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Analysis of the Relationship between the Key Parameters of Grain Yield in Two Maize (*Zea mays L.*) Genotypes

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Abstract

We studied the relationship between key components of maize grain yield using two maize populations derived from two strains (BLC and JNE genotypes) with contrasting values of yield components. The BLC genotype has higher grain filling rate and heavier kernels while the JNE genotype has longer effective filling period and larger number of kernels per ear. In both populations, we observed a highly significant relationship between grain filling rate and kernel weight ($r \geq 0.90$, $p<0.001$). Kernel weight was also correlated with effective filling period, but at a lower magnitude ($r=0.29$ for JNE genotype, and 0.30 for BLC genotype, $p<0.05$). These observations clearly showed that selecting for higher grain filling rate had a strong additive genetic effect on kernel weight. However, final grain yield per plant was much more influenced by number of kernels than kernel weight at a planting density of 42000 plants ha^{-1}. A principal component analysis reveals that larger number of kernels and longer effective filling period are characteristics of the JNE genotype that had higher grain yield. Higher grain filling rate and heavier kernels were attributes of the BLC genotype that had comparatively lower grain yield.

Keywords: Key components; Genotype; Maize; Grain yield; Principal components analysis

Introduction

Maize (*Zea mays L.*) is an important crop species used for human consumption, animal feed, and as raw material in various industrial transformations (i.e., corn syrup, sweetener, fuel,) and its importance in human lives justifies the enormous resources allocated worldwide to research in maize improvement, especially maize grain yield. Maize grain yield is roughly defined as the product of kernel weight and the number of kernels per unit area. The maize kernel weight is determined by the rate of dry matter accumulation in the developing kernel and the duration of dry matter accumulation. The duration of dry matter accumulation divides into three phases: The lag phase, the phase of linear growth, and the phase of grain dry-down. These three phases describe a logistic curve [1]. The lag phase starts with the double fertilization of the egg and central cell by two male gametes from the pollen grain to respectively form the diploid embryo and the triploid endosperm [2,3]. Both the embryo and the endosperm develop concomitantly within the maternal tissues of the ovule but with different genome combinations and separate pathways [4,5]. In maize, the endosperm constitutes the majority of the mature kernel [6], and in general cereal seed size positively correlates with endosperm cell number [7,8]. Soon after fertilization, the endosperm undergoes nuclear divisions to form a coenocyte [5]. Then, cellularization and differentiation of cells follow to form the basal endosperm transfer cells, the embryo-surrounding region, the aleurone, and immature endosperm starch [9]. The formation of the basal endosperm transfer cells signals that the fertilized ovules are now the most active sink in the whole plant. The lag phase continues with active cell divisions, increased water content [10] and the determination of kernel sink capacity that is linked to the number and size of the endosperm cells [11,12]. There is little to no dry matter accumulation at the end of the lag phase. Any stress during this phase may result in kernel abortion and a significant reduction in number of kernels on the cob and in final grain yield.

The lag phase is followed by the phase of linear grain filling. The grains take an appearance of blister, and the start of the linear grain growth is called the blistering stage. During the phase of linear grain growth, both grain wet and dry weight rapidly increases through 40 d after pollination [13]. Starch synthesis during the first three weeks of the phase of linear grain growth is diverted to the developing grain. Total starch content of the developing grain rapidly increase through 30 d after pollination. Then wet weight starts to decline while dry weight continues to increase through 50 d after pollination [13]. Several metabolic activities take place in the developing grain during the phase of linear grain filling. The most important activities with direct effect on grain yield are those linked to starch synthesis. They include the activities of soluble invertase, sucrose synthase and ADP glucose pyrophosphorylase that show maximum activities at different times during the linear phase of grain filling [14]. Synthesis of the other commercially important components of the maize grain, the class of lipids, actively occurs during the phase of linear grain growth, between 15 to 45 days after pollination [15]. The polar lipids, abundant in the early development of the maize kernel are progressively replaced by triglycerides as the grain mature. During this phase, moisture content decreases almost linearly until physiological maturity [16]. The physiological maturity marks the end of the development of the maize grain with the presence of a black layer at the base of the kernel. The grain has accumulated maximum dry matter and its moisture content is about 30%. The phase of grain dry-down comes right after the maize kernel has reached physiological maturity. It is mostly characterized by a loss of moisture and a drying of the maize kernel. It ends when the grain reaches harvest maturity.

Grain filling can be extended if the environment allows the maize plant to stay green for a longer period after silking [17]. That assertion is explained by the fact that early-maturing maize genotypes yield 15% to 30% less than the late-maturing ones. Tao adds that high yielding maize plants have longer reproductive growth period with green leaves and high leaf area index that persist longer after silking to maintain photosynthetic activities and accumulate more dry matter in the developing kernel. And, compared to older maize hybrids, the newer ones consistently have higher kernel weights that are related to higher leaf nitrogen at silking and a persistence of functional green leaves during grain filling [18]. Increased photosynthetic activities for a longer period after silking results in higher maize kernel weight and an increased grain yield. However, the contribution of maize kernel weight to the increase in grain yield is only a portion of the effort to improve maize grain yield. A greater determinant of maize grain yield is kernel number per plant [19,20]. And the observed increase in maize grain yield in the last fifty years in the US and Canada is attributed to an increased number of kernels per unit area. Prolificity and higher plant density associated with tolerance to crowding stress account in large part to that increase in grain yield. Improved plant growth rate in the period around silking, delayed leaf senescence and increased radiation use efficiency during the grain filling period are favorable attributes that resulted in a larger number of kernels per ear, an increased dry matter accumulation to the developing kernels and the improved maize grain yield in North America [21].

Improved plant growth rate in the period around silking determines the number of kernels and kernel weight is affected by photosynthetic activities during the linear grain filling phase [22]. In addition to the environmental effects on yield, genotypic differences account in large part to maize grain yield improvement. Understanding the interconnection of grain yield parameters, or secondary yield traits, should help to design effective selection procedures in order to further increase maize grain yield. Given the exponential increase in world population coupled with the increasingly reduced agricultural land, yield improvement of crops such as maize commands a considerable amount of resource and relentless research effort around the globe. In this study, we aim to elucidate the relationship between maize grain filling rate, effective duration of grain filling, final kernel weight, and kernel number per plant and how they relate to grain yield per plant of two genotypes with contrasting yield parameters.

Materials and Methods

Plant material

Two maize strains were used in this study, the BLC and JNE strains. The BLC strains had translucent kernels, wider leaves and taller plants. In addition, the BLC strains had heavier kernels. In contrast, the JNE strain had yellow kernels, comparatively narrower leaves, and a larger number of kernels per ear. None of the two strains was prolific. Seeds from the F3 and F4 plants of the two genotypes were planted during spring 2017 at the experimental station of the University Nangui Abrogoua, (5°18′ 34″ N and 4°00′ 45″ W), Abidjan, Cote d'Ivoire, in a completely randomized experiment on a sandy-clay soil. Each plot consisted of either genotype and plots were completely randomized. Fertilizers were added to the soil to adjust to recommendation and the field was thinned to 42000 plants ha^{-1}, three weeks after planting. Emerging ear shoots were covered with paper bag to prevent unwanted pollen fertilization of ovules. Randomly selected plant from each strain in a plot was pollinated with a bulk of pollen from several male inflorescences of the same strain and the procedure was repeated the following day to insure that all the ovules on the ear were pollinated.

Data collection

About 14 d after pollination, five kernels from the midsection of the ear were sequentially sampled at 5-day intervals and were oven-dried for 3 d at 70°C. At the end of the 3 day period, the set of 5 kernels was weighed to obtain the dry weight of the developing kernels for each sampling day. The method of Mostafavi and Cross (1990) was used to compute the Grain Filling Rate (GFR) and Effective Filling Period (EFP). At harvest, kernels per selected ear were weighed to determine Kernel Weight (KW). The Number of Rows of Kernel (NKR) and Number of Kernels Per Row (NKPR) were counted. We should note that the products, NKR^*NKPR and KW^*NKR^*NKPR respectively gives number of kernels and grain yield per plant. However, given their redundant nature, we removed them from the correlation analysis.

Statistical analysis

The aims of this study were to provide information on the field that helps to elucidate the relationship between key components of maize grain filling and grain yield of two maize genotypes. We conducted an analysis of variance and a comparison of means using the Least Significant Difference (LSD) criterion, at a level of significance $\alpha=0.05$. Those two procedures led to identify genotypic mean values of components that were significantly different. We also computed the coefficients of variation to understand the overall variability of a key component with respect to its mean. In addition, we computed the Pearson coefficient of correlation between the components to understand the nature of the relationship between the parameters of grain yield. We complemented the correlation analysis with a principal component analysis to evaluate the liens between the grain yield parameters and genotypes. With the principal component analysis, we constructed a biplot [23,24]. A predictive graphical model using the first two principal components that summarize most of the variability in the original data matrix. The biplot yielded a graphical display of the association between the parameters of grain yield and the genotypes.

Results and Discussion

Mean values of the components of yield

The means for the components of grain yield are reported in Table 1. In general, there were no significant differences between the parents and their offspring for all five measured components. However, genotypes significantly differed for all of the components. The BLC genotype had significantly higher rates of dry matter accumulation (7.66 mg d^{-1} and 7.84 mg d^{-1}) than the JNE genotype (6.60 mg d^{-1} and 6.41 mg d^{-1}) during the linear phase of grain filling. In addition, the BLC genotype had higher kernel weight (216.37 mg and 221.73 mg) than the JNE genotype (204.83 mg and 199.53 mg). In contrast, the JNE genotype had longer effective filling period (31.02 d and 31.10 d), larger number of rows of kernels on the cob (13.40 rows and 13.83 rows) and a larger number of kernels on each row (25.90 kernels per row and 26.50 kernels per row) The BLC genotype had effective filling periods averaging 28.17 d and 28.23 d, with 12.66 and 12.80 rows of kernels on the cob, and 21.60 and 23.16 kernels per row, respectively for parents and offspring. Kernel weight was significantly higher for the BLC genotypes compared with the JNE genotypes. Because none of these genotypes was prolific, the number of kernels per plant was given by the product of number of rows of kernels to number of kernels per row and that variable multiplied by kernel weight gave the average grain yield per plant. To eliminate any redundancy, the variables

Number of Kernels per Year and grain yield per plant were not considered in the statistical analysis.

Components	**Grain yield components**				
	GFR ($mg\ d^{-1}$)	**EFP (d)**	**KW (mg)**	**NKR (units)**	**NKPR (units)**
BLC (parent)	7.66	28.17	216.37	12.66	21.60
BLC (offspring)	7.84	28.23	221.73	12.80	23.16
JNE (parent)	6.60	31.02	204.83	13.40	25.90
JNE (offspring)	6.41	31.10	199.53	13.83	26.50
LSD (0.05)	0.44	0.24	13.71	0.80	3.30
CV (%)	12.08	1.58	12.73	11.89	26.62
F-statistic	21.37**	371.30**	4.35**	3.59*	3.82*

**Significant at the 0.01 level of probability; *Significant at the 0.05 level of probability

Table 1: Means, Least Significant Difference (LSD) for comparison of means, Coefficient of Variation (CV) and F statistics for Grain Filling Rate (GFR), Effective Grain Filling Period (EFP), average Kernel Weight at harvest (KW), Number of Rows of Kernels on the cob (NKR), and average Number of Kernels Per Row (NKPR) for two maize genotypes (BLC and JNE) and their offspring.

JNE genotype had a larger number of kernels per plant than the BLC genotype as it had significantly higher numbers of rows of kernels and numbers of kernels per row. The comparatively reduced number of kernels per ear of the BLC genotype was compensated by the weights of those kernels which were heavier than the kernels of the JNE genotypes. Based on the averages, the JNE genotype had a higher grain yield per plant than the BLC genotype [25]. They identified kernel number and kernel weight as the two key components that determine maize grain yield [26]. They found that the number of kernels on the cob of the ear was totally controlled by the female plant and the growing condition particularly during the critical period around silking. They added that maize kernel weight was determined by physiological activities during the phase of grain filling when the developing kernel was the most active sink of the whole plant [27]. In this study, kernel number played a prominent role in the increase of grain yield than kernel weight when we compared the two genotypes, BLC and JN. A strong link between maize grain yield and number of kernels per unit area was found [21,28,29]. The latter two added that most of the increase in grain yield of newer hybrids was due to an increased number of kernels per unit area instead of kernel weight because these new hybrids were tolerant to stress associated with higher planting densities. The observations in this study are in line with their findings except that the planting density in this study was 42000 plants ha^{-1} which was more comfortable for the individual plants in the populations studied. This finding leads to the conclusion that kernel number is the most important grain yield component.

Correlation analysis

In this study, we dissected kernel number per plant into number of rows of kernels and number of kernels per row to see if there is any relationship between kernel weight, rate of grain filling, effective filling period, and number of kernels based on their architectural dispositions on the cob. Because the two genotypes have contrasting component values, pooling them together will produce biased measures of coefficients of correlation. We therefore computed the Pearson coefficients of correlation between the components of grain yield for each genotype. We found a very significant coefficient of correlation ($r>/=0.90$, $p<0.001$) between the rate of grain filling and kernel weight on an individual basis for each of the two genotypes shows in Table 2. We also found a significant correlation coefficient between kernel weight and effective filling period ($r=0.30$ for BLC and $r=0.29$ for JNE, $p<0.05$). Computed partial correlation coefficients did not reveal any new significant information. Previous reports have indicated the direct links between grain filling parameters (Grain Filling Rate and Effective Filling Period) and yield [30].

Grain yield components	**GFR**	**KW**	**EFP**	**NKR**	**NKPR**
GFR	-	0.90**	0.18	0.14	0.14
KW	0.94**	-	0.29*	0.15	0.15
EFP	0.18	0.30*	-	0.12	0.09
NKR	0.00	0.03	0.29*	-	0.21
NKPR	-0.02	-0.04	-0.17	0.07	-

**Significant at the 0.01 level of probability; *Significant at the 0.05 level of probability

Table 2: Coefficients of correlation between Kernel Weight (KW), Grain Filling Rate (GFR), Effective Grain Filling Period (EFP), Number of Kernel Rows on the cob (NKR), and Number of Kernels Per Row (NKPR) for JNE genotype (upper diagonal) and BLC genotype (lower diagonal).

A study conducted by was led to the finding of a strong relationship between kernel weight and the rate of grain filling as estimated by the coefficient of correlation ($r=0.79$, $p<0.001$) between those two traits [31]. The authors also found a significant relationship between effective grain filling period and kernel weight, but at a lower magnitude ($r=0.32$, $p<0.001$). The results obtained in this study corroborate their findings and estimated values of the coefficients of correlation are very close to the ones they reported. A significant relationship ($r=0.29$, $p<0.05$) was found between number of rows of kernels and effective filling period in the BLC population, but not in the JNE population. However, the biological interpretation of the significant relationship between the number of rows of kernels and the effective filling period may be limited. The number of ovules is set during the critical period around silking and depends on the growing condition of the female plant [32]. There is a strong relationship between plant growth rate around silking and the number of kernels per plant [27]. Therefore, the potential number of kernels on the cob is predetermined before fertilization and ways before the parameters of the grain filling activity (i.e. grain filling rate and effective filling period). Hence, the observed significant relationship between number of rows of kernels and the effective filling period may be a random association between the two traits in the BLC genotype, or a particularity of the BLC genotype that adds to its differences with the JNE genotype. Based on this comparative study, plants with larger number of kernels also have longer effective filling period. We found no other significant coefficient of correlation between the other traits.

Principal component analysis

This analysis helped to elucidate the importance of the components of yield and their discriminative power on the two genotypes. The first two principal components account for 71% of the total variability in the original data and their correlations with the components of yield is given in Table 3, below. The first principal component represents a contrast between the characteristics of grain filling and number of grain on the cob of the ear. Therefore, the first principal component is a contrast between the two components of grain yield: Kernel weight and kernel number. It increases with increased kernel weight, and decreases with increased number of kernels. In the other hand, the second principal component is a weighted average of all five variables. The two most important ones are number of rows of kernels and number of kernels per row whose increases significantly increase the second principal component compared to the other three variables. The second principal component is mainly defined by the characteristics of number of kernels on the cob.

Analysis	PC1	PC2
KW	0.57	0.40
GFR	0.65	0.21
NKR	-0.20	0.55
NKPR	-0.15	0.56
EFP	-0.42	0.41
Standard Deviation	1.48	1.16
Proportion of Variance	0.44	0.27
Cumulative Proportion	0.44	0.71

Table 3: The first two principal components with 71% of total variability and importance of the components of yield.

A visualization of the first two principal components is given in Figure 1. It can be seen that the variables kernel weight and grain filling rate significantly move individuals to the right and lower-right. Most of the individuals concerned are of the BLC genotype [33-36]. In contrast, number of rows of kernels, number of kernels per row, and effective filling period move individuals to the left and upper-left, and they are mostly individuals of the JNE genotype [37-40]. In general, most of the individuals of the BLC genotypes cluster together to the right and are mostly defined by the variables kernel weight and grain filling rate, whereas most of the individuals of the JNE genotypes are on the left and are mainly influenced by the variables number of rows of kernels, number of kernels per row and effective filling period [41]. This predictive graphical model indicates that an individual plant with higher grain filling rate and heavier kernel is likely to be of the BLC genotype and an individual maize plant with larger number of kernels on the ear and longer effective filling period is more inclined to belong to the JNE genotype [42].

General Summary and Conclusion

Two maize populations derived from two genotypes (BLC and JNE) with contrasting yield parameters have been used in this study to elucidate the relationships between those parameters and how their affect final grain yield per plant. In each population, it was found that the relationship between grain filling rate and kernel weight was very strong ($r \geq 0.90$, $p \leq 0.001$) revealing the direct link between those two traits. Irrespective of the genotype, a plant with higher grain filling rate has heavier kernels. This observation leads to the conclusion that grain filling rate determines the weight of the maize kernel and provides support to earlier findings by the reporter that a reduction in grain filling rate with plant defoliation at silking resulted in a correlated reduction in kernel weight. Breeding theory indicates that correlated responses between two traits are the expression of an additive genetic correlation.

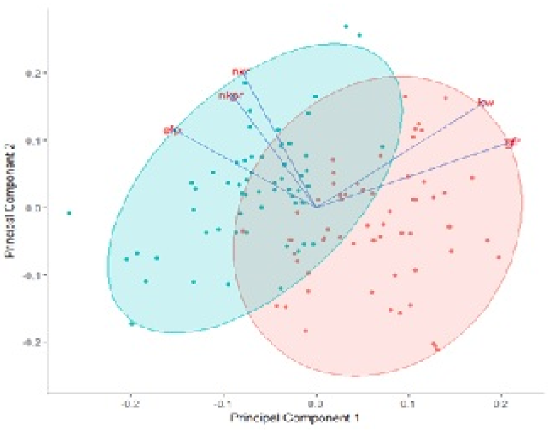

Figure 1: Visual display of the distribution of the individual plants of the two genotypes (BLC and JNE) with respect to the first two principal components.

A significant relationship ($r=0.30$ for BLC and 0.29 for JNE, $p \leq 0.05$) was also found between effective filling period and kernel weight indicating a significant contribution of that parameter to final grain weight, but not as much as the contribution of grain filling rate. In the population issued from the BLC genotype, it was observed a significant relationship between effective filling period and number of rows of kernels on the cob. But that relationship may be spurious in nature, or a random association of the two traits in that genotype. The JNE genotype has a larger number of kernels than the BLC genotype, though the kernels from the BLC genotype were heavier. On the average, the JNE genotype has a higher grain yield per plant largely due to the larger number of kernels per plant. Kernel weight significantly contributes to grain yield, but the number of kernels per plant is the most determinant of grain yield. This result is in line with the findings on North American and Argentinean recent maize hybrids with the plant material used in this study, individual plants with higher grain filling rate had larger kernel mass and almost surely identified with the BLC genotype and plants with longer effective filling period had larger number of kernels and largely identify with the JNE genotype.

Conflict of Interest Statement

The authors declare no conflict of interest

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