

GENETIC ANALYSIS OF CHLOROPHYLL CONTENT IN MAIZE BY MIXED MAJOR AND POLYGENE MODELS

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Irfan M., J. Sun[#], Y. Liu, X. Li, and S. Yang (2014): *Genetic analysis of chlorophyll content in maize by mixed major and polygene models*- Genetika, Vol 46, No. 3, 1037-1046

Chlorophyll is an important factor which also affects the yield in maize. In this study, genetic analysis of chlorophyll content was conducted by joint segregation analysis of four generations P₁, P₂, F₁ and F_{2:4} from the cross Shen3336 × Shen3265 using the mixed major genes and polygenes inheritance models. Genetics of chlorophyll revealed that chlorophyll “a” was controlled by two main gene having additive-dominance-epistasis effects. The heritability of these genes were 56.3%. Chlorophyll “b” was controlled by two pairs of codominant major gene plus additive-dominance polygene. The heritability of these major genes and polygenes were 1.12% and 93.26% respectively. Chlorophyll “a+b” was controlled by two pairs of additive-dominance-epistatic major genes plus additive-dominance polygene having heritability of 56.2% and 5.2% respectively.

Key words: Chlorophyll, SSR, QTL, Maize

INTRODUCTION

The most abundant pigment on earth is chlorophyll which absorbs sunlight during photosynthesis (HÖRTENSTEINER and KRÄUTLER, 2011). This pigment plays an important role in electron transport and charge separation within reaction centers, thus harvesting solar energy (TANAKA and TANAKA, 2006). All heterotrophic organisms including humans depend on this energy. Chlorophyll is green in color and this color seems to have a positive psychological effect on humans (PRETTY *et al.*, 2007). In rice breeding programs, chlorophyll content is used as an effective index of high photosynthetic efficiency (KANNANGARA, 1991).

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Maize (*Zea mays* L.) is an important cereal crop which is grown in irrigated and rain fed areas through out of the world (IRSHAD *et al.*, 2002). Among all crops, maize is on number third position after wheat and rice globally. All over the world scientist's major goal is to achieve greater production using advanced molecular technology due to increased demand of this crop. This crop is being widely used as food for human and animals. Currently scientist's using QTL mapping for exploring the genetic architecture for agro-economical traits in breeding. This technique has been widely applied for crop improvement (KUMAR and KUMAR, 2009). Researchers found so many molecular markers as SSR, which are linked with traits and QTLs controlling these traits and have been cloned (ZHOU *et al.*, 2011). In maize so many traits having QTLs were mapped to all (10) chromosomes (TSONEV *et al.*, 2009; QIU *et al.*, 2011). This study was aimed to explore the genetics of chlorophyll content in maize using population of 235 F_{2,3} individuals.

MATERIALS AND METHODS

Plant Materials

To study genetics of chlorophyll content, maize hybrid Shenyu21 (F₁), bred by the Breeding Institute, Shenyang Academy of Agricultural Sciences, was used to construct a segregation population. The female parent Shen3336 had high photosynthetic efficiency and the male parent Shen3265 had weak photosynthetic efficiency. Shenyu21 seeds were grown in San Taizi experiment field of Shenyang Academy of Agricultural Sciences for F₂ seed production in May 1, 2010. In the same year, F₃ lines were advanced from individual F₂ plants in Hainan Province, China. During the 2011 crop season, the parents, Shenyu21 (F₁) and F₃ population were planted at San Taizi experiment field of Shenyang Academy of Agricultural Sciences on April 28. Sixty Shenyu21 (F₁) seeds were planted along 4 rows with 15 seeds in one row. For the 222 F₃ lines, about 15 seeds from each line were planted in a 4 m row with 0.6 m apart between rows. Because of limited seed quantities, only one experiment field (site) was conducted and replications were not possible in 2011. In 2012, the parents, Shenyu21 (F₁) and F₄ population were sown on 2nd May at San Taizi experiment field, 4th May at New Chengzi experiment field of Shenyang Leiao Seed Company. The experimental plots were completely randomized with three replications at each site. F₃ and F₄ lines were advanced from individual F₂ plants through single seed-descent. The ear leaves from 5 normal plants per line were sampled at filling stage with 3 replications.

Measurement of chlorophyll contents in leaves

The determination of chlorophyll content was carried out with the use of acetone-extract method. 0.5g ear leaves of five plants in each line were sheared, put into a test tube with 10ml ethanol/acetone extraction liquid (1:1), and were incubated 2 hrs at 65°C. After that, the liquid extracts were diluted 20 times with ethanol/acetone (1:1). The absorption of the extracts at wavelengths of 663nm (D663) and 645 nm (D645) were measured with a UV1102 spectrophotometer. The concentrations of total chlorophyll (Chl-t) were then calculated using the equations as follow according to ARNON *et al.*, (1949): $Chl-t = 20.31 A_{645} + 8.05 A_{663}$.

Statistical analysis

Joint segregation analysis of 4 generations (P₁, P₂, F₁ and F_{2,4}) from cross shen3336× shen3265 was carried out to investigate the inheritance of chlorophyll content using the mixed major gene plus polygene genetic models (GAI and WANG, 1998). The 24 genetic models were categorized into five models groups which are; (A) inheritance controlled by one pair of major genes, (B) two pairs of major genes, (C) polygenes, (D) one pair of major genes plus polygene and

(E) two pairs of major genes plus polygenes. Distribution parameters were calculated by maximum log likelihood and IECM (Iterated expectation and conditional maximization) method. The best candidate genetic model was selected according to Akaike's information criterion (AIC) value. Further, the best-fitting model was determined by 5 statistical parameters (U_1^2 , U_2^2 , U_3^2 , nW^2 and D_n). The gene effects and genetic variances were estimated by the component distribution parameters of best-fitting models using least squares estimation (LSE). The genetic variances of major gene (σ_{mg}^2) and polygene (σ_{pg}^2) were computed as $\sigma_{mg}^2 = \sigma_p^2 - \sigma_f^2$ and $\sigma_{pg}^2 = \sigma_f^2 - \sigma_e^2$, respectively, with σ_p^2 , the phenotypic variance of population; σ_f^2 , the distribution variance of population; σ_e^2 , the error variance. The heritability of major gene (h_{mg}^2) and polygene (h_{pg}^2) were obtained according to formula $h_{mg}^2 = \sigma_{mg}^2 / \sigma_p^2 \times 100$ and $h_{pg}^2 = \sigma_{pg}^2 / \sigma_p^2 \times 100$.

RESULTS AND DISCUSSION

Descriptive statistics of Chlorophyll content

The descriptive statistics of chlorophyll content among 4 generations derived from the cross shen3336 x shen3265 were listed in table 1. The chlorophyll contents of F_1 plants were little higher than parents. The coefficients of variation (CV %) among $F_{2;4}$ generation were higher than those of P_1 , P_2 and F_1 generations, indicating the existence of real variations of heredity. As shown in Figure 1, chlorophyll contents showed a continuous distribution, suggesting quantitative inheritance. The distribution curve of chlorophyll "a" "b" and "a+b" showed some major peaks indicating that chlorophyll content was controlled by some major gene while modified by several minor genes.

Table 1 Descriptive Statistical analysis of chlorophyll content among 4 generations derived from shen3336 x shen3265

Trait	Generation	Maximum	Minimum	Range	Mean	SD	CV%
Chlorophyll a	P_1	3.74	2.72	1.02	3.21	0.20	6.23
	P_2	2.88	2.42	0.46	2.67	0.15	5.61
	F_1	4.37	3.45	0.92	3.74	0.28	7.48
	$F_{2;4}$	4.27	1.22	3.05	2.94	0.45	15.3
Chlorophyll b	P_1	0.99	0.80	0.19	0.87	0.05	5.74
	P_2	0.79	0.60	0.19	0.73	0.05	6.84
	F_1	1.17	1.00	0.17	1.059	0.04	3.77
	$F_{2;4}$	1.26	0.38	0.87	0.87	0.13	14.94
Chlorophyll a + b	P_1	5.92	3.98	1.94	4.55	0.48	11.0
	P_2	3.77	2.75	1.02	3.0	0.29	9.7
	F_1	5.00	3.8	1.20	4.50	0.33	7.0
	$F_{2;4}$	5.52	1.61	3.91	3.82	0.57	15.0

Inheritance analysis of Chlorophyll content in maize

By using 24 genetic models of mixed major gene plus polygene inheritance, coded as A-E, were tested with the data of chlorophyll content from P_1 , P_2 , F_1 and $F_{2;3}$ from the cross shen3336 x shen3265 (Table 2). For chlorophyll "a" the model B-1 and C-1, for chlorophyll "b" the model C-0 and E-6 while for chlorophyll "a+b" the model C-0 and E-1 were chosen as the candidate models

for the inheritance analysis due to the lower Akaike's information criterion (AIC) values of these models than the others. According to the fitness, evaluation was done by using 5 statistical parameters such as U_1^2 , U_2^2 , U_3^2 , nW^2 , and D_n as shown in Table 3. After all evaluations, the model B-1, E-6 and E-1 was the best-fitting model for chlorophyll "a", "b" and chlorophyll "a + b" content respectively.

Table 2. Max-likelihood values and Akaike's information criterion (AIC) values of chlorophyll content under different genetic models.

Trait	Model	Max log likelihood value	AIC value	Model	Max log likelihood value	AIC value
Chlorophyll a	A-1	-169.524918	347.049835	D-0	-137.762238	291.524475
	A-2	-189.458984	384.917969	D-1	-148.322968	310.645935
	A-3	-179.826263	365.652527	D-2	-148.323975	308.647949
	A-4	-194.178635	394.357269	D-3	-148.333298	308.666595
	B-1	-126.729912	273.459839	D-4	-148.322723	308.645447
	B-2	-165.835846	343.671692	E-0	-137.764175	303.528351
	B-3	-188.898666	385.797333	E-1	-128.296539	282.593079
	B-4	-205.624146	419.248291	E-2	-137.617615	293.235229
	B-5	-182.326218	374.652435	E-3	-148.319595	310.639191
	B-6	-192.823166	393.646332	E-4	-148.319595	308.639191
	C-0	-137.764175	287.528351	E-5	-148.319839	310.639679
	C-1	-148.319595	306.639191	E-6	-148.319580	308.639160
	Chlorophyll b	A-1	191.362579	-374.725159	D-0	231.434891
A-2		171.006424	-336.012848	D-1	230.967941	-447.935883
A-3		180.981308	-355.962616	D-2	231.181519	-450.363037
A-4		167.450470	-328.900940	D-3	231.119476	-450.238953
B-1		207.023849	-394.047699	D-4	231.183289	-450.366577
B-2		195.533691	-379.067383	E-0	231.419739	-434.839478
B-3		171.248291	-334.496582	E-1	231.420624	-436.841248
B-4		154.982559	-301.965118	E-2	229.978149	-441.956299
B-5		185.278503	-360.557007	E-3	231.185471	-448.370941
B-6		168.116165	-328.232330	E-4	231.185471	-450.370941
C-0		231.419739	-450.839478	E-5	231.185501	-448.371002
C-1		231.185471	-452.370941	E-6	231.185486	-450.370972
Chlorophyll a + b		A-1	-251.835220	511.670410	D-0	-220.692993
	A-2	-257.457886	520.915771	D-1	-226.644119	467.288239
	A-3	-252.575760	511.151489	D-2	-226.613892	465.227783
	A-4	-264.913361	535.826721	D-3	-226.615326	465.230652
	B-1	-233.664856	487.329712	D-4	-226.612122	465.224243
	B-2	-241.446838	494.893677	E-0	-220.635803	469.271606
	B-3	-252.363266	512.726562	E-1	-210.133057	446.266113
	B-4	-274.194641	556.389282	E-2	-220.604538	459.209076
	B-5	-252.123398	514.246826	E-3	-226.609344	467.218689
	B-6	-256.017059	520.034119	E-4	-226.609344	465.218689
	C-0	-220.635803	453.271606	E-5	-226.609375	467.218750
	C-1	-226.609344	463.218689	E-6	-226.609329	465.218658

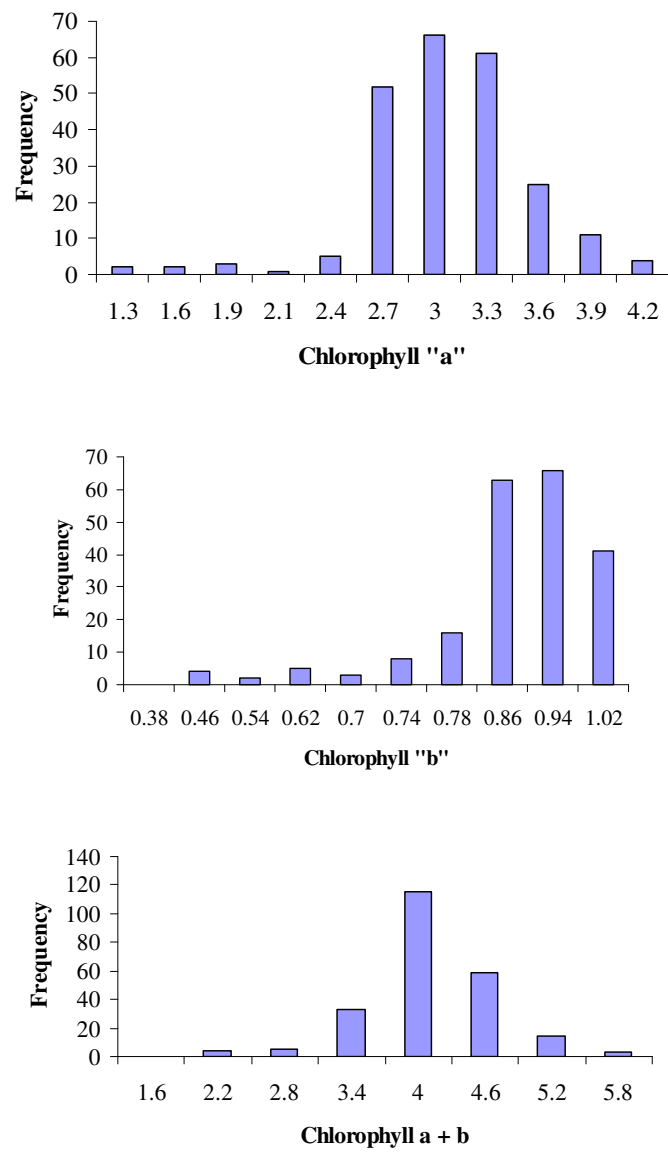


Figure 1. Frequency distribution of chlorophyll content in $F_{2:4}$ maize population.

Table 3. Tests for goodness-of-fit of candidate models for chlorophyll content.

Trait	Model	Generation	U_1^2	U_2^2	U_3^2	nW ²	D _n
Chlorophyll a	B-1	P ₁	0.219(0.6401)	0.088(0.7668)	0.390(0.5323)	0.0866	0.1856(CD(0.05)=0.3206)
		P ₂	0.800(0.3710)	0.414(0.5200)	0.795(0.3726)	0.2509	0.2865(CD(0.05)=0.3206)
		F ₁	0.002(0.9653)	0.146(0.7027)	2.874(0.0900)	0.1716	0.2037(CD(0.05)=0.3206)
		F _{2;4}	0.021(0.8843)	0.001(0.9753)	0.472(0.4919)	0.0505	0.0345(CD(0.05)=0.0899)
		P ₁	0.023(0.8806)	0.002(0.9613)	0.602(0.4378)	0.0665	0.1606(CD(0.05)=0.3206)
	E-1	P ₂	0.682(0.4088)	0.378(0.5389)	0.549(0.4588)	0.2341	0.2799(CD(0.05)=0.3206)
		F ₁	0.000(0.9966)	0.203(0.6520)	3.195(0.0739)	0.1773	0.2074(CD(0.05)=0.3206)
		F _{2;4}	0.057(0.8117)	0.010(0.9192)	0.267(0.6051)	0.0487	0.0384(CD(0.05)=0.0899)
		<hr/>					
Chlorophyll b	C-0	P ₁	0.102(0.7491)	0.018(0.8918)	0.483(0.4872)	0.0871	0.1670(CD(0.05)=0.3206)
		P ₂	0.057(0.8115)	0.416(0.5187)	2.748(0.0974)	0.1513	0.2055(CD(0.05)=0.3206)
		F ₁	0.585(0.4445)	0.621(0.4306)	0.037(0.8480)	0.1757	0.1809(CD(0.05)=0.3206)
		F _{2;4}	0.206(0.6500)	0.122(0.7271)	9.944(0.0016)	0.3801	0.0875(CD(0.05)=0.0899)
		P ₁	0.319(0.5720)	0.125(0.7240)	0.603(0.4376)	0.1121	0.1866(CD(0.05)=0.3206)
	E-6	P ₂	0.190(0.6626)	0.680(0.4097)	2.585(0.1079)	0.1671	0.2198(CD(0.05)=0.3206)
		F ₁	0.257(0.6123)	0.239(0.6250)	0.000(0.9939)	0.1285	0.1585(CD(0.05)=0.3206)
		F _{2;4}	1.049(0.3058)	0.044(0.8342)	9.792(0.0018)*	0.4636	0.0994(CD(0.05)=0.0899)
		<hr/>					
Chlorophyll a + b	C-0	P ₁	0.795(0.3726)	0.551(0.4578)	0.234(0.6288)	0.2014	0.2189(CD(0.05)=0.3206)
		P ₂	0.010(0.9213)	0.132(0.7160)	1.151(0.2834)	0.0479	0.1185(CD(0.05)=0.3206)
		F ₁	0.057(0.8107)	0.030(0.8630)	0.057(0.8121)	0.1169	0.1789(CD(0.05)=0.3206)
		F _{2;3}	0.037(0.8481)	0.192(0.6613)	6.222(0.0126)	0.2633	0.0673(CD(0.05)=0.0899)
		*					
	E-1	P ₁	0.867(0.3519)	0.597(0.4399)	0.266(0.6060)	0.2106	0.2226(CD(0.05)=0.3206)
		P ₂	0.021(0.8854)	0.165(0.6848)	1.135(0.2868)	0.0494	0.1166(CD(0.05)=0.3206)
		F ₁	0.045(0.8327)	0.020(0.8865)	0.061(0.8046)	0.1149	0.1764(CD(0.05)=0.3206)
		F _{2;3}	0.048(0.8261)	0.008(0.9288)	0.243(0.6217)	0.0494	0.0439(CD(0.05)=0.0899)

Note: * Means significant difference at 0.05; U_1^2 , U_2^2 and U_3^2 are statistics of Uniformity test; nW² is the statistic of Smirnov test. The critical value of nW² is 0.461 at 0.05 level; D_n is the statistic of Kolmogorov test.

Genetic parameter estimation

The first order and the second order parameters were estimated by using the IECM method, max-likelihood values of parameter distribution means of the best-fitting models (Table 4). Two major genes controlling chlorophyll "a" and additive effect of second gene (0.227623) was more than the first gene (0.040997). First gene was strongly dominant over second gene. Additive x additive effects of both genes was 0.190744 while dominance x dominance effects was 2.065368. Variance of these major genes was 0.116 with heritability of 56.3%. For chlorophyll "b" the model selected was E-6 having major genes and polygenes. The additive affects of one main gene and polygenes was 0.001661 and 0.064690 respectively. The dominance affects of these polygenes were 0.247361. Variations in polygenes were higher than that of main gene. The heritability of these polygenes and main gene was 93.26% and 1.12% respectively.

Table 4. The estimates of genetic parameters of chlorophyll content of $F_{2:4}$ population

Trait	Model	1 st order parameter	Estimate	1 st order parameter	Estimate	2 nd order parameter	Estimate
Chlorophyll a	B-1	m	3.307905	j_{ab}	-0.068033	σ_e^2	0.015
		d_a	0.040997	j_{ba}	-0.645202	σ_p^2	0.206
		d_b	0.227623	1	2.065368	σ_{mg}^2	0.116
		h_a	0.754876			h_{mg}^2	56.3%
		h_b	-				
		i	1.496448				
Chlorophyll b	E-6	m	0.806799			σ_e^2	0.001
		d_a	0.001661			σ_p^2	0.018
		[d]	0.064690			σ_{mg}^2	0.0002
		[h]	0.24736			σ_{pg}^2	0.0166
		1				h_{mg}^2	1.12%
						h_{pg}^2	93.26%
Chlorophyll a+b	E-1	m	3.903294	j_{ab}	1.251403	σ_e^2	0.132753
		d_a	0.000000	j_{ba}	0.219850	σ_p^2	0.32114
		d_b	0.000000	1	1.457208	σ_{mg}^2	0.180364
		h_a	0.481714	[d]	0.685533	σ_{pg}^2	0.008023
		h_b	-0.182698	[h]	-1.122663	h_{mg}^2	56.2%
		i	-0.034057			h_{pg}^2	2.5%

Note: d, Additive effect; h, Dominance effect; I, Additive×Additive effect; j, Dominance×Additive effect; 1, Dominance×Dominance effect; [d], Additive effects of the polygenes; [h], Dominance effects of the polygenes; σ_{mg}^2 , Major gene variance; σ_{pg}^2 , Polygene variance; h_{mg}^2 , Major gene heritability; h_{pg}^2 , Polygene heritability. Subscript a and b refer to two major genes.

There were no additive effects between two major genes controlling chlorophyll contents. The dominance effects of the two major genes were 0.481714 and -0.182698, respectively, larger effect by the first gene. The additive ($[d]=0.685533$) and dominance ($[h]=-1.122663$) effects of polygenes can be either positive or negative among crosses, which shows differences in their polygenic background. The additive×additive interaction effect (i) was -0.034057, whereas the dominance×dominance interaction effect (l) was 1.457208. Both additive×dominance (j_{ab}) and dominance×additive (j_{ba}) were 1.251403 and 0.219850 respectively. Heritability of major gene was greater ($h_{mg}^2=56.2\%$) than heritability of polygenes ($h_{pg}^2=2.5\%$). The fluorescence of chlorophyll was controlled by additive type of gene action (FARSHADFAR *et al.*, 2011). Total chlorophyll content in plants (cucumber, rice) was controlled by mini-polygene which was

affected by environmental factors (LI *et al.*, 2009; YANG *et al.*, 2006). ZHANG *et al.*, (2009) reported that the heritability of chlorophyll *a* and *b* was high in wheat. Chlorophyll content and photosynthetic rate is correlated with each other, thus an effective way to increase the biomass production and grain yield in crops is to increase the chlorophyll content in crops (WANG *et al.*, 2008).

ACKNOWLEDGEMENT

This study was supported from the key project of introducing foreign experts on technology management system in Liaoning province under the project “construction of crop molecular breeding technology system” and sponsored by the “Planned Science and Technology Project of Shenyang, China” (NO.F12-277-1-24).

Received August 29th, 2014

Accepted October 22th, 2014

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GENETIČKA ANALIZA SADRŽAJA HLOROFILA U SELEKCIJI KUKURUZA KORIŠĆENJEM KOMBINOVANIH I POLIGENOG MODELA

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Izvod

Hlorofil je važan faktor koji, takođe utiče na prinos kukuruza. U ovoj studiji, genetska analiza sadržaja hlorofila je vršena kombinacijom analize zajedničke segregacije četiri generacije P1, P2, F1 i F2:4 posle ukrštanja Šen3336 × shen3265 koristeći kombinaciju modela nasleđivanja major gena i modele za nasleđivanje poligenih osobina. Genetičkim istraživanjima hlorofila je otkriveno da je chlorophyll "a" pod kontrolom dva glavna, major gena koji imaju kombinaciju aditivnih - dominantnih i epistatičnih efekata. Heritabilnost ovih gena je 56,3 %. Chlorophyll "b" je pod kontrolom dva para kodominantnih major gena plus aditivno - dominantnih poligena. Heritabilnosti ovih gena i poligena je 1,12 % odnosno 93,26 %. Hlorofil "a" + "b" je pod kontrolom dva para aditivno - dominantno - epistaznih major gena plus aditivno - dominantnih poligena čija heritabilnost je 56,2% odnosno 5,2 % .

Prilmeno 29. VIII.2014.

Odobreno 22. X. 2014.