} (Supplementary Table 2). The highest grain carbon stock was recorded for genotype TZE COMP3 DT-C2 (1.47 t ha^{-1}), followed by DT-STR-Y-SYN14 (1.31 t ha^{-1}), whilst the lowest GCs were recorded for genotypes TZ-35 (0.46 t/ha), TZ-41 (0.45 t ha^{-1}), and CKDHL037 (0.43 t ha^{-1}) (Supplementary Table 2). The shoot carbon stock of the tested maize genotypes ranged between 0.76 t ha^{-1} and 2.29 t ha^{-1} (Supplementary Table 2).

TABLE 5 Analysis of variance and significance tests for the 25 tested genotypes and significance tests for carbon stocks.

SOV	df	GCc	SCc	RCc	GCs	SCs	RCs	RCs/SCs	PCs
Replication	1	0.11	0.33	5.70	281.30	145.00	17.66	0.28	224.80
Block	2	0.23	1.82*	36.90*	307.70	1334.00*	30.49	0.18	1858.80*
Genotype	24	0.45	1.20*	15.59	546.20*	627.40*	18.72	0.40*	762.10*
Residual	21	0.33	0.53	10.69	212.10	277.60	11.34	0.37	350.40
Trial statistics									
CV		1.30	1.72	7.38	64.77	76.91	40.78	97.39	62.91
LSD (5%)		2.32	0.63	3.24	9.44	8.23	7.64	6.22	8.35

* Significant at $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; SOV, source of variation; df, degrees of freedom; CV, coefficient of variation; PCs, total plant carbon stocks; SCs, shoot carbon stock; RCs, root carbon stock; RCs/SCs, root to shoot carbon stock ratio; GCs, grain carbon stock; SCc, shoot carbon content; RCc, root carbon content; GCc, grain carbon content; LSD, least significant difference.

TABLE 6 Mean values for nine agronomic traits of the 10 best-selected genotypes and five bottom-performing genotypes based on grain yield (GY) after evaluating 45 maize genotypes across two locations in South Africa during the 2022/23 growing season.

Maize genotype	DTF	DTM	PH	GY	SB	RB	HI	RS	PB
Top 10 genotypes									
TZCOMP3 DT-C2	60	112.25	212.33	3.3	4	2.08	45.22	0.47	9.38
TZE (OMP3DT/WHITable DT STRSYN)CZ	50.75	112.5	222.58	3.1	5.42	2.95	37.49	0.52	11.47
DT-STR-Y-SYN14	64	108.25	201.83	2.91	3.18	1.58	48.77	0.49	7.67
9022-13	59	108.75	213.92	2.78	5.21	2.34	34.57	0.45	10.33
TZ-44	57.25	105.75	199.67	2.69	3.44	1.37	44.64	0.42	7.49
TZ COM1/ZDP	58.5	110.75	200.67	2.6	3.97	1.37	39.03	0.34	7.94
ZDIPLOBC4-C3-W	55	101	252.25	2.47	4.56	2.18	35.26	0.47	9.21
T81	60	111	212.5	2.42	3.77	1.51	39.12	0.4	7.7
TZ-30	56	107.25	250.75	2.32	3.92	1.91	36.99	0.48	8.15
DT-STR-W-SYN11	56.5	109.5	218.63	2.23	4.34	2.45	39.07	0.59	9.01
Bottom 5 genotypes									
UK1-55	58	111	175.08	1.06	2.19	1.1	34.85	0.52	4.34
TZ-41	56.75	118.5	203.5	1.02	1.82	1.09	36	0.6	3.93
TZ-35	55	108.75	157	1.02	1.95	0.99	34.21	0.51	3.95
CKDHL0378	55	120	177.25	0.95	1.78	0.99	35.99	0.56	3.72
CML393	64.5	111.75	145.37	0.92	2.93	1.91	25.88	0.67	5.76
Summary statistics									
Mean	58.79	110.64	195.28	1.83	3.14	1.56	37.87	0.51	6.53
Median	58.75	110.5	200.67	1.73	3.08	1.48	36.99	0.5	6.36
Minimum	50.75	101	131.42	0.92	1.72	0.88	23.8	0.34	3.72
Maximum	67.25	120	252.25	3.3	5.42	3.12	51.86	0.67	11.47
Q1	55.5	108.25	179.5	1.49	2.29	1.21	33.96	0.47	5.2
Q3	61.5	113	212.33	2.17	3.77	1.88	41.86	0.55	7.68
SD	3.96	3.89	28.87	0.58	0.98	0.51	6.69	0.06	1.83
SE	0.59	0.58	4.3	0.09	0.15	0.08	1.00	0.01	0.27
cv%	6.73	3.52	14.79	31.59	31.17	32.37	17.67	11.79	28.07
Skewness	0.27	-0.08	-0.39	0.60	0.48	1.20	0.14	0.04	0.67
Kurtosis	-0.62	0.33	-0.04	0.00	-0.42	1.58	-0.2	1.13	0.12

SD, standard deviation; SE, standard error; DTF, days to 50% flowering; DTM, days to 50% maturity; PH, plant height (cm); PB, total plant biomass (g plant⁻¹); SB, shoot biomass (g plant⁻¹); RB, root biomass (g plant⁻¹); RS, root to shoot biomass ratio; GY, grain yield (g plant⁻¹); HI, harvest index (%).

The genotypes that allocated more carbon to the shoots with the highest shoot carbon stock were TZE (OMP3DT/WHITE DT STRSYN)CZ, 9022-13, and ZDIPLOBC4-C3-W, with mean values of 2.29, 2.23, and 1.94 t ha⁻¹, respectively (Supplementary Table 2).

The mean root carbon stock for the tested maize genotypes was 0.68 t ha⁻¹ (Supplementary Table 2). The highest root carbon stock was observed for genotype TZE (OMP3DT/WHITE DT STRSYN)CZ (1.25 t ha⁻¹) followed by ZDIPLOBC4-C3-W (1.00 t ha⁻¹) and ZDIPLO-BC4-C3-W-DTC1 (0.98 t ha⁻¹), whilst the lowest root carbon stock was recorded for TZ-5 (0.37 t ha⁻¹). The total plant carbon stocks varied from 1.13 t ha⁻¹ and 3.55 t ha⁻¹, with a mean value of 2.05 t ha⁻¹ (Supplementary Table 2). The maize genotypes which sequestered more carbon with the highest total plant carbon stock were TZE (OMP3DT/WHITE DT STRSYN)CZ, 9022-13, and ZDIPLOBC4-C3-W, with mean values of 3.55, 3.06, and 2.94 t ha⁻¹, respectively, whilst the lowest mean PCs values were recorded for

TZ-41 (1.26 t ha⁻¹), CKDHL0378 (1.20 t ha⁻¹), and TZ-5 (1.13 t ha⁻¹) (Supplementary Table 2).

3.3 Variance components, heritability, and genetic advance for agronomic traits

The phenotypic coefficient of variation (PCV) and genotypic coefficient of variation (GCV) for the assessed traits ranged from 6.67 to 88.11% and 4.23 to 53.67%, respectively (Table 8). The PCV and GCV values in the present study were categorized as low when less than 10%, moderate when between 10–20%, and high when greater than 20%. The highest PCV values were recorded for total plant biomass (88.11%), followed by HI (83.05%), GY (80.83%), RB (80.25%), and SB (75.41%) (Table 8). The highest GCV values were recorded for GY (53.67%), SB (35.61%), PB (29.56%), and PH (27.31%). The remaining traits had either low or medium PCV and

TABLE 7 Mean values for carbon storage traits of the best ten genotypes and bottom five genotypes arranged based on total plant carbon stock.

Maize genotype	GC _c	SC _c	RC _c	GC _s	SC _s	RC _s	RC _s /SC _s	PC _s
Top 10 genotypes								
TZE (OMP3DT/WHITable DT STRSYN)CZ	44.08	42.32	42.49	1.37	2.29	1.25	0.55	3.55
9022-13	44.39	42.68	35.58	1.23	2.23	0.83	0.37	3.06
ZDIPLOCB4-C3-W	44.98	42.57	45.70	1.11	1.94	1.00	0.51	2.94
ZDIPLO-BC4-C3-W-DTC1	45.24	42.33	46.65	0.56	1.84	0.98	0.53	2.82
TZE COMP5C7/TZE COMP39TCZ	44.83	41.21	46.50	0.75	1.82	0.91	0.50	2.73
CML540	43.92	41.98	47.18	0.92	1.70	0.90	0.53	2.59
TZCOMP3 DT-C2	44.59	41.53	43.00	1.47	1.66	0.90	0.54	2.56
TZ-30	45.33	42.36	45.72	1.05	1.66	0.87	0.53	2.53
TZ-50	44.34	43.92	46.07	0.51	1.55	0.79	0.51	2.34
SAMMAZ-16	45.09	40.70	42.45	0.77	1.37	0.80	0.58	2.17
Bottom 5 genotypes								
UK1-6	45.37	43.07	47.02	0.68	0.82	0.45	0.55	1.27
TZ-35	44.62	42.30	44.48	0.46	0.82	0.44	0.53	1.26
TZ-41	43.98	42.31	44.67	0.45	0.77	0.49	0.63	1.26
CKDHL0378	44.91	42.77	44.32	0.43	0.76	0.44	0.57	1.20
TZ-5	43.82	42.59	42.36	0.82	0.76	0.37	0.49	1.13
Summary statistics								
mean	44.55	42.30	44.29	0.86	1.36	0.68	0.51	2.05
SD	0.48	0.81	3.02	0.31	0.47	0.23	0.07	0.68
SE	0.10	0.16	0.60	0.06	0.09	0.05	0.01	0.14
Skewness	0.06	-0.12	-1.71	0.36	0.26	0.68	-1.21	0.35
kurtosis	-1.10	-0.27	2.70	-0.93	-0.93	-0.14	2.60	-0.78

SD, standard deviation; SE, standard error; GC_c, grain carbon content (%); SC_c, shoot carbon content (%); RC_c, root carbon content (%); GC_s, grain carbon stock (t/ha); SC_s, shoot carbon stock (t/ha); RC_s, root carbon stock (t/ha); RC_s/SC_s, root to shoot carbon stock ratio; PC_s, total plant carbon stocks (t/ha).

GCV values. Furthermore, the heritability estimates were categorized as low (0–30%), moderate (30–60%), and high (60% and above). In the present study, the highest broad sense heritability (H^2) was recorded for DTF (70.56%) and by PH (61.57%), medium H^2 were recorded for GY (44.09%), DTM (40.32%), and RS (32.19%). The lowest H^2 values

were recorded for RB, PB, HI, and SB, with values of 0.73%, 2.84%, 3.45%, and 3.99%, respectively. The highest genetic advance values (GA) were recorded for plant height (86.22), while grain yield exhibited a moderate GA value of 25.22. The remaining agronomic traits showed very low genetic advance (<10). The highest and

TABLE 8 Variance components, heritability and genetic advance for nine agronomic traits of 45 maize genotypes assessed under different South African agro-ecological zones during the 2022/23 growing season.

Traits	Parameters								
	σ_p^2	σ_g^2	σ_e^2	σ_{ge}^2	PCV	GCV	H^2	EGA	GAM
DTF	45.38	32.02	0.05	13.31	11.46	9.63	70.56	9.79	16.66
DTM	54.44	21.95	25.69	6.80	6.67	4.23	40.32	6.13	5.54
PH	4620.55	2844.90	2782.70	-1007.05	34.81	27.31	61.57	86.22	44.15
GY	770.86	339.89	702.23	-271.25	80.83	53.67	44.09	25.22	73.42
SB	11016.14	439.32	20176.93	-9600.11	75.41	35.61	3.99	8.62	14.65
RB	2475.76	18.15	4574.67	-2117.06	80.25	14.56	0.73	0.75	2.57
HI	993.79	34.26	1752.03	-792.49	83.05	15.42	3.45	2.24	5.90
RS	0.01	0.004	0.01	0.001	22.86	12.97	32.19	0.08	15.16
PB	23860.44	678.49	43966.49	-20784.55	88.11	29.56	2.84	9.05	10.27

DTF, days to 50% flowering; DTM, days to 50% maturity; PH, plant height (cm); GY, grain yield (g plant⁻¹); SB, shoot biomass (g plant⁻¹); RB, root biomass (g plant⁻¹); HI, harvest index (%); RS, root to shoot biomass ratio; PB, total plant biomass (g plant⁻¹); σ_p^2 = phenotypic variance, σ_g^2 = genotypic variance, σ_e^2 = environmental variance, σ_{ge}^2 = genotype by environment interaction variance, PCV, phenotypic coefficient of variation; GCV, genotypic coefficient of variation; H^2 , broad sense heritability; GA, genetic advance; GAM, genetic advance as a percentage of the mean.

moderate genetic advance as a percentage of the mean (GAM) was recorded for GY (73.42%) and PH (44.15%), respectively. Combined high H^2 and GA values were recorded for DTF (70.56%) and PH (86.22%), respectively (Table 8).

3.4 Variance components, heritability, and genetic advance for carbon storage traits

The PCV and GCV values in the present study were categorized as low when less than 10%, moderate when between 10–20%, and high when greater than 20% (Table 9). The highest PCV were recorded for GCs (88.71%), RCs/SCs (83.60%), SCs (80.11%), and PCs (76.96%). The highest GCV values were recorded for GCs (86.86%), SCs (64.73%), RCs/SCs (23.76%) and PCs (46.82%) (Table 9). Both PCV and GCV values were very low for GCc (1.40%, 0.55%), SCc (2.20%, 1.37%), and RCc (8.18%, 3.53%) in that order. Meanwhile, traits such as RCs (37.96%, 18.81%) had moderate PCV and GCV. Furthermore, the heritability estimates were categorized as low (0–30%), moderate (30–60%) and high (60% and above). In the present analysis, moderate heritability was recorded for GCs (44.06%), SCc (38.733%), SCs (38.65%), and PCs (37.01%), while RCs (24.55%), RCc (18.65%), and GCc (15.38%) had moderate heritability. Very low heritability was recorded for RCs/SCs (3.9%) (Table 9). High genetic advance values were recorded for PCs, GCs, and SCs, with values of 17.98, 17.67, and 16.94%, respectively. Very low genetic advance was reported in RCs/SCs, GCc, SCc, RCc, and RCs with values of 0.05, 0.20, 0.74, 1.39, and 1.96, respectively. The following traits exhibited the highest GAM values: GCs (80.51%), SCs (82.9%), and PCs (58.67%) had the highest GAM. While moderate to low GAM values were recorded for RCs (19.2%) and RCs/SCs (9.66%) GCc (0.44%), SCc (1.75%), RCc (3.14) (Table 9).

3.5 Correlation analysis

3.5.1 Agronomic traits

Pearson's correlation coefficient I showed the relationship among eight agronomic traits of 45 maize genotypes evaluated across the two locations in South Africa (Figure 1). Grain yield showed a positive correlation with PH ($r = 0.42$, $p < 0.01$), SB ($r = 0.58$, $p < 0.001$), RB ($r =$

0.44, $p < 0.01$), HI ($r = 0.48$, $p < 0.001$) and PB ($r = 0.54$, $p < 0.001$), and a significant negative correlation with RS ($r = -0.47$, $p < 0.01$) (Figure 1). In addition, RB exhibited a strong and significant ($p < 0.001$) correlation with SB ($r = 0.91$) and PB ($r = 0.98$).

3.5.2 Carbon storage traits

Pearson correlation between the carbon allocation and storage traits of the 25 tested genotypes is presented in Figure 2. The grain carbon content showed a significant ($p < 0.05$) and negative correlation with shoot carbon content ($r = -0.45$). Carbon content traits, including grain carbon content, shoot carbon content and root carbon content, exhibited non-significant correlation with root carbon stocks, shoot carbon stocks and total plant carbon stocks. Shoot carbon stocks were strongly correlated with root carbon stocks ($r = 0.94$, $p < 0.001$) and total plant carbon stocks ($r = 0.99$, $p < 0.001$) (Figure 2). Furthermore, the results indicated that there is no strong or consistent relationship observed between earliness and carbon storage capacity (Figure 2).

3.6 Principal component analysis

3.6.1 Agronomic traits

The interrelationships between agronomic traits and 45 maize genotypes were explored by principal component biplot analysis (PCA-biplot) (Figure 3). The first two PCs with Eigen value greater than one accounted for 68.13% (Table 10). The PCA showed that the first principal component (PC1) explains 45.24% of the total variation and exhibited a positive association with DTM, DTF, PH, GY, SB, RB and PB. Smaller angles between dimension vectors in the same direction suggest a strong correlation between the traits in terms of their ability to discriminate genotypes. The principal component 2 (PC2) accounted for 22.89% of the data variation and had a strong positive correlation with DTM, DTF and RS, and a negative association with HI and GY (Figure 3). Genotypes that perform well in a particular trait are plotted closer to the trait and furthest to the vector line. Genotypes TZECOMP3 DT-C2 (1), TZE (OMP3DT/WHITE DT STRSYN)CZ (2) and DT-STR-Y-SYN14 (3) were grouped together based on high grain yield GY, SB and PB exhibited positive correlation (Figure 3). The agronomic traits that contributed the most

TABLE 9 Variance components, heritability and genetic advance for carbon storage traits of twenty-five maize genotypes selected from a pool of 45 maize genotypes based of yield potential.

Parameters	σ_p^2	σ_g^2	σ_e^2	PCV	GCV	H^2	EGA	GAM
GC _c	0.39	0.06	0.33	1.40	0.55	15.38	0.20	0.44
SC _c	0.87	0.34	0.53	2.20	1.37	38.73	0.74	1.75
RC _c	13.14	2.45	10.69	8.18	3.53	18.65	1.39	3.14
GC _s	379.15	167.05	212.10	88.71	86.86	44.06	17.67	80.51
SC _s	452.50	174.90	277.60	80.11	64.73	38.65	16.94	82.90
RC _s	15.03	3.69	11.34	37.96	18.81	24.55	1.96	19.20
RC _s /SC _s	0.39	0.02	0.37	83.60	23.76	3.90	0.05	9.66
PC _s	556.25	205.85	350.40	76.96	46.82	37.01	17.98	58.67

GC_c, grain carbon content (%); SC_c, shoot carbon content (%); RC_c, root carbon content (%); GC_s, grain carbon stock (g plant⁻¹); SC_s, shoot carbon stock (g plant⁻¹); RC_s, root carbon stock (g plant⁻¹); RC_s/SC_s, root to shoot carbon stock ratio; PC_s, total plant carbon stocks (g plant⁻¹); σ_p^2 = phenotypic variance, σ_g^2 = genotypic variance, PCV, phenotypic coefficient of variation; GCV, genotypic coefficient of variation; H^2 , broad sense heritability; GA, genetic advance; GAM, genetic advance as a percentage of the mean.

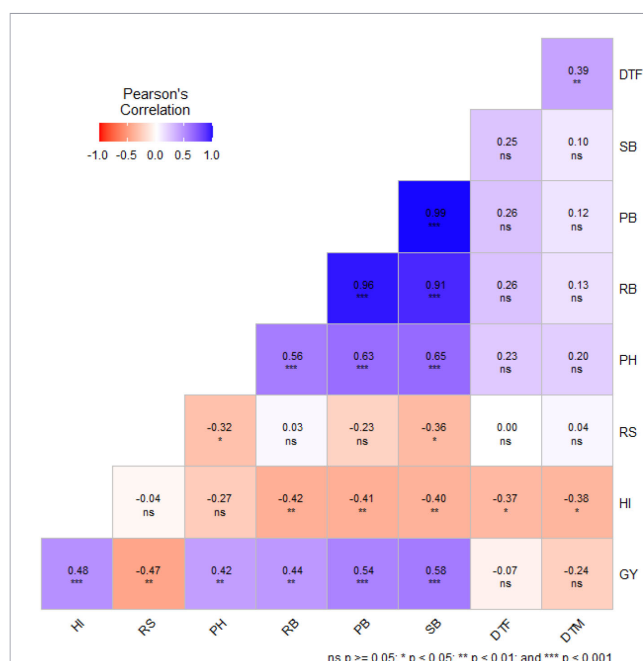


FIGURE 1

Pearson correlation plot showing the association of eight agronomic traits of 45 maize genotypes evaluated across two locations in South Africa. The colour variation indicates the magnitude of correlations; traits with deep blue are strongly and positively correlated, while deep red is strongly negatively correlated. *, **, and *** denote the level of significance associations of traits at 0.05, 0.01, and <0.001 probability values, respectively, and ns, non-significant; DTF, days to 50% flowering; DTM, days to 50% maturity; PH, plant height; PB, total plant biomass; SB, shoot biomass; RB, root biomass; RS, root to shoot biomass ratio; GY, grain yield; HI, harvest index.

in PC4 were DTF (0.75) and DTM (0.63). Genotypes TZ-35, CKDHL0378 and CML393 were grouped together and possessed high RS (Figure 3).

3.6.2 Carbon storage traits

The interrelationship between carbon allocation traits and 25 tested maize genotypes was evaluated using a principal component biplot analysis (PCA) (Figure 4). Four principal components (PC1 to PC4) attributed to 88.76% of the total variation for carbon storage traits (Table 11). The PCA showed that the first principal component (Dim 1) explains 40.68% of the data variation and positively correlated with RCs, PCs, SCs, GCs and GCc. In addition, the second principal component accounts for 21.17% of the total variation and had a higher positive correlation with RCc, RCc/SCs and SCc (Figure 4). The GCs and GCc were strongly negatively associated with RCc, RCc/SCs and SCc (Figure 4). The carbon storage traits that contributed the most in PC3 were GCs (0.20), RCc (0.88) and RCs (0.33). The maize genotypes TZ-35, UK1-6 and TZECOMP3 DT-C2 strongly associated with RCs, PCs and SCs (Figure 4).

4 Discussion

4.1 Agronomic performance of maize genotypes

Maize cultivars with high yield and carbon sequestration potential can sustain maize production and productivity in the

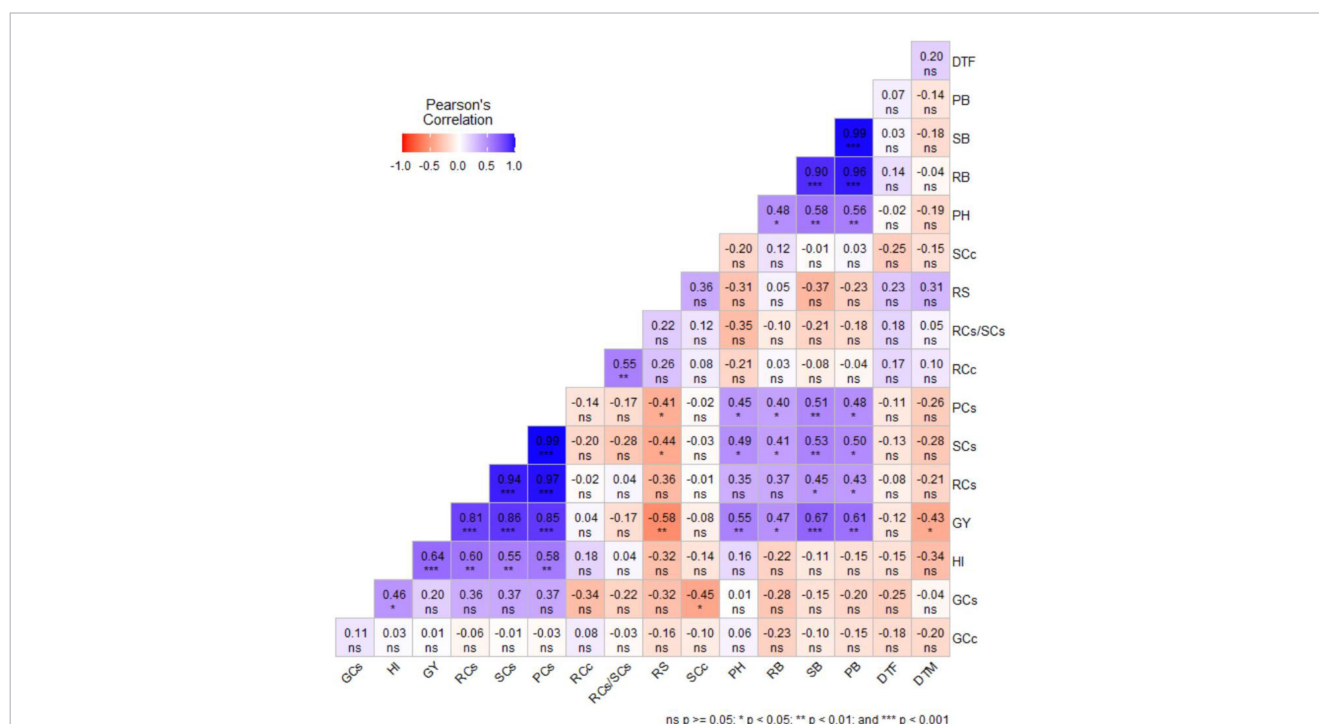


FIGURE 2

Pearson correlation coefficient between agronomic traits and carbon storage traits of the 25 selected maize genotypes. The colour variation indicates the magnitude of correlations; traits with deep blue are strongly and positively correlated, while deep red is strongly negatively correlated. *, **, and *** denote the level of significance associations of traits at 0.05, 0.01, and <0.001 probability values, respectively, and ns, non-significant. SCc, shoot carbon content; RCc, root carbon content; GCc, grain carbon content; PCs, total plant carbon stocks; SCs, shoot carbon stock; RCs, root carbon stock; RCs/SCs, root to shoot carbon stock ratio; GCs, grain carbon stock.

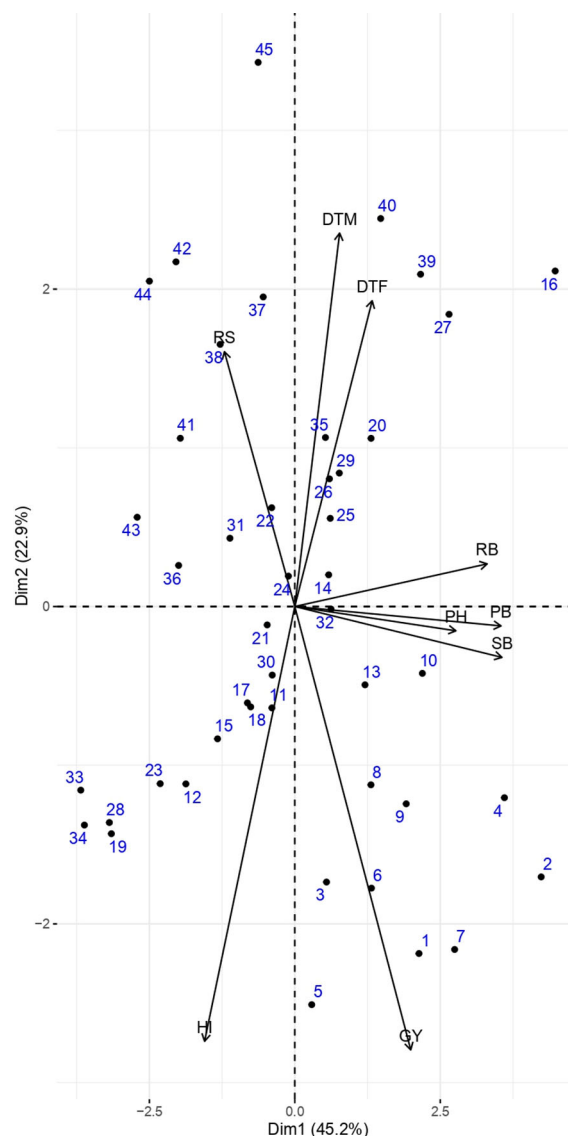


FIGURE 3

Principal component biplot analysis showing the relationship between agronomic traits and 45 maize genotypes evaluated under two environmental conditions in South Africa. DTF, days to 50% flowering; DTM, days to 50% maturity; PH, plant height; PB, total plant biomass; SB, shoot biomass; RB, root biomass; RS, root to shoot biomass ratio; GY, grain yield; HI, harvest index. The genotypes were coded with numbers as recorded in [Supplementary Table 1](#).

marginal areas of sub-Saharan Africa, including South Africa. The present study evaluated 45 maize genotypes across two locations for their agronomic performance and carbon storage traits to identify genotypes with improved grain yield and carbon sequestration for direct cultivation and breeding. Combined analysis of variance revealed significant ($p < 0.05$) variation among the test genotypes for the studied agronomic traits ([Table 4](#)), indicating the availability of marked genetic variation among the genotypes in developing maize varieties with high grain yield and enhanced carbon storage. [Korsa et al. \(2024\)](#) also reported a significant variation in agronomic traits among the 25 maize inbred lines evaluated in the field at the Ambo Plant Protection Research Centre of Ethiopia.

Significant genotypic $\times$ location ($p < 0.05$) interactions were recorded for grain yield, shoot biomass, root biomass and total plant biomass production ([Table 4](#)), indicating the effect of the environment on the performance of these genotypes. These results

agree with [Azrai et al. \(2022\)](#), who reported a significant genotype $\times$ location interaction on yield and yield components in tropical maize hybrids. Therefore, understanding the effect of genotype $\times$ location interaction assists in predicting the phenotypic response to various environmental conditions, which is vital in improving the selection efficiency of high-yielding maize genotypes. A vast majority of the genotypes showed unstable performances across the two locations. Related findings have been reported by [Alam et al. \(2022\)](#), who found that a change in the environment led to genotype $\times$ environment interaction on maize. This could be attributed to the differences among the breeding materials and their genetic behavior in the different environments. The significant differences ($p < 0.05$) observed among genotypes, locations, and genotype $\times$ location interactions for grain yield highlight the importance of developing varieties specifically adapted to environmental conditions, as well as those exhibiting exceptional stability

TABLE 10 Principal components showing variation and contribution by nine agronomic traits among 45 maize genotypes evaluated during the 2022/23 growing season in South Africa.

Traits	Principal components			
	PC1	PC2	PC3	PC4
DTF	0.03	0.00	0.12	0.75
DTM	0.01	-0.03	0.16	0.63
GY	0.15	0.06	-0.80	0.17
PH	0.60	-0.80	0.02	-0.04
SB	0.42	0.30	-0.01	0.01
RB	0.20	0.19	0.09	-0.05
RS	-0.01	0.01	0.01	-0.01
HI	-0.06	-0.04	-0.55	0.07
PB	0.63	0.48	0.08	-0.03
Eigenvalues	4.07	2.06	1.04	0.74
Explained variance (%)	45.24	22.89	11.60	8.32
Cumulative variance (%)	45.24	68.13	79.74	88.05

PC, principal component; DTF, days to 50% heading; DTM, days to 50% maturity; PH, plant height; PB, total plant biomass; SB, shoot biomass; RB, root biomass; RS, root to shoot biomass ratio; GY, grain yield; HI, harvest index. The highest loading scores for each PC are highlighted in bold.

across diverse environments (Masila and Langat, 2020). However, in the present study, genotypes such as TZECOMP3DT-C2, TZE (OMP3DT/WHITEDTSTRSYN)CZ, DT-STR-Y-SYN14, TZ-44, and ZDIPLOBC4-C3-W showed near-perfect performances, exhibiting better yields across the locations. Ideal maize genotypes have high grain yield and wide adaptability across different environmental conditions (do Couto et al., 2023). Maize breeders should develop stable hybrids across various environments to be widely accepted by farmers and seed producers. These hybrids are more likely to endure challenging conditions such as low-fertility soils, excessive rainfall, or drought. Water stress can lower crop yields by reducing the CO₂ assimilation area, decreasing leaf number and total leaf area, the net assimilation rate, and affecting yield components such as ear size, kernel count per ear, and kernel weight, ultimately leading to a decline in biomass production (Laskari et al., 2022; Deribe, 2024).

The findings of this study further highlight the critical role of climatic conditions during the growing season in influencing maize yield and genotype performance. Climatic factors such as temperature, rainfall distribution and their interaction with soil conditions significantly affect crop growth, biomass accumulation, and grain yield formation. For instance, Božović et al. (2022) demonstrated that maize productivity varied significantly under contrasting climatic conditions, emphasizing the interaction between environmental factors and management practices. Similarly, Šimon et al. (2023) reported that temperature and precipitation patterns strongly influence maize developmental stages and final yield outcomes. In Zimbabwe, Mazibuko et al. (2024) showed that long-term genetic gains in maize yield are closely linked to adaptation to changing climatic conditions, highlighting the importance of selecting climate-resilient genotypes. Furthermore, Rajčić et al. (2025) and Stojiljković et al. (2025) emphasized that interactions

between genotype, climatic variables, and agronomic practices such as sowing time and plant density significantly influence yield performance. These findings support the results of the present study, where significant genotype × location interactions were observed, suggesting that environmental variability between Ukulinga and Bethlehem likely influenced genotype performance, biomass production, and carbon allocation patterns. Therefore, the identification of stable and high-performing genotypes requires multi-environment evaluation to capture the complexity of genotype responses under varying climatic conditions.

The five best-yielding genotypes were 9022-13, TZECOMP3 DT-C2, TZE (OMP3DT/WHITE DT STRSYN)CZ, TZ-44, and DT-STR-Y-SYN14, and TZECOMP3 DT-C2 was the highest yielder (Table 4). This superior performance may be associated with their relatively tall stature and enhanced biomass production. However, yield advantage in taller genotypes is also influenced by optimal ear placement along the stem (Nzuve et al., 2014). The genotypes with ear placement at approximately mid-plant height tend to exhibit better structural stability and reduced susceptibility to lodging compared to those with excessively high ear placement. This observation is consistent with Stubbs et al. (2023), who highlighted the importance of balanced plant architecture in achieving high yield potential. Furthermore, it suggests that tall genotypes are more efficient in supporting kernel growth by mobilizing stem reserves (D'Andrea et al., 2016). Previous studies have demonstrated that increased shoot biomass accumulation and grain yield in maize are linked to the stay-green trait in leaves, supported by more effective mobilization of stored carbon before silking (Yin et al., 2016; Qi et al., 2019). Additionally, a larger total leaf area during the late growth stages of wheat has been shown to prolong the duration of photosynthesis. Therefore, when breeding for high yield, biomass allocation, and carbon storage, the focus should be on selecting genotypes with the stay-green trait to prolong photosynthesis and support grain filling through efficient carbon mobilization (Araus et al., 2008). In addition, selecting genotypes with larger leaf areas and taller plant stature can further enhance biomass accumulation and nutrient use efficiency.

4.2 Carbon storage of the tested maize genotypes

The significant differences among the 25 tested maize genotypes for carbon storage traits and carbon stocks (GCs, PCs, SCs, RCs, RCs/SCs, and GCs) (Table 5), indicate the presence of genetic diversity among the test maize genotypes for carbon sequestration. These results agree with Datta et al. (2018) and Ngidi et al. (2024a), who reported a significant variation in these carbon storage traits and carbon stocks in diverse sorghum genotypes. Furthermore, breeding programs should exploit these variations to develop new maize cultivars with high yield, enhanced carbon sequestration and better adaptability (Magar et al., 2021).

Maize genotypes TZE (OMP3DT/WHITE DT STRSYN) CZ, 9022-13, and ZDIPLOBC4-C3-W sequestered more carbon as they accumulated the highest total plant carbon stocks (Table 7). This is due to their high biomass production, which increases their ability to sequester more carbon. Genotypes TZ-5, TZ-41, and CKDHL0378 recorded the lowest total plant biomass production

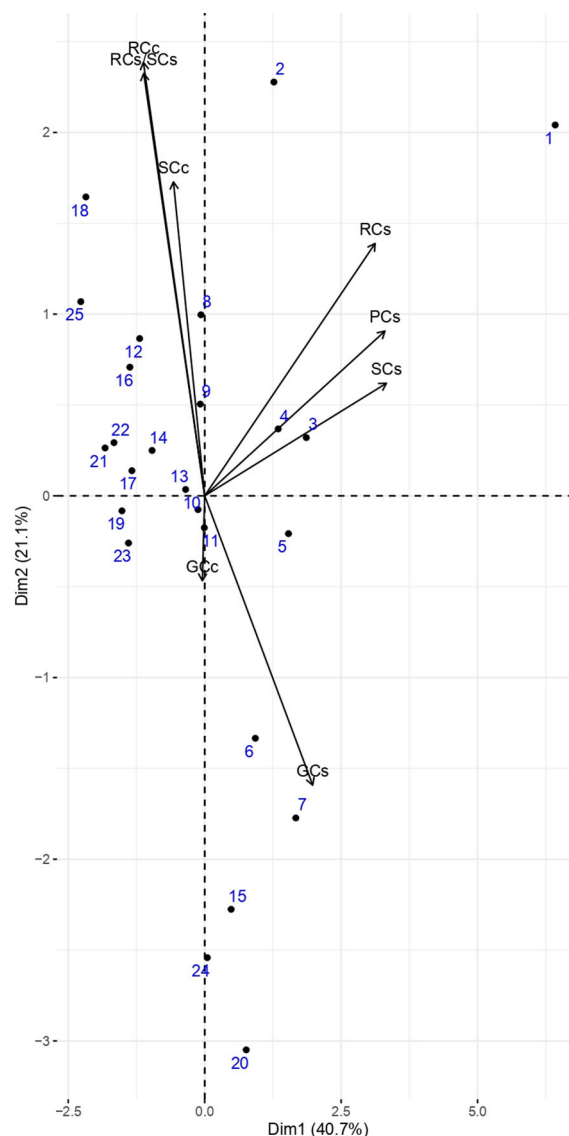


FIGURE 4

Principal component biplot analysis showing the relationship between carbon storage traits and selected maize genotypes tested for carbon storage. SCc, shoot carbon content; RCc, root carbon content; GCc, grain carbon content; PCs, total plant carbon stocks; SCs, shoot carbon stock; RCs, root carbon stock; RCs/SCs, root to shoot carbon stock ratio; GCs, grain carbon stock. The genotypes were coded with numbers as recorded in [Supplementary Table 2](#).

which causes them to have a poor carbon sequestration potential ([Table 7](#)). These findings are consistent with [Ngidi et al. \(2024a\)](#), who highlighted that crop genotypes with low plant biomass productions are associated with poor carbon sequestration potential or vice versa.

Genotype TZE (OMP3DT/WHITE DT STRSYN)CZ combines both high grain yield and high carbon storage traits, including GCs, SCs, RCs and PCs. The genotype would be a valuable resource for developing new maize cultivars with enhanced grain yield and carbon sequestration. The mean shoot carbon stocks of all the tested maize genotypes were higher than their respective root carbon stocks ([Supplementary Table 2](#)). This confirms that the maize plants store more carbon in their shoots compared to their roots. The carbon allocation pattern could influence how these maize genotypes are managed for optimal growth, carbon sequestration strategies, and possibly their resilience to diverse environmental conditions.

4.3 Genetic variability

Genetic variability is a key to success in plant breeding. Assessing the extent of variability among the evaluated genotypes for the target traits aided in the selection of desirable genotypes for future maize improvement. Higher values of PCV and GCV were recorded for GY, HI, PB, RB, SB, GCs, SCs, RCs/SCs, and PCs ([Tables 8, 9](#)), suggesting a wide range of variability for these traits. These findings agree with [Bartaula et al. \(2019\)](#), who reported high PCV and GCV values for grain yield. Moderate PCV and GCV values were recorded for PH ([Table 8](#)). These results are consistent with the findings of [Magar et al. \(2021\)](#) who also reported moderate PCV and GCV values for plant height. The computed PCV and GCV values of plant height were not variable after flowering, indicating that these traits were less influenced by the test locations unlike the report; [Kashiani et al. \(2010\)](#). The coefficient of variation

TABLE 11 Response of maize genotypes for yield and yield components and organic carbon storage in the shoot and root systems.

Parameters	Principal components			
	PC1	PC2	PC3	PC4
GC _c	0.01	-0.01	0.01	0.09
GC _s	-0.12	-0.97	0.20	0.06
PC _s	-0.80	0.11	0.06	-0.13
RC _c	0.02	0.20	0.88	0.42
RC _s	-0.28	0.06	0.33	-0.68
RC _s /SC _s	0.01	0.01	0.02	-0.04
SC _c	0.01	0.07	-0.03	-0.09
SC _s	-0.52	0.05	-0.27	0.56
Eigenvalues	3.25	1.69	1.22	0.92
Variance (%)	40.68	21.17	15.32	11.58
Cumulative variance (%)	40.68	61.86	77.17	88.76

PC, principal component; SC_c, shoot carbon content; RC_c, root carbon content; GC_c, grain carbon content; PC_s, total plant carbon stocks; SC_s, shoot carbon stock; RC_s, root carbon stock; RC_s/SC_s, root to shoot carbon stock ratio; GC_s, grain carbon stock. The highest loading scores for each PC are highlighted in bold.

indicates a substantial degree of genetic variation; however, heritability estimates and genetic gain are the only genetic parameters that can be used to determine the amount of heritable variation (Adhikari et al., 2018).

4.4 Heritability and genetic advance

In the current study, high to moderate broad sense heritability values were recorded for DTF, PH, GY, DTM, RS, GCs, SCc, SCs, and PCs (Tables 8, 9). High heritability indicates that the environmental influence on the tested traits is minimal. Therefore, the traits can be successfully selected for enhanced biomass production, grain yield, and carbon storage. Medium to high heritability values were recorded for GY, PH, DTF and DTM (Table 8). These results are in agreement with those of Ogunniyan and Olakojo (2014). However, as broad sense heritability is based on total genetic variance, which includes additive, dominant, and epistemic variances, selecting for the improvement of such traits would not be helpful. High heritability combined with high genetic advance suggests that the observed variation is primarily due to additive genetic effects, indicating that selection for these traits will likely be more effective (Bello et al., 2012). Traits such as grain yield, grain carbon stock, shoot carbon stock, and total plant carbon stock expressed high heritability coupled with high genetic advance. Therefore, direct selection of such traits would be influential in improving the yield and carbon storage.

4.5 Association between agronomic traits

The degree of relationship between the agronomic traits in improving grain yield in maize genotypes guides the simultaneous selection of traits in future maize breeding programs. Grain yield was

positively correlated with shoot biomass and total plant biomass (Figure 1). This indicates that genotypes with enhanced assimilate production and partitioning capacity are more likely to achieve higher grain yield under the tested environments. Similar relationships have been reported with quantitative values showing moderate to strong positive correlations ($r = 0.60\text{--}0.85$) between biomass and grain yield in maize, sorghum and wheat (Ghassemi-Golezani and Dalil, 2014; Ngidi et al., 2024a; Mutanda et al., 2025), supporting the consistency of this trend. Higher shoot biomass contributes to improved grain yield through increased leaf area index, enhanced light interception and higher photosynthetic capacity, which collectively support assimilate availability during grain filling (Shamuyarira et al., 2022). Therefore, the genotypes exhibiting these traits are physiologically more efficient in converting intercepted radiation into economic yield (Xing et al., 2018). Furthermore, the positive association between grain yield and root biomass observed in the present study (Figure 3), indicates the significance of root traits in improving grain yield production in maize. These findings align with Xu et al. (2022), who reported significant positive correlations between grain yield and root biomass, suggesting that genotypes with larger root systems can sustain higher productivity. The increase in root size improves nutrient and moisture uptake by plants (Mutanda et al., 2025), which is crucial in dryland farming systems where plants are highly dependent on rainfall and deeper root systems can forage for water in the soil profile. This explains why some of the superior genotypes identified in this study combined high root biomass with high grain yield, indicating efficient belowground resource acquisition and utilization under the prevailing environmental conditions.

In addition, root-to-shoot ratio was negatively associated with plant height, shoot biomass, root biomass and total plant biomass (Figure 3). This suggests a trade-off in assimilate allocation between aboveground and belowground plant components, where increased allocation to shoots may limit proportional investment in roots. Such allocation patterns are regulated by hormonal balance (e.g., auxins and cytokinins) and carbon partitioning dynamics. These findings are consistent with those of Qi et al. (2019), who reported a negative correlation between root-to-shoot ratio, plant height, and aboveground biomass. Some studies conducted in other cereals such as sorghum (Ngidi et al., 2024a) and wheat (Shamuyarira et al., 2022; Mutanda et al., 2024) reported this trend of correlations, indicating that excessive allocation to roots relative to shoots may reduce overall biomass accumulation and grain yield. Therefore, increasing RS has a negative impact on grain yield production, as reflected in maize genotypes such as TZ-35, CKDHL0378 and CML393 which have lower grain yield and high RS values. However, a high RS is essential for improving nutrient acquisition and plant survival in drought-prone and nutrient-poor production areas. Therefore, selection should optimize root development to enhance nutrient uptake and maize productivity (Comas et al., 2013).

4.6 Link between carbon allocation traits

The present study exhibited a high contribution and strong association of RCs/SCs, RCs, PCs, and SCs to both PC1 and PC2, indicating the importance of these traits for selection. The maize

genotypes showing increased and desirable mean performances in these targeted traits should be selected for the production and development of carbon sequestration hybrids. In addition, the results showed that PCs was negatively associated with RCs/SCs, suggesting that excessive allocation of carbon to roots relative to shoots may reduce overall plant carbon accumulation. This may be due to lower photosynthetic capacity associated with reduced shoot biomass (Kumar et al., 2020), which limits total carbon fixation. These findings are consistent with Ngidi et al. (2024), who reported a significant negative correlation between total plant carbon stocks (PCs) and the root-to-shoot carbon ratio (RCs/SCs). Similar trends have also been observed in other studies (Mathew et al., 2017; Ngidi et al., 2024a), with reported values indicating moderate negative correlations ($r = -0.40$ to -0.70), reinforcing the trade-off between root allocation and total carbon gain. However, several reports suggest that the relationship between root-to-shoot carbon allocation and total carbon storage can vary depending on genotype and environmental conditions (Chaplot et al., 2023; Joshi et al., 2023; Arellano Vazquez et al., 2024; Ngidi et al., 2024b), indicating that genotype $\times$ environment interactions play a critical role in determining carbon partitioning strategies.

The superior genotypes identified in this study likely achieved higher carbon stocks due to their ability to maintain high shoot biomass (supporting photosynthesis and carbon fixation) while also sustaining adequate root biomass for nutrient and water uptake. This balance enables efficient carbon assimilation and storage under field conditions. Furthermore, environmental factors such as soil type, moisture availability, and temperature at the two study locations may have influenced carbon allocation patterns, contributing to the observed genotype differences. Therefore, these results demonstrate that selection for carbon sequestration in maize should prioritize genotypes with high total biomass and balanced carbon allocation, rather than those with extreme allocation to either shoots or roots. Integrating these traits into breeding programs can enhance both productivity and environmental sustainability under diverse agro-ecological conditions.

5 Conclusion

The present study evaluated 45 genetically diverse maize genotypes for agronomic performance and carbon storage capacity. Significant variation existed for key agronomic and carbon-related traits, with higher biomass genotypes exhibiting greater total plant carbon stocks, highlighting their superior carbon sequestration potential. Grain yield was positively associated with plant height, shoot and root biomass, and total biomass, indicating that vegetative growth contributes to productivity and carbon storage. Notably, genotypes TZE COMP3 DT-C2, TZE (OMP3DT/WHITE DT STRSYN)CZ, DT-STR-Y SYN14, TZE (OMP3DT/WHITE DT STRSYN)CZ, TZ-50 and TZE COMP5C7/TZE COMP39TCZ demonstrated superior performance in both grain yield and carbon storage. These genotypes are recommended for adoption in maize production systems and for use in breeding programs aimed at enhancing yield and promoting climate-resilient agriculture.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author.

Author contributions

MM: Writing – original draft, Writing – review & editing. SF: Writing – original draft, Writing – review & editing. AN: Writing – original draft, Writing – review & editing. ST: Writing – original draft, Writing – review & editing. VC: Writing – original draft, Writing – review & editing. HS: Writing – original draft, Writing – review & editing.

Funding

The author(s) declared that financial support was received for this work and/or its publication. The authors would like to thank the Water Research Commission (WRC) for funding this work. This article is based on research under the project titled “Knowledge validation of water use efficiency and soil carbon sequestration of selected indigenous and modern crop cultivars for sustainable agriculture intensification and climate change mitigation” funded by the Water Research Commission (Project No. C2020/2021-00646), with grants awarded and managed by the University of South Africa (UNISA). The contents of the article are the authors sole responsibility and should not be regarded as reflecting the views and positions of the WRC and UNISA.

Acknowledgments

The University of South Africa, the African Centre for Crop Improvement of the University of KwaZulu Natal, the Institut de Recherche pour le Développement (France) and the Agricultural Research Council-Small Grain Institute (South Africa) are thanked for their overall research support.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fagro.2026.1798511/full#supplementary-material>

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