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ANALYSIS OF A CROSSBREEDING EXPERIMENT BETWEEN TWO STRAINS OF ANGORA RABBITS IN TWO ENVIRONMENTS.

WANG K. Z., ZHENG W.

Sichuan Agricultural University, YAAN, Sichuan - China

SUMMARY :
In this paper, weighted least square analysis is used to study the genotype-environment interaction of major economic traits of Angora rabbit for three generations in two environments. The heterosis of the economic traits was analyzed by the estimated parameters and the theory of relative heritability. The results indicate that there are significant additive effects and interactions between the additive effect and the environment among some traits of wool producing performances of Angora rabbits, and significant environment effects existed in some reproductive traits. The heterosis of the wool yield is mainly due to gene dispersion, and the increase of reproduction performances is dependent on the improvement of environment. The theory of relative heritability could be used conveniently for the heterosis analysis, but significance test and the genotype-environment interaction could not be conducted or analyzed, which is the shortage of the theory.

RESUME : Analyse d'une expérience de croisement entre deux souches de lapins Angora dans deux environements.
Dans cet article, on utilise les moindres carrés pour étudier les interactions entre le génotype et le milieu pour les principaux caractères d'intérêt économique chez le lapin Angora pour trois générations élevées dans deux milieux. On a estimé les effets d'hétérosis pour les principaux caractères en utilisant la théorie de l'héritabilité relative. Il y a des effets génétiques additifs et des effets d'interaction significatifs pour quelques caractères de production de poil ainsi que des effets du milieu pour quelques caractères de reproduction. L'effet d'hétérosis sur la production de poil est du principalement à la génétique, alors que l'amélioration des performances de reproduction dépend surtout de l'amélioration du milieu. La théorie de l'héritabilité relative est utile pour l'analyse des effets d'hétérosis mais l'abscence de tests statistiques et l'impossibilité d'analyser les interactions génotypes–milieu sont gênantes.

INTRODUCTION

Many researches have been made on the selection and breeding of Angora rabbits using the theory of quantitative genetics, which have accelerated the improvement of the animal (KONG, 1982 ; Bayerische Landesanstalt für Tierzucht, 1987). In order to conduct early selection and increase wool yield by taking advantage of heterosis, the past researches on quantitative traits were chiefly focused on the estimation of genetic parameters and the formulation of selection indexes. So far, there are no reports on the genetic effects and genotype-environment interaction of the major economic traits of Angora rabbits.

Quantitative traits are controlled by some specific minor gene system. Their phenotypic value is the sum of the genotypic and the environmental values. The genotypic value can be divided into additive effect, dominant effect and epistatic effect. Therefore it is necessary to study the genotype effect of some economic traits. In this paper, the genotype effect of some leading economic traits of Angora rabbits and the genotype-environment interaction are analysed by the weighted least square method (GAO, 1986 ; FALCONOR, 1989) and heterosis of some major economic traits of Angora rabbits is also studied in order to provide some theoretical basis for the breeding of Angora rabbits.

MATERIAL AND METHODS

Rabbits and environments of the experiment :

The experiment was carried out from 1983 to 1985 on the Rabbit Farm of Sichuan Agricultural University (Environment 1) and on Shu Fangba Rabbit Farm of Anyue County, Sichuan province (Environment 2), respectively. It's more comfortable in environment 1 than in environment 2, and it's much hotter in summer in environment 2. The university farm is a teaching and research rabbitry. There were four combinations, which were German Angora x German Angora, Chinese Angora x Chinese

Angora, F_1 and F_2 paternal upgrading of German Angora on each farm.

Measuring traits :

Seven traits, which are wool yield of both male and female rabbits (from birth to 12 months old), yearly wool production rate (yearly wool yield x 100 % / body weight at 12 months old), litter size (total number of rabbits at birth), newborn litter weight, weaning litter size and weaning weight of litter (weaned at 60 days old), were measured.

Statistical analyses :

1 - With the additive dominant model, the genotype effects and the genotype-environment interaction effects were estimated by means of weighted least square (GAO, 1986 ; MA, 1982).

2 - Heterosis estimation (GAO, 1986 ; PEI, 1983).

$$* \ RH = \frac{[h] + g_{hj}}{m + e_j}$$

RH : rate of heterosis ; m : population means ; j : environment number ; e_j : environment effects ; [H] : dominant effects ; g_{hj} : interaction of dominant effect and environment.

** The heterosis estimation was carried out by using the parental genetic transmitting relationship of the theory of relative heritability as the linear addition.

$a_1 = (\bar{F}_1 - \bar{P}_2) / (\bar{P}_1 - \bar{P}_2)$
$a_2 = (\bar{P}_1 - \bar{F}_1) / (\bar{P}_1 - \bar{P}_2)$ and $a_1 + a_2 = 1$
a_1, a_2 : relative heritability
$\bar{P}_1$: mean of German Angora (P_1)
$\bar{P}_2$: mean of Chinese Angora (P_2)
$\bar{F}_1$: mean of the crossbred offsprings from German males x Chinese females (F_1)

Assuming there existed the dominance, then :

$\bar{F}_1 = AM + (\bar{P}_1 - \bar{P}_2)(a_1 - 0.5)$
$\bar{F}_2 = AM + 0.5(\bar{P}_1 - \bar{P}_2)(a_1 - 0.5)$
$\bar{F}_2$: mean of the offsprings from German males x F_1 females (F_2)
AM : average value of the 2 parents.

And the heterosis measurement would be :

$\mu_1 = \bar{F}_1 - AM = (\bar{P}_1 - \bar{P}_2)(a_1 - 0.5)$
$\mu_2 = \bar{F}_2 - AM = 0.5(\bar{P}_1 - \bar{P}_2)(a_1 - 0.5)$
μ_1, μ_2 are the heterosis measurements of the 2 strains of rabbits.

3 - The additive effect, dominant effect and the effect of each environment situation are estimated by the additive-dominant genetic model.

Table 1 : Genetic analysis of wool-producing and reproductive performances of different generation under two environments.

G	E	Male wool yield (g)	Female wool yield (g)	Wool prod. rate %	Litter size	Newborn litter weight (g)	Weaning litter size	Weaning litter weight (kg)	Model					
		x ± s	x ± s	x ± s	x ± s	x ± s	x ± s	x ± s	m	[d]	[h]	el	gdl	ghl
P1	1	544.4±18.99 (13)	743.8±18.75 (13)	15.8±1.54 (26)	7.6±1.23 (16)	343.2±56.98 (16)	6.2±0.8 (16)	4077±317.6 (16)	1	1	0	1	1	0
P1	2	371.9±75.02 (43)	338.7±78.78 (36)	13.7±2.68 (79)	5.8±1.24 (33)	262.9±55.77 (33)	4.9±1.05 (33)	2420±553.6 (33)	1	1	0	−1	−1	0
P2	1	110.9±8.28 (19)	198.0±9.45 (18)	5.9±2.13 (37)	6.9±0.96 (23)	336.0±44.70 (23)	5.8±0.74 (23)	3631±411.3 (23)	1	−1	0	1	−1	0
P2	2	230.4±49.31 (37)	234.7±54.78 (40)	11.0±2.55 (77)	6.7±1.36 (37)	263.5±46.57 (37)	4.8±1.08 (37)	2184±400.8 (37)	1	−1	0	−1	1	0
F1	1	369.5±90.39 (36)	401.9±342.4 (35)	14.4±2.89 (71)	6.9±1.43 (14)	394.3±49.55 (14)	6.4±1.05 (14)	4203±372.8 (14)	1	0	1	1	0	1
F1	2	236.5±57.99 (36)	237.5±56.99 (42)	9.2±2.62 (78)	5.5±1.28 (31)	249.3±58.55 (31)	4.5±0.74 (31)	2211±245.2 (31)	1	0	1	−1	0	−1
F2	1	351.8±52.53 (5)	493.4±106.7 (24)	15.0±2.87 (29)	7.5±1.32 (16)	403.6±52.53 (16)	5.6±1.32 (16)	3658±343.6 (16)	1	0	0.5	1	0	0.5
F2	2	268.8±55.63 (34)	281.6±53.95 (38)	11.0±2.83 (72)	6.6±1.21 (38)	295.8±55.63 (38)	4.7±1.21 (38)	2204±324.5 (38)	1	0	0.5	−1	0	−0.5

[d] : additive effect ; gdl : interaction of additive effect and environment ; ghl : interaction of dominant effect and environment
G : generation ; E : environment ; numbers in ( ) are sample size.

Table 2 : Estimated values of each division in each traits.

Division	Male Wool yield	Female wool yield	Wool prod. rate	Litter size	Newborn litter weight	Weaning litter size	Weaning litter weight
m	312.3±20.40 **	315.6±19.72 **	11.9±0.94 **	6.6±0.48 **	312.2±20.18 **	5.4±0.36 **	3087±141.5 **
[d]	142.9±22.60 **	96.6±23.98 **	3.1±1.13 **	−0.1±0.60	4.0±25.42	0.1±0.47	183.9±214
[h]	−1.3±66.29	21.1±65.31	0.3±3.23	0.6±1.43	45.3±64.42	−0.04±1.32	−65.9±383.9
el	15.1±21.12	21.3±20.66	−0.7±1.12	0.5±0.59	41.7±25.07 a	0.6±0.46	729.2±207.9 **
gdl	73.7±22.78 **	41.9±24.15 a	1.7±1.13	0.4±0.60	3.0±25.60	0.1±0.47	48.4±209.6
ghl	55.5±79.49	46.4±71.53	3.5±3.69	−0.4±1.70	−5.2±72.82	0.2±1.54	241.1±520.6

** : P<0.01 ; a : P<0.1.

RESULTS

The analyses of genotype effects of the leading economic traits :

The wool yield, wool production rate, litter size, newborn litter weight, average weaning size of litter and weaning weight of litter are listed in Table 1, which was obtained by the additive-dominant model analysis. The genotype effects are in table 2.

According to the estimated value in table 2, the expected means of the seven traits of every generation have been calculated and compared with the measured means. Their differences are not significant by Chi-square test (P>0.05), which indicate that it is suitable to study the genotype-environment interaction of all the wool-producing and reproductive traits of the Angora rabbit by means of he additive-dominant model.

The significance test of each divided value in table 2 indicates that the wool producing performances, such as wool yield (male and female) and wool production rate, population means (m) additive effect (d) are significant (P<0.01). The interaction effects between the additive effect and the environment (gdl) of wool yield are significant (P<0.01 or P<0.1). The population means of the four reproductive traits (average litter size, newborn litter weight, weaning litter size, weaning litter weight) are significant, respectively (P<0.01). The environment effects on newborn litter weight and weaning litter weight are significant (P<0.01 or P<0.1) (table 2).

The estimation of heterosis:

The estimation of the heterosis rate :

The heterosis rate are in Table 3, which were estimated by means of the values in Table 2 and the

Table 3 : Heterosis rates of each traits : (unit %).

E	Male wool yield	Female wool yield	Wool prod. rate	Litter size	Newborn litter weight	Weaning litter size	Weaning litter weight
1	16.56	20.04	34.06	3.59	11.33	4.82	4.59
2	−21.47	−17.18	−25.60	−11.95	−5.31	−6.41	−3.92

Table 4 : Relative heritability of each trait.

Realtive herita-bility	E	Male wool yield	Female wool yield	Wool production rate	litter size	newborn litter weight	weaning litter size	weaning weight
a_1	1	0.597	0.739	0.864	−0.015	8.138	1.318	1.283
a_2	1	0.403	0.261	0.136	1.042	−7.138	−0.318	−0.283
a_1	2	0.043	0.026	−0.683	1.125	23.032	−5.800	0.118
a_2	2	0.957	0.974	1.163	−0.125	−22.032	6.800	0.882

Table 5 : Heterosis measurement (μ) of each trait.

Heterosis measu-rement	E	Male wool yield	Female wool yield	Wool production rate	Litter size	Newborn litter weight	Weaning litter size	Weaning litter weight
$\mu 1$	1	41.92	65.96	3.58	–0.36	54.69	0.36	348.68
$\mu 2$	1	20.96	32.98	1.79	–0.18	27.35	0.18	174.34
$\mu 1$	2	–64.67	–49.26	–3.17	–0.75	–13.97	–0.32	–90.28
$\mu 2$	2	–32.34	–24.63	–1.59	–0.38	–6.99	–0.16	–45.14

Table 6 : Comparison of [h] and $\mu 1$ of all the traits.

	E	Male wool yield	Female wool yield	Wool production rate	Litter size	Newborn litter weight	Weaning litter size	Weaning litter weight
[h]	1	41.93	65.96		–0.36	54.69	0.36	346.16
[h]	2	–62.64	–42.12	–3.02	–0.78	–4.91	–0.24	–77.88
$\mu 1$	1	41.92	65.96	3.58	–0.36	54.69	0.36	348.68
$\mu 1$	2	–64.67	–49.26	–3.17	–0.75	–13.97	–0.32	–90.28

RH formula appearing in the Material and Methods part.

The estimation of the heterosis measurement by the sum-difference genetic model of the relative heritability theory :

Based on the theory of relative heritability, the seven leading economic traits of the wool productive capacity and the reproductive ability were studied, and the obtained relative heritability and the heterosis are listed in Table 4 and Table 5.

From the results listed in Table 3 and 5, it is obvious that the estimated heterosis rate (RH) and the heterosis measurement (μ) estimated by the relative heritability are inconsistent in the two environments. But in the same environment, the heterosis of each trait estimated by the two different methods is almost identical, which indicates that the environment factors have a great influence upon the heterosis.

The results of dominant effect and heterosis measurements of all traits in each environment are listed in Table 6.

DISCUSSION

1 - The result of this research shows that there are significant or very significant interaction effects between the genotype and the environment (the interaction gdl between the additive effect and environment) in the traits of wool produving performances, such as the wool yield and the wool procuction rate. Although the traits of the reproductive performances, such as the litter size, newborn litter weight, weaning size of litter and the weaning weight of litter, are suitable to the additive-dominant genetic pattern, the interaction effects between the genotype and the environment are not significant, but the environmental effects are generally significant. Other studies already discovered that the heritability of Angora rabbit's wool clip per year is high and that of the German Angora is 0.5 - 0.7 (YANG, 1992 ; CHENG *et al.*, 1988.) and that of Chinese Angora is 0.27 (estimated by the author), as to the heritability of the wool production rate per year, the German Angora is 0.4341 and Chinese Angora is 0.4669 (estimated by the author). Although the two traits are of high heritability, only in favorable environment, can the excellent genetic characteristics be fully manifested. So, it's easy to understand why they are significant or very significant interactions between the additive genetic effect and the environment among those traits such as the wool clip and the wool production rate. This is identical with other studies (KONG, 1982 ; CHENG, 1984 ; ROCHAMBEAU, 1989 ; BAYERISCHE LANDESANSTALT FÜR TIERZUCHT, 1987).

The heritability of breeding traits is generally low, for instance, the heritability of livability in German Angora is only 0.118 (CHENG *et al.*, 1988). The least square analyses shows that there are significant or very significant difference (P<0.05 or

$P<0.01$) among the four breeding traits in the two environments, respectively, which suggests that the environmental factors play a dominant role in the phenotypic value of the four breeding traits (WANG, 1987 ; ZHAO, 1987 ; ROCHAMBEAU, 1989). As the nutrition level, the feeding and management and the environment variate, the four breeding traits will change widely.

2 - The heterosis has close relationship with the genetic difference and complementation of genes of the two cross parents. The results in Table 2 indicate that the heterosis of the wool clip and the wool production rate is dominantly from the dissemination of genes with the same effect. The additive (d) and the dominant genetic effect (h) of the four reproductive traits are not significant ($P<0.05$). The result of least square analysis and multiple comparison on the reproductive performances of the two parents shows that the difference between the two parents is not significant ($P>0.05$), which suggests that the genetic difference between the two parents is slight and there exists no complementation between their traits. This, perhaps, is related to the blood blending during the rearing of the variety. As discussed before, it is clear that the environmental factors are the mojor cause to influence the reproductive performances. Therefore, we think that ir is almost impossible to increase the reproductive performances, especially the litter size of Angora rabbits by crossbreeding. Generally, the litter size of German Angora and Chines Angora is almost the same, that is 6-8 heads (CHENG, 1989) which has been proved by many other studies (KONG, 1982 ; WANG, 1987 ; ZHAO, 1987 ; CHENG, 1984 ; ROCHAMBEAU, 1989). The major way to raise up the reproductive performance of Angora rabbit is to improve the environment conditions, including the reproductive techniques.

3 - It is considered by the relative heritability theory that the genetic traits and genetic transfering ability of the parents are the major basis for the selection of mating parents in crossbreeding. The genetic transfering ability or the heritability is an ability for the crossing parents to transfer traits to the offsprings, which is a intrinsic attribue that organisms posses and change in degree or strength among different strains or different traits. In crossbreeding the traits of the crossbreds are determined by the relative strength of the gentic transfering ability or the relative heritability between the two parents (PEI, 1983). From the heterosis measurements in the two environments (Table 5), it is clear that there exists comparatively great differences. In environment 1 the heterosis measurements of all the traits are generally positive (except the litter size), but in environment 2 all the heterosis measurements of the traits are negative. This futherly indicates that there are genotype–environment interactions in woll yield producing performance, but the reproductive performance are mainly affected by environment factors.

4 - The average value of generation Fn ($\bar{F}_n$) can be measured by the parameter m and [h], which may be estimated by gene effect analyses, or by heterosis measurements $\mu 1$, which may be estimated by relative heritability a_1. The formulae are in the following :

$$\bar{F}_n = m + (\tfrac{1}{2})^{n-1} [h]$$
$$\bar{F}_n = Am + (\tfrac{1}{2})^{n-1} \mu 1$$

Am may be considered as the unbiassed estimate of m, so [h] and $\mu 1$ should have the same meaning and be equal to each other (see Table 6). From the formulae for [h] and $\mu 1$ estimation, it is much easier to estimate $\mu 1$. But the significance test for the existence of $\mu 1$ cannot be carried out, which cannot but be a shortage of the method.

5 - Using the above two formulae, the average value of F_n ($\bar{F}_n$) can be estimated by m and [h] or Am and $\mu 1$. So in crossbreeding, we can calculate $\bar{F}n$ first, then decide when to carry out the crossing fixation according to the value of $\bar{F}n$. This may have profound importance in animal breeding practice.

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Correspondance to :
Dr WANG Kangning
Sichuan Agricultural University
YAAN
Sichuan 625014
CHINA

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