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Screening of maize inbred lines for resistance to *Aspergillus flavus* and agronomic traits for semi-arid areas

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ABSTRACT

Maize is a main cereal crop meeting food demand for approximately 300 million people in Sub-Saharan Africa (SSA). A fast-growing human population and production challenges have surged the demand for maize grains. Tropical climate, in addition to poor pre- and post-harvest practices, has resulted in the highest levels of mycotoxin accumulation in several food products, including maize in SSA. Aflatoxin contamination has a negative impact on food safety, often resulting in outbreaks, especially in Kenya. Aflatoxin contamination in Africa is aggravated by limited resistant maize lines. Therefore, this study screened certain commercial inbreds against *A. flavus* that can be developed into more resistant and resilient hybrids suited for both subsistence and commercial use in regions with limited rainfall. The aim of this study was to determine if the aflatoxin resistance and agronomic performance and yield stability in the inbred lines are influenced solely by genes or by interactions with the environment. Field experiments were conducted at Kenya Agricultural and Livestock Research Organization (KALRO) in Katumani and Kiboko sub-centres using five maize inbred lines (ML312, KABML018, KABML 658-3, KABML 308-2-2, and KABML 6-2-1). Maize inbreds were grown following a 3 x 5 lattice randomized complete block design and inoculated with *Aspergillus flavus* S strain during 50% silking using silk channel method. The aflatoxin accumulation (levels) as was assessed from 20-gram sample of flour using an ELISA-based Reveal Q+ Kit. Agronomic performance (anthesis-silking intervals, days from silking to maturity, plant height, ear height, grain moisture and grain yield) for the inbreds were evaluated from five randomly selected plants in each replicate. General combining ability of each inbred line was computed. Aflatoxin accumulation and agronomic performance datasets were subjected to analysis of variance in Minitab software. This study revealed that KABML6-2-1 and KABML018 exhibited excellent performance and show promise for creating hybrids with built-in resistance in semi-arid farming systems. KABML658-3 and KABML308-2-2 can be used as secondary resistance sources. This study recommends testing resistant parental lines, such as KABML6-2-1 and KABML018, before commercial distribution through multi-location experiments to confirm their resistance, stability, and adaptability.

Keywords: Introgression; Aflatoxin; Semi-arid areas

INTRODUCTION

About 1.2 billion people worldwide and 300 million people in Sub-Saharan Africa (SSA) rely on maize (*Zea mays* L.) as a staple food and income crop (IITA, 2025). Africa's rising population has increased demand for more food. Amid the increasing population increase and subsequent surge demand for maize as well production challenges in SSA, the availability of maize grains has decreased significantly, often resulting in a skyrocketing price (Simane *et al.,* 2025). According to the Food and Agriculture Organization (FAO), maize contains roughly 365 kilocalories per 100 grams and contributes 35% of total caloric intake (FAOSTAT, 2019). One important bottleneck is pre- and post-harvest losses, ranging from

12% to over 30%, due to insect, rodent, and fungal damages, as well as improper handling and storage of maize grains (Kumar & Kalita, 2017; Tefera, 2012). Insect infestations and damage by rodents create conditions for the infestation by mycotoxin-causing fungi, which further deteriorate the grains and render them unsafe for human consumption (Okori *et al.*, 2022; Shukla *et al.*, 2025). Furthermore, climate change has not only contributed to pre-harvest loss of maize but also amplified the infestation and proliferation of mycotoxin-causing fungi (Ngum *et al.*, 2022).

African nations have encountered the elevated levels of mycotoxin contamination partly due to their tropical climatic conditions (Ngum *et al.*, 2022). *Aspergillus, Penicillium,* and *Fusarium* are among the fungal genera that naturally produce mycotoxins, which are poisonous substances. Maize grains, for example, is the most prone to contamination by *Aspergillus fungus*, particularly *A. flavus* and *A. parasiticus,* which thrive in high-temperature, highhumidity, and drought-stressed conditions (Okoth *et al.*, 2012). These fungi produce substantial amounts of mycotoxins, especially aflatoxins, and have been a major contributor to food poisoning outbreaks in Kenya since 1960 (Kang'ethe *et al.*, 2020; Omara *et al.*, 2021). Aflatoxin exposure in Kenya is around 21.3 ng/kg bw/day (Omara *et al.*, 2021) and about 16% of maize flour samples have above permissible limit (10 ppb) (Hoffman *et al.*, 2025). Contaminations of food products by aflatoxin have negatively impacted food safety and trade because of its toxic nature. These aflatoxins have associated with health concerns when consumed in large quantities over an extended period of time (Dhakal *et al.*, 2023; Syraji *et al.*, 2025).

The widespread and severity of aflatoxin contamination in Africa is aggravated by limited resistant maize lines, poor field agronomic methods (such as low farm input), inappropriate grain storage, adverse weather conditions (such as limited rainfall and high temperatures), and limited knowledge and insufficient technical support in controlling and managing the problem (Ngum *et al.*, 2022; Nji *et al.*, 2022). Numerous management strategies have been proposed, such as the use of resistant maize, good agricultural practices, biocontrol agents (like Aflasafe), timely and proper harvesting, processing, drying, and storing methods, and chemical treatments (Kwigizile *et al.*, 2025). Using host plant resistance is one potential, economical method of lowering pollution (Guo *et al.*, 2017). Previous studies have screened and identified maize germplasms that resistant to *A. flavus* for potential hybridization projects (Moral *et al.*, 2022; Suwarno *et al.*, 2019; Warburton *et al.*, 2015). According to reports, the presence of carotenoid compounds in maize plants can suppress colonization by aflatoxin-producing fungi and *in vitro* development of aflatoxins (Mollel *et al.*, 2025; Suwarno *et al.*, 2019).

Finding the source of resistance with desired agronomic traits in commercial materials is an additional possibility; however, there is scarce information on aflatoxin accumulation in commercial cultivars. In order to find the source of resistance to be included in the breeding initiatives, a thorough screening of the current inbreds and commercial materials should be carried out. Thus, the purpose of this study was to assess the phenotypic screening of certain commercial inbred lines against *A. flavus* that can be used to develop more resistant hybrids suitable for both subsistence and commercial uses in semi-arid areas. Alongside this, agronomic performance and yield stability for the inbreds were evaluated. Additionally, the study will determine if the aflatoxin resistance and agronomic performance and yield stability in the inbred lines are influenced solely by genes or by interactions of genes with the environment.

MATERIALS AND METHODS

Study area

The study was conducted at the research stations of the Kenya Agricultural and Livestock Research Organization (KALRO) in Katumani (1° 34' 60" S, 37° 15' 0" E) and Kiboko (2° 10' S, 37° 40' E) in southeast Kenya (Figure 1). The two locations were chosen due to variability in weather conditions as well as past aflatoxicosis epidemics. Situated 1600 m above sea level (a.s.l.) in Machakos County is the KALRO Katumani Centre. It is a semi-arid with tropical climate. The centre experiences bimodal rainfall pattern receiving mean rainfall of 655 mm, annually. The centre experiences mean maximum temperatures of 24.7 °C and mean lowest temperatures of 13 °C. Chromic luvisols are the predominant soil type in this region. KALRO Kiboko is located in Makindu sub-county, Makueni County. The station is 975 m a.s.l. and has a bimodal rainfall pattern, with averages ranging from 545 to 629 mm. Kiboko has a hot, dry climate, with temperatures ranging from 16.5°C to 28.6°C. Acri-rhodic ferralsols are the area's major soil type. Long rain falls from March to May at both places, whereas brief rain falls from October to January.

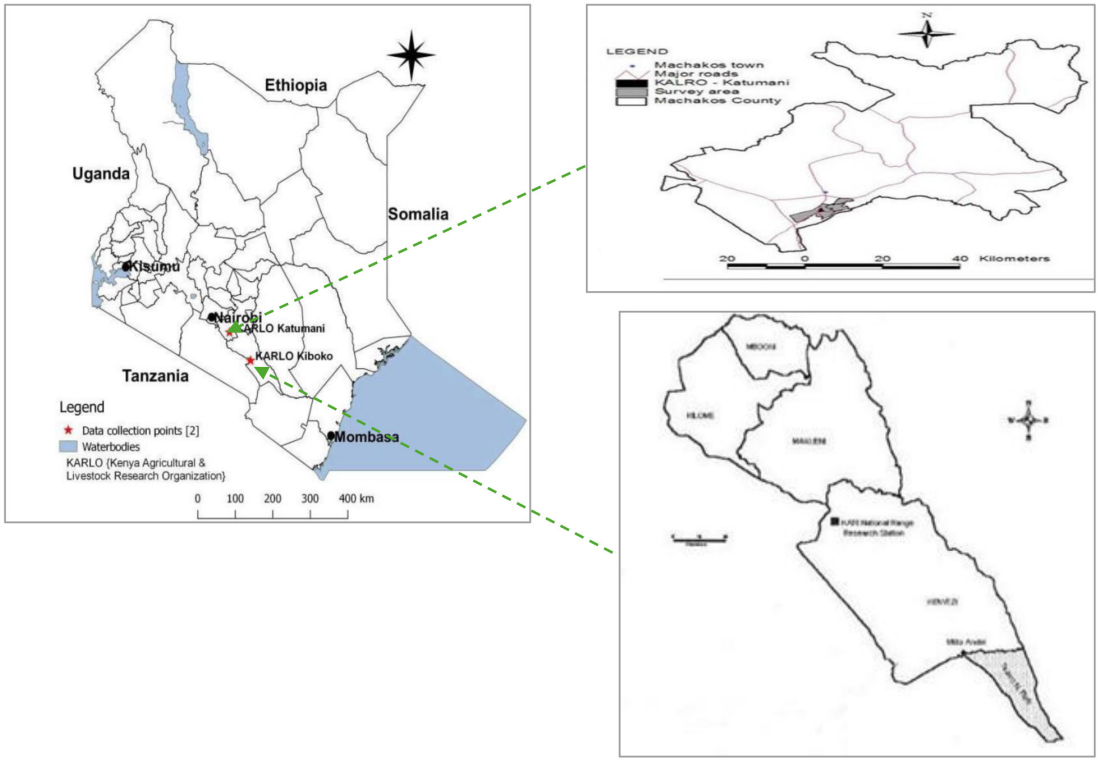

Figure 1. Map representing study sites in Kenya Agricultural and Livestock Research Organization (KALRO) research stations in Kiboko and Katumani, located in Machakos County and Makueni County, respectively.

Experimental materials and sources

Maize inbred: The maize germplasm was sourced from the International Maize and Wheat Improvement Centre (CIMMYT). The five inbred lines for the aflatoxin trial in both KARLO Kiboko and Katumani were CML312, KABML018, KABML 658-3, KABML 308-2-2, and KABML 6-2-1.

Inoculum: *Aspergillus flavus* S strain with aflatoxin production of over 5000 ppb, previously isolated from Machakos County farmers' farms and stored in the repository at KALRO Katumani laboratories.

Experimental design

Maize was planted in plots organized in a 3 x 5 lattice randomized complete block design (Figure 2). Each maize inbred line was planted in one plot per block and replicated five times. A plot measured 3 m × 3 m, and there was a 1 m passage between each plot and a 2 m road between each block. This resulted in a total of 15 plots in each block that were duplicated three times. The distance between planting hills was 75 cm by 25 cm.

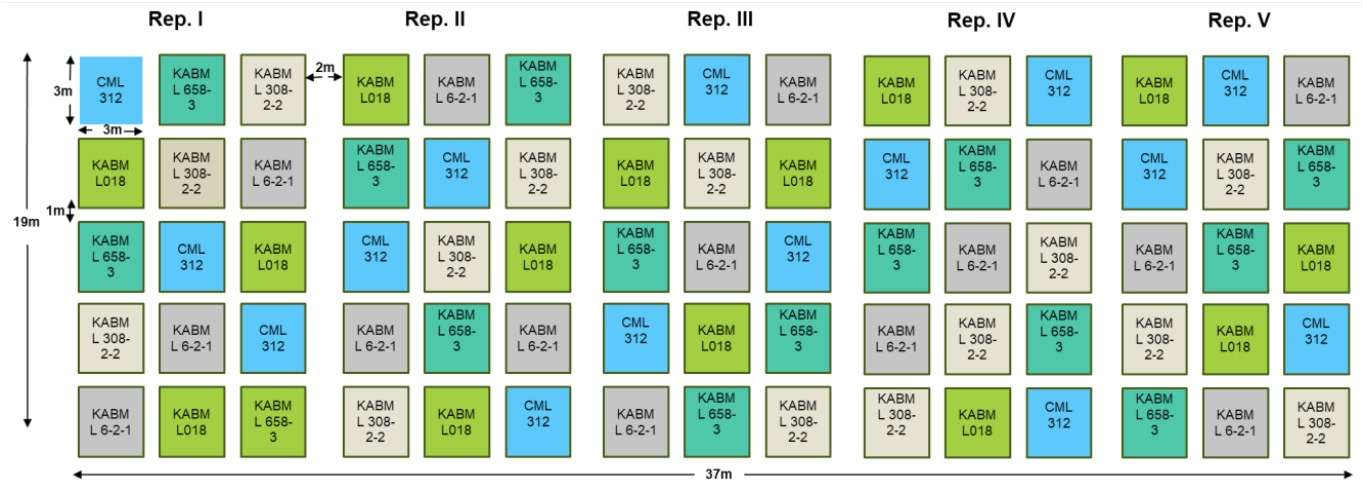

Figure 2. Illustration of experimental lay out organized in a randomized complete block design with five maize inbred lines.

Crop management practices

The rate of planting was two seeds per hill. Each hill received 8 g of phosphatic fertiliser. To boost the likelihood of germination, two seeds were placed; they were subsequently reduced to one seedling per hill by thinning. Good agronomical practices were adhered to, and they included appropriate weeding during the growing season, irrigation when needed, and topdressing with nitrogenous fertilizer just after thinning the plants. At a rate of 8 g per hill, calcium ammonium nitrate (CAN 21%) is used to supplement the plant nitrogen requirement. Bagging was done after the ear emerged but before emergence of silk to prevent the silk from getting pollen from an undesirable source. Maize plants were de-tasselled when the tassel was visible above leaf whorl and before pollen shedding started. In each plot, maize cobs were harvested after they reached physiological maturity when the moisture level was around 18– 20% and packaged separately. The maize ear was shelled, and data on grain weight and moisture content were recorded. Grain samples were transported to the laboratory for aflatoxin assessment.

Inoculation of maize with A. *flavus* S strain

Strain of *A. flavus* S was cultured by placing a mycelial disc in a sterile potato dextrose agar (PDA) in a 9 cm-diameter Petri dish. To guarantee enough spore yield, about 10 Petri dishes were inoculated and incubated at room temperature (22–25°C) for two weeks following previously described protocols (Kumar *et al.,* 2024). Resulting spores were harvested by adding distilled water to cultures. Mycelia were eliminated from the suspension by passing it through cheesecloth. Spore suspension was extracted using a Gilson pipette, and the end of the pipette tip was gently placed at the edge of the chambers to fill the hemocytometer. By using capillary action, sample was drawn out of pipette, and the fluid ran to the edges of the grooves only. Using a compound light microscope at 400× magnification, haemocytometer estimated up to 100 spores per millilitre. Spore cultures were maintained in slant universal bottles and stored at 4°C until subsequent use in the field. Inoculation of inbred lines occurred soon after at least 50% silk creation. Silk channel method was employed to inoculate the maize ears in the fields (Zummo and Scott, 1989). A syringe and sterilized needle were used to gently inject around 5 ml of the well-mixed spore slurry into each maize ear through the silk channel. Inoculation occurred on the seventh day when 50% of plants had emerged with silk. Sampled plants received a 5 ml spore suspension of the *A. flavus* S strain, while controls received 5 ml of water. Before inoculation, the inoculum was agitated to ensure that the conidia were evenly distributed.

Data collection

Agronomic performance of maize cultivars

Data on agronomic performance and yield for inbred lines of maize were collected from blocks and replications in the two study sites. Anthesis-silking intervals, which indicate the number of days between the date on which 50% of the maize plants tassel and shed pollen and the appearance of silks, were recorded. Number of days between the day when 50% of the silk emerges and physiological maturity, representing "days from silking to maturity", was also recorded. Plant height was collected from five randomly selected maize plants per plot using a graduated stick to measure height from the ground to the node with flag leaf. The same plants used to measure the heights were also used to measure the height of the ears, which was measured from ground level to the node bearing the topmost ear. In the inoculated block, maize cobs were manually collected at maturity, one plot at a time. The initial step involved harvesting all the inoculated maize, labelling it, and placing it in various sacks according to the inbred. Additionally, the inbred lines in non-inoculated plots were harvested and put in separate sacks for each inbred. Grain from harvested maize cobs was shelled separately for each treatment and plot after being dried to a moisture level of about 13%. Measurement of moisture content was done using a moisture reader (Superpro Moisture Analyzer), followed by the grain weight assessment using a weighing balance immediately after shelling. The grain yield from each plot was extrapolated to tonnes per hectare (t/ha).

Aflatoxin resistance

Maize samples for aflatoxin screening were ground into a fine powder using a Kenwood kitchen blender. A 20-gram sample of flour was weighed and analyzed for aflatoxin using an ELISA-based Reveal Q+ Kit according to the manufacturer's instructions. The kit's maximum and lower detection limits are 150 µg/kg and 2.0, respectively. Using an orbital shaker (HS501 IKA-WERKE, Germany) set at 200 rpm for three minutes, the samples were extracted using 100 ml of 65% ethanol. Whatman No. 1 filter paper was used to filter the supernatant after it had settled for a few minutes. 0.1% potassium hydroxide was used to bring the extract's pH down to 6.0. About 100 µl of the extract were combined with 500 µl of the sample diluent included in the kit, and 100 µl of the mixture was transferred to a sample cup. The sample cup containing the mixture was filled with a Reveal Q+ lateral flow strip, which was then allowed to process for six minutes. Sample cup was then placed inside the sample cartridge. Aflatoxin levels were measured in parts per billion (ppb) after cartridge was placed into the Accusan Gold scanner.

General combining ability and aflatoxin resistance

General combining ability measure of the additive genetic effects. The combining ability of the inbred lines was estimated using the methods and protocols established by Griffing (1956), model 1: $Xij=u+gi+gj+sij$, where u is the overall mean of all entries in the diallel design, gi is the general combining ability of the ith parent, gj is the general combining ability of the jth parent, and sij is the specific combining ability between the ith and jth parents.

Data analysis

Minitab software was used for all analyses. Analysis of variance (ANOVA) was used to examine agronomic performance data on anthesis-silking interval, silking-maturity interval, plant height, ear height, grain yield, moisture content, and aflatoxin concentration which served as response variables with inbred lines and study sites as explanatory variables. To identify which particular group means differ significantly, separation of means was carried out using Tukey's Honestly Significant Difference (HSD).

RESULTS

Aflatoxin levels and general combining ability (GCA) for selected inbred lines

CML 312 had the strongest positive GCA (17.13) and moderate resistance (9.86 ppb and 14.53 ppb) against aflatoxin, implying it to be poor for breeding programs. In Kiboko and Katumani, positive but lowest GCA was expressed by KABML658-3 (1.17; 1.19) and KABML308-2-2 (0.11; 0.21). However, KABML658-3 had the highest accumulation (23.99 ppb and 23.23 ppb), while KABML308-2-2 had moderate aflatoxin (12.84 ppb; 13.86 ppb). KABML018 (GCA: -3.42, -3.42; aflatoxin: 19.34 pp, 16.31 ppb) and KABML6-2-1 (GCA: -15, -13; aflatoxin: 7.62 pp, 10.25 ppb), displayed negative GCAs and lowest to moderate resistance in Kiboko and Katumani, respectively, implying their high suitability for breeding. Table 1 shows aflatoxin levels and general combining ability of the five selected inbred lines (KABML018, KABML308-2-2, CML312, KABML6-2-1, and KABML658-3) in the Kiboko and Katumani study sites.

Table 1. Aflatoxin levels for the selected inbred lines

Inbred lines	Mean aflatoxin level (ppb)		GCA	
	Kiboko	Katumani	Kiboko	Katumani
KABML018	19.34±0.33^{b}	16.31±0.29^{b}	-3.42	-5.42
CML 312	9.86±0.29^{d}	14.53±0.46^{c}	17.13	18.12
KABML658-3	23.99±0.21^{a}	23.23±0.05^{a}	1.17	1.19
KABML308-2-2	12.84±0.07^{c}	13.86±0.05^{c}	0.11	0.21
KABML6-2-1	7.62±0.29^{e}	10.25±0.04^{d}	-15.00	-13.00

Values expressed as mean ± SEM for five replications per group (n=5). Different superscript letters show significant differences across inbred lines according to Tukey's test HSD ($p<0.05$).

Aflatoxin changes were site-specific in inbred lines (Figure 3). Aflatoxin levels were higher in Katumani than in Kiboko for three inbred lines (CML 312, KABML308-2-2, and KABML6-2-1). In contrast to Kiboko, Katumani exhibited the lowest aflatoxin levels in KABML018 and KABML658-3.

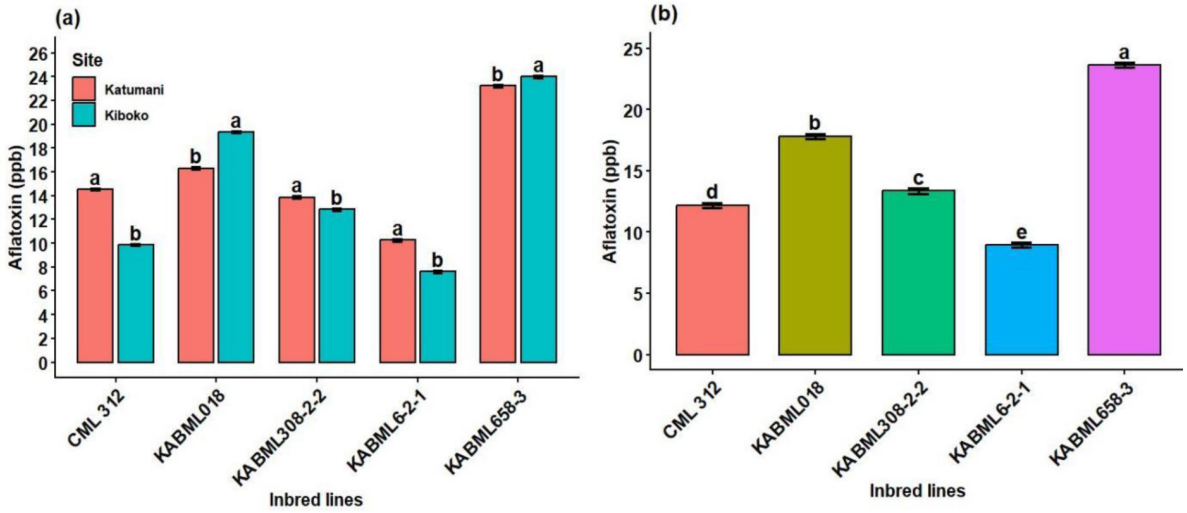

Figure 3. Comparison of aflatoxin levels between study sites for each parental line. Different small letters above error bars show significant differences between study sites according to Tukey's HSD test at p=0.05.

Agronomic performance of selected inbred lines

The inbred lines differed significantly in agronomic and yield parameters ($p<0.05$) (Table 2). Except for grain moisture content, all agronomic traits (plant height, ear height, days between anthesis and silking, days between silking and maturity, and grain yields) were significantly impacted by environmental factors (the study sites). Except for days to maturity and moisture levels, most agronomic traits showed a substantial interaction between inbred lines and the study site. The majority of agronomic traits showed high heritability (H^2 = 0.660.97), indicating significant genetic control of the characteristics, except for grain yield, which had low broad-sense heritability across settings (H^2 = -0.45).

Table 2. ANOVA results of agronomic parameters for parent lines, study site and interaction

Source	DF	Mean square					
		Plant height	Ear height	Days between anthesis-silking	Days between silking-maturity	Yields	Moisture
aGenotype (G)	4	1743.9***	419.7***	1.74***	30.6***	0.25*	1.48**
bEnvironment (E)	1	623.7***	27.1***	0.38*	279.5***	0.35*	0.12ns
G x E	4	45.5*	63.1***	0.58***	1.43ns	0.36*	0.06ns
Residual	38	17.4	0.69	0.08	3.28	0.14	0.28
Variances							
G		169.8	35.6	0.12	2.92	-0.01	0.14
E		121.2	5.29	0.06	55.2	-0.02	-0.03
G x E		5.62	12.45	0.10	-0.37	0.05	-0.05
Residual		17.4	0.68	0.08	3.28	0.14	0.29
Heritability (H2)		0.97	0.85	0.66	0.95	-0.45	0.96

aInbred lines, bStudy sites. ns denotes not significant, while asterisks * = $p<0.05$, ** = $p<0.01$ and *** = $p<0.001$.

There were notable differences in the agronomic traits of the inbred lines (Supplementary Figure S1). In both research stations, the agronomic characteristics of the inbred lines also differed considerably (Table 3). The inbred lines KABML658-3 and KABML308-2-2 had the lowest plant heights in both research stations, while KABML6-2-1, KABML018, and CML 312 had the highest mean plant heights. In the Kiboko research station, the inbred KABML308-2-2 exhibited the longest intervals between anthesis and silking, followed by CML 312 and KABML658-3, while KABML6-2-1 showed the shortest intervals. In contrast, KABML018 had the best anthesis-silking intervals at Katumani Research Station, followed by KABML6-2-1 (2.932) and CML 312 (2.817), while KABML658-3 (2.234) and KABML308-2-2 (2.312) had the lowest intervals. The number of days between silking and maturity varied considerably amongst inbred lines ($p<0.05$). KABML018 had the longest interval between silking and maturity at the Kiboko research site, followed by CML 312, KABML658-3, and KABML308-2-2, while KABML6-2-1 had the shortest. Regarding silkingmaturity, KABML018 and CML 312 had the longest intervals at Katumani Research Station, followed by KABML658-3 and KABML308-2-2, while KABML6-2-1 had the shortest interval. The mean ear heights of the evaluated inbred lines ranged from 60.1 to 77.7 cm. The inbred lines CML 312 and KABML6-2-1, followed by KABML308-2-2, had the highest mean ear height at the Kiboko research site, while KABML658-3 and KABML018 had the lowest. KABML6-2-1 had the highest mean ear height at the Katumani research site, followed by CML 312, KABML018, and KABML308-2-2, while KABML658-3 had the lowest. In the Kiboko research station, inbred line CML 312 had the lowest grain yield, while inbred line KABML018 had the highest. At the Katumani research station, KABML018, CML 312, and KABML6-2-1 had the highest yield, while KABML658-3 and KABML308-2-2 had the lowest. In the Kiboko research station, inbred line CML 312 had the lowest grain yield, while inbred line KABML018 had the highest. At the Katumani Research Station, KABML018, CML 312, and KABML6-21 had the highest yield, while KABML658-3 and KABML308-2-2 had the lowest. The grain moisture contents in five inbred lines ranged from 10.18 to 11.13%. The four other inbred lines had the lowest grain moisture content in both research sites, while KABML308-2-2 had the greatest.

Table 3. Agronomic performance of inbred lines on agronomic traits in Kiboko and Katumani research station

Agronomic traits	Inbred lines				
	KABML018	CML 312	KABML658-3	KABML308-2-2	KABML6-2-1
Kiboko research station					
Plant height (cm)	205.9±0.08^{a}	188.3±0.16^{b}	175.8±1.62^{c}	177.2±0.14^{c}	206.3±0.23^{a}
Ear height (cm)	61.1±0.43^{c}	77.5±0.26^{a}	61.0±0.43^{c}	70.5±0.21^{b}	77.3±0.02^{a}
Anthesis-silking intervals (days)	3.26±0.04^{a}	2.70±0.33^{ab}	2.66±0.00^{ab}	2.65±0.02^{ab}	2.34±0.10^{b}
Silking-maturity interval (days)	40.39±0.66^{a}	38.67±1.64^{ab}	37.48±0.12^{ab}	37.64±0.18^{ab}	36.14±0.32^{b}
Yields (t/ha)	2.17±0.03^{a}	1.81±0.05^{b}	2.11±0.06^{ab}	1.97±0.09^{ab}	2.11±0.09^{a}
Moisture (%)	10.25±0.22^{b}	10.32±0.55^{b}	10.07±0.15^{b}	11.14±0.05^{a}	10.76±0.11^{ab}
Katumani research station					
Plant height (cm)	191.6±4.8^{ab}	185.2±1.8^{b}	170.3±1.5^{c}	171.9±0.4^{c}	198.9±0.7^{a}
Ear height (cm)	68.1±0.18^{b}	72.5±0.78^{a}	60.0±0.33^{d}	65.5±0.26^{c}	73.2±0.18^{a}
Anthesis-silking intervals (days)	3.71±0.01^{a}	3.13±0.14^{b}	2.26±0.02^{c}	2.30±0.08^{c}	3.02±0.08^{b}
Silking-maturity interval (days)	44.9±0.25^{a}	44.7±1.6^{a}	42.3±0.31^{ab}	42.3±0.13^{ab}	40.2±0.40^{b}
Yields (t/ha)	2.15±0.08^{ab}	2.37±0.46^{a}	1.66±0.05^{d}	1.87±0.02^{c}	2.42±0.16^{a}
Moisture (%)	10.46±0.23^{b}	10.54±0.10^{b}	10.20±0.25^{b}	11.27±0.18^{a}	10.63±0.12^{b}

Values expressed as mean ± SEM for five replications per group (n=5). Different superscript letters show significant differences across inbred lines according to Tukey's test HSD ($p<0.05$).

When comparing the agronomic characteristics of the inbred lines between the two study locations, none of the inbred lines showed a significant change in moisture levels. However, a number of important agronomic parameters showed site-specific variations in the majority of the inbred lines (Figure 4). In Kiboko, maize plants of inbreds KABML018, KABML658-3, and KABML6-2-1 were taller than those in Katumani. In Katumani, only CLM 312 showed a significantly better grain yield than in Kiboko. While KABML658-3 showed higher anthesissilking intervals in Kiboko than in Katumani, CLM 312, KABML018, and KABML6-2-1 showed higher anthesis-silking intervals in Katumani. In comparison to Kiboko, all inbreds in Katumani showed longer silking-maturity intervals. Greater ear height was observed in CLM 312, KABML308-2-2, and KABML6-2-1 when grown in Kiboko than in Katumani. In Katumani, only KABML018 had taller ear height than those in Kiboko.

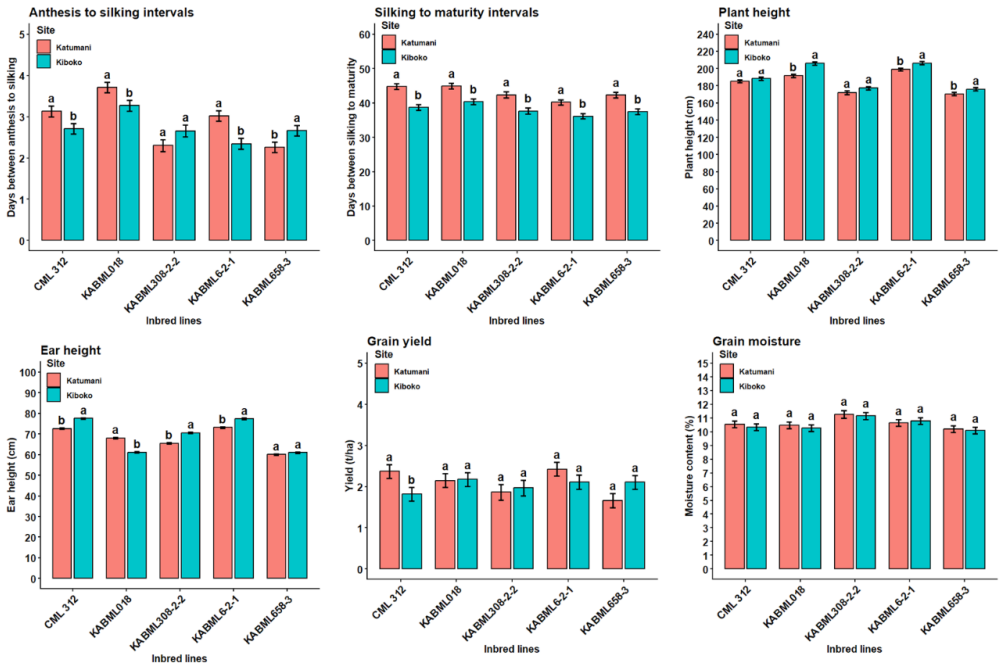

Figure 4. Comparison of the performance of agronomic traits for inbred lines in different research stations. Different small letters above error bars show significant differences between study sites according to Tukey's HSD test at p=0.05.

Combining abilities of the selected inbred lines

GCA of selected female inbred lines

The average yield and overall combining ability for the female inbred lines are summarised in Table 4. In Kiboko, the female genotype CML312 had the highest and positive GCA estimate (0.16). In Katumani, the genotype also displayed the highest and positive GCA of 0.18. With an average yield of 2.60 and 2.70 t/ha in Kiboko and Katumani, respectively, this showed a significant beneficial impact of CML312 on yield improvement. In contrast, in both Kiboko and Katumani, the female genotype KABML6-2-1 had the lowest GCA estimate of 0.03, implying it is a poor general combiner. With an average yield of 1.04 and 1.02 t/ha in Kiboko and Katumani, respectively, this indicates a less positive effect on yield. The moderate GCA values of the other female genotypes (KABML308-2-2, KABML6-2-1, and KABML658-3) ranged from -0.16 to 0.03, indicating their comparatively balanced contributions.

Table 4. General combining ability for the yield parameter in female inbred lines

Female inbred lines	Mean yield (t/ha)		GCA	
	Kiboko	Katumani	Kiboko	Katumani
KABML018	1.04±0.02^{b}	1.02±0.08^{b}	-0.16	-0.17
CML 312	2.60±0.83^{a}	2.70±0.09^{a}	0.16	0.18
KABML658-3	2.57±0.07^{a}	1.75±0.01^{ab}	0.02	0.03
KABML308-2-2	1.88±0.03^{b}	1.90±0.01^{ab}	0.01	0.03
KABML6-2-1	1.48±0.70^{a}	1.16±0.04^{a}	-0.03	-0.03

Values expressed as mean ± SEM for five replications per group (n=5). Different superscript letters show significant differences across inbred lines according to Tukey's test HSD ($p<0.05$).

GCA of selected male inbred lines

In Kiboko and Katumani, respectively, the male genotype CML312 showed the highest GCA estimate of 0.15 and 0.16 with a yield mean of 2.85 and 2.65 t/ha, demonstrating its considerable favourable influence in breeding combinations (Table 5). Male genotypes KABML018 (GCA = 0.13; 0.14) and KABML658-3 (GCA = 0.10; 0.12) also showed positive contributions, with mean yields of 2.03 and 1.75 t/ha in Katumani and 2.17 and 2.17 t/ha in Kiboko, respectively. Male KABML308-2-2, on the other hand, had the lowest yield mean (1.69; 1.50 t/ha) in Katumani and Kiboko, respectively, and negative GCA estimations (-0.27; -0.29), indicating a limited beneficial genetic impact. The male genotype KABML6-2-1 had yield means of 1.94 and 1.72 t/ha in Kiboko and Katumani, respectively, and a somewhat negative GCA (-0.12; -0.14).

Table 5. General combining ability (GCA) for the yield parameter in male inbred lines

Female inbred lines	Mean yield (t/ha)		GCA	
	Kiboko	Katumani	Kiboko	Katumani
KABML018	2.17±0.70^{a}	2.17±0.04^{a}	0.13	0.14
CML 312	2.85±0.83^{a}	2.65±0.09^{a}	0.15	0.16
KABML658-3	2.03±0.07^{ab}	1.75±0.01^{ab}	0.10	0.12
KABML308-2-2	1.69±0.03^{b}	1.50±0.01^{b}	-0.27	-0.29
KABML6-2-1	1.94±0.02^{b}	1.72±0.08^{b}	-0.12	-0.14

Values expressed as mean ± SEM for five replications per group (n=5). Different superscript letters show significant differences across inbred lines according to Tukey's test HSD ($p<0.05$).

Aflatoxin levels for selected inbred lines

ANOVA showed that the aflatoxin level in both inbred lines showed significant variations across genotypes, environment (study sites) and genotypes×environment interactions, with the strongest heritability (H^2 =0.93) (Table 6).

Table 6. ANOVA results of aflatoxin levels in parent lines, study site and their interaction.

Predictors	DF	Mean square
[a]Genotype (G)	4	1930.1***
[b]Environment (E)	1	58.5***
G x E	4	132.9***
Residual	38	0.27
Variances:		
G		179.7
E		11.6
G x E		26.5
Residual		0.26
Heritability (H^2)		0.93

[a]Inbred lines, [b]Study sites. [ns] denotes not significant, while asterisks * = p<0.05, ** = p<0.01 and *** = p<0.001.

DISCUSSION

Aflatoxin resistance of inbred lines

The purpose of this research was to identify genotypes that are high-yielding, stable inbreds across both sites, resistant to aflatoxin contamination, and have strong agronomic qualities for future hybrid development. Genotype variability may give new or advantageous alleles for improvement or identification of parental lines for the creation of better hybrids that combine aflatoxin resistance and high yield (Oppong *et al.*, 2022; Warburton & Williams, 2014).

GCA provides insight into the potential performance of parental genotypes in hybrids as well as their additive genetic impact. Breeders can create hybrids that lower *Aspergillus flavus* contamination while preserving good yields by identifying inbred lines with strong negative GCA effects for aflatoxin accumulation. The results of this study offer vital information about the genetic potential of specific inbred lines for resistance to aflatoxin accumulation in maize, especially in farming systems in semi-arid regions. Of the five inbred lines assessed, line CML 312 stood out the most since it had a significant positive GCA score (+17.13) and the lowest to moderate aflatoxin concentration (9.9–14.5 ppb). This indicates that CML 312 is not a good donor for breeding operations since it not only accumulates aflatoxin but also has a negative impact on hybrid progeny.

Inbred line KABML6-2-1 showed negative GCA values and high resistance to aflatoxin, while KABML018 showed negative GCA values and moderate resistance to aflatoxin; both can be deemed appropriate for hybridization projects. Lines such as KABML658-3 exhibited the lowest resistance but low positive GCA scores, while KABML308-2-2 was resistant to aflatoxin and had low positive GCA estimates, reducing its chance for breeding. These findings are in line with earlier research that used GCA to evaluate the frequency of additive gene activity and aflatoxin resistance in inbred lines (Meseka *et al.*, 2018; Oppong *et al.*, 2021). Importantly, this analysis clearly emphasizes the connections between genotype and environment. A key breeding objective is environmental stability, which is demonstrated by the capacity of KABML6-2-1 and KABML018 to perform well in both varying agroecological settings. Conversely, the underperforming lines may be more vulnerable to environmental changes or lack high-resistance alleles. The moderately resistant lines with low positive GCA may contribute to resistance, but they may require complementing crossings or the combination of several desirable genes to provide more powerful effects. This is consistent with existing breeding methods for aflatoxin-resistant maize, which emphasise persistent genetic resistance across habitats and backgrounds, since significant environmental variability may hamper performance (Oppong *et al.*, 2022).

The findings provide several useful breeding recommendations. For future crosses that seek to increase resistance and decrease aflatoxin accumulation, KABML6–2–1 and KABML018 should be given priority as parental lines. Their positive GCA indicates that they regularly pass on favourable alleles. Second, lines like KABML658-3 and KABML308-2-2 may be used as secondary parental lines in pyramiding schemes, but their modest GCA estimates suggest caution; they may need to be coupled with strong combiners or perfect hybrids to maximize effect. Third, lines like CLM 312 with extremely high positive GCA scores might not be included in resistance-focused breeding pipelines unless they possess other desired features. Finally, because some crossings have demonstrated notable variation, breeders should evaluate both parental GCA in a variety of environmental settings to guarantee stability.

Agronomic performance of inbred lines

Agronomic properties varied among the inbred lines of maize, indicating genotyping factors of the parental line. This indicates that each line has unique genotypic expressions inherited from its parents. Quantitative trait loci (QTLs), which influence agronomic variables like plant height, ear height, and grain yield, are often associated with these differences across inbred lines (Badu-Apraku *et al.*, 2023). However, several inbred lines, including KABML018, KABML6–2–1, and KABML308–2–2, had agronomic qualities like yield that did not vary throughout the study locations, suggesting that environmental variables had no effect on inbred lines. These inbred lines have a significant genetic buffering capacity or stability, which is a highly desirable feature in maize breeding efforts (Kamara *et al.*, 2020).

Genetic factors are the main determinant of maize plant height. Inbred KABML018 and KABML6-2-1 had the highest plant heights in both research sites, followed by CML 312, while KABML658-3 and KABML308-2-2 had the lowest. Plant height is another important agronomic feature that is often associated with biomass accumulation and photosynthetic efficiency, both of which influence grain yield. The moderate to high plant height under various climatic conditions supports the genetic stability of these inbred lines with regard to vegetative development. The yield also showed comparable patterns, suggesting a strong correlation between the inbred lines' production and plant growth parameters (height). Reportedly, taller genotypes tend to assimilate more matter to reproductive structures, ultimately enhancing biomass and yield (Meseka *et al.*, 2018; Sabiel *et al.*, 2014). However, Ma *et al.* (2025) also demonstrated that moderate plant height is associated with improved photosynthetic efficiency, reduce lodging risk, and increase yield.

However, ear height revealed a significant trend. Inbred lines CML 312 and KABML62-1 showed higher ear heights than KABML018, KABML308-2-2, and KABML658-3. Differences in ear height between inbred lines reflect different photosynthetic partitioning and stem elongation patterns, which under optimum development conditions are typically more influenced by genotype than environment (Yan & Frégeau-Reid, 2018). This could be explained by environmental factors like temperature and soil fertility as well as genetic variables that regulate internode elongation. The findings are consistent with earlier research demonstrating that, in favourable conditions, enhanced ear placement may indicate robust vegetative growth despite being linked to lodging risks (Zhao *et al.*, 2022). In line with the goal of many breeding programs, the moderate ear height improves standability and harvestability.

The five inbred lines differed in the number of days between silking and maturity, but the small range indicates that the assessed crossings were comparatively synchronized in flowering, a favourable characteristic for hybrid seed production and drought adaptability. For moisture-deficient areas like Kiboko and Katumani, early flowering hybrids are essential because they enable plants to finish their life cycle before terminal stress occurs. For areas with a moisture deficit, early flowering is a crucial maize characteristic because it enables the plant to finish its life cycle before terminal drought stress occurs without reducing grain yield (Sabagh *et al.*, 2020). In both research sites, KABML6-2-1 had the lowest gap between anthesis and silking, while KABML018 had the longest period of 3.3 and 3.7 days. Inbred lines KABML308-2-2, CML 312, and KABML658-3 have equal intervals between anthesis and silking (2.7 days). KABML6-2-1 had a shorter interval (2.3 days), indicating a shorter reproductive time, making them better suited to drought-prone environments. This trait promotes early maturation, reducing exposure to heat and drought stress (Chiuta & Mutengwa, 2025). However, only KABML018 showed longest interval between silking to maturity (40.4 days). Such longer grain filling times and more dry matter accumulation can increase final grain weight and yield (Ajala *et al.*, 2020). Ear height trends that are consistent across research locations provide support to the hypothesis that genetics, rather than environmental variables, primarily influence the reproductive period of inbred lines.

The results revealed that the grain production of inbred line KABML018 was the highest in both locations (2.17 and 2.17 t/ha in Kiboko and Katumani, respectively). However, the inbred line CML 312 had the lowest grain production in Kiboko (1.85 t/ha), whereas KABML658-3 had the lowest yield in Katumani (1.75 t/ha). Superior production may relate to increased plant height and extended grain-filling time as observed in KABML018. The grain moisture content in five inbred lines ranged from 10.18 to 11.13%, falling within the acceptable range of ≤13%. This is beneficial since aflatoxin infection and multiplication may be predisposed to by high grain moisture content (>13%) (Mutiga *et al.*, 2015). Every inbred line reached the right moisture content, indicating that the genotypes matured properly and were harvested on time. This reduces post-harvest losses and ensures grain storability. As a result, the inbred lines demonstrated potential acceptability for use in hybrid breeding initiatives.

General combining ability for the yield trait

The line tends to increase the value of the advantageous characteristic when the GCA is significant and positive. Conversely, negative GCA values indicate that an inbred

line may cross with other lines to produce children with lower values for a certain characteristic. Benefits like early maturation or lodging resistance may arise from this, which is advantageous for characteristics like plant height or days to flowering. The GCA of five inbred lines for yield in two sites in dryland agricultural systems offers a useful insight into how additive genetic effects might be advantageous in a hybrid-breeding effort. In Kiboko and Katumani, female genotype CML312 expressed highest and positive GCA values of 0.16 and 0.18, respectively, with yields of 2.60 and 2.70 t/ha. Such high GCA values lend support to the idea that high GCA suggests additive gene activation, which is critical in parent line selection. This shows that CML312 consistently contributes favourable alleles across a wide range of crosses and conditions. This is consistent with prior research revealing that GCA, which derives from additive effects, is a major predictor of the effectiveness of inbred in hybrid combinations (Kamweru *et al.*, 2023).

On the other hand, the genotype KABML6-2-1 had the lowest GCA estimate of -0.03 in both locations, as well as low yields of 1.04 t/ha at Kiboko and 1.02 t/ha at Katumani. Such negative GCA values indicate that this line may not be very useful as a parental line when yield is the major goal, as it tends to produce alleles with worse average hybrid performance for yield across all pairings. A negative GCA in breeding indicates that a line is unlikely to be a significant general contributor through additive gene activity. This does not, however, imply that the line is worthless because it might still be valuable in specific combinations (via special combining ability). In general, research on maize combining ability has supported this theory (Awad-Allah *et al.*, 2022). For example, lines with negative or low GCA are less favourable when additive gene activity is dominating. For this group of inbred lines, the breeding strategy could prioritize utilizing CML312 as the major female parent in crosses meant to boost yield since strong positive GCA values of this gene suggest the presence of beneficial additive alleles that may be continuously passed on. For lines like KABML6-2-1 and the intermediate lines KABML308-2-2 and KABML658-3, a more refined approach is necessary if a high-yield trait is the goal of the breeding program. Instead of being the primary parents that boost yield, these lines might be used as line components or testers in the establishment of certain heterotic groups, or they could be employed in targeted crossings where they complement the advantageous alleles of high-GCA parents (Liu *et al.*, 2020).

The male genotype CML312 was the most promising parent, with the best grain yields (2.85 t/ha and 2.65 t/ha) and GCA values (0.15 and 0.16), respectively, in Kiboko and Katumani. These findings indicate that CML312 has beneficial alleles that consistently improve yield performance, making it a strong candidate for inclusion in breeding efforts intended to increase productivity in semi-arid conditions (Hallauer *et al.*, 2010). Similarly, the male genotypes KABML018 and KABML658-3 displayed positive GCA values in both locations. KABML018 recorded GCA values of 0.13 and 0.14 with mean yields of 2.17 t/ha in Kiboko and 2.17 t/ha in Katumani, whereas KABML658-3 reported GCA values of 0.10 and 0.12 with yields of 2.03 t/ha and 1.75 t/ha, respectively. These results imply that both male genotypes contribute additive genes that are beneficial for raising yield, however not to the same extent as CML312. The consistently positive performance across locations highlights these genotypes' stability and their potential to improve hybrid vigour in a range of environmental circumstances (Kamara *et al.,* 2024).

Conversely, the GCA values of the male genotypes KABML6-2-1 and KABML308-22 were negative. This implies that their genetic additive contributions to yield were negligible. KABML308-2-2 had the lowest GCA values (-0.27 and -0.29) and yield averages of 1.69 and 1.50 t/ha, respectively, in Kiboko and Katumani. This male genotype's low GCA value suggests that it has alleles that don't enhance yield performance (Kamutando *et al.*, 2018). Similarly, KABML6-2-1 had significantly negative GCA values (-0.12 and -0.14) and mean yields of 1.94 t/ha and 1.72 t/ha at both sites. These genotypes might be useful in certain crosses where complementarity with high-GCA genotypes makes up for their shortcomings, even if they might not be the best general combiners. These findings demonstrate how important it is to select inbred lines based on their GCA in order to maximize breeding efficiency. The most promising male genotype was determined to be CML312 because of its high GCA estimates and improved yield performance, which is consistent with other research that emphasizes the importance of strong general combiners in hybrid production (Hallauer *et al.*, 2010).

However, breeding operations may need to selectively use genotypes with negative GCA, such as KABML308-2-2 and KABML6-2-1, perhaps in combination with high-GCA parents, in order to benefit from special combining ability (SCA) effects. Therefore, GCA calculations must be incorporated into hybrid development methods to enhance genetic gain and yield stability under a range of environmental conditions.

CONCLUSION

The study unequivocally demonstrates the value of combining ability measurements (GCA) with parental line performance (in terms of agronomic variables and

aflatoxin resistance) to breed maize with high yield, reduced aflatoxin accumulation, and resistance to environmental stressors like heat and drought. While the outstanding performance of KABML018 and KABML6-2-1 indicates potential for developing hybrids with inherent resistance, the cross-site study also highlights the necessity of testing in diverse environments. Furthermore, even when additive genetic influences (shown in GCA) appear to be central, nonadditive and environmental interactions (indicated in SCA and cross-specific performance) are still crucial for optimizing results. Therefore, a multidimensional approach should be used in breeding projects to reduce aflatoxin: choosing parents with high GCA for resistance, evaluate significant specific crosses for stability and SCA, and test them in a range of agro-ecologies to find broadly suited resistant materials.

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COMPETING INTEREST

The authors declare that there are no competing interests.

AVAILABILITY OF DATA AND MATERIALS

The datasets used and analyzed in this study are accessible from the corresponding author upon request.

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Supplementary materials

Figures

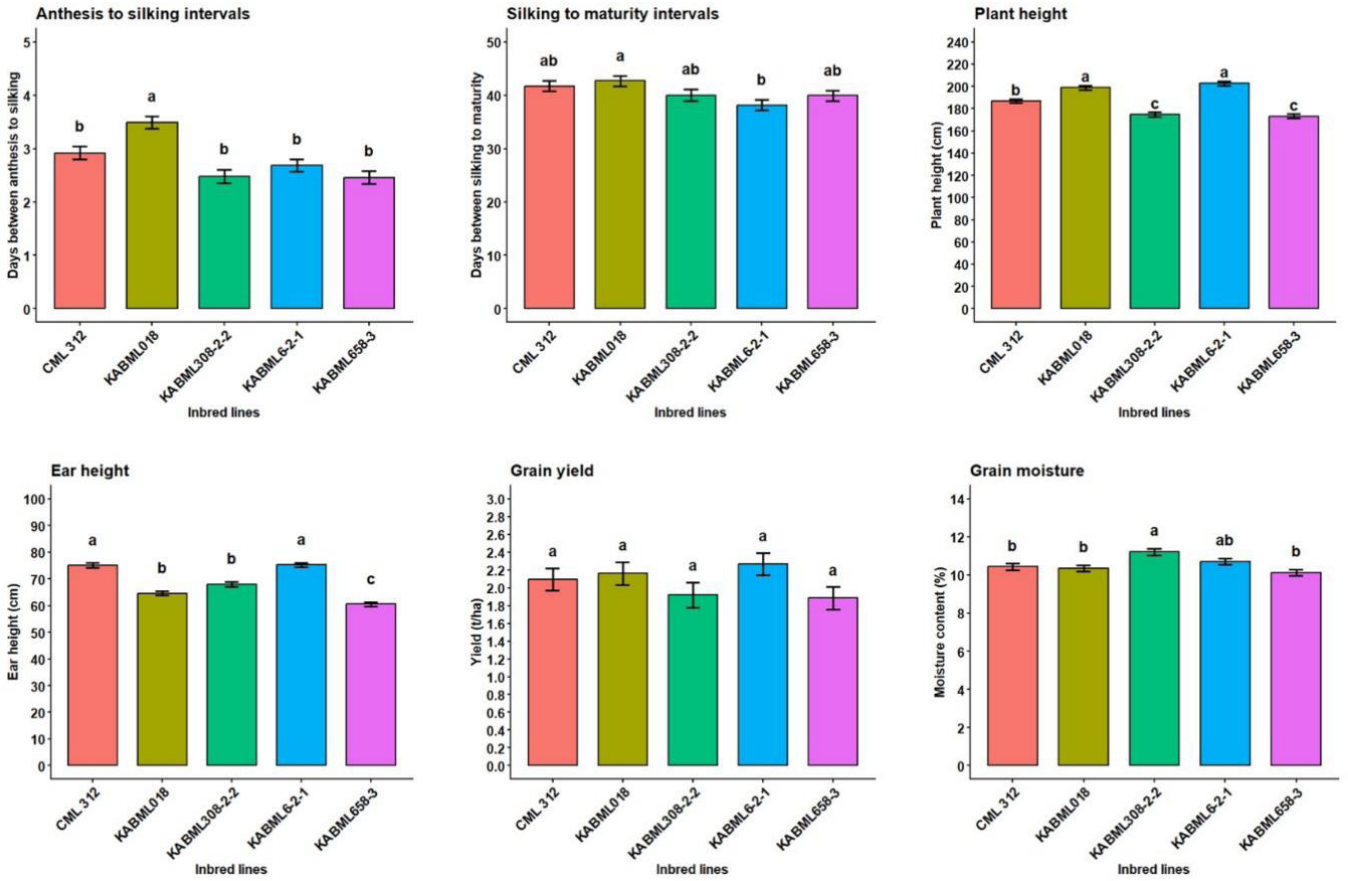

Figure S1. Comparison of the performance of agronomic traits for specific single inbred lines combined for research stations. Different small letters above error bars show significant differences between study sites according to Tukey's HSD test at p=0.05.