

RESEARCH ARTICLE

Inheritance of Yield and Yield-related Traits in Highland Maize Hybrids of Uganda

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Received: August 18, 2017 / Revised: October 03, 2017 / Accepted: October 13, 2017

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Abstract

Although many studies have been conducted on gene action of grain yield and yield related traits in maize, none of them focused on highland maize in Uganda. This study was conducted to establish the gene action controlling inheritance of yield and its related traits in highland maize hybrids. Thirty-six F₁ hybrids generated from a 9 x 9 half diallel mating design, were planted with two local checks in three highland locations; Kalengyere, Kachwekano, and Buginyanya with two replications using a 2 x 19 alpha (0, 1) lattice design. Results showed that inheritance of ear length and anthesis-silking interval was controlled by both additive and non-additive gene action while the inheritance of days to anthesis, days to silking was mainly controlled by additive gene action. The inheritance of grain yield and other yield related traits was greatly influenced by environment and genotype x environment interaction. Considering the great influence of the environment and genotype x environment interaction on most of the traits including grain yield, further testing in additional locations over more seasons and broadening the genetic base of the parents is encouraged.

Key words : Heritability, highland, hybrids, gene action, grain yield, *Zea mays*

Introduction

Maize is globally grown in a wide range of agro-ecological zones (FAO 2015). In East Africa, it is the most important staple cereal grain and provides over 50% of the daily calorie and protein intake of the population (Twumasi-Afriyie et al. 2001). The Global production of maize in 2014 was about 1 billion metric tons (MT), with East Africa contributing 31.7 million MT and Uganda only 2.8 million MT (FAOSTAT 2016). Maize is grown throughout Uganda in low, mid, and high altitudes areas. According to UBOS (2014) maize production in mid-altitude areas outweighs highland areas. However, while maize produced in the mid altitudes is primarily sold on the local market, maize produced in highlands is mainly exported to neighboring countries both as seed and grain (Dr. Frank Kagoda, personal communication 2014). Highland production is, therefore, emerging as a potential

avenue for production to supplement the mid-altitude production and target new markets (Twumasi-Afriyie et al. 2001). While production is scaling out to highland areas, the productivity of varieties grown by farmers is however low (Kagoda 2013).

The yield potential for maize in Uganda is estimated at 4.5-7.0 t ha⁻¹ (CIMMYT 2001) but on average, the actual yield on-farm is 2.7 t ha⁻¹ (FAOSTAT, 2016) and in highland areas, it hardly exceeds 2 t ha⁻¹ (Kagoda 2013). This is due to the occurrence of pests and diseases, stalk lodging, frost effects, and lack of high-yielding genotypes adapted to highland conditions of Uganda (Twumasi-Afriyie et al. 2001). Farmers in highland plant unsuitable varieties which, in reality, were developed for low and mid altitude zones; consequently, these varieties yield very poorly (Twumasi-Afriyie et al. 2001). There was therefore a need to develop improved maize varieties that are adapted to Ugandan highland conditions. In this regard, the Buginyanya Zonal Agricultural Research and Development

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Institute introduced highland maize inbred lines from CIMMYT-Ethiopia in 2013 to develop high-yielding and adapted hybrids for the highlands in Uganda. These lines being exotic, in order to define an appropriate breeding strategy for quantitative traits such as yield, breeders need to consider the relative contributions of the genetic (additive and non-additive) and environmental variances to phenotypic variation (Agoyi et al. 2016).

Grain yield is a very important, though complex, trait in maize breeding. This is because its expression is determined by several genes and influenced by environmental conditions, which have the ability to influence the expression of the trait. Dominance gene action is preferred for developing hybrids and additive gene action denotes the standard selection protocols that will be effective in improving the traits (Kumar et al. 2012). Several inheritance studies have been conducted on grain yield and yield-related traits. Shahrokhi et al. (2013) reported the significance of additive genes and additive x additive interactions effects in the control of traits like ear height, 100 kernel weight, and grain yield measured in six generations of maize. Other previous researchers reported predominance of non-additive genetic effects for days to silking, plant height and ear height (Alam et al. 2008), number of kernels (Srdic et al. 2007), ear length and grain yield (Rezaei and Roohi 2004) and leaf area (Suneeta et al. 2000). Kumar et al. (1998), showed that both additive and non-additive gene actions were important for number of kernels per row and grain yield in maize. These inconsistencies show that the gene action controlling yield and yield-related traits is specific to the genetic material used and the testing environment. It was, therefore, crucial to establish the gene action governing grain yield and its components in the newly introduced highland maize inbreds prior to improvement so as to guide in the choice of the appropriate breeding strategy. The objective of this study was therefore to determine the mode of gene action controlling the inheritance of yield and yield-related traits of maize in the highlands of Uganda. The study contributed knowledge in a relatively new area that had not been ventured into by maize breeders in Uganda.

Materials and Methods

Experimental sites

The study was conducted at three highland sites of Uganda, namely Buginyanya in Bulambuli District, Kachwekano in Kabale District, and Kalengere satellite station in Kabale District (Table 1). The three highlands are found under the

Montane agro-ecology (Wortman and Eledu 1999), characterized by elevations between 1500-3000 m above sea level, annual average rainfall of 1500-2000 mm, average minimum temperature of 15 °C and maximum of 28 °C, and 80% relative humidity.

Germplasm and population development

A total of 59 inbred lines were sourced from CIMMYT-Ethiopia in 2013 and were screened on-station at Buginyanya Zonal Agricultural Research and Development Institute (Bugi ZARDI), Ikulwe Satellite Station in eastern Uganda during the first rainy season of 2014 (April to June) to enable selection of superior genotypes based on resistance to biotic and abiotic stresses. Criteria for selection involved: resistance to major diseases in the tropics mainly Turcicum Leaf Blight (TLB), Grey Leaf Spot (GLS), Maize Streak Virus (MSV), and Maize Lethal Necrosis (MLN); a low anthesis-silking interval, resistance to lodging, and prolificacy. At the end of the season, one set of nine most promising inbred lines (Table 2) were crossed on-station in a half-diallel mating design $p(p-1)/2$ to get 36 single cross F1 hybrids. Hybrids were evaluated in the rainy season of 2015 from March to October across the three highland sites.

Experimental design and management

The 36 single crosses were planted in Kachwekano, Kalengere, and Buginyanya using a 2×18 alpha (0, 1) lattice design, with two replications per site. Two plants were planted per hill and later thinned to one. Each hybrid was planted in single row plot of 4.2-m long, spaced at 0.3×0.75 m within and between rows which gave a total 15 plants per plot. Diammonium phosphate (DAP) fertilizer was applied at planting at a rate of 125 kg ha⁻¹ and urea top dressed at same rate when plants had at least 7-8 leaves.

Data collection

According to CIMMYT/IBPGR (1991), data was collected on days to anthesis (AD) and days to silking (SD) which were recorded per plot as number of days from sowing to 50% tasseling, and when silks have emerged on 50% of the plants, respectively. Anthesis-silking interval was computed as the difference between SD and AD. At harvest plant count was estimated, number of ears per plot was counted, and number of ears per plant was calculated as the ratio of number of ears per plot and plant stand count. Data were also collected on number of kernel rows in the central part of the uppermost ear, number of kernels per row, ear diameter (cm), ear length (cm), 1000-kernel weight (g), field weight per plot (kg), and moisture content (%) of grain for each plot. Grain yield

Table 1. Geographical and climatic characteristics of the experimental sites.

Location	Longitude	Latitude	Altitude (masl)	Temperature (°C)	Annual average rainfall (mm)
Buginyanya	34° 09' E	01° 22' N	1800	12-22	1297
Kachwekano	29° 41' E	01° 17' S	1980	6-23	1170
Kalengere	30° 30' E	01° 15' S	2450	10-23	1000

Table 2. List of the maize parental inbred lines.

NAME	PEDIGREE	ORIGIN	REMARKS
AMH704-14	[KIT/SNSYN[N3/TUX]]c1F1-##(GLS=2.5)-34-2-1-1-1-#####	AMB10A-AMB10EN18-14	Medium height, semi-dent seed texture, small seed size, medium maturity and electrophile leaf type.
AMH704-22	[POOL9Ac7-SR(BC2)]FS59-4-1-2-1-1-2-1-2-#####	AMB10A-AMB10EN18-22	Medium height, semi-dent seed texture, medium seed size, early maturity and semi-erect leaf type.
AMH704-43	[POOL9Ac7-SR(BC2)]FS69-1SR-1-2-2-2-#-1-#####	AMB10A-AMB10EN18-43	Medium height, dent seed texture, large seed size, early maturity and semi-erect leaf type.
AMH701-9	[POOL9Ac7-SR(BC2)]FS232-4-1-3-1-2-2-1-#####	AMB10PN19-9	Medium height, semi-dent seed texture, medium seed size, early maturity and planophile leaf type.
AMH701-20	[ECU/SNSYN[SC/ETO]]c1F1-##(GLS=2.5)-36-2-1-1-#####	AMB10PN19-20	Semi-dent seed texture, small seed size, late maturity and semi-erect leaf type.
AMH703-22	[POOL9Ac7-SR(BC2)]FS45-3-2-2-1-2-#*4-#####	AMB10A-AMB10KN20-22	Short, dent seed texture, large seed size, late maturity and semi-erect leaf type.
AMH703-34	[POOL9Ac7-SR(BC2)]FS211-1SR-1-1-1-#####	AMB10A-AMB10KN20-34	Tall, dent seed texture, small seed size, early maturity and planophile leaf type.
AMH703-35	SRSYN95[ECU//SC/ETO]F1-##(GLS=3.5)-20-2-1-1-#####	AMB10A-AMB10KN20-35	Tall, dent seed texture, large seed size, early maturity and semi-erect leaf type.
AMH703-37	[POOL9Ac7-SR(BC2)]FS67-1-2-3-1-#####	AMBO	Medium height, dent seed texture, medium seed size, late maturity and planophile leaf type.

adjusted to 12.5% moisture content (Sesay et al. 2016) was calculated as:

$$GY(t.ha^{-1}) = \frac{FW_P * 0.8 * (100 - MC) * 10,000}{(100 - 12.5) * 3.15 * 1000}$$

Where: FW_P = Field weight (kg) of maize per plot, MC = moisture content of grain for each plot, 0.8 = Shelling coefficient, 3.15 m² = Plot area

Data analysis

Combining ability analysis was performed as a fixed effects model 1 method IV of Griffing (1956) across the three sites using Diallel-SAS05 program for Griffing analysis (Zhang et al. 2005). The linear model for consideration during analysis was: $Y_{ijk} = \mu + L_k + g_i + g_j + s_{ij} + gL_{ik} + gL_{jk} + sL_{ijk} + e_{ijk}$; where, Y_{ijk} = value of F1 cross of the i^{th} female and the j^{th} male in the k^{th} site μ = population mean; L_k = main effect of the k^{th} site; g_i and g_j = GCA effects of i^{th} and j^{th} inbred parents, respectively; s_{ij} = SCA effect ($SCA_{ij} = SCA_{ji}$); gL_{ik} and gL_{jk} = effects of the interaction between the GCA of i^{th} and j^{th} parents and the k^{th} site effect respectively; sL_{ijk} = effect of interaction between the SCA of the i^{th} and j^{th} parents and the k^{th} site; e_{ijk} = experimental error.

Components of genotypic variances were determined and used to estimate heritability in form of broad-sense coefficient of genetic determination (BS.CGD), which is the total genetic variations and narrow-sense coefficient of genetic determination (NS.CGD) which is the proportion of the phenotypic variation explained by additive effect (Dabholkar 1992). The relative importance of the additive gene effects over non-additive genes effects in determining the predictability of progeny

performance was assessed in terms of Baker's (1978) ratio. BS.CGD, NS.CGD, and Baker's ratio estimates across environments were computed as:

$$BS.CGD = \frac{2 * \sigma^2 gca + \sigma^2 sca}{2 * \sigma^2 gca + \sigma^2 sca + (\sigma^2 gca * site + \sigma^2 sca * site) / 3 + (error) / 6}$$

$$NS.CGD = \frac{2 * \sigma^2 gca}{2 * \sigma^2 gca + \sigma^2 sca + (\sigma^2 gca * site + \sigma^2 sca * site) / 3 + (error) / 6}$$

$$Baker's\ ratio = \frac{2 * \sigma^2 gca}{2 * \sigma^2 gca + \sigma^2 sca}$$

Individual parent's GCA and individual F₁ hybrids SCA effects were tested by a two-sided t-test to determine if they significantly differed from 0, based on the standard error associated with their estimation (Dabholkar 1992).

Results

Analysis of variance across the three highland environments

The combined analysis of variance (Table 3) showed significant environment mean squares ($P < 0.01$) for all the traits except ear length, grain yield, and number of kernel rows. The F₁ maize hybrids family had significant mean squares for days to anthesis, ear length ($P < 0.01$), days to silking ($P < 0.05$), and anthesis-silking interval ($P < 0.001$). The parents had significantly different GCA effects for anthesis days to silking, anthesis-silking interval and ear length at

Table 3. Analysis of variance of 36 crosses: mean squares for yield and yield-related traits of hybrids evaluated across three highland locations of Uganda.

SOV	df	AD	SD	ASI	E_P	ED	EL	GY	KR	K_R	SW
ENV	2	2545.35**	2561.72**	10267.63***	1.54**	322.28**	34.54 ^{ns}	368.27 ^{ns}	5.36 ^{ns}	198.74 ^{ns}	297085.51**
REP(ENV)	3	35.81 ^{ns}	21.5 ^{ns}	0.074 ^{ns}	0.02 ^{ns}	7.42***	4.12 ^{ns}	46.05***	4.69*	65.5**	2401.32 ^{ns}
HYBRID	35	46.79**	55.6*	378.29***	0.29 ^{ns}	3.4 ^{ns}	11.57**	4.27 ^{ns}	3.98 ^{ns}	46.33 ^{ns}	6895.3 ^{ns}
GCA	8	125.2*	174.01*	1555.48*	0.31 ^{ns}	1.84 ^{ns}	19.2*	5.03 ^{ns}	9.78 ^{ns}	57.74 ^{ns}	9518.18 ^{ns}
SCA	27	23.55 ^{ns}	20.51 ^{ns}	29.49***	0.29 ^{ns}	3.86 ^{ns}	9.31*	4.05 ^{ns}	2.26 ^{ns}	42.95 ^{ns}	6030.78 ^{ns}
ENV*HYBRID	70	22.07***	28.96*	120.8***	0.24***	3.09***	5.03*	4.36***	3.55***	37.33***	7346.52 ^{ns}
ENV*GCA	16	41.27***	62.42***	501.57***	0.17**	3.31**	5.97*	5.57**	4.3**	43.71***	5400.15 ^{ns}
ENV*SCA	54	16.38*	19.05 ^{ns}	7.98***	0.26***	3.03***	4.75 ^{ns}	4.01**	3.32**	35.44***	8770.97*
ERROR	105	10.09	18.12	2.71	0.07	1.2	3.41	2.22	1.7	15.8	5264.22
V.GCA	4	5.31	50.19	0.01	-0.07	0.63	-0.03	0.26	0.67	171.58	
V.SCA	2.39	0.49	7.17	0.01	0.28	1.52	0.01	-0.35	2.5	-913.4	
V.GCA x ENV	4.45	6.33	71.27	0.01	0.3	0.37	0.05	0.37	3.99	16.99	
V.SCA x ENV	6.29	0.93	5.27	0.19	1.83	1.34	-1.21	1.62	19.64	3506.75	
BS.CGD	0.66	0.67	0.81	0.23	0.23	0.71	0.02	0.36	0.27	0.14	
NS.CGD	0.51	0.64	0.75	0.13	0	0.32	0	0.36	0.09	0.14	
BR	0.77	0.96	0.93	0.57	0	0.45	0	1	0.35	1	

Significance level, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, SOV=Source of Variation, df=Degrees of Freedom, AD=Days to Anthesis, ASI=Anthesis silking Interval, E_P= Number of ears per plant, ED=Ear diameter, EL=Ear length, GY= Grain yield, KR=Number of kernel rows, K_R=Number of kernels per row, SD=Days to silking, SW= 1000 Seed weight, GCA= General combining ability, SCA= Specific combining ability. ENV= Environment, V.GCA= Variance due to GCA, V.SCA=Variance due to SCA, V.GCA x ENV=Variance due to interaction between genotype (GCA) and Environment. V.SCA x SCA=Variance due to interaction between crosses (SCA) and Environment, BS.CGD&NS.CGD=Broad sense and Narrow sense Coefficients of genetic determination, BR= Bakers ratio.

Table 4. Estimates of GCA effects for grain yield and yield-related traits of maize inbred lines across three highland locations in Uganda.

ENTRY	AD	SD	ASI	ED	EL	GY	KR	K_R	SW
AMH704-14	0.83	1.67	0.97*	0.19	-0.33	-0.09	0.52*	0.28	-30.77*
AMH704-22	-2.01*	-2.16*	-0.46	0.01	0.19	0.31	-0.26	1.82*	4.36
AMH704-43	0.34	0.31	0.23	-0.27	0.48	-0.18	-0.1	-0.87	-15.63
AMH701-9	-2.16*	-2.04*	-0.05	0.04	0.89**	0.32	0.19	0.39	-8.48
AMH701-20	2.43*	2.19*	-0.01	0.08	-0.80**	0.06	0.35	-0.56	11.43
AMH703-22	-0.09	-0.05	0.08	0.29	0.08	0.49	0.31	-1.25	5.31
AMH703-34	-2.09*	-2.61*	-0.55	0.04	0.44	-0.56	-0.48*	0.39	14.01
AMH703-35	1.69	3.09*	0.73	-0.39	-1.25***	0.05	0.4	-1.63*	-0.48
AMH703-37	1.05	-0.38	0.95*	0.01	0.29	-0.4	-0.93***	1.42	20.26

Significance level, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, AD=Days to Anthesis, ASI=Anthesis silking Interval, E_P= Number of ears per plant, ED=Ear diameter, EL=Ear length, GY= Grain yield, KR=Number of kernel rows, K_R=Number of kernels per row, SD=Days to silking, SW= 1000-Seed weight

0.05 probability level. The specific combining ability effects of the hybrids only showed significant differences for anthesis-silking interval ($P < 0.001$) and ear length ($P < 0.05$). Environment x hybrids and environment x GCA interactions effects were highly significantly different for grain yield and all the yield-related traits except 1000-seed weight. The interaction effects of environment x SCA were highly significant for grain yield and all the yield-related traits except days to silking and ear length.

The estimate broad-sense coefficient of genetic determination (BS.CGD) was relatively high ($0.66 < \text{BS.CGD} < 0.81$) for days to anthesis, days to silking, anthesis-silking interval, and ear length, moderately low ($0.22 < \text{BS.CGD} < 0.36$) for number of ears per plant, ear diameter, number of kernel rows, and kernel per row and significantly low ($\text{BS.CGD} < 0.2$) for grain yield and 1000-seed weight. The estimate of narrow-sense coefficient of genetic determination (NS.CGD)

was fairly high for days to silking (0.64) and anthesis-silking interval (0.75); moderate for days to anthesis (0.50), moderately low for ear length (0.32) and number of kernel rows (0.36); and significantly low ($\text{BS.CGD} < 0.2$) for the remaining traits including grain yield. Coming to the estimate of Baker's ratio (BR), it was high for days to anthesis, days to silking, number of kernel rows, 1000-seed weight, and anthesis-silking interval ($\text{BR} > 0.76$); moderate for number of ears per plant, ear length, and number of kernels per row ($0.34 < \text{BR} < 0.56$); and very low for ear diameter and grain yield.

General combining ability effects of parental lines

The general combining ability effects for individual parents across the three highland environments are presented in Table 4. None of the highland maize inbred lines had a significant GCA effect for grain yield and ear diameter. Parental lines AMH704-22, AMH701-9, and AMH703-34

had significant ($P \leq 0.05$) negative GCA effects for days to anthesis and days to silking while inbred AMH701-20 had a significant ($P \leq 0.05$) but positive GCA effect for the same traits. Two inbreds AMH704-14 and AMH703-37 had significant ($P \leq 0.05$) positive GCA effects for anthesis-silking interval. Coming to number of kernel rows, the former had a positive while the latter had a negative GCA effect. Inbreds AMH701-20 and AMH703-35 had significant ($P \leq 0.01$) negative GCA effects while AMH701-9 had a positive GCA effect for ear length. The inbred line AMH704-22 had the highest significant ($P \leq 0.05$) positive GCA effect for number of kernels per row whereas AMH704-14 had the highest significant ($P \leq 0.05$) negative GCA effect for 1000-seed weight.

Specific combining ability effects of hybrids

The specific combining ability effects of the highland maize hybrids across the three environments are presented in Table 5. There were no hybrids with significant SCA effects for grain yield, across the three highland sites (Table 5). Hybrid AMH 701-20/AMH703-35 had significant ($P \leq 0.05$) positive SCA effects for days to anthesis and significant ($P \leq 0.05$) negative effects for ear diameter, ear length, number of kernels per row and 1000-seed weight. Hybrids AMH701-20/AMH703-35 and AMH704-43/AMH703-34 had the highest significant ($P \leq 0.05$) negative SCA effect for 1000-seed weight.

Table 5. Hybrids' SCA effects for grain yield and yield related traits of maize hybrids across three highland sites.

HYBRIDS	AD	E_P	ED	EL	KR	K_R	NE	SW
AMH704-14/AMH704-22	1.23	-0.09	0.21	0.00	-0.74	0.73	-1.50	30.86
AMH704-14/AMH704-43	-1.13	0.03	-0.2	1.34	-0.07	-0.92	1.48	-21.21
AMH704-14/AMH701-9	-0.96	0.03	-0.64	-0.77	0.14	-1.18	0.12	4.64
AMH704-14/AMH701-20	1.27	0.08	1.23	1.2	0.14	2.27	0.05	42.32
AMH704-14/AMH703-22	0.96	-0.14	-0.72	-1.52*	-0.64	-3.37	-3.31	-56.74
AMH704-14/AMH703-34	0.13	0.1	-0.17	0.53	0.98	0.49	0.38	38.59
AMH704-14/AMH703-35	-1.49	0.05	0.17	-0.83	0.26	1.85	2.31	-22.01
AMH704-14/AMH703-37	-0.01	-0.07	0.12	0.03	-0.07	0.13	0.38	-16.45
AMH704-22/AMH704-43	-1.44	0.1	-0.03	-0.3	0.55	0.37	-1.14	-22.18
AMH704-22/AMH701-9	3.23	-0.23	-0.41	0.66	0.43	-2.23	2.62	-1.76
AMH704-22/AMH701-20	-1.54	0.32*	0.52	-0.18	0.26	2.23	-1.24	3.03
AMH704-22/AMH703-22	-2.18	-0.23	-0.34	-0.21	-0.19	-1.92	-0.38	4.5
AMH704-22/AMH703-34	-0.68	-0.16	-0.54	-0.59	0.1	-3.56*	0.38	-6.47
AMH704-22/AMH703-35	1.04	-0.04	0.05	0.87	-0.95	3.63*	-2.67	10.78
AMH704-22/AMH703-37	0.35	0.34*	0.54	-0.24	0.55	0.75	-0.90	-18.75
AMH704-43/AMH701-9	-0.30	-0.11	0.02	0.29	-0.9	1.63	-0.93	13.06
AMH704-43/AMH701-20	-2.06	-0.23	0.45	1.01	0.1	1.25	0.10	16
AMH704-43/AMH703-22	1.30	0.22	-0.66	-1.05	0.81	-1.56	2.36	3.17
AMH704-43/AMH703-34	-0.04	-0.21	-0.49	-0.43	-0.9	-2.2	2.74	-26.23
AMH704-43/AMH703-35	1.18	0.41**	0.78	-0.24	0.55	1.15	0.55	15
AMH704-43/AMH703-37	2.49	-0.21	0.13	-0.63	-0.12	0.27	2.07	22.39
AMH701-9/AMH701-20	-3.06	0.1	-0.15	0.62	-0.52	-1.18	0.50	17.93
AMH701-9/AMH703-22	1.13	0.22	0.31	-0.99	0.19	-1.15	1.14	-31.83
AMH701-9/AMH703-34	2.63	0.29*	0.22	-1.24	-0.52	3.54	-1.33	-22.38
AMH701-9/AMH703-35	-1.32	-0.09	0.69	0.85	0.1	0.73	-5.90**	25.62
AMH701-9/AMH703-37	-1.35	-0.21	-0.04	0.58	1.10*	-0.15	0.81	-5.28
AMH701-20/AMH703-22	0.04	-0.07	0.33	1.16	0.19	2.63	1.90	0.24
AMH701-20/AMH703-34	-0.13	0.01	0.71	0.38	0.64	1.65	0.48	15.89
AMH701-20/AMH703-35	4.92*	-0.21	-2.97***	-4.30****	-0.4	-8.82***	0.88	-74.79*
AMH701-20/AMH703-37	0.56	0.01	-0.11	0.11	-0.4	-0.04	0.19	-20.62
AMH703-22/AMH703-34	0.73	0.29	0.45	0.62	-0.14	1.18	-2.17	42.46
AMH703-22/AMH703-35	-0.06	-0.26	1.21	1.63*	0.64	2.54	1.60	13.92
AMH703-22/AMH703-37	-1.92	-0.04	-0.57	0.34	-0.86	1.65	1.07	24.27
AMH703-34/AMH703-35	-3.39	-0.18	-0.01	1.47*	-0.07	0.23	-0.57	-12.41
AMH703-34/AMH703-37	0.75	-0.14	-0.16	-0.75	-0.07	-1.32	-1.07	-29.44
AMH703-35/AMH703-37	-0.87	0.32	0.08	0.55	-0.12	-1.3	-0.98	43.88

ASI, GY and SI were not included in this table because they were not significant across all hybrids. Significance level, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, AD=Days to Anthesis, E_P= Number of ears per plant, ED=Ear diameter, EL=Ear length, HC=Husk cover (%), KR=Number of kernel rows, K_R=Number of kernels per row, NE=Number of ears per plot, SW= 1000 Seed weight.

Discussion

Genetic variation and mean performance of highland maize hybrids

Significant differences were observed among the hybrids mean performance for days to anthesis (AD), days to silking (SD), anthesis silking interval (ASI), and ear length (EL) indicating that there was high genetic diversity among the parental lines and the subsequent hybrids regarding these traits. The main goal of every breeding program is to achieve high genetic gain which depends, to a great extent, on the presence of genetic diversity in the breeding population (Falconer 1989). Thus, genetic diversity is of paramount importance in crop improvement as it provides a wide genetic base for selection (Govindaraj et al. 2015). The results of this study show therefore that selection can, be made among these maize inbreds for breeding for early-maturing (AD, SD, and ASI) varieties with long ears (EL) in highland areas.

Genetic and environmental factors are the two main sources that determine the phenotypic variability observed in plant populations (Rubaihayo 1996). Among these, the environmental factors usually have a great influence on the phenotypic expression of quantitative traits like yield. Expectedly, in this study, significant environment effects were observed for most of the yield-related traits indicating that the overall performance of the hybrids at each of the three highlands sites were different. Similarly, the mean squares of environment x hybrids interaction effects for grain yield and all the yield related traits except 1000-seed weight were also significant, showing that the relative difference observed in these hybrids' performance was not consistent across environments because of the influence of their specific interaction with each environment. This implies that there is a need of testing these hybrids in more highland locations and over two or more seasons in order to detect and quantify more clearly the hybrids by environment interaction.

The overall performance of the hybrids across the three highland sites showed that AMH704-43/AMH701-9 had the shortest period for days to anthesis, days to silking, and anthesis silking interval. This hybrid has therefore a good early maturity and can be used for developing early-maturing maize hybrids which are more suitable for drought-prone areas especially with the increasing adverse effects of climate change. Coming to the hybrids that showed the best performance for other yield related traits, AMH703-22/AMH703-35 had the largest maize cob with the highest number of kernel rows while AMH704-43/AMH703-35 had the highest number of ears per plant. The highest number of kernel per row was observed on AMH704-22/AMH703-37 while AMH704-14/AMH703-35 produced the longest cob with a high number of kernels per row. The hybrids that had the best performance for the yield related traits had the best contribution to the grain yield of these hybrids.

Combining ability and heritability

General combining ability (GCA) is the average performance of a parent in hybrid combination while specific combining ability (SCA) refers to the positive or negative deviation of a hybrid performance from what would be expected on the basis of average performance of the parents involved (Griffing 1956). From the partitioning of the genetic variance, GCA is associated with additive effects of the genes while SCA is associated with non-additive effects (dominance and epistasis) (Aguiar et al. 2003). In this study, the mean squares of the parents' overall GCA effects across the three highland sites were significant for AD, SD, ASI, and EL indicating the involvement of additive gene action in the control of these traits (Dhasarathan et al. 2015). The environment x GCA interaction effects were also significant for grain yield and all the yield-related traits except SW suggesting that the degree of transmission of these traits from parental lines to hybrids differed from one location to the other. In other words, the additive genes effects involved in the inheritance of these traits were differential to the environment. Different inbred lines could therefore be selected to generate cross combination for specific environment to improve grain yield and the yield-related traits (Nzuve et al. 2013). Coming to the SCA effects, the mean squares were significant for yield related traits like ASI, EL, and 1000-seed weight (SW) which is an evidence of non-additive genes effect being involved the control of these traits. These results are consistent with those of Rezaei and Roohi (2004) and Srdić and Mladenović-Drnić (2007) who reported that ear length is controlled by non-additive gene effects. The environment x SCA interaction effects were also significantly different for grain yield and all the yield-related traits except SD and EL, which implied that the crosses had different SCA effects for these traits from one environment to the other. The non-additive gene effects responsible for the inheritance of these traits were also differential to the environments hence the selection of hybrid with a desirable SCA effect would preferably be environment-specific.

Both additive and non-additive gene effects were responsible for the inheritance of grain yield and most of to yield-related traits though they were mainly altered by the environmental variations. Comparing the contribution of GCA and SCA to the genetic variance component, relatively high Baker's ratio values showed that GCA had a higher contribution for AD, SD, ASI, KR, SW, and number of ears per plant indicating predominance of additive gene action in control of most of these traits. This suggests for such traits, that hybrids performance would be well predicted based on the GCA effects of the parental lines. On the hand, SCA had a higher contribution than GCA for grain yield, EL, ED, and K_R which indicated predominance of non-additive gene action in control of most of these characters. This suggests poor predictability of these traits based on the GCA effects of the parental lines hence there is a need for more crosses to be made while including more genetically diverse parents in the crossing scheme.

The estimates of broad sense heritability (BS.CGD) for ASI, EL, SD, and AD were high indicating that high percentage of variation (BS.CGD > 60%) among the hybrids which was due to genetic causes. Going further, only the flowering traits (AD, ASI, and SD) had a high and moderate narrow-sense heritability (NS.CGD) as non-additive gene effects are predominant in the inheritance of EL. This shows that the variation among hybrids for the flowering traits was mainly due to transmissible genetic effects, in other words, additive genetic effects. Early-generation selection would therefore be effective for these traits and a moderate number of hybrids would be sufficient for an effective evaluation and performance prediction since the environmental variation did not have so much influence. This is in consonance with Mohsen et al. (2013) whose study reported that additive gene action is important for days to silking, days to anthesis. On the other hand, grain yield and the other yield-related traits had low values for both BS.CGD and NS.CGD suggesting that for these traits most of the phenotypic variation observed among the hybrids was due to the effect of environment and the interaction between environment and hybrids. These results are similar to those of Shrestha (2013) who reported that genotype by environment interaction had a significant effect on the expression of grain yield. This study had revealed that in highland maize, just like in most crops, grain is a quantitative trait thus highly influenced by environmental variation (Bernado 2010; Rubaihayo 1996). Consequently, an effective selection for yield improvement in highland maize would require an evaluation in several locations over many seasons and at advanced generation.

Combining ability effects

A parent is deemed desirable if it has significant GCA effects in the right direction for that particular trait (Dabholkar 1999; Singh and Chaudhary 2004). The most desirable parents for AD and SD were AMH704-22, AMH701-9, and AMH703-34 as they contributed to the earliness of the anthesis and silking by an average of 2 days. This means a short growth period will be attained whenever these inbreds are included in a cross, which is a desirable attribute in any breeding program because early-maturing hybrids would escape drought stress. Inbred AMH701-9 had the most desirable GCA effect for ear length with an average contribution of 0.89 cm towards the production of longer cobs which would lead to an increase of the grain yield. Coming to number of kernel rows and number of kernels per row the most desirable parents were AMH704-14 and AMH704-22, respectively. In this study, although some inbreds had significant desirable GCA effects for the yield related traits, none of them had a significant overall (GCA across the three highlands) contribution towards higher grain yield. As regard, in addition to including more genetically diverse parents in the crosses specifically for grain yield, the inbred lines with desirable GCA effects for the yield related traits, would also have a good contribution towards improvement of these traits and yield when used in a breeding program for the three highland locations.

The hybrids AMH704-43/AMH703-35, AMH704-22/AMH703-37, and AMH704-22/AMH701-20 produced a higher number of cobs per plants than what would be expected on the basis of the GCA effects of their parents. Besides these hybrids also had the longest cobs. Hybrid AMH703-22/AMH703-35 had the best SCA effect for ear length as it produced cobs that are 1.63 cm longer than what would be expected for ear length. This was further confirmed by the fact that this hybrid had a mean performance of the third longest cob. These hybrids with good SCA effects could be considered by the breeding programs for the development of hybrids with long cob, and number of cobs per plant and, indirectly, high grain yield.

This study showed that the inheritance of ear length and anthesis-silking interval was controlled by both additive and non-additive gene action, days to anthesis, and days to silking were mainly controlled by additive gene action while grain yield and other yield-related traits were greatly influenced by environment and genotype x environment interaction. Depending on the estimate narrow sense heritability, early generation selection would be effective for the flowering traits while advanced generation testing and selection would be more appropriate for grain yield and other yield-related traits. Considering the major influence of the environment and hybrid x environment interaction on most of the traits including grain yield, further testing in additional locations over more seasons should be done to further dissect the effects of hybrids x environment and choose the appropriate strategy between breeding for broad or specific adaptations.

Acknowledgements

We gratefully acknowledge Alliance for Green Revolution in Africa (AGRA) for funding this research and National Crops Resources Research Institute (NaCRRI), Buginyanya Zonal Agricultural Development Institute (BugiZARDI), and Makerere University for their collaboration which has eased conducting this research.

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