GENETIC RELATIONSHIP BETWEEN PLANT GROWTH, SHOOT AND KERNEL SIZES IN MAIZE (*Zea mays* L.)

A. S. P. NGUETTA[1] et H. Z. CROSS[2]

[1]Université de Cocody-Abidjan, Côte d'Ivoire, UFR de Biosciences ; Laboratoire de Génétique 22 B.P. 582 Abidjan 22.

[2]Department of Plant Sciences, North Dakota State University, Fargo, ND 58105, USA.

ABSTRACT

Maize (*Zea mays* L.) ear vascular tissue transports nutrients that contribute to grain yield. To assess kernel heritabilities that govern ear development and plant growth, field studies were conducted to determine the combining abilities of parents that differed for kernel-size, grain-filling rates and shoot-size. Thirty two hybrids were derived from large (LG) and small (SM) kernel plants by inter-crossing parents that differed for shoot-size at silking [Long-Shoot (LS) and Small-Shoot (SS)]. Each hybrid was grown in replicated experiments at Fargo and Casselton stations, N.D., USA in 2002. Juvenile plant height, leaf number and mature leaf length, number and width were measured to determine leaf area per mature plant. Ear length, diameter, and fresh weight at 7 and 14 days after silking were estimated at early ear development. Compared to LG parents, the SM parents, produced 5 % taller juvenile plants, 3 % more and 7 % larger mature leaves. Compared to LS x LG hybrids, SS x SM hybrids, produced 7 % taller juvenile plants, 3 % wider mature leaves and 2 to 3 % less leaves at juvenile stage. Compared to LS x LS (LG x LG) hybrids, SS x SS (SM x SM) hybrids, also produced 3 % taller mature plants. Shoot-size parents differed in combining abilities for plant growth traits but not for ear-size traits, suggesting that this trait is lowly heritable. Pollen-type parents did not affect early ear development.

Key words : Maize, ear, genotype, shoot, USA, Ivory Coast

RESUME

RELATION GENETIQUE ENTRE LA CROISSANCE DE LA PLANTE, LES TAILLES DES GRAINES ET DES EPIS DU MAÏS (Zea mays L.)

Le tissu vasculaire de l'épi de maïs (Zea mays L.) transporte les nutriments utilisés dans le rendement des grains. Pour connaître l'héritabilité du développement de l'épi et de la plante, des études ont été conduites au champ pour estimer les aptitudes à la combinaison des parents qui diffèrent par la taille des graines, de l'épi et la vitesse de remplissage des graines. Des génotypes ayant de grosses (LG) et de petites (SM) graines ont été inter croisés avec des génotypes ayant de grands [Long-Shoot (LS)] et de petits [Short-Shoot (SS)] épis pour produire 32 hybrides. Chaque hybride a été semé dans un dispositif 6 x 6 simple lattice à Fargo et Casselton, N.D., USA en 2002. La taille et le nombre de feuilles des jeunes plants, ainsi que la longueur, le nombre et le diamètre des feuilles pour déterminer la surface foliaire des plantes à maturité ont été mesurés. La longueur, le diamètre et le poids frais de l'épi, après 7 et 14 jours suivant la sortie des fleurs femelles ont permis d'estimer le développement précoce de l'épi. Comparés à LG, les parents SM ont produit les plus grands jeunes plants et les plus grandes feuilles à maturité. Comparés à LS x LG, les hybrides SS x SM ont produit les plus grands jeunes plants et les plus larges feuilles à maturité. Comparés à LS x LS (LG x LG), les hybrides SS x SS (SM x SM) ont produit aussi les plus grandes plantes à maturité. Les plantes qui diffèrent par la taille des épis diffèrent également dans les aptitudes à la combinaison pour le développement des plantes, mais pas pour la croissance des épis, indiquant que ce trait a une faible héritabilité. Le type de pollen n'a pas affecté le développement de l'épi.

Mots clés : *Maïs, épi, génotype, taille, USA, Côte d'Ivoire*

INTRODUCTION

Kernel mass is an important maize yield component that is controlled by both maternal and xenia effects (Seka and Cross, 1995 a). Seka *et al.,* (1995) reported that sucrose supply and paternal, as well as maternal genes in the kernel influence cob dry weight, kernel dry matter and water contents during *in vitro* kernel development.

Assimilates accumulation in the endosperm during kernel development may be associated with water uptake during early kernel growth. Cavalieri and Smith (1985) found that the rate of dry matter accumulation influences kernel moisture content during early kernel development. Kernel moisture per growing-degree-day decreased during the grain-filling period (Kang *et al.,* 1986). A positive relationship between kernel moisture reduction per growing-degree-day and the rate of grain-filling was observed.

Daynard and Kannenberg (1976) reported that genes controlled the rates and durations of effective dry matter accumulation. Selection for heavy kernels increased kernel mass in two genetic backgrounds by increasing the rate of grain-filling (Cross and Mostafavi, 1994). Alexander and Cross (1983) measured the grain-filling characteristics of high (HC), random (RC), and low (LC) R *n-j* color expression strains developed from an early-maturing synthetic by three cycles of mass selection. The HC strain accumulated dry matter rapidly for a short effective filling period. The LC strain accumulated dry matter more slowly over a longer effective filling period. The RC strain was intermediate for both growth rate and effective filling period in the developing kernel.

Nguetta and Cross (1997) also observed that HC selections produced 3 % longer and 6 % heavier ears at 7 d, and had 5 % more, 3 % wider and 4 % larger leaves per plant than LC selections. The authors concluded that the earlier ear development of HC strains may contribute to higher kernel growth rates. Due to larger leaves per plant, HC strains also may produce more photosynthate for translocation into the developing kernels.

General (GCA) and specific combining abilities (SCA) measure the potential genetic values of inbred sources for producing hybrids (Falconer, 1960). The GCA refers to the average performance of a line in hybrid combination. The SCA measures instance in which certain hybrid combinations are either better or poorer than would be expected from average performance of the parent inbred lines included (Sprague and Tatum, 1942). Genes having largely additive effects produce GCA, and genes having dominance and epistatic effects produce SCA. Estimates of GCA and SCA are relative to and depend on the particular set of inbred lines tested (Sprague and Tatum, 1942).

Seka and Cross (1995 b) measured the rates of grain-filling of large (LG) and small (SM) kernel-weight strains developed by five cycles of mass selection from the same early maturing synthetic population were also measured. The authors indicated that kernels pollinated with LG pollen, compared to SM pollen, accumulated dry matter 5.2 % faster, had 0.4 % shorter lag phases, and were 3.9 % heavier at maturity in field studies.

Pollen from LG strains, compared to SM strains, increased both kernel and cob piece dry weights *in vitro* culture. Cob pieces from explants pollinated with LG pollen, compared to SM pollen, were heavier at 7 d *in vitro* culture (Seka *et al.,* 1995). Genes contributed to the kernel from the pollen apparently influenced *in vitro* growth of cob tissue containing only genes contributed by the plant before pollination. The authors suggested that genes in the explanted kernel may have stimulated vascular tissue growth, or that larger kernels may have increased the rate of sugar transport into the endosperm by increasing sink demand. The results showed that genes in one tissue (via hormones or unknown factors) influenced growth of tissues lacking these genes.

Using the *R-nj* aleurone color strains known to differ for rate of grain-filling, Seka *et al.,* (1995) produced 12 strains hybrids in two sets. The authors reciprocally inter-crossed the three HC, RC, and LC strains to large- (LG) and small-seeded (SM) strains.

Laboratory studies showed that *in vitro* cultured cob pieces of LG hybrids grew better than cob pieces of SM hybrids. Seka and Cross (1995 a) observed in field studies that hybrids from LG strains had increased rates of grain-filling and kernel dry weights compared to hybrids from SM strains.

After studying several inbred lines, Leng (1949) reported that pollen parents directly affected the size of crossed kernels. The author observed that pollen of inbred R4 reduced the period of dry matter translocation to the kernels. Crossed kernels with R4 as a pollen parent were invariably smaller and of poorer quality at maturity than when other inbreds were used as a pollen source.

To better understand how ear and plant development relate to grain filling in early- maturing maize, a study was conducted on the combining abilities of parents selected for the rate of grain-filling (via the *R-nj* gene), mature kernel-size and shoot-size.

MATERIAL AND METHODS

32 hybrids (16 hybrids x 2 sets) were produced in two sets by hand-pollination during the summer of 1992. At silking, four plants each from large (LG) and small (SM) strains developed by five cycles of mass selection from NDSC sub-strains, were selected by measuring the shoot-size. Long-shoot (LS) parental plants had shoots measuring 10 to 12 cm, compared to 4 to 5 cm for shoots of the short-shoot (SS) parental plants. Each selected parental plant was pollinated with bulked pollen from 10 LG or 10 SM plants on two dates (two sets) to derive the 32 hybrids used in this experiment (Table 1).

Table 1 : Mating design used to produce each of the two sets of 16 maize hybrids.

Plan de croisement utilisé pour produire chacun des 2 groupes de 16 hybrides de maïs.

Parental group 2	Parental group 1			
	LG LS	LG SS	SM LS	SM SS
LG LS	LGLS x LGLS	LGLS x LGSS	LGLS x SMLS	LGLS x SMSS
LG SS	LGSS x LGLS	LGSS x LGSS	LGSS x SMLS	LGSS x SMSS
SM LS	SMLS x LGLS	SMLS x LGSS	SMLS x SMLS	SMLS x SMSS
SM SS	SMSS x LGLS	SMSS x LGSS	SMSS x SMLS	SMSS x SMSS

LG, SM, LS, and SS stand for large-kernel, small-kernel, long shoot, and short shoot, respectively.

Field experiments were conducted at the Agricultural Experiment Stations on a Fargo soil (Fargo clay loam, Vertic Haplaquoll) and at Casselton, N.D., USA (Beardon silty clay loam, Aeric Calciaquoll) during the summer of 2002. These soils have slow permeabilities, high water holding capacities and medium fertilities. A 7.0 by 0.75 m single-row plots arranged in a 6 x 6 simple lattice design with four replications per location was used. Each plot was seeded and plants were later thinned to 58.000 plants/ha. Standard cropping practices recommended for high yields were followed.

Approximately 45 days after planting, 5 plants were randomly selected in each plot and juvenile plant height (cm from the ground to the tip of the uppermost leaf) and number of leaves (leaves with visible collars) was recorded. Immediately after all plants had silked, the same (five) plants were measured for mature plant height, leaf number, ear-leaf length, and ear-leaf width using the procedure outlined by Cross (1990). Leaf area per plant was estimated using the following equation : leaf area = leaf number x ear-leaf length x ear-leaf width x 0.75 (Cross, 1991).

Ear development was monitored at three maturity stages (early-, intermediate-, and late-silking dates) within strains and replications by marking (with spray painting) plants that silked the same day.

Paper shoot bags protected silks that were pollinated in each replication with bulked pollen from 10 LG or 10 SM plants grown adjacent to the plot area. Eight plants were randomly pollinated (four each with LG and SM pollen on the same day) from each hybrid in each plot. After 3 d, the shoot bags were removed to allow

any unpollinated kernels to open pollinate. At 7 and 14 d after silking for each maturity stage and for each replication, the ears from each strain were sampled and dissected and ear length, diameter, and fresh-weight were measured. For each trait, the differences between ear measurements were computed to estimate ear growth parameters. Analyses of variance (ANOVA) using a modified design II (3) linear model produced statistics for means separations. The model treated locations and replications as random and kernel-size and shoot-size strains as fixed effects.

RESULTS

POLLEN SOURCE EFFECTS

The analysis of variance (ANOVA) (not reported) did not show significant effects due to pollen types for several traits of plant growth. However, previous studies indicated that the pollen source affected different traits associated with kernel development.

GCA FOR KERNEL-SIZE PARENTS

Kernel-size showed significant GCA for plant growth traits. Compared to LG plants, the SM plants, produced longer, wider, and larger leaf areas per mature plant in both independent parental groups (Table 2).

The SM parents produced 5 % taller and 2 % more juvenile plants, 3 % more and 7 % larger

mature leaves than LG parents in the first parental group. In the second parental group, compared to LG hybrids, SM hybrids, also produced 2 % longer and 4 % larger mature leaves, but LG hybrids grew 3 % more leaves at juvenile stage than SM hybrids.

SCA FOR KERNEL-SIZE CROSSED TO SHOOT-SIZE PARENTS

The ANOVA showed significant ($P < 0.05$) SCA between independent groups of shoot-size and kernel-size parents for juvenile plant height, leaf number, and mature leaf width (Table 3).

Compared to LS x LG hybrids, SS x SM hybrids, produced 7 % taller juvenile plants, 2 to 3 % less juvenile leaves and 3 % wider mature leaves. Compared to SS x LG and LS x SM hybrids, SS x SM hybrids, produced also 8 % and 5 % taller juvenile plants, respectively and 3 % less mature leaves.

The ANOVA also revealed significant SCA between independent groups of shoot-size parents and between kernel-size of independent parental groups for juvenile leaf number and mature plant height (Table 4).

Compared to LS x LS (LG x LG) hybrids, SS x SS (SM x SM) hybrids, grew 3 % taller mature plants and 2 % less juvenile leaves. Compared to SS x LS (SM x LG) hybrids, SS x SS (SM x SM) hybrids, produced also 4 % less juvenile plants and 0.7 % less taller mature plants.

Table 2 : Means* of GCA of kernel size for the two independent parental groups (P1 and P2).

Moyennes des AGC relatives à la taille des épis pour les 2 groupes parentaux indépendants P1 et P2.

Kernel genotypes	GCA of kernel size							
	P1					P2		
	PHJ	LNJ	LNM	LWM	LAM	LNJ	LLM	LAM
	cm	n°.	------- cm -------		cm^2	n°.	cm	cm^2
LG	31.03	8.10	27.82	3.20	603	8.20	28.05	614
SM	32.60	8.20	28.76	3.20	648	8.00	28.54	637
LSD (0.05)	0.96	0.10	0.39	0.10	19	0.10	0.39	19

* average across replications, parent P2, parent P1, shoot-size, sets, and environments ;
PHJ, LNJ, LLM, LWM, and LAM stand for juvenile plant height, juvenile leaf number, mature leaf length, mature leaf width, and mature leaf area, respectively ; n°. : number
LG and SM stand for large-kernel and small-kernel genotypes, respectively.
AGC : Aptitudes Générales à la Combinaison

Table 3 : Means* of SCA between shoot size and kernel size of two maize independent parental groups (S x P).

Moyennes des ASC entre les tailles d'épi et de grain de maïs relativement aux deux groupes parentaux idépendants (S x P).

	SCA					
	S1xP1	S1xP1	S1xP2	S2xP1	S2xP2	S2xP1
Plant type	PHJ		LNJ			LWM
	cm	---------------------- n°. ---------------------				cm
LS x LG	31.20	8.10	8.30	8.20	8.10	3.10
SS x LG	30.80	8.00	8.20	8.30	8.00	3.20
LS x SM	31.80	8.20	8.00	8.00	8.10	3.30
SS x SM	33.30	8.10	8.10	8.00	8.20	3.20
LSD (0.05)	1.30	0.10	0.10	0.10	0.10	0.10

* average across replications, sets, and locations ;
PHJ, LNJ, and LWM : juvenile plant height, juvenile leaf number, and mature leaf width, respectively ; n°. : number
LS, SS, LG, and SM : long-shoot, short-shoot, large-kernel, and small-kernel genotypes, respectively.
ASC : Aptitudes Spécifiques à la Combinaison

Table 4 : Means* of SCA between shoot size of two maize independent parental groups (S1 x S2) and (P1 x P2).

Moyennes des ASC entre les tailles d'épi de deux groupes parentaux indépendants de maïs (S1 x S2) et (P1 x P2).

	SCA		
	S1 x S2	P1 x P2	
Plant type	LNJ	LNJ	PHM
	n°.	n°.	cm
LS x LS (LG x LG)	8.20	8.10	57.24
SS x LS (SM x LG)	8.10	8.30	59.26
LS x SS (LG x SM)	8.10	8.00	59.25
SS x SS (SM x SM)	8.20	8.00	58.83
LSD (0.05)	0.10	0.10	1.33

* average across replications, sets, and locations ;
LNJ and PHM stand for juvenile leaf number and mature plant height, respectively ; n°. : number
LS, SS, LG, and SM stand for long-shoot, short-shoot, large-kernel, small-kernel genotypes, respectively.

DISCUSSION

The results indicated no significant differences between several traits associated to ear and plant growth. However, Seka and Cross (1995 b) found that pollen did not affect sporophyte growth, but affected traits associated with kernel growth. The LG pollen increased kernel-size over SM-pollinated kernels (Odhiambo and Compton, 1987; Seka and Cross, 1995 a ; Seka *et al.,* 1995). When compared to SM pollen, LG pollen, increased kernel size (sink), in this study, there was no detectable response in early ear growth and plant development.

Significant GCA was observed for several plant growth traits associated with LG or SM parents, but not for ear-growth traits. These results may suggest that kernel-size genes are genetically associated with plant-growth traits. In this experiment, ear sizes were unaffected by kernel-size parental source. This may be due to a lower power of the test (fewer environments).

The SCA for shoot-length parents mainly affected juvenile plant growth traits and mature plant growth traits, suggesting that some genetic associations probably exist between shoot-size and growth traits associated with plants. The ANOVA did not detect GCA or SCA for shoot-size parents for any ear-size growth traits. This lack of detectable genetic effects for shoot-size parents for ear length at 7 and 14 d suggested that this trait is lowly heritable or that the direct selection response (ear length at silking) has disappeared after 7 d after silking.

CONCLUSION

Kernel-size strains differed in combining abilities for plant growth traits, but not for ear growth traits. The SM plants produced longer leaves and larger leaf areas per plant, implying that they produced more photosynthates for translocation into the developing-kernels. Shoot-size parents affected juvenile plant growth traits, but did not differ in combining abilities for ear-size traits associated in early ear development. Therefore, plant growth is genetically associated with kernel-size, but only weekly associated with shoot-size parents. In this study, pollen-type parents did not affect early ear development.

REFERENCES

Alexander,(W.L.), and (H.Z.) Cross. 1983. Grain-filling characteristics of early maize strains selected for variable *R-nj* expression. Euphytica 32 : 839-843.

Cavalieri, (A.J.), and (O.S.) Smith. 1985. Grain filling and field drying of a set of maize hybrids released from 1930 to 1982. Crop Sci. 25 : 856-860.

Comstock, (R.E.), and (H.F.) Robinson. 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics 4 : 254-266.

Cross, (H.Z.) 1990. Selection for rapid leaf expansion in early-maturing maize. Crop Sci. 30 : 1029-1032.

Cross, (H.Z.) 1991. Leaf expansion rate effects on yield and yield components in early-maturing maize. Crop Sci. 31 : 579-583.

Cross, (H.Z.), and (M.R). Mostafavi, 1994. Grain filling of *R-nj* color-selected maize strains divergently selected for kernel weight. Can. J. Plant Sci. 64 : 455-460.

Daynard, (T.B.), and (L.W.) Kannenberg. 1976. Relationship between length of the actual and effective grain filling periods and the grain yield of corn. Can. J. Plant Sci. 56 : 237-242.

Falconer, (D.S.) 1960. Introduction to quantitative genetics. Ronald Press, New York.

Kang, (M.S.), (M.S.) Zuber, (T.R.) Colbert, and (R.D.) Horrocks. 1986. Effects of certain agronomic traits on and relationship between rates of grain-moisture reduction and grains fill during the filling period in maize. Field Crops Res. 14 : 339-347.

Leng, (E.R.) 1949. Direct effect of pollen parent on kernel size in dent corn. Agron. J. 41 : 555-558.

Nguetta, (A.S.P.), and (H.Z.) Cross. 1997. Correlated responses in ear and plant traits in maize synthetics selected for *R-nj* color expression. Crop Sci. 37 : 739-744.

Odhiambo, (M.O.), and (W.A.) Compton. 1987. Twenty cycles of divergent mass selection for seed size in corn. Crop Sci. 27 : 1113-1116.

Seka, (D.), and (H.Z.) Cross. 1995 a. Xenia and maternal effects on maize kernel development. Crop Sci. 35 : 80-85.

Seka, (D.), and (H.Z.) Cross. 1995 b. Xenia and maternal effects on maize at three densities. Crop Sci. 35 : 86-90.

Seka, (D.), (H.Z.) Cross, and (P.E.) McClean. 1995. Maize kernel development *in vitro* : Sucrose concentration, xenia, and maternal effects. Crop Sci. 35 : 75-79.

Sprague, (G.F.), and (L.A.) Tatum. 1942. General vs specific combining ability in single crosses of corn. J. Am. Soc. Agron. 34 : 923-932.