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RESEARCH ARTICLE

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Analysis of embryo, cytoplasm and maternal effects on fatty acid components in soybean (*Glycine max* Merill.)

Abstract The quality of oil determined by the constituents and proportion of fatty acid components, and the understanding of heredity of fatty acid components are of importance to breeding good quality soybean varieties. Embryo, cytoplasmic and maternal effects and genotype × environment interaction effects for quality traits of soybean [*Glycine max* (L.) Merrill.] seeds were analyzed using a general genetic model for quantitative traits of seeds with parents, F_1 and F_2, of 20 crosses from a diallel mating design of five parents planted in the field in 2003 and 2004 in Harbin, China. The interaction effects of palmitic, stearic, and linoleic acid contents were larger than the genetic main effects, while the genetic main effects were equal to interaction effects for linolenic and oleic acid content. Among all kinds of genetic main effects, the embryo effects were the largest for palmitic, stearic, and linoleic acids, while the cytoplasm effects were the largest for oleic and linolenic acids. Among all kinds of interaction effects, the embryo interaction effects were the largest for fatty acids. The sum of additive and additive × environment effects were larger than that of dominance and dominance × environment effects for the linolenic acid content, but not for other quality traits. The general heritabilities were the main parts of heritabilities for palmitic and oleic acid contents, but the interaction was more important for stearic, linoleic, and linolenic acid contents. For the general heritability, maternal and cytoplasm heritabilities were the main components for palmitic, oleic, and linolenic acid contents. It was shown for the interaction heritabilities that the embryo interaction heritabilities were more important for oleic and linolenic acid contents, while the maternal interaction heritabilities were more important for linoleic acid content. Among selection response components, the maternal and cytoplasm general responses and /or interaction responses were more important for palmitic, stearic, oleic, and linoleic acid contents. The main selection response components were from the embryo general response and / or interaction response for linolenic acid content. It suggested that the selection of palmitic, stearic, oleic, and linoleic acid contents in offspring should be in maternal plants, while linolenic acid content should be improved by screening or selecting the single seed in higher generations.

Keywords soybean, fatty acid, embryo effect, cytoplasmic effect, maternal effect, heritability

1 Introduction

Soybean [*Glycine max* (L.) Merrill.] is one of the most important oil crops, and its oil quality is determined by content and ratio of fatty acid composition in the oil. It is important to understand the genetic mechanisms for an oil quality breeding program, which is an important approach to improve fatty components. There have been some reports about the inheritance theories of fatty acids in soybean seeds. Fatty acid component inheritance of soybean embodies quantitative traits with normal distribution and positive or negative exceed-parents phenomena in F_2 (Martin et al., 1983; Hu et al., 1990; Zhang, 1991). Seed traits should be controlled by embryo, cytoplasm, and maternal plant effects. Some experiments were conducted by reciprocal cross, but the conclusions were inconsistent. Brim et al. (1968) and Singh and Hadley (1968) found that the maternal effects could control the fatty composition content in F_1, but Wilson et al. (1981), Martin et al. (1983), Fu and Yang (1994) and Primomo et al. (2002a) found there were no maternal effects in F_1. Liu et al. (1988) and Hu et al. (1990) estimated the heritability of five fatty acid compositions in F_2. The above-mentioned analysis on heritability focused on nuclear inheritance and ignored cytoplasm and maternal effects in single environment. Furthermore, as a result of the meteorological element (Rennie and Tanner, 1989; Ma et al., 1999), there was inconsistency in different environments (Zhang et al., 1990; Schnebly and Fehr, 1993; Nian et al., 1997; Rebetzke et al., 2001; Primomo

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et al., 2002b), which would interfere in the efficiency of selection for improving fatty compositions in early generations. Zhu (1997) proposed a general seed genetic model which was gene main effect and genotype × environment interaction effects including embryo, cytoplasm and maternal effects. Some studies had been carried out using the model (Wu et al., 1995; Shi et al., 1996; Wang et al., 2003). In the present experiment, a two-year data of 20 crosses from diallel mating design of five parents were analyzed by the general seed genetic model (Zhu, 1997) in the embryo, cytoplasm and maternal effects and genotype × environment interaction effects related to fatty acid compositions in soybean. Our objective was to find a theoretical basis for soybean breeding.

2 Materials and methods

2.1 Genetic experiment

The mating design used in this experiment was a diallel cross with five parents, Dongnong42 (P1), Dongnong46 (P2), Dongnong7819 (P3), Nongda5129 (P4), and Heinong35 (P5) that were spring soybean genotypes from Heilongjiang Province of China. All parents were crossed with each other in 2002. Seeds of parents, F_1 and F_2 were sown in the field of Northeast Agricultural University, Harbin, in 2003 and 2004, respectively. The experiments were laid out in a randomized block design with three replications. There were 15 plants in each plot for parents, F_1 and F_2 at a spacing of 8 cm within rows and 65 cm between rows. Seed samples were taken when matured from each plant of parents, F_1 and F_2, and the fatty composition content of a bulk sample of 10 g from each plot was determined by gas chromatography (Wang and Xiang, 2000).

2.2 Data analysis

Generation means were analyzed by a genetic model for quantitative traits of embryo, cytoplasmic and maternal effects for diploid plant seeds (Zhu, 1997). Genetic components of embryo additive variance (V_A), embryo dominance variance (V_D), cytoplasmic variance (V_C), maternal additive variance (V_{Am}), maternal dominance variance (V_{Dm}), embryo additive interaction variance (V_{AE}), embryo dominance interaction variance (V_{DE}), cytoplasmic interaction variance (V_{CE}), maternal additive interaction variance (V_{AmE}), maternal dominance interaction variance (V_{DmE}), covariance between seed and maternal additive interaction variance ($C_{A.AmE}$), covariance between seed, and maternal dominance interaction variance ($C_{D.DmE}$) were estimated by the MINQUE(0/1) method (Zhu 1997). The variance of residual effects (Ve) was also estimated. Embryo additive effect, embryo dominance effect, cytoplasmic effect, maternal additive effect, maternal dominance effect, embryo additive interaction effect, embryo dominance interaction effect, cytoplasmic interaction effect, maternal additive interaction effect, and maternal dominance interaction effect were predicted by Adjusted Unbiased Prediction (AUP) method (Zhu 1997). Estimates of variances and covariances were further used for calculating seed heritability $h^2{}_o = V_A/V_p$, cytoplasmic heritability $h^2{}_c = V_C/V_p$, maternal heritability $h^2{}_m = V_{Am}/V_p$, seed interaction heritability $h^2{}_{oE} = V_{AE}/V_p$, cytoplasmic heritability $h^2{}_{CE} = V_{CE}/V_p$, and maternal heritability $h^2{}_{mE} = V_{AmE}/V_p$. The Jackknife method (Zhu, 1997) was used to derive the standard errors of estimated components of variance and predicted genetic effects by sampling the generation means of genetic entries. All data were analyzed by the software program of Zhu (1997).

3 Results

3.1 Variance component analysis

Variance components of genetic main effects, genotype × environment interaction effects and residual effects are summarized in Table 1.

Table 1 Estimation of variance components for genetic main effects and genotype × environment interaction effects of fatty acid components in soybean seeds

Parameter	Palmitic acid	Stearic acid	Oleic acid	Linoleic acid	Linolenic acid
V_G					
V_{Ao}	0.00	0.00	0.00	0.00	0.00
V_{Do}	5.50 **	0.70 **	0.52 **	0.92 **	0.00
V_C	2.60 **	0.00	2.24 **	0.00	49.50 **
V_{Am}	0.00	0.00	0.00	0.00	0.00
V_{Dm}	0.00	0.00	1.14 **	0.00	26.90 **
V_{GE}					0.00
V_{AoE}	0.00	0.00	0.65 **	0.00	75.90 **
V_{DoE}	11.50 **	2.30 **	3.31 **	1.79 **	0.00
V_{CE}	0.00	0.40 **	0.00	0.65 **	0.00
V_{AmE}	0.00	1.70 **	0.00	0.00	0.00
V_{DmE}	0.40 **	0.00	0.00	0.00	0.00
V_e	5.90 **	7.10 **	1.19 **	0.73 **	68.60 **
V_P	0.00	0.00	0.00	0.00	0.00

Note: *: $P<0.05$; **: $P<0.01$.

Palmitic, stearic, and linoleic acids were mainly controlled by genotype × environment interaction effects (V_{GE}), which accounted for 59.5%, 86.2%, and 72.5% of total variance ($V_G + V_{GE}$), while genetic main effects accounted for 40.5%, 13.7%, and 27.5% of total variance ($V_G + V_{GE}$). It suggested that the genetic main effects could have a little important role, the environment could affect performances and the selection efficiency would be inconsistent with improving these three traits in different years or locations. Genetic main effects proved to be equal to genotype × environment interaction effects for oleic and linolenic acids, and genetic main variance and genotype × environment interaction variance accounted for 50% of total variance ($V_G + V_{GE}$).

Among all kind of genetic main effects, the embryo effect was the largest for palmitic, stearic, and linoleic acids, whose ratios of embryo variances to total genetic variance were 67.9%, 100%, and 100%, respectively. Cytoplasm effect was the largest for oleic and linolenic acids, whose cytoplasm variances accounted for 57.5% and 64.7% of total genetic variance. The second largest one was maternal effects for oleic and linolenic, whose maternal variances accounted for 29.2% and 35.3% of total genetic variance.

In all kinds of genotype×environment interaction effects, embryo interaction effect was the largest for all fatty compositions, and the embryo interaction variances accounted for 96.6%, 52.3%, 100%, 73.4%, and 100% of total genotype × environment interaction variance for palmitic, stearic, oleic, linoleic, and linolenic acids, respectively. The ratio of maternal × environment variance to total genotype × environment interaction for stearic was 38.6% and that of cytoplasm × environment variance to total genotype × environment interaction for linoleic was 26.6%. Among the three genetic systems controlling the performances of fatty acid components, the embryo genetic system was prone to be affected by the environment, and the sensitivities of cytoplasm and maternal to the environment were varied according to different traits.

For palmitic, stearic, oleic, and linoleic acids, the sum of additive and additive interaction variance ($V_{Ao}+V_C+V_{Am}+V_{AoE}+V_{CE}+V_{AmE}$) was less than 50% of total variance (V_G+V_{GE}). It means that selection for these four fatty acids would be less efficient in early generations. Linolenic acid was mainly controlled by additive and additive interaction effects, and the sum of embryo additive variance, cytoplasm variance, maternal additive variance ($V_{Ao}+V_C+V_{Am}$) and embryo additive interaction variance, cytoplasm interaction variance, and maternal additive interaction variance ($V_{AoE}+V_{CE}+V_{AmE}$) accounted for 32.5% and 49.8% of total variance (V_G+V_{GE}), respectively. It means that selection for improving linolenic acid would be efficient in early generations. Larger sum of embryo additive interaction variance, cytoplasm interaction variance, and maternal additive interaction variance ($V_{AoE}+V_{CE}+V_{AmE}$) than that of embryo additive variance, cytoplasm variance, and maternal additive variance ($V_{Ao}+V_C+V_{Am}$) indicated that selecting efficiency would be significantly varied in different sites and years. Dominance and/or dominance interaction variance, due to embryo and maternal plant, reached significance for the five fatty acid components, which showed dominance and/or dominance interaction effects would interfere the efficiency on selection in early generations for these traits.

3.2 Heritability analysis

Heritabilities of fatty acid components are summarized in Table 2.

Total narrow-sense heritabilities of palmitic, stearic, oleic, linoleic, and linolenic acid components were estimated as 56.8%, 10%, 16.7%, 32%, and 15.8%, respectively. In comparison with the amount of interaction heritability, general heritability was lager than the interaction heritability for palmitic and oleic acids, and the interaction heritability was larger than the general heritability for stearic, linoleic, and linolenic acids. It was suggested that the results of selection for improving palmitic and oleic acids would be stable and those of stearic, linoleic and linolenic acids would be inconsistent in different environments.

Table 2 Estimated heritabilities for fatty acid components

Acid	h^2_G /%			h^2_{GE} /%		
	h^2_{Go}	h^2_C	h^2_{Gm}	h^2_{GoE}	h^2_{CE}	h^2_{GmE}
Palmitic	0.000	10.000 **	0.000	0.000	0.000	0.000
Stearic	0.000	0.000	0.000	0.000	13.800 **	2.900
Oleic	0.000	24. 800 **	0.000	7.200 *	0.000	0.000
Linoleic	0.000	0.000	0.000	0.000	0.000	15.800 **
Linolenic	0.000	22.400 **	0.000	34.400 **	0.000	0.000

Note: *: $P<0.05$; **: $P<0.01$.

Among general heritabilities, cytoplasm heritability was the largest for palmitic, oleic and linolenic acids, so the efficiency would be expected with simple selecting procedure and reducing rate by selection of maternal parents in cross-mating. For the insignificant general narrow-sense heritability, the selection for improving stearic and linoleic acids would not get better results in early generations. The amounts of interaction heritability and embryo interaction heritability were the largest for oleic and linolenic acids, the cytoplasm interaction heritability would be the largest for stearic acid, the maternal interaction heritability would be the largest for linoleic acid, while there were no significant interaction components for palmitic acid. It indicated that the embryo additive effect on oleic and linolenic acids would be likely affected by the environment, while the cytoplasm effects on stearic acid would be affected by the environment, and the maternal additive effects on linoleic acid would be affected by environment; efficiency would be stable according to different environments.

3.3 Selection response analysis

Estimated values of selection response components are listed in Table 3.

Table 3 Estimation of selection response components for fatty acid contents

Acid	R_G /%			R_{GE} /%		
	R_{Go}	R_C	R_{Gm}	R_{GoE}	R_{CE}	R_{GmE}
Palmitic	0.000	0.970 *	0.000	0.000	0.000	0.000
Stearic	0.000	0.000	0.000	0.000	0.430	2.020 *
Oleic	0.000	6.620 **	0.000	1.930	0.000	0.000
Linoleic	0.000	0.000	0.000	0.000	1.280 *	0.000
Linolenic	0.000	7.360 **	0.000	11.290 **	0.000	0.000

Note: *: $P<0.05$; **: $P<0.01$.

Total selection responses of palmitic, stearic, oleic, linoleic, and linolenic acids were estimated as 0.97%, 2.45%, 8.55%, 1.28%, and 18.65%, which showed it was possible to improve these five traits by selection. Among five fatty acid components, the linolenic acid component could be improved with the highest efficiency for its largest response of 18.65%, and the stearic, oleic, and linoleic acid components could be improved with better genetic advance.

Compared with the genotype × environment response, the general genetic responses were higher for palmitic, oleic, and linolenic acids, which were 0.97%, 6.62%, and 7.36%, respectively, indicating that changes of environment would slightly influence these three traits, and selecting under different environment could achieve a similar efficiency. However, the genotype × environment responses were higher for stearic and linoleic acids (2.45% and 1.28%), which showed that effects of environments on genetic variation of stearic and linoleic acids were higher, which would further influence the genetic advance in selecting stearic and linoleic acid components with difference at various sites and in different years.

The sums of cytoplasm general response, maternal general response, cytoplasm × environment response and maternal × environment response ($R_C+R_{Gm}+R_{CE}+R_{GmE}$) were higher than those for palmitic, stearic, oleic, and linoleic acids. It showed that the acids were mainly controlled by the cytoplasm and maternal effects, and selecting for improving these four traits should be conducted by single plant according to its performance. The embryo general response and embryo × environment response ($R_{Go}+R_{GoE}$) were higher than those of cytoplasm general response, maternal general response, cytoplasm × environment response, and maternal × environment response ($R_C+R_{Gm}+R_{CE}+R_{GmE}$) for linolenic acid, which indicated that performance of linolenic acid was mainly controlled by the embryo effect, and the improvement of linolenic acid trait should be carried out by screening single seed or selecting single plant in later generations.

4 Discussion

Quality trait improvement in soybean has become one of the main breeding goals all over the world. Genetic theories are of importance to breeding in soybean quality. In previous researches, cytoplasm and maternal plant effects were confused with each other, and some experiments were carried out by reciprocal crosses to analyze cytoplasm and maternal effects (Brim et al., 1968; Singh and Hadley, 1968; Wilson et al., 1981; Fu and Yang, 1994; Primomo et al., 2002a). In our study, fatty acid compositions in soybean seeds were analyzed by a general seed genetic model, and the results showed that fatty acid compositions were controlled by embryo, cytoplasm and maternal plant effects and genotype × environment interaction effects. In all kinds of genetic main effects, palmitic, stearic and linoleic acids were mainly controlled by the embryo effects, while oleic and linoleic acids were mainly controlled by the cytoplasm effect. Among various genotype × environment interaction effects, fatty acids were controlled significantly by embryo × environment interaction effects. If some traits were mainly controlled by the maternal additive effects and/or cytoplasm effects (or higher maternal heritability and/or cytoplasm heritability), there would be no large separation in seeds in maternal plants in early generations, and good response to selection could be expected by selection of performance maternal plants. It is also important to select parents, especially maternal parents, in the mating of crosses. In this paper oleic and linolenic acids were mainly controlled by the cytoplasm effects, which suggested that these two traits should be selected by performance of maternal plants. If some traits were largely controlled by the embryo additive effects or had a higher embryo heritability, there would be large separation in seeds in early generations, therefore, selection should be conducted by single seed or in later generations. For example, palmitic, stearic, and linoleic acids are controlled by embryo effects in our research, and these traits should be selected by scanning single seed or in later generations. Quality traits with high dominant effects should be selected in late generations, but dominant effects from different genetic system could lead to various breeding efficiency. When traits are controlled by maternal dominant effects, there would be no significant separation in F_2 seeds growing in F_1 plants. If traits are controlled by the embryo dominant effects, obvious separation would be detected in F_2 seeds growing in F_1 plants and seeds become a mixture of various genotype.

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