

Genetic Variation and Path Coefficient Analysis of Introgressed Maize Inbred Lines for Economic Traits

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Abstract

Knowledge of the effects of introgressing temperate maize germplasm in tropical elite inbred lines on genetic variation and relationship between grain yield and its components is limited. In this study, the objective was to evaluate introgressed maize inbred lines for selected economic traits. Field evaluation was carried out on 122 inbred lines comprising sets of introgressed lines from three selection environments, parental inbred lines and two common checks. Genetic variation was significant ($P < 0.05$) for all the major economic traits among inbred lines within and across sets. Heritability estimates ranged from low (0.21%) to high (91%) for stalk lodging and silking days, respectively. Comparison of means of inbred lines sets illustrated that environmental effect had influence on grain yield of introgressed lines. Grain yield and ear prolificacy performance across sets also illustrated that introgression of temperate germplasm in tropical elite inbred lines was effective. Spearman's rank correlation analysis on grain yield and ear prolificacy highlighted correlation between selection environments. Correlation among traits demonstrated that grain yield had significant ($P < 0.05$) positive correlation with plant and ear aspects, plant height, root and stalk lodging, ear prolificacy and grain moisture content at harvest. Further, decomposing of correlation using path coefficient analysis showed significant ($P < 0.05$), and moderate direct effects of ear prolificacy and plant height on grain yield; indicating that these traits had the highest contribution towards grain yield. Generally indirect effects of secondary traits on grain yield potential of inbred lines was negligible. Therefore, direct selection of plant height and ear prolificacy will be emphasised during introgression of temperate germplasm in tropical elite inbred lines.

Keywords: maize, genetic variability, heritability, correlation, grain yield, grain yield components

1. Introduction

Maize (*Zea mays* L.) is a major staple cereal crop widely grown across environments for its productivity. In South Africa maize has a commercial value that determines social, economic and political stability of the region. South African maize industry is regarded as a net earner of foreign currency, rendering this market highly lucrative for both breeding programmes operating from tropical and temperate environments. However, tropical germplasm directly introduced into the South African environments mainly by breeding programmes operating outside the South African temperate environments has been characterized by lack of adaptability.

In the current study, the focus was on developing new maize inbred lines introgressed with genes from temperate germplasm to enhance adaptability to the South African warm temperate environments. Introgressed inbred lines were developed through the use of a single common temperate donor inbred line as source of genes from temperate germplasm into 12 elite tropical inbred lines. Introgressed lines were selected from three distinct environments in South Africa and Zimbabwe based on important economic traits that are desirable for the South African market and are usually lacking in directly introduced germplasm namely: ear prolificacy; low grain moisture content at harvest; good plant standing ability; and high grain yield (Abadassi & Herve, 2000).

In maize breeding programmes amount of genetic variability and level of heritability determines rate of breeding progress. According to Bello et al. (2012) the success of any crop improvement programme depends upon the amount of genetic variability existing in the germplasm and the extent to which it is heritable, which sets the

limit of progress that can be achieved through selection. Therefore, in this study there was need to establish knowledge of the genetic variation of desired economic traits, the level of heritability among traits if increased genetic gains were to be achieved in improving desired economic traits (ear prolificacy, good standing ability, early physiological maturity and high grain yield) for the South Africa market. Literature reports significant genotypic variability and heritability among maize genotypes for various morphological traits. However, the complex nature of economical traits such as grain yield and its components in breeding programmes makes it difficult to explore this genetic variability to achieve desired genetic gain in grain yield. In addition, changes in environments generally affects yield mainly through its components, hence there is need to establish the relationship between yield and its components, and influence of the environment for effective selection.

Direct selection for grain yield may not be the most efficient method for crop improvement. Indirect selection for other yield related traits that are closely associated with yield and heritability estimates can be more effective (Akeel-Wannows et al., 2010). Hence there is need to understand and exploit the relationships between grain yield and its components during the selection process thus ensuring grain yield improvement. According to Hefny (2011) yield components do not only directly affect selection but also indirectly by affecting other yield components in a negative or positive direction. A number of studies have reported relationship between traits using correlations and path coefficient analysis techniques. However due to inadequacy of correlation coefficients to successfully predict success of selection, several studies have explored the use of path-coefficient analysis. Path coefficient analysis has been reported in a number of studies as an efficient method for establishing correlation between grain yield and its components. Muge Mangango and Kumar (2011), reports that path coefficient analysis technique establishes the exact correlation in terms of cause and effect through: identification of the direct, indirect and total (direct and indirect) casual effects. In this study Pearson's correlation and path coefficient analysis techniques were used to establish relationship of grain yield and its components.

Thus, the objective of this study was to evaluate genetic variation, heritability for selected economic traits, and to determine the relationships between traits in the new introgressed inbred lines. Importantly, the effect of selection environment on genetic variation and mean performance should be established in order to identify suitable sites for development of introgressed inbred lines. Environments that have high discrimination capacity would be desired to enhance breeding gains.

2. Method

The experimental material comprised 123 inbred lines: 76 introgressed inbred lines that combined temperate and tropical germplasm. These inbred lines were selected from three distinct environments to form three sets of introgressed inbred lines and were considered as test genotypes. There was also a set of 26 temperate inbred lines including the donor inbred line that were used as a set of positive control inbred lines for the study. They were used as positive controls because they are adapted to the South African warm temperate environments. Additionally, a set of 21 tropical inbred lines was included as negative control maize inbred lines. They were considered as negative controls because they are not adapted to South African environments. The lists of these inbred lines are indicated in Appendix 1-3. Consequently, the new introgressed inbred lines were evaluated in the study relative to the tropical and temperate control inbred lines.

2.1 Experimental Design

Augmented alpha lattice experimental design (Lin & Poushinsky, 1983; Scott & Miliken, 1993; Spehar, 1994) was used to evaluate the trial. A total of 122 inbred lines (76 introgressed inbred lines plus sets of tropical and temperate control inbred lines) were randomly assigned into six blocks, in each block 10 test entries were randomly assigned to plots within each block and two common tropical control lines (SC21 and SC19; repeated checks) were also randomly assigned in each block.

2.2 Field Layout and Agronomic Management

Field layout and agronomic management was carried out at Rattray Anorlrd Research Station (RARS), Kadoma Research Centre (KRC), Cedara Research Station (CRS) and Ukulinga Research Stations (UKRS) in Zimbabwe and South Africa in 2012-13 summer season. In South Africa, at UKRS each entry was planted to single row plots of 5m length, spaced at 0.3 m in-row and 0.75 m between row spacing to achieve a total plant population density of at least 44,000 plants ha⁻¹. At CRS, single 5m row plots, in-row spacing 0.3 m and inter-row 0.9 m were used to achieve a plant stand of at least 37,000 plants ha⁻¹. In Zimbabwe, at RARS and KRC each entry was planted to single row plots of 10m length, space at 0.3 m in-row and 1.5 m between row spacing to achieve a total plant population density of at least 22,000 plants ha⁻¹. Standard cultural management practices for growing maize were carried out at all sites. Irrigation was only applied to achieve uniform establishment and also to

supplement rainfall as and when necessary. Fertilizer application was done at a rate of: 120 kg Nitrogen (N), 33 kg Phosphorous (P), and 44 kg Potassium (K) at CRS and URS; 145 kg Nitrogen (N), 56 kg Phosphorous (P), and 28 kg Potassium (K) at RARS; and 88.4 kg Nitrogen (N), 56 kg Phosphorous (P), and 28 kg Potassium (K) at KRC.

2.3 Variables Measured

Comprehensive data was collected following standard procedures used at International Maize and Wheat Improvement Centre, CIMMYT (1985) for the following traits:

- a) Anthesis days (AD): number of days to 50 % pollen shedding from day of planting.
- b) Silking days (SD): number of days to 50% silk emergence from day of planting.
- c) Plant height (m) (PH): distance between the base of a plant to the auricle of the flag leaf.
- d) Ear height (m) (EH): distance between the ground level and the base of the primary ear.
- e) Stalk lodging (SL): percentage of plant per plot that had their stems broken.
- f) Root lodging (RL): percentage of plant per plot which had their stems inclined by at least 45°.
- g) Number of ears per plot-Ear Prolificacy (EPP) as a fraction number of plants.
- h) Moisture content at harvest (MC): percentage grain moisture content at harvest.
- i) Grain yield (t ha⁻¹) (GYD): grain mass per plot adjusted to 12.5 % moisture content.

2.4 Statistical Analyses

Data for grain yield and other agronomic traits from individual sites was analysed for variance using PROC GLM of SAS (SAS Institute Inc., 2010). Combined analysis of variance was carried out after testing for homogeneity of variance following Leven test and Welch's test using GLM procedure of SAS (SAS Institute Inc., 2010). Analysis of variance was performed using PROC GLM of SAS (SAS Institute Inc., 2010) for combined data across sites. The means of lines were predicted for each selection environment which constituted sets. The mean of inbred lines across the sets were also predicted. Correlation between the environments was calculated using the Spearman's rank correlation.

2.5 Estimation of Heritability

Estimate of narrow sense heritability were performed as described by Hallauer and Miranda (1988) using the variance components analysis in SAS (SAS Institute, 2010). The heritability estimates were classified according to Robinson et al. (1949) into 3 classes; low 0-30%, medium 31-60% and > 60% as high. Based on variance components narrow sense heritability was estimated as:

$$h^2 = \delta_g^2 / (\delta_g^2 / re + \delta_{ge}^2 / e + \delta_g^2) \quad (1)$$

Where, δ_g^2 is variance of inbred lines, δ^2 is error variance, δ_{ge}^2 is site x entry interaction variance and e is sites.

2.6 Estimation of Correlations

Pearson's correlation coefficients values were calculated using PROC CORR (SAS Institute, 2010). Path coefficient analysis was used to calculate direct and indirect effects of secondary traits on grain yield using the PathSAS programme (SAS Institute, 2010) developed by Cramer et al. (1999). The path coefficient is estimated by solving sets of simultaneous equations indicating the basic relationship between correlation and path coefficients (Mugemangango & Kumar, 2011). Path coefficient direct and indirect effect values were classified into scales suggested by Lenka and Mishra (1973) namely; negligible 0.00-0.09, low 0.01-0.19, and moderate 0.20-0.29, and high 0.30-0.99. In this regard negligible values indicate non-significant contribution to grain yield potential.

$$r_{iy} = P_{iy} + r_{i1}P_{1y} + r_{i2}P_{2y} + \dots + r_{i(i-1)}P_{iy}; \quad i = 1, 2, 3, \dots n \quad (2)$$

Where, n is the number of independent characters; r_{1y} to r_{iy} denote coefficient of correlation between casual factors 1 to i and dependent character y , r_{i2} to $r_{i(i-1)}$ the coefficients of correlation among all possible combinations of casual factors and P_{1y} to P_{iy} denote the direct effects of character 1 to i on the character. The indirect effect of i th variable through j th variable on y the dependent variable is computed as $P_{jy} \times r_{ji}$.

3. Results

3.1 Genetic Variation

Combined analysis of variance for grain yield and its components for the 123 inbred lines across sites is presented in Table 1. Mean square values for all the traits were significantly ($P < 0.001$) different for site effects. Control entries were significant ($P < 0.01$) for all the traits excluding root and stalk lodging. Experimental entries were significantly ($P < 0.05$) different for anthesis and silking days, plant and ear heights, ear prolificacy, grain moisture content at harvest and grain yield. Genotype-by-environment interaction effects were significant ($P < 0.05$) for anthesis and silking days, root and stalk lodgings, ear prolificacy, grain moisture content at harvest and grain yield.

3.2 Environmental Effect

Analysis of variance of grain yield and its components at individual sites showed that the four sites were able to discriminate the traits for the genotypes under study as shown in Table 2. Check entries at RARS were significant ($P < 0.05$) for the majority of the traits which included root lodging, grain moisture content at harvest, and grain yield. At KRC, anthesis and silking days, ear prolificacy and grain yield were significant ($P < 0.05$) traits for the check entries. The majority of the traits; anthesis and silking days, ear height, ear prolificacy, grain moisture content at harvest and grain yield were significant ($P < 0.05$) at URS. At CRS the following traits; root and stalk lodging, and ear prolificacy were significant ($P < 0.05$). Experimental entries at RARS were significant ($P < 0.05$) for anthesis and silking days, plant height, stalk lodging and grain yield. At KRC silking days and grain yield were significant ($P < 0.05$). Experimental entries were significant ($P < 0.05$) at URS for silking days, ear height, stalk lodging, ear prolificacy, grain moisture content at harvest and grain yield. At CRS stalk lodging and ear prolificacy were the only significant ($P < 0.01$) traits.

Table 1. Combined analyses of variances for grain yield and its components for 123 maize inbred lines across sites

Trait/Source of variation	Site	Control inbred lines	X-Experimental inbred lines (Control)	Site*Control	Site*X(Control)	MS (Error)
Grain yield ($t\ ha^{-1}$)	13.53***	0.41**	1.54***	0.27***	0.53***	0.05
Ear prolificacy	1.52***	4.07***	0.38***	0.34***	0.12***	0.02
Moisture content (%)	237.48***	11.63**	9.23	8.80**	4.59**	2.19
Anthesis days	6291.36***	146.19***	25.21***	25.45***	7.36***	2.79
Silking days	6381.31***	446.75***	33.04***	38.16***	6.97*	4.04
Plant height (m)	37217***	2813.17**	1528.96***	181.33	377.15	342.72
Ear height (m)	3198.56***	3839.19***	562.98***	112.51	107.06	133.93
Root lodging (%)	1960.66***	95.05	89.97**	275.50***	96.55*	41.2
Stalk lodging (%)	973.88***	29.91	52.33***	36.56	52.92***	18.78

Note. *, **, *** indicates the data is significant at $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$; grain moisture content at harvest (%), percentage grain moisture at harvest; Site, environment; Control, check entry; X(Control), experimental inbred lines nested within checks; Site*Control, check-by-environment interaction; Site*X(Control), environment-by-experimental inbred lines nested within checks interaction.

Table 2. Mean squares from analysis of variances for grain yield and its components for the 123 maize inbred lines at four individual sites

Trait/Source of variation	Control inbred lines				Experimental inbred lines			
	RARS	KRC	URS	CRS	RARS	KRC	URS	CRS
Grain yield (t ha ⁻¹)	0.09	0.37***	0.70*	0.03	0.95**	0.13*	1.67***	0.14
Ear prolificacy	1.69***	0.07*	1.80***	1.50**	0.16**	0.04	0.32**	0.19**
Moist content (%)	29.77	4.99	1.81**	1.26	7.41	11.57	1.27**	1.61
Anthesis days	98.86***	24.55**	97.40**	2.05	12.77***	5.07	22.68	5.86
Silking days	207.60***	173.30***	155.42**	23.57	15.268**	11.74*	21.89*	4.36
Plant height (m)	1279.63*	504.63	1340.35	403.26	478.59*	424.52	1082.85	517.66
Ear height (m)	1696.02*	501.05	780.52**	1177.3	248.06	174.19	213.63*	216.57
Root lodging (%)	20	150.5	2.75	730.56*	44.68	68.28	2.75	222
Stalk lodging (%)	1.77***	130.14	5.82	1.12***	4.56***	87.54	95.23*	12.59***

Note. DF (check) = 3 and DF (Test lines) = 122 at all sites; *, **, *** indicates the term is significant at $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$; RARS-Ratray Anorld Research Station; KRC-Kadoma Research Centre; URS-Ukulinga Research Station; CRS-Cedara Research Station.

Summary statistics of combined data indicated that all the data was significant ($P < 0.05$) for the entries (Table 3). Anthesis and silking days had both minimum of 42 days and a maximum of 90-91 days. Plant and ear height had ranges of 0.80-2.88 m and 0.35-1.00 m, respectively. Stalk and root lodging both had minimum values of 0% with maximum 37% and 100%, respectively. Variation for ear prolificacy had the smallest range 0-0.35. Large variation was also observed for the following traits: grain moisture content at harvest and grain yield.

Table 3. Summary statistics of combined data for the 123 maize inbred lines across sites

Variable	Mean	Std Dev	Minimum	Maximum	R ²	CV	P value	Heritability
Grain yield (t ha ⁻¹)	1.30	0.99	0.00	9.92	1.00	16.60	***	0.54
Ear prolificacy	1.17	0.49	0.00	3.50	1.00	8.75	***	0.83
Grain moisture	14.84	2.90	0.00	33.30	0.98	10.57	***	0.80
Anthesis days	68.00	11.38	42.00	91.00	1.00	2.44	***	0.80
Silking days	72.00	11.43	42.00	90.00	1.00	2.93	***	0.91
Root lodging (%)	6.32	10.61	0.00	100.00	0.97	91.28	*	0.39
Stalk lodging (%)	4.54	8.31	0.00	37.00	0.99	85.21	***	0.21
Plant height (m)	1.78	36.54	0.80	2.88	0.98	11.17	***	0.70
Ear height (m)	0.78	16.26	0.35	1.50	0.97	16.23	***	0.84

Note. *, **, *** indicates the term is significant at $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$; Grain moisture-grain moisture at harvest; Std Dev-standard deviation; R²-R-square value.

3.3 Heritability

High heritability ($h^2 > 0.70$) was exhibited for the following traits: anthesis and silking days, grain moisture content at harvest, plant and ear heights, and ear prolificacy (Table 3). Moderate heritability (0.54) was estimated for grain yield. Low heritability estimates were observed for root and stalk lodging.

3.4 Comparison Between Breeding Environments

Data for the two principal traits yield and ear prolificacy was used to determine the associations between test environments. Spearman's rank correlation coefficients for grain yield data between environments indicated highest positive correlation (0.81) between CRS and URS, both in South Africa. Low correlations were noted between RARS and KRC (-0.34) in Zimbabwe, and between CRS and KRC (0.17) (Table 4).

Table 4. Environmental correlation

	RARS	KRC	CRS	URS
<i>Spearman's rank correlation between the environments using grain yield ($t\ ha^{-1}$) data</i>				
RARS	1.00	-0.34	-0.01	0.01
		<u>0.00</u>	<u>0.89</u>	<u>0.87</u>
KRC		1.00	0.17	0.11
			<u><.0001</u>	<u>0.22</u>
Cedara			1.00	0.81
				<u><0.001</u>
Ukulinga				1.00
<i>Spearman's rank correlation between the environments using ear prolificacy data</i>				
RARS	1.00	0.04	0.46	0.09
		<u>0.65</u>	<u><.0001</u>	<u>0.32</u>
KRC		1.00	0.17	0.42
			<u>0.06</u>	<u><0.001</u>
Cedara			1.00	0.26
				<u>0.00</u>
Ukulinga				1.00

Note. RARS-Rattray Anorld Research Station; KRC-Kadoma Research Centre; URS-Ukulinga Research Station; CRS-Cedara Research Station; Underlined numbers-significance value.

Spearman's rank correlation coefficients values for ear prolificacy data between environments indicated weak but significant ($P < 0.001$) association between CRS and RARS (0.46), and KRC and URS (0.42). Lowest association for ear prolificacy was observed between CRS and URS (0.26) (Table 4).

3.5 Comparison of Means of Lines Derived in Different Environments

Results of least significant mean data for grain yield and its components of inbred line sets across sites were significant ($P < 0.05$) for: silking days, ear prolificacy, grain moisture content at harvest and grain yield (Table 5). Inbred line sets (introgression and controls) were different for grain yield potential. Grain moisture content at harvest data indicated no differences among the inbred line sets with the only difference observed between recipient inbred lines (tropical elite inbred lines) and donor parental inbred line (temperate inbred lines). Ear prolificacy showed difference among introgressed lines bred at RARS and the other two sets of introgressed lines from KRC and URS. Control inbred line sets were different for ear prolificacy in tropical and temperate germplasm. Least significant means values for silking days showed difference between donor line and tropical inbred lines, while introgressed lines were not different. The results in Table 5 indicates that the donor parent (temperate) was superior for the principal traits, grain yield, ear prolificacy, grain moisture content at harvest and silking days. The tropical set of inbred lines was generally inferior to both the donor lines and the set of temperate lines for the economic traits. Although recipient lines (founder parents) displayed higher grain yield than the introgression sets, they were inferior to their progenies with respect to ear prolificacy grain moisture content at harvest and silking days.

3.6 Correlations Analysis Between Traits

Significant ($P < 0.05$) positive and negative correlations were observed between primary and secondary traits (Table 6). The main primary trait, grain yield had positive correlation with plant and ear height, root and stalk lodging, ear prolificacy and grain moisture content at harvest; but negative correlation with anthesis days and silking days. Ear prolificacy had positive correlation with plant and ear height, and anthesis days; while negative correlation was observed with root and stalk lodging. Secondary traits had positive correlation observed between traits namely: anthesis days and silking days, ear height and flowering days (anthesis and silking days), root lodging and anthesis days, ear height and plant height, root lodging and flowering days, and grain moisture content at harvest and flowering days. Negative correlation was also detected among secondary traits namely; plant height and flowering days, stalk lodging and flowering days, stalk lodging and plant height, stalk lodging and ear height.

3.7 Path Coefficient Analysis

In this study, the correlation coefficients of secondary traits on grain yield were further partitioned into direct and indirect effects using path coefficient analysis. Plant height and ear prolificacy showed significant ($P < 0.05$)

direct effect on grain yield (Table 7). This study categorizes of path coefficient values suggested by Lenka and Mishra (1973) were used as: negligible 0.00-0.09, low 0.01-0.19, and moderate 0.20-0.29, and high 0.30-0.99. Significant ($P < 0.05$) and moderate positive direct effect values for grain yield were observed on plant height and ear prolificacy (Table 8). Plant height had a moderate positive direct effect (0.27) on grain yield and it also illustrated negligible positive indirect effect via the following traits; silking days (0.04), stalk lodging (0.03), ear prolificacy (0.01) and grain moisture content at harvest (0.03). Plant height also illustrated negligible negative indirect effect via: anthesis days (-0.01) and ear height (-0.03). Ear prolificacy showed moderate direct effect (0.24) on grain yield and it also illustrated negligible positive indirect effect via; silking days (0.06), and plant height (0.01), while negligible negative indirect effect was observed via; anthesis days (-0.01), stalk lodging (-0.01) and grain moisture content at harvest.

Table 5. Least significant means for grain yield and its components of maize inbred lines sets across sites

Set	GY	EPP	MC	AD	SD	PH	EH	RL	SL
Introgressed lines ex-KRC	1.33b	1.47d	13.52ab	66.53a	66.02a	44.37ab	18.39	4.61	4.85
Introgressed lines ex-RARS	1.43c	1.41c	13.88ab	67.76bc	67.83bc	49.43ab	19.1	4.42	4.17
Introgressed lines ex-UKS	1.11a	1.49d	13.75ab	68.47bc	68.38bc	48.3ab	20.28	4.8	3.88
<i>Controls</i>									
A-recipient lines	1.77d	1.11b	15.06b	68.67e	69.52ab	45.77	20.21	4.04	4.64
B-donor line	2.59e	1.75e	13.01a	66.21d	65.44a	49.92	17.21	4.95	7.82
C-tropical lines	1.28b	1.06a	14.60ab	70.79	72.63b	47.83	23.04	3.43	2.69
D-temperate lines	1.47c	1.75e	13.77ab	69.80f	69.53ab	41.41	18.64	3.75	3.77
Trial mean	1.57	1.43	13.94	68.32	68.48	46.72	19.55	4.29	4.54
CV (%)	68.78	30.89	20.58	8.69	16.63	129.12	124.38	121.54	148.26
LSD _(0.05)	0.06	0.03	1.66	0.86	6.58	6.50	4.17	1.92	2.03
Pr>F	***	***	*	NS	*	NS	NS	NS	NS

Note. Ex-KRC, introgressed lines bred at Kadoma Research Centre; Ex-RARS, introgressed lines bred at Rattray Anorlrd Research Station; Ex-UKS, Introgressed lines bred at Ukulinga Research Station; *, **, *** indicates the term is significant at $P \leq 0.05$, $P \leq 0.01$, $P \leq 0.001$; NS, not significant.

Table 6. Correlation coefficients for grain yield and its components of maize inbred lines

	Anthesis days	Silking days	Plant height	Ear height	Root Lodging	Stalk lodging	Ear prolificacy	Grain moisture	Grain yield
Anthesis days	1	0.98***	-0.13***	0.21***	0.23***	-0.32***	0.10*	0.48***	-0.07*
Silking days		1	-0.16***	0.21***	0.19***	-0.35***	0.04	0.5***	-0.16***
Plant height			1	0.6***	-0.03	-0.15***	0.32***	-0.01	0.38***
Ear height				1	0.03	-0.11*	0.17***	0.36***	0.30***
Root Lodging					1	0.25***	-0.12***	0.03***	0.14***
Stalk lodging						1	-0.27***	-0.17***	0.19***
Ear prolificacy							1	0.05	0.26***
Grain moisture								1	0.16*
Grain yield									1

Note. $R^2 = 0.66$; $n = 525$; *, **, ***-Significant at 0.5, 0.01, 0.001, respectively; grain moisture-grain moisture content at harvest.

Table 7. Parameter estimates for direct effects based on regression

Trait	Parameter estimate	Standard Error	t Value	Pr > t
Intercept	-0.064	0.059	-1.070	0.287
Anthesis days	0.150	0.146	1.020	0.309
Silking days	-0.274	0.154	-1.780	0.079
Plant height	0.266	0.109	2.440	0.017*
Ear height	-0.042	0.109	-0.380	0.703
Root lodging	0.000	0.070	0.000	0.996
Stalk lodging	0.145	0.078	1.850	0.068
Ear prolificacy	0.240	0.090	2.670	0.009**
Grain moisture	0.096	0.097	0.980	0.329

Note. *, **, ***-Significant at 0.5, 0.001, respectively.

Table 8. Direct and indirect effects of secondary traits on grain yield of maize inbred lines

	Anthesis days	Silking days	Plant height	Ear height	Root lodging	Stalk lodging	Ear prolificacy	Grain moisture	Total correlation with GYD
Anthesis days	<u>0.15</u>	-0.24	-0.02	-0.01	0.00	-0.04	-0.02	0.04	-0.07
Silking days	0.13	<u>-0.27</u>	-0.03	-0.01	0.00	-0.04	-0.05	0.04	-0.17
Plant height	-0.01	0.04	<u>0.27</u>	-0.03	0.00	0.03	0.01	0.03	0.38*
Ear height	0.02	-0.04	0.21	<u>-0.04</u>	0.00	0.03	0.00	0.05	0.30
Root lodging	-0.02	0.03	0.07	-0.01	<u>0.00</u>	0.05	0.00	0.02	0.14
Stalk lodging	-0.04	0.08	0.06	-0.01	0.00	<u>0.14</u>	-0.02	0.00	0.19
Ear prolificacy	-0.01	0.06	0.01	0.00	0.00	-0.01	<u>0.24</u>	-0.01	0.26***
Grain moisture	0.07	-0.12	0.09	-0.02	0.00	0.00	-0.02	<u>0.10</u>	0.16

Note. $R^2 = 0.66$; $n = 525$; Bold font and underlined for direct effects; *, **, ***-Significant at 0.5, 0.1, 0.01, respectively; grain moisture-grain moisture content at harvest.

4. Discussion

4.1 Genetic Variability Among Inbred Lines

The amount of genetic variability in maize breeding population sets the limit of genetic gain that can be attained in improving traits of economic importance. Significant variation was observed among inbred lines within and among sets for all the traits which was an indication that genetic variation for the traits under study was present. Morrissey et al. (2010), through the breeders' equation indicates that for any breeding programme to achieve desirable genetic gain per breeding cycle there is need to exploit genetic variation existing in germplasm and applying correct selection intensity (i) and high level of precision in implementation the breeding programme. Therefore, this indicates that traits that illustrated genetic variation in current study can be exploited for improvement. However, breeding progress might be slow as genotype-environment interaction was also observed to be significant. A number of studies have also reported genetic variation for economic traits such as: anthesis and silking days (Hefny, 2011; Akeel-Wannows et al., 2010); plant and ear height (Kage et al., 2013; Bello et al., 2011); root and stalk lodging (Prasanna, 2012); ear prolificacy (Kesomkeaw et al. 2009; Golam et al., 2011); grain moisture content at harvest (Filipenco et al., 2013); and grain yield (Bello et al., 2011).

Combined analysis of variance was significant ($P < 0.001$) due to site effect for all the traits. Therefore, the sites were different from each other and provided contrasting environments for testing inbred lines' performance. Check entries were significant for all the traits under study excluding percentage root and stalk lodging. This showed that the check entries gave a wide spectrum of traits to compare against the introgressed lines; an indication that they were appropriate checks which can be used for similar studies in the future. However, in future studies, there is also the need to select checks that accommodate all the traits under study. Genotype-by-environment interaction was significant ($P < 0.05$) for the majority of the traits. This illustrates that phenotypic selection of economic traits under study was influenced by environmental effects, an indication that there may be slow breeding progress, because $G \times E$ compromises heritability.

4.2 Genetic Variability Across Inbred Lines Sets

Least significant mean values for grain yield and its components of inbred line sets across sites were significant ($P < 0.05$). Grain yield illustrated that there was genetic variation among the introgressed lines bred from different environments. This was an indication that there are environmental effects for grain yield potential of introgressed lines bred at different environments. Environment at each site influences genetic grain yield potential through different agrotechnical elements namely; effective crop rotation, fertilization and water supply. Chen et al. (2018) also illustrates that yield is different across environments due to a complex of sub-optimal management practices that may result in errors. Grain yield for the control entries were significant illustrating genetic variation for grain yield potential of temperate and tropical germplasm used in this study. Inbred line sets (introgressed and controls) were different for grain yield potential. Grain moisture content at harvest indicated no differences among the inbred line sets. This can be attributed to the common donor parental inbred line that was used during introgression. In addition, recipient tropical inbred lines used during introgression came from an established tropical breeding programme; and breeders are known to recycle breeding material during trait improvement. Therefore, this may account for no difference observed for grain moisture content at harvest among inbred lines within and across sets. Differences observed between recipient inbred lines and donor parental inbred line for grain moisture content at harvest can be attributed to difference in germplasm backgrounds. Temperate germplasm has low grain moisture content at harvest relative to tropical germplasm (Abadassi & Herve, 2000). Similar results have been reported by Tarter et al. (2004) of high grain moisture content at harvest in tropical maize germplasm relative to temperate maize germplasm. However, it is clear that further introgression of temperate germplasm in the introgressed lines will be required to boost variation for grain moisture content at harvest. This is one of the principal traits that will confer adaptation of inbred lines in temperate environments.

Difference noted in ear prolificacy among introgressed lines bred at Rattray Anorld Research Station and sets of introgressed lines bred at Kadoma Research Centre and Ukulinga Research Station indicates the influence of breeding environments in discriminating ear prolificacy among inbred lines (Table 4). Hence Rattray Anorld Research Station was a unique environment for selecting ear prolificacy during breeding. Introgression of temperate germplasm for ear prolificacy was effective as indicated by general difference in ear prolificacy among the introgressed lines. Control inbred line sets were different for ear prolificacy in tropical and temperate germplasm. This can be attributed to differences in germplasm background. According to Brathwaite and Brathwaite (2002) and Kesomkeaw et al. (2009) genetic diversity and high heritability for ear prolificacy is more pronounced in temperate germplasm relative to tropical germplasm. Silking days indicated differences between the donor line and tropical inbred lines, indicating effect of germplasm background on flowering. Introgressed lines were not different for silking days which can be attributed to common donor parent line used during introgression. Therefore, further introgression of the lines using different donor parental inbred lines will be pursued to obtain ample genetic variation for silking days in introgressed lines.

4.3 Environmental Correlation

Correlation between sites was also observed to be significant ($P < 0.001$) between RARS and URS, KRC and CRS, and KRC and URS, using grain yield data (Table 5). However, only KRC and URS had a high correlation coefficient value of 0.80, indicating only one of the sites could be recommended for utilization during breeding and trial evaluation as they have the same discriminating effect. However, this result is in sharp contrast with known records as KRC is situated in tropical environments of Zimbabwe; while URS is a temperate environment in South Africa. The remaining sites RARS and URS; and KRC and CRS had weak correlation coefficient values (0.29) and (0.17), respectively. The sites offer contrasting environmental effects hence they can be used as different selection environments. Similar trend was also observed for these environments using ear prolificacy trait.

Analysis of variance for grain yield and its components at the four individual sites illustrated difference in discriminating effect of desirable economic traits for the genotypes at each site used. Significant differences for anthesis days and silking days for all the environments except CRS indicates differences in genetic variation to flowering and also influence of environmental factors such as day length, temperature effect, and growing degree units per season during flowering in maize (Abadassi and Herve, 2000; Edmeades et al., 2000; Xu et al., 2009). Ukulinga Research Station illustrated significant differences ($P < 0.01$) for ear height for entries an indication that the environment can effectively discriminate inbred lines for ear height hence it can be used for phenotypic selection of ear height in introgressed lines. Significant difference ($P < 0.05$) for root lodging were observed at CRS only which can be attributed to excessive wind storms that are experienced at this site, qualifying it as the best site to screen introgressed lines for standing ability.

Number of ears per plant was observed to be significantly different ($P < 0.05$) at all the sites except for KRC environment. Therefore, these environments can discriminate ear prolificacy in inbred lines under study and can effectively be utilized for phenotypic selection in future studies. Lack of ear prolificacy at KRC can be attributed to the drought stress associated with below normal rains that were received during the growing season. Edmeades et al. (1997) also reports that ear prolificacy is a secondary trait in maize production which is affected by barrenness under drought stress. This is contrary to Varga et al. (2004) who reported increased number of ears per plant under stress environment. Percentage grain moisture content at harvest was observed to be significant ($P < 0.001$) at RARS only, which can be attributed to early harvesting that was carried out at this site. Therefore, in future studies, time of harvesting of trials should be standardized across sites based on physiological maturity. Grain yield data also illustrated that all the sites were able to discriminate inbred lines and showed genetic variation for grain yield which enables selection. Therefore, phenotypic selection can be carried out on introgressed lines at these sites based on grain yield potential. Breeding programmes prefer inbred lines with outstanding grain yield potential in seed production.

4.4 Heritability

High narrow sense heritability estimates were observed for the following traits: anthesis and silking days, percentage grain moisture content at harvest, plant and ear height and ear prolificacy. This illustrates that these traits can be successfully selected for using phenotypic selection during breeding. Based on the high heritability estimates, these traits can also be used as part of the selection index for the improvement of introgressed lines in future projects. Similar results have been reported in a number of studies for the following traits: anthesis and silking days (Beyene, 2005; Sumathi et al., 2005); plant and ear height (Smalley et al., 2003; Akeel-Wannows et al., 2010; Bello et al., 2011). Moderate heritability was detected for grain yield. This indicates that grain yield is a complex trait that is strongly influenced by environment during selection thus slow progress is expected during selection. Contrasting reports on the magnitude of heritability for grain yield has also been reported: low heritability (Sumathi et al., 2005; Iqbal, 2009) and high heritability (Beyene, 2005; Akeel-Wannows et al., 2010). Differences in the heritability values among researchers can be attributed to differences in genetic materials that were used as well as environments used during the studies. Low heritability estimates for root and stalk lodging were detected. This indicates that the traits were influenced by environmental factors that mask genetic effects during selection. Therefore, they are difficulties in direct selection of inbred lines through introgression. Further breeding gains for these traits can be obtained by increasing genetic variance, increase selection intensity and improving quality of experiments to minimise errors during assessment.

4.5 Correlation Among Traits

A number of traits in maize have complex inheritance hence they are difficult to directly select for in breeding programmes, therefore there is need to indirectly select these traits using other closely related traits. In this study, Pearson's correlation coefficient and path coefficient values were used to establish relationships among grain yield and its components.

4.6 Correlation Analysis

The traits under study illustrated that there was significant ($P < 0.05$), positive and negative correlation between traits. Grain yield had positive correlation with plant and ear height, ear prolificacy and grain moisture content. This shows that grain yield is a complex trait that is affected by both yield and growth aspects of the plant. Varga et al. (2004) reports that ear prolificacy is a yield component that has a direct effect on grain yield. In current study, growth aspects were observed to have positive effect on grain yield. This reveals that indirect selection of growth aspects; plant and ear height and grain moisture content at harvest may result in improved grain yield. Similar results have been reported of positive correlation of grain yield with ear prolificacy (Varga et al., 2004) and plant height (Iqbal, 2010). In contrast, anthesis and silking days had negative correlation with grain yield. This may illustrate that these traits have an inverse relationship with grain yield; selection for anthesis and silking days may lead to low grain yield. Ear prolificacy illustrated positive correlation with plant and ear height, and anthesis days. This indicates that selection of these plant attributes will result in an increased ear prolificacy. Secondary traits that demonstrated positive correlation between each other may suggest that these traits can be indirectly selected for each other thus ensure parallel improvement of these traits. An improvement in one of the traits has a direct effect on the corresponding trait during selection. However, negative correlation was also observed between secondary traits an indication that these traits have an inverse relationship. An increase in one trait will lead to a decline in the corresponding trait, therefore there has to be a compromise during selection when breeding for both traits.

4.7 Path Coefficient Analysis

This study revealed that there was significant ($P < 0.05$), moderate and positive direct effects of plant height and ear prolificacy on grain yield, an indication that these traits had the highest contribution towards grain yield. It is evident that an increase in ear prolificacy and plant height can result in an increase grain yield. This may reveal that plant height and ear prolificacy maybe given a high selection preference during breeding. Beside positive direct effect on grain yield, plant height also revealed negligible positive indirect effect via silking days, stalk lodging, ear prolificacy and grain moisture content at harvest. Thus by selecting for plant height one would also be selecting for these traits. Similarly, when selecting for ear prolificacy indirect selection for silking days and plant height will also be achieved.

5. Conclusion

The study revealed genetic variation among inbred lines within sets and among sets for all the economic traits evaluated. Heritability estimates were detected varying from low (21%) to high (91%) for stalk lodging and silking days, respectively. Comparison of means of introgressed lines bred from different environments illustrated that selection environments had an effect on grain yield of inbred lines. Difference and ear prolificacy performance of the new progeny lines across sets illustrated that introgression of temperate germplasm into tropical elite inbred lines was effective. Spearman's rank correlations on grain yield and ear prolificacy showed correlation between environments. This indicated that KRC would be suitable environment to evaluate germplasm to be deployed in the South Africa environments. Correlation analysis showed that grain yield had positive correlations with plant and ear height, root and stalks lodging, and also yields components such as ear prolificacy and grain moisture content at harvest. Further breakdown of the correlations by path analysis revealed that there was significant ($P < 0.05$), and moderate direct effect of plant height and ear prolificacy on grain yield. This indicates that these are the most important traits contributing towards grain yield. The indirect effects of secondary traits on grain yield were generally small to negligible. In sum it indicated that plant height and ear prolificacy must be emphasised during the introgression strategy to enhance adaptation of tropical germplasm in South African warm temperate environments.

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Appendix A**Description of maize inbred lines used in the study**

Entry	Code	Breeding Environment	Germplasm Background	Homozygosity
1	KRC_1	KRC-Zimbabwe	Introgressed lines	0.90
2	KRC_2	KRC-Zimbabwe	Introgressed lines	0.92
3	KRC_4	KRC-Zimbabwe	Introgressed lines	0.94
4	KRC_5	KRC-Zimbabwe	Introgressed lines	0.68
5	KRC_6	KRC-Zimbabwe	Introgressed lines	0.99
6	KRC_7	KRC-Zimbabwe	Introgressed lines	0.63
7	KRC_8	KRC-Zimbabwe	Introgressed lines	0.74
8	KRC_9	KRC-Zimbabwe	Introgressed lines	0.80
9	KRC_11	KRC-Zimbabwe	Introgressed lines	1.00
10	KRC_22	KRC-Zimbabwe	Introgressed lines	0.98
11	KRC_23	KRC-Zimbabwe	Introgressed lines	0.56
12	KRC_24	KRC-Zimbabwe	Introgressed lines	1.00
13	KRC_25	KRC-Zimbabwe	Introgressed lines	1.00
14	KRC_27	KRC-Zimbabwe	Introgressed lines	0.98
15	KRC_28	KRC-Zimbabwe	Introgressed lines	0.99
16	KRC_29	KRC-Zimbabwe	Introgressed lines	1.00
17	KRC_30	KRC-Zimbabwe	Introgressed lines	0.95
18	KRC_31	KRC-Zimbabwe	Introgressed lines	0.95
19	KRC_33	KRC-Zimbabwe	Introgressed lines	1.00
20	KRC_34	KRC-Zimbabwe	Introgressed lines	1.00
21	KRC_35	KRC-Zimbabwe	Introgressed lines	0.99
22	KRC_38	KRC-Zimbabwe	Introgressed lines	0.85
23	KRC_39	KRC-Zimbabwe	Introgressed lines	0.96
24	KRC_41	KRC-Zimbabwe	Introgressed lines	0.71
25	KRC_43	KRC-Zimbabwe	Introgressed lines	0.69
26	RARS_1	RARS-Zimbabwe	Introgressed lines	0.66
27	RARS_2	RARS-Zimbabwe	Introgressed lines	0.94
28	RARS_3	RARS-Zimbabwe	Introgressed lines	0.94
29	RARS_4	RARS-Zimbabwe	Introgressed lines	1.00
30	RARS_5	RARS-Zimbabwe	Introgressed lines	0.99
31	RARS_6	RARS-Zimbabwe	Introgressed lines	0.98
32	RARS_7	RARS-Zimbabwe	Introgressed lines	0.96
33	RARS_8	RARS-Zimbabwe	Introgressed lines	0.58
34	RARS_9	RARS-Zimbabwe	Introgressed lines	0.99
35	RARS_11	RARS-Zimbabwe	Introgressed lines	0.98
36	RARS_12	RARS-Zimbabwe	Introgressed lines	1.00
37	RARS_16	RARS-Zimbabwe	Introgressed lines	0.95
38	RARS_17	RARS-Zimbabwe	Introgressed lines	0.96
39	RARS_18	RARS-Zimbabwe	Introgressed lines	0.94
40	RARS_19	RARS-Zimbabwe	Introgressed lines	0.96
41	RARS_20	RARS-Zimbabwe	Introgressed lines	0.98

Appendix B**Description of maize inbred lines used in the study**

Entry	Code	Breeding Environment	Germplasm background	Homozygosity
42	RARS_21	RARS-Zimbabwe	Introgressed lines	0.93
43	RARS_22	RARS-Zimbabwe	Introgressed lines	0.89
44	RARS_23	RARS-Zimbabwe	Introgressed lines	1.00
45	RARS_24	RARS-Zimbabwe	Introgressed lines	1.00
46	RARS_25	RARS-Zimbabwe	Introgressed lines	1.00
47	RARS_26	RARS-Zimbabwe	Introgressed lines	0.99
48	RARS_27	RARS-Zimbabwe	Introgressed lines	1.00
49	RARS_28	RARS-Zimbabwe	Introgressed lines	0.99
50	RARS_29	RARS-Zimbabwe	Introgressed lines	1.00
51	DLMF7_3	URS-South Africa	Introgressed lines	0.99
52	DLMF7_7	URS-South Africa	Introgressed lines	1.00
53	DLMF7_14	URS-South Africa	Introgressed lines	0.59
54	DLMF7_17	URS-South Africa	Introgressed lines	0.95
55	DLMF7_20	URS-South Africa	Introgressed lines	1.00
56	DLMF7_28	URS-South Africa	Introgressed lines	0.99
57	DLMF7_30	URS-South Africa	Introgressed lines	0.98
58	DLMF7_33	URS-South Africa	Introgressed lines	0.96
59	DLMF7_38	URS-South Africa	Introgressed lines	0.98
60	DLMF7_41	URS-South Africa	Introgressed lines	0.95
61	DLMF7_45	URS-South Africa	Introgressed lines	0.99
62	DLMF7_49	URS-South Africa	Introgressed lines	1.00
63	DLMF7_51	URS-South Africa	Introgressed lines	1.00
64	DLMF7_53	URS-South Africa	Introgressed lines	1.00
65	DLMF7_54	URS-South Africa	Introgressed lines	0.68
66	DLMF7_59	URS-South Africa	Introgressed lines	0.99
67	DLMF7_65	URS-South Africa	Introgressed lines	0.99
68	DLMF7_72	URS-South Africa	Introgressed lines	0.99
69	DLMF7_79	URS-South Africa	Introgressed lines	1.00
70	DLMF7_84	URS-South Africa	Introgressed lines	1.00
71	DLMF7_88	URS-South Africa	Introgressed lines	0.81
72	DLMF7_90	URS-South Africa	Introgressed lines	0.99
73	DLMF7_93	URS-South Africa	Introgressed lines	0.62
74	DLMF7_96	URS-South Africa	Introgressed lines	0.99
75	DLMF7_112	URS-South Africa	Introgressed lines	0.95
76	DLMF7_124	URS-South Africa	Introgressed lines	0.99
77	TE36	URS-South Africa	Temperate	1.00
78	TE101	URS-South Africa	Temperate	0.98
79	TE102	URS-South Africa	Temperate	0.99
80	TE115	URS-South Africa	Temperate	0.96
81	TE92	URS-South Africa	Temperate	1.00
82	TE33	URS-South Africa	Temperate	0.99

Appendix C

Description of maize inbred lines used in the study

Entry	Code	Breeding Environment	Germplasm background	Homozygosity
83	DTAB_93	URS-South Africa	Temperate	1.00
84	DTAB_49	URS-South Africa	Temperate	0.99
85	DTAB_28	URS-South Africa	Temperate	1.00
86	DTAB_15	URS-South Africa	Temperate	0.99
87	DTAB_104	URS-South Africa	Temperate	1.00
88	DTAB_103	URS-South Africa	Temperate	1.00
89	DTAB_19	URS-South Africa	Temperate	0.96
90	DTAB_1	URS-South Africa	Temperate	0.98
91	DTAB_30	URS-South Africa	Temperate	1.00
92	DTAB_105	URS-South Africa	Temperate	0.99
93	DTAB_45	URS-South Africa	Temperate	0.98
94	DTAB_59	URS-South Africa	Temperate	0.94
95	DTAB_69	URS-South Africa	Temperate	0.98
96	DTAB_39	URS-South Africa	Temperate	1.00
97	DTAB_111	URS-South Africa	Temperate	0.99
98	DTAB_22	URS-South Africa	Temperate	0.94
99	DTAB_41	URS-South Africa	Temperate	0.99
100	DTAB_118	URS-South Africa	Temperate	1.00
101	DTAB_114	URS-South Africa	Temperate	0.96
102	08CED6_7_B	URS-South Africa	Temperate donor parent line	0.95
103	SC01	RARS-Zimbabwe	Tropical	1.00
104	SC02	RARS-Zimbabwe	Tropical	0.72
105	SC03	RARS-Zimbabwe	Tropical	1.00
106	SC04	RARS-Zimbabwe	Tropical	0.98
107	SC05	RARS-Zimbabwe	Tropical	1.00
108	SC06	RARS-Zimbabwe	Tropical	1.00
109	SC07	URS-South Africa	Tropical	1.00
110	SC08	URS-South Africa	Tropical	1.00
111	SC09	RARS-Zimbabwe	Tropical	0.95
112	SC10	RARS-Zimbabwe	Tropical	1.00
113	SC11	RARS-Zimbabwe	Tropical	0.99
114	SC12	RARS-Zimbabwe	Tropical	1.00
115	SC13	RARS-Zimbabwe	Tropical	0.99
116	SC14	RARS-Zimbabwe	Tropical	0.64
117	SC15	RARS-Zimbabwe	Tropical	1.00
118	SC16	RARS-Zimbabwe	Tropical	0.99
119	SC17	RARS-Zimbabwe	Tropical	1.00
120	SC18	RARS-Zimbabwe	Tropical	1.00
121	SC19	RARS-Zimbabwe	Tropical check inbred line	1.00
122	SC20	RARS-Zimbabwe	Tropical check inbred line	0.96
123	SC21	RARS-Zimbabwe	Tropical check inbred line	0.95

Note. Introgressed-tropical maize inbred lines introgressed with genes from temperate germplasm, temperate, temperate germplasm background, and tropical-tropical germplasm lines recipient parents. Homozygosity of the lines obtained using SNP markers.

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