J. Dairy Sci. 87:1496–1505

Genetic Comparison of Breeding Schemes Based on Semen Importation and Local Breeding Schemes: Framework and Application to Costa Rica

B. Vargas[1] and J. A. M. van Arendonk[2]
[1]Posgrado Regional en Ciencias Veterinarias Tropicales,
Universidad Nacional de Costa Rica, Heredia, Costa Rica
[2]Animal Breeding and Genetics Group, Wageningen University,
6700 AH Wageningen, The Netherlands

ABSTRACT

Local breeding schemes for Holstein cattle of Costa Rica were compared with the current practice based on continuous semen importation (SI) by deterministic simulation. Comparison was made on the basis of genetic response and correlation between breeding goals. A local breeding goal was defined on the basis of prevailing production circumstances and compared against a typical breeding goal for an exporting country. Differences in genetic response were <3%, and the correlation between breeding goals was 0.99. Therefore, difference between breeding objectives proved negligible. For the evaluation of genetic response, the current scheme based on SI was evaluated against a progeny testing (PT) scheme and a closed nucleus (CN) breeding scheme, both local. Selection intensities and accuracy of selection were defined according to current population size and reproduction efficiency parameters. When genotype × environment interaction (G × E) was ignored, SI was the strategy with the highest genetic response: 5.0% above the CN breeding scheme and 33.2% above PT. A correlation between breeding values in both countries lower than one was assumed to assess the effect of G × E. This resulted in permanent effects on the relative efficiencies of breeding strategies because of the reduction in the rate of genetic response when SI was used. When the genetic correlation was assumed equal to 0.75, the genetic response achieved with SI was reduced at the same level as local PT. When an initial difference in average genetic merit of the populations was assumed, this only had a temporal effect on the relative ranking of strategies, which is reverted after some years of selection because the rate of change in genetic responses remains unchanged. Given that the actual levels of genetic correlation between countries may be around 0.60, it was concluded that a local breeding scheme based on a nucleus herd could provide better results than the current strategy based on SI.
(**Key words:** breeding scheme, genetic comparison, dairy cattle)

Abbreviation key: CN = closed nucleus, **CR** = correlated response, **ER** = economic response, **G × E** = genotype × environment interaction, **PT** = progeny testing, **SI** = semen importation, **TPI** = total production index.

INTRODUCTION

Breeding schemes have contributed to genetic improvement of dairy cows in most Western countries. Regression of average breeding values for 305-d milk yield in Holstein dairy cows from USA (AIPL-USDA, 2003) results in an average genetic increase of 82.2 kg/yr. Genetic improvement in the Holstein population has benefitted from the international exchange of semen and breeding animals. The genetic improvement of other dairy cattle populations was accelerated in the 1970s by importation of genetic material from North America. Subsequently, these countries implemented modern breeding strategies for improvement of their own populations. These breeding schemes have decreased the need for importation of genetic material.

An efficient progeny testing (**PT**) scheme within a country is built on participation of a large group of farmers in AI and performance recording. Not all countries can afford the implementation of such a functional but costly breed improvement organization. Open nucleus breeding schemes may provide an alternative to PT schemes (Smith, 1988; Mpofu et al., 1993; Peters, 1993). Some advantages that have been mentioned for this scheme are that the entire breeding program is operated as a single herd with a high degree of operational control over the determinants of genetic progress (Meuwissen, 1990). In addition, generation intervals are shorter, and important characters can be measured at a relatively low cost under the same conditions. Potential disadvantages that have been mentioned for this scheme are possible increases of inbreeding, major risk for spreading diseases, high initial investment and op-

Received September 12, 2003.
Accepted December 20, 2003.
Corresponding author: J. Van Arendonk; E-mail: Johan.vanarendonk@wur.nl.

erating costs, and organizational considerations (Hodges, 1990; Meuwissen, 1990).

As an alternative to having their own breeding scheme, countries could decide to rely entirely on importation of semen, embryos, or both from other countries. Performance testing on a relatively small number of farms is required to evaluate the merit of genetic material from different exporting countries. Both genetic as well as economic issues are involved in choosing the most appropriate improvement strategy for a country.

For example, the dairy cattle population in Costa Rica consists of approximately 200,000 cows located on 6400 farms (MAG-CORFOGA, 2001). Although these farms are technologically advanced, no official milk recording scheme is carried out, and <20% of the farmers perform some kind of milk recording. There is a need to explore the opportunities of different breeding strategies to meet the needs of the Costa Rican dairy farmers. The main question is whether the current breeding practices, based on importation of semen, should be continued or whether there is room for a transition to a more local breeding scheme.

Livestock production systems vary in production intensity, access to infrastructure, and markets. Differences between countries in environmental or market conditions may lead to differences in breeding goals and genotype × environment interaction (**G × E**) between countries.

From a conceptual point of view, importation of semen to improve the local cattle population is advised only under the following circumstances (Smith, 1988): 1) breeding goals for the exporting and importing populations are similar, 2) exotic stocks are better than domestic stocks for traits in the breeding goal, or 3) G × E effects are not important.

No good framework is available for evaluating the importance of each of these factors. Such a framework is needed for a genetic and economic comparison of the different breeding alternatives for a population.

This paper presents a framework for the genetic comparison of schemes based on semen importation (**SI**) and local breeding schemes, i.e., PT and closed nucleus (**CN**) breeding. The study first addresses the consequences of differences in breeding goals between the local and exporting country. Subsequently, differences in genetic level and rates of genetic gain between the populations are evaluated in relation to the structure of the breeding scheme and the degree of G × E between countries. The framework is demonstrated for the Costa Rican Holstein population, which currently relies heavily on importation of semen from North America.

MATERIALS AND METHODS

Breeding Goal

We considered a breeding goal for Holstein cows in Costa Rica and a breeding goal for an exporting country. Consequences of differences in breeding goals were assessed by calculating the correlations among breeding goals, correlations among selection index of sires, and response to selection. We applied some differences between countries in the traits included in the breeding goal, the selection index of sires, and the relative weights given to these traits in the breeding goal. Three production traits (carrier, fat, and protein) and 2 functional traits (rumen capacity, survival rate) were chosen on the basis of the analysis performed by Vargas et al. (2002). It was assumed that selection of sires in the exporting country is on the basis of performance of 100 daughters for production traits and survival rate. Selection in Costa Rica was also based on performance of 100 daughters for all traits, including rumen capacity.

Genetic and phenotypic parameters used in this analysis are given in Table 1. Parameters were taken from the literature (Groen, 1990; Visscher and Goddard, 1995) and assumed equal for both countries. In this way, we ensured that observed differences between countries are due to differences in breeding goals or breeding schemes and not due to differences in genetic parameters. Economic values for traits in the breeding goal for Holstein cattle in Costa Rica (Table 1) were calculated by Vargas et al. (2002) assuming a fixed milk-output evaluation base.

Economic values used for the exporting country (Table 1) reflect the relative weights in the total production index (**TPI**) economic index used for selection of Holstein cattle in US (Holstein USA, 2003). The TPI index included production (fat, protein), type (type, udder, feet, and legs), and health traits (productive life, SCS) with relative weights of 4:2:1. In determining the economic values for production traits, the ratio of economic values for protein and fat in the exporting country was set equal to 5:2, and the total value (fat + protein) was assumed equal to the total value for Costa Rica. An earlier study (Vargas et al., 2002) demonstrated that the economic value for survival rate in Holstein cattle of Costa Rica was in the same range as in other countries. Therefore, survival rate was given the same economic value in the exporting country and Costa Rica. Rumen capacity was assumed to have an economic value of zero in the exporting country.

Selection index coefficients (b) were derived using the following equation (Hazel, 1943):

$$b = \mathbf{P}^{-1}\mathbf{G}\mathbf{v} \quad [1]$$

where P is the variance-covariance matrix between traits in the selection index, **G** is the variance-covariance matrix between traits in the index and traits in

Table 1. Means, phenotypic standard deviations (σ_p), heritabilities (diagonal), phenotypic correlations (above diagonal), genetic correlations (below diagonal), and economic values for traits included in a breeding goal for Holstein cattle in Costa Rica and an exporting country.

								Economic value	
Trait	$\overline{\chi}$	σ_p	Carrier[1]	Fat[1]	Protein[1]	Rumen capacity[2]	Survival rate[3]	Costa Rica[4]	Exporting country
Carrier	5170.3	1034.0	**0.30**	0.81	0.92	0.65	0.32	–0.04	0.00
Fat	202.1	50.5	0.73	**0.34**	0.87	0.65	0.34	3.53	1.84
Protein	157.8	39.5	0.88	0.85	**0.31**	0.65	0.33	2.91	4.60
Rumen capacity	8.652	1.003	0.70	0.70	0.70	**0.25**	0.60	45.59	0.00
Survival rate	92	12	0.62	0.64	0.69	0.70	**0.05**	3.18	3.18

[1]305-d kg of carrier, fat, and protein for a Holstein heifer (28 mo old), 1-yr calving interval, producing 5530.2 kg of 305-d milk yield, fat content = 3.65%, protein content = 2.85%. Correlations and h^2 from Groen (1990).

[2]Obtained as 0.021 × heifer BW. Correlations and h^2 obtained from Groen (1990).

[3]Probability of a Holstein heifer not to be culled by mortality, health, disease, or udder and teat problems during 1 yr. Correlations with carrier, fat, and protein were taken from Visscher and Goddard (1995).

[4]Economic values under a fixed milk output base of evaluation from Vargas et al. (2002).

the breeding goal, and **v** is a vector with economic values for traits in the breeding goal.

The correlation between the breeding goal for Costa Rica (H_{cr}) and the breeding goal in the exporting country (H_{exp}) was derived as follows (Gibson and van Arendonk, 1998):

$$r_{Hcr,Hexp} = \frac{\mathbf{v}'_{cr}\mathbf{C}\mathbf{v}_{exp}}{\sqrt{\mathbf{v}'_{cr}\mathbf{C}\mathbf{v}_{cr}} \times \sqrt{\mathbf{v}'_{exp}\mathbf{C}\mathbf{v}_{exp}}} \quad [2]$$

where **C** is the variance-covariance matrix between traits in the 2 breeding goals and **v** is as defined in Eq. [1]. Note that matrix **C** is the same within and between countries because of the assumption that the same parameters apply in both countries and that there is no genotype × country interaction. Equation [2] can be modified in situations where there are differences in parameters between countries or when G × E is present (Gibson and van Arendonk, 1998).

The correlation between the selection index of sires obtained for Costa Rica (I_{cr}) and the selection index in the exporting country (I_{exp}) is equal to:

$$r_{Icr,Iexp} = \frac{\mathbf{b}'_{cr}\mathbf{P}\mathbf{b}_{exp}}{\sqrt{b'_{cr}Pb_{cr}} \times \sqrt{b'_{exp}Pb_{exp}}} \quad [3]$$

where **P** is as defined in Eq. [1] and $\mathbf{b}_{cr}$ and $\mathbf{b}_{exp}$ are the vectors with selection index coefficients for proven sires in Costa Rica and the exporting country, respectively. The expressions in the denominator of Eq. [3] are the products of the standard deviation of the index (σ_I) in both countries.

Alternative Breeding Schemes

General concept. The objective of the following analysis was to determine the relative efficiency of alternative breeding schemes for the current Holstein population in Costa Rica using deterministic simulation. Three strategies were analyzed: SI, PT, and CN breeding schemes.

Information sources for the selection indexes were defined according to breeding scheme and selection path. The assumptions made for the different breeding schemes are described in the following sections.

SI. For this strategy, it was assumed that genetic improvement of the local Holstein cattle population relies entirely on the importation of semen from the exporting country. This strategy has been suggested for situations in which the exotic stock suits the local production and marketing conditions, and there are no major effects of G × E (Smith, 1988). Genetic resources available worldwide can be used locally at a reasonable price because of the increasing number of competitors for this market (Meuwissen, 1990). In the present study, it was assumed that all imported semen was purchased from a single country. This country has a long-standing PT scheme operating on a large dairy cow population. Cattle population parameters assumed for Costa Rica and the exporting country are given in Table 2. Figures for the exporting country were based on data for the Holstein cattle population in the US (Wiggans, 1997), which is currently the major provider of germplasm for Costa Rica. Selection intensities for the different selection paths were derived from these figures, considering restrictions in size of population for PT-Costa Rica and CN. It was also assumed that all cows in the population were inseminated using imported semen. No selection was performed within the local population; therefore, genetic improvement for this strategy relied exclusively on the genetic progress generated in the exporting country. Traits included in the selection index are given in Table 3. Genetic evaluation of sires was based on daughter performance for

Table 2. Population parameters assumed for a progeny testing scheme for Costa Rican Holstein cattle and selection intensities and generation intervals for selection paths: sires of sons (SS), sires of daughters (SD), dams of sons (DS), and dams of daughters (DD).

	Exporting country		Costa Rica	
Parameter.	Efficiency	Value	Efficiency	Value
Total population	. . .	4,400,000	. . .	200,000
Breeding population (AI + milk recording)	50%	2,200,000	35%	70,000
Population of cows to select DS	10%	220,000	10%	7000
First lactation cows bred by AI[1]	25%	550,000	25%	17,500
Number of young bulls tested/yr	. . .	1500	. . .	50
Daughters/young bull[2]	. . .	100	. . .	100
Selection intensity				
SS	15/1500	2.66	4/50	1.80
SD[3]	45/1500	2.27	8/50	1.49
DS[4]	8570/220,000	2.17	286/7000	2.14
DD[5]	109/130	0.31	50/60	0.29
Generation interval, yr				
SS	. . .	6.0	. . .	6.0
SD[6]	. . .	5.9	. . .	5.9
DS	. . .	5.0	. . .	5.0
DD	. . .	6.0	. . .	6.0

[1]All first-parity cows are assumed to be bred by young bulls.

[2]Number of daughters = [number of first-parity cows/number of young bulls] × conception rate (0.70) × sex ratio (0.50) × survival rate until first lactation (0.90) × rate of success of first lactation (0.90).

[3]It is assumed that imported semen is from sires in the top 10% of the ranking in the exporting country.

[4]Number of dams = number of young bulls/[conception rate (0.70) × sex ratio (0.50) × survivability (0.50)].

[5]Average number of heifers = [herd size × conception rate (0.70) × sex ratio (0.50) × survivability (0.50)]. Number of heifers + later parity cows = heifers/0.25.

[6]L_{SD} = proportion young bulls (0.25) × 2.5 yr + proportion proven bulls (0.75) × 7 yr = 5.9.

production traits and survival, with no measurements on rumen capacity.

Calculations for SI were initially performed assuming no effect of G × E and no initial difference in genetic level between populations. The effect of G × E was further examined by assuming 2 different levels of genetic correlations (0.50 and 0.75) between traits measured in both countries (the same genetic correlation for all traits). The effect of initial differences of 1.25, 1.50, and 2.0 standard deviations in overall genetic merit was also evaluated.

PT. For this strategy, it was assumed that a PT scheme was initiated within the local population. Table 2 summarizes assumptions made about the size of the local population and the structure of the PT scheme. Given the small population size, it is obvious that the number of bulls needed to sire all cows in the base population could be very low. Therefore, a minimum of

Table 3. Traits included in the selection index and information sources for breeding strategies based on semen importation (SI), progeny testing (PT), and closed nucleus (CN) breeding schemes.

	Traits in the selection index[1]					
Breeding strategy	Carr	Fat	Prot	RC	SR	Information sources
SI						
Sires of sons/sires of daughters	x	x	x	—	x	100 daughters
Dams of sons/dams of daughters	x	x	x	—	x	performance + breeding values for sire and grandsire
PT						
Sires of sons/sires of daughters	x	x	x	x	x	performance (rumen capacity) + 100 daughters (production traits and survival)
Dams of sons/dams of daughters	x	x	x	—	x	performance (production traits and survival) + breeding values for sire and grandsire (all traits)
CN						
Sires of sons/sires of daughters	x	x	x	x	x	performance (rumen capacity) + 4 full sisters and 12 half sisters (all traits)
Dams of sons/dams of daughters	x	x	x	x	x	performance + 3 full sisters and 12 half sisters (all traits)

[1]Carr = carrier, Prot = protein, RC = rumen capacity, and SR = survival rate.

Table 4. Parameters assumed for a closed nucleus (CN) breeding scheme in the Costa Rican Holstein population.

Parameter	Efficiency	Value
Number of cows in the nucleus herd[1]	. . .	256
Number of donor cows in the nucleus herd	. . .	32
Embryos per cow[2]	. . .	16
Male and female offspring per cow[3]	. . .	4/4
Number of full sibs per bull candidate	. . .	4
Number of half sibs per bull candidate	. . .	12
Selection intensity	. . .	
Males[4]	8/32	1.24
Females	32/256	1.64
Generation interval, yr		
Males	. . .	3.50
Females	. . .	4.25

[1]Cows are assumed to be culled after their second lactation; therefore, 130 replacements are needed per year.

[2]Number of embryos assumes 4 flushes with 2 surviving males/females per flush.

[3]Assuming 60% success of embryo transfer and 90% calf survival after birth.

[4]Eight males are selected from a total of 128 available in the herd, but a maximum of one male is allowed per full sib family to minimize inbreeding. Therefore, male selection is within families, and the fraction selected becomes 8/32.

4 sires to breed sons and 8 sires to breed dams was used to avoid rates of inbreeding that were too high. Traits in the selection index and information sources for this strategy are specified in Table 3. It was assumed that all cows under milk recording were sired by bulls selected from the local PT scheme. It was also assumed that production traits and survival rate were measured on the entire cow population participating in the breeding program; rumen capacity information was only available on performance of sires.

CN. This strategy assumed that a nucleus breeding herd was established in Costa Rica. The nucleus herd used multiple ovulation and embryo transfer. In our analysis, we considered multiple ovulation and embryo transfer on adult cows within a closed nucleus. Potential donors were selected on the basis of performance during first lactation and on information on first lactation performance of full-sibs and half-sibs. Selection of sires and dams was performed only within the CN herd. Genetic gain in the base population was, therefore, entirely determined by the genetic gain within the nucleus. Data on structure and efficiency parameters assumed for the nucleus are given in Table 4 and were based on field data (Meuwissen, 1990). Traits included in the selection index and information sources are given in Table 3. Note that for this strategy we assumed that rumen capacity was measured not only on males, but also on females.

Genetic response for this strategy was compared against SI and PT assuming the same genetic merit at the start of the different programs, which is probably not a very realistic assumption because the nucleus herd could be selected from outstanding individuals available in the exporting country (e.g., US). Therefore, initial genetic level of cows in the nucleus is much higher than the genetic level of the commercial population. The effect of the initial genetic level on the comparison between strategies will also be discussed.

Comparison criteria and sensitivity. Total genetic response (R) expressed in US dollars per year was used as the criteria for comparison. This result was obtained from the following equation (Rendel and Robertson, 1950):

$$R = \frac{\sum_{s=1}^{4} ER_s}{\sum_{s=1}^{4} L_s} \quad [4]$$

where ER_s and L_s are, respectively, the economic response (**ER**) in the breeding goal and the average generation interval for selection path *s*. Details on calculation of ER_s are given in Table 5. The change in genetic (co-)variance caused by selection (Bulmer, 1971) and effects of family structure and population size on selection intensity were ignored, which lead to an over-prediction of genetic gain in particular for the CN scheme (McGuirk, 1989). Inbreeding effects were only taken into account by setting a minimum number of sires to select in the PT scheme and by setting a restriction of one bull selected per family in the CN scheme. The main objective of the present analysis was to provide a framework for comparing the results of alternative breeding schemes.

RESULTS AND DISCUSSION

Breeding Goal

The correlation between breeding goals was 0.987, and the correlation between selection indexes of sires was 0.976, which indicates that the difference in breeding goals between the 2 countries does not result in major differences in the ranking of sires when selecting for either of the 2 breeding goals.

Traits with the highest contribution to the overall genetic gain were protein and fat (see ER, Table 5), but the relative importance differs between countries. Fat and protein account for 61.4 and 35.5% of the total response in Costa Rica, respectively. For the exporting country, the contributions are 32.5 and 63.6%, respectively. Rumen capacity contributes an additional 8.0% to the genetic response in Costa Rica, and the contribution of survival rate is <4% in both countries.

Table 5. Selection index coefficients (**b**) for selection of sires, genetic superiorities (GS), economic response (ER), and correlated response (CR) for traits in breeding goal in Costa Rica and the exporting country assuming a selection intensity (i) equal to 1.

	Costa Rica			Exporting country			
Parameter	**b**	GS[1]	ER[2]	**b**	GS	ER	CR[3]
Carrier	–0.07	416.8	–16.67	–0.01	455.4	0.00	–18.22
Fat	6.98	27.50	97.08	3.51	26.11	48.04	92.17
Protein	5.60	19.29	56.13	8.71	20.41	93.89	59.39
Rumen capacity	13.39	0.35	15.96	. . .	0.34	0.00	15.68
Survival rate	2.58	1.77	5.63	0.94	1.78	5.66	5.66
Total response (R),[4] US $/yr per cow	. . .	. . .	158.1	. . .	. . .	147.6	154.7
Standard deviation index (σ_I)	158.1			147.6			
Standard deviation breeding goal (σ_H)	167.0			156.0			
Accuracy of the index (R_{IH})	0.95			0.95			

[1]Genetic superiority (GS) = (i **b′** $\mathbf{G}_j$)/σ_I for j = 1 to 5 traits in the breeding goal where $\mathbf{G}_j$ = column j of **G**, the variance-covariance matrix between traits in the index and traits in the breeding goal (see Eq. [1]).

[2]Economic response (ER) = GS_j $\mathbf{v}_j$; for j = 1 to 5 traits in the breeding goal.

[3]Correlated response (CR) in Costa Rica when selection is on breeding goal in the exporting country.

[4]Total response (R) = i σ_I with i = 1, R = σ_I.

A comparison of the differences in breeding goals can also be based on the correlated response (**CR**), i.e., the economic response in Costa Rica resulting from selection of sires in the exporting country for the breeding goal of the exporting country (Table 5). In this case, the total genetic response includes the contribution of rumen capacity, which is the correlated response achieved for this trait when selecting for other traits in the breeding goal. The correlated response in Costa Rica from selection for the exporting country is 2.2% lower than the response from direct selection for the Costa Rican breeding goal. The relative contribution of traits to the total economic response is very similar for both alternatives.

In summary, the breeding goals between Costa Rica and the exporting country differed in the traits included as well as the economic weights of breeding goal traits. The results show that selection for the breeding goal for the Costa Rican Holstein population would lead to similar rates of genetic response as selection for the breeding goal in the exporting country. The differences between breeding objectives are not a major factor in evaluating importation of semen and breeding schemes based on the local Holstein population.

Breeding Schemes

Initial situation. The genetic response achieved for each breeding strategy and selection path is shown in Table 6. This table also gives information on selection intensities and accuracy of selection. Note that the results shown for SI correspond to the correlated response in Costa Rica when selection is performed in the exporting country, assuming a genetic correlation of one (no G × E effect), but different economic values for traits in the breeding goal. Strategy SI resulted in the highest rate of economic response. The response was 5.0 and 33.2% higher compared with CN and PT (Table 6). Cumulative genetic responses are plotted in Figure 1, assuming a time horizon of 25 yr and no initial genetic differences between populations. The genetic distance between populations will increase over time because of the differences in rates of genetic gain.

The advantage of SI over PT was mainly caused by the higher selection intensity for the selection paths: sires of sons and sires of daughters in the exporting country. This was, in part, the result of the differences in population size. The reduced size of the Holstein population in Costa Rica implies that the number of bulls that can be progeny tested is very low. The inclusion of rumen capacity in the selection index for Costa Rica did not produce a substantial increase in genetic response because of the relatively low contribution of this trait. As previously discussed, the economic response is mainly determined by production traits. An earlier study also found a superiority of strategies based on SI over local PT schemes when genetic correlation between countries was assumed equal to one (Mpofu et al., 1993).

Progeny testing schemes have been successfully practiced for a long time in countries with a large dairy cattle population. Selection of sires and dams can be performed directly within the same population to be improved. On the other hand, this strategy requires a widespread milk recording scheme and extensive use of AI for the estimation of breeding values of selection candidates, which are not the norm in a developing country (Meuwissen, 1990). Genetic gain largely depends on the effective size of the population. In addition,

Table 6. Economic response (ER; US$/yr) for strategies based on semen importation (SI), progeny testing (PT), and closed nucleus breeding scheme (CN) assuming a genetic correlation of 1.0 between traits in the breeding goal in the 2 countries.

Path	σ_I	σ_H	R_{IH}	I	Genetic superiority[1]					ER	
					Carr	Fat	Prot	RC	SR	(US$/yr)	(%)
SI[2]											
Sires of sons	147.6	156.0	0.95	2.66	455.4	26.1	20.4	0.34	1.78	68.58	42
Sires of daughters	147.6	156.0	0.95	2.27	455.4	26.1	20.4	0.34	1.78	44.82	28
Dams of sons	95.4	156.0	0.61	2.17	265.8	17.4	13.0	0.21	1.12	44.26	27
Dams of daughters	95.4	156.0	0.61	0.31	265.8	17.4	13.0	0.21	1.12	5.27	3
										162.93	
PT											
Sires of sons	158.1	167.0	0.95	1.80	416.8	27.5	19.3	0.35	1.77	47.44	39
Sires of daughters	158.1	167.0	0.95	1.49	416.8	27.5	19.3	0.35	1.77	25.24	21
Dams of sons	104.2	167.0	0.62	2.14	235.2	18.4	12.2	0.22	1.08	44.64	36
Dams of daughters	104.2	167.0	0.62	0.29	235.2	18.4	12.2	0.22	1.08	5.04	4
										122.36	
CN											
Sires of sons	100.0	167.0	0.60	1.24	260.2	17.0	11.9	0.27	1.18	35.43	23
Sires of daughters	100.0	167.0	0.60	1.24	260.2	17.0	11.9	0.27	1.18	35.43	23
Dams of sons	109.2	167.0	0.65	1.64	253.7	19.1	12.8	0.24	1.16	42.14	27
Dams of daughters	109.2	167.0	0.65	1.64	253.7	19.1	12.8	0.24	1.16	42.14	27
										155.14	

[1]The response given for SI corresponds to the correlated response in Costa Rica when selection is on the breeding goal of the exporting country. Carr = carrier, Prot = protein, RC = rumen capacity, and SR = survival rate.

[2]Genetic superiority is given in the respective units of the trait.

the inclusion of additional traits in the selection requires the implementation of a recording scheme.

From Table 6, we can also see that the superiority of CN over PT mainly originates from the increased reproductive capacity of females and the shorter generation intervals (Tables 2 and 4). As observed, most of the genetic gain was obtained through the dam paths (54%); for SI and PT, these 2 paths only contributed 30 and 40% of the total ER, respectively. Especially, the contribution of the dams to breed dams pathway becomes important in CN. Superiority of CN over PT schemes has been reported before (Nicholas and Smith, 1983; McGuirk, 1989; Mpofu et al., 1993).

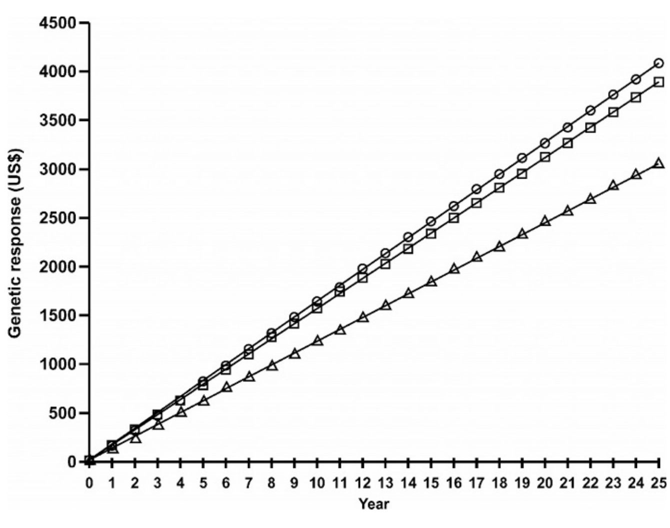

Figure 1. Genetic response (US$) for strategies based on progeny testing (△), semen importation (○), and closed nucleus (□) breeding schemes assuming no genotype × environment interaction effect and no initial difference in genetic merit between populations.

Effect of G × E. The effect of G × E was evaluated by simulating different degrees of genetic correlation between traits in the exporting country and Costa Rica. Three levels of genetic correlations were analyzed: 0.50, 0.75, and 1.0. The genetic responses for these 3 levels were compared against the genetic response obtained for strategy PT. The results are shown in Figure 2. As observed, when the genetic correlation was 0.50, the rate of response achieved by SI was lower than that by PT. With a genetic correlation of one, the genetic response from PT was 75.1% of the response from SI. Consequently, the strategies SI and PT produced almost the same genetic response for a genetic correlation of 0.75 (Figure 2). Based on these results, importation of semen is justified from a genetic point of view when the genetic correlation between countries is >0.75, which is in agreement with results found in previous studies (Goddard, 1992; Mpofu et al., 1993).

Initial differences in genetic merit. For strategy SI, genetic responses were also analyzed assuming initial differences in genetic merit of the population in

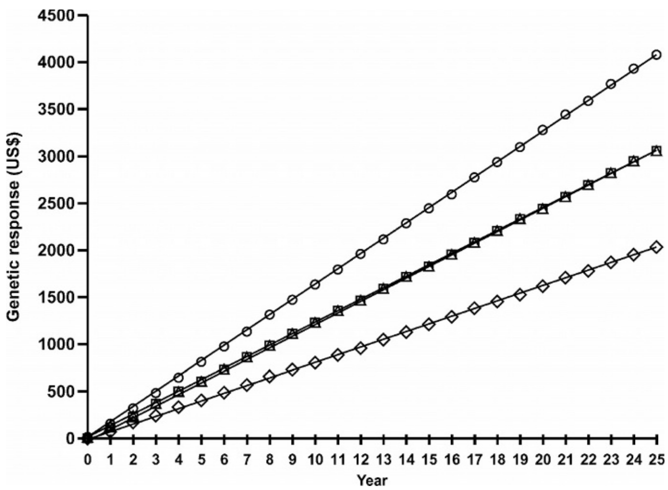

Figure 2. Genetic response (US$) for breeding strategies based on progeny testing (△) and semen importation assuming genetic correlations of 1.0 (○), 0.75 (□), and 0.50 (◇) between traits in the breeding goals in the exporting country and Costa Rica.

the exporting country for a situation with a genetic correlation of 0.50 between traits in both countries. Results were compared against strategy PT for a time horizon of 15 yr only, to appreciate differences more clearly (Figure 3).

Initial differences in genetic merit will shift the line of ER along the y-axis, but the rate of change in genetic response will remain at the same level. When the genetic correlations are high, the lines for SI and PT will never cross, and SI will always be higher than PT. When genetic correlations are low, as shown in Figure 3, the line for PT will start below SI and will intersect SI at some point in time because of the higher rate of genetic gain. The point of intersection will be determined by the initial difference in genetic merit and can be obtained as x = IGD/(R_{SI} – R_{PT}), where x is the time in years, IGD is the initial difference in genetic merit for the index ([1.25, 1.50, or 2.0] × $\sigma_{H\text{-}PT}$) (Table 5), and R_{SI} – R_{PT} is the difference in annual genetic responses between SI and PT (162.93 – 122.36). For the cases illustrated in Figure 3, the point of intersection is located at 5.1, 6.2, and 8.2 yr for 1.25, 1.50, and 2.0, respectively.

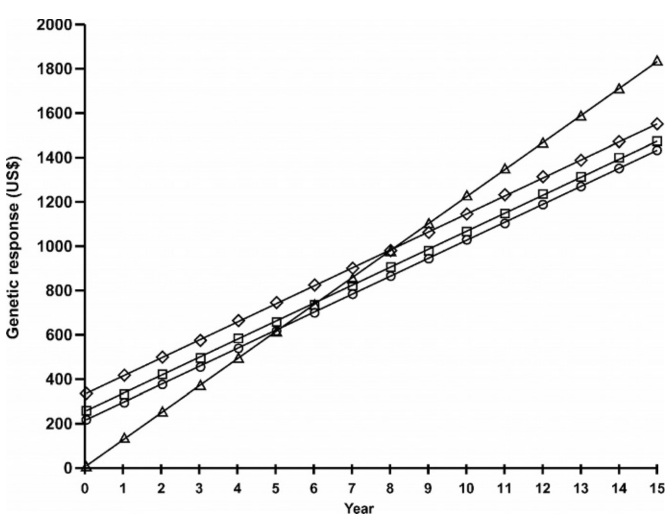

Figure 3. Genetic response (US$) for breeding strategies based on progeny testing (△) and semen importation assuming initial differences of 1.25 (○), 1.50 (□), and 2.00 (◇) genetic standard deviations in overall genetic merit for the exporting country and Costa Rica and a genetic correlation (genotype × environment interaction) of 0.50.

Other genetic considerations. The time between the start of a breeding program and the realization of genetic gain in the commercial cow population will differ between strategies. The SI scheme relies on the importation of semen from selected sires and has a direct effect on the commercial cow population. Genetic gain in CN will take longer to reach the commercial population compared with SI and PT. These differences in timing do not affect the rate of genetic gain. The consequences can be visualized by moving the respective lines of ER along the x-axis.

The G × E can also be present in the CN, where the performance recorded on cows may not be the same in the nucleus herds as in the commercial population. In this case, the same reasoning would apply as for SI.

Differences between schemes with respect to inbreeding have been ignored in the present study. A way to consider this could be to adjust the genetic response achieved under different strategies by the expected rate of inbreeding (Goddard, 1992). Higher predicted rates of inbreeding are reported for the CN scheme; however, a previous study (Leitch et al., 1994) demonstrated that inbreeding within CN might be reduced effectively by using restrictive mating strategies and with little effect on genetic responses. In addition, the most likely local scheme will continue to import some genetic material to overcome the bottlenecks of a small population and to provide an international benchmark for the local population.

Final considerations. The present results have clear implications for the design of a breeding program for dairy cattle in a small country such as Costa Rica. For this specific case, it seems that the choice between a local vs. externally based breeding program depends largely on the level of G × E, because no major differences in breeding objectives were found. In a preliminary study (Vargas and Solano, 1995), a correlation of 0.62 was found between breeding values for milk yield of Holstein sires in the US and Costa Rica. Other studies performed on AI Holstein sires from the US used in Latin America showed even lower estimates (Powell et al., 1990; Stanton et al., 1991; Houri Neto et al., 1996). Powell et al. (1990) reported a correlation between PTA of 0.42 for Holstein sires evaluated in the US and Ecuador. A similar study in Brazil found genetic correlations in the range of 0.50 to 0.68 (Houri Neto et al., 1996). Other studies, however, report correlations >0.90 (Powell and Wiggans, 1991). If the estimate of 0.62 found for Costa Rica is close to reality, there is a clear prospect to establish a local breeding scheme.

Our findings on the impact of G × E are in agreement with earlier results (Banos and Smith, 1991; Goddard, 1992). Banos and Smith (1991) found that when the genetic correlation between objectives in both countries was 0.7, each country stopped selecting bulls from the other country after a few generations. Goddard (1992), however, pointed out that inbreeding effects and the large size of the world population work to prevent complete isolation. He concluded that a possible future course is one in which, following the global bottleneck resulting from the introduction of American Holstein in the global Black and White populations, some differences between local populations re-emerge, but these local populations continue to exchange genes and do not become isolated strains. His latter conclusion, however, depends heavily on the degree of G × E between countries. The degree of G × E should be evaluated for total genetic merit and not just milk production (Goddard, 1992). When differences in production environments increased (e.g., feeding regimen, temperature, disease pressure), the importance of functional traits for the overall genetic merit is likely to be larger in the poor environment. Consequently, the degree of G × E will increase.

The implementation of a PT scheme requires the participation of a large number of farmers in milk recording and AI. This might be difficult to realize given the relatively low participation of farms in milk recording schemes. A small-scale milk performance recording scheme is also required in the case of SI. The results are needed to judge the value of genetic material from different exporting countries. Strategies based on nucleus herds rely less on the collection of information in the commercial cow population. However, establishing an effective nucleus breeding scheme puts high demands on technical skills and management conditions (Meuwissen, 1990). Such conditions are rarely attained in developing countries. A few studies reported on the results of implementation of multiple ovulation and embryo transfer programs in developing countries (Wagner, 1987; Niemann, 1992). Results showed large variation between countries with low efficiency levels in general.

Apart from the technical comparison of schemes discussed thus far, operating costs and general economic developments need to be taken into account when considering the future of dairy breeding in a country such as Costa Rica. Current trends in dairy breeding seem to converge toward the globalization of breeding programs. Under these circumstances, it is highly probable that international breeding companies will continue to play an important role on genetic improvement of the cattle population in developing countries. Several countries are already participating in a project for international evaluation of sires under the guidance of INTERBULL. Access to information on genetic evaluations performed worldwide can now be easily gained through the Internet. These transformations will also have an effect on breeding of dairy cattle in developing countries, because these countries represent a potential market for international breeding programs. However, these programs will have to meet the requirements of the new markets, i.e., future generations of sires will have to satisfy the specific demands of specific countries and productive sectors.

Collective efforts among similar countries in a regional breeding program, rather than several programs at the national level, may be a more sound option for small developing countries with similar production conditions. Breeding companies may play a role in setting up these programs and providing the necessary expertise to run them efficiently, while still making profit by fulfilling the requirements of a broader market.

ACKNOWLEDGMENTS

The authors thank Stichting Samenwerkings Verband IO-instellingen & LUW (SAIL), The Netherlands, for their financial support.

REFERENCES

AIPL-USDA. 2003. Trend in milk breeding values. http://aipl.arsusda.gov/dynamic/trend/ current/trndx.html. Accessed August 08, 2003.

Banos, G., and C. Smith. 1991. Selecting bulls across countries to maximize genetic improvement in dairy cattle. J. Anim. Breed. Genet. 108:174–181.

Bulmer, M. G. 1971. The effect of selection on genetic variability. The Am. Nat. 105:201–211.

Gibson, J. P., and J. A. M van Arendonk. 1998. Introduction to the design and economics of animal breeding strategies. Lecture notes. Post-graduate course. Warsaw Agricultural University, Poland. 259 pp.

Goddard, M. E. 1992. Optimal effective population size for the global population of Black and White dairy cattle. J. Dairy. Sci. 75:2902–2911.

Groen, A. F. 1990. Influences of production circumstances on the economic revenues of cattle breeding programmes. Anim. Prod. 51:469–480.

Hazel, L. N. 1943. The genetic basis for constructing selection indices. Genetics 28:476–490.

Hodges, J. 1990. Genetic improvement of livestock in developing countries using the Open Nucleus Breeding Systems. Pages 13–23 in Conf. Open Nucleus Breeding Syst., Poland. M. Zurkowski, ed. FAO Animal Science Papers and Reports no. 6, Warsaw, Poland.

Holstein USA, 2003. The new TPI index. http://www.holsteinusa.com/html/newtpi.html. Accessed August 02, 2003.
Houri Neto, M., H. M. Silva, and J. A. G. Bergmann. 1996. Vantagens e Desvantagens do uso do semen importado para producao de leite no Brasil. Arquivo Brasileiro de Medicina Veterinaria y Zootecnia. 48:755–762.
Leitch, C. H., Smith, C. Burnside, E. B., and M. Quinton. 1994. Genetic response and inbreeding with different selection methods and mating designs for nucleus breeding programs of dairy cattle. J. Dairy Sci. 77:1702–1718.
MAG-CORFOGA. 2001. Análisis de Censo Ganadero 2000. 13 pp.
Meuwissen, T. H. E. 1990. The use of increased female reproductive rates in dairy cattle breeding schemes. Anim. Prod. 52:21–31.
McGuirk, B. 1989. The relevance of MOET programmes to developing countries. Theriogenology 31:29–40.
Mpofu, N., C. Smith, and E. B. Burnside. 1993. Breeding strategies for genetic improvement of dairy cattle in Zimbabwe 1. Genetic evaluation. J. Dairy Sci. 76:1163–1172.
Nicholas, F. W., and C. Smith. 1983. Increased rates of genetic change in dairy cattle by embryo transfer and splitting. Anim. Prod. 26:341–353.
Niemann, H. 1992. The use of frozen/thawed embryos from livestock in developing countries. Pages 140–147 in Proc. Symp. Potentials and Limitations of Biotechnology in Livestock Production in Developing Countries. Part 1: Animal Reproduction and Breeding. H. Niemann, H. Franzen and D. Smidt, ed. Institut fur Tierzucht und Tierverhalten (FAL), Mariensee, Germany and Council for Tropical and Subtropical Agricultural Research (ATSAF), Stuttgart, Germany.
Peters, K. J. 1993. Selection and breeding strategies for sustainable livestock production in developing countries, with particular reference to dairy cattle production. Pages 119–128 in Animal Production in Developing Countries. M. Gill, E. Owen, G. E. Pollott, and T. L. J. Lawrence, ed. Occasional Publ. 16, British Society of Animal Science, Penicuik, Scotland.
Powell, R. L., and G. R. Wiggans. 1991. Animal model evaluation for Mexican Holsteins. J. Dairy Sci. 74:1420–1427.
Powell, R. L., G. R. Wiggans, and R. D. Plowman. 1990. Evaluations of Holstein bulls and cows in Ecuador. J. Dairy Sci. 73:3330–3335.
Rendel, J. M., and A. Robertson. 1950. Estimation of genetic gain in milk yield by selection in a closed herd of dairy cattle. J. Genet. 50:1–8.
Smith, C. 1988. Genetic improvement of livestock using nucleus breeding units. World Anim. Rev. 65:2–9.
Stanton, T. L., R. W. Blake, R. L. Quaas, and L. D. Van Vleck. 1991. Response to selection of United States Holstein sires in Latin America. J. Dairy Sci. 74:651–664.
Vargas, B., A. Groen, M. Herrero, and J. A. M. van Arendonk. 2002. Economic values for production and functional traits in Holstein cattle of Costa Rica. Livest. Prod. Sci. 75:101–116.
Vargas, B., and C. Solano. 1995. Genetic and environmental trends in milk production of dairy cattle in Costa Rica. Arch. Latinoam. Prod. Anim. 3:165–176.
Visscher, P. M., and M. E. Goddard. 1995. Genetic parameters for milk yield, survival, workability and type traits for Australian Dairy Cattle. J. Dairy Sci. 78:205–220.
Wagner, H. G. R. 1987. Present status of embryo transfer in cattle. World Anim. Rev. 64:2–11.
Wiggans, G. R. 1997. Genetic evaluation systems in the United Status: Present ethod and proposed changes. 32nd Int. Symp., Anim. Prod. Advances in Technology, Accuracy, and Management, Milan, Italy.