

RESEARCH PAPER

Striga Infestation Responses, Heterotic Alignment, and Genetic Diversity of Inbred Maize Lines

Jean Paul Barutwanayo^{1,3}, Ilesanmi Oluyinka², Abdoul Raouf Sayadi Maazou², Catherine W. Muui^{1*} and Harun I. Gitari⁴

¹Department of Agricultural Science and Technology, School of Agriculture and Environmental Sciences, Kenyatta University, Nairobi, Kenya

²International Institute of Tropical Agriculture (IITA), Oyo Road, Ibadan PMB 5320, Nigeria

³International Institute of Tropical Agriculture (IITA), Kabondo, Bujumbura, Burundi

⁴Department of Agricultural Science and Technology, School of Agriculture and Environmental Sciences, Kenyatta University, Nairobi, Kenya

*Corresponding author: muui.catherine@ku.ac.ke (ORCID ID: 0000-0001-6782-0626)

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ABSTRACT

Maize (*Zea mays* L.) production in Sub-Saharan Africa has been declining due to *Striga* infestation. This study evaluated the response of 176 inbred maize lines to *Striga* infestation, refined heterotic grouping, and their genetic diversity at IITA, Ibadan, Nigeria. Each line was replicated three times in a rhizotron in a completely randomized design. Pre-germinated *Striga* seeds were spread on maize roots. Height, number of leaves, and internodes were recorded per maize plant. *Striga* damage was scored using a scale; the number of *Striga* plants attached to maize roots was counted, and the striga biomass was recorded. Leaf tissues of maize were sampled for DNA extraction. STRUCTURE software and harvester were used to assess population structure; TASSEL software for principal component analysis, and means were separated using Tukey's HSD. GenAIEx software and Power Maker were used for genetic diversity and heterozygosity. TZISTR2004 attained the highest plant height (94.77cm) while TZISTR1873 recorded the lowest (38.33cm). TZISTR2042 recorded the highest number of leaves, while TZISTR2247 had the lowest (11.33cm). Internodes were highest (15.67) in TZISTR2042, while lowest (10.33) was on TZISTR2275 and TZISTR2247. Plant scorching was highest (9.00) in TZISTR2100, TZISTR2269, TZISTR2287, whereas TZISTR1318 recorded 1.00. TZISTR1126 had 18.72 striga attached while TZISTR2175, TZISTR2241, TZISTR2102, TZISTR2270, TZISTR2287 had none. Striga biomass was highest (22.72g) on TZISTR2129, and TZISTR2175 attained the least weight. Heterozygosity ranged between 0.0 to 0.85. Major allele frequency ranged between 0.5-1.0, whereas gene diversity ranged from 0 to 1.0. The identified lines with resistance to *Striga* could be utilized in maize breeding programmes to enhance production in Sub-Saharan Africa.

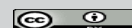
HIGHLIGHTS

- ① *Striga* infestation significantly reduced the plant height, internode length, and number of leaves of the inbred maize lines, which have low or no resistance to the parasite.
- ② The number of *Striga* attached to the roots and biomass was lowest in resistant lines, attributed to reduced production of the *Striga* germination stimulants and a reduction in nutrients from the host.
- ③ SNP markers assigned the inbred maize lines into heterotic groups based on their genetic makeup, background, and the source population, aligning lines from the same pedigree in one subpopulation.
- ④ The inbred lines have the potential to contribute new alleles, which can be utilized in future breeding programs for resistance to *striga*.

Keywords: Genetic diversity, Heterozygosity, Inbred maize lines, Resistance, *Striga* infestation

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Cereals are the main source of nourishment, providing approximately half of the total caloric content requirements in humans (Fisher *et al.* 2015) “maize is life,” due to its importance to food security and economic wellbeing. Around 40 % of Africa’s maize-growing area faces occasional drought stress, resulting in yield losses of 10–25 %. Around 25 % of the maize crop suffers frequent drought, with losses of up to half the harvest. To reduce vulnerability and improve food security, the Drought Tolerant Maize for Africa (DTMA). Unlike other cereals, maize, wheat, and rice are the most important sources of human food, accounting for approximately 94% of the global cereal consumption (Ranum *et al.* 2014; Nduwimana *et al.* 2020). In Sub-Saharan Africa (SSA), maize is one of the staple foods for more than 1.2 billion people (Cooper *et al.* 2013; Ochieng *et al.* 2023). Apart from being a human food, the crop is one of the major sources of animal feed (Aslam *et al.* 2013).

The maize plant’s capability to thrive in various soil types in different agroecological zones has significantly contributed to the increased usage in many African countries (Ranum *et al.* 2014; Psiwa *et al.* 2022; Krishna *et al.* 2024; Maheswari *et al.* 2025). Burundi is densely populated and has a high population growth, and only 36% of the country is arable. Furthermore, its climate has resulted in diminished water availability, which is likely to pose a food security threat in Burundi (Warner, 2018). Maize, among other crops, particularly in SSA, is constrained by pest and disease infestations, climate change, poor soil fertility, and salinity stress (Ngaiza *et al.* 2026; Maitra *et al.* 2025; Raza *et al.* 2025; David *et al.* 2022; Santosh *et al.* 2024). Drought, increased temperatures, and soil salinity significantly reduce maize yields (Manasa *et al.* 2018; Seife, 2021; Truşcă *et al.* 2023). In addition, the decline in soil fertility occasioned by the continuous use and limited replenishment with necessary inputs has resulted in deficiency of macronutrients such as nitrogen, phosphorus, and calcium; and micronutrients such as copper and zinc in soils, hence poor maize yields (Bhusal *et al.* 2021; Mugo *et al.* 2021; Ngowi *et al.* 2025; Cheptoet *et al.* 2021).

Striga infestation is amongst the common biotic factors affecting maize production, increasing food insecurity and poverty levels in SSA (Hossain *et al.* 2021; David *et al.* 2022; Ray *et al.* 2025). This

parasitic plant thrives in high-temperature regions of SSA and some parts of the Middle East and Asian continent. According to David *et al.* (2022), more than 50 million hectares of land under cereal cultivation have been infested by *Striga* spp. The infestations of this parasite have resulted in approximately 75% loss of cereals, resulting in an annual loss of about \$10 billion. Similarly, 80% of farmers have been forced out of their cereal farms due to the infestation of the *Striga* parasite (David *et al.* 2022).

Striga has been reported in Eastern African countries, including Burundi, Kenya, Uganda, Ethiopia, Rwanda, Tanzania, and Sudan. The invasion of these parasitic weeds, especially on cereals, has significantly led to reduced their production in Sub-Saharan countries (Rodenburg *et al.* 2010). The reduction in cereal production affects approximately 300 million people who depend on these cereals for food in Saharan Africa (Atera *et al.* 2013). Studies have shown that *striga* affects approximately 217,000 hectares of maize farms in western Kenya. This accounts for a reduction in maize yields of approximately 182,227 tons annually. The loss depends on the host affected, average weather conditions, the varieties of cereals cultivated, the nature of soils, and the degree of infestation (Mudereri *et al.* 2020).

Striga thrives in adverse conditions such as drought and low-nutrient soils, making it very detrimental to farms (Atera *et al.* 2013), especially in Sub-Saharan Africa. Management of the *Striga* is expensive to farmers, and often, they may not find a remedy, hence the continued decrease in cereal production (Mwangangi *et al.* 2021). The small-scale farmers use low-cost management methods, which include hand weeding, short crop rotation, trap rotation, and conventional biocontrol methods (Atera *et al.* 2013; Mukesh *et al.* 2024; Mohammad *et al.* 2025). Despite these efforts, these low-cost management methods are not effective.

Maize resistant lines have been developed to overcome the *Striga* constraint in production (Menkir *et al.* 2014; Maitra *et al.* 2024; Sairam *et al.* 2025). However, the performance of the maize *Striga*-resistant lines may differ based on environmental conditions in the region where the crop is grown (Elemosho *et al.* 2020). According to Annor *et al.* (2019), the resistant lines mature early even under



drought and low nitrogen levels in the soil. Due to these vital features, *Striga*-resistant maize increases maize production and consequently increases the income and livelihood of the maize farmers (Menkir *et al.* 2012). Additionally, it enhances the suitability of the maize seed-producing companies (Menkir, 2006).

Previously, the International Institute of Tropical Agriculture (IITA) has introgressed *Striga* resistance in maize inbred lines through long-term breeding. The resistance can be conferred by constructing a pyramid of several characters for a variety of purposes in *Striga* endemic environments. The maize resists *Striga* invasions by developing less branch root structure, developing resistance to attachments to the *Striga* sprouting close to the maize roots (Rich and Ejeta, 2008). The resistance in maize lines can be detected earlier in the early life cycle of the parasites since *Striga* has been linked to much damage during the establishment stage.

Heterotic grouping enables the discovery and availing of information on inbred lineages that produce superior hybrids (Temesgen, 2021; Manasa *et al.* 2021; Mohapatra *et al.* 2023; Majeed *et al.* 2023) information on combining ability is required to determine the crossing pairs in the production of hybrid varieties. Heterosis is the expression of an F1 hybrid's dominance over its parents in a given feature, as measured not by the trait's absolute value, but by its practical use. To put it another way, heterosis is defined as an increase in the character value of F1 hybrids when compared to the average value of both parents. A plant breeder's ultimate goal is to achieve desirable heterosis (hybrid vigor). This provides maximum advantage of the germplasm through leveraging complementary lines to develop higher hybrids (Temesgen, 2021) information on combining ability is required to determine the crossing pairs in the production of hybrid varieties. Heterosis is the expression of an F1 hybrid's dominance over its parents in a given feature, as measured not by the trait's absolute value, but by its practical use. To put it another way, heterosis is defined as an increase in the character value of F1 hybrids when compared to the average value of both parents. A plant breeder's ultimate goal is to achieve desirable heterosis (hybrid vigor). Therefore, this study characterized the heterotic patterns of the new *Striga*-resistant maize inbred

lines, established their genetic diversity, and their response to artificial *Striga* infestation. The findings will provide a heterotic database of maize lines in IITA that are resistant to *Striga*. Besides, it will enable identification of maize lines that can be utilized to produce high output maize cultivars, which can be used in breeding programmes and shared with farmers to enhance maize production in Burundi and the entire Sub-Saharan Africa. Additionally, the findings will provide adequate data that can be used in policy formulation regarding the improvement of maize varieties to meet demand and increase the productivity of maize.

MATERIALS AND METHODS

Site description

The research was conducted at the International Institute of Tropical Agriculture (IITA) Maize Unit screen house in Ibadan, Nigeria, from April to November 2022. The Institute is located at longitude 7° 30'8" N and latitude 3°54'37" E, at an elevation of 240 meters above sea level.

Experimental design and establishment

A total of 176 inbred maize lines were obtained from the maize improvement project of IITA, Ibadan. The maize inbred lines had been evaluated for drought and *Striga* resistance in the field at IITA-Nigeria. The study was carried out in the greenhouse using a rhizotron to enable real-time monitoring of attachment and development of *striga* on roots without destroying the maize plants. All 176 inbred maize lines were used for molecular characterization, whereas 79 lines were selected for evaluation of maize inbred lines' responses to artificial *Striga* infestation. The selected 79 lines had been previously established to contain *Striga*-resistant genes. The inbred maize lines were planted in a completely randomized design (CRD) with each line replicated three times.

Striga seeds obtained from IITA were preconditioned based on methods developed by Mbuvi *et al.* (2017). The seeds were first surface sterilized for ten minutes with little agitation in 10% w/v commercial bleach, after that, washed three times with distilled water, then placed in a plastic cup with Whatman filter paper. For preconditioning, sterile distilled water



was added, and the *striga* seeds were incubated at 29 °C for 11 days.

Ten maize seeds from each inbred line were surface sterilized to remove any potential contaminants on the surface. Surface sterilization was done for 15 minutes using a half-strength standard treatment solution comprising 15 percent commercial bleach and 0.01 percent Triton X-100. To enhance germination, seeds were covered and placed in the dark for 2 days in plates. After seven days of seed germination, 2 seedlings from each line were transferred to the rhizotron based on methods developed by Mbuvi *et al.* (2017). The seedlings were provided with 50 ml of nutrient solution (40% Long Ashton solution with ammonium nitrate) twice daily for ten weeks.

Eleven days after transfer into the rhizotron, the maize plants were infested by spreading 20-25mg of pre-germinated *Striga* seeds on the exposed roots' surface using a soft brush. Seven days later, after the emergence of new maize roots, more *Striga* seeds were added. Height (cm), number of leaves, and number of internodes were recorded per individual maize plant after week eight to evaluate the reduction in host growth. Damage caused by *Striga* was visually assessed utilizing a scale of 1 to 9, where 1 = no obvious indicators of damage on the host plant and 9 = all leaves totally scorched, resulting in premature mortality for each infected line 10 weeks after planting. The total number of *Striga* plants attached to the maize roots was counted at week eight. After that, the biomass (g) of *Striga* was evaluated by drying the seedlings for 7 days at 45°C before weighing using a scale balance.

Two weeks after planting, samples of 4-5 young leaves were obtained from each plant of the 176 inbred maize lines and pooled into shoot bags. The pooled leaf samples were then placed in a freezer at a temperature of approximately -75°C. The lyophilized leaf samples were sampled into 96-well plates for crushing into powder for 1.5 minutes. Crushing was done using Geno/Grinder, an automated high-throughput tissue homogenizer, shaking the tissues at 1500 strokes per minute.

Genomic DNA was extracted from the ground leaf tissues following the CTAB DNA extraction protocol (Offord *et al.* 2022). Genotyping was carried out using a panel of medium-density DARTag

markers. DArTseq, part of the Diversity Arrays Technology (DART), is used in genotyping to identify polymorphism across different genomes. These markers utilize the next-generation sequencing with a proprietary array-based platform to detect variations such as single-nucleotide polymorphisms (SNPs). This process involved digesting DNA with specific restriction enzymes and selecting a reproducible subset of the fragments, and thereafter sequencing. The unique genomic sequences (DART markers) were identified and used to genotype the individual inbred maize lines based on the *Striga* resistant gene presence or absence.

In addition, based on the genotyping output, the population structure of the inbred maize lines and the optimal number of inherent sub-populations were inferred. Comparison between populations was done using the Analysis of Molecular Variance (AMOVA) based on the GenAlEx software. The genetic diversity output was used to generate the genetic diversity indices, major allele frequency (MAF), heterozygosity, and Polymorphism Information Content (PIC) value.

Data analysis

Analysis of variance (ANOVA) was used to estimate and determine the means for parameters measured on maize and *striga* plants using statistical analysis software (SAS). For mean separations and genotype groupings according to their resistance to *Striga*, Tukey's Honest Significant Difference (HSD) test ($p < 0.05$) was used to separate the means. R software, version 4.2.1, was used to perform all statistical analyses. Population structure was assessed using STRUCTURE software, version 2.3.4, and the optimal number of inherent sub-populations was inferred using STRUCTURE Harvester. TASSEL software, version 5.2.92, was used to perform principal component analysis (PCA). Genetic diversity was analysed using the GenAlEx software version 6.1 and Power Marker, V3.25. Power Marker software was used to produce genetic diversity indices major allele frequency (MAF), unbiased genetic diversity estimate, detected heterozygosity, and Polymorphism Information Content (PIC) value. Genetic distances were used to develop dendrograms.



RESULTS

Response of maize inbred lines to *Striga* infestation

The height of maize plants upon infestation of *Striga* differed significantly ($p=0.0001$) between the inbred maize lines (Table 1). Inbred maize lines TZISTR2004, TZISTR1119, and TZISTR2017 recorded the highest height, with a mean ranging from 89-94 cm per plant. The lowest height was reported in inbred maize lines, TZISTR1131, TZISTR1181, TZISTR2002, and TZISTR1873.

Table 1: Plant height (cm) of inbred maize lines under *Striga* infestation

Lines	Height (cm)	Lines	Height (cm)
TZLCOMP1-1368 STR	45.67±12.01e	TZISTR2129	84.33±4.70a
TZISTR1119	91.67±6.93a	TZISTR2131	50.83±2.09cde
TZISTR1121	55.53±12.89cde	TZISTR2133	77.33±2.85ab
TZISTR1126	51.17±3.09cde	TZISTR2139	60.17±2.24bcd
TZISTR1130	59.03±5.50cde	TZISTR2145	67.83±1.69bcd
TZISTR1131	40.50±1.04e	TZISTR2149	53.33±1.45cde
TZISTR1178	51.77±6.09cde	TZISTR2150	86.70±2.35a
TZISTR1181	40.40±7.79e	TZISTR2152	66.33±4.76bcd
TZISTR1214	45.67±10.53e	TZISTR2158	61.43±3.94bcd
TZISTR1224	87.23±9.57a	TZISTR2163	74.93±3.97ab
TZISTR1248	40.80±1.41e	TZISTR2175	72.67±1.09ab
TZISTR1303	73.43±3.47bc	TZISTR2186	70.67±4.81ab
TZISTR1305	76.03±6.86ab	TZISTR2205	78.17±4.60ab
TZISTR1318	43.33±6.91e	TZISTR2208	63.17±4.49bcd
TZISTR1323	48.50±13.25e	TZISTR2211	59.67±4.41cde
TZISTR1336	66.83±8.08 bcd	TZISTR2221	65.00±10.50bcd
TZISTR1870	62.90±5.06bcd	TZISTR2225	68.67±4.18bcd
TZISTR1873	38.33±1.86ef	TZISTR2227	66.60±4.66bcd
TZISTR1876	56.68±7.31cde	TZISTR2229	54.17±3.66cde
TZISTR1878	86.13±2.89a	TZISTR2231	88.67±6.89a
TZISTR2002	40.17±2.92e	TZISTR2235	60.83±2.42bcd
TZISTR2004	94.77±4.62a	TZISTR2239	55.83±5.58cde
TZISTR2008	51.83±1.69cde	TZISTR2241	52.00±8.74cde
TZISTR2017	89.47±3.02a	TZISTR2247	47.83±4.49e
TZISTR2036	85.67±14.04a	TZISTR2251	44.33±0.73e
TZISTR2039	72.83±11.41bc	TZISTR2256	76.50±4.67ab
TZISTR2042	57.10±1.73cde	TZISTR2260	76.50±2.29ab
TZISTR2043	86.80±10.10a	TZISTR2266	71.33±3.33abc
TZISTR2047	63.07±7.91bcd	TZISTR2267	67.67±0.93bcd
TZISTR2049	58.67±14.41cde	TZISTR2269	87.17±2.46a

TZISTR2054	58.43±7.67cde	TZISTR2270	65.87±3.43bcd
TZISTR2059	55.47±10.59cde	TZISTR2272	79.87±10.20ab
TZISTR2064	75.83±2.16ab	TZISTR2275	66.10±9.88bcd
TZISTR2100	81.00±20.00a	TZISTR2279	49.17±0.88e
TZISTR2102	58.17±1.97cde	TZISTR2287	76.20±7.95ab
TZISTR2107	78.50±9.73bc	Z.diplo.BC4-472-2-2-16-4B-B	76.57±0.54ab
TZISTR2115	65.17±2.35bcd	1368 STR	78.70±8.41ab
TZISTR2120	67.17±1.88bcd	5057	83.07±10.94a
TZISTR2121	66.13±1.33bcd	9540	74.33±14.68ab
TZISTR2125	72.03±10.68ab		
P-value	<0.0001		<0.0001

Means with the same letters within the same column are not statistically different.

Comparison of the number of leaves showed a significant difference ($P=0.0001$) between the inbred maize lines (Table 2). The inbred maize lines TZ1STR1303, TZ1STR2042, TZ1STR2152, and TZ1STR2163 had significantly higher numbers of leaves, ranging from 15-16 per plant. In contrast, maize lines TZ1STR1336, TZ1STR2247, and TZ1STR2275 had significantly lower leaves with a mean of 11 leaves per plant.

Table 2: Number of leaves formed on inbred maize lines under *Striga* infestation

Lines	No. of leaves	Lines	No. of leaves
TZLCOMP1-1368 STR	12.67±1.76bcde	TZISTR2129	14.33±0.33abcde
TZISTR1119	13.67±0.33abcde	TZISTR2131	12.67±0.33 bcde
TZISTR1121	12.00±0.58cde	TZISTR2133	13.33±0.33bcde
TZISTR1126	13.33±0.33bcde	TZISTR2139	12.67±0.33 bcde
TZISTR1130	13.00±0.00abcd	TZISTR2145	13.33±0.33bcde
TZISTR1131	12.00±0.58cde	TZISTR2149	14.00±0.00abcde
TZISTR1178	13.67±0.88abcde	TZISTR2150	14.33±0.33abcde
TZISTR1181	12.67±0.67bcde	TZISTR2152	15.67±0.33ab
TZISTR1214	13.67±0.33abcde	TZISTR2158	14.67±0.33abcd
TZISTR1224	14.33±0.33abcde	TZISTR2163	15.67±0.33ab
TZISTR1248	12.33±0.33cde	TZISTR2175	13.00±0.00bcde
TZISTR1303	15.00±0.58abc	TZISTR2186	13.33±0.33bcde
TZISTR1305	14.00±0.00abcde	TZISTR2205	13.33±0.67bcde
TZISTR1318	12.67±0.33bcde	TZISTR2208	13.33±0.67bcde
TZISTR1323	13.00±0.00bcde	TZISTR2211	12.67±0.33 bcde
TZISTR1336	11.67±0.33cde	TZISTR2221	12.00±0.57 cde
TZISTR1870	13.00±0.00bcde	TZISTR2225	12.33±0.33 cde
TZISTR1873	12.67±0.88bcde	TZISTR2227	13.33±0.33bcde



TZISTR1876	12.00±0.58cde	TZISTR2229	12.33±0.33 cde
TZISTR1878	14.00±0.58abcde	TZISTR2231	14.00±0.57abcde
TZISTR2002	14.67±0.33abcd	TZISTR2235	12.67±0.33 bcde
TZISTR2004	14.67±0.67abcd	TZISTR2239	12.33±0.33 cde
TZISTR2008	13.33±0.33bcde	TZISTR2241	13.00±0.00 bcde
TZISTR2017	14.33±0.33abcde	TZISTR2247	11.33±0.88 e
TZISTR2036	13.67±0.33abcde	TZISTR2251	14.00±0.58abcde
TZISTR2039	14.00±1.00abcde	TZISTR2256	14.00±0.58abcde
TZISTR2042	16.67±0.67a	TZISTR2260	12.67±0.33 bcde
TZISTR2043	14.67±0.88abcd	TZISTR2266	12.67±0.33 bcde
TZISTR2047	13.67±0.67abcde	TZISTR2267	13.00±0.58 bcde
TZISTR2049	12.67±1.20 bcde	TZISTR2269	13.00±0.00 bcde
TZISTR2054	14.67±0.33abcd	TZISTR2270	12.67±0.33 bcde
TZISTR2059	13.00±1.53 bcde	TZISTR2272	13.33±0.33bcde
TZISTR2064	13.67±0.33abcde	TZISTR2275	11.33±0.33
TZISTR2100	14.00±0.00abcde	TZISTR2279	12.33±0.33 cde
TZISTR2102	13.67±0.33abcde	TZISTR2287	12.67±0.33 bcde
TZISTR2107	14.00±0.00 abcde	Z.diplo. BC4-472-2-2- 16-4B-B	14.00±0.00abcde
TZISTR2115	14.00±0.00 abcde	1368 STR	13.50±0.62bcde
TZISTR2120	13.33±0.33 bcde	5057	14.00±1.15abcde
TZISTR2121	14.33±0.67abcde	9540	13.00±0.58bcde
TZISTR2125	14.00±1.15abcde		
P-value	<0.0001		<0.0001

Means with the same letters within the same column are not statistically different.

The scorching of maize plants by the *Striga* differed significantly ($p=0.0001$) between the inbred maize lines (Table 3). Inbred maize lines TZISTR2100 and TZISTR2269 had a significantly high scorching score of 9.00 per plant. The lowest scores were recorded in inbred maize lines TZISTR2279, TZISTR1318, TZISTR2064, ranging from 1.0-1.5 per plant.

Table 3: Scores of scorching on inbred maize plants

Lines	Scorching of plants	Lines	Scorching of plants
TZLCOMP1-1368 STR	6.00±1.73abcde	TZISTR2129	6.00±1.73abcde
TZISTR1119	4.50±0.00abcdef	TZISTR2131	4.50±0.00abcdef
TZISTR1121	6.50±0.00abcd	TZISTR2133	3.50±0.50bcdef
TZISTR1126	3.00±0.50cdef	TZISTR2139	3.00±0.00cdef
TZISTR1130	4.50±0.00abcdef	TZISTR2145	2.00±1.00def
TZISTR1131	6.00±0.00abcde	TZISTR2149	3.50±0.501bcdef
TZISTR1178	7.00±1.00abc	TZISTR2150	7.00±1.00abc
TZISTR1181	5.00±2.00abcdef	TZISTR2152	5.00±1.00abcdef

TZISTR1214	3.00±0.00cdef	TZISTR2158	3.00±0.00cdef
TZISTR1224	6.00±1.73abcde	T1ZISTR2163	4.00±1.00bcdef
TZISTR1248	5.00±2.00abcdef	TZISTR2175	6.00±0.00abcde
TZISTR1303	3.00±0.00cdef	TZISTR2186	3.00±0.00cdef
TZISTR1305	5.00±1.00abcdef	TZISTR2205	4.50±0.00abcdef
TZISTR1318	1.00±0.50	TZISTR2208	3.00±0.00cdef
TZISTR1323	3.00±0.00cdef	TZISTR2211	3.00±0.00cdef
TZISTR1336	5.50±0.50abcdef	TZISTR2221	4.50±0.87abcdef
TZISTR1870	4.50±0.00abcdef	TZISTR2225	3.00±0.00cdef
TZISTR1873	4.50±0.00abcdef	TZISTR2227	4.00±1.00bcdef
TZISTR1876	6.00±0.00abcde	TZISTR2229	4.50±0.00abcdef
TZISTR1878	6.00±0.00acde	TZISTR2231	3.00±0.00cdef
TZISTR2002	3.00±0.00cdef	TZISTR2235	4.50±0.00abcdef
TZISTR2004	5.00±1.00abcdef	TZISTR2239	4.50±0.00abcdef
TZISTR2008	3.00±0.00cdef	TZISTR2241	4.50±0.00abcdef
TZISTR2017	5.00±1.00abcdef	TZISTR2247	4.50±0.00abcdef
TZISTR2036	5.00±1.00abcdef	TZISTR2251	6.00±0.00abcde
TZISTR2039	7.00±1.00abc	TZISTR2256	5.50±0.50abcdef
TZISTR2042	4.00±1.00bcdef	TZISTR2260	4.50±0.00abcdef
TZISTR2043	4.00±1.00bcdef	TZISTR2266	1.50±1.50ef
TZISTR2047	5.00±1.00abcdef	TZISTR2267	4.50±0.00abcdef
TZISTR2049	5.00±1.00abcdef	TZISTR2269	9.00±0.00a
TZISTR2054	3.00±0.00cdef	TZISTR2270	5.00±1.00abcdef
TZISTR2059	4.00±1.00bcdef	TZISTR2272	4.00±1.00bcdef
TZISTR2064	1.50±0.00ef	TZISTR2275	5.00±1.00abcdef
TZISTR2100	9.00±0.00a	TZISTR2279	1.50±1.50ef
TZISTR2102	3.00±0.00cdef	TZISTR2287	9.00±0.00a
TZISTR2107	3.00±0.00cdef	Z.diplo. BC4-472-2-2- 16-4B-B	4.50±0.00abcdef
TZISTR2115	3.00±0.00cdef	1368 STR	5.00±1.00 abcdef
TZISTR2120	3.00±0.00cdef	5057	7.00±1.00 abc
TZISTR2121	8.00±1.00ab	9540	3.00±0.00 cdef
TZISTR2125	6.00±1.73abcde		
P-value	<0.0001		<0.0001

Means with the same letters within the same column are not statistically different.

The number of maize plant internodes differed significantly between maize lines at $p=0.0001$ (Table 4). The highest number of internodes was recorded in maize lines TZISTR2042, TZISTR2152, and TZISTR2163, ranging between 14-16 internodes per plant. The lowest number of internodes was recorded in maize lines TZISTR2247, TZISTR2275, and TZLCOMP1, each with an average of 10 internodes per plant (Table 4).



Table 4: Number of internodes of inbred maize plants

Lines	No. of internodes	Lines	No. of internodes
TZLCOMP1-1368 STR	11.67±1.76bcde	TZISTR2129	13.33±0.33abcde
TZISTR1119	12.67±0.33abcde	TZISTR2131	11.67±0.33bcde
TZISTR1121	11.00±0.58abcde	TZISTR2133	12.33±0.33abcdea
TZISTR1126	12.33±0.33abcde	TZISTR2139	11.67±0.33bcde
TZISTR1130	11.67±0.33bcde	TZISTR2145	12.33±0.33abcde
TZISTR1131	11.00±0.58abcde	TZISTR2149	13.00±0.00abcde
TZISTR1178	12.68±0.88acde	TZISTR2150	13.33±0.33acde
TZISTR1181	11.67±0.67bcde	TZISTR2152	14.67±0.33ab
TZISTR1214	12.67±0.33abcde	TZISTR2158	13.67±0.33abcd
TZISTR1224	13.00±0.58abcde	T1ZISTR2163	14.67±0.33ab
TZISTR1248	11.33±0.33bcde	TZISTR2175	12.00±0.00bcde
TZISTR1303	14.00±0.57abc	TZISTR2186	12.33±0.33abcde
TZISTR1305	13.00±0.00abcde	TZISTR2205	12.33±0.67abcde
TZISTR1318	11.67±0.33bcde	TZISTR2208	12.33±0.67abcde
TZISTR1323	12.00±0.00bcde	TZISTR2211	11.67±0.33bcde
TZISTR1336	10.67±0.33abcde	TZISTR2221	11.00±0.58abcde
TZISTR1870	12.00±0.00bcde	TZISTR2225	11.33±0.33abcde
TZISTR1873	11.67±0.88bcde	TZISTR2227	12.33±0.33abcde
TZISTR1876	11.00±0.58abcde	TZISTR2229	11.33±0.33bcde
TZISTR1878	13.00±0.58abcde	TZISTR2231	13.00±0.58abcde
TZISTR2002	13.67±0.33abcd	TZISTR2235	12.00±0.00bcde
TZISTR2004	13.67±0.67abcd	TZISTR2239	11.33±0.33bcde
TZISTR2008	12.33±0.33abcde	TZISTR2241	12.00±0.00bcde
TZISTR2017	13.33±0.33abcde	TZISTR2247	10.33±0.88abcde
TZISTR2036	12.67±0.33abcde	TZISTR2251	13.00±0.57abcde
TZISTR2039	13.00±1.00abcde	TZISTR2256	12.67±0.88abcde
TZISTR2042	15.67±0.67a	TZISTR2260	11.67±0.33bcde
TZISTR2043	13.67±0.88abcd	TZISTR2266	11.67±0.33abcde
TZISTR2047	12.67±0.67abcde	TZISTR2267	12.00±0.58bcde
TZISTR2049	11.67±1.20bcde	TZISTR2269	12.00±0.00bcde
TZISTR2054	13.67±0.33acd	TZISTR2270	11.67±0.33bcde
TZISTR2059	12.00±1.53bcde	TZISTR2272	12.33±0.33abcde
TZISTR2064	12.67±0.33abcde	TZISTR2275	10.33±0.33bcde
TZISTR2100	13.00±0.00abcde	TZISTR2279	11.00±0.58bcde
TZISTR2102	12.67±0.33abcde	TZISTR2287	11.67±0.33bcde
TZISTR2107	13.00±0.00abcde	Z.diplo.BC4-472-2-2-16-4B-B	13.00±0.00
TZISTR2115	13.00±0.00abcde	1368 STR	12.50±0.62 abcde
TZISTR2120	11.33±0.33bcde	5057	13.00±1.15 abcde
TZISTR2121	13.33±0.67abcde	9540	12.00±0.58 abcde
TZISTR2125	13.00±1.15abcde		

Means with the same letters within the same column are not statistically different.

Striga infestation on the maize inbred lines

The number of *Striga* attached to the inbred maize roots differed significantly (p=0.0001) (Table 5). Inbred maize lines TZISTR1126, TZISTR2256, and TZISTR2211 recorded the highest number of *Striga* attached to the maize plant roots. However, the results showed that Inbred maize lines TZISTR2102, TZISTR2175, TZISTR2241, TZISTR2270, and TZISTR2287 had no *Striga* attached to their roots.

Table 5: Number of *Striga* attached to the roots of inbred maize plants

Lines	No. of striga	Lines	No. of striga
TZLCOMP1-1368 STR	2.13±1.34bc	TZISTR2129	8.29±5.93bc
TZISTR1119	6.40±4.22bc	TZISTR2131	1.42±0.89bc
TZISTR1121	3.13±1.95bc	TZISTR2133	4.33±2.46bc
TZISTR1126	18.72±4.33a	TZISTR2139	1.56±0.49bc
TZISTR1130	0.13±0.13c	TZISTR2145	0.50±0.42bc
TZISTR1131	0.20±0.20c	TZISTR2149	2.33±1.76bc
TZISTR1178	0.40±0.20bc	TZISTR2150	0.13±0.13c
TZISTR1181	0.13±0.13c	TZISTR2152	0.42±0.42bc
TZISTR1214	2.87±2.77bc	TZISTR2158	0.25±0.25bc
TZISTR1224	0.40±0.23bc	T1ZISTR2163	3.60±1.61bc
TZISTR1248	0.20±0.20c	TZISTR2175	0.00±0.00c
TZISTR1303	1.27±0.44bc	TZISTR2186	0.33±0.33bc
TZISTR1305	0.20±0.20c	TZISTR2205	2.94±2.10bc
TZISTR1318	3.94±1.44bc	TZISTR2208	1.42±0.63bc
TZISTR1323	4.28±1.70bc	TZISTR2211	8.61±1.79b
TZISTR1336	3.28±2.64bc	TZISTR2221	1.00±0.92bc
TZISTR1870	1.27±1.27bc	TZISTR2225	2.91±1.47bc
TZISTR1873	0.40±0.40bc	TZISTR2227	0.47±0.29bc
TZISTR1876	0.47±0.24bc	TZISTR2229	4.06±2.02bc
TZISTR1878	5.20±2.00bc	TZISTR2231	2.72±0.44bc
TZISTR2002	4.89±2.36bc	TZISTR2235	0.67±0.19bc
TZISTR2004	0.67±0.57bc	TZISTR2239	1.06±0.63bc
TZISTR2008	0.89±0.34bc	TZISTR2241	0.00±0.99c
TZISTR2017	4.67±1.40bc	TZISTR2247	1.24±1.05bc
TZISTR2036	2.47±2.07bc	TZISTR2251	9.33±2.46b
TZISTR2039	2.47±1.57bc	TZISTR2256	5.06±2.41bc
TZISTR2042	2.08±0.92bc	TZISTR2260	2.83±1.42bc
TZISTR2043	0.80±0.40bc	TZISTR2266	2.11±2.11bc
TZISTR2047	0.47±0.07bc	TZISTR2267	3.83±1.11bc
TZISTR2049	0.33±0.18bc	TZISTR2269	2.06±0.87bc
TZISTR2054	1.40±0.83bc	TZISTR2270	0.00±0.00c
TZISTR2059	0.40±0.23bc	TZISTR2272	1.27±0.24bc
TZISTR2064	1.28±0.31bc	TZISTR2275	0.67±0.24bc



TZISTR2100	1.80±0.61bc	TZISTR2279	1.67±1.17bc
TZISTR2102	0.00±0.00c	TZISTR2287	0.00±0.00c
TZISTR2107	0.28±0.15bc	Z.diplo.BC4-472- 2-2-16-4B-B	1.11±0.59bc
TZISTR2115	1.83±0.51bc	1368 STR	0.80±0.39bc
TZISTR2120	2.28±1.03bc	5057	1.20±0.76bc
TZISTR2121	1.40±0.58bc	9540	0.40±0.20bc
TZISTR2125	0.40±0.23bc		
P-value	<0.0008		<0.0008

Means with the same letters within the same column are not statistically different.

The biomass of *Striga* attached to the roots differed significantly between the inbred maize lines ($p=0.0001$), as shown in Table 6. *Striga* attached to the Inbred maize line TZISTR2100 had the significantly highest biomass of 40.30 mg per plant. Biomass of *Striga* attached to Inbred maize lines TZISTR225, 5057, TZISTR2129, TZISTR2211, and TZISTR2251 recorded high weight ranging from 22-26 mg per plant. However, *striga* biomass on inbred maize lines TZISTR2287, TZISTR2175 attained low weight.

Table 6: Biomass (g) of *Striga* attached to the inbred maize plants

Lines	Biomass (g)	Lines	Biomass (g)
TZLCOMP1- 1368 STR	0.00±0.00b	TZISTR2129	22.72±19.80ab
TZISTR1119	17.94±5.31ab	TZISTR2131	2.65±1.67b
TZISTR1121	2.87±1.27b	TZISTR2133	9.60±5.41ab
TZISTR1126	10.14±5.64ab	TZISTR2139	1.52±1.39b
TZISTR1130	0.00±0.00b	TZISTR2145	0.09±0.09b
TZISTR1131	0.00±0.00b	TZISTR2149	3.86±3.44b
TZISTR1178	0.00±0.00b	TZISTR2150	0.84±0.84b
TZISTR1181	0.00±0.00b	TZISTR2152	0.49±0.49b
TZISTR1214	13.54±13.15ab	TZISTR2158	0.19±0.19b
TZISTR1224	0.00±0.00b	T1ZISTR2163	1.07±0.09b
TZISTR1248	0.77±0.39b	TZISTR2175	0.00±0.00b
TZISTR1303	3.80±1.43b	TZISTR2186	0.00±0.00b
TZISTR1305	0.00±0.00b	TZISTR2205	5.07±2.59b
TZISTR1318	3.05±2.37b	TZISTR2208	1.06±0.59b
TZISTR1323	4.00±3.07b	TZISTR2211	21.84±12.31ab
TZISTR1336	1.71±1.54b	TZISTR2221	0.22±0.22b
TZISTR1870	6.76±6.76b	TZISTR2225	1.21±0.68b
TZISTR1873	6.34±6.17b	TZISTR2227	0.98±0.98b
TZISTR1876	4.60±2.08b	TZISTR2229	2.88±2.03b
TZISTR1878	15.24±4.83ab	TZISTR2231	1.83±0.92b
TZISTR2002	5.94±2.58b	TZISTR2235	0.38±0.07b

TZISTR2004	0.84±0.84b	TZISTR2239	0.52±0.29b
TZISTR2008	1.25±1.09b	TZISTR2241	0.00±0.00b
TZISTR2017	3.34±2.16b	TZISTR2247	0.47±0.38b
TZISTR2036	0.89±0.89b	TZISTR2251	25.92±4.27ab
TZISTR2039	0.00±0.00b	TZISTR2256	8.86±6.85b
TZISTR2042	16.66±8.34ab	TZISTR2260	4.29±4.29b
TZISTR2043	1.21±1.21b	TZISTR2266	2.75±2.75b
TZISTR2047	1.22±1.22b	TZISTR2267	6.25±1.92b
TZISTR2049	0.58±0.58b	TZISTR2269	2.07±2.03b
TZISTR2054	3.04±2.67b	TZISTR2270	2.50±2.50b
TZISTR2059	0.66±0.66b	TZISTR2272	0.91±0.91b
TZISTR2064	4.44±1.39b	TZISTR2275	2.62±2.62b
TZISTR2100	40.30±28.96a	TZISTR2279	1.33±1.33b
TZISTR2102	0.00±0.00b	TZISTR2287	0.00±0.00b
TZISTR2107	0.47±0.41b	Z.diplo.BC4-472- 2-2-16-4B-B	0.52±0.26b
TZISTR2115	4.29±2.36b	1368 STR	14.84±8.48ab
TZISTR2120	3.15±1.57b	5057	23.70±16.46ab
TZISTR2121	2.55±1.87b	9540	5.95±3.08b
TZISTR2125	1.64±1.64b		
P-value	<0.0001		<0.0001

Means with the same letters within the same column are not statistically different.

Heterotic grouping of the maize lines

The population structure analysis of the 176 inbred maize lines showed that delta K values from the mean log-likelihood probabilities peaked at $k = 3$ (Fig. 1). At $k = 3$, 100% of the maize inbred lines were placed into three subpopulations, with 65% of the lines falling into the mixed group as admixtures. In addition, 35 inbred maize lines were assigned to subpopulation 1 (red). This subpopulation was characterized by the majority of the individual inbred lines being genetically homogenous (primarily assigned to one subpopulation) except three lines (TZ1STR2235, TZ1STR2236, and TZ1STR2163), which were admixtures. The second subpopulation (green) comprised 47 inbred lines. The majority of the inbred lines were homogenous, with a few being heterogeneous, including lines TZ1STR2155, TZ1STR1339, TZ1STR2281, TZ1STR2286, TZ1STR2129, and TZ1STR2111. The existence of admixtures in these subpopulations showed that the admixtures share ancestry and are derived from 2 or more germplasm sources (subpopulations 1 and 2). The third subpopulation (blue) comprised 87 lines, and the controls (5057,

9540, 1368 STR, 9071 STR). All the inbred lines in this subpopulation were admixtures derived from germplasm of subpopulations 1, 2, and 3 (Fig. 1).

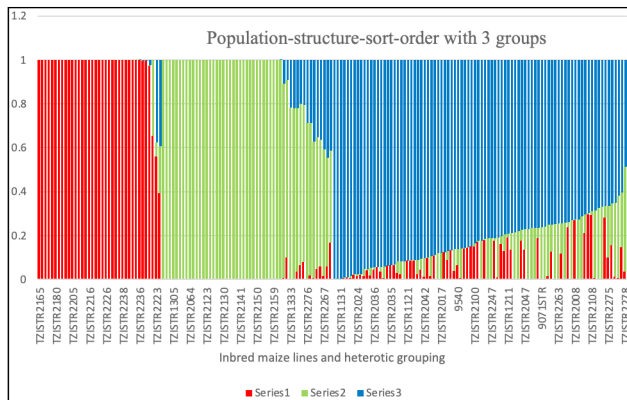


Fig. 1: Population structure obtained from STRUCTURE based on $k = 3$. Each vertical bar plot represents a single maize inbred, while the three different colors represent the subpopulations (clusters). Red-Subpopulation 1 with 35 inbred lines, Green-Subpopulation 2 with 47 inbred lines, and Blue-Subpopulation 3 with 87 inbred lines

The heterozygosity of the inbred maize lines ranged between 0.0 to 0.85, with fewer lines below 0.8 (Fig. 2). Besides, the major allele frequency (MAF) in the 10 chromosomes ranged between 0.0 and 1.0, and an average of 0.80. The MAF indicates that the major allele for most of the SNPs was present in 34.60%-100% of the maize lines. Therefore, there was a high degree of genetic uniformity among the inbred maize lines for most of the SNP markers used in this study.

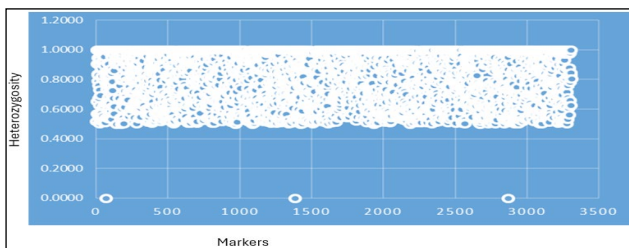


Fig. 2: Heterozygosity of the inbred maize lines based on the DArTag marker system

The PCA revealed that the majority of the inbred lines clustered together (Fig. 3). The clustering was consistent with that provided by phylogenetic analysis. PC1 captures most variance (-5.6-4.8) followed by PC2 and PC3. Therefore, the inbred lines in PC1 share common alleles than those clustering at PC2 (-4.8-5) and PC3 (-2-1.5). In PC3, a few maize lines have unique SNP marker patterns (Fig. 3).

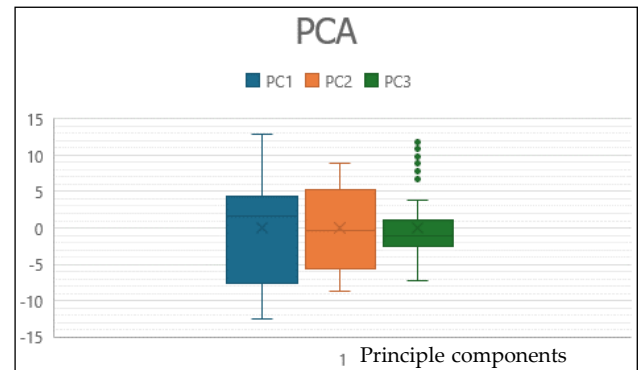


Fig. 3: Principal Component Analysis (PCA) of the inbred maize lines. Blue-Subpopulation 1, Orange-Subpopulation 2, and Green-Subpopulation 3

Genetic diversity of the inbred maize lines using molecular markers based on the DArTag marker system

A total of 3305 DArTag SNP markers were used to assess the genetic diversity of the 176 maize inbred lines, including the controls. Quality assessment was done using the DArTag marker system, and 2385 DArTag SNP markers were of high quality and were retained for the determination of the genetic diversity. Based on the retained SNP markers, the inbred maize lines were genetically diverse (Fig. 4). The gene diversity ranged from 0 - 1.0, recording an average gene diversity of 0.26. A few of the inbred maize lines exhibited genetic diversity values of 1.0, suggesting a higher genetic diversity. However, the majority of inbred maize lines had genetic diversity below 0.4 (Fig. 4).

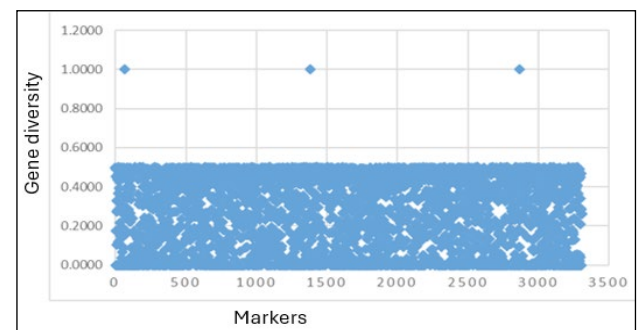


Fig. 4: Gene diversity of the 176 inbred maize lines based on the DArTag marker system

In this study, the majority of polymorphism information content (PIC) values were below 0.4. All the PIC values ranged between 0.2 to 0.4 (Fig. 5). The PIC values were distributed evenly across the 10 chromosomes and had an average of 0.21. This

shows that most of the markers had low to moderate informativeness. These markers had low allele frequency differences or could be monomorphic. However, none of the markers used in this study had a PIC value of 1.0; hence no highly informative markers in the inbred maize lines dataset (Fig. 5). The consistent range of the PIC values indicates a stable level of genetic diversity among the inbred maize lines.

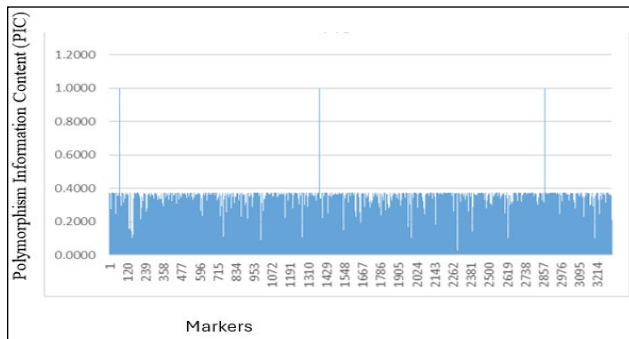


Fig. 5: Polymorphism Information Content (PIC) based on the DArTag marker system

The results on the inbred lines population structures analysis were confirmed by phylogenetic analysis (Fig. 6). The phylogenetic tree grouped the 176 genotyped inbred maize lines into three subpopulations. Subpopulation 1 (red) comprised 87 inbred lines, subpopulation 2 (green) comprised 55 inbred lines, and subpopulation three (blue) had the fewest lines with 34 inbred lines (Fig. 6).

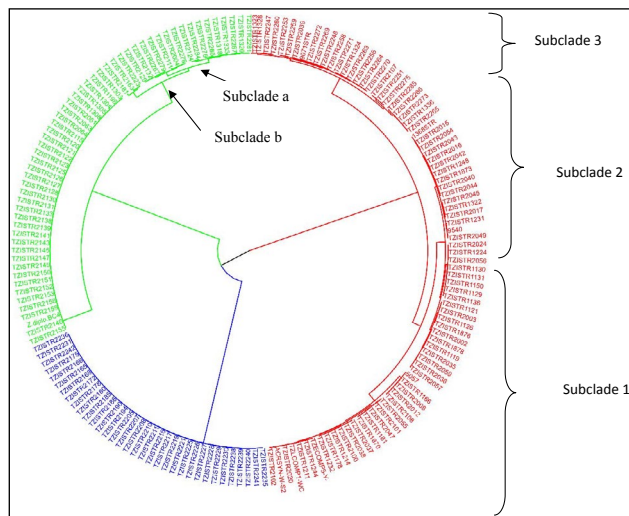


Fig. 6: Genetic distances and phylogenetic analysis of the 176 inbred maize lines inferred using the neighbour-joining clustering method

Subpopulation 3 had one clade, while subpopulation 2 was made of one main clade and two subclades.

Subpopulation one had one main clade and three subclades. Control 5050 clustered in subclade 1, control 9540 and 13685STR subclade 2, while control 9071STR clustered in subclade 3. The branch lengths in the dendrogram differed significantly between the clades. The clustering of the inbred maize lines into three subpopulations shows genetic similarity within each group and genetic differences between the subpopulations.

DISCUSSION

Response of maize inbred lines to *Striga* infestation

In this study, *Striga* infestation significantly reduced the plant height and length of the internodes of the inbred maize lines. This may be attributed to nutrient deprivation by the *Striga*. According to Mwangangi *et al.* (2024), when *Striga* attaches to the maize roots, it siphons off the plant's essential nutrients and water. This deprives the plant of the resources required for growth, thus reducing plant height. Besides, *Striga* infestation, particularly in maize, results in disruption of the plant hormonal balances, especially those involved in plant growth, including auxins, gibberellins, and cytokinin. The disruption is associated with abnormal growth in plants and subsequently reduced plant height and length of internodes (Mwangangi *et al.* 2024). Moreover, *Striga* infestation impedes the development of roots in the maize plant, thus a weaker root system and delayed overall development, hence significantly reduced height.

Additionally, *Striga* infestation occasions hormonal imbalances in maize, which in turn suppress the development of new leaves on the growing points within the plant. Consequently, the number of leaves is lower in the *Striga*-infested plants than in the non-infested plants. *Striga* triggers the production of stress-related hormones such as abscisic acid (ABA), which limits the formation of leaves in plants as a survival strategy to water stress. This is associated with a low number of leaves, as reported in this study for some maize lines. *Striga* absorbs nutrients available for the plant, and the unavailability of these nutrients to the plant results in fewer leaf formations in the plants (Mwangangi *et al.* 2024).



Striga infestation has significant deleterious effects on the host plants. Inbred maize lines with high *Striga* attachment on the roots had reduced plant height and number of leaves than the inbred maize lines that had no *Striga* attachment on the roots (Unachukwu *et al.* 2020). Reduced number of plant leaves affects the stomatal conductance, which is vital for the acquisition of carbon (IV) dioxide. *Striga* infestation in maize results in reduced stomatal conductance, thus stomatal closure in the *Striga* host plant while increasing the stomatal conductance of the *Striga* parasite (David *et al.* 2022). Therefore, the available water and nutrients from the host plant are directed to the *Striga* parasite. Consequently, the host plant's photosynthetic capacity and production are reduced (Cimmino *et al.* 2018).

The scorching of plants by *Striga* differed between the inbred maize lines. This may be attributed to differences in metabolic support from the different inbred maize lines. The flow of nutrients, particularly from *Striga*-susceptible inbred maize lines, is low compared to the *Striga*-resistant inbred lines, hence the differences in scorching (Zebire *et al.* 2020). *Striga* susceptible inbred lines have limited nutrients for the *Striga*, hence higher scorching (Mwangangi *et al.* 2024).

Striga infestation on the maize inbred lines

The number of *Striga* attached to the roots differed between the maize inbred lines. This may be attributed to the differences in the stimulation ability of the maize lines or the reduced production of the *Striga* germination stimulants by the different maize lines. According to Unachukwu *et al.* (2020), the differences in genes of the maize lines result in differences in the strigolactone in root exudates, hence differences in *Striga* attachment on the inbred maize lines. Some maize inbred lines could have been resistant to the *Striga* infestations, hence slow or no *Striga* attachment compared to the susceptible inbred lines. These finding corroborates with Hu *et al.* (2020) who reported that inbred maize lines resistant to *Striga* intrinsically induce either biochemical or physiological defense responses to parasitism, particularly on the *Striga* parasite.

Moreover, the differences in the number of *Striga* attached to the inbred maize roots can be attributed to the *Striga* germination and dynamics.

The *Striga* seeds require specific conditions to germinate, including a signal from the maize roots (strigolactones). The attachment phase starts during the early weeks, and later the parasitism peaks (Unachukwu *et al.* 2020). The *Striga* develops haustoria (specialized roots) to extract nutrients, leading to a significant increase in the number of attached parasitoids. Additionally, some maize lines exhibit genetic resistance to *Striga*, which might have affected the attachment rates (Hu *et al.* 2020). Maize with strong resistance mechanisms may show fewer *Striga* parasites, while the susceptible lines supported continuous *Striga* growth and higher attachment numbers.

The response of *Striga* to the resistant inbred lines could be attributed to the accumulation or deposition of the plant exudates and substances that interfere with the *Striga* parasite *haustoria*, leading to poor nutrient absorption from the inbred maize lines. With low nutrients absorbed, the *Striga* will have retarded growth (Cimmino *et al.* 2018). Similarly, the *Striga* retarded growth or attachment on the roots could be attributed to host-plant induced compounds, which are toxic to the parasite, thus low germination and low attachment on the inbred maize lines (Kim and Adetimirin, 2001).

Additionally, different inbred lines have differences in the root architecture, hence differences in attachment of the *Striga* (Li *et al.* 2018). *Striga* is a root parasite, and in maize lines with fewer roots, there is a significantly lower likelihood of *Striga*-host root contact (Gobena *et al.* 2017). The *haustoria* help in connecting the *Striga* with the host plant, consequently resulting in the flow of water and nutrients from the host plant to the *Striga*, thus damaging the latter (Cimmino *et al.* 2018).

The *Striga* biomass differed between the inbred maize lines, and this could be attributed to differences in host nutrients. *Striga* relies on the host plants for water and nutrients. Influx of these nutrients allows the *Striga* to grow and invest in vertical growth, which increases the biomass in healthy plants compared to unhealthy plants (Mwangangi *et al.* 2024). If the maize plant is heavily infested by the maize parasite, the *Striga* may experience stunted growth due to limited supply of nutrients and water, hence reduced biomass.



Heterotic grouping of the maize lines using molecular markers

In this study, 176 inbred maize lines were assessed for their genetic diversity using 3305 SNP markers. Besides, 35% of the markers were present as homogenous, while 65% were present as heterozygous. The 3305 SNP markers revealed the presence of three subpopulations ($K=3$) within the 176 inbred maize lines. The inbred maize lines from the same pedigree clustered in one subpopulation. Therefore, the SNP markers assigned the inbred maize lines into heterotic groups based on their genetic makeup, background, and the source population. This agrees with Ayesiga *et al.* (2023) which is an important parameter that enables breeders to select parental lines and designing breeding systems. We assessed the level of genetic diversity and population structure in a panel of 151 tropical maize inbred lines using 10,940 SNP (single nucleotide polymorphism, who reported that the SNP markers assign the inbred lines to different subpopulations based on the inbred maize lines' genetic background and phenotypic features such as endosperm color. According to Adu *et al.* (2024), the SNP marker's ability to assign inbred lines to homogenous groups demonstrates the effectiveness of these markers in genotyping. Use of a large number of SNP markers facilitates better interpretation of the heterotic groupings and inferences on the population structure of the inbred maize lines.

Apart from a homogenous population, the population structures analysis showed inherent grouping within the population, particularly in subpopulation 3. The existence of inherent grouping presents a stable and reliable grouping of individual inbred maize lines within the genotypes tested, hence it can be used to select inbred maize lines from different groups for purposes of heterotic hybridization as described by Ertiro *et al.* (2017) we investigated the genetic purity, relatedness and population structure of 265 maize inbred lines from the Ethiopian Institute of Agricultural Research (EIAR). In addition, it shows that the inbred maize lines in subpopulation 3 were genetically diverse than those in subpopulations 1 and 2.

The grouping of the inbred maize lines into the same subpopulation shows that lines in the same

groups share common ancestry and are genetically related. This is in agreement with Badu-Apraku *et al.* (2021), who indicated that common ancestry and genetic relatedness of maize lines place these lines in the same subpopulation. Furthermore, it is in line with Adu *et al.* (2022), who indicated that inbred lines in distinct heterotic groups have significantly higher genetic distances between them and vice versa.

Additionally, there was a large number of inbred lines with admixtures, accounting for 65% of the tested lines. Detection of a large number of admixtures is attributed to the mixed genetic background and the generation of the inbred maize lines. At F1, there is a possibility that in this generation, there might be limited generation advancement and selection to allow division of these lines into distinct groups as established by Badu-Apraku *et al.* (2023).

The heterozygosity of the inbred maize lines ranged between 0.0 and 0.85 an average of 0.03. Besides, the major allele frequency in the 10 chromosomes ranged from 0.50 to 1.0, and an average of 0.80. According to Semagn *et al.* (2012), inbred lines are considered to be pure if the proportion of the heterozygous SNP loci is less than 5%. The significantly high heterozygosity observed in this study is attributed to the inbred maize lines' early generation (F1). This finding contrasts with Josia *et al.* (2021), who reported low heterozygosity in S4 early generation, and the inbred lines were considered pure. The existence of pure inbred lines is significantly influenced by the inbreeding technique that is used during the advancement of the tested lines. According to Ertiro *et al.* (2017), the number of reading generations required for the production of homozygous lines is significantly reduced when many individuals are selected phenotypically while segregating the desired progenies for the subsequent inbreeding. Similarly, it is reduced when there is negative selection of the heterotic traits, such as the maize height, days to anthesis, and leaf number, are considered (Adu *et al.* 2024).

The mean PIC of 0.21 recorded in the inbred lines indicates that the markers showed high polymorphism in the inbred lines and present a potential chance for these markers to be used in further selection. This finding corroborates a



previous study by Adu *et al.* (2024), where a PIC value of 0.23 was recorded, and this was high polymorphism among the inbred maize lines. Besides, it agrees with Zhang *et al.* (2016), who recorded a PIC value ranging from 0.25-0.39 in maize. However, this study reported significantly higher PIC than the previous study done by Adu *et al.* (2019), who reported an average PIC of 0.19. Based on genotyping of inbred maize lines done by IITA using 1057 markers, PIC average values of 0.218 and MAF values of 0.202 were reported. Similarly, CIMMYT reported an average PIC value of 0.256 and a peak distribution ranging from 0.02-0.375 in inbred maize lines (Dao *et al.* 2014). Despite the genotyping done using similar markers, the PIC values differ. These differences can be attributed to various factors, including the composition of the experimental material, the number of markers used, and the population size, as described by Yan *et al.* (2010).

Genetic diversity of the inbred maize lines using molecular markers based on the DArTag marker system

Molecular analysis is vital in determining the extent of genetic diversity present in a population. In plant breeding, high gene diversity provides an opportunity for selecting plant lines with wide adaptation to a range of constraints and traits. The gene diversity in this study ranged from 0-1.0 an average gene diversity of 0.26. This implies abundant genetic diversity within the 176 inbred maize lines, hence allowing significant progress in parental line selection, which can contribute to high genetic gain and heterosis for the desired traits. This is in agreement with Lu *et al.* (2009), who reported gene diversity of 0.27, and Adu *et al.* (2019), who reported gene diversity of 0.22. However, this was significantly lower compared to the gene diversity reported by Ayesiga *et al.* (2023) and Josia *et al.* (2021), where the gene diversity was 0.39 and 0.45, respectively. These differences in the gene diversity in these studies are accounted for by the differences in the set of germplasm used in the experiment and the number of SNP markers used (Serrote *et al.* 2020) According to Xia *et al.* (2005), genetic distances are vital in establishing the degree of relatedness between individuals in a population. Based on this study finding, the genotyped inbred maize lines

had wide variability and low genetic distances. Therefore, these inbred lines are unique and have the potential to contribute new alleles that can be utilized in future breeding programs.

CONCLUSION

Striga infestation significantly reduced the plant height, length of the internodes, and number of leaves of the inbred maize lines, which have low or no resistance to the parasite. The number of *Striga* attached to the roots and biomass was lowest in resistant lines, attributed to reduced production of the *Striga* germination stimulants and a reduction in nutrients from the host. The SNP markers grouped the 176 inbred maize lines into three (3) distinct subpopulations: 1, 2, and 3 with 35, 47, and 87 inbred maize lines, respectively. Based on the DArTag marker system and the 3305 SNP markers, the inbred maize lines were genetically diverse. The genetic diversity differed across the inbred lines' subpopulations. The gene diversity ranged from 0-1.0 an average of 0.26. The inbred lines have the potential to contribute new alleles that can be utilized in future breeding programs for resistance to *striga*.

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