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Genetic Analysis of Plant Potassium Accumulation under Potassium Deficiency Stress at Filling Stage in Maize (*Zea Mays* L.)

X.H. Zhao, Y. Liu, C.J. Jiang, X.G. Wang, M.J. Cao, H.Q. Yu *
College of Agronomy, Shenyang Agricultural University, Shenyang, China

***Corresponding Author**
Name: Haiqiu YU
Email: haiqiuyu@163.com

Abstract: Six generations, including P_1, P_2, F_1, B_1, B_2 and F_2, were constructed by 90-21-23 (tolerance to K deficiency) and D937 (sensitive to K deficiency) in maize (*Zea Mays* L.). The genetic analysis of plant potassium Accumulation were evaluated under natural potassium deficiency experimental field using a mixed genetic model of major gene plus polygene. The results showed that the plant potassium Accumulation were controlled by two major genes with additive-dominance-epistatic effects plus polygenes (E_1_0 model). The heritability of the major gene plus polygene in B_1, B_2 and F_2 was estimated to be 57.99%, 58.94% and 52.99% respectively, and thus environment variance accounted for 41.06%~47.01% of phenotype variance. These results indicated that the most efficient selection tolerance to potassium deficiency was in the B_2 generation. The polygenes and the environmental effect also play an important role in phenotypic variation. These results indicated that advanced backcross or recurrent selection should transfer the potassium tolerance gene and selection should not perform in early generation. This study recommends that the segregation analysis can be used by maize breeder who have related segregation data to obtain important information on the inheritance of tolerance breeding material, and could be benefit breeder to improve breeding program in maize.

Keywords: Maize, Tolerance to potassium deficiency, Plant potassium Accumulation

INTRODUCTION

Potassium (K) as an essential nutrient plays an important role in crop growth and development, metabolism and yield formation process [1, 2]. According to statistics, 22.5% of the world's arable land subjected to severe nutrient stress, of which 40 percent was due to K deficiency [3]. Maize (*Zea Mays* L.) is sensitive to K deficiency in whole growth stage. Therefore, the poor potash supplying has become a limiting factor in maize production. Factors on soil K deficiency and potash mineral resources insufficient, the lack of enough import potash, more expensive potash imports, increasing cost of cultivation, are becoming a series conflicts urgently to be solved [4, 5]. Therefore, it necessary to cultive maize genotypes efficient use of potassium and to clarify its genetic mechanism of tolerance to low K stress, which should benefit to improve yield in maize.

The total amount of K absorbed by crop was compositely affected by some factors, including the crop species, the amount of K^+ availability in the soil, the amount of fertilizer K^+ applied, the growth conditions and the field management [6, 7]. The majority of K^+ uptake in soybean and cotton occur after flowering [8, 9]. On the other hand, most of K^+ uptake in maize takes place at silking stage [10]. In addition, some studied indicated that the crop varieties resistant to low K by adjusting the root morphology and the absorption ability to adapt K deficiency stress [11, 12].

A genetic model named as mixed major gene and polygene inheritance model was proposed by Gai and Wang [13]. The exsitance of major genes and polygenes can be evaluated by modifing the mixed genetic model. In addition, the genetic parameters for major and minor genes can be estimated. So far, there were many reports about the application of the mixed genetic model [14, 15]. The researches evaluating the inheritance of various traits have been reported by joint various segregations, such as maize [16], wheat [17], rice [18], cotton [19], soybean [20]. The joint segregation of five populations were used to analysis the inheritance of erucic acid in *Brassica napus* L. by method of mixed major gene plus polygene genetic model, which indicated that inheritance of erucic acid was controlled by two major genes with additive-dominance-epistatic effects plus polygenes [21]. However, these are few studies in genetic traits under nutrition deficiency condition.

In this study, six generations, including P_1, P_2, F_1, B_1, B_2 and F_2, were measured the plant K Accumulation under K deficiency stress field using a mixed genetic model of major gene plus polygene in maiz. The objectives are to explain the genetic regulation of plant K Accumulation under K deficiency stress and to afford the scientific method to improve breeding program for nutrition deficiency in maize.

MATERIALS AND METHODS

The experiment was carried out in Manduhu Town (41°32′N, 122°43′E), Liaozhong County, Shenyang City, Liaoning Province located on the Northeast China Plain in 2012. The soil of experimental field is classified as sandy with lack of K. The initial soil nutrition elements were available K 48.3 mg/kg, alkaline hydrolysis N 87.3 mg/kg, Olsen-P 43.1 mg/kg. Two inbred lines, 90-21-3 (P_1 tolerance to K deficiency) was from "Ludahongu" group and D937 (P_2 sensitive to K deficiency) was from "Reid" group, were used to construct the genetic group including F_1, B_1 ($F_1 \times P_1$), B_2 ($F_1 \times P_2$) and F_2. The F_1, B_1, B_2 were constructed using 90-21-3 and D937 in 2011. In the same year, F_2 population was developed from self-cross of F_1 seed in Hainan Province, China. Six generations (P_1, P_2, F_1, B_1, B_2 and F_2) were cultured on 6th May 2012. 30 seeds of P_1, P_2 and F_1 were planted along 3 rows with 10 seeds in one row. Randomized block design with three replications was used. For B_1, B_2 and F_2, 190 seeds were planted in a 6.5m row with 0.6m apart between rows.

At filling stage, 10 representative plants of P_1, P_2 and F_1 were collected in each test plot, while all plants of B_1, B_2 and F_2 population were collected. Each leaf, stem, tassel, ear and roots were dried at 105℃ for 30 min, then kept at 75℃ until completely dry (about 2days). Grinding mill prototype of each leaf, stem, tassel, ear and roots, with the H_2SO_4-H_2O_2 digestion [22], using flame photometer (Sherwood M410 Flame photometer, England). Using the formula K accumulation (mg) = K Accumulation (mg/g) × sample dry weight (g) calculation of plants in different parts of K accumulation.

The software of mixed genetic model of major gene plus polygene was used to analysis the genetic character of plant K Accumulation reported by Gai and Wang [13] and zhang et al. [23]. By maximum log likelihood method and IECM (Iterated expectation and conditional maximization), component distribution parameters of the above four generations were calculated and candidate genetic models were selected referring to Akaike's information criterion (AIC) value. Further, the best-fitting model was determined by 5 statistical parameters ($U1^2$, $U2^2$, $U3^2$, 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 ($\sigma^2 mg$) and polygene ($\sigma^2 pg$) were computed as $\sigma^2 mg=\sigma^2 p-\sigma^2 f$ and $\sigma^2 pg=\sigma^2 f-\sigma^2$, respectively, with $\sigma^2 p$, the phenotypic variance of population; $\sigma^2 f$, the distribution variance of population; σ_e^2, the error variance. The heritability of major gene ($h^2 mg$) and polygene ($h^2 pg$) were obtained according to formula $h^2 mg=\sigma^2 mg/\sigma^2 p \times 100\%$ and $h^2 pg=\sigma^2 pg/\sigma^2 p \times 100\%$.

RESULT AND DISCUSSION

Frequency distribution

The distributions of plant k accumulation of six generations were showed in table 1. The results showed the plant K Accumulation of P_1 is mainly distributed in the range of 0.30～0.75 g/plant, while plant K Accumulation of P_2 is mainly distributed in 0.30～0.60 g/strain range. F_1 plants are mainly distributed in the range of 0.45～1.35 g/plant. However, the groups of B_1, B_2 and F_2 separation range is larger than tow parents, the separation phenomenon is more obvious. The plant k Accumulation of B_1 and B_2 was changed from 0.30～1.35 g/plant and 0.15～1.35 g/plant. It was worthy note that the variation of F_2 was changed 0.30～1.65 g/plant. It is unimodal distribution of F_2 generation, while two backcross generations of B_1 and B_2 showed the multi-peak distribution (Fig. 1). These results indicated that plant K Accumulation was controlled by one major gene while modified by several minor genes. The positive and negative transgressive advantages were observed in F_2 population.

Table 1: Frequency distribution of plant K Accumulation in various generations

Generation	K Accumulation in plant (g/plant)												
	0	0.15	0.3	0.45	0.6	0.75	0.9	1.05	1.2	1.35	1.5	1.65	No.
P_1			6	10	4	3							23
P_2			11	10	2								23
F_1				1	1	7	9	1	2	2			23
F_2			10	33	38	20	8	5		1	1	1	117
B_1			15	25	33	23	14	6	2	4			122
B_2		2	14	31	31	19	9	5	1	2			114

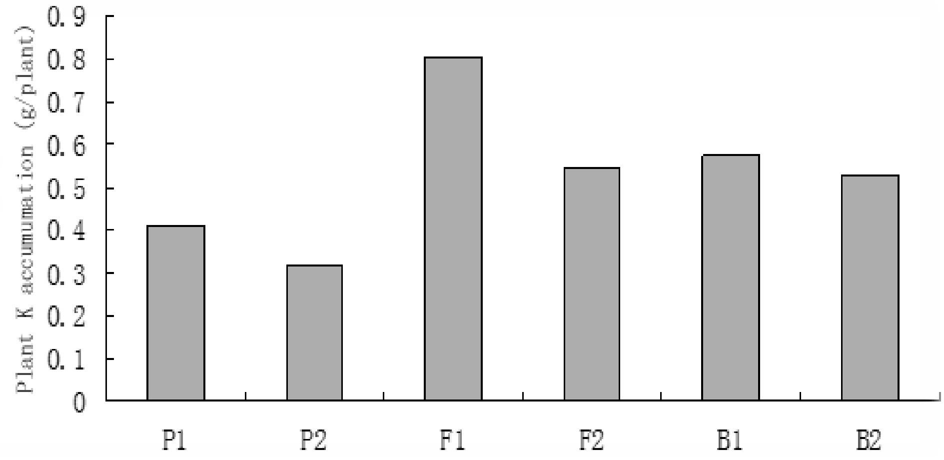

Fig. 1: Distribution of plant K Accumulation in various generations

Potassium tolerance is an important quantitative trait for screening of maize genotypes on infertile field. In our previous study, the inbred line 90-21-3 was screened and indicated it can absorb more potassium than other inbred lines to maintain normal growth [24]. In this study, variation of plant K Accumulation in B_1, B_2, F_1, F_2 generally somewhat wider than the value of 90-21-3 tolerance to K deficiency and most families were gather near the mid-parent values. Distribution of genetations showed that the inheritance of K tolerance should be controlled by two major genes plus polygene.

AIC value of variant inheritance models

The AIC value of variant inheritance models for K Accumulation in plant were showed in table2 in 6 various generations. Total 24 model were used to evaluated the optimum AIC value, while those of B_1_1, E_1_0 and E_1_1 models were lower than other models, were -61.49,-60.70 and -60.70, respectively. Preliminary, B_1_1, E_1_0 and E_1_1 models were screened as the alternative models to further analysis. Then a set of suitable detections were used to check the above three model test, which the model showed the least significant should be selected as the most suitable model.

Table 2: AIC value of variant inheritance models for K Accumulation in plant in various generations

Model	*AIC* value	Model	*AIC value*
A_1	-18.9023	D_0	-40.0985
A_2	23.14241	D_1	-
A_3	9.533322	D_2	-
A_4	24.97872	D_3	-37.9748
B_1_1	-61.4855	D_4	-51.2768
B_1_2	-29.9081	E_1_0	-60.6975
B_1_3	111.4479	E_1_1	-56.525
B_1_4	23.02276	E_1_2	-41.7614
B_1_5	9.123119	E_1_3	-38.5426
B_1_6	7.122762	E_1_4	-37.1201
C_0	-34.9485	E_1_5	-35.1082
C_1	-39.1117	E_1_6	-

The tests for goodness-of-fit of inheritance models were evaluated by 5 statistical parameters as shown in table 3. Three tests for goodness-of-fit, equal distribution (U_1^2, U_2^2, and U_3^2), Smirnov (nW^2) and Kolmogorov test (Dn) were applied o determine the goodness-of-fit. The results showed that 8 statistical parameters (U_1^2, U_2^2, U_3^2, nW^2 and Dn) were significant for model E_1_0. Thus E_1_1 model has 4 statistic parameters (U_2^2, U_3^2, nW^2 and Dn) reached significant level. However, only one statistic parameter (U_3^2) was reached significant level for E_1_0. Due to the differences between the model which holding the least significant statistics and other selected models were not significant, the model which holding the least significant statistics was the best fitting model. Therefore, the "additive-dominance-epistatic +polygene" model was chosen as the candidate models for the inheritance analysis due to the lower AIC values of these models than the others.

Table 3: Tests for goodness-of-fit of inheritance models for K Accumulation in plant

Model	Generation	U_1^2	U_2^2	U_3^2	nW^2	D_n
B_1_1	P_1	0.853(0.3556)	0.605(0.4369)	0.219(0.6399)	0.1957	0.1955
	F_1	4.186(0.0407) *	2.259(0.1328)	3.657(0.0558)	0.5900*	0.3190*
	P_2	2.705(0.1001)	5.043(0.0247) *	6.828(0.0090) *	0.6103*	0.3010*
	B_1	0.014(0.9048)	0.044(0.8347)	0.138(0.7101)	0.0514	0.0493
	B_2	0.837(0.3602)	1.633(0.2014)	2.455(0.1172)	0.2354	0.126
E_1_0	F_2	1.690(0.1936)	3.598(0.0579)	6.513(0.0107) *	0.4074	0.1224
	P_1	0.121(0.7276)	0.034(0.8536)	0.374(0.5410)	0.1144	0.1539
	F_1	0.379(0.5384)	0.107(0.7436)	1.155(0.2826)	0.1318	0.1833
	P_2	0.012(0.9135)	0.753(0.3855)	9.306(0.0023) *	0.307	0.2475
	B_1	0.754(0.3852)	1.094(0.2956)	0.674(0.4118)	0.1179	0.0808
	B_2	0.816(0.3665)	1.453(0.2281)	1.750(0.1858)	0.2886	0.126
E_1_1	F_2	0.687(0.4072)	0.978(0.3228)	0.556(0.4561)	0.153	0.1006
	P_1	2.210(0.1371)	1.208(0.2717)	1.854(0.1733)	0.363	0.248
	F_1	2.190(0.1389)	0.993(0.3191)	3.050(0.0807)	0.3669	0.2657
	P_2	0.035(0.8525)	0.340(0.5600)	9.309(0.0023) *	0.3025	0.2618
	B_1	0.008(0.9298)	0.118(0.7315)	1.064(0.3023)	0.0568	0.0491
	B_2	3.430(0.0640)	4.249(0.0393) *	1.150(0.2835)	0.5978*	0.1603*
	F_2	0.007(0.9316)	0.035(0.8521)	1.163(0.2809)	0.071	0.0677

Note: Value in Parenthesis means Probability, *indicate the significant at 5%.

Estimates of inheritance parameters

Table 4 showed the estimates of genetic parameters for relative conductivity by additive-dominant- epistatic+ polygene model. According the model, the plant K Accumulation was controlled by two pairs of main genes, which showed dominant and additive by additive, dominance x dominant and additive x dominant effect.

Table 4: Estimates of inheritance parameters for K Accumulation in plant

1st order parameter	Estimate	2nd order parameter	Estimate		
			B_1	B_2	F_2
m_1	-0.06	σ_p^2	0.061	0.063	0.055
m_2	0.84	σ_{mg}^2	0.035	0.005	0.026
m_3	0.47	σ_{pg}^2		0.032	0.003
m_4	0.44	$\sigma^2 e$	0.026	0.026	0.026
m_5	0.66	h_{mg}^2 (%)	57.99	7.54	47.28
m_6	0.58	h_{pg}^2 (%)		51.4	5.71
d_a	0.16	$h_{mg}^2 + h_{pg}^2$ (%)	57.99	58.94	52.99
d_b	0.16				
h_a	-0.09				
h_b	-0.09				
i	0.15				
j_{ab}	-0.09				
j_{ba}	-0.09				
l	0.15				

σ^2_p: phenotypic variance; σ^2_{mg}: major gene variance; σ^2_{pg}: polygene variance; σ^2_e: environmental variance; h^2_{mg} *(%)*: heritability of major gene; h^2_{pg}*(%)*:heritability of polygene.

The additive effect (*da*) of first pair of main gene and the additive effect (*db*) of second pair of main gene were 0.16 and 0.16, which indicated that they have a positive additive effect. The dominant effect (*ha*) of first pair of main genes and the dominant effect (*hb*) of second pair of main gene were -0.09 and -0.09, which indicated that the two pair of main genes showed a negative effect. The inheritances of main gene were 7.54% and 47.28% in B_2 and F_2 generations, which it was 57.99% in B_1 generation. The genetic ratios of polygene were 0, 51.4% and 5.71% in B_1, B_2 and F_2 generations, respectively. However, the main gene+polygene genetic ratio were 57.99%, 58.94% and 52.99%, respectively. These results showed indicated that the plant K Accumulation was controlled by main gene and significantly affected by minor polygene. So it is more efficient to screen higher K Accumulation inbred lines in B_1 generation. The genetic variation coefficient of in B_1, B_2 and F_2 generations were changed from 52.99%～58.94%. It was worthy note that the environmental variation coefficient contributed 43.36% to the phenotypic variation coefficient, indicating the environment effect was important in breeding for tolerance to K deficiency.

The classic Mendelian method indicates the quantitative traits as multigenes and overall estimates gene effect sizes and modes of gene action. However, the mixed inheritance model of major genes and polygenes suit foe segregation analysisand could provides an efficient way to evaluate the inheritance of complex traits [25]. Korir *et al*. [26] evaluated the inheritance of aluminum tolerance using recombinant inbred line population in soybean based on major gene plus polygene mixed inheritance model. They indicated that the major genes and polygenes contributed about 50% and 30% to the phenotypic variation were both important in breeding for Al tolerance. In addition, Rezende *et al*. [27] reported the inheritance of anthracnose leaf blight was evaluated in maize by mixed model using six generations. Results indicated that mixed model major genes and polygenes were benefit to explain the inheritance of anthracnose leaf blight in maize. In this study, Six generations constructed by 90-21-3 (tolerance to K deficiency) and D937 (sensitive to K deficiency) were carried out to measure the genetic analysis of plant K Accumulation in maize using a mixed genetic model of major gene plus polygene. The results indicated that the two pair main genes and polygenes played the same important role for plant K accumulation, and the environmental effect largely affect the trait variation. It implies that the effect of polygene and environmental effect should be paying more attention on crop breeding program.

The appropriate breeding means should improve the breeding program, so it is necessary to explain the the major gene and polygene genetic rule of quantitative traits. In crop breeding program, single cross recombination or simple backcross is usually used to transfer positive major genes for quality traits. However, polymerization backcross or recurrent selection is employed to cumulate potitive polygenes for quantitative traits. Zhang *et al*. [28] constructed six generations populations from cross H077×H113 and evaluated the inheritance of cryotolerance in cotton by the mixed genetic model of major gene and polygene during the overwintering period. They indicated that the whole heritability in F_2 was always higher than that in B_1 and B_2 in each cross. So the method of single cross recombination or single backcross should be adopted to transfer major genes, and the selection in F_2 would be more efficient than that in other generations. However, the inheritances of main gene and the main gene plus polygene were higher in B_1 generation than those in B_2 and F_2 generations. These results indicated that, for potassium tolerance, it is need advanced backcross o with tolerance parent recurrent to transfer the potassium tolerance gene and selection should not perform in early generation.

CONCLUSION

The plant K Accumulation were controlled by two major genes with additive-dominance-epistatic effects plus polygenes. The major genes and polygenes were equivalently controlling the plant K Accumulation. The environmental effect also plays an important role in phenotypic variation. Advanced backcross or recurrent selection should be used to transfer the K tolerance gene and selection should not perform in early generation.

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