Full Length Research Paper

Genetic analysis of yield in peanut (*Arachis hypogaea* L.) using mixed model of major gene plus polygene

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A recombinant inbred line (RIL) population with 215 lines derived from a cross between a highly yield line Zheng8903 (female parent) and a variety Yuhua No.4 (male parent) was used in this research. The RILs population was grown in three environments to make a genetics analysis of yield from F_7 to F_9. Jointly segregating analysis was used to analyze the genetics of yield in the combination of Zheng8903×Yuhua No.4 using the method of major gene plus polygene mixed inheritance model. The results indicated that the optimum model of yield trait was two major genes plus polygenes mixed inheritance models and its expression could be greatly influenced by different environments. The heritability of major gene for the yield trait in the RILs was 70.73, 40.29 and 37.79% at Zhengzhou, Sanya and Yuanyang, respectively. The yield had significant major gene effect and the results implied that not only should the two major genes' effects be considered but also the polygene's effect should be considered in breeding to increase peanut yield.

Key words: Peanut, yield, major gene plus polygene inheritance model, genetic analysis.

INTRODUCTION

Peanut consists of diploid (2n = 2x = 20), tetraploid (2n = 4x = 40) and aneuploid species (2n = 2x = 18), belonging to the genus *Arachis* that incorporates 69 species. The domesticated peanut (*Arachis hypogaea* L.) is an important legume worldwide and provides a major source of digestible protein, cooking oil and also is a significant source of animal feed and important raw materials for many industrial products (Mouecoucou et al., 2004; Liu et al., 2008). China is the major producer and the planting acreages and its yield accounts for one third of those in the world (Yang, 2009; Liu et al., 2009b).

Yield is a very important quantitative trait, which is easily affected by the environment and difficult to

investigate. The polygenic nature of many characteristics and the phenotypic plasticity inherent in environmental effects makes the study of the genetic basis and architecture for polygenic traits more difficult than mono-genic traits (Xu, 2002). Selection for yield ever has been the basis for improving groundnut productivity in the world (Nigram et al., 1991), but gain from such selection is slow due to large environmental effects. Reports show that it is an important method to increase yield through standard plant breeding in recent years (Liu et al., 2009a). Yield improvement is the most important component and research to improve yield has gained extensive attention (Yang et al., 2005).

The use of physiological models offer a means of identifying traits linked with yield and may contribute to improvements in the efficiency of breeding. The exploitation of this approach in segregating populations has been hampered by the difficulties of measuring physiological traits on individual plants without either destroying the plant or incurring great cost. Additional or improved selection criteria and procedures are needed.

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Previous studies suggest that, the inheritance of yield was mainly controlled by the effect of genes and also by the interaction of genotype and environment. Some experiments indicated that, the inheritance of yield was conducted by additive and non-additive genetic effects (Layrisse et al., 1980; Yin et al., 2005). The other reports demonstrated that, the non-additive genes effects were more important than additive genes effects in peanut trait of yield (Sandhu and Khehra, 1976).

A simple yield model provides a frame work for the understanding of yield variation among different geno-types in different environments (Duncan et al., 1978). There are investigations on the genetic model of yield to increase peanut yield, but no report about mixed genetic model of yield in peanut is known. This work presents a joint analysis of mixed genetic model of major gene plus poly-genes of peanut yield in three environments.

MATERIALS AND METHODS

Plant materials

Peanut line Zheng8903 and cultivar Yuhua No.4 which had difference genetic background and big differences in yield were used as the parents. Germplasm Zheng8903 was an elite line developed by the peanut Laboratory of Henan Academy of Agricultural Science, under both favorable and adverse environmental conditions. Yuhua No. 4 is a market-type peanut cultivar also released by peanut Laboratory of Henan Academy of Agricultural Sciences.

Recombinant inbred line (RILs) population (Zheng8903×Yuhua No.4) was constructed by Henan Academy of Agricultural Science, in 2001 through the method of single seed descent (SSD) from generation F_2 to F_7.

Experimental methods

Field experiments were conducted by the peanut Laboratory of Henan Academy of Agricultural Science. The field trial was a randomized complete design. The RILs and both parents were grown in three locations which were Zhengzhou, Sanya and Yuanyang farm, in 2007, 2007 and 2008 growing seasons, respectively. These sowing dates were expected to coincide with the suitable weather conditions conducive to the seed germination. There were different planting dates to ensure sufficient variation in yield for the RILs in the three environments.

The materials were composed of three generations (P_1, P_2, and RILs). Parents P_1, P_2 and RILs planting were randomized in each place; length and width of the row were 3.0 and 0.4 m, respectively. The trial consisted of single row plots of dimension containing 20 plants.

The yield measurements were carried out in the harvest season. The yield of P_1, P_2 and RILs was measured using JJ2000B precise balance. The parents and populations were analyzed with 5 data-mining of each row. Descriptive statistics of yield in different condition was performed to test the differences among the RILs. Genetic variability among the RILs, coefficient of variance (CV), kurtosis and skewness values were estimated, respectively. All necessary computation for yield was performed with the SPSS 13.0 software.

Genetic analysis

The genetic analysis method adopted the mixed genetic model of major gene plus polygenes (Gai, 2006). Under the modifications of polygene and environment, it was supposed that the effects of major gene in segregation generation display an independent normal distribution and then, the whole segregation generation could be seen as a mixed distribution made up by many independent normal distributions. Statistical deduction can be regarded as an estimation of probability distribution of observed value according to the principle of entropy maximization suggested by Akaike. Therefore, comparison of the goodness-of-fit of practical frequency distributions with the standard curves can approximate the inheritance model of a quantitative trait. The most-fitting genetic model was chosen according to Akaike's information criterion (AIC). Akaike suggested that, the hypothesis maximizing the expected entropy should be selected as the most fitting model. The smallest AIC value is the most-fitting genetic model. Next, the selected models were further tested for goodness-of-fit to find the best-fitted model.

Calculated software was provided by Soybean Research Center of Nanjing Agricultural University. Inheritance parameters were estimated with the method of Gai et al. (2003).

RESULTS

Statistical analysis of yield

Descriptive statistics showed variation of yield in the parents and RILs (Table 1). The means of yield per plant of P_1 and P_2 in Zhengzhou were 30.59 and 15.43 g, respectively. The means of yield per plant of P_1 and P_2 in Sanya were 39.03 and 12.04 g, respectively. The means of yield per plant of P_1 and P_2 in Yuanyang were 33.69 and 7.17 g, respectively. Obviously, the RILs population had a tendency toward the female parent in Sanya and Yuanyang; but the RILs population had a tendency toward the male parent in Zhengzhou. The yield of RIL population in the three environments showed a wide range of variation and a great number of lines exceeding the parents were found. The range of yield per plant in Zhengzhou was 5.34 to 34.51 g, the variance of yield in Sanya was 11.89 to 59.19 g and the range of yield in Yuanyang was 6.33 to 48.38 g. The range of coefficient of variance % of yield was 24.96 to 33.77% in different conditions. The kurosis and skewmess value indicated that the yield of RIL in different condition was continuity and slightly positive skew distribution. Figure 1 suggested that, the distribution characteristics of yield in RIL population in different condition are a mixture of normal distributions, showing a character of obvious mixed major gene plus polygenes.

Genetic analysis on mixed model of yield

Selection for fitting model
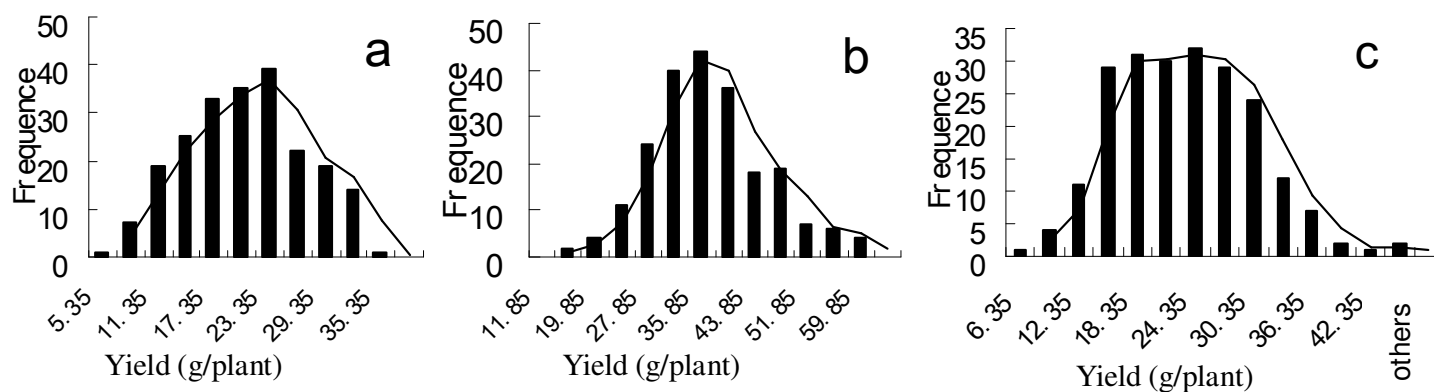
Table 2 showed that model E-1-5 was the fitting model in

Table 1. Variation parameters in parents and RILs population.

Trait	Environment	Parent			RIL population						
		Female (P₁)	Male (P₂)	Mid-parent	Mean	Min	Max	SD	CV%	Kurtosis	Skewness
Yield per plant (g)	Zhengzhou	30.59	15.43	23.01	19.22	5.34	34.51	6.49	33.77	-0.61	0.08
	Sanya	39.03	12.04	25.53	34.94	11.89	59.19	8.72	24.96	0.16	0.36
	Yuanyang	33.69	7.17	20.43	22.71	6.33	48.38	6.48	31.98	1.02	0.48

Table 2. AIC value of yield analyzed in the different environments.

Environment	Model code	Implication of model	AIC value
Zhengzhou	E-1-5	MX2-AER-A	1391.43
	E-1-4	MX2-AED-A	1391.43
	E-1-1	MX2-AI-I	1391.88
Sanya	E-1-0	MX2-AI-I	1525.25
	E-2-0	MX2-AI-I	1526.60
	E-2-7	MX2-ACE-A	1526.89
Yuanyang	E-1-5	MX2-AER-A	1429.99
	C-0	PG-ADI	1430.55
	E-1-9	MX2-AIE-A	1430.60

MX, Mixed major gene plus polygene model; PG, polygene model; A, additive effect; AD, additive + dominance; I, interaction (additive + additive); ED, epistatic dominance; ER, epistatic recessiveness; CE, complementary effect; IE, inhibiting effect.

Figure 1. Frequency distribution of yield in RILs at the three environments. a, Zhengzhou; b, Sanya; c, Yuanyang.

Zhengzhou. AIC value of model E-1-5 was the least, been 1391.43. Also, Table 2 indicated that, E-1-0 was the best fitting model in Sanya among the mentioned E models. AIC value of model E-1-0 was the lowest, been 1525.25. For the model of Yuanyang, E-1-5 was the suitable model. AIC value of model E-1-5 was 1429.99.

Tests of goodness-of-fit for better genetic model

Comparison of the expected distributions with the observed distributions can determine the fitness of the selected model with the observed data. Three tests for goodness-of-fit; equal distribution (U_1^2, U_2^2 and U_3^2), Smirnov ($_nW^2$) and Kolmogorov test (D_n) were applied to determine the goodness-of-fit. Table 3 suggests that, the statistics of the three genetic models of the three environments had no significant differences among E-1-5, E-1-0 and E-1-5 which were the fitting genetic models for yield.

Table 3. Tests of goodness-of-fit in the three selected genetic models.

Environment	Model	AIC	Generation	Statistic				
				U_1^2	U_2^2	U_3^2	nW^2	Dn
Zhengzhou	E-1-5	1391.43	P_1	0.00(0.99)	0.02(0.88)	0.40(0.53)	0.06	0.34 (p > 0.05)
			P_2	0.00(0.99)	0.02(0.88)	0.40(0.53)	0.06	0.34 (p > 0.05)
			RIL	0.01(0.91)	0.04(0.85)	0.13(0.73)	0.04	0.060(p > 0.05)
Sanya	E-1-0	1525.25	P_1	0.00(0.99)	0.03(0.87)	0.40(0.53)	0.06	0.34 (p > 0.05)
			P_2	0.00 (1.00)	0.03(0.87)	0.40(0.53)	0.06	0.34 (p > 0.05)
			RIL	0.04(0.84)	0.12(0.73)	0.34(0.56)	0.05	0.043(p > 0.05)
Yuanyang			P_1	0.00(0.99)	0.03(0.87)	0.40(0.53)	0.06	0.34 (p > 0.05)
	E-1-5	1429.99	P_2	0.00(0.99)	0.03(0.87)	0.40(0.53)	0.06	0.34 (p > 0.05)
			RIL	0.11(0.74)	0.07(0.79)	0.04(0.84)	0.05	0.05(p > 0.05)

The value in parentheses after U_1^2, U_2^2 and U_3^2 means the probability and after Dn means the significant level.

Table 4. Genetic parameters estimated for the most fitting model of yield.

Environment	Model	Genetic parameters						
		m	da	db	i	σ_p^2	σ_{mg}^2	h_{mg}^2 %
Zhengzhou	E-1-5	19.16	0.15	4.00	-	42.14	29.81	70.73
Sanya	E-1-0	35.04	3.36	3.18	3.15	76.05	30.64	40.29
Yuanyang	E-1-5	21.98	3.72	-3.10	-	49.03	18.53	37.79

m, mean of population; d, means additive effect of major gene; I, the means additive×additive interaction; σ_P^2, the means of phenotypic variance; h_{mg}^2% , means of heritabilities of major gene.

Estimation of genetic parameters for the most fitting model

Yield was controlled by two additive major gene plus additive and polygenes. Table 4 demonstrates that, the heritabilities of the major gene in Zhengzhou were 70.73%, in Sanya was 40.29% and in Yuanyang was 37.79%. At Zhengzhou, the additive effect of the two major genes was 0.15 and 4.00, respectively. The additive effect of one major gene in Sanya was 3.36 and the other major gene was 3.18 indicating that, the allele in the parents increased the yield in Sanya. In Sanya, the additive×additive interaction was 3.15. In Yuanyang, the additive effect of one major gene was 3.72 and the other major gene was -3.10, indicating that the allele in the parents increased and decreased the yield in Yuanyang.

DISCUSSION

Yield and related traits are important quantitative traits closely affected by the environment and their inheritances are very complicated. It reflects the interaction of the environment with all growth processes that occur throughout the life cycle, for example, the yield of peanut.

Therefore, the results in literature are quite controversial. Some researches indicated that, yield was affected by additive and non-additive genes (Layrisse et al., 1980; Yin et al., 2005). Other reports showed that the yield was affected by non-additive genes (Sandhu and Khehra, 1976).

The permanent segregation population of RILs was very effective for genetic analysis. This work adopted RILs and experiments in multiple environments to assess genotype × environment interactions. If a joint segregation analysis of multiple generations is used to study the inheritance of yield, a comprehensive result could be obtained. Segregation of the effects of major genes from polygenes and the environments is important for understanding the expression of a major gene in relation to its genetic background and for predicting the segregation of a cross in breeding (Jiang et al., 1994). In order to eliminate the effects of the environment, in this research, the segregation generations of RILs were investigated in three environments. The results indicated that, genetic model E was the most fitting genetic model for the trait. In other words, the yield of peanut was controlled by two major genes plus polygenes. Mather (1955) proposed that, genes interaction or epistatic effect was one of the key factors about heterosis. The work showed both

maternal effect and epistatic influence of genes.

The results revealed a very wide variation in the segregation populations of RILs and a mixture of normal distributions. The heritability of the major gene in Zhengzhou was higher than that in Sanya and Yuanyang. Therefore, it would have a high efficiency when selection for high yield is conducted in different environments in breeding. A joint analysis with multiple generations estimated genetic parameters more precisely and also indicated that, the mixed model of major gene and polygenes was applicable to analyze the inheritance of yield in peanut.

In addition, it was found that 12, 62 and 9 segregate individuals expressed yield higher to those of their parents in Zhengzhou, Sanya and Yuanyang, respecttively. Among the transgressive lines in Sanya, 6 were common with that in Zhengzhou and 3 were common with that in Yuanyang, respectively. Presumably, because the peanut originated in South America, tropical environment and external factors can induce the full play of its own characteristics. The same lines that were better than those of the parents in the different locations should have stable genetic factors. The stable genetic factors will be the research focus for further work.

ACKNOWLEDGEMENT

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