Genetic Selection to Improve the Quality and Composition of Beef Carcasses

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Introduction

The livestock and meat industry is under increasing pressure to reduce fat while maintaining tenderness and palatability of its products. In the case of slaughter cattle, considerable variation exists in composition of beef carcasses and tenderness of product, a significant part of which is genetic in origin. In this paper, results from the Germplasm Evaluation (GPE) program at the Roman L. Hruska U. S. Meat Animal Research Center (MARC), Clay Center, Nebraska are reviewed to assess between and within breed selection opportunities to reduce fat and improve palatability of retail product from beef carcasses. Then the potential of using genetic markers from a bovine genomic map to assist selection for carcass and meat characteristics will be discussed.

Germplasm Evaluation Program

Table 1 shows the mating plan for five cycles of the Germplasm Evaluation Program. Topcross performance of 29 sire breeds have been, or are being, evaluated in calves out of Hereford, Angus dams or crossbred dams. F_1 cross cows produced in Cycle I were mated to Brahman, Devon, Holstein and Angus or Hereford sires in the final phase of Cycle I and F_1 cows produced in Cycle II were mated to Brangus, Santa Gertrudis, and Angus or Hereford sires in the final phase of Cycle II. In addition to the Hereford and Angus cows, composite MARC III cows (1/4 each Angus, Hereford, Red Poll, and Pinzgauer) are being used to initiate Cycle V. This review will focus primarily on data from 20 sire breeds involved in the first three cycles of the program which have been completed.

Data presenting results pooled over Cycles I, II and III were obtained by adding the average differences between Hereford-Angus reciprocal crosses and other breed groups (two-way and three-way F_1 crosses) within each cycle to the average of Hereford-Angus reciprocal crosses over the three cycles. The pooled results will be presented for nineteen F_1 crosses (two-way and three-way) grouped into seven biological types based on relative differences (X lowest, XXXXXX highest) in growth rate and mature size, lean-to-fat ratio, age at puberty and milk production (Table 2). The breed group means presented in this review are from previous reports for carcass and meat characteristics (Koch et al., 1976, Koch et al., 1979, Koch et al., 1982b, Young et al., 1978) of steers. Mean differences between breeds will be expressed in actual units and in standard deviation units for breeding value [$S_g = h(S_p)$, where h is the square root of heritability, and S_p is the phenotypic standard deviation] computed from the GPE program (Koch et al., 1982a, MacNeil et al., 1984; Cundiff et al., 1986).

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Genetic Variation Among and Within Breeds

Average differences between breeds are primarily attributable to additive effects of genes present at diverse frequencies in different breeds. Breeds which have been kept separate from each other, either by pedigree barriers imposed by man or by geographic barriers, have diverged in frequency for genes affecting expression of many characteristics due to forces of chance, mutation and natural selection for components of fitness and adaptation to diverse environments. Breed differences are usually greatest for characteristics which have responded to many generations of selection directed by man toward different goals (e.g., milk production, size, fatness, leanness, color, horn characteristics and other visually appraised characteristics). Topcross comparisons in the GPE program estimate one-half of the additive genetic difference among sire breeds, assuming effects of heterosis are similar among different specific crosses. This assumption is generally true, except for Bos indicus X Bos taurus crosses (e.g., Bos indicus breeds include Brahman, Sahiwal, Nellore and Boran) which yield significantly more heterosis than crosses of Bos taurus breeds (e.g., all other sire breeds except Tuli). This is a more important consideration for lowly heritable traits that display large effects of heterosis (e.g., reproduction rate) than for highly heritable traits that display small effects of heterosis such as carcass and meat traits.

Retail Product

Throughout the GPE program, we have obtained closely trimmed-boneless retail product, i.e., steaks and roasts (trimmed to 8 mm of external fat and boneless except for the short loin and rib roasts) and lean trim (trimmed and processed into ground beef with 25% fat content based on chemical analysis) from the right side of each carcass. In the first three cycles of the GPE program, these data were obtained at Kansas State University under the direction of Dr. Michael E. Dikeman. In Cycle IV of the program, these data were obtained in our own laboratory, with Dr. Dikeman still collaborating to assure continuity with previous cycles of the program. Recently, in the GPE program we have obtained data on retail product with two levels of trim. After

Table 1. Sire Breeds Used in Germplasm Evaluation Program.

Cycle I (1970-72)	*Cycle II (1973-74)*	*Cycle III (1975-76)*	*Cycle IV (1986-90)*	*Cycle V (1992-94)*
		F_1 crosses from Hereford or Ancus dams (Phase 2)		
Hereford	Hereford	Hereford	Hereford	Hereford
Angus	Angus	Angus	Angus	Angus
Jersey	Red Poll	Brahman	Longhorn	Tuli
S. Devon	Brown Swiss	Sahiwal	Salers	Boran
Limousin	Gelbvieh	Pinzgauer	Galloway	Belgian Blue
Simmental	Maine Anjou	Tarentaise	Nellore	Brahman
Charolais	Chianina		Piedmontese	Piedmontese
			Charolais	
			Gelbvieh	
			Pinzgauer	
		3-way crosses out of F_1 dams (Phase 3)		
Hereford	Hereford			
Angus	Angus			
Brahman	Brangus			
Devon	Santa Gertrudis			
Holstein				

Table 2. Breed Crosses Grouped into Biological Types for Four Criteria[a].

Breed group	*Growth rate & mature size*	*Lean to fat ratio*	*Age at puberty*	*Milk production*
Jersey (J)	X	X	X	XXXXX
Hereford-Angus (HA)	XX	XX	XXX	XX
Red Poll (R)	XX	XX	XX	XXX
Devon (D)	XX	XX	XXX	XX
South Devon (Sd)	XXX	XXX	XX	XXX
Tarentaise (T)	XXX	XXX	XX	XXX
Pinzgauer (P)	XXX	XXX	XX	XXX
Brangus (Bn)	XXX	XX	XXXX	XX
Santa Gert. (Sg)	XXX	XX	XXXX	XX
Sahiwal (Sw)	XX	XXX	XXXXX	XXX
Brahman (Bm)	XXXX	XXX	XXXXX	XXX
Brown Swiss (B)	XXXX	XXXX	XX	XXXX
Gelbvieh (G)	XXXX	XXXX	XX	XXXX
Holstein (Ho)	XXXX	XXXX	XX	XXXXX
Simmental (S)	XXXXX	XXXX	XXX	XXXX
Maine Anjou (M)	XXXXX	XXXX	XXX	XXX
Limousin (L)	XXX	XXXXX	XXXX	X
Charolais (C)	XXXXX	XXXXX	XXXX	X
Chianina (Ci)	XXXXX	XXXXX	XXXX	X

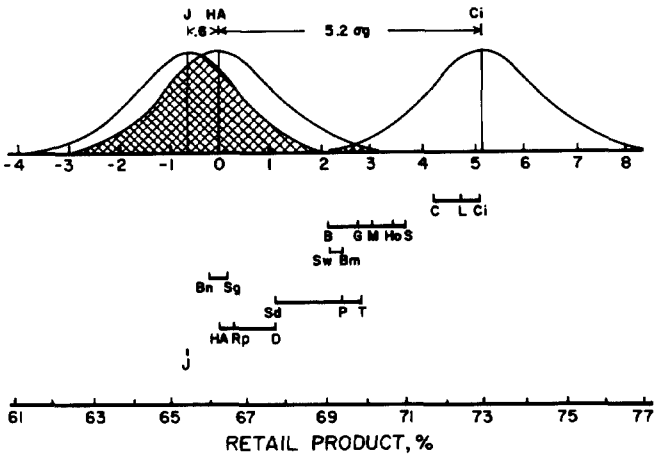
[a]Increasing number of X's indicate relatively higher values.

weights for closely trimmed retail product from each wholesale cut are recorded, retail cuts are trimmed to 0 mm outside fat and made entirely boneless. The fat trim removed between 8 mm and 0 mm accounted for 4.6% of the side weight of yield grade 1 cattle and from 5.3, 5.5 and 5.5% of the side weight of yield grades 2, 3 and 4 cattle, respectively (Crouse et al., 1988). Thus, a high degree of association exists between closely trimmed (8 mm) and zero trimmed (0 mm) retail product, especially in cattle of yield grades 2, 3 and 4.

Results for retail product expressed as a percentage of carcass weight at 458 days of age are summarized in Figure 1. Significant genetic variation exists between and within breeds for retail product percentage when comparisons are made at the same age or weight. In Figure 1, the spacing on the vertical axis is arbitrary but the ranking from the bottom to top reflects increasing increments of mature size. Steers sired by bulls of breeds with large mature size produced a significantly higher percentage of retail product than steers sired by breeds of small mature size. Differ-

Figure 1

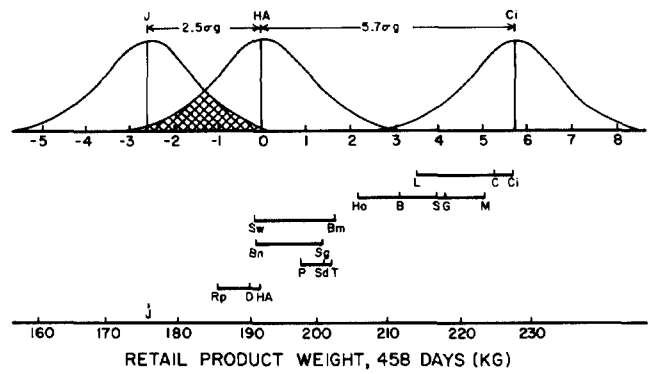
VARIATION BETWEEN AND WITHIN BREEDS



Breed group means (lower axis) and genetic variation between and within breeds (upper axis) for percentage retail product at 458 days of age (Cundiff et al., 1986). See Table 2 for abbreviations.

Figure 2

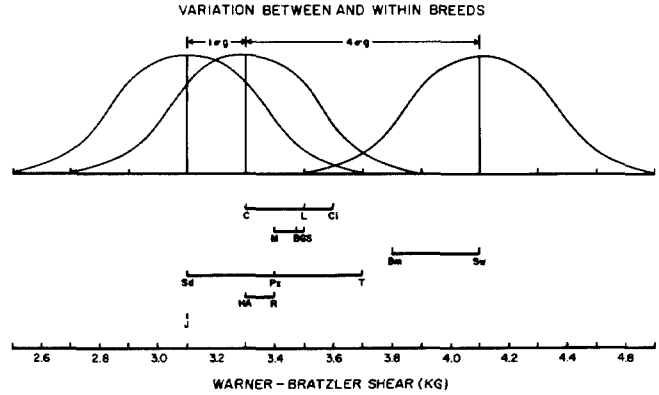
VARIATION BETWEEN AND WITHIN BREEDS



Breed group means (lower axis) and genetic variation between and within breeds (upper axis) for weight of retail product at 458 days of age (Cundiff et al., 1986). See Table 2 for abbreviations.

Figure 3

VARIATION BETWEEN AND WITHIN BREEDS



Breed group means (lower axis) and genetic variation between and within breeds (upper axis) for Warner-Bratzler shear estimates of tenderness at 458 days of age (Cundiff et al., 1986). See Table 2 for abbreviations.

ences have been doubled in the upper horizontal scale to reflect variation among pure breeds relative to a S_g within pure breeds. Frequency curves, shown for Jerseys, the average of Herefords and Angus, and Chianinas, reflect the distribution expected for breeding values of individual animals within pure breeds. The breeding value of the leanest Jersey was not expected to equal that of the fattest Chianina and the leanest Hereford and Angus were only equal to the fattest Chianina in genetic potential for percentage of retail product at 458 days. The range for mean differences between breeds, was estimated to be about 5.8 S_g (i.e., standard deviation units for breeding value) between Chianina and Jersey steers. Genetic variation, both between and within breeds, was important for percentage of retail product. When both between and within breed genetic variations are considered, the range in breeding value from the smallest Jersey steers to the heaviest Chianina steers was estimated to be about 30%.

Variation among breeds relative to that within breeds was even greater for growth of retail product (Figure 2) than for percentage of retail product at a constant age (Figure 1). The range for mean differences between breeds was estimated to be about 5.7 S_g Chianina and Hereford or Angus steers and about 8.2 S_g between Chianina and Jersey steers. When both between and within breed genetic variations are considered, the range in breeding value from the smallest Jersey steers to the heaviest Chianina steers was estimated to be 180 kg, or 88% of the overall mean.

Quality (Tenderness and Marbling)

Results for Warner-Bratzler shear determinations of tenderness of tenth-rib longissimus muscle steaks (1.27 cm cores oven-broiled at 177 C to an internal temperature of 65°C) are summarized in Figure 3. Steaks from progeny of Bos indicus sire breeds (Sahiwal and Brahman) were significantly less tender than steaks from progeny of Bos taurus sire breeds. Sensory panel evaluations of tenderness corresponded closely to Warner-Bratzler shear estimates (Table 3). High levels of acceptance were found for steaks from all Bos taurus breed groups when the steers were fed and managed alike and slaughtered at 14 to 16 months of age. In these studies, sensory scores were assigned on a 9-point scale from 1 = extremely undesirable (e.g., extremely tough), 5 = acceptable, up to 9 = extremely desirable (e.g., extremely tender).

Average taste panel scores and Warner-Bratzler shear determinations for tenderness did tend to improve as marbling increased when comparisons were at the same age, but the change was very small (Table 3). Although, breed groups differed significantly in average marbling scores and in percentage of carcasses that had adequate marbling to grade USDA Choice or better, average sensory panel evaluations of tenderness, flavor and juiciness were acceptable for all breed groups.

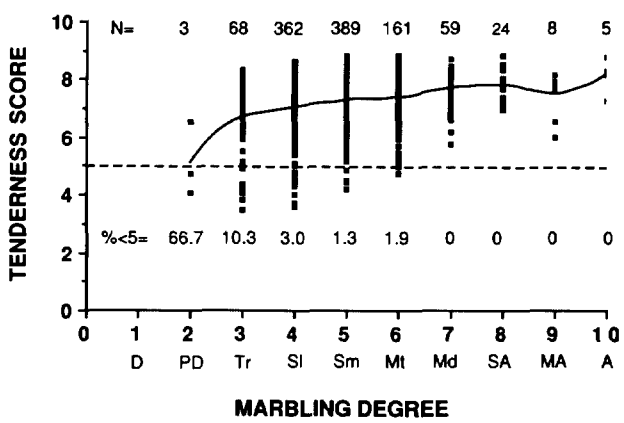
However, variation in sensory panel tenderness scores

Table 3. Breed Group Means For Factors Identified With Meat Quality.

Breed group	Marbling score[a]	Percent USDA Choice	Warner-Bratzler shear[b] (kg)	Sensory panel scores[c] Tender-ness	Flavor	Juici-ness
Chianina-X	8.3	24	3.6	6.9	7.3	7.2
Limousin-X	9.0	37	3.5	6.9	7.4	7.3
Brahman-X	9.3	40	3.8	6.5	7.2	6.9
Gelbvieh-X	9.6	43	3.5	6.9	7.4	7.2
Sahiwal-X	9.7	44	4.1	5.8	7.1	7.0
Simmental-X	9.9	60	3.5	6.8	7.3	7.3
Maine-Anjou-X	10.1	54	3.4	7.1	7.3	7.2
Tarentaise-X	10.2	60	3.7	6.7	7.3	7.0
Charolais-X	10.3	63	3.3	7.3	7.4	7.3
Brown Swiss-X	10.4	61	3.5	7.2	7.4	7.2
Pinzgauer-X	10.8	60	3.4	7.1	7.4	7.2
South Devon-X	11.3	76	3.1	7.4	7.3	7.4
Hereford-Angus-X	11.3	76	3.3	7.3	7.3	7.3
Red Poll-X	11.5	68	3.4	7.3	7.4	7.1
Jersey-X	13.2	85	3.1	7.4	7.5	7.5

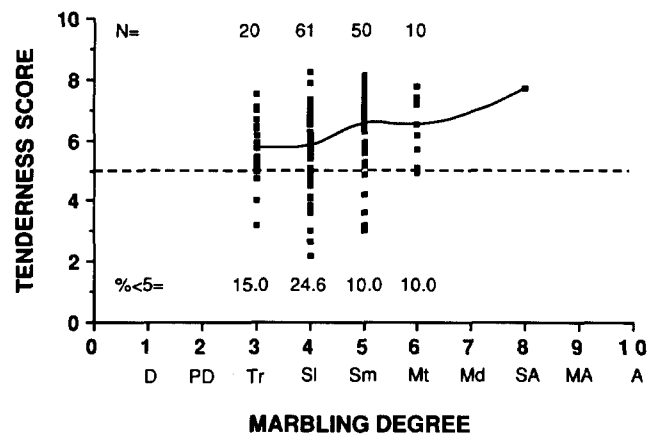
[a]Marbling: 8 = slight, 11 = small, 14 = modest, 17 = moderate.
[b]Shear force required for a 1.27 cm core of cooked steak.
[c]Scores: 2 = undesirable, 5 = acceptable, 7 = moderately desirable.

Figure 4
BOS TAURUS TENDERNESS, BY MARBLING



Effects of marbling on mean sensory panel tenderness in Bos taurus breeds. Sensory panel scores for tenderness ranged from 1 - extremely tender, 5 - acceptable, 9 extremely tender. Bos taurus breed groups are Angus, Brown Swiss, Charolais, Chianina, Gelbvieh, Hereford, Jersey, Limousin, Maine Anjou, Pinzgauer, Red Poll, Simmental, South Devon and Tarentaise sired topcrosses out of Hereford and Angus dams (Koch et al., 1988).

Figure 5
BOS INDICUS TENDERNESS, BY MARBLING

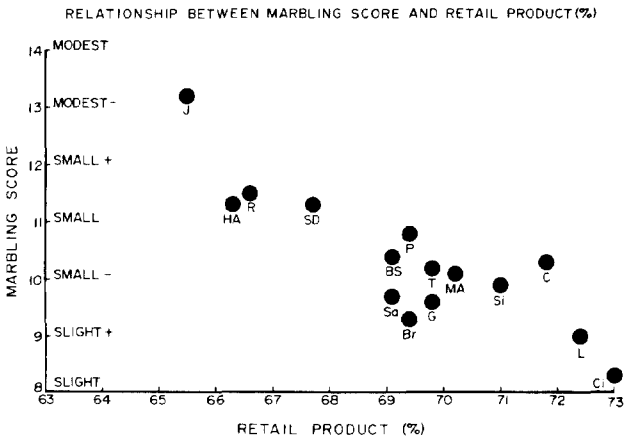


Effects of marbling on mean sensory panel tenderness in Bos indicus sired topcrosses (Brahman and Sahiwal) out of Hereford and Angus dams. Sensory panel scores for tenderness ranged from 1 = extremely tender, 5 = acceptable, 9 = extremely tender (Koch et al., 1988).

(see ranges in Figure 4 for Bos taurus x Bos taurus breed crosses and Figure 5 for Bos indicus x Bos taurus breed crosses) tended to be greater in cattle with low levels of marbling than in cattle with high levels of marbling (Koch et al., 1988). This in turn leads to greater risk of at least some steaks having less than acceptable tenderness at low levels of marbling. In Bos taurus sired cattle with a Slight degree of marbling (USDA Select), 3% of the steaks were scored as less than acceptable (sensory panel scores of <5) in tenderness. In Bos taurus sired cattle with Moderate or greater degrees of marbling (USDA high Choice or Prime), 0% of the steaks were scored as less than acceptable (i.e., 100% had scores ≥ 5). Sensory panel scores for steaks from Bos indicus sired steers were lower for tenderness than those from Bos taurus sired steers, even at the same degree of marbling.

Unfortunately, breeds that rank highest for percentage of retail product rank lowest for marbling (Figure 6). Thus,

Figure 6



Breed group means for retail product percentage versus marbling score at 458 days of age (Koch et al., 1979; Koch et al., 1979; Koch et al. 1982b). See Table 2 for abbreviations (except Si - Simmental, Sa - Sahiwal, Br - Brahman).

only limited opportunity exists from between breed selection for genetically increasing marbling without increasing fat trim and reducing percentage of retail product. This antagonistic relationship between percentage of retail product and marbling has deterred the substitution of breeds that excel in leanness for those with higher yield grades and higher USDA quality grades. This deterrence has not necessarily been undesirable. Since breeds that excel in leanness had relatively large mature size and in many instances relatively high genetic potential for milk production, a total substitution of one biological type for the other would have had undesirable effects on cow size, milk production and efficiency in many cow herds. Considering all traits that are important for specific environments and market targets, performance is often more nearly optimized in crosses of breeds representing diverse biological types than in crosses of breeds representing the same biological type.

Results for shear force estimates of tenderness are presented in Figure 7 for steers differing in the ratio of Bos indicus (Brahman, Sahiwal) to Bos taurus (Hereford, Angus) inheritance. Reciprocal backcross and F_2 matings produced steers with 0:100 , 25:75 , 50:50 and 75:25 ratios of Bos indicus to Bos taurus inheritance. Shear force required to slice through 1.27 cm cores from rib steaks cooked to an internal temperature of 65°C increased .75 kg for each 25% increase in Brahman inheritance and 1.3 kg for each 25% increase in Sahiwal inheritance (Crouse, et al., 1989).

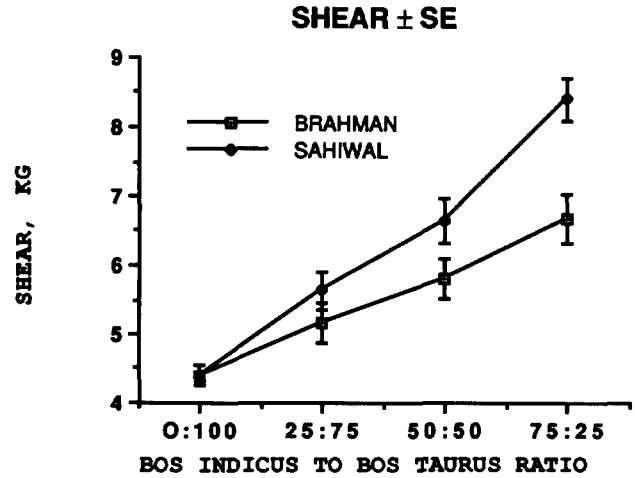
Preliminary Results from Cycle IV of the GPE Program

Breed cross means for final weight and carcass and meat traits are presented in Table 4 for steers from the first four of five calf crops to be produced in cycle IV of the GPE program. Attention is directed to results for Piedmontese crosses, a breed believed to have a high gene frequency for a major gene that causes muscle hyperplasia (double muscling). Piedmontese breeders in Italy have applied significant selection pressure for double muscling for at least 50 years. Although Piedmontese crosses ranked ninth in final weight, comparable to original Hereford-Angus crosses, they ranked second only to Charolais in weight of totally trimmed (.0 in) retail product due to high dressing percentage and significantly higher retail product percentages than other breeds. Piedmontese crosses had larger rib eyes and less fat thickness than any other breed. Although Piedmontese crosses ranked lowest in marbling, they ranked second lowest to Pinzgauer in shear force estimates of tenderness. A major proportion of these effects are likely associated with the major gene double muscling. Assuming most bulls introduced into North America and sampled in our experiment were homozygous for double muscling, most of the F_1 crosses out of Hereford and Angus cows should possess one copy of the double muscling gene. In cycle V, Belgian Blue have been included to obtain comparative data on another breed with a high gene frequency double muscling.

Carcasses from Galloway and Longhorn crosses had higher percentage retail product, but were lighter in weight than Hereford-Angus crosses. Salers crosses were intermediate in growth rate to weaning and yearling ages. Marbling score was low but retail product yield as a percentage of carcass weight was relatively high in Salers crosses. Salers, Gelbvieh and Nellore crosses were comparable in lean growth potential as reflected in weight of retail product at 417 days of age.

Breed crosses ranked differently for marbling score than they did for shear force estimates of tenderness. Shorthorn crosses and Hereford-Angus crosses excelled in marbling score but shear estimates of tenderness were comparable

Figure 7



Shear force estimates of tenderness in rib steaks from steers differing in the ratio of Bos indicus (Brahman, Bm; Sahiwal, Sw) to Bos taurus (Hereford, H; Angus, A) inheritance, Reciprocal backcross and F_2 matings produced steers with 0:100 (HxAH, HxHA, AxAH, AxHA, HAxHA, AHxHA, HAxAH, AHxAH), 25:75 (HxBmH, AxBmA, HxSwH, AxSwA), 50:50 (BmHxBmH, BmAxBmA, SwHxSwH, SwAxSwA) and 75:25 (BmxBH, BmxBA, SwxSwH, SwxSwA) Bos indicus to Bos taurus inheritance (Crouse et al,, 1989).

Table 4. Breed Group Means for Final Weight and Carcass Characteristics of Steers in Cycle IV of GPE Program (Preliminary, 1986-1989 Calf Crops)[a].

Breed group of steer	No.	Final wt. kg	Dress. pct. %	Marbling score[b] %	WB shear kg	Fat thickness mm	Rib eye area sq cm	Retail product 8 mm trim %	Retail product 0 mm trim %	Retail product 8 mm trim kg	Retail product 0 mm trim kg
Orig HAx	69	505	62.0	539	5.4	167	71	68.0	62.2	203	186
Cur. HAx	29	544	62.2	528	5.7	158	71	68.3	62.5	222	203
Charolais	71	562	62.0	499	5.8	95	80	71.2	66.0	239	221
Gelbvieh	94	537	61.9	503	5.4	91	79	71.7	66.5	229	212
Pinzgauer	84	530	61.1	527	4.9	104	74	70.3	65.0	220	203
Shorthorn	72	542	62.0	564	5.6	119	72	68.3	62.7	220	202
Galloway	64	483	62.3	516	5.7	116	73	70.9	65.3	205	188
Longhorn	76	455	61.8	514	5.9	93	70	70.5	65.2	190	176
Nellore	82	521	64.6	489	7.1	125	75	70.2	64.6	227	209
Piedmontese	63	507	63.8	497	5.4	76	86	74.5	69.9	231	217
Salers	68	538	62.4	500	6.2	102	77	70.9	65.6	228	211

[a]Means for weight and carcass traits at average slaughter age of 417 days.
[b]Marbling: Slight = 400 to 499, small = 500 to 599, etc.

to those of other Bos taurus sired breed groups with lower levels of marbling. Marbling score was relatively low, but steaks were relatively tender in Piedmontese crosses. Marbling score also was low in Nellore crosses and their shear values were higher than all other crosses. Steaks from Nellore crosses, like Bos indicus breeds evaluated earlier (Brahman and Sahiwal), were less tender than those from Bos taurus sire breeds.

In cycle V of the GPE program, two tropically adapted breeds that have evolved in Africa have been included to characterize their meat tenderness and other traits relative to Brahman, Belgian Blue, Piedmontese, Hereford and Angus sired F_1 crosses. Tuli are a non-indicus, sanga type of cattle from Zimbabwa and Boran are a Bos indicus type from East Africa. Semen is being introduced from Australia in cooperation with CSIRO scientists, who along with a consortium of private breeders imported these breeds as frozen embryos into Australia a few years ago. Experiments comparing two or more of these breeds are being conducted cooperatively with USDA, ARS locations at El Reno, Oklahoma and Brooksville, Florida and with State Agricultural Experiment Stations in Tifton, Georgia and McGregor, Overton, and Ulvalde, Texas to extend the evaluations to subtropical regions of the U.S.

Genetic Variation Within Breeds

The range for differences between breeds is comparable in magnitude to the range for breeding value of individuals within breeds for most bioeconomic traits important to beef production. Thus, significant genetic change can result from selection both between and within breeds. Between-breed differences are more easily exploited than genetic variation within breeds because they are more highly heritable. Also, use of genetic variation within breeds is often complicated by difficulties of measurement for characteristics such as carcass and meat traits. Breeds can be selected to optimize performance levels and match market targets with a high level of precision much more quickly than intrapopulation selection.

However, once between-breed genetic variation has been exploited by selection of the desired breed or breeds used in a crossbreeding program or in foundation of a composite population, continued genetic improvement is dependent on intrapopulation selection and genetic variation available within the breeds or composite population. Intrapopulation (i.e., within breed or composite) variation is virtually restored generation after generation by the Mendelian process; while variation between populations, accruing only very slowly as a result of different selection goals, genetic drift (associated with inbreeding) or rare mutations, can only be exploited rarely (e.g., at times abrupt changes in selection goals are indicated and exotic germplasm is available). Intrapopulation response to selection is dependent on heritability and selection pressure applied. Response in other traits, not subject to direct selection, is dependent on the genetic correlations and heritability of direct and correlated traits.

Estimates of heritability and genetic correlations among certain quality and composition traits from the GPE program are presented in Table 5 (Koch et al., 1982a). Weight and percentage of retail product were among the most highly heritable of traits studied. Marbling also had a relatively high heritability. Meat tenderness based on Warner-Bratzler shear determinations was moderately heritable.

Table 5. Heritability and Genetic Correlations Among Carcass and Meat Traits in the GPE Program (Koch, 1982[a]).

Trait	Heritability	Retail prod. Wt	Retail prod. %	Marbling	Shear
Carcass wt	.43	.81	–.11	.25	.00
Retail prod. wt	.58		.46	–.02	–.07
Retail prod. %	.63			–.37	–.16
Marbling	.40				–.25
Shear	.31				

The genetic correlation between carcass weight and percentage retail product was low, indicating that selection for growth to yearling ages would have negligible effects on carcass composition. This result is consistent with our recent estimates of genetic trends in Hereford and Angus cattle in the U.S. In cycle IV of the GPE program, Hereford (14 horned and 18 Polled) and Angus (30) sires born from 1982 to 1984 were compared to original Hereford (8 horned, 3 Polled) sires born from 1963-1969 and Angus (14) sires born from 1968-1970. The means for F_1 crosses shown in Table 4 for original versus current Hereford-Angus crosses estimate half of the genetic change in Hereford and Angus breeds during this time span. Although weight at 417 days of age changed significantly, carcass composition, as reflected by percentage retail product at 8 mm and 0 mm levels of fat trim, and marbling changed very little. These results indicate that selection for size will not change composition. Direct selection pressure will have to be applied to composition or to fat thickness and other predictors to change carcass composition.

The genetic correlation between marbling and percentage retail product was -0.37. A similar antagonistic relationship was observed between marbling and percentage retail product among breeds (Figure 6). This antagonism makes it necessary to progeny test a large number of sires with a large number of progeny per sire to identify even a few sires with truly favorable breeding values for both marbling and percentage retail product.

Estimates of heritability and for shear and marbling and the relatively low genetic correlation between marbling and shear indicate that single trait selection for shear would have more impact on tenderness than single trait selection for marbling. However, these genetic parameters indicate that multiple trait prediction of breeding value based on shear and marbling would be more effective than single trait selection for either trait alone. Again, the primary problem with selection for carcass and meat characteristics is trait measurement. Carcass and meat traits cannot be measured in bulls and females used for breeding. A limited number of bulls are progeny tested for carcass and meat traits. However, it is expensive and progress is slow because of the long generation interval in cattle. Without a more value-based marketing system, return on investment is too low to justify use of progeny testing to improve carcass and meat traits. Thus, carcass and meat traits are especially good candidates for newly emerging techniques of genetic selection based on use of genetic markers.

Genome Mapping and Marker-Assisted Selection

Marker-assisted selection techniques based on use of DNA markers closely linked to favorable alleles at quantitative trait loci (QTL's) appear promising for carcass and meat traits because they are highly heritable. When traits are highly heritable, it should be possible to find a number of markers that are closely linked to QTL's with consistent average effects on phenotype, regardless of other genes present in the genotype.

Recent successes with plant species provide incentive to develop a genomic map and identify DNA markers associated with quantitative traits in livestock species. In the work reviewed by Patterson et al. (1988), F_1 crosses between domestic and wild type South American green fruited tomatoes were backcrossed to domestic tomatoes. Three agriculturally important quantitative traits in tomato production were studied: Fruit mass, soluble solids concentrations and pH which affects preservation of tomatoes. The scientists had previously developed a genetic linkage map with 300 RFLP's and 20 isozyme markers on 12 chromosomes of tomato. For QTL mapping, a subset of markers at approximately 20 cM (1 centiMorgan is the distance along the chromosome with a recombination frequency of one percent) intervals, displaying polymorphisms between the domestic and wild type strains of tomato, were selected. A total of 70 markers were scored for each of 237 backcross progeny.

Fruit mass was found to be significantly associated with 6 markers on 6 chromosomes. The QTL's identified accounted for 58% of the phenotypic variation in fruit mass in the backcross progeny. In each case, the domestic alleles had the favorable effect on fruit mass. It was estimated that each allele added 3.5 to 6 g, accounting for about 1/2 of the difference between the domestic and wild type strains (28 g). Soluble solids concentration was associated with four markers on 4 chromosomes, accounting for 44% of the phenotypic variation. Again, favorable alleles were all from domestic germ plasm. In the case of pH, 48% of the phenotypic variation was accounted for by markers on 5 chromosomes. Because domestic and wild strains did not differ in pH, results indicated that domestic alleles did not all produce effects in the same direction.

With similar approaches, we are optimistic that markers associated with meat tenderness, leanness, etc., can be identified in progeny of diverse breed crosses after an adequate map has been developed in cattle. No single breed excels in all traits of importance to beef production. For example, Bos indicus X Bos taurus crosses (Brahman or Sahiwal X Hereford or Angus) are exceptionally productive (Cundiff et al., 1986) and efficient (Green et al., 1991) especially in subtropical (Olson et al., 1991) or tropical climates (Frisch and Vercoe, 1978), but they are relatively late to reach puberty (Gregory et al., 1979) and produce beef that is significantly less tender than Bos taurus x Bos taurus breed crosses, Thus, it is not likely that all the desirable genes will come from one parent breed.

Quantitatively, the challenge will be to develop genetic prediction procedures that accurately assess breeding value of animals, Reliance on markers will depend on the percentage of genetic variation (additive and nonadditive) that can be accounted for by markers. For traits that are easily measured phenotypically (e.g., weights at birth and subsequent ages, milk production in dairy cows, etc.), a high percentage of the genetic variance will need to be accounted for before phenotypic measures are no longer required. In the meantime, there will be need to develop genetic prediction procedures that appropriately assess and weight both sources of information.

For traits that are not so easily measured in seedstock animals, such as carcass and meat characteristics, it will

be worthwhile to rely on marker information even at early stages of development of the genomic map and data base when only low percentages of genetic variation are accounted for by markers. Marker searches should be most fruitful for traits that are moderate to highly heritable because they are likely to be influenced by a number of genes with consistent additive effects, regardless of other genes present in the genotype.

Unfortunately, identification of QTL's will be much more difficult for lowly heritable traits such as components of reproduction, survival and disease resistance which show large effects of heterosis in crosses of specific breeds and inbred lines. When traits are lowly heritable, nonadditive gene effects are expected to account for most of the genetic variation in a trait. If intra-locus interaction (dominance or overdominance) and inter-locus interaction (epistasis) are important, the effect of a QTL will differ depending on presence of alleles at the same locus or other loci. Eventually, as the genomic map becomes more saturated and well defined, it may be possible to develop prediction models that account for significant percentages of nonadditive genetic variation in important traits. To manage and exploit markers that account for nonadditive genetic variation, breeding strategies are likely to involve selection for divergence among strains that complement each other in the maximum number of loci when crossed. Similar strategies may come into play to manage antagonistic genetic relationships among moderately to highly heritable traits (e.g., calving ease versus growth rate, meat tenderness versus tropical tolerance, etc.).

The first step is to develop a comprehensive genomic map in the bovine. Efforts to map the bovine genome are well underway in laboratories at Texas A&M (Womack and Moll, 1986), Switzerland (Fries et al., 1989) and Australia (Hetzel, 1989). Within the last year, we have assembled a group of eight scientists at MARC trained in molecular biology and genetics to work on mapping the genome of cattle, swine and sheep. Objectives of the project are to 1) Identify marker genes and develop a genetic linkage map in cattle, sheep and swine, 2) Determine relationship of marker genes to traits of biological and economic importance, such as carcass and meat characteristics, and 3) Develop and evaluate marker-assisted selection procedures to more accurately assess the breeding value of animals used for breeding.

To provide reference families on which to base a linkage map, in the case of cattle, three generation reference families were initiated in 1990, using multiple ovulation and embryo transfer to produce 20 to 30 full sibs per family. To maximize heterozygosity, backcrosses and four-way crosses were made among diverse Bos taurus (Angus, Hereford, Gelbvieh, Simmental, Longhorn, Piedmontese) and Bos indicus (Brahman and Nellore) breeds to establish the families. The approach incorporates use of microsatellite and cosmid probes to identify and map random evenly spaced marker loci.

While the map is being developed, we are obtaining data on all animals in the reference families on a comprehensive series of quantitative traits including carcass and meat characteristics of males. We also are obtaining blood samples from many of the cattle in our genetics and breeding populations including: 1) GPE program (Table 1), 2) Germplasm Utilization program (three composite populations and nine pure breeds which contributed to the three composite populations), 3) Hereford unselected control line and lines selected for weaning weight, yearling weight, or an index of yearling weight and muscling score, and 4) Twinning population (a composite population selected for twinning rate, current mean twinning rate is 25%).

We anticipate that this effort will contribute markers to a national and international effort to construct an evenly spaced interval map of the bovine genome. We believe that free and open exchange of probes, reference DNA, and information, as well as a consensus on anchor loci is required among scientists working in this area for effective development of a genomic map and development of marker-assisted genetic prediction procedures. These and other cooperative endeavors will be required for effective development and transfer of this promising new technology to the livestock industry.

Conclusions

Genetic variation found between breeds is comparable in magnitude to that found within breeds for growth for most carcass and meat traits. Thus, significant genetic change can result from selection both between and within breeds. Between-breed differences are more easily exploited than genetic variation within breeds.

Within breeds, phenotypic variation is highly heritable for growth and percentage of retail product. Quality characteristics such as tenderness and marbling are moderately heritable. An antagonistic genetic correlation between marbling and percentage retail product complicates selection efforts to improve composition and marbling simultaneously.

The fact that carcass and meat characteristics are highly heritable but difficult to measure in live animals used for breeding make them especially good candidates for newly emerging marker-assisted selection techniques. Before these techniques can be effective, it will be necessary to develop a comprehensive genomic map and identify sufficient markers to account for a high percentage of the genetic variation in carcass composition and meat quality characteristics.

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