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HETEROSIS AND LINE-BY-TESTER COMBINING ABILITY ANALYSIS FOR GRAIN YIELD AND PROVITAMIN A IN MAIZE

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SUMMARY

Developing a high-yielding and provitamin A-rich maize variety is one of the best approaches to reduce malnutrition and increase production, especially in regions where maize is a staple food, such as, the former Katanga Province in the Democratic Republic of the Congo. However, it requires a good knowledge of combining ability and heterosis for grain yield and provitamin A. Thus, evaluating grain yield, provitamin A content and other agronomic traits of eight lines, four testers, and their 32 hybrids occurred during the 2015-2016 and 2016-2017 cropping seasons. The results showed that genetic parameters related to combining ability and heterosis among various F_1 hybrids influenced all the studied traits except plant height. The parental genotypes P6 and P10 were suitable for improving 100-kernel weight, grain yield, stature at ear insertion, and provitamin A content. The parental genotypes P7, P4, and P2 were promising for provitamin A content, while the parental genotype P3 was leading for grain yield. Five hybrids (P10 × P5, P10 × P6, P10 × P7, P10 × P8, and P11 × P5) showed distinction as the best specific combinations for improving productivity and provitamin A content. The F_1 hybrid P10 × P6 with desirable specific combining ability revealed that it is helpful as the best combination in producing double and triple hybrids with the highest yield and provitamin A potential. Crosses P10 × P5 and P11 × P5 can serve as the best cross combinations for grain yield, while hybrids P10 × P7 and P10 × P8 showed promising for provitamin A content. The presented results could benefit future breeding programs to develop maize genotypes with high yield and provitamin A elements, alleviating food insecurity and malnutrition.

Keywords: Maize (*Zea mays* L.), heterosis, line-by-tester combining ability, GCA and SCA, grain yield, provitamin A

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Key findings: The presented study indicates that both additive and non-additive effects contribute to the genetic control of grain yield and provitamin A content in maize (*Zea mays* L.). Some parental lines, testers and their hybrids have better mean performance for the assessed traits. The parental line P6 and tester P10 appeared as the best general combiners suitable for hybridization to improve the grain yield and provitamin A content. The F_1 hybrid P10 × P6, followed by P10 × P5, P10 × P7, P10 × P8 and P11 × P5, was the best cross combination for desirable heterotic and combining ability effects for higher grain yield and provitamin A content.

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INTRODUCTION

Maize (*Zea mays* L.) is one of the most multipurpose crops with worldwide economic importance, widely used as food, fodder, and raw material for industrial products (Ghosh *et al.*, 2018). In the Democratic Republic (DR) of the Congo, the maize sector has rapidly grown over the past two decades. In 2020, the planted area increased and reached 2,735,473 ha, with an increase of more than 84%, compared with the year 2000. On production, an increase of more than 78% occurred, varying from 1,184,000 t (2000) to 2,111,786 t (2020). However, its average production is due to inadequate grain yields (0.7 t ha^{-1}) compared with Zambia and other Southern African countries (FAOSTAT, 2021).

Maize is a widely grown crop in the former Katanga Province, DR Congo, and is vital in alleviating food insecurity for the local population (Nyembo *et al.*, 2018). In this region, white maize, which is deficient in provitamin A, is widely consumed (Menkir *et al.*, 2008; Li *et al.*, 2013). Insufficient intake of provitamin A can lead to deficiency, causing night blindness (Meda *et al.*, 2000; OMS, 2011; Black *et al.*, 2013; Stevens *et al.*, 2015), increases the risk of child morbidity and mortality (Meda *et al.*, 2000; OMS, 2011; Black *et al.*, 2013) and premature birth and maternal anemia (Radhika *et al.*, 2002). DR Congo is one of many countries with a high prevalence of vitamin A deficiency (Stevens *et al.*, 2015), a public health problem (PRONANUT, 2015; Taleon *et al.*, 2019). The rate of vitamin A deficiency in DR Congo is 61% among children aged 6-36 months (PRONANUT, 2015). Therefore, the search for maize varieties rich in provitamin A is essential to remedy this situation.

Despite the importance of maize in the human diet of the population in DR Congo in general and the former Katanga province in particular, its production covers only one-third of the total demand, partly due to using degenerated varieties (Nyembo *et al.*, 2018). Consequently, it becomes necessary to use hybrid varieties, known for their high productivity (Duvick, 2005a, 2005b; Hochholdinger and Baldauf, 2018). In maize hybrids, exploiting heterosis obtains their high yield potential (Duvick, 2005a; Hochholdinger and Baldauf, 2018; Yi *et al.*, 2019).

Since introducing the concept of heterosis, maize breeders have made great efforts to take advantage of it. Several heterotic studies in maize for quantitative traits like yield components and grain yield explored the phenomenon of heterosis and heterobeltiosis (Singh *et al.*, 2012; Wegary *et al.*, 2013; Dorina and Viorica, 2015; Owusu *et al.*, 2017; Ghosh *et al.*, 2018; Al-Naggar *et al.*, 2022). However, in the current context of vitamin A deficiency malnutrition, improving maize quality is as important as quantity. Thus, a range of maize biofortification breeding initiatives has evolved and used maize inbred lines with high levels of provitamin A to develop new hybrids with good yield and provitamin A potential (Babu *et al.*, 2013; Pixley *et al.*, 2013). In addition, these newly developed hybrids must have desirable agronomic characteristics with higher grain yields, increasing the farming community's preference (Azmach *et al.*, 2021).

In this regard, knowledge of heterosis and combining ability is imperative for a breeding program to develop hybrid and composite varieties with higher grain yield and provitamin A content. Previous studies on the combining ability in maize inbred lines showed significant general combining ability (GCA) and specific combining ability (SCA) effects for grain yield and provitamin A content (Suwarno *et al.*, 2014). However, Egesel *et al.* (2003) and Senete *et al.* (2011) indicated the dominance of GCA compared with SCA, which implied an additive type of gene action for yield-related traits and grain yield.

The success in commercial production of hybrid maize depends on extensive assessment of inbred lines. Therefore, the presented investigation studied the magnitude of heterosis and combining ability for grain yield and provitamin A (PVA) content in single cross hybrids and their parental genotypes by adopting a line-by-tester model in maize.

MATERIALS AND METHODS

Study area and genetic material

The recent research materialized at the Kasapa Research Station, Faculty of Agronomy, Université de Lubumbashi, Lubumbashi, Democratic Republic of the Congo (27° 28'37" E, 11° 36'44" S, and 1274 m altitude). The maize (*Zea mays* L.) genetic material used in this study consisted of 44 genotypes, including 12 parental genotypes (eight lines, four testers) and their 32 F_1 hybrids. In the 2014-2015 cropping season, four white maize genotypes (used as female parents) were crossed to eight male parent inbreds (PVA donors) to generate 32 F_1 crosses (Table 1). These four white maize genotypes, characterized by good yields and resistance to diseases, such as, grey leaf spot (*Cercospora zeae-maydis*), maize streak virus, and southern corn leaf blight (*Bipolaris maydis*), are the most widely grown in the former Katanga province.

Table 1. Maize parental lines and testers used in the study.

No.	Code	Pedigree	Source
Provitamin A maize lines			
1	P1	SAM4(ProA)BC1c2FS	CIMMYT
2	P2	(CML489/[BeTASYn]Bc1–2-$^{\#}$/CML300)-B-26–1-1-B	CIMMYT
3	P3	(Ac8730SR-$^{\#\#}$-124–1-5-B-1-$^{\#}$/[BeTASYn]Bc1–5-$^{\#}$-B-B//Ac8730SR-$^{\#\#}$-124–1-5-B-1-$^{\#}$/[BeTASYn] Bc1–5-$^{\#}$-B/CML304)-5–1-B	IITA
4	P4	P33c2(STE)-12-1-B-2-B*4 $^{\#}$/(CML 324)	CIMMYT
5	P5	(MAS[206/312]-23–2-1–1-B-B-B/[BETASYN]BC1–10–2-1-$^{\#}$/CML-305-B)-B-9–1-B	ZARI
6	P6	(MAS[206/312]-23-2-1-1-B-B-B/[BETASYN]BC1-11-3-1- $^{\#}$/CML-304-B)-B-13–1	ZARI
7	P7	SA4-C2HC(21/26)- 1-2-2-2-B-B-B-B-B-B$^{\#}$/CML 438	CIMMYT
8	P8	P33c2(STE)-102-2-B-1-B*3 $^{\#}$/CML 323	CIMMYT
White maize testers			
1	P9	UNILU	UNILU
2	P10	KATANGA	UNILU
3	P11	NSIMA	UNILU
4	P12	BABUNGO	INERA

CIMMYT: Centro Internacional de Mejoramiento de Maíze y Trigo (International Maize and Wheat Improvement Center); IITA: International Institute of Tropical Agriculture; ZARI: Zambia Agricultural Research Institute; UNILU: Université de Lubumbashi; INERA: Institut National pour l'Etude et la Recherche Agronomiques.

Field experiment

The 32 hybrids and their 12 parents were raised in a randomized complete block design (RCBD) with three replications during the wet season of 2015–2016 and 2016–2017 cropping seasons. The plot size has three rows with five meters in length and a spacing of 75 cm × 25 cm, at the rate of one seed per hole. Following Nyembo *et al*. (2018) and Ilunga *et al.* (2018) recommendation, 300 kg ha^{-1} of NPKS 10-20-10-6 and urea were applied, respectively, at the sowing time and 30 days after sowing. Manual weeding (hoeing) continued twice (four weeks after planting and seven weeks after planting, combined with tied ridging) to control weeds.

Data recorded and laboratory measurements

Data collection was recorded on 10 randomly selected healthy plants for the parameters, i.e., plant height (PH), ear height (EH), and 100-kernel weight (100-KW). Grain yield (GY) calculation in tons per hectare was from the shelled plot grain weight adjusted to 12.5% moisture using the non-selfed ears. Provitamin A (PVA) content determination was measured on 10 randomly selected self-pollinated ears followed the HarvestPlus culture approach. Provitamin A analysis, including extraction, separation, and quantification, ensued following HarvestPlus laboratory protocols (Rodriguez-Amaya and Kimura, 2004) at the Kalambo Biofortification Laboratory in South Kivu, using a spectrophotometer.

Biometrical analysis

Using the Agricolae package of R i386 4.1.2 software analyzed the data. Given the non-significant results of the homogeneity test required a combined analysis of the variance of the RCBD over the two cropping seasons. Heterosis for various traits' estimates were the percentage increase or decrease of F_1 over mid- and better parent. Heterosis (H) relative to the mid-parent (MP) and better parent (BP) for each F_1 hybrid calculation followed Hallauer *et al.* (2010) and Al-Naggar *et al.* (2022) with the formula below:

$$\text{MPH (\%)} = \frac{F_1 - MP}{MP} \times 100$$

$$\text{BPH (\%)} = \frac{F_1 - BP}{BP} \times 100$$

where:
F_1 = is the mean of the F_1 hybrid performance
MP = Mid parent value of the particular F_1 cross
BP = Better parent value of the particular F_1 cross

RESULTS

Genetic variation among lines, testers, and hybrids

The analysis of variance showed significant variability among the lines, testers, and their F_1 hybrids for various studied traits (Table 2). The parents and parents vs. crosses also have wide genetic variation for all the features. In terms of F_1 hybrids, highly significant variations occurred for all the studied traits except ear height. Variance due to lines showed significant differences for all the studied traits, while variance due to testers emerged relevant for all attributes under the study except plant height. Line-by-tester effects, also called SCA effects, were significant for all the traits except ear height and 100-kernel weight.

General combining ability

Estimates of general combining ability effects of lines and testers for all the studied traits are in Table 3. None of parents (line or tester) showed significant GCA effects for all traits studied. For plant height, four out of eight lines showed significant GCA effects. Maximum positive GCA effect was with parental lines P3

Table 2. Analysis of variance (F statistics) of line-by-tester combining ability for various traits in maize.

Source of variation	d.f.	Plant height (cm)	Ear height (cm)	100-kernel weight (g)	Grain yield (t/ha)	Provitamin A (µg/g)
Replications	5	812.79	170.47	147.78***	6.33*	0.31
Genotypes	43	3205.67***	654.75***	95.42***	16.72***	25.22***
Parents	11	7891.18***	1359.73***	133.44***	33.21***	86.52***
Parents vs. Crosses	1	20304.93***	9060.67***	1640.98***	231.18***	62.82***
Crosses	31	991.48**	133.44	32.08***	3.95**	2.25***
Lines	7	2295.71**	229.02*	22.31*	3.39*	2.54*
Testers	3	555.13	332.23*	219.03***	13.65**	4.94*
Lines × Testers	21	619.07*	73.19	8.63	2.75*	1.78***
Error	215	550.26	145.44	9.89	2.05	0.23

*, **, *** - Significant at 5%, 1%, and 0.1% levels of probability, respectively.

Table 3. General combining ability (GCA) effects of parental lines and testers for various traits in maize.

Maize genotypes	Plant height (cm)	Ear height (cm)	100-kernel weight (g)	Grain yield (t/ha)	Provitamin A (µg/g)
Lines (Provitamin A maize)					
P1	3.966	-2.284	-1.05*	-0.646*	0.167*
P2	9.499*	-1.302	-1.135*	0.255	0.267*
P3	10.765**	2.046	-0.195	0.532*	-0.208*
P4	4.980	-3.316*	0.95*	-0.042	-0.483*
P5	-6.928*	-1.494	-0.487	0.029	-0.158*
P6	2.239	3.186*	0.7	0.33*	0.367**
P7	-18.146**	-2.113	-0.317	-0.286	0.342**
P8	-6.376	5.278*	1.533**	-0.171	-0.295*
S.E. (GCA for line)	4.788	2.463	0.642	0.29	0.098
S.E. (gi - gj)line	6.771	3.481	0.91	0.41	0.139
Testers (White maize)					
P9	4.969	1.589	-2.356**	-0.697**	-0.058
P10	-1.775	2.718*	-0.763*	0.599**	0.342***
P11	-0.659	-1.266	0.399	0.004	-0.414***
P12	-2.535	-3.041*	2.72***	0.094	0.130*
S.E. (GCA for tester)	3.386	1.741	0.45	0.21	0.07
S.E. (gi - gj)tester	4.788	2.462	0.64	0.29	0.098

*, **, *** - Significant at 5%, 1%, and 0.1% levels of probability, respectively.

(10.77) and P2 (9.50), while maximum negative GCA effect was with parental lines P7 (-18.15) and P5 (-6.93). For the tester, the result showed that no tester exhibited a significant GCA effect (Table 3). For ear height, three out of eight lines and two out of four testers exhibited significant GCA effects. The parental lines P8 (5.278) and P6 (3.186), as well as tester P10 (2.718) showed positive GCA effects, while parental line P4 (-3.316) and tester P12 (-3.041) exhibited negative GCA effects (Table 3).

For 100-kernel weight, two parental lines, P1 (-1.05) and P2 (-1.135), showed significant negative GCA effects, while parental P8 (1.533) and P4 (0.95) displayed considerable positive GCA effects (Table 3). For testers, 100-kernel weight GCA effects revealed that a significant positive value was with P12 (2.72), while a suggestive negative value was by P9 (-2.356) (Table 3). As for grain yield, two lines, P3 (0.532) and P6 (0.33), and one tester P10 (0.599) gave significant positive GCA effects, while substantial negative GCA effects came from parental line P1 (-0.646) and tester P9 (-0.697). In terms of provitamin A content, parental lines P1 (0.167), P2 (0.267), P6 (0.367), P7 (0.342), and testers P10 (0.342) and P12 (0.13) indicated meaningful positive GCA, while lines P3 (-0.208), P4 (-0.483), P5 (-0.158), and P8 (-0.295) and tester P11 (-0.414) revealed relevant negative GCA effects.

Specific combining ability

Among 32 cross combinations, overall, three hybrids showed significant SCA effects for plant height (Table 4). The recorded maximum positive SCA effect was with hybrid P11 × P8 (16.22), with the maximum negative recorded by hybrids P9 × P5 (-20.43) and P10 × P8 (-13.97) for plant height (Table 4). For ear height and 100-kernel weight, none of the cross combinations showed significant SCA effects. For grain yield, five crosses gave relevant SCA effects, three of them (P10 × P5, P10 × P6, and P11 × P5) were in the positive direction, while two hybrids (P9 × P5 and P12 × P5) provided negative SCA effects (Table 4). For provitamin A content, seven F_1 hybrids, viz., P9 × P2, P9 × P5, P10 × P6, P10 × P7, P10 × P8, P11 × P3, and P12 × P1, displayed substantial positive effects, with significant negative SCA effects recorded in 10 F_1 hybrids, i.e., P9 × P1, P9 × P8, P10 × P1, P10 × P3, P10 × P5, P11 × P2, P11 × P6, P11 × P7, P12 × P5, and P12 × P7.

Heterotic effects

Among 32 F_1 hybrids, the mid and better parent heterosis ranged from -7.96% to 35.45% and -26.83% to 7.76%, respectively, for plant height. Results revealed that for plant height, out of 32 crosses, eight and 21 hybrids exhibited negative mid- and better-parent heterotic values, respectively (Table 5). However, 10 hybrids gave significant positive mid-parent heterosis, while none showed significant better-parent heterosis for plant height. Among F_1 hybrids, for ear height, the mid- and better-parent heterosis ranged from -28.90% to 32.34% and -41.60% to 4.78%, respectively. For ear height, out of 32 crosses, six hybrids exhibited positive for mid-parent and one for better-parent heterotic effects. However, two and 13 crosses revealed meaningful positive and negative mid-parent heterosis, respectively, for ear height. The 16 hybrids showed significant negative better-parent heterosis, but none gave significant positive better-parent heterotic effects for ear height.

For 100-kernel weight among F_1 hybrids, the mid- and better-parent heterosis ranged from -2.76% to 42.47% and -12.56% to 12.65%, respectively (Table 5). Among 32 hybrids, 31 and 16 hybrids exhibited positive mid- and better-parent heterotic effects, respectively, but 16 and seven crosses revealed significant positive mid- and better-parent heterosis, respectively, for 100-kernel weight. Among F_1 hybrids, the mid- and better-parent heterosis ranged from -12.00% to 82.94% and -16.94% to 19.57%, respectively, for grain yield. The 30 and 11 hybrids displayed positive mid- and better-parent heterotic effects, respectively; however, 12 and five F_1 hybrids showed significant positive mid- and better-parent heterosis, respectively, for grain yield.

For provitamin A among F_1 hybrids, the mid- and better-parent heterosis ranged from 12.44% to 66.89% and -28.00% to 1.83%, respectively (Table 5). All the hybrids exhibited positive mid-parent heterosis for provitamin A, but only 17 were significant. Two F_1 hybrids revealed significant positive better-parent heterosis for provitamin A. Overall, five hybrids, viz., P10 × P6 (14.36%), P11 × P3 (15.23%), P11 × P4 (15.60%), P11 × P5 (19.57%), and P11 × P8 (14.96%) exhibited significant positive better-parent heterosis for grain yield. For provitamin A, two F_1 hybrids, i.e., P12 × P6 (1.83%) and P12 × P1 (1.58%) had positive better-parent heterosis. These promising F_1 hybrids need further study for developing high-yielding and provitamin A-rich cultivars in maize.

Table 4. Estimates of specific combining ability (SCA) effects among the F_1 hybrids for various traits in maize.

F_1 Hybrid	Crosses	Plant height (cm)	Ear height (cm)	100-kernel weight (g)	Grain yield (t/ha)	Provitamin A (µg/g)
PVAH-21L	P9 × P1	4.571	-1.261	-1.563	0.585	-0.642***
PVAH-14L	P9 × P2	-6.195	-0.684	-1.180	-0.088	0.408**
PVAH-24L	P9 × P3	-0.670	-3.332	1.285	-0.155	-0.267
PVAH-20L	P9 × P4	7.867	1.354	-0.796	0.066	-0.092
PVAH-16L	P9 × P5	-20.43**	3.012	0.108	-0.985*	0.933***
PVAH-32L	P9 × P6	4.986	2.214	-0.178	0.479	0.108
PVAH-28L	P9 × P7	6.385	-1.067	1.310	-0.065	-0.067
PVAH-12L	P9 × P8	3.482	-0.236	1.013	0.163	-0.380*
PVAH-27L	P10 × P1	-7.279	2.359	1.084	-0.110	-0.392*
PVAH-11L	P10 × P2	-1.059	-2.075	0.103	-0.232	0.108
PVAH-2L	P10 × P3	6.871	5.314	-1.301	0.450	-0.317*
PVAH-22L	P10 × P4	1.075	-1.432	-0.111	-0.367	-0.142
PVAH-3L	P10 × P5	12.812	2.327	0.214	0.948*	-0.717***
PVAH-1L	P10 × P6	-10.428	-4.590	0.148	0.926*	0.589***
PVAH-6L	P10 × P7	2.843	1.055	-0.256	0.325	0.933***
PVAH-5L	P10 × P8	-13.966*	-2.958	0.119	-0.609	0.620*
PVAH-25L	P11 × P1	-2.660	2.015	-0.380	-0.155	0.164
PVHA-17L	P11 × P2	-3.563	-0.696	-0.105	-0.079	-0.636*
PVAH-30L	P11 × P3	-7.880	-4.811	-1.058	-0.195	0.589*
PVAH-9L	P11 × P4	-1.297	-2.108	1.032	0.889	-0.092
PVAH-7L	P11 × P5	10.048	-0.991	0.328	1.15**	0.089
PVAH-19L	P11 × P6	8.617	3.815	1.162	-0.547	-0.286*
PVAH-31L	P11 × P7	-10.356	-2.569	-1.80	-0.815	-0.361*
PVAH-13L	P11 × P8	16.222*	5.344	-0.120	-0.249	0.027
PVAH-15L	P12 × P1	5.367	-3.113	1.084	-0.321	0.870***
PVAH-10L	P12 × P2	10.817	3.455	0.103	0.398	0.120
PVAH-29L	P12 × P3	1.679	2.829	-1.301	-0.100	-0.005
PVAH-18L	P12 × P4	1.485	2.186	-0.111	-0.588	-0.180
PVAH-26L	P12 × P5	-2.431	-4.348	0.214	-1.114**	-0.305*
PVAH-4L	P12 × P6	-12.307	-1.438	0.148	0.474	0.270
PVAH-23L	P12 × P7	1.128	2.581	-0.256	0.555	-0.505*
PVAH-8L	P12 × P8	-5.738	-2.150	0.119	0.686	-0.267
S.E. (SCA effects)		9.577	4.923	1.284	0.585	0.197
S.E. (sij - skl)		13.543	6.963	1.81	0.827	0.278

*, **, *** - Significant at 5%, 1%, and 0.1% levels of probability, respectively.

Table 5. Heterosis over mid- and better-parents among the F_1 hybrids for various traits in maize.

F_1 Hybrids	Crosses	Plant height (cm)			Ear height (cm)			100-kernel weight (g)			Grain yield (t/ha)			Provitamin A (µg/g)		
		Means	MPH (%)	BPH (%)	Means	MPH (%)	BPH (%)	Means	MPH (%)	BPH (%)	Means	MPH (%)	BPH (%)	Means	MPH (%)	BPH (%)
PVAH-21L	P9 × P1	237	16.75*	-4.12	73	-20.20*	-23.30**	25.65	-2.76	-0.67	7.25	-1.85	-14.53*	6.85	29.44*	-15.00*
PVAH-14L	P9 × P2	231	6.31	0.90	75	-19.60*	-27.60**	25.94	5.14	-10.13	7.47	-3.97	-5.56	8.00	47.98**	-9.02
PVAH-24L	P9 × P3	238	12.16*	-3.36	75	-9.76	-16.54	29.35	17.09*	8.98*	7.68	18.20	4.19	6.85	20.14	-23.00**
PVAH-20L	P9 × P4	241	12.09*	-8.39	75	-19.40*	-27.60**	28.41	9.78	-10.32	7.34	8.76	-6.81	6.75	13.92	-28.00**
PVAH-16L	P9 × P5	201	4.582	-8.26	78	4.18	-15.34	27.88	17.58*	5.62	6.39	1.51	-8.89	8.10	66.89*	-0.54
PVAH-32L	P9 × P6	235	7.85	-5.06	82	-4.22	-11.39	28.78	18.97*	7.10*	8.09	26.00	-2.21	7.80	52.38**	-3.79
PVAH-28L	P9 × P7	216	4.33	-12.77	74	-14.10	-23.20**	29.25	17.16*	8.23*	6.98	11.76	-13.54	7.60	27.98	-20.00*
PVAH-12L	P9 × P8	225	32.57**	4.08	82	32.34	-2.20	30.81	16.63	9.22*	7.31	42.39*	-2.15	6.65	13.16	-26.00**
PVAH-27L	P10 × P1	218	1.20	-14.16	78	-15.58	-34.20**	29.89	8.42	-5.58	7.83	17.76	-16.94*	7.50	38.83*	-9.81
PVAH-11L	P10 × P2	230	-0.10	-13.07	74	-19.90*	-33.60**	28.82	8.93	-0.03	8.58	23.68	-5.11	8.10	46.03*	-11.00
PVAH-2L	P10 × P3	239	5.18	-6.04	85	3.02	-17.45	28.36	8.16	-8.00	9.51	70.03*	-6.72	7.20	23.31	-23.00**
PVAH-22L	P10 × P4	227	-0.81	-8.52	73	-21.20*	-38.70**	30.69	13.15	6.39	8.17	37.82*	-7.69	7.10	17.30	-28.00**
PVAH-3L	P10 × P5	227	11.55*	-14.97	79	3.89	-1.14	29.58	17.52*	5.47	9.50	74.51**	-5.53	6.85	37.43*	-3.48
PVAH-1L	P10 × P6	222	-4.42	-15.79	76	-10.07	-19.41	30.70	21.62*	3.57	8.49	51.23*	14.36*	8.00	52.04**	-6.95
PVAH-6L	P10 × P7	206	-7.25	-26.83	77	-10.26	-20.07*	29.28	11.28	-2.21	8.60	50.68*	-13.7	9.00	48.22**	-21.00*
PVAH-5L	P10 × P8	201	10.98*	-12.43	80	24.63*	4.78	31.50	13.31	9.35*	7.81	82.94**	-9.41	8.05	34.01*	-27.00**
PVAH-25L	P11 × P1	224	9.66*	5.11	74	-19.50*	-31.00**	29.59	15.30	1.24	7.22	2.84	-3.95	7.30	39.30*	-9.48
PVHA-17L	P11 × P2	228	3.26	-0.28	72	-23.20*	-35.20**	29.77	21.54*	10.13*	8.16	10.20	-5.24	6.60	22.49	-10.78
PVAH-30L	P11 × P3	225	4.33	3.23	71	-13.68	-15.76	29.76	22.49*	1.15	8.31	38.79*	15.23*	7.35	29.66	-19.00
PVAH-9L	P11 × P4	217	-0.60	0.50	68	-26.30*	-28.20**	34.00	35.15**	10.98*	8.80	40.31*	15.60*	6.90	17.08	-28.00
PVAH-7L	P11 × P5	226	17.20*	3.65	71	-5.06	-10.56	30.86	33.76*	-2.63	9.12	58.81*	19.57**	6.90	42.69*	-3.98
PVAH-19L	P11 × P6	233	5.32	7.76	81	-4.42	-16.07	32.88	42.47**	12.65*	7.78	30.01	8.06	7.05	38.46*	-2.90
PVAH-31L	P11 × P7	194	-7.96	5.02	69	-18.80*	-22.71*	28.84	19.64*	2.45	6.93	16.67	8.03	6.95	17.59	-19.00*
PVAH-13L	P11 × P8	232	35.45**	-0.37	85	28.50*	-13.82	32.43	25.43*	0.77	7.58	68.36*	14.86*	6.70	14.61	-25.00**
PVAH-15L	P12 × P1	230	11.34*	-1.11	67	-28.90*	-39.10**	33.14	10.06	-4.95	7.14	-12.00	0.28	8.55	56.91**	1.58
PVAH-10L	P12 × P2	241	7.13	1.06	74	-22.40*	-35.50**	33.38	15.08	-9.87	8.71	3.89	-4.47	7.90	41.62*	-12.00
PVAH-29L	P12 × P3	233	6.60	0.21	77	-8.978	-8.79	34.21	19.38*	-12.56*	7.49	5.95	-13.10	7.30	24.48	-20.00*
PVAH-18L	P12 × P4	227	2.94	0.52	71	-24.90*	-41.60**	33.16	12.27	-6.08	7.47	1.74	-1.86	6.85	12.44	-28.00**
PVAH-26L	P12 × P5	211	8.13	-10.44	66	-14.10	-9.03	32.20	16.52	-2.01	7.03	2.08	8.76	7.05	40.76*	-3.20
PVAH-4L	P12 × P6	210	-6.61	-9.91	74	-15.46	-19.07	32.90	18.82*	-4.30	8.85	26.25	5.30	8.15	53.91**	1.83
PVAH-23L	P12 × P7	204	-5.10	-16.48	73	-17.30*	-26.44*	33.82	17.33*	-1.99	8.33	19.29	-9.54	7.35	20.30	-18.00
PVAH-8L	P12 × P8	208	21.09*	-13.43	75	15.70	-11.32	33.86	12.19	-5.69	8.58	51.55*	-11.58	6.95	14.90	-24.00**

*, ** Significant at 5% and 1% levels of probability, MPH: Mid-parent heterosis (%), BPH: Better-parent heterosis (%).

DISCUSSION

In general, the studied maize genotypes showed a high level of genetic variability for all the traits. The significant differences observed in the lines, testers, and line-by-tester suggested both additive and non-additive gene effects exist in controlling the traits (Kumar *et al.*, 2015). These results corroborate with past findings reported for provitamin A content (Egesel *et al.*, 2003; Suwarno *et al.*, 2014; Duo *et al.*, 2021), yield-related traits and grain yield (Pswarayi and Vivek, 2008; Badu-Apraku *et al.*, 2013; Owusu *et al.*, 2017; Gami *et al.*, 2018), with the improvement in these traits achieved through selection and hybridization in maize.

The presented results showed that the variance due to GCA effects among lines and testers was higher than that due to SCA among the hybrids for all the studied traits except plant height. It shows the predominance of additive effects crucial to fixing traits and rapidly identifying the best parents (Islam *et al.*, 2015), and using simple selection for improving these traits in *Zea mays* L. (Dhasarathan *et al.*, 2015). Additionally, Barnard *et al.* (2002) and Walkowiak *et al.* (2022) argued that lines with high GCA should be selected for use in the future breeding program because of having more favorable alleles for improving the suggested traits. Furthermore, Fellahi *et al.* (2018) reported that breeders should choose parental genotypes based on the following principle - "Cross the best with the best to get the best.’’

Based on these results, the parental lines P1, P2, P6, and P7 proved promising and indicated improvement in provitamin A content. Such important maize genotypes need usage in future maize breeding programs to alleviate severe acute provitamin A malnutrition, as observed in the former Katanga province, DR Congo. Moreover, this province also has low production due to low maize yields. Thus, lines P6 and P3 can play a vital role due to their significant positive GCA, reflecting their potential to increase grain yield based on the positive correlation between grain yield and 100 or 1000-kernel weight reported by previous research (Cai *et al.*, 2012; Ram Reddy and Jabeen, 2016; Shim *et al.*, 2017). The lines P4 and P8 can play a vital role due to their significant positive GCA, reflecting their potential to increase 100-kernel weight, subsequently increasing grain yield. Furthermore, the 100 or 1000-kernel weight is not only one of the components that positively influence grain yield, but it also has a crucial role in the seed weight for use on a given area (Ilunga *et al.*, 2018).

The SCA effects are crucial to identify promising cross combinations concerning the selection of specific traits (Islam *et al.*, 2022). In addition, the SCA effects are also helpful in classifying hybrids into heterotic groups (Pswarayi and Vivek, 2008; Legesse *et al.*, 2009). A high SCA effect can result either from the a) combination of two parents with good GCA, b) from the combination of two parents with one good GCA, or c) the combination of two parents with poor GCA (Murtadha *et al.*, 2018). Examining the relationship between the performance of the parental genotypes and their hybrids, the hybrids with significant SCA for provitamin A result from either combining parents with poor GCA (P11 × P3), combining parents with high GCA (P10 × P6, P10 × P7, and P12 × P1), or combining parents with one of them having significant GCA (P10 × P8 and P9 × P2) and combining parents with medium and low GCA (P9 × P5).

For grain yield, significant positive SCA effects emerged in the hybrids, viz., P10 × P5, P10 × P6, P11 × P5, P9 × P5, and P12 × P5. Seeing the significant and positive SCA effects, the hybrid P10 × P6 was a cross between two parents with good GCA. Meanwhile, P10 × P5 was a cross with a significant positive GCA and medium GCA. Furthermore, the hybrid P11 × P5 comes from parents with medium GCA. These results also agree with those of Khan *et al.* (2016), who reported hybrids with significant positive SCA effects obtained from two parents with medium and significantly positive GCA or between parents with medium GCA. The superiority of significant negative × negative GCA observed in P11 × P3 for provitamin A content or the combination of parental genotypes with medium GCA for grain yield, noted in the cross P11 × P5, might be due to genetic diversity among parents, transgressive segregation, and complementation (Kulshreshtha and Singh, 2011). Furthermore, the high SCA effects observed in the hybrids P10 × P8 and P9 × P2 crosses for provitamin A content and hybrid P10 × P5 for grain yield are probably due to the interaction of positive alleles among the parent cultivars (Tefera *et al.*, 2020). The significant positive SCA effect obtained by three single hybrids (P10 × P5, P10 × P6, P11 × P5) and five hybrids (P9 × P5, P10 × P6, P10 × P7, P10 × P8, and P12 × P1) for grain yield and provitamin A content, respectively, as well as, the significant negative SCA effect obtained by the F1 hybrids P9 × P5 and P10 × P8 for plant height, suggest that these F1 hybrids can also be helpful to produce two- or three-way hybrids. These categories of crosses are less productive than single hybrids (Hallauer *et al.*, 2010; Meseka *et al.*, 2016; Makinde *et al.*, 2021), but their seed production is less expensive (Hallauer *et al.*, 2010). Furthermore, three-way and double hybrids have a broader adaptation than single-cross hybrids (Meseka *et al.*, 2016; Makinde *et al.*, 2021). It continues to make them desirable, especially in areas such as the former Katanga province.

The heterosis results showed that hybrids expressed positive gain for grain yield except for P12 × P1, P9 × P1, and P9 × P2. However, this genetic gain was significant for 41% of hybrids only, such as P10 × P8, P10 × P5, P10 × P3, P11 × P8, P11 × P5, P12 × P8, P10 × P6, P10 × P7, P9 × P8, P11 × P4, P11 × P3, P10 × P4 and P11 × P6. Indeed, the expression of the highest heterosis was due to the genetic diversity among the parental maize genotypes (Lee *et al.*, 2007; Siyuan *et al.*, 2018; Ghosh *et al.*, 2018). The presented results validate the findings of past researchers who observed significant variation in average heterosis for grain yield and its components (Dorina and Viorica, 2015; Owusu *et al.*, 2017).

For provitamin A content, the mid-parent heterosis was positive among all the hybrids; however, significant only for the crosses. i.e., P9 × P2, P9 × P5, P9 × P6, P10 × P1, P10 × P5, P10 × P6, P11 × P1, P11 × P2, P11 × P5, P11 × P6, P12 × P1, P12 × P5, and P12 × P6. These results indicate not only the presence of diversity among the mated parents but also the absence of a bidirectional variation in dominance (Owusu *et al.*, 2017). However, the provitamin A content was between the contents of the two parents. It led to negative better-parent heterosis for all the hybrids except two crosses, P12 × P6 and P12 × P1. Though, some crossbreeds expressed positive better-parent heterosis for grain yield, including P9 × P3, P10 × P6, P11 × P3, P11 × P4, P11 × P5, P11 × P6, P11 × P7, P11 × P8, and P12 × P1. Thus, the hybrids P10 × P5, P10 × P6, P10 × P7, P10 × P8, and P11 × P5 expressed better mid-parent heterosis for provitamin A content and grain yield. The significant heterosis combined with the better mean performance for grain yield and provitamin A content is a good indication for the selection of the genotypes. However, their dissemination requires an evaluation of the stability of their performance in various environments.

CONCLUSIONS

The higher variance of GCA compared with SCA for most traits indicates the predominance of additive gene action. Thus, improving such features should be based on exploiting the additive effects. The parental line P6 was the best general combiner for ear height, 100-kernel weight, grain yield, and provitamin A content. The lines P7, P4, and P2 presented relevant positive GCA effects for the provitamin A element. In addition, line P3 had significant positive GCA effects for grain yield, which means the favorable alleles were transferred to their progenies for these traits through hybridization. In the context of malnutrition and low yield observed in the former province of Katanga, the parental line P6 could form the base population for enhancing grain yield and provitamin A content. Based on SCA and heterosis, five hybrids (P10 × P5, P10 × P6, P10 × P7, P10 × P8 and P11 × P5) showed superior best specific combinations for improving productivity and provitamin A content. Furthermore, the hybrid P10 × P6 can also benefit the production of either two- or three-way hybrids to improve the grain yield and provitamin A content. Crossbreeds P10 × P5 and P11 × P5 can also be helpful for the production of two- and three-way hybrids with high yield potential, with P10 × P7 and P10 × P8 for high provitamin A content. The performance of these hybrids could vary according to weather and soil conditions; therefore, it is crucial to study the stability of these hybrids in different environments.

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