

Developments in quantitative genetics methodology as applied to national genetic improvement programs for swine

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Abstract: Genetic selection in pigs through BLUP was very successful. However, strong selection mainly on growth and number of born alive decreased fitness and reduced environmental changes that animals can tolerate especially under suboptimal environments. Additional challenges are genetic differences between purebreds (selected animals) and crossbreds (commercial animals), and possibly different environments for these groups of animals. A successful genetic selection at this time requires comprehensive data for all levels of the pyramid, multitrait models for a variety of traits including categorical and survival, and software that can implement complicated models while supporting large data sets. Many projects in pig genetic evaluation are carried out at the University of Georgia. Those studies are supported by software family called BGR90.

Key words: quantitative genetics; breeding software; national swine breeding program

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For a long time, purebred pigs were evaluated in a nucleus for several growth, meat quality and reproduction traits including growth, backfat and number of piglets alive^[1]. The evaluation was using BLUP with all traits treated as linear and also assuming a normal distribution. Animals down the pyramid were not evaluated; it was assumed that most if not all of the gains of selection at the nucleus level transferred to the commercial level. The selection based on the evaluations seemed to be successful as all the traits seemed to improve. Perhaps the most commonly used software used in the evaluation of pigs was PEST^[2]. This software allowed for a multitrait evaluation for several traits of quite large data sets.

Later, additional traits were added, for example associated with meat quality^[1]. Also, an effort was made to identify QTL's associated with major traits^[3]. The most well known group to utilize markers on a large scale is Pig Improvement Company (PIC). Because the number of traits increased and methodologies to incorporate genetic markers are compute intensive, traits and markers are now analyzed in groups.

Lately, questions have been raised whether the selection at the nucleus level was efficient at the commercial level, whether traditional or by molecular markers. At Smithfield (Culbertson Personal comm., 2004), while growth and the number of piglets increased, the mortality increased, the meat quality decreased, sows pro-

ductive life decreased and susceptibility to diseases increased. This was attributed to less than optimal environment at those farms (Rothschild personal comm., 2004). Such a statement is supported by observations in Denmark (Berg personal comm., 2004) where the genetic progress in commercial animals was found to closely trace that in the nucleus animals. In Denmark the environments at the nucleus and the commercial levels are similar. However, an interesting picture can be drawn from a French experiment where pigs were inseminated with frozen semen from boars born in 1977 and 1998. Daughters of younger boars had 1.6 more born piglets but only 0.4 more born alive.

There are many possible reasons why performance gains in the nucleus may not transfer well to the commercial level. First, the nucleus and commercial environments may be different. In this context, the environment contains a number of attributes including not only a geographical location but also type of management, feeding, the quality of labor and the stocking rate. Subsequently, animals may be not selected for environments in which they have to produce. In particular, traits that are unimportant and unselected for in the nucleus may be important in the commercial population. Second, commercial animals are usually 3 or more way crosses, and the correlation between purebreds and crossbreds in the presence of dominance and epistasis may be smaller than one and even negative^[4]. In beef or dairy cattle, F_1 crosses among diverse breeds are very productive while other crosses are not^[5-6]. This was attributed to recombination loss. The correlation between purebreds and crossbreds was estimated to be between 0.20 and 0.99^[7-8].

Part of the problem with selection in pigs could be due to selection for few major traits while ignoring other, mostly low heritability traits.

Waaïj et al.^[9] documents decrease of fitness in major species as a response to selection mainly for production. According to their work, animals are selected for greater capability for production. This way, less energy is left for "fitness". In environments where survival requires more energy than is available, the most productive animals are more likely to die or become unproductive.

That genetically "improved" animals require better environment was clearly documented in broilers by Eitan and Soller^[10]. Over the past fifty years, the slaughter age in chicken has been reduced from 120 to 40 days with a large improvement in average feed conversion ratio. However, these came at a cost of lower fertility, different levels of sexual maturity in sexes, and decreased disease resistance. New problems are handled by improved management like artificial light, supplementation of cocks, antibiotics in food etc. Under less than optimal environment, the "modern" chicken would not function well.

Napel^[11] argues for creation of a more robust pig which would function well under a variety of environments including environments changing with time due to external conditions. Theories exist how to select such a pig^[12]. However, a "robust" genotype may be less productive in a very specialized environment than a "specialized" genotype.

1 Selection of profitable pigs

In order for the selection to be profitable at the commercial level, the following conditions need to be met: (1) The evaluation needs to include all traits of current economic importance including mortality, diseases and survival. (2) The evaluation needs to be at the level of commercial animals. (3) Selection of purebreds should occur in similar conditions as in commercial animals, otherwise, genotypes need to be

flexible enough so that they would function well across environments

The last two conditions are related. If commercial and nucleus animals are raised in different environments, the genetic correlations between traits of nucleus and purebreds will be reduced.

The above conditions create require collection of comprehensive data, the collection should be at all levels of the breeding pyramid and possibly in different environments. Also, new statistical tools are needed to handle the complexity of the data. These include methods for multitrait evaluation where some traits may be non-normally distributed, censored, and methods where differences between purebreds and various kinds of crossbreds are accounted for.

2 Work done at UGA

Genetic analyses and genetic evaluation can be done only if there is appropriate software available. Usually two types of software are used. One type is used for exploratory studies and parameter estimation. This type usually can accommodate only small data sets. Another type is used for evaluation, where very large data sets can be accommodated, however, with less flexibility or possibility for parameter estimation. When new types of models need to be supported, an important feature of software is ease of modification. Only when the source code is available then modifications to the software can be done. Depending on design of software, the program may be easier, difficult or even impossible to modify. Large statistical packages like SAS are not suitable for genetic analyses.

2.1 Package BGF90

A software called BGF90 or a BLUPF90 family of programs has been developed at the University of Georgia to support animal breeding

research and genetic evaluation. The software was developed with the purpose of supporting a large number of models for both data and the genetic evaluation, with simplicity that would aid modifications when needed and with reasonable efficiency (Misztal 1999, Misztal et al 2002). Most of the software is free for research use and is available on the Web at <http://nce.uga.edu/~ignacy>. This software, which is continuously modified for needs of new projects, allows scientists at UGA and collaborators to conduct new types of analyses. Many specific methodologies are available. For example, for standard analyses, AI-REML methodology is usually fast and accurate. However, for some analyses, particularly involving traits of low heritability and high genetic correlations, this software fails. In this case, a slower approach of EM-REML is often more reliable. REML methodology usually fails with a large number of traits or when the data size is too large. In this case, Bayesian methodologies based on Gibbs sampling may be applicable. In analyses where a very large data set is crucial for obtaining accurate estimates, like for estimation of non-additive effects, both REML and Bayesian methodologies are too expensive. In this case, a Method R may be applicable at a cost of somewhat higher standard errors. Unique features of BGF90 are uniformity of parameter files across the programs and availability of programs using iteration on data that can analyze very large data sets. For more detailed information about the programs see the Appendix.

2.2 Studies in pig breeding or useful for pig breeding at UGA

This section highlights work in new evaluation methods at UGA with discussion of relevant issues especially related to methodologies.

2.2.1 Joint evaluation of purebreds and crossbreds

Lo et al.^[4] developed a theory for

joint analyses of purebreds and crossbreds. For all crossbreds including F_1 , backcrosses, F_2 , etc., their model is very complicated. However, that model simplifies for a terminal cross data when the only populations are purebred and F_1 ^[13]. In such a situation, each pure breed has its own additive effect, and crossbreds have two corresponding to parental lines. Additionally, the dominance effect is fit. Such a methodology allows for estimation of genetic correlations between each purebred and F_1 and for a different additive variance for each breed or each parental effect in each F_1 . Necessary software requires the ability to support multiple additive effects and dominance effect, all of which are supported by BLUPF90. In a study by Lutaaya et al.^[7], this model was applied to Landrace (breed A) and Large White (breed B). The genetic correlations between purebreds and crossbreds (rpc) for lifetime daily gain were 0.99 (A-C) and 0.62 (B-C); for backfat the correlations were 0.32 (A-C) and 0.70 (B-C). Thus, breed A transmitted to F_1 predominantly daily gain and breed B predominantly backfat. Lutaaya et al.^[14] also evaluated animals based on purebred only or on combined purebred- F_1 performance. Rankings were similar because data beyond purebreds was very limited. Both studies have shown a need for data collection beside the nucleus. It is desirable to develop a realistic methodology for joint evaluation of purebreds and crossbreds beyond F_1 as commercial animals are at least 3 way crosses.

2.2.2 Genetic analyzes of farrowing mortality As piglet mortality is increasing, there is a question whether that increase is due to response to a selection on growth and fecundity. Arango et al.^[15] looked at genetic parameters for farrowing mortality, litter size, and test performance of Large White sows. Because the distribution of pigs born dead is far from normal, this

trait was treated as categorical and analyzed by the threshold model; other traits were treated as normally distributed. Estimates confirmed that selection for less backfat and higher growth increased the number of pigs born dead. To find whether pigs born dead and born alive were genetically similar traits across parities, another analysis involved a 6 trait model: pigs born dead in 3 parities analyzed as categorical traits and pigs born alive in 3 parities analyzed as linear traits. Analyzing categorical traits by the threshold model accounts for incidence differences across time and farms and provides more realistic assessments of gains by genetic selection. All analyses were by THRGIBBSF90.

2.2.3 Estimation of competitive effects

One reason why genetic gains for some traits do not transfer well from nucleus to commercial could be competitive effects. In commercial environments, the pig density in a pen is high. Pigs selected as the fastest growing could be those who are also the most dominant. Under feed restrictions, such pigs are likely to enforce their dominance status, causing retarded growth in the remaining pigs in the pen. Thus, the average performance of the pigs in one pen is low. Muir and Schinckel^[16] developed a theory to evaluate the animals for general and competitive (or cooperative) effects. A good pig would be the one who grows fast yet does not inhibit the capability of other pigs to grow. Arango et al.^[17] used their model for on test average daily gain of Large White gilts. In this model, each observation contains not only the effect of a pig with that observation but also effects of all remaining pigs in the same pen. With pen sizes up to 16 but varying, a model for an observation could contain up to 16 additive effects. Also, different pen size influenced weights of competitive effects. Programs BLUPF90, REMIF90, and GIBBSF90 handled the competitive effect model.

without any modification. The estimate of the competitive effects had a very large error because of large pen sizes. More precise estimates can be obtained when pen sizes are smaller and when the competitive model is refined. The model by Muir and Schinckel assumes that competitive effects are expressed on the normal scale. In fact, these effects are expressed categorically: the most competitive pig is the most likely to become dominant while all the remaining pigs are likely to be passive. A work on the refinement continues.

2.2.4 Analyses of sow removal disposal
Sows survive shorter than in the past. There are many reasons for sow removal. One question is whether all those reasons are independent genetically or are they due to a general deterioration of fitness. Arango et al.^[18] combined over 40 different reasons into 3 general groups: reproduction diseases, and others. Three traits created were: parity at removal for reproduction (R), parity at removal for disease (D), and parity at removal for other (O) reasons. Because a sow is removed only for one reason, only one trait is recorded for each sow. However, if a sow is removed from the herd for one reason, it means that it was not removed for other reasons, but might have been removed for those reasons later. For example, if a sow was removed for disease at parity 3, her potential removal for other reasons certainly did not happen at parities 1-2 but could have happened in parities 3 (after disposing for disease) or later. Therefore, one trait would be observed and two censored:

$$R \geq 3, D = 3, O \geq 3.$$

Even though there is no direct observation on censored traits, using censored data allows one to utilize more information and subsequently leads to more accurate analyses. An extra bonus is ability to estimate genetic correlations among the traits. In analyses by Arango et al.^[18], a

multitrait program GIBBS2 F90 was modified to allow censoring; the new program was named GIBBS2 C90. Estimated genetic correlations among all traits were high, indicating that a general decrease in fitness is causing low sow survival.

In general, traits like productive life would be best analyzed by a survival model^[19]. Such a model takes into account risks of disposal at each unit of time and inherently takes account of censoring. However, at this time, the survival model cannot easily be used in multitrait models or in models with an animal effect except in small data sets^[20].

2.2.5 Changes in genetic parameter over time
In most evaluation systems, it is assumed that genetic parameters stay constant over time. This means that variances and genetic correlations do not change. Tsuruta et al.^[21, 22] analyzed up to 25 traits in Holstein cows. The analyses used program GIBBS2 F90, which supports large number of traits. Many genetic parameters changed greatly over a period of 20 years. Some genetic correlations changed from positive to negative. The most long-lived animals 20 years ago milked well and were tall. Now, long-living animals are shorter and are not necessarily the highest producing but have good reproduction. This is because the genetic selection over the years produced cows that are taller than the optimum. Also, cows selected as most productive have worse reproduction and more health problems than the average.

Environments change over time, and the changes increase importance of some traits while decreasing the value of other traits. For example, many farms are getting larger and each animal receives less individual attention. Subsequently, ongoing health problems may not be detected in time and heat may not be observed. Both of these factors increase the importance of immune resistance and fertility.

Changing genetic parameters over time illustrate limited value of very old data in predicting the genetic values of current animals and the need for time adjustments in models used for genetic evaluations. The need for adjustments may not be realized unless specific tests are made. For instance, dairy bulls for many breeds are evaluated globally by Interbull (<http://www.interbull.org>). This organization combines genetic evaluations from individual countries into evaluations that take into account data from all the countries. To guarantee quality evaluations from each country Interbull requires that their evaluations pass many tests. Evaluations from many countries could not pass the tests before often complicated time adjustments were made. Often the changes reduced the estimate of genetic trend in half or even to none^[23] providing less optimistic assessment of the selection work done so far.

3 Recommendations

Use of imported lines is justifiable if the environment from the importing countries can be duplicated. Otherwise a genetic selection

scheme would select animals best suited for a local environment. A recording scheme needs to be set up that includes major traits of economic importance with emphasis on those limiting productivity locally. Traits under recording need to be analyzed with a model that can fully account for their complexity. The selection requires a research component so that current challenges are identified, models are modified and new genetic evaluations provided.

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Appendix

The table 1 describes computer program available at UGA for problems associated with quantitative genetics, molecular genetics and genetic evaluation. All programs are written in Fortran 95. Most programs are modifications of a BLUP program called BLUPF90. The design of that program has been described in class notes for a course on “Computing Methods in Animal Breeding” taught as ADSC 8200 at the University of Georgia; this course has also been taught as a short course by J. Misztal on five continents. Most of the programs are available at <http://nce.ads.uga.edu/~ignacy/newprograms.html>.

Table 1 Computer program

type ^{a)}	Program	description	features
I	BLUPF90	Calculates BLUP for multiple trait models; supports missing traits and different models for each trait	Matrices kept in memory; solutions by iteration or by sparse matrix factorization; suitable for small to medium data sets
	REMLF90	Variance component estimation by EM REML	Slow but reliable; works with random regression models only if starting values too large and not too small
	AREMLF90	Variance component estimation by AI REML	Usually much faster than REMLF90; less reliable for some models
	AREMLRES	As above but with estimation of heterogeneous residual variances	BYT Druet
	QXPAK	Joint analysis for polygenic and QTL effects	BYM Perez Enciso

Continued Tab 1

type	Program	description	features
I	CBLUP90	Solutions for bivariate linear threshold model	Thresholds not computed
	CBLUP90 THR	Solution for multiple trait models with one categorical trait	Thresholds computed
	GIBBSF90	Variance component estimation using Bayesian methods and Gibbs sampling; block sampling	Creates new matrices every round, simple but slow
	GIBBS F90	As above modified for speed	Sets matrices only once, much faster than GIBBSF90 especially for large number of traits
	GIBBS2 F90	As above but adds joint sampling of correlated effects	Faster mixing for maternal and random regression models
	GIBBS3 F90	As above with support for heterogeneous residual variances	
	POSTGIBBSF90	Graphical analyses of samples from the GIBBS family of programs	Version with graphics version available for Linux
II	MRF90	Variance component estimation by Method R	BY T Druet, supports very large data sets
III	THRGIBBSF90	Variance component estimation for any number of categorical and linear traits; uses Bayesian methods	BY D K Lee, a modification of GIBBS2 F90
	THRGIBBS F90	Simplified version of above	BY S Tsuruta, much easier to correct than above but some features not implemented
	GIBBSCF90	Variance component estimation for multiple trait linear censored models	BY J Arango
	RENUMF90	Renumbering for animal effects and large data sets	Supports multiple additive effects; eliminates unnecessary pedigrees, only binaries available on the Website
IV	BLUP90 DD	As BLUPF90 but with support for very large data sets	BY Shogo Tsuruta
	CBLUP90 DD	As CBLUP90 THR but with support for very large data sets	
	ACC90	Approximation of accuracies for multiple trait models very large data sets	Maternal effects supported

I) I : Programs available on the Web II: Programs below available by request III: Programs under development IV: Programs available only under research agreement
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Example of a parameter file

This is an implementation of a terminal cross model for joint evaluation of two purebreds (A and B) and F₁ (AB) by Lo et al.^[13] and used by Lu et al.^[7].

Model

breed A $y_a = c_g + u_a + e_a$
breed B $y_b = c_g + u_b + e_b$
F₁: $y_{ab} = c_{gb} + u_{ab} + u_{bab} + e_{ab}$

Data file (data_cross)

- 1. cg A (85 levels)
- 2. cg B (110 levels)
- 3. cg crossbred (87 levels)
- 4. animalbreed A (2 400 animals) or parent from breed A
- 5. animalbreed B (3 000 animals) or parent from breed B
- 7. y_a
- 8. y_b
- 9. y_c

Pedigree files

pedig_A for breed A and pedig_B for breed B

Parameter file

```
# Example of a terminal cross model
DATAFILE
data_cross
NUMBER_OF_TRAITS
3
NUMBER_OF_EFFECTS
3
OBSERVATION(S)
6 7 8
WEIGHT(S)
EFFECTS POSITIONS IN DATAFILE NUMBER_OF_LEVELS TYPE_OF_EFFECT
1 2 3 110 cross ! contemporary group effect
4 0 4 2400 cross cross ! additive effect of breed A
0 5 5 3000 cross ! additive effect of breed B
RANDOM_RESIDUAL_VALUES
100 0 0
0 100 0
0 0 100
RANDOM_GROUP
2
RANDOM_TYPE
add_animal
FILE
pedig_A
(CO)VARIANCES
```

```
40 0 30
0 0 0
30 0 50
RANDOM_GROUP
3
RANDOM_TYPE
add_animal
FILE
pedig_B
(CO) VARIANCES
0 0 0
0 50 30
0 30 40
40 30
```

References

[1] Swine Improvement Program Guidelines (SIPG) [EB/OL]. <http://www.nsisf.com/>. 2005.

[2] GROENEVELD E, KOVAC M, WANG T. PEST: a general purpose BLUP package for multivariate prediction and estimation [A]. Proc of 4 th World Cong on Genet Appl To Livestk Prod Edinburgh [C]. 1990. XII: 488—491.

[3] DEKKERS J C M. Commercial application of marker and gene-assisted selection in livestock: Strategies and lessons [J]. J Anim Sci 2004; 82: E313—E328.

[4] LO L L, FERNAND R L, CANIETR J C et al. Theory for modeling means and covariances in a two-breed population with dominance inheritance [J]. Theor Appl Genet 1995; 90: 49—62.

[5] RUTLEDGE J J. Greek temples, tropical kine and recombination load [J]. Livestock Production Science 2001; 68: 171—179.

[6] MADALENA F E, TEODORO R L, LEMOS A M et al. Evaluation of strategies for crossbreeding of dairy cattle in Brazil [J]. J Dairy Sci 1990; 73: 1 887—1 901.

[7] LUTAAYA MISZTAŁ E, I MABRY J W et al. Genetic parameter estimates from joint evaluation of purebreds and crossbreds in swine using the crossbred model [J]. J Anim Sci 2001; 3 002—3 007.

[8] MERKS J W M, HANENBERG E H A T, KNOL E F. Developments in international pig breeding programmes [A]. Paper C5. 3 56 th annual meeting of the European Association for Animal Production June [C]. 2005.

[9] van der WAAL J E H. A resource allocation model describing consequences of artificial selection under metabolic stress [J]. J Anim Sci 2004; 82: 973—981.

[10] EITAN Y, SOLLER M. Associated effects of sixty years of commercial selection for juvenile growth rate in broiler chickens: Endo/exo-physiological or genetic? [A]. Proc of 7 th World Cong on Genet Appl to Livestk Prod Montpellier: Communication 19 — 10 [C]. 2004.

[11] NAPEL J ten. Biological robustness of pigs [A]. Paper P2. 1 56 th annual meeting of the European Association for Animal Production June [C]. 2005.

[12] SIRANDBERG E. Environmental sensitivity and robustness [A]. Paper P2. 7 56 th annual meeting of the European Association for Animal Production June [C]. 2005.

[13] LO L L, FERNANDO R L, GROSSMAN M. Genetic evaluation by BLUP in two-breed terminal crossbreeding systems under dominance [J]. J Anim Sci 1997; 75: 2 877—2 884.

[14] LUTAAYA MISZTAŁ E, I MABRY J W et al. Joint evaluations of purebreds and crossbreds in swine [J]. J Anim Sci 2002; 80: 2 263, 2 266.

[15] ARANGO J, MISZTAŁ E, I TSURUTA S et al.

Threshold linear estimation of genetic parameters for farrowing mortality, litter size and test performance of Large White sows [J]. J Anim Sci 2005 83: 499—506

[16] MUR W M, SCHNCKEL A. Incorporation of competitive effects in breeding programs to improve productivity and animal well being [A]. 7 th World Congress of Genetics Applied to Livestock Production, Montpellier, France, Communication No14—07 [C]. 2002

[17] ARANGO J, MISZTAL J, TSURUTA S, et al. Estimation of variance components including competitive effects of Large White growing gilts [J]. J Anim Sci 2005 83: 1 241—1 246

[18] ARANGO J, MISZTAL J, TSURUTA S, et al. Study of codes of disposal at different parities of Large White sows using a linear censored model [J]. J Anim Sci 2005

[19] DUCROCQ V, SÖIKNER J. The Survival Kit: a Fortran package for the analysis of survival data [A]. Proc 5 th World Congress on Genetics Applied to Livestock Production [C]. 1994: 2 251—2 252

[20] HOLM L H. Quantitative genetic analysis of survival: linear Gaussian and ordered categorical traits [D]. Royal Veterinary and Agricultural University, Frederiksberg, Denmark, 2004

[21] TSURUTA S, MISZTAL J, LAWLOR T J. Genetic correlations among production, body size, udder and productive life traits over time in Holsteins [J]. J Dairy Sci 2004 87: 1 457—1 468

[22] TSURUTA S, MISZTAL J, LAWLOR T J. Current day's prediction of a changing trait: productive life of US Holsteins [J]. J Dairy Sci 2005 88: 1 156—1 165

[23] DUCROCQ V. An improved model for the French genetic evaluation of dairy bulls on length of productive life of their daughters [J]. Anim Sci 2005 80(3): 249—257

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译文

数量遗传学方法应用于国家猪育种计划

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摘要: 利用 BLUP对猪进行遗传选择非常成功。不过, 由于对猪生长和产活仔数的高度选择降低了适应性, 削弱了个体在不良环境下的应变能力。此外, 还面临包括纯种 (育种群) 和杂种 (商品群) 间的遗传差异, 以及这些群体所处环境差异等方面的挑战。目前, 成功的遗传改良需要利用金字塔育种体系中的所有群体的综合信息, 包括不同性状的多性状模型, 如分类性状和生存性状, 以及可以处理各种大批量数据为基础的复杂模型的软件。在乔治亚大学已经开展了多个猪遗传改良计划研究, 这些研究所用的软件称为 BGP90系列软件。

关键词: 数量遗传学; 育种软件; 国家猪育种计划

长期以来, 对核心群纯种猪进行评估的性状包括生长性状、肉质性状和繁殖性状, 如生长速度、背膘厚和窝初生活仔猪数等^[1]。BLUP把所有性状当作线性来处理, 而且假定它们服从正态分布。金字塔下层的个体是不进行评定的, 这时假定几乎所有的核心群选择进展都传递到了商品群。利用这种方式评估基本上是成功的, 因为所有性状都得到了改良。猪育种中最常用的软件可能是 PEST^[2]。这种软件可

以利用多性状 BLUP模型处理大量数据。随后, 评估时增加了其他的性状, 比如, 与肉质有关的性状。还有, 可以利用与主要性状相关联的 QTL信息^[3]。众所周知大规模利用标记的组织是 PIC集团。因为遗传评定的性状数量增加了, 以及结合了遗传标记的信息, 计算比以前更为复杂, 因此性状和标记数据是分组进行分析的。最近, 人们开始怀疑, 无论是传统方法还是增加