

Full Length Research Paper

Inheritance of maize (*Zea mays* L.) leaf traits

Seka, D.^{1*}, Bonny, B. S.¹, Adjoumani, K.², Alla Eby, Y. G. H.¹, Yoboué, A. N.³, Sié, R. S.¹ and Adepo-Gourene B. A.¹

¹School of Natural Sciences, University Nangui Abrogoua, 02 BP 801 Abidjan, Côte d'Ivoire.

²Department of Sciences and Technology, Teacher's Training College of Abidjan, 08 BP 10 Abidjan 08, Côte d'Ivoire.

³School of Environmental Sciences, Jean Lorougnon Guédé University, B.P. 150, Daloa, Cote d'Ivoire.

Received 10 October, 2019 ; Accepted 22 November, 2019

Maize leaf plays an important role in the synthesis of organic compounds. It hosts the interception of light energy and conversion to organic energy, and the capture and assimilation of carbon dioxide in order to produce food. In this study, we explore the heritability of the maize leaf length, leaf width, and the number of leaves of two maize genotypes, JNE and BLC. The estimates of heritability varied from 0.2 to 0.44. Only estimates for leaf width and leaf length are significant. The coefficients of genotypic correlation were between 0.45 and 0.66, and like the estimates of heritability, only the genotypic correlations between parents and offspring are significant for leaf length and leaf width of the two genotypes. The estimates of degree of genetic determination also known as heritability in the broad sense are all high. They range between 0.52 and 0.85. We determined a significance criterion for the degree of genetic determination, the critical value at the level of significance $\alpha = 0.05$. We evaluated three methods for finding the critical value. With two methods based on the algebraic transformation of a function of the Snedecor's F and a simulation based on that function of F , it can be concluded that the estimates of the degree of genetic determination of leaf width of both the JNE and BLC genotypes are significant. With the third method that is based on fitting a Beta distribution, the critical value helped to conclude that none of the estimates of the degree of genetic determination is significant. The Pearson coefficients of correlation between plant height and all three leaf traits showed significant correlation between them, except leaf length and number of leaves.

Key words: Heritability, genotypic correlation, degree of genetic determination, genotype, significance test.

INTRODUCTION

The leaves of maize plant produce food for the growth and development of the plant. They are the main source of assimilate production that feeds the growth and

development of the plant; soon after the third leaf fully emerges and photosynthesis starts. This important role of maize leaves carries on until senescence. They

*Corresponding author. E-mail: sekadag@hotmail.com, seka.d@iugb.edu.ci. Tel: (225)0936 6895.

significantly contribute to the production of food and raw materials for human use, and generate an enormous interest in maize improvement. Maize is the third most important food crop in terms of worldwide use (Leakey et al., 2004) and demand for maize's harvest continues to increase. The continuous improvement of maize grain yield needed to meet the increasing demand requires finding ways to increase photosynthesis per unit leaf area. There has been little change in the rate of photosynthesis per unit leaf area and any effort to improve the rate of photosynthesis would further increase yield (Richards, 2000; Long et al., 2006). The enzyme, ribulose-1,5-biphosphate carboxylase/oxygenase (Rubisco), which catalyzes the carbon fixation for the production of assimilate has been the effect of extensive studies to see how it can be used to improve the rate of photosynthesis (Salesse-Smith et al., 2018; Parry et al., 2012; Crafts-Brandner and Salvucci, 2002; Richards, 2000; Morales et al., 1999). Recently, Salesse-Smith et al. (2018) found that the addition of the Rubisco assembly chaperone results in an increase of the content of maize leaf Rubisco and CO₂ assimilation. That finding suggests that maize plant biomass and yield could be significantly improved by improving efficiency of the plant leaf to assimilate more CO₂ molecules (Salesse-Smith et al., 2018; Long et al., 2006; Crafts-Brandner and Salvucci, 2002). Higher amount of Rubisco activase in the maize leaf is also needed to activate Rubisco and increase photosynthesis (Morales et al., 1999; Martinez-Barajas et al., 1997). Increasing the enzyme contents of Rubisco and Rubisco activase in the leaf of maize plant will certainly increase net assimilate production per unit leaf area. However, more exposure of maize leaf surface to sunlight is needed to complement that effort.

In addition to their role in providing food for human consumption, maize leaves are at the forefront of the struggle against the rising earth temperature. Even though the enzyme Rubisco activase is sensitive to heat stress (Ainsworth and Ort, 2010; Parry et al., 2012; Craft-Brandner and Salvucci, 2000), the maize plant does adjust to heat stress by synthesizing an enzyme that is similar to Rubisco activase (Craft-Brandner and Salvucci, 2002) and causes the activation of Rubisco at relatively high temperature. That property of maize leaves makes the plant suitable for a possible increase of earth temperature linked to the continuous burning of fossil fuels. In addition, CO₂ uptake and photosynthesis significantly increase with the concomitant efficient use of water under projected increase of atmospheric CO₂ concentration (Leakey et al., 2004).

It is therefore crucial to identify cultivars with architecturally distributed leaves around the plants that reduce shading of leaves and harvest more sunlight and intercept more CO₂ molecules for increased photosynthesis (Huang et al., 2017). Different combinations of leaf area and leaf angle define the canopy structure and influence canopy photosynthesis

(Stewart et al., 2013). Leaf angle has shown to be the most important trait in the rearrangement of canopy structure to better adapt to higher plant densities and still maintain high photosynthetic activities and higher yield (Lauer et al., 2012; Pendleton et al., 1968). The natural inclination of the maize leaf to orient itself in order to capture the most sunlight, the effect of planting density, the environment, and the genetic effect control leaf angle. With the progressive increase in planting densities in the past few decades, the genetic basis of leaf angle has got more attention in the attempt to develop new hybrids with more upright leaves that harness more energy from the sunlight, increase the rate of photosynthesis per unit leaf area and yield (Li et al., 2015; Chen et al., 2015; Tian et al., 2011; Mickelson et al., 2002). Leaf area and canopy architecture are important parameters to consider in the attempt to increase yield per plant. In addition to leaf angle that has received enormous attention, understanding the genetics of maize leaf length, leaf width and number of leaves will enhance maize breeding programs and help to develop maize hybrids that respond to the increasing human needs. The objectives of this current work were to study the inheritance of maize leaf traits. The objectives include the determination of the heritability in the broad sense and in the narrow sense of maize leaf length, leaf width and number of leaves of two maize genotypes, BLC and JNE. They also include the evaluation of the genotypic correlation between parents and offspring and the Pearson coefficients of correlation between the measured traits.

MATERIALS AND METHODS

Two genotypes of maize (*Zea mays* L.), BLC and JNE, are used in this study. The BLC genotype has translucent kernels, wider and longer leaves and taller plants. In contrast, the JNE genotype has yellow kernels, and comparatively smaller leaves. The F₂ and F₃ seed of the two genotypes, BLC and JNE, generated the four experimental populations used in this study. The seeds were planted in the Spring 2017, in a completely randomized factorial experiment at the experimental station of University Nangui Abrogoua, Abidjan, Côte d'Ivoire. Planting density and agricultural practices were done as described previously (Seka et al., 2019). Plots were tagged with identification number that identified each parent and its progeny. At silking, the day when about 50% of the plants in a plot developed silks, randomly sampled plants were used to obtain plant height as the length of the plant from the soil surface to the tip of the male inflorescence. The number of leaves was determined by counting nodes. We measured ear leaf length and maximum ear leaf width, and computed leaf area as suggested previously (Cross, 1991). These metrics were used to conduct a multivariate analysis of variance (MANOVA). The mean vectors of the levels of a factor (genotype) that were significantly different were used in a canonical discriminant analysis to further explain how they were different and which features, or phenotypic traits, best distinguished the levels of the factor. We supplemented with an analysis of variance for each measured canopy trait. The components of variance from the expected mean-squares of the analysis of variance helped to identify the genotypic and phenotypic variances (Hanson, 1963; Searle et al., 2006) for the three leaf traits (Table A1).

The heritability in the broad sense, H , as the ratio of the genotypic variance (σ_G^2) to the phenotypic variance (σ_P^2), $H = \sigma_G^2 / \sigma_P^2$ was determined (Falconer, 1989). The parameter H is distributed on the unit interval and a candidate density function for H is the Beta (shape 1, shape 2) density function. A significance test for this parameter was based on simulation using the method of moments and a critical value was obtained for the level of probability $\alpha = 0.05$. Other methods for finding a critical value for the significance of H were also explored. Those methods included the algebraic evaluation of a function of $F_{(1-\alpha, df1, df2)}$ (Appendix), and a consideration of the ninety-fifth percentile of simulated ten thousand random variables based on that transformation of $F_{(1-\alpha, df1, df2)}$. The heritability in the broad sense has been termed the degree of genetic determination (Falconer, 1989). And for the remainder of the text, we will refer to H as degree of genetic determination to avoid any confusion with the heritability in the narrow sense which is the true indicator of heredity. The heritability in the narrow sense, or simply heritability, h^2 , is the ratio of the additive genetic variance (σ_a^2) to the phenotypic variance, $h^2 = \sigma_a^2 / \sigma_P^2$. It is the proportion of phenotypic variation that is due to additive genetic values (Holland et al., 2003; Hallauer and Miranda, 1981; Hanson, 1963). An equivalent statement of heritability is the ratio of the genetic covariance of offspring and parents $Cov(P, O)$ to the variance of parents $Var(P)$ (Falconer, 1989), $h^2 = Cov(P, O) / Var(P)$. A significance test for h^2 is given by $t = \frac{\hat{h}^2}{s_{\hat{h}^2}}$ which has a Student's t distribution with $n-2$ degrees of freedom. And $s_{\hat{h}^2}$ is the standard error of the estimate. The genotypic correlation between relatives is given as $h = \sqrt{h^2}$. The significance of h is the same as h^2 . We computed the Pearson coefficient of correlation between the leaf traits and plant height to evaluate any relationship between the height of the plant and leaf length, leaf width, and number of leaves. All statistical analyses were performed with R (R Core Team, 2017).

RESULTS

Means and distribution of maize leaf traits

The multivariate analysis of variance indicates highly significant differences ($p < 0.01$) between genotypes for all the measured traits except number of leaves. The BLC genotype shows wider and longer leaves (Table 1). As a result, leaf area (la) per plant is significantly higher ($p < 0.01$) for the BLC genotype than the JNE genotype. In addition, plants from the BLC genotype are significantly taller than plants from the JNE genotype ($p < 0.01$). Leaf width of F3 and F4 plants from the BLC genotype are not significantly different. However, leaves of the F4 plants from the JNE genotype are wider than leaves of the F3 plants ($p < 0.05$). In addition, parents and offspring are significantly different for all measured leaf traits when

averaged across genotypes. The results show that the collection of seed from F3 plants based on the look of the plants significantly augmented leaf traits, resulting in an increase of leaf area per plant.

We complemented the multivariate analysis of variance with a canonical discriminant analysis. In this second analysis, we used the two variables, leaf length and leaf width, that show significant differences between the two genotypes in the MANOVA test. These two traits considered together provide the best basis for discriminating between the two genotypes. In general the BLC genotype has longer and wider leaves than the JNE genotype, and corroborates the results observed with the MANOVA test. However, they do not form distinct groups. The distributions of leaf length and leaf width of the two genotypes overlap.

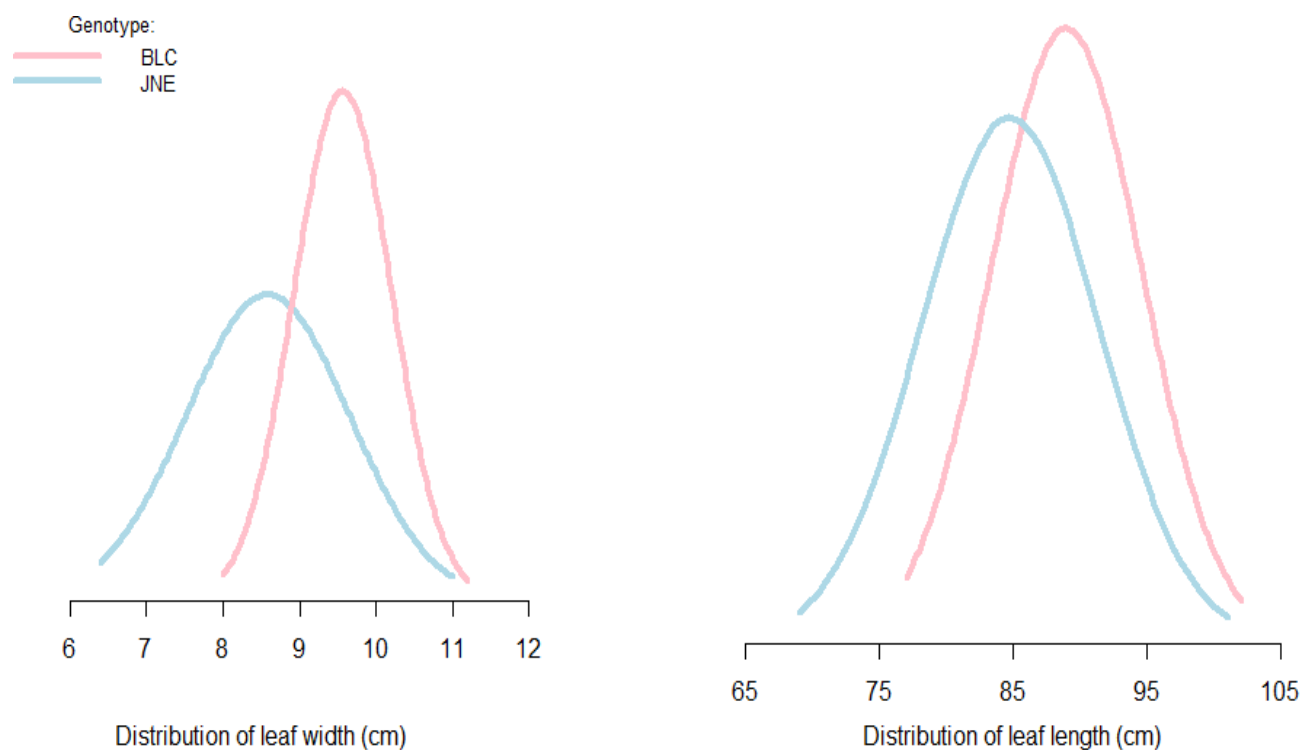
The density plots of the distributions of leaf length and leaf width for the two genotypes are given in Figure 1. The distribution of leaf width as shown in the first panel of Figure 1 shows that leaf width of the JNE genotype has a platykurtic distribution compared to the distribution of leaf width of the BLC genotype that is relatively leptokurtic. More width measurements had values concentrated around the mean, giving a taller density plot for the BLC genotype. The center of the distribution for the BLC genotype was to the right. The BLC genotype has wider leaves. The distribution of leaf length is presented in the second panel of Figure 1. The distributions appear to have the same shape. However, the center of the density plot for the BLC genotype moved to the right and is slightly higher than the JNE genotype. It shows that the BLC genotype has relatively longer leaves, than the JNE genotype. More leaves have length concentrated around the mean leaf length. The two traits, leaf length and leaf width, resulted in a significantly higher leaf area for the BLC genotype. The larger leaf surface area for the BLC genotype can be interpreted as having a larger exposure to sunlight energy, and possibly, increased capture of carbon dioxide and higher rate of photosynthesis.

Heritability of maize leaf traits

The estimates of heritability for the three traits are reported in Table 2. The broad-sense heritability, H , is referred to as degree of genetic determination. It is the ratio of the genotypic variance, σ_G^2 , to the phenotypic variance, σ_P^2 . That is, $H = \sigma_G^2 / \sigma_P^2$. The degree of genetic determination is the proportion of the phenotypic variance that is attributable to genotypic variation. The genotypic variation is caused by the effects of the additive actions of the genes, the effect of dominance at different loci, and the interaction between the genes also called epistasis, $\sigma_G^2 = \sigma_a^2 + \sigma_d^2 + \sigma_e^2$, (Falconer, 1989). The denominator is given by $\sigma_P^2 = \sigma_G^2 + \sigma_E^2$ where, σ_E^2

Table 1. Mean values of leaf width (lw), leaf length (ll), leaf number (ln), total leaf area (la), and plant height of two F3 and F4 maize strains.

Factor	Levels of factor	lw (cm)	ll (cm)	ln (cm)	la (cm)	Height (cm)
Generation	F3	8.85	86.41	12.17	7003.56	226.22
	F4	9.37	88.51	12.58	7845.76	224.95
	LSD	0.29	1.76	0.38	383.61	8.14
	CV	8.83	5.57	8.69	14.28	9.98
Genotype	BLC	9.63	89.81	12.45	8081.86	233.68
	JNE	8.59	85.12	12.30	6767.48	217.48
	LSD	0.29	1.76	0.38	383.61	8.14
	CV	8.83	5.57	8.69	14.28	9.98
Genotype (generation)	BLC(F3)	9.46	88.90	12.23	7718.86	235.87
	JNE(F3)	8.24	83.93	12.10	6288.29	216.57
	BLC(F4)	9.80	90.73	12.66	8444.86	231.50
	JNE(F4)	8.93	86.30	12.50	7246.67	218.40

**Figure 1.** Density plot of the distributions of leaf length and leaf width for the two maize genotypes, BLC and JNE.

is the error variance (Wolfe et al., 2013; Falconer, 1989; Lamkey and Halauer, 1987). And in replicated trials, the denominator becomes $\sigma_p^2 = \sigma_G^2 + \sigma_E^2/r$ with r denoting the number of replications (Gitonga et al., 2014; Holland et al., 2003; Hanson, 1963). Therefore H generally overestimates the true contribution of heredity in the spread of

the phenotypes for a specific trait. In a single environment, the degree of genetic determination is:

$$H = \begin{cases} 1 - 1/F & \text{if } F > 1 \\ \text{undefined,} & \text{otherwise} \end{cases}$$

Table 2. Heritability estimates and genotypic correlations for leaf width, leaf length, and leaf number of two F3 and F4 maize genotypes.

Variety	Leaf length	Leaf number	Leaf width
Degree of genetic determination			
JNE	0.60	0.60	0.85
BLC	0.72	0.52	0.85
Heritability			
JNE	0.33*	0.26	0.42**
BLC	0.32*	0.20	0.44**
Correlation between parents and offspring			
JNE	0.57*	0.51	0.65**
BLC	0.56*	0.45	0.66*

*Significantly different from zero at level of probability $\alpha = 0.05$. **Significantly different from zero at level of probability $\alpha = 0.01$.

Where, $F = MSG/MSE$ is the Snedecor's F statistic for testing for differences between the means of relatives for the measured trait in the population, MSG is the genotype mean-square and MSE is the error mean-square (Appendix). The estimates of the degree of genetic determination are between 0.52 for number of leaves of the BLC genotype and 0.85 for leaf width of both the BLC and the JNE genotypes (Table 2). A decision on the significance of the estimates of degree of genetic determination (or the null hypothesis $H_0: H = 0$) depends on the method used to determine the critical values. Critical values determined by the algebraic transformation of the function of $F_{(1-\alpha, df1, df2)}$ and simulation based on that function of $F_{(1-\alpha, df1, df2)}$ are 0.7504 (Appendix) and 0.8318 (Table 3), respectively. Based on those two critical values, leaf width of both the BLC and the JNE genotypes have significant estimates of the degree of genetic determination. Based on the fitted Beta (shape 1, shape 2) distribution, the critical value is 0.8777 and none of the estimates of the degree of genetic determination is significant. Despite the high values observed for the estimates of the degree of genetic determination, the contribution through heredity is quite low due to the fact that unquantified effects from other sources such as epistatic and environmental effects are compounded in the reported estimates.

The narrow-sense heritability is defined as the true heritability and is referred to as heritability in this paper. It is the statistic that measures the genetic advances through selection. It is given by the ratio of the additive variance, σ_a^2 , to the phenotypic variance, and is $h^2 = \sigma_a^2 / \sigma_p^2$, (Falconer, 1989). The heritability measures the effects of genes transmitted from parents

in the expression of the phenotypes, or the degree of resemblance between parents and offspring. The heritability is also given as the ratio of the covariance between parents and offspring to the variance of the parents, $h^2 = Cov(P, O) / Var(P)$. And the genotypic correlation between parents and offspring is $r_{OP} = h = \sqrt{h^2}$, a statistic that indicates how progeny are related to their parents (Falconer, 1989). The estimates of heritability vary from 0.20 for number of leaves of the BLC genotype to 0.44 for leaf width of the BLC genotype (Table 2). Based on the analysis of the parent-offspring regression, only estimates for leaf length and leaf width of the BLC and JNE genotypes are significant. The coefficients of genotypic correlation between parents and offspring ranged from 0.45 for number of leaves of the BLC genotype to 0.66 for leaf width of the BLC genotype. It should not surprise that only the leaf length and the leaf width of both the

BLC and the JNE genotypes are significant. The p -value for testing the hypothesis $H_0: \beta = 0$ is the same as the p -value for the hypothesis $H_0: \rho = 0$. Based on the estimates of heritability, gain from selection is likely to be achieved much easily for the traits leaf width and leaf length compared to number of leaves.

Correlation between plant height and leaf traits

The correlation analysis indicates low to moderate coefficients of correlation. The correlations between plant height and all three leaf traits are highly significant. The correlations between plant height and leaf length ($r = 0.43^{**}$) and plant height and number of leaves ($r = 0.42^{**}$) are the strongest. Taller plants have relatively

Table 3. Critical values for the degree of genetic determination H at the level of significance $\alpha = 0.05$.

Method	Critical value	Bootstrap confidence interval (95%)
Simulation based		
On the transformation of F	0.8318	[0.8247; 0.8383]
Fitted Beta (α, β) distribution	0.8777	[0.8705; 0.8850]

Table 4. Matrix of coefficients of correlation between maize plant height, leaf width, leaf length and number of leaves.

Parameter	Leaf width	Leaf length	Number of leaves
Plant height	0.28** (low)	0.43** (moderate)	0.42** (moderate)
Leaf width		0.37** (low)	0.25** (low)
Leaf length			0.18 ^{ns} (low)

*, **Significantly different from zero at level of probability $\alpha = 0.05$ and $\alpha = 0.01$, respectively.

greater number and longer leaves. In addition, they have wider leaves. Plant with longer leaves also have wider leaves ($r = 0.37^{**}$). Leaf length is not correlated with number of leaves (Table 4).

DISCUSSION

The study of the distribution of the three leaf traits shows that leaf length and leaf width have large variations compared to number of leaves. Significant differences are observed for those two traits. The curves of the distributions of leaf length and leaf width indicate that, on the average, the BLC genotype has larger and longer leaves than the JNE genotype. But the number of leaves does not vary much between genotypes and between parents and offspring. The estimates of degree of genetic determination, also known in the literature as heritability in the broad sense, are high. They are all greater than 0.50. Estimates of degree of genetic determination reported elsewhere are also very high. For example, in a genetic study on cotton varieties, *Gossypium hirsutum*, the computed estimates of degree of genetic determination are greater than 0.99 (Ahsan et al., 2015). In a work on tetraploid rose, *Rosa x hybrida*, the estimates are between 0.40 for number of side shoot and 0.96 for number of petals (Gitonga et al., 2014). And the reported estimates of the degree of genetic determination are between 0.49 for harvest index and 0.99 for lodging in finger millet, *Eleusine coracana* (Wolie et al., 2013). The degree of genetic determination is a broad measure of heritability. And the generally high estimate may be due to the fact that it includes other components such as dominance, epistatic and environmental variances that are compounded in its estimation. In addition, traits such as leaf length, leaf width and number of leaves are quantitative in nature. They are polygenic traits, and they

are very sensitive to the environment, particularly planting density, agricultural practices, and bioclimatology that greatly contribute to the overestimation of the degree of genetic determination. Therefore, the high estimate of degree of genetic determination does not necessarily mean a great hereditary contribution. But, that parameter of inheritance is often used in modern genetic and genomic analyses (Visscher et al., 2008). That makes it very compelling to have a test of significance for the degree of genetic determination. It is mentioned that an estimate of the degree of genetic determination that is very high, greater than 0.8, may indicate that the phenotype is a true expression of the genotype; therefore a genetic gain may be achieved from selection (Singh, 2001). However, because that rule-of-thumb benchmark cannot be applied to all situations and experimental works, we propose the determination of a critical value and a critical region for the degree of genetic determination based on either the reciprocal of the Snedecor's F (for $F > 1$) that depends on its degrees of freedom or the $Beta$ distribution (for $0 < H < 1$) that depends on its shape parameters. In this study, the three computed critical values ranged from 0.7504 to 0.8777 and they do not deviate too much from the suggested benchmark.

Heritability in the narrow sense is simply called heritability (Falconer, 1989). This parameter is a true measure of heredity. It measures the effect of additive genes transmitted from the parents to the progeny. The estimates of heritability vary from a low of $h^2 = 0.20$ to a moderate value of $h^2 = 0.44$. They are determined with the regression of offspring on parents. The estimates obtained in this study are within the range of previously reported estimates of heritability for kernel hardness in wheat, *Triticum aestivum* (Seka and Frohberg, 2016), and for yield traits in wheat (Eid, 2009), where the method of parent-offspring regression was used. The use

of the restricted maximum likelihood method in the estimation of heritability produced a moderately high estimate for the softening rate of apple (*Malus domestica*) fruits (Iwanami et al., 2008). Because the estimation of heritability uses the regression method in this study, test of significance is based on the *t* distribution with its degree of freedom, and we do not need to elaborate on the test as it is found in most statistics books. The genotypic correlation between parents and offspring is given as the square-root of the heritability. An equivalent *t*-test for significance of the coefficient of genotypic correlation yields the same *p-value* as the significance test of heritability. Only leaf width and leaf length of both the BLC and the JNE genotypes have significant estimates of heritability and coefficients of genotypic correlation between parents and offspring. Computation of the Pearson coefficients of correlation between plant height, leaf length, leaf width and number of leaves gives low to moderate values. But all the coefficients are highly significant except the correlation between number of leaves and leaf length.

Conclusion

Estimates of heritability were significantly high for leaf width and leaf length indicating that the proportion of phenotypic variation that is due to additive genetic values was considerable for those two traits. In addition, those two traits showed significant differences between the two genotypes in the analysis of variance. Besides, the canonical discriminant analysis showed that those two traits were mostly responsible for distinguishing the two genotypes. Under the same growing conditions, leaf number did not vary significantly between the two genotypes and from one generation to the next except when averaged across genotypes. Sunlight energy and carbon dioxide enter the cycle of production of organic molecules from the plant leaf surface. Understanding the genetics of the canopy traits would certainly lead to a more efficient production of assimilate and increased yield. The computed degree of genetic determination was generally very high. Given, its frequent use in the determination of heritability in modern genetic and genomic researches, it becomes necessary to develop a significance test for proper inferences.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

REFERENCES

Ahsan MZ, Majidano MS, Bhutto H, Soomro AW, Panhwar FH, Channa AR, Sial KB (2015). Genetic variability, coefficient of variation, heritability and genetic advance of some *Gossypium hirsutum* L. accessions. *Journal of Agricultural Science* 7(2):147-151.

Ainsworth EA, Ort DR (2010). How Do We Improve Crop Production in a Warming World? *Plant physiology* 154(2):526-530.

Chen X, Xu D, Liu Z, Yu T, Mei X, Cai Y (2015). Identification of QTL for leaf angle and leaf space above ear position across different environments and generations in maize (*Zea mays* L.). *Euphytica* 204(2):395-405.

Crafts-Brandner SJ, Salvucci ME (2002). Sensitivity of Photosynthesis in a C4 Plant, Maize, to Heat Stress. *Plant Physiology* 129(4):1773-1780.

Crafts-Brandner SJ, Salvucci ME (2000). Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO₂. *Proceedings of the National Academy of Sciences* 97(24):13430-13435.

Cross HZ (1991). Leaf expansion rate effects on yield and yield components in early maturing maize. *Crop Science* 31(3): 579-583.

Eid MH (2009). Estimation of heritability and genetic advance of yield traits in wheat (*Triticum aestivum* L.) under drought condition. *International Journal of Genetics and Molecular Biology* 1(7):115-120.

Falconer DS (1989). *Introduction to Quantitative Genetics* (3rd ed.). Harlow: Logman Scientific and Technical.

Gitonga VW, Koning-Boucoiran CFS, Verlinden K, Dolstra O, Visser RGF, Maliepaard C, Krens FA (2014). Genetic variation, heritability and genotype by environment interaction of morphological traits in a tetraploid rose population. *BMC Genetics* 15(1):146.

Hallauer AR, Miranda JB (1981). *Quantitative genetics in maize breeding* (Vol. 6). Springer Science and Business Media.

Hanson WD (1963). Heritability. In Hanson WD and Robinson HF, Eds., *Statistical Genetics and Plant Breeding*. NAS-NRC. Washington, DC. pp. 125-140.

Holland JB, Nyquist WE, Cervantes-Martinez CT (2003). Estimating and interpreting heritability for plant breeding: an update. *Plant Breeding Reviews* 22:9-112.

Huang S, Gao Y, Li Y, Xu L, Tao H, Wang P (2017). Influence of plant architecture on maize physiology and yield in the Heilonggang River valley. *The Crop Journal* 5(1):52-62.

Iwanami H, Moriya S, Kotoda N, Takahashi S, Abe K (2008). Estimations of Heritability and Breeding Value for Postharvest Fruit Softening in Apple. *Journal of the American Society for Horticultural Science* 133(1):92-99.

Lamkey KR, Hallauer AR (1987) Heritability estimated from recurrent selection experiments in maize. *Maydica* 32(1):61-78.

Lauer S, Hall BD, Mulaosmanovic E, Anderson SR, Nelson B, Smith S (2012). Morphological changes in parental lines of Pioneer Brand maize hybrids in the U.S. Central Corn Belt. *Crop Science* 52(3):1033-1043.

Leakey ADB, Bernacchi CJ, Dohleman FG, Ort DR, Long SP (2004). Will photosynthesis of maize (*Zea mays*) in the US Corn Belt increase in future [CO₂] rich atmospheres? An analysis of diurnal courses of CO₂ uptake under free-air concentration enrichment (FACE). *Global Change Biology* 10(6):951-962.

Li C, Li Y, Shi Y, Song Y, Zhang D, Buckler ES, Zhiwu Z, Tianyu W, Yu Li. (2015). Genetic control of the leaf angle and leaf orientation value as revealed by ultra-high density maps in three connected maize populations. *PLoS ONE* 10(3): p e0121624.

Long SP, Zhu X-G, Naidu SL, Ort DR (2006). Can improvement in photosynthesis increase crop yields? *Plant, Cell and Environment*. 29(3):315-330.

Martinez-Barajas E, Molina-Galan J, Sanchez de Jimenez E (1997). Regulation of Rubisco activity during grain-fill in maize : possible role of Rubisco activase. *The Journal of Agricultural Science* 128(2):155 - 161.

Morales A, Ortega-Delgado ML, Molina-Galan J, Sanchez de Jimenez E (1999). Importance of Rubisco activase in maize productivity based on mass selection procedure. *Journal of Experimental Botany* 50(335):823-829.

Mickelson SM, Stuber CS, Senior L, Kaeppeler SM (2002). Quantitative trait loci controlling leaf and tassel traits in a B73 x Mo17 population of maize. *Crop Science* 42(6):1902-1909.

Parry MAJ, Andralojc PJ, Scales JC, Salvucci ME, Carmo-Silva AE, Alonso H, Whitney SM (2012). Rubisco activity and regulation as targets for crop Improvement. *Journal of Experimental Botany* 64(3):717-730.

- Pendleton JW, Smith GE, Winter SR, Johnston TJ (1968) Field investigation of the relationships of leaf angle in Corn (*Zea mays* L.) to grain yield and apparent photosynthesis. *Agronomy Journal* 60(4):422-424.
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richards RA (2000). Selectable traits to increase crop photosynthesis and yield of grain crops. *Journal of Experimental Botany* 51:447-458.
- Salesse-Smith CE, Sharwood RE, Busch FA, Kromdijk J, Bardal V, Stern DB (2018). Overexpression of Rubisco subunits with RAF1 increases Rubisco content in maize. *Nature Plants* 4(10):802-810.
- Searle SR, Casella G, McCulloch CE (2006). *Variance components*. John Wiley and Sons, Inc, Hoboken, New Jersey.
- Seka D, Bonny BS, Yoboué AN, Sié SR, Adopo-Gourène BA (2019). Identification of maize (*Zea mays* L.) progeny genotypes based on two probabilistic approaches: Logistic regression and naïve Bayes. *Artificial Intelligence in Agriculture* 1:9-13.
- Seka D, Frohberg CR (2016). Inheritance of kernel hardness in spring wheat as measured by near-infrared reflectance spectroscopy. *Euphytica* 209(3):679-688
- Singh BD (2001). *Organisation for crop improvement in India. Plant Breeding: Principles and Methods*. Kalyani Publishers, Ludhiana, pp. 801-830.
- Stewart DW, Costa C, Dwyer LM, Smith DL, Hamilton RI, Ma BL (2013) Canopy Structure, Light Interception, and Photosynthesis in Maize. *Agronomy Journal* 95(6):1465-1474.
- Tian F, Bradbury PJ, Brown PJ, Hung H, Sun Q, Flint-Garcia S, Rocheford TR, McMullen MD, Holland JB, Buckler ES (2011). Genome-wide association study of leaf architecture in the maize nested association mapping population. *National Genetics* 43(2):159-162.
- Visscher PM, Hill WG, Wray NR (2008). Heritability in the genomics era - concepts and misconceptions. *Nature Reviews Genetics* 9(4):255-266.
- Wolie A, Dessalegn T, Belete K (2013). Heritability, variance components and genetic advance of some yield and yield related traits in Ethiopian collections of finger millet (*Eleusine coracana* (L.) Gaertn.) genotypes. *African Journal of Biotechnology* 12(36):5529-5534.

Appendix

Table A1 . Layout of the analysis of variance with the expected mean squares for a single environment (Hanson, 1963; Searle et al., 2006).

Source of variation	Degree of freedom	Mean Square	Expected Mean Square
Replication	$r - 1$		
Genotypes	$g - 1$	MSG	$\sigma_E^2 + r\sigma_G^2$
Error	$g(r-1)$	MSE	σ_E^2

- i. Estimation of the degree of genetic determination (heritability in the broad sense):

$$H = \frac{\sigma_G^2}{\sigma_P^2} \text{ with } \sigma_P^2 = \sigma_G^2 + \sigma_E^2/r.$$

The estimators of σ_G^2 and σ_E^2 are $\hat{\sigma}_G^2 = \frac{MSG - MSE}{r}$ and $\hat{\sigma}_E^2 = MSE$. And the estimator of the degree of genetic determination becomes $\hat{H} = \frac{MSG - MSE}{MSG} = 1 - 1/F$ for $F > 1$, undefined otherwise, with $F = MSG/MSE$.

- ii. Finding the critical value for H based on the F distribution:

$Q(p) = F^{-1}(f) = f$ such that $\Pr(F < f) = p$. For probability $p = 0.95$, the critical value H_{cr} is given by $1 - 1/f_{(p, df1, df2)} = 1 - f_{(1-p, df2, df1)} = 0.7504$.