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GENOTYPE BY ENVIRONMENT INTERACTIONS IN LIVESTOCK BREEDING PROGRAMS: A REVIEW

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In a simple genetic model for a quantitative trait, the phenotype is considered as the sum of independent genetic and environmental effects. Often, such a model is not satisfactory for the range of situations to which it is applied. If a genotype by environment interaction (GEI) exists, this independence is lost, and the simple model does not fit the data properly (Falconer, 1989). A possible remedy is to extend the model by including a term for GEI. Dickerson (1962) defined the GEI as "additional variation due to the joint effects of the genotype and environment, not predictable from their separate average effects" and added that "They are important to the extent that use of the best combination of genotype and environment would permit more efficient animal production."

Genotype by environment interactions may affect the efficiency of selection programs by reducing the response in the performance traits (i.e., growth, milk production) in animals raised under environmental conditions different to that of the selected ones. These reductions may involve reproduction and survival rates in genotypes raised at particular locations. The effect of genotype x environment interactions resulting from the lack of adaptation of particular genotypes to specific conditions may reduce economic performance when the environmental conditions of the selected animals are different from those of the commercial population.

Genotype by environment interaction is a potential source of reduced efficiency in genetic improvement programs involving animals in tropical areas and developing countries for three main reasons:

1) The utilization of germplasm selected or developed in regions with other climatic conditions and production systems is very common (Bondoc *et al.*, 1989). This approach reflects the limited number of efficient breeding programs based on local performance data.
2) The climate and other characteristics of production systems in tropical areas create numerous environmental challenges (food, housing, temperature, pathogens) to efficient production (Vercoe and Frisch, 1992). Adaptability traits are commonly mentioned and used in selection programs in tropical areas (Horst, 1982), but appear to be less important in more favorable environments.
3) Economic characteristics of markets in tropical regions, which may be different from those where the animals were selected, would lead to novel genotype x (economic) environment interactions.

Vercoe and Frisch (1986) identified the main environmental limitations for animal performance in tropical areas as being climatic factors (e.g., high temperatures, humidity and solar radiation), external parasites (e.g., ticks and other arthropods), internal parasites (e.g., gastrointestinal helminthes), protozoan, bacterial, fungal and viral diseases, and variations in the quantity and quality of available food.

The possible levels for studying genotype x environment interactions in animals (Barlow, 1985) are economic considerations, production traits, trait components of production traits, indirect traits (physiological traits), and direct genetic variation (DNA).

From the practical point of view, implications of GEI should be evaluated preferably at the economic level. However, studies performed at the other levels could help in a better understanding of GEI implications in animal improvement.

Previous reviews have emphasized methods for estimating GEI in animals and the biological-statistical evidence for GEI (Barlow, 1981; Vercoe and Frisch, 1992; Warwick, 1972; Wilson, 1974).

This paper reviews the implications of parameter estimates associated with GEI on design of genetic improvement programs for animals, with particular emphasis on tropical areas and developing countries. For completeness, some basic methodological principles and some old and some new biological-statistical evidence for GEI in animals are also included.

KEY WORDS / Production Systems / Breeding Systems / Selection / Genetic Resources / Breeds / Developing Countries /

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Types of genotype by environment interactions

Initially, interactions caused by heterogeneity of genotypic variances among environments must be distinguished from those caused by a lack of correlation between genotypic performance in different environments (Yamada, 1962; Falconer, 1989). Dickerson (1977) considered the genetic correlation between environments (r_g) as the most useful criterion for assessing the importance of GEI in animal breeding. Genetic correlations lower than 0.8 are expected to cause important reductions in the efficiency of breeding programs (Robertson, 1959).

In the absence of GEI, the expected value of r_g is one. Only when the genetic correlation among environments is less than one does GEI impede response to selection because it can change the optimal composition of the selection and rejected groups across environments (Cooper and DeLacy, 1994). Heterogeneity of variances in situations where the genetic correlations are unity is largely regarded as an effect of scale and not a cause of reranking.

Estimation Methods

There are three main methods for measuring GEI: components of variance, genetic correlations among environments, and pattern analysis (Cooper and DeLacy, 1994). Heterogeneity of genotypic variances among environments and correlation among genotypic performance in different environments are confounded when a standard ANOVA is used to estimate a GEI variance component (Muir *et al.*, 1992). Mixed model methodology has been used (see review by Cameron, 1993) to estimate r_g unbiasedly. Genetic evaluations using mixed model methodology in the presence of heterogeneous variances have also been described and their effectiveness evaluated (Garrick and Van Vleck, 1987; Reverter *et al.*, 1997).

An approximate genetic correlation between two environments can be obtained from the observed correlation between the predicted breeding values (I) of progeny tested sires in two environments ($r_{I(1),I(2)}$), using the equation (Brascamp *et al*., 1985):

$$rg \approx r_{I(1),I(2)} / \sqrt{(\, r^2_{AI(1)}\ r^2_{AI(2)})} \qquad (1)$$

where $r^2_{AI(1)}$ and $r^2_{AI(2)}$ are average reliabilities (repeatabilities) of the indices based on progeny testing, i.e., the squared correlation between the index and the breeding value (A) within environments 1 and 2. This correlation is expected to be lower than the genetic correlation, because the indices are predictions of A which contain error terms. For this reason, the use of uncorrected correlation estimates between sire or other replicated family group indices (predicted breeding values) in two environments as direct evidence of GEI can be misleading (Lynch and Walsh, 1998). In addition, when using this method, it is necessary to set one minimum value for r^2_{AI} (e.g. 0.7) in each environment for each sire, since equation (1) applies only if the sum of random environmental deviations of the progeny in each environment equals zero. This is true only in sires with predictions obtained using enough progeny numbers in both environments.

Another theoretical approach, particularly popular in plant breeding, is the concept of stability, which expresses the ability of one genotype to be less 'sensitive' to environmental influences. If the genotypes are considered fixed effects in a linear model (i.e., breeds), and the environments are a random sample of many possible production environments (locations or herds), 'stable' genotypes will have less steep regression lines across ordered environmental levels than 'non stable' ones (Eberhart and Russell, 1966; Muir *et al.*, 1992; Lynch and Walsh, 1998). This approach may help in selecting genotypes more adapted to difficult conditions by retaining for breeding those which perform better at lower environmental levels, rather than those with the maximum average performance.

DNA studies have identified sequences related to major genes for quantitative traits. These can be used for marker-assisted selection (Jansen, 1993). In the future, molecular biology techniques may help geneticists identify animals which carry specific genes with large effects on quantitative traits or quantitative trait loci (QTL) capable of increasing the productivity or product quality in specific environments. Identification of an important number of interacting QTL capable of increasing productivity in specific environments, management systems or markets, could help to develop a population with specific advantages under certain environmental conditions or limitations (Drinkwater and Hetzel, 1991).

TABLE I
TYPES OF GENOTYPE X ENVIRONMENT INTERACTIONS IN ANIMALS

Types	Variation		Examples
	Genotypes	Environments	
1	Small	Small	Sire families in one herd
2	Large	Small	Breeds in one herd
3	Small	Large	Sire families in different herds
4	Large	Large	Breeds in different areas

Adapted from Dunlop (1962).

Biological-statistical evidence of genotype by environment interactions in animals

Dunlop (1962) developed a scale of increasing likelihood for the presence of GEI in animals which involved increasing degrees of environmental and genetic variation from 1 to 4 (Table I). Interactions are most likely to be expected in category 4 (breeds in different areas). A classic example of the latter category occurs when both *Bos taurus* and *Bos indicus* cattle are raised in temperate and tropical areas. An example of category 3 (sire families in different herds) would be with poultry where the genetic correlation between sire progenies reared on the floor and in cages is as low as 0.7 (Pirchner, 1983). Interactions in situations of types 1 (sire families in one herd) or 2 (breeds in one herd) are less common.

Where the environment cannot, or can only partially, be controlled, as with plant and fish production, or with range animals, GEI are important. In contrast, where environmental control is feasible, as with dairy or poultry production, GEI are less important. With dairy cattle, GEI are small within the same geographic area, or between temperate regions. Thus, for example, GEI for productive traits in Holstein was small among the states of California, New York and Wisconsin, and between the US and Spain (Carabaño, 1988; Carabaño *et al.*, 1990). Most studies in temperate areas show little or no evidence for strong interactions between genotype and nutrition in dairy cattle (Syrstad, 1976).

Selection responses to the use of selected US Holstein sires for milk production in Latin America were estimated to be 53% to 78% of the response observed in the USA. The genetic correlations ranged from 0.78 to 0.91. Most of the reduction was attributed to heterogeneous variances (Stanton *et al.*, 1991). Costa *et al.* (2000) reported relatively large genetic correlations (0.85-0.88) for milk and fat production between Brazil and the USA although heritabilities and phenotypic variances were smaller in Brazil. In a study with data from Mexico and USA, Cienfuegos-Rivas *et al.* (1999), found genetic correlations ranging from .60 to .93 for milk production between countries. Correlations were higher between data from herds with similar production ranking in both countries.

Some unpublished estimates for Holstein herds with extremely high or low production levels in Mexico showed a low genetic correlation (0.40) for the first lactation records. This estimate is very close to the estimate of 0.38 for the genetic correlation between the genetic values in the Southern and Northern regions of Mexico obtained by Valencia (2001) with the same data. Ron and Hillel (1983) found significant interactions for genotype x lactation number in Holsteins in Israel but a very low interaction genotype x farm production level. These authors also attempted to determine differences in 'stability' of expressions of sires' genotypes across herd production levels, but there was no evidence of GEI.

Abubakar *et al.* (1987) observed a lower breeding efficiency and survival in high-milk estimated breeding value (EBV) Holstein bulls compared with low-milk EBV bulls in Mexico and Colombia. The relationship between milk production and survival was the opposite of that observed in the USA, suggesting a possible genotype x environment interaction. Valencia (2001) however, found a positive genetic correlation (0.33 to 0.64) between milk production and survival traits in Holstein with Mexican data.

Castillo-Juárez *et al.* (2000) found changes in correlations between milk production and somatic cell score and conception rate at first service with groups of herd environment. The genetic correlations between pairs of traits were consistently smaller in high environment herds, suggesting that differences in management between the two environment levels lessened the antagonistic genetic association between the traits studied. The authors suggested that a long-range plan for low environment herds should focus on improving the level of management, which would greatly reduce the unfavorable correlated changes in lactation mean somatic cell score and conception rate at first service associated with the genetic improvement of mature equivalent milk yield.

Syrstad (1990) indicated that there was no evidence of interaction of production levels (environments) x genotypes, represented by several European x Zebu or European x native crosses, on milk production. Significant genetic group x farm interactions for age at calving, length of lactation and calving interval were found in India. Genetic groups where Holstein x Sahiwal crosses with a different Holstein proportion ranging from 50 to 87.5% (Rao *et al.*, 1992).

Different economic conditions may lead to GEI when instead of one trait the economic value of the total production is considered. For example, the upgrading of European dual-purpose cattle with Holstein has increased milk yield but decreased carcass value. The improvement in dairy performance requires a high level of feeding. If a high level of feeding is uneconomical, but beef performance remains economically attractive, dual-purpose cattle may be more profitable under this new 'environment.' Similar examples can be drawn from beef breeding. A Simmental x Hereford cross may be generally more productive than pure Herefords, but in poor grazing regions, its higher milk potential may lead to unsatisfactory fertility and make the pure beef breed superior. The breeding goal should, therefore, be determined by the economic conditions of each particular situation (Pirchner, 1983).

Morris *et al.* (1993) studied genotype x location effects on reproductive and maternal traits in beef cattle using bulls of 11 breeds in crosses with Angus cows. Important GEI were observed for a number of reproductive, maternal and composite traits, including weight of calf weaned per cow mated (productivity) and cow 'efficiency' (the ratio of productivity to cow weight).

Important GEI were also found when comparing *Bos taurus x Bos indicus* crosses (TI) *vs. B. taurus x B. taurus* crosses (TT) in Nebraska and Florida (Olson *et al.*, 1991). The genotype x environment interaction was important for pregnancy rate; the advantage of TI over TT cows being greater in Florida (6%) than in Nebraska (2%). GEI also were observed for weaning weight and weight per cow exposed to breeding. Advantage for weight per cow exposed to breeding for TI *vs.* TT cows was greater in Florida (28%) than in Nebraska (6%).

In pigs, research has shown important GEI for body weight and backfat thickness when the same sires were used on test stations and commercial farms in the Netherlands (Merks, 1988a,b; 1989). Sire x herd interactions explained 11-23% of the variance for several traits. The genetic correlations between performances in central stations and farms were 0.41 for daily gain and 0.70 for backfat thickness.

Webb and Curran (1986) reviewed numerous studies in pigs, which showed that the interaction genotype x restricted or *ad libitum* feeding affected growth rate, and the interaction of genotype x test location (station *vs.* on-farm) was significant for feed efficiency.

Similarly, important GEI were found for growth traits in sheep in the United Kingdom under different commercial environments and according to sex. The genetic correlation for growth between males reared under intensive conditions and females reared on pasture was only 0.37 (Bishop *et al.*, 1996).

Selection response in a second environment

When animals, such as artificial insemination dairy sires, selected in environment 1 are used in a second environment 2, expected genetic response in environment 2 is:

$$\Delta G_{2.1} = r_G r_{AI_1} \sigma_{A_2} i_1$$

where r_G is the genetic correlation between environments 1 and 2, r_{AI_1} is selection accuracy for animals selected on environment 1, σ_{A_2} is the genetic additive standard deviation of the trait on environment 2 and i_1 is selection intensity on environment 1. Response to selection within environment 2 is:

$$\Delta G_{2.2} = r_{AI_2} \sigma_{A_2} i_2$$

where r_{AI_2} is selection accuracy for animals selected on environment 2 and i_2 is selection intensity on environment 2. Assuming i_1=i_2, if r_G r_{AI_1}>r_{AI_2}, selecting in environment 1 will give a greater selection response in environment 2. Conversely, if r_G r_{AI_1}<r_{AI_2}, selection within environment 2 will give greater response. Also in situations where $i_1 > i_2$, where say, more sires are tested in environment 1, use of sires selected on environment 1 may be more efficient than within population selection on environment 2.

Selection in several environments

Animal breeders often wish to improve overall performance in a range of environments. James (1961) derived formulae for maximizing the average selection response for two environments using a selection index approach. Kinghorn and Swan (1991) described how to apply a multitrait, best linear, unbiased prediction model to optimal multiple-environment evaluation with variance-covariance structures among relatives in different environments, including the numerator relationship matrix.

With two environments, there are several options for selection (Falconer, 1952). They are selection in one environment (either 'good' or 'bad'), separate selection of two strains in both environments, and selection on an index combining performance in both environments.

Falconer (1990) defined selection performed in a bad environment as 'antagonistic' and selection performed in a good environment as 'synergistic'. In laboratory organisms, 'antagonistic' selection is significantly better for improving the average mean of the selected traits. In a classical experiment with pigs (Fowler and Ensminger, 1960), two populations were selected for growth rate on *ad libitum* and restricted feeding. When switched to the opposite regime, the population selected under restricted feeding grew faster in both regimes.

Using genotype by environmental interaction parameters to optimize selection programs

Genotype by major environment interactions will change the ranking of the genotypes within each major environment, suggesting the possible need to design as many breeding programs as environments. In small scale breeding programs, this strategy may involve increased costs and reduced selection efficiency. Methods are therefore required to evaluate the possible outcomes of alternative designs.

Once the magnitude and biological and economic nature of the GEI have been evaluated, these parameters could be used to evaluate the effectiveness of selection across or within major production-marketing environments (Dickerson, 1962, 1977). The main parameters are genetic correlations among economic objectives for different environments.

Interactions Among Genotype and Random Environments

Total response to selection in several environments is proportional to the genetic correlation between genotypes in different environments (r_g). The ratio of selection response at constant selection intensity, derived by averaging selection responses measuring performance within k random environments relative to selecting in one environment, is (Dickerson, 1962):

$$[(1+(nk-1)\,h^2)/(1+(n-1)\,h^2 + n\,(k-1)\,r_g\,h^2)]^{1/2} \tag{2}$$

if a total of nk animals are tested (n in each environment). For nk=1000 animals tested, progress of the ratio with k is shown in Table II for different levels of r_g and heritability.

TABLE II
EFFECT OF INCREASING THE NUMBER OF TESTING ENVIRONMENTS (K) ON GENETIC RESPONSE IN A POPULATION OF 1000 ANIMALS

k	**h^2/r_g***								
	0.2/0.2	**0.2/0.4**	**0.2/0.8**	**0.4/0.2**	**0.4/0.4**	**0.4/0.8**	**0.8/0.2**	**0.8/0.4**	**0.8/0.8**
1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
5	2.22	1.49	1.22	1.10	1.05	1.02	1.01	1.01	1.00
10	3.11	1.76	1.32	1.15	1.07	1.04	1.02	1.01	1.00
20	4.31	2.06	1.43	1.20	1.09	1.05	1.02	1.01	1.01
50	6.47	2.52	1.58	1.26	1.12	1.06	1.03	1.01	1.01
100	8.47	2.87	1.69	1.30	1.14	1.07	1.03	1.02	1.01

* h^2/r_g = heritability/genetic correlation among environments.

The impact of increasing k will be greater when the trait has a low heritability and a low genetic correlation. GEI may significantly reduce the accuracy of estimates of the genetic values of the genotypes by introducing additional sources of variation into the phenotype (genotype x random environment interaction).

Merks (1988a) extended formula (2) to a full sib design to estimate the effect of genotype x random environmental interactions of a breeding program in pigs. Assuming each sire has m litters of size n in N herds, selection in all herds simultaneously produce a response of ΔG_N with Nmn individuals per sire. In the case of selection in a single herd, the response is ΔG_1. The formula (3) for the increase in selection response with increasing measured environments and constant selection intensity is

$$\frac{\Delta G_N}{\Delta G_1} = \left[\frac{(1+(n-1)(0.5h^2+c^2)+n(mN-1)0.25h^2}{(1+(n-1)(0.5h^2+c^2)+n(m-1)0.25h^2+nm(N-1)0.25h^2 r_g}\right]^{0.5} \tag{3}$$

were c^2 stands for the common environmental and non-additive effects between littermates within herds and h^2 is the heritability of the trait. This formula shows that the advantage of increase N is to minimize the error from r_g when measuring the suitability of each genotype by distributing the representatives of the genotype over as many herds (environments) as possible (Merks, 1988a).

Interactions Among Genotype and Major Environments

If GEI occur among k important production environments, choice between separate initial genotypes and selection programs in each environment *vs.* a single initial genotype with continuing selection for general adaptability to all k environments can be based upon the heritability (h^2_i) and the relative economic importance (e_i) of the performance in each environment and their genetic correlations ($r_{g\,ij}$). If e_i are equal, average response at constant selection intensity in the specific i-th environment from selection based upon average adaptability to k environments (P_k) relative to selection in one environment will be roughly (Dickerson, 1977):

$$\frac{\Delta G_1 \text{fromP}_k}{\Delta G_1 \text{fromP}_1} = \frac{(h_1 + \sum_1^{(k-1)} h_j r_{g\,ij})}{h_1 \sqrt{k[1+(k-1)\overline{\overline{h_i h_j r_{g\,ij}}}\,]}} \tag{4}$$

Equation (4) may be used whether or not a higher response will be obtained by performing selection for general adaptation to k major (e.g., regional) environments. Assuming equal heritability in each environment and equal genetic correlation among all pairs of environments, equation (4) simplifies to:

$$(1 + (k-1)\,r_g)/(k\,[1 + (k-1)\,h^2\,r_g])^{0.5} \tag{5}$$

TABLE III

AVERAGE EXPECTED RESPONSE FOR WITHIN ENVIRONMENT SELECTION AS A PROPORTION OF THE AVERAGE RESPONSE IN K MAJOR ENVIRONMENTS

k	**h^2/r_g***								
	0.8/0.8	**0.8/0.5**	**0.8/0.3**	**0.5/0.8**	**0.5/0.5**	**0.5/0.3**	**0.3/0.8**	**0.3/0.5**	**0.3/0.3**
1	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
2	0.99	0.90	0.83	1.08	0.95	0.86	1.14	0.99	0.88
3	0.99	0.86	0.76	1.12	0.94	0.81	1.23	1.01	0.85
4	0.99	0.84	0.72	1.15	0.94	0.79	1.30	1.04	0.84
5	1.00	0.83	0.70	1.16	0.95	0.78	1.34	1.06	0.84
100	1.00	0.79	0.62	1.26	1.00	0.77	1.61	1.27	0.98
1000	1.00	0.79	0.61	1.26	1.00	0.77	1.63	1.29	1.00

***** h^2/r_g = heritability/genetic correlation among environments.

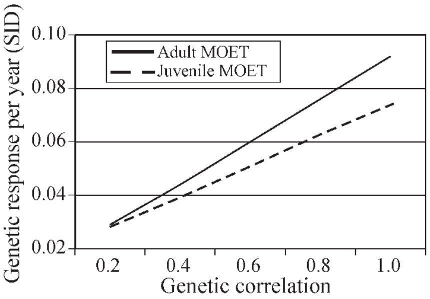

Figure 1. Genetic response per year in standard deviation units (SD) for the commercial population using adult and juvenile MOET nucleus with different genetic correlation.

Application of equation (5) shows that unless the value of heritability is high and the genetic correlation is low, the response in one environment is not reduced significantly with an increase in the number of major testing environments (Table III). For 1-5 major environments, with heritability values ranging from 0.3 to 0.5, a reduction in efficiency would be expected only with values of $r_g < 0.3$. Programs based on the evaluation of genotypes for several major environments would seem to be robust against reductions in r_g values and number of testing environments. The simplified assumptions in equation (5), however, may not be realistic for many cases.

Figure 1 depicts the effect of different values of r_g between adult and juvenile multiple ovulation and embryo transfer (MOET) nucleus and commercial populations in dairy cattle (Bondoc and Smith, 1993). The responses are expressed in standard deviations of the commercial population. A linear relationship exists between the expected response and r_g associated with each selection program. This relationship may also occur when a country is importing semen from sires evaluated in another country. If the first country is evaluating bulls by using progeny testing with data obtained at the commercial level, the entire system could be considered as another major environment if the test environment is different from that of the importing country. This case is similar to that when sires or semen from a nucleus population are used in the commercial population of one country.

Hierarchical Systems

In hierarchical improvement programs such as in pig breeding, two types of genetic correlations can be defined with respect of the consequences of GEI on genetic progress (Brascamp *et al.*, 1985; Merks, 1988a).

1) r_G is defined as the genetic correlation across levels of a genetic program and is typically the correlation between the test (nucleus) and commercial environments.
2) r_g is defined as the common genetic correlation among random environments (herds) within one level of a genetic program. If $r_g < 1$, the GEI will reduce the accuracy of the estimation of breeding values if insufficient numbers of random environmental levels (herds, locations) are used. Collecting data for evaluation from several herds will help overcome this problem.

Evaluating the impact of GEI in a hierarchical genetic program may involve interactions between and within the major environments, for which four parameters are necessary; h_T^2 the heritability of the trait (or index) at the level of the testing population (nucleus), h_C^2, the heritability at the level of the commercial population; and r_G and r_g as defined before.

In this case, the genetic response at the commercial level is reduced when r_G or r_g values are less than one, and possibly by $r_g \geq r_G$, which means that testing at the commercial level could help increase the genetic response. Generally $h_T^2 > h_C^2$, because the animals tested in the nucleus population usually perform in a more uniform environment and because more traits can be measured more accurately. In this situation, the best approach is to make the test environment as similar as possible to the commercial environment and to incorporate procedures, such as progeny testing or two-stage selection to evaluate animals at the commercial level (Merks, 1988a). A similar conclusion has been expressed with respect to the convenience of using information from commercial crossbred animals to evaluating purebred candidates, even when the genetic correlation is < 1 (Wei and van der Werf, 1994).

Discussion

In many species, the population is stratified into nucleus, multiplier and commercial production levels. These levels are not always conceptually recognized. In developing countries, where nucleus or even multiplier animals (germplasm) are usually imported, there is an increased possibility of GEI affecting the economic expression of the desired improvement. Studies on the practical implications of GEI in these countries and on the ways to circumvent such interactions are few. An exception is milk production traits in Holstein cattle among temperate areas, where GEI are of minor importance. Adequate assessment of the economic importance of GEI for many species is not available. In pigs, the practical importance of GEI is high (Brascamp *et al.*, 1985; Webb and Curran, 1986). Negative economic consequences of importation of animals when genetic correlations are less than unity, could be sometimes partially offset using rational selection criterion such as selecting dairy bulls on profit (Montaldo, 1997).

As an option to increase productivity by selection under difficult environments, some authors have stressed the importance of considering physiological or adaptability traits as selection criteria in breeding programs for tropical areas (Horst, 1982; Vercoe and Frisch, 1992). The incorporation of these traits into the selection process is not easy or straightforward because of the lack of knowledge about their economic value and the cost of measuring such traits.

Crossbreeding for exploitation of heterosis is often an option for combining adaptability and productivity in difficult environments. Heterosis is generally greater in more severe environments (Barlow, 1981). In tropical environments, the offspring of Brahaman x (Hereford x Shorthorn), have the same growth potential as the Hereford x Shorthorn parents and are almost as resistant to environmental stress as the Brahaman. In this case, the crossed offspring outperform both parental types in all but very low stress or very high stress environments (Vercoe and Frisch, 1992).

If 'antagonistic' selection is more efficient than 'synergistic' selection for developing animals adapted to a range of heterogeneous environments, this may imply that important changes are required in current improvement methods, where animals selected under favorable conditions are expected to produce progeny in unfavorable environments.

Webb and Curran (1986) found that for pigs the solution to the problem of low correlation between the performance in testing station and farm environments was to conduct the performance testing in a commercial environment. They suggested that identification of factors that cause the GEI (level of feeding, number of pigs per pen) may help in designing adequate tests in the future.

Other than GEI, the main practical consequences of subdividing a population for selection, are increased inbreeding and reduced selection intensity in smaller populations (Smith and Quinton, 1993). Operational and cost considerations related to the size of the program are also important. These factors usually encourage the development of a single breeding program for a relatively large population over a range of environments (Drinkwater and Hetzel, 1991).

Important limitations on selection of animals adapted to specific conditions, particularly pasture systems, include lack of adequate characterization of the environment and the presence of environmental conditions that change rapidly, e.g., drought and disease, or that make profitable animal production difficult or impossible.

Because economic returns from a given breeding program are obtained over several generations, economic and environmental conditions may change. For this reason, evaluation of the consequences of GEI need to be projected into the future.

In populations adapted to specific environments that are difficult to change, selection for locally adapted populations may be the best option. For any situation, comparative economic performance of candidate genotypes under conditions of the local environment should be evaluated before a decision is taken. Few comparisons have been made among exotic, local and crossbreed genotypes under commercial conditions in developing countries. In many cases, the experimental evidence is compromised by severe deficiencies in the experimental design and by poor characterization and sampling of the local breeds (Montaldo and Meza, 1999).

If nucleus breeding strategies based on MOET are used, distribution of the nucleus among several sites and data collection from the base population level may help reduce the negative effects of GEI, particularly when the r_g is low (Bondoc and Smith, 1993). Thus, in the presence of GEI, an important potential advantage exists for dispersed rather than centralized, and for open rather than closed nucleus populations. In many cases, disease control standards may limit the use of animals selected from the base commercial population in the nucleus population. Similar restrictions occur in traditional improvement schemes which use closed, purebred studs to provide males for the multiplier and commercial populations. The accurate estimation of GEI parameters is critical to assess the effectiveness of breeding programs for production systems in developing countries. Use of evaluation schemes such as progeny testing with artificial insemination in several locations and herds, could reduce the effect of GEI on the response to selection.

Conclusions

The practical and economic implications of GEI will continue to dominate the organization of animal breeding programs. Biological-statistical evidence for GEI needs to be considered together with economic information during decision-making processes involving all traits of interest. Despite biological evidence for GEI for many individual traits in animals, the implications of GEI on the organization of more efficient animal breeding programs are frequently difficult to evaluate. Current research on effects of GEI on total productivity in tropical areas and developing countries should, therefore, be done at the commercial level.

Improvements based on closed elite stud or nucleus breeding systems and on importation of germplasm are more likely to be negatively affected by GEI than those based on extensive recording of all important traits at the commercial level. In this strategy, identification of the key major environmental factors associated with GEI will help optimize the environments for testing in hierarchical improvement schemes.

Current biological evidence suggests that 'antagonistic' selection under a 'bad' environment is a better option for producing animals adapted to a wide range of environmental conditions than 'synergistic' selection under 'good' environmental conditions. In many cases, this is the opposite of the current practice in animal breeding where the nucleus and stud herds are better managed than average commercial operations. However, many examples exist of successful use of genetic material selected under different environmental conditions. In many cases, crossbreeding and creation of new synthetic breeds might be the most profitable option to combine high production levels with resistance to environmental conditions. Continued selection under commercial conditions will help to increase the frequency of the alleles required to increase productivity under that environment, as long as the program uses rational selection criteria.

The evidence and relationships reviewed show the importance of using replicated random environments and of incorporating records of animals at commercial level into evaluation systems to minimize the potentially negative effects of GEI on the rate of genetic progress.

Adaptability and economic value of recently introduced populations should be assessed under commercial environmental conditions including reasonable restrictions which are a part of the production system in the future. Removal of obvious environmental restrictions for productivity is to be considered in most cases, before looking for genetic 'adaptation' of animal populations to bad or irrational management practices. Comparative studies with appropriate experimental design are mandatory for adequate decision-making regarding conservation, introduction and crossbreeding of local and recently introduced populations.

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