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Variability of grain-filling traits in early maturing CIMMYT tropical maize inbred lines

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ABSTRACT

Grain-filling rate (GFR), effective grain-filling duration (EGFD) and total grain-filling duration (TGFD) are important physiological traits of maize (*Zea mays* L.) grain yield (GY) formation. To devise effective breeding strategies, the genetic nature of these traits is a pre-requisite for improvement in early maturing maize. A study was conducted at CIMMYT-Zimbabwe using an α-lattice design with two replications in two environments to investigate the genetic variability of grain-filling traits in eighteen early maturing tropical maize inbred lines derived from CIMMYT germplasm. Highly significant differences were observed for GY, 1000 grain weight (TGW), GFR, EGFD,TGFD, kernels per rows (KR) and rows per cob (RC). The broad sense coefficient of genetic determination (the fixed parent equivalent of broad sense heritability) was above 70% for all of the traits. The highest GY was obtained from the inbred line T032-30 (79.2 g plant^{-1}) and the lowest from inbred line CML506 (37.6 g plant^{-1}), respectively. Therefore, selecting for higher GFR and longer TGFD, especially the EGFD, can increase GY of early maize without extending days to physiological maturity.

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Abbreviations: GY, grain yield; GFR, grain-filling rate; EGFD, effective grain-filling duration; TGFD, total grain-filling duration; DPM, days to physiological maturity; TGW, 1000 grain weight, KR, kernels per row; RC, rows per cob.

Maize is the main and preferred staple food with consumption averaging 42 kg capita^{-1} year^{-1} and exceeding 100 kg capita^{-1} year^{-1} in sub-Saharan Africa (SSA)(Ninno et al., 2007; Chauvin et al., 2012). It is grown in major agro-ecological zones in southern Africa covering over 12 million hectares for more than 200 million inhabitants (FAOSTAT, 2003). However, maize yields in this region still remain low, averaging 1.4 t ha^{-1} compared to yields in developed countries (FAOSTAT, 2010). The crop is produced either as a late or early maturing crop depending on the agro-ecological conditions. Early maturing maize varieties provide early harvests after a long dry season and thus are an ideal crop for food security (Langyintuo and Setimela, 2007). Not only does it provide food early in the season, but it also escapes late season drought, making it suitable for early or late planting depending on the onset of rains. The term 'early maturing maize' is used relatively to refer to maize varieties that take up to 65 days to 50% anthesis and 130 days to reach physiological maturity (Magorokosho et al., 2009).

Early maturing maize is characterised by shorter plant height, less number of leaves, early maturing and a shorter total grain-filling duration (TGFD) and low grain yield (GY) in comparison to late maturing ones. The maturity period is influenced by heat units or growing degree days which have been adopted universally to classify maturity groups in maize and other crops (Dwyer et al., 1999). However, yield differences in maize varieties that take the same number of days to physiological maturity have been reported by several researchers (Magorokosho et al., 2009;

Pswarayi and Vivek, 2008). This raises the possibilityof improving yield capacity of early maturing maize varieties to meet the increasing demand for maize.

Maize improvement has resulted in gains as much as 144 kg ha^{-1} year^{-1} in tropical maize under drought when stress was imposed at flowering (Edmeades et al., 1999). In temperate germplasm, the progress has been estimated at 73 kg ha^{-1} year^{-1}for mild stress (Duvick, 1977). Selection in maize has led to increases in yield; the net effect of this has been the reduction of genetic variability among germplasm (Lee and Tollenaar, 2007), which compounds the amount of genetic gains that can be achieved through breeding (Halluaer and Mirander, 1988). Grain yield in maize is a function of grain number, size and weight (Luque et al., 2006). Grain number is determined by plant growth rate during silking and ear attributes such as the number of kernel rows and kernels per row (Andrade et al., 1999). Kernel weight is a heritable trait that is dependent on dry matter accumulation (Borras et al., 2009) and there is a positive genetic relationship between kernel growth rate (grain-filling rate) and grain-filling duration (Talbert et al., 2001; Borras et al., 2009). Grain-filling duration starts after fertilisation and continues until physiological maturity (Lee and Tollenaar, 2007). Genotypic variability in the length of the TGFD has been reported in maize (Wang et al., 1999; Gambin et al., 2007; Borras et al., 2009). Therefore, increasing the TGFD in early maize without extending the days to maturity can help to increase yield due to the long period available for the accumulation of photo-assimilates. However, this requires screening of the tropical maize inbred lines for the variability in TGFD before evaluating the heritability of this trait.

Grain yield in cereals depends of the total amount of dry-matter accumulation in the grains during the grain-filling period. However, grain-filling occurs in three stages: lag phase (rapid cell division and differentiation), linear phase (rapid dry matter accumulation) and final phase (maturation drying). Over 90% of the total dry matter in the grain is accumulated during the linear phase (Lee and Tollenaar, 2007). The length of the linear grain-filling phase is therefore considered the effective grain-filling duration (EGFD), while the rate of dry matter accumulation during this linear phase is called the grain-filling rate (GFR). The EGFD is more important because over 90% of the dry matter is accumulated during this period. Grain-filling rate (GFR) is measured during the EGFD, starting about two weeks post-fertilisation and is highly heritable in maize (Wang et al., 1999) and other cereals such as wheat (Mashiringwani et al., 1994).

Understanding the physiological mechanisms that determine crop growth and increased yield is a pre-requisite for plant breeders to develop screening tools to improve genotypic selection in target environments (Andrade et al., 2005). One of the physiological traits,GFR, is known to be influenced by the accumulation of photo-assimilates (source factors) and their partitioning (sink factors) and the interactions between the source and sink factors (Lee and Tollenaar, 2007). These sink and source attributes have been used as indirect selection for improving yields of various crops (Lee and Tollenaar, 2007). Indirect selection using traits with high heritability and correlation with a complex trait such as GY is more effective. In maize, genetic variability for grain-filling traits have not been fully exploited to improve productivity, particularly GFR, EGFD and TGFD.

Maize inbred lines represent a fundamental resource for studies in genetics and breeding and are used extensively in hybrid maize production (Anderson and Brown, 1952). Knowledge of genetic diversity in maize germplasm helps to ensure that a broad genetic base of breeding materials is maintained, not just for sustaining genetic improvement but also for reducing genetic vulnerability to various stresses.

They can help maize breeders in efficiently assigning lines to heterotic groups and guide them in the choice of parents for the development of new hybrids. Both conventional and molecular breeding approaches depend on genetic variability for the trait of interest. The aim of this study was to determine the genetic variability of grain-filling traits in early maturing tropical maize inbred lines.

MATERIALS AND METHODS

Plant materials

Eighteen elite maize inbred lines from CIMMYT Zimbabwe tropical breeding program were selected based on earliness, drought and disease tolerance, and overall adaptation to Zimbabwe.

Trial management and experimental design

The trials were conducted at CIMMYT-Zimbabwe station located at an altitude of 1,500 m above sea level and longitude and latitude of 31^{o}E and 17^{o}43' S, respectively. The mean annual rainfall exceeds 700 mm, mostly occurring during a single growing season that ranges from early November to mid-April each year. The field experiments received 350 kg ha^{-1} of basal fertiliser, compound D with NPK ratio of 7:14:7 and a top-dressing of 300 kg ha^{-1} ammonium nitrate with 37.5% N. Eighteen maize inbred lines were evaluated using an α-lattice design with two replications. A plot consisted of three rows, 4 m long, spaced 75 cm apart with 25 cm spacing between plants within the row in all trials. Two experiments were conducted: one under irrigation, with the other under rain-fed conditions. Day was used as a unit of time, instead of thermal unit, because the temperature was very moderate throughout the growing season, with little variation during the grain-filling period of the two experiments (27-28^{o}C for day and 19-20^{o}C for night).

Data collection

To assess various grain-filling parameters, destructive sampling was performed weekly by the removal of developing maize cobs, starting two weeks after pollination. In each plot, plants from which developing cobs were removed were left standing to maintain the initial plant density. From each sampled cob, 10 g of grain (fresh weight) was obtained from the middle part of the cob to reduce variation that might result from sampling different parts of the same cob. Dry weights were measured after drying the grains in a forced-air oven at 80^{o}C for 96 h. The same procedure was repeated weekly until the crop reached physiological maturity, as indicated by the formation of a black layer at the point where the kernel is attached to the cob. At physiological maturity there was no further increment in grain weight.

Statistical Analyses

A log-linear equation $Y= b \ln (x) + a$, was fitted on the data, where ‘Y’ is the percentage of dry matter at sampling time x, ‘b’ is the slope of the curve (rate of percentage dry matter increase on a log scale) and ‘x’ is the sampling point in time (weekly basis) and ‘a’ is the constant. The start of the linear phase is when the maize kernels reach 87% moisture content (13% dry matter content) and the end is when the kernels reach 36% moisture content (64% dry matter content) (Borras et al., 2009). This equation was fitted to the weekly dry matter content data per plot to predict the start of the linear phase. The period prior to the linear phase was designated the lag phase duration. The period from the start of the linear phase until physiological maturity was considered the effective grain-filling duration (EGFD). Days to physiological maturity (DPM) were recorded as the days from sowing until the kernels developed a black layer at the point of their attachment to the cob. The grain-filling rate (GFR) (g day^{-1}) was calculated as the final GY per plant divided by the EGFD. The total grain-filling duration (TGFD) was calculated by subtracting the days to silking from the days to physiological maturity (DPM). Data were also recorded on number of kernels per row (KR), number of rows per cob (RC), and GY. The GY per plant was obtained by dividing the total grain weight per plot by the number of harvested cobs per plot.

Analysis of variance was conducted using Genstat software version 14 (Genstat, 2010) using the following mixed model as described by Dabholker(1999): $P_{ijk} = \mu + g_i + t_j + (gt)_{ij} + e_{ijk}$ where μ is the population mean, g_i is the effect of the inbred line *i*, t_j is the effect of the environment *j*, $(gt)_{ij}$ is the inbred line x environment interaction effect associated with inbred line*i* and environment *j*, and e_{ijk} is the within environment error associated with inbred line *i*, environment *j* and the replicate *k*. A t-test was used to compare the mean performance for GY, TGW, GFR, EGFD, TGFD, KR and RC between the top nine and the worst nine inbred line performers.

The phenotypic correlations among GY, TGW, GFR, EGFD, TGFD, KR and RC were computed as described by Singh and Chaudhary (2004) as $r_p= [Cov_P/(\delta_{P(X)}\delta_{P(Y)})]$, where r_p is the phenotypic correlation between X and Y, Cov_P is the phenotypic covariance between X and Y, $\delta_{P(X)}$ is the phenotypic standard deviation of X and $\delta_{P(Y)}$ is the phenotypic standard deviation of Y. The genotypic correlations among traits were computed as $r_A = [Cov_A)/ (\delta_{A(X)}\delta_{A(Y)})]$, where r_A is the genetic correlation between X and Y, Cov_A is the genetic covariance between X and Y, $\delta_{A(X)}$ is the genetic standard deviation of X and $\delta_{A(Y)}$ is the genetic standard deviation of Y. The genetic variances and covariances were obtained by subtracting the error variances and covariances from their respective phenotypic variances and covariances based on the 18 genotype means. Genotypic path analyses of TGW, GFR, EGFD, TGFD, KR and RC on GY were calculated as described by Singh and Chaudhary (2004). The assumption made for path analysis is that there are unidirectional causal relationships among the yield determining traits in early maize inbred lines.

RESULTS

There were significant differences among the maize inbred lines at $P<0.001$for GY, TGW, GFR, EGFD, TGFD, KR and RC (Table 2). The broad sense coefficient of genetic determination (the fixed parent equivalent of broad sense heritability) was above 70% for all of the traits. The inbred line by environment interaction was significant at ($P<0.05$) for GY and GFR.

The highest GY was obtained from the inbred line T032-30 (79.2g plant^{-1}) and the lowest from inbred line CML506 (37.6g plant^{-1}), respectively (Table 3). The highest GFR (above 2.7 g day^{-1}) was observed in the inbred lines V547-178 and T032-30 while the longest EGFD (above 30 days) was found in the inbred lines VL057967, CML507 and VL08526. There was no significant difference in days to physiological maturity among the inbred lines. There were significant differences ($P<0.05$) between the mean of the high yielding inbred lines group and the lower yielding ones for GY, GFR, TGFD and TGW (Table 3). The group mean yield of the high yielding inbred lines exceeded the mean yield of the low yielding inbred lines by 42.7% (3.4tha^{-1} vs. 2.4tha^{-1}). Furthermore, the high yielding group had 23.6% higher

GFR (2.25g day^{-1}vs. 1.82g day^{-1}), 7.3% longer TGFD (57.56 days vs. 53.64 days), 10.7% longer EGFD (non-significant) and 24.1% more TGW (202.45g vs. 163.10g).

Grain yield was significantly ($P<0.05$) positively correlated with TGW ($r=0.67$), GFR ($r=0.61$), EGFD ($r=0.47$) and TGFD ($r=0.52$) (Table 4), but less so to KR and RC.The TGW was positively correlated with EGFD ($r=0.53$) and TGFD ($r=0.52$) while GFR was positively correlated with RC ($r=0.59$) and KR ($r=0.79$)(Table 4). However, GFR and EGFD were negatively correlated ($r= -0.40$) (Table 4).

The direct effects of GFR (0.93) and TGFD (0.80) on GY were positive and large (Table 5), accounting for their respective positive correlation between GY (Table 4). However, direct effects of TGW and KR were negligible and negative. The EGFD had a negative direct effect (-0.12) on GY (Table 5) but a positive correlation with GY (Table 4). However, TGFD had an indirect effect (0.35) on yield via EGFD.The indirect effects of KR (0.73) and RC (0.54) on GY via GFR were positive and large.

Discussion

Variability of grain yield, grain-filling traits and other related traits

Improvement of GY depends on genetic variability for yield and its components. There were significant differences for GY, TGW, RC, KR, GFR, EGFD and TGFD among the early maize inbred lines (Table 2), which indicated the variability that breeders can exploit to improve GY of early maize. The utility of this variability is evident in the best inbred lines (T032-30, VL08526, VL055063) which had a combination of high GFR, longer EGFD and TGFD in addition to high TGW and high kernel number (RC*KR). In line with this observation, inbred lines with the lowest yield (CML506 and CML197) either had low GFR, short EGFD or a combination of these two. In this study, it is evident that the difference between the high yielding and low yielding inbred lines is attributable to the differences in the grain-filling traits (Table 2). The high broad sense coefficient of genetic determination values of these grain-filling traits suggests the repeatability of these measurements in different environments. In line with this observation, Wang et al. (1999) reported significant general and specific combining ability for grain-filling traits in temperate maize, thus raising possibilities of developing superior hybrids that combine long EGFD and high GFR that translates into developing hybrids with high GY potential. In the past, the focus on maize improvement targeted TGW and kernel number (KR*RC) as indirect selection traits for improving GY (Derera et al., 2009; Banziger et al., 2004; Hallauer and Miranda, 1988). However, future genetic improvements of the yield of early maize must incorporate GFR, EGFD and TGFD as new potential traits. Although the genotype-by-environment interaction (GEI) was significant for GY and GFR, it was not present for EGFD and TGFD. The absence of GEI for EGFD and TGFD shows that these grain-filling traits could be used to predict maize GY with greater accuracy irrespective of the testing environment used.

Relationships of grain yield, grain-filling traits and other traits

The results showed a strong positive correlation of GY with the grain-filling traits that include GFR, EGFD and TGFD. This positive correlation observed between GY and grain-filling traits (GFR, EGFD and TGFD) shows the influence of these traits on GY formation in maize. High GFR and longer EGFD and TGFD results in the accumulation of more photo-assimilates in the grains during grain-filling (Lee and Tollenaar, 2007). High rate of grain-filling also influences seed size and seed number, the two major components of GY. Longer grain-filling durations imply more dry matter accumulation and hence high kernel weight that translates into high yield (Gasura et al., 2013). Furthermore, increased availability of current photo-assimilates reduces embryo abortion and results in high kernel numbers per cob. Kernel number, size and weight are traits that largely contribute to yield (Luque et al., 2006; Andrade et al., 2005). Therefore, this explains the large positive correlations observed for these traits and GY suggesting their importance in GY improvement. Previous studies also showed positive correlation of GFR and yield in maize (Wang et al., 1999) and wheat (Mashiringwani et al., 1994). Kernel weight is determined by rate (GFR) and duration (TGFD especially the EGFD) of dry matter accumulation (Andrade et al., 2005). This explains the positive correlation that exists between TGW and EGFD and/or TGFD. The length of the grain-filling period (EGFD or TGFD) is critical in yield formation since there is no remobilisation of assimilates from the stem reserves in maize (Lee and Tollenaar, 2007), unlike in rice (Yang et al., 2003), wheat (Yang et al., 2000) and sorghum (Blum et al., 1997).The negative relationship between GFR and EGFD observed in this study was not absolute as evidenced by some exceptional inbred lines that were above the regression line. This suggests the possibility of having hybrids that can combine both high GFR and longer EGFD, which may translate into high yield.

Direct and indirect effects of grain-filling traits and other traits on grain yield

The GFR and EGFD had positive direct effects on GY that were larger than the correlations between GY and these traits, suggesting that GFR and EGFD have a true effect on GY. Singh and Chaudhary (2004) reported that if the direct effects are larger than the correlations, then the indirect selection method would be the best. To this regard, GFR and EGFD become excellent traits to use in supplementing other traits used to select for high GY. Large and positive direct effects of GFR and EGFD on GY were also reported by Wang et al. (1999) in temperate maize germplasm. Path analyses showed EGFD to have a large and indirect effect via TGFD while TGFD had large indirect effect on yield via TGW. In this case, TGFD can be considered in the selection for GY. The large indirect effects of KR and RC on GY via GFR show that increasing KR and RC increase GFR, and in this case GFR becomes a critical trait to select when improving GY.

In the past, maize breeders selected lines that had high kernel number (KR and RC), harvest index and TGW as major yield components (Luque et al., 2006), as well as improved resource capture and stress tolerance (Tollenaar and Wu, 1999; Duvick and Cassman, 1999). However, it is important to consider other traits for the improvement of GY. The grain-filling traits identified in this study can be used to complement other traits for selection to improve GY. A better selection index can be developed if GFR and EGFD are included in the equation rather than based on TGW, KR and RC alone. The advantage of the grain-filling traits is that they still have variability that be exploited compared to other traits commonly used in breeding. Furthermore, the absence of GEI on EGFD and TGFD makes them more accurate in predicting GY across varied environments. Lee and Tollenaar(2007) noted that not all variability is useful in GY. They emphasised that there will be less variability from the harvest index and other source and sink factors. However, grain-filling traits are a product of the various sources and sink factors and thus present much variability that can be exploited in pushing up the yield of early maturity maize. Improving the yield of early maize can be achieved by selecting for a combination of high GFR and long EGFD.

The breeding progress relies on genetic variability for the traits of interest, high selection intensity, high heritability of the traits of interest and their strong genetic correlation with yield. Furthermore, there must be a genetic correlation between yield in the selection environment and the target population of environments (Falconer, 1989). This demonstrates the possible utility of GFR and EGFD duration in improving yield. These traits not only showed genetic variability, but also a strong genetic correlation with yield. Furthermore, they showed high broad sense heritability coupled with some reports that showed that these traits are largely controlled by additive gene action (Wang et al., 1999), suggesting that these traits might have high narrow sense heritability values. The absence of GEI on EGFD and TGFD selection of yield based on these traits is desirable since it is not influenced by the selection environment.

Conclusions

This study revealed genetic variability of GFR, EGFD and TGFD and their associations with GY in tropical early maize inbred lines. These traits could be used as additional traits in the improvement of maize GY in early maize without extending the DPM by selecting for a combination of high GFR and long EGFD. In this study, inbred lines with high GFR (V547-178 and T032-30) and long EGFD (VL057967, CML 507 andVL08526) were identified and can be used in future genetic studies.

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Table 1.Names and pedigrees of the CIMMYT maize inbred lines used in this study

Inbred line name	Inbred line pedigree
T032-30	ZEWAc2F2-183-2-B-B-B
VL08526	ZEWBc2F2-101-2-B
VL055063	[Ent320:92SEW2-77/[DMRESR-W]EarlySel-#I-2-4-B/CML386]-B-11-3-B-2-#-B*4
VL057967	ZEWAc1F2-219-4-3-B-1-B*4-2-4
C389-92	ZM523B-29-2-1-1-B*6
VL05615	ZEWBc1F2-216-2-2-B-2-B*4-2-4
VL057903	ZEWAc1F2-151-6-1-B-1-BBB-2-6
VL0536	[CML389/CML176]-B-29-2-2-B*5
VL08528	ZEWBc2F2-110-1-B
CML507	[[[K64R/G16SR]-39-1/[K64R/G16SR]-20-2]-5-1-2-B*4/CML390]-B-38-1-B-7-#-B*6
V547-178	03SADVEA-#-28-1-2-1-1-B
VL057847	ZEWAc1F2-300-2-2-B-1-B*4-3-4
VL0536	[CML389/CML176]-B-29-2-2-B*5
VL05128	WWO1408-1-1-2-B*4-#-B
CML508	[89[G27/TEWTSRPool]#-278-2-X-B/[COMPE2/P43SR//COMPE2]F#-20-1-1]-B-32-2-B-4-#-2-B*5
VL058014	ZEWAc1F2-254-2-1-B-1-BBB
CML197	Ent52:92SEW1-2/[DMRESR-W]EarlySel-#L-2-1-B/CML386]-B-22-1-B-4-#-1-B*5-B-B
CML506	[EarlyMid1/KatumaniSR]-#-169-2-4-B-1-#-BBB

Table 2. Summary ANOVA, variance components and broad sense heritability values

Source	DF	Grain Yield (g plant^{-1})	[a]1000 kernel weight (g)	Grain filling rate (g day^{-1})	Effective grain filling duration (days)	Total grain filling duration (days)	Rows per cob	Kernels per row
Environments	1	2493.31*		1.97*	28.48	1.13	2.70	45.71
Environments.Replications	2	28.66	52.10	0.04	15.92	3.74	0.50	12.81
Genotypes	17	578.13***	2098.10***	0.79***	80.38***	71.27***	9.80***	42.06***
Genotype*Environment	17	72.66*		0.24*	12.50	3.42	0.94	6.54
Error	34	37.15	150.80	0.11	11.52	4.38	0.73	8.38
Total	71							
Error variance component		37.15	150.80	0.11	11.52	4.38	0.73	8.38
GxE variance component		16.26		0.07	0.49	-0.48	0.11	-0.92
Genotype variance component		127.12	973.65	0.14	16.97	16.96	2.22	8.88
Broad sense heritability								
Single plot basis		0.70	0.87	0.44	0.59	0.81	0.73	0.54
Across envrionments basis		0.88		0.70	0.84	0.95	0.90	0.84

*** significant at 0.1% probability level, * significant at 5% probability level. [a] traits recorded in one environment.

Table 3. Grain yield and related traits performance of the top nine and bottom nine yielding maize inbred lines

Inbred line name	Grain yield (g plant^{-1})	1000 kernel weight (g)	Grain filling rate (g day^{-1})	Effective grain filling duration (days)	Total grain filling duration (days)	^{a}Days to physiological maturity (days)	Rows per cob	Kernels per row
Top nine (9)								
T032-30	79.22	224.98	2.76	28.64	57.50	122.00	12.83	23.08
VL08526	76.46	210.47	2.38	32.38	60.75	127.00	13.50	24.83
VL055063	67.74	169.09	2.42	28.52	54.25	127.00	14.33	25.92
VL057967	64.85	211.79	1.94	33.65	59.75	128.00	10.90	22.83
V553/1	59.69	181.17	2.45	24.51	53.50	125.00	16.67	23.17
VL05615	58.31	158.47	2.27	25.92	58.25	128.00	15.83	22.25
VL057903	57.83	240.14	2.02	29.92	62.75	127.00	13.08	16.76
CML509	54.26	245.08	1.95	27.97	55.00	127.00	11.50	18.17
VL08528	54.21	180.83	2.08	26.70	56.25	127.00	12.17	23.75
Mean	63.62	202.45	2.25	28.69	57.56	126.44	13.42	22.31
Standard deviation	9.22	31.35	0.28	2.95	3.12	1.88	1.91	2.98
Bottom nine (9)								
CML507	52.05	190.75	1.60	32.51	57.00	131.00	11.00	17.00
V547-178	48.49	147.37	2.90	17.16	55.00	120.00	12.67	26.33
VL057847	47.97	184.07	1.52	31.62	57.00	129.00	12.00	23.75
VL0536	44.38	138.65	1.64	27.21	49.25	130.00	13.33	22.58
VL05128	43.75	169.82	2.09	21.23	44.50	127.00	12.83	24.58
CML508	43.16	167.68	1.40	31.11	54.50	127.00	12.50	17.75
VL058014	42.89	168.07	1.67	25.72	54.25	122.00	10.83	16.25
CML197	41.12	143.24	2.18	20.10	58.75	127.00	13.17	22.08
CML506	37.58	158.22	1.40	26.68	52.50	127.00	12.00	20.25
Mean	44.60	163.10	1.82	25.93	53.64	126.67	12.26	21.18
Standard deviation	4.32	17.88	0.49	5.45	4.41	3.57	0.89	3.57
Difference	19.02	39.35	0.43	2.76	3.92	-0.22	1.16	1.13
% Difference	42.65	24.13	23.63	10.66	7.30	-0.18	9.50	5.34
Standard error of difference	3.39	12.03	0.19	2.07	1.80	1.34	0.70	1.55
t-value	5.60	3.27	2.30	1.34	2.17	-0.17	1.66	0.73
t-probability	0.000	0.005	0.035	0.200	0.045	0.871	0.117	0.476
Minimum value	9.22	31.35	0.28	2.95	3.12	120.00	1.91	2.98
Mean	54.11	182.80	2.04	27.31	55.60	126.56	12.84	21.74
Maximum value	79.22	245.08	2.90	33.65	62.75	131.00	16.67	26.33
P-value (for 18 inbred lines)	<.001	<.001	<.001	<.001	<.001		<.001	<.001
5% least significant difference	12.28	25.37	0.65	6.97	4.23		1.72	5.96
Coefficient of variation (%)	11.30	6.70	16.00	12.40	3.80		6.60	3.90

[a] traits recorded in one replication of one environment.

Table 4. Genotypic (lower diagonal) and phenotypic (upper diagonal) correlation coefficients of grain yield and yield determining traits

	Grain Yield (g plant^{-1})	1000 kernel weight (grams)	Grain filling rate (g day^{-1})	Effective grain filling duration (days)	Total grain filling duration (days)	Rows per cob	Kernels per row
Grain yield (g plant $^{-1}$)	1.00	0.60	0.61	0.42	0.49	0.28	0.34
1000 kernel weight (grams)	0.67	1.00	0.11	0.55	0.49	-0.23	-0.29
Grain filling rate (g day $^{-1}$)	0.61	0.15	1.00	-0.44	0.18	0.49	0.61
Effective grain filling duration (days)	0.47	0.53	-0.40	1.00	0.43	-0.28	-0.32
Total grain filling duration (days)	0.52	0.52	0.21	0.45	1.00	-0.04	-0.18
Rows per cob	0.30	-0.21	0.59	-0.34	-0.07	1.00	0.41

Genotypic and phenotypic correlations were calculated based on genotype means across locations. The r critical values at 10%, 5% and 1% levels are 0.39, 0.46 and 0.58, respectively.

Table 5. Direct and indirect effects of grain-filling and related traits on grain yield

	weight (grams)	(g day^{-1})	duration (days)	duration (days)	cob	row
1000 kernel weight (grams)	-0.02	0.00	-0.01	-0.01	0.01	0.01
Grain filling rate (g day^{-1})	0.14	0.93	-0.37	0.20	0.54	0.73
Effective grain filling duration (days)	-0.06	0.05	-0.12	-0.05	0.04	0.05
Total grain filling duration (days)	0.41	0.17	0.35	0.80	-0.06	-0.16
Rows per cob	-0.02	0.06	-0.03	-0.01	0.10	0.04
Kernels per row	0.03	-0.06	0.04	0.02	-0.03	-0.08