The impact of quantitative genetics on productive, reproductive and adaptive traits in beef cattle

LV Cundiff

US Meat Animal Research Center, Agricultural Research Service, US Department of Agriculture, Clay Center, Nebraska USA

Introduction

Efficiency of beef production has been impacted greatly by implementation of genetic evaluation procedures that have increased accuracy and effectiveness of selection and by use of crossbreeding or composite populations to exploit heterosis and match genetic potential with the climatic environment, feed resources, and consumer preferences for lean tender beef products. The impact of improved genetic evaluation procedures and the impact of experimentation with beef cattle on choice of breeds and breeding systems used to improve productive, product quality, reproductive, and adaptive traits in beef cattle will be the focus of this review.

Genetic Improvement Within Breeds

Expected progeny differences (EPDs) have provided the beef industry with an effective tool to impact genetic improvement in beef cattle. Genetic trends in EPDs for birth weight, direct and maternal components of weaning weight and yearling weight are shown in figures 1- 6 for six breeds that play a prominent role in beef production in North America. In the 1960's genetic evaluation were based on estimated breeding values (EBVs) computed within herds. Widespread use and acceptance of artificial insemination in the 1970's provided for multi-herd comparisons which paved the way for use of best linear unbiased prediction (BLUP) methodology (Henderson, 1975) and reduced animal model estimation procedures (Pollak and Quass, 1983) to compute EPDs. Accuracy of estimates were greater for EPDs than EBVs and rate of genetic change for growth traits was increased by the mid to late 1970's in most breeds (e.g., Hereford genetic trends, figure 2) as a result of increased use of AI and improved genetic evaluation procedures. More recently effectiveness of genetic evaluations have been improved by use of multi-trait genetic evaluations (BIF, 2002). Multi-breed genetic evaluations (Pollak and Quaas, 2005) have also been an important development in genetic evaluations, especially for producers of F1 seedstock or composite breeds.

The EPD technology has had a much greater impact on growth traits than other traits, primarily because growth traits have been recorded for more animals over a longer period of time. Genetic trend slopes for weaning and yearling weights have been steeper in British breeds (Angus and Hereford) than in Continental-European breeds (Charolais, Limousin, Gelbvieh and Simmental), an indication that the latter have exerted more selection pressure on calving ease or against birth weight. Genetic trends for calving ease EPDs have been significant for Simmental and Gelbvieh because they were introduced by these breeds much earlier than by other breeds. Hereford, Red Angus, and Limousin have published calving ease EPDs in recent years. Most breeds have relied solely on use of birth weight EPDs as the basis for genetic improvement in calving ease.

By the mid-1990's EPDs for scrotal circumference were included in genetic evaluations by the Hereford and Limousin breeds and they have been included in more recent genetic evaluations by Angus, South Devon, Charolais, Gelbvieh, Salers, and Beefmaster. Some breeds have introduced EPDs for stayability (Red Angus, Salers and Gelbvieh), docility (Limousin, Salers), mature weight (Angus, Simmental, and Salers), and mature height (Angus, Limousin) in recent years.

The EPDs for carcass traits were introduced in the late 1990's. Records on carcass traits were sparse, so EPDs were not available for many bulls. However, with development and increased use of ultrasound estimates for ribeye area, fat thickness and intramuscular fat (marbling) estimates of EPDs for fat thickness, ribeye area and marbling have been provided for at least three years by 11 breeds (Angus, Red Angus, Hereford, Shorthorn, Limousin, Simmental, Charolais, Gelbvieh, Maine Anjou, Salers, and Brangus). In a recent analysis (Van Vleck and Cundiff, unpublished), we estimated coefficients of regression for carcass traits in steers (n = 2,602) produced in our Germplasm Evaluation Program at the U.S. Meat Animal Research Center (MARC) on EPDs for their sires (402 sires) from 2005 genetic evaluations of these 11 breeds. Regression coefficients of 1.07 + 17 for marbling, 2.8 + .35 for fat thickness, and 0.88 + 0.19 for ribeye area suggest that EPDs can predict with reasonable precision variation in carcass traits

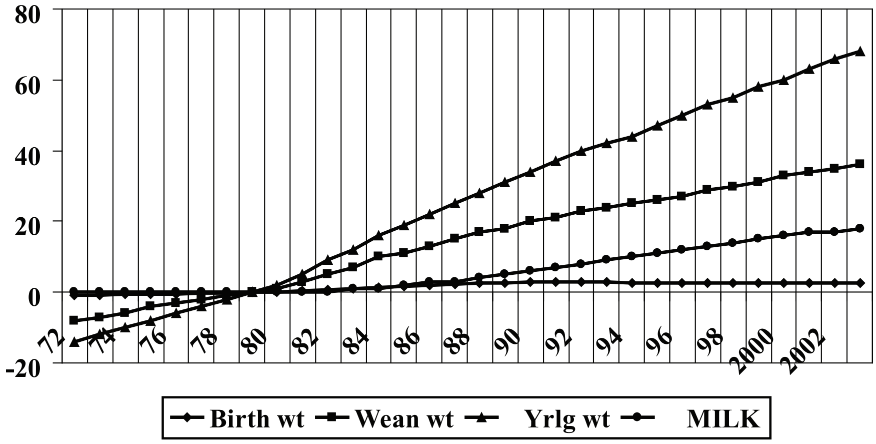

Figure 1. Angus Genetic Trends, EPDs

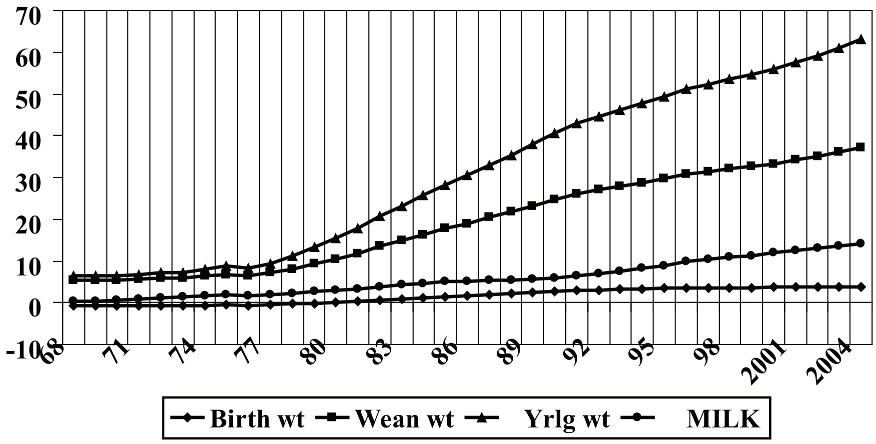

Figure 2. Hereford Genetic Trends, EPDs

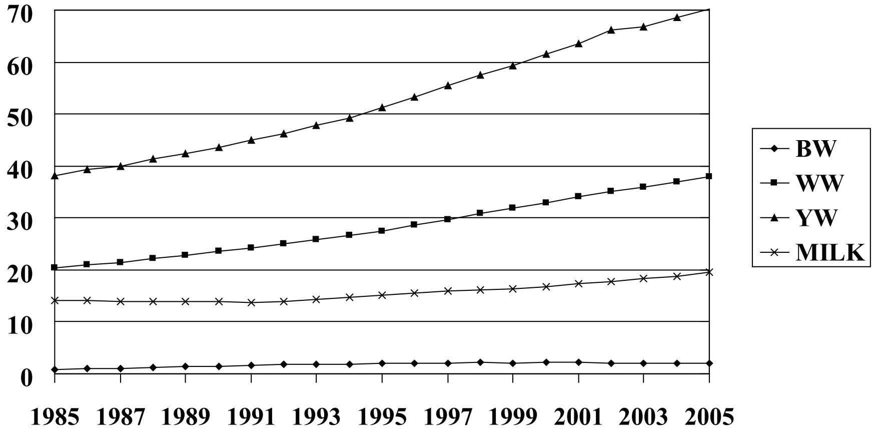

Figure 3. Genetic Trend in Limousin

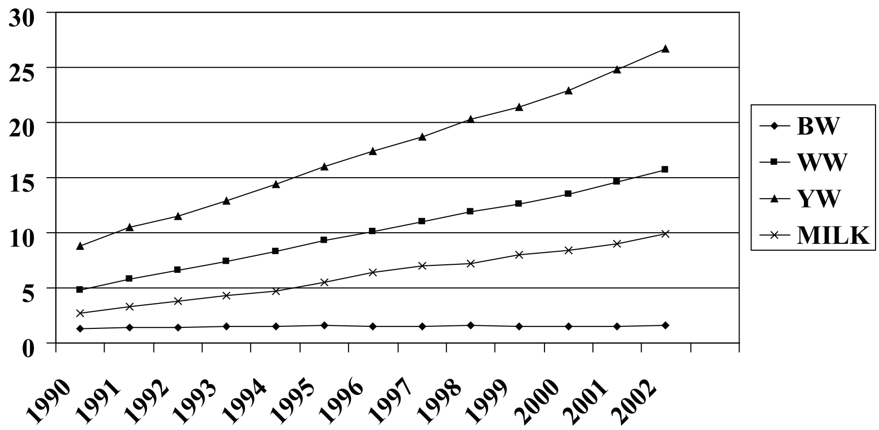

Figure 4. Genetic Trend in Charolais

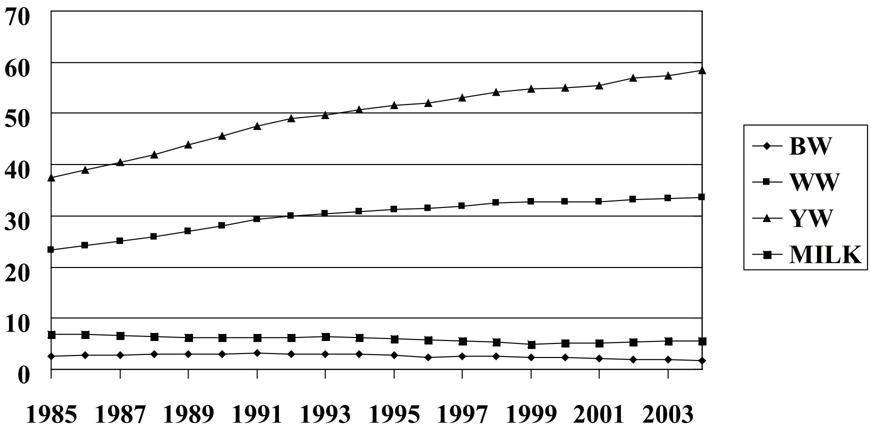

Figure 5. Genetic Trend in Simmental

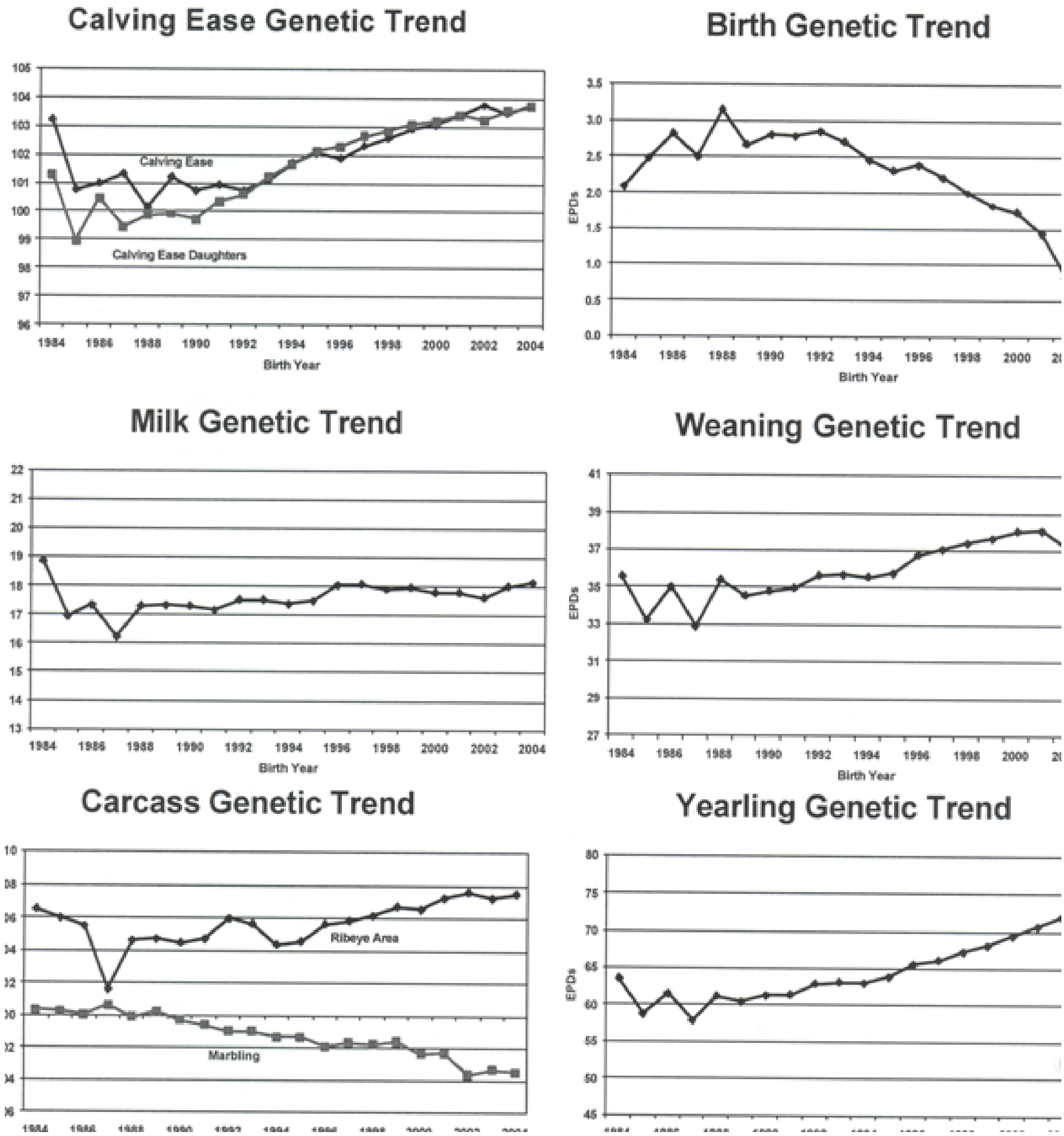

Figure 6. Gelbvieh Genetic Trends

of steers fed and managed to relatively heavy slaughter weights (mean = 590 kg) and degrees of fatness (means of 1.08 cm for fat thickness) typical of commercial production systems in the U.S. It is not surprising that the regression coefficient for fat thickness (2.8) was greater than unity since the EPDs were based primarily on ultrasound estimates taken in seedstock herds on yearling bulls or yearling heifers developed for use as replacements. We are encouraged by these results indicating that significant progress can be made by use of EPDs for carcass traits based primarily upon live animal ultrasound estimation of marbling, fat thickness, and ribeye area.

Heterosis

Experiments conducted in the 1970's demonstrated effects of heterosis increase production per cow about 20-25% in crosses of Bos taurus breeds (e.g., Cundiff et al., 1974). More than half of this advantage was dependent on use of crossbred cows. We have repeated comparison of Hereford X Angus reciprocal crosses to straightbred Hereford and Angus cows in Cycles II, IV, and VII of the Germplasm Evaluation Program at MARC and results have continued to be very similar to these earlier results. Results from experiments Bos indicus X Bos taurus breed crosses have found even higher levels of heterosis, increasing production per cow at least 50% (Cartwright et al., 1964; Koger et al., 1975; Crocket et al., 1978, Peacock et al., 1979). Effects of heterosis increase production per cow about 20 to 25 percent in Bos taurus crosses (e.g., Angus X Hereford) and at least 50 percent in Bos indicus X Bos taurus breed crosses (e.g., Brahman X Shorthorn). Significant levels of heterosis are maintained by rotational systems of crossbreeding (Gregory and Cundiff, 1980) or by use of composite populations founded from crosses of two or more Bos taurus breeds (Koch, et al., 1985; Gregory et al, 1991; 1999). Results from experiments involving Bos taurus breed crosses have indicated that heterosis is retained proportional to heterozygosity with either rotational crossing systems or in composite populations, as expected from dominance model predictions of heterosis.

Experimental evidence concerning heterosis retention in inter se mated Bos indicus X Bos taurus breed crosses has been mixed and not as conclusive. Results from rotational crossing experiments conducted in Texas (Cartwright et al., 1964); Louisiana (Turner and McDonald, 1969; McDonald and Turner, 1972; Boston et al., 1969), and Florida (Koger et al., 1975; Peacock and Koger, 1979) are consistent with expectations that heterosis was proportional to heterozygosity and expectations from dominance model predictions. However, results reported by Arthur et al. (1999) indicate that weaning weight declined significantly in advanced generation Brahman-Hereford rotational crosses due to significant negative epistatic effects. Sanders et al. (2005b) reported results from an experiment comparing Brahman X Hereford and Brahman X Angus F1 and F2 progeny to their respective parental purebreds. Results for calf crop born, calf crop weaned, calf survival, weaning weight, and 4-year-old cow weight were mixed and not conclusive. Results indicated that more heterosis was lost in Brahman X Angus F2 cows than would be predicted from a dominance model, but that less heterosis was lost in a Brahman X Hereford F2 cows than would be predicted from a dominance model.

Breed Differences in Germplasm Evaluation Program at MARC

The Germplasm Evaluation Program at the U.S. Meat Animal Research Center (MARC) has been conducted to characterize breeds of cattle for a comprehensive series of bio-economic traits. Table 1 shows the mating plan for the first eight Cycles of the GPE Program. Each Cycle has been an experiment conducted over a time span of about 10 years. Topcross performance of 37 sire breeds has been evaluated in F1 calves out of Hereford, Angus, or Composite MARC III (Composite MARC III is ¼ each Angus, Hereford, Pinzgauer, and Red Poll) dams. Hereford and Angus sires have been used in each Cycle of the program to provide ties for analysis of data pooled over Cycles. Some of the Hereford and Angus sires used in Cycle I were repeated in Cycles II, III and IV (60'-70's sires). Later, many of the Hereford and Angus sires used for the first time in Cycle IV were repeated in Cycle V (80's sires). Similarly, many of the Brahman sires used in Cycle III (70's sires) were repeated in Cycle V and compared to a new sample of Brahman sires born in the 1980's (80's sires). As a general rule in each Cycle, about 200 progeny per sire breed were produced from artificial insemination (AI) to 20-25 sires per breed. Sires were sampled representing young herd sire prospects (non progeny tested sires) for each breed. Starting with Cycle VII, about half of the sires sampled were chosen from lists of the 50 most widely used bulls in each breed according to registrations.

Prominent Bos taurus breeds. In Cycle VII of the GPE Program (Cundiff et al., 2004), the seven most prominent beef breeds in the U.S. were evaluated, according to registrations in breed associations (National Pedigreed Livestock Council, 2005-2006). Among registrations reported, 83% were for these seven breeds: Angus, Hereford, Limousin, Simmental, Charolais, and Gelbvieh were first characterized in Cycle I and II of the GPE Program (Table 2). Red Angus was evaluated for the first time in Cycle VII. In general, management practices have been similar to those used in commercial production in the U.S. Cundiff et al.,

Table 1. Sire breeds used in Germplasm Evaluation Program at MARC

Cycle I (1970-72)	Cycle II (1973-74)	Cycle III (1975-76)	Cycle IV (1986-90)	Cycle V (1992-94)	Cycle VI (1997-98)	Cycle VII (1999-2000)	Cycle VIII (2001-2002)
				F_1 crosses (Hereford or Angus dams)[a]			
Hereford	Hereford	Hereford	Hereford	Hereford	Hereford	Hereford	Hereford
Angus	Angus	Angus	Angus	Angus	Angus	Angus	Angus
Jersey	Red Poll	Brahman	Longhorn	Tuli	Wagyu	Red Angus	Brangus
S. Devon	Braunvieh	Sahiwal	Salers	Boran	Norwegian Red	Limousin	Beefmaster
Limousin	Gelbvieh	Pinzgauer	Galloway	Belgian Blue	Swedish Red&White	Charolais	Bonsmara
Simmental	Maine Anjou	Tarentaise	Nellore	Brahman	Friesian	Simmental	Romosinuano
Charolais	Chianina		Shorthorn	Piedmontese		Gelbvieh	
			Piedmontese				
			Charolais				
			Gelbvieh				
			Pinzgauer				
	3-way crosses out of F_1 dams						
Hereford	Hereford						
Angus	Angus						
Brahman	Brangus						
Devon	Santa Gertrudis						
Holstein							

[a]Composite MARC III cows (1/4 each Angus, Hereford, Red Poll and Pinzgauer) also were included in Cycles V, VI, and VII. MARC III cows completely replaced Hereford cows in Cycle VIII.

(2004) provided further details concerning management of steers and heifers and procedures used in analyses of data.

Sire breed means for preweaning traits are shown in Table 2. Sire breed means for final weight, percentage and weight of retail product, marbling score, percentage of carcasses grading USDA choice, and Warner-Bratzler shear estimates of tenderness for longissimus steaks are shown in Table 3. Sire breed means for estimates for postweaning efficiency of live weight gain (gain, g/Mcal feed intake) of steers for time (0 to 187 days), weight (340 to 590 kg), fat thickness (0 days to 1.1 cm fat thickness), marbling (0 days to Small00 marbling), percentage fat trim (0 days to 24.8% fat trim), and retail product weight (0 days to 225 kg retail product) intervals of evaluation are shown in Table 4. Sire breed means for 400-day weight, 550-day weight, 18-month height, frame score, age at puberty, and pregnancy rate (%) of females are shown in Table 5. Sire breed means for percentage calf crop born and weaned per cow exposed, calving difficulty score, percentage unassisted births, birth weight, and 200-day weaning weight of progeny produced by the F1 females with MARC III sired calves produced at 2 years of age are presented in Table 6. Sire breed means for percentage calf crop born and weaned per cow exposed, calving difficulty score, percentage unassisted births, birth weight, and 200-day weaning weight of progeny produced by the F1 females at 3 – 6 years of age are shown in Table 7. Sire breed means for height, condition score (1 for very thin to 9 for very fat), weight, and weight adjusted for conditions score of the F1 females at 5 years of age are shown in Table 8. The mean least significant difference (LSD < .05) shown for each trait can be used to assess specific sire breed contrasts (sire within sire breed mean square was used as the error term).

Table 2. Breed group means for preweaning traits of calves

Sire breed of calf	No. calves born	Calvings unassist. %	Calving diff. sc	Birth wt. kg	200-d wt. kg
Hereford	190	95.6	1.24	41.0	237.7
Angus	189	99.6	1.01	38.1	241.9
Red Angus	206	99.1	1.06	38.3	238.7
Simmental	201	97.7	1.10	41.8	251.0
Gelbvieh	209	97.8	1.10	40.2	242.2
Limousin	200	97.6	1.13	40.6	235.3
Charolais	199	92.8	1.40	42.5	245.0
LSD < .05		3.6	.21	1.5	6.4

Angus and Red Angus sired calves require less assistance at calving than those by other British or Continental-European sire breeds (Table 2). Even so, calving ease has improved significantly for calves sired by Continental-European breeds, especially Simmental and Gelbvieh, relative to those by British breeds since the Continental-European breeds were first introduced into the U.S. Sire breed of calf differences for birth weight between Continental-European and British breeds are less than half as great in recent years as they were 30 years earlier.

Sire breed of dam differences for calving ease and birth weight for 2-year-old first calf heifers progeny (Table 7) were not significant, reflecting significant improvement in calving ease for Continental breeds relative to British breeds over a 30 year period. Simmental has made the most improvement in calving ease for 2-year-old first calf heifers. In Cycle I, Simmental sired 2-year-old females required 6% more assistance than Hereford-Angus reciprocal crosses. In Cycle VII, Simmental sired 2-year-olds required 11% less assistance than Hereford and Angus sired crosses. These results, suggest that Continental-European breeds have emphasized selection for components of calving ease relatively more than British breeds during this time span.

Steer progeny of British and Continental-European sire breeds did not differ in postweaning average daily gain or final slaughter weight at 445 days of age (Table 3). In evaluations conducted 30 years earlier, Continental-European sire breeds had significantly faster average daily gains and were 1- 3 standard deviations heavier at yearling ages than British breeds (Cundiff et al., 1986). Similarly, heifers by British and Continental-European sire breeds did not differ in 400-day and 550-day weights (Table 5). These results, are consistent with slopes for genetic trends for yearling weight reported by breed association for these breeds (figures 1-6) indicating that selection emphasis for growth rate to weaning and yearling ages has been emphasized more in British breeds than in Continental-European breeds during the past 30 years.

Although, steers progeny of British and Continental-European sire breeds did not differ significantly in live weight at 445 days, Continental-European sire breeds still produced progeny with significantly heavier retail product (15 kg) due to higher retail product yields (3.9%) than British sire breeds (Table 3). Steers by British sire breeds had significantly greater marbling and a higher percentage of carcasses grading USDA

Table 3. Sire breed means for final weight and carcass traits of F_1 steers (445 days)

Sire breed	N	Final wt kg	Retail product %	Retail product kg	Marbling sc	USDA Choice %	WB shear kg
Hereford	97	599.6	60.7	217.8	526	65.4	4.12
Angus	98	619.3	59.2	221.3	584	87.6	4.02
Red Angus	93	604.7	59.1	215.1	590	89.9	4.15
Simmental	92	617.9	63.0	237.0	527	65.7	4.30
Gelbvieh	90	595.0	63.8	231.1	506	57.7	4.51
Limousin	84	583.0	63.7	228.5	504	56.9	4.31
Charolais	95	611.2	63.5	237.3	517	61.9	4.34
LSD < .05		18.4	1.3	7.3	28	10.7	.31

Choice than those by Continental-European sire breeds. Results indicate that differences between Continental-European and British breeds for carcass composition, marbling, and tenderness remain nearly as great today as they were 30 years ago (Cundiff et al., 1986), a result that is not surprising because EPDs have only recently been introduced for carcass traits and results have shown that correlated response for carcass composition or marbling to selection for growth is low (e.g., Koch et al., 2004).

As a result of these relative changes in growth rate, British and Continental-European breeds no longer differ significantly in efficiency of postweaning live weight gain (gain, kg/Mcal metabolizable energy consumed) to age or weight end-points (Table 4). In Cycles I and II, steers by Continental-European sire breeds were significantly more efficient than those by British sire breeds, especially to weight end-points (Cundiff et al., 1986). However, to fatness end-points (1.1 cm fat thickness, 25% carcass fat trim, or small00 marbling), progeny by British sire breeds were still significantly more efficient than those by Continental-European sire breeds just as they were 30 years earlier. Also, to a weight of retail product end-point (0 days to 225 kg), progeny by Continental-European sire breeds were still significantly more efficient than those by British sire breeds.

Breeds that have had a long history of selection for milk production (e.g., Simmental and Gelbvieh), still produce females that reach puberty at younger ages than those that have not been selected for milk production (Limousin, Charolais, Hereford, Angus or Red Angus) much as they did 30 years earlier (Cundiff et al., 1986).

Differences among sire breeds for F1 daughters percentage calf crop born or weaned at 2 years of age (Table 6) or at 3 – 6 years of age (Table 7) were not significant in recent or earlier evaluations (Cundiff et al., 1986). Weaning weights of progeny of F1 daughters are still greater for Simmental and Gelbvieh, that have had a history of selection for milk production, than for those by Charolais, Limousin, Angus, Red Angus, Hereford that were never used for dual purpose dairy and beef production (Tables 6 and 7). However, magnitude of contrasts for direct and maternal components of weaning weight between Continental-European and British breeds are less than half as great in the current evaluations as those 30 years earlier (Cundiff et al., 1986).

Recent estimates indicate that Continental-European and British breeds do not differ significantly in estimates of cow weight or height at 5 years of age, with one exception Gelbvieh are significantly lighter than females by other sire breeds. Results indicate that the reduced cow weight for Gelbvieh is associated with strong negative genetic trends for birth weight in the Gelbvieh breed, contrasted to slightly positive or null genetic trends for birth weight in other breeds.

Table 4. Feed efficiency (live weight gain, g/Mcal) for alternative intervals and endpoints

Sire breed	Time 187d	Weight change 340 to 590 kg	Fat thick. 1.1 cm	Marbling score Small 00	Fat trim 24.8%	Retail prod. wt. 225 kg
Hereford	59.2	57.8	60.5	58.5	60.4	57.0
Angus	56.6	56.1	59.5	61.0	59.8	55.1
Red Angus	55.7	54.5	57.8	60.3	58.5	52.6
Simmental	57.4	57.6	55.6	56.7	55.9	60.3
Gelbvieh	55.4	54.5	53.8	53.6	53.6	56.5
Limousin	58.1	55.8	56.4	55.5	56.6	59.0
Charolais	54.5	54.5	52.2	53.1	52.5	57.4
LSD < .05	3.7	4.3	3.4	3.3	3.3	4.2

These results are consistent with preliminary results from a selection experiment at MARC, in which response to selection for lighter birth weight and heavier yearling weight, reduced birth weight and mature cow weight significantly while yearling weight was increased (G. L. Bennett, personal communication). The lack of differences among breeds for cow weight and height, contrast sharply with comparisons made 30 years earlier when cows by Continental-European sire breeds were on average 2.3 cm taller and about 15 kg heavier than those by British sire breeds (Arango et al., 2004a,b).

Table 5. Sire Breed Least Squares Means for Growth and Puberty Traits of Heifers in Cycle VII of the GPE Program (1999-2000 Calf Crops)

Sire breed of female	No.	400-d wt. kg	550-day wt. kg	18-mo ht. cm	Frame score sc	Age at puberty	Preg. rate %
Hereford	81	381.5	430.9	128.4	5.5	342	94
Angus	85	394.2	424.5	127.2	5.3	340	88
Red Angus	106	393.7	432.5	126.9	5.2	339	91
Simmental	103	385.3	435.8	130.2	5.9	335	90
Gelbvieh	111	366.1	418.4	128.8	5.6	322	83
Limousin	109	373.6	423.3	129.9	5.8	363	87
Charolais	103	375.4	430.7	129.5	5.8	348	91
LSD $\leq$ .05		14.0	14.7	1.6	.3	15	13

Adaptation to Temperate and Subtropical Environments

In choosing breeds for a specific production system it is very important to consider climatic adaptation of breeds. Frisch and Vercoe (1978) and Utech et al., (1978) have documented the advantages of using Bos indicus X Bos taurus crosses (e.g., Brahmans X Shorthorn or Brahman X Hereford) to cope with ticks, gastrointestinal helminthes, high ambient temperature, solar radiation, and nutritional stress in a tropical environment. Use of some tropically adapted germplasm is also important in subtropical climates (e.g., Cartwright et al., 1964; Koger et al., 1975; Thrift and Thrift, 2005). In a cooperative effort between the Subtropical Agricultural Research Station, (ARS, USDA and the University of Florida), Brooksville, Florida and MARC, weaning weight per cow exposed was significantly greater for the Bos indicus X Bos taurus F1 crosses (Brahman X Hereford, Brahman X Angus, Sahiwal X Hereford, Sahiwal X Angus) than for the Bos taurus X Bos taurus F1 crosses (Hereford X Angus, Angus X Hereford, Pinzgauer X Hereford, Pinzgauer X Angus) at both locations, but the advantage was especially large in Florida (Olson et al., 1991). Results at MARC have also indicated that cow efficiency (pounds of calf gain per unit of feed consumed by the cow and calf), estimated during lactation in summer months, was exceptional for Bos indicus X Bos taurus relative to Hereford X Angus crosses (Green et al., 1991), which were in turn relatively efficient compared to other Bos taurus X Bos taurus crosses (Jenkins et al, 1991). Reproduction rate, weaning weight per cow exposed and cow efficiency is outstanding in Bos indicus X Bos taurus F1 crosses, especially in subtropical climatic environments, but their advantages are tempered by older age at puberty and reduced meat tenderness as the proportion of Bos indicus increases (Crouse et al., 1989). Concerns about meat quality and reproduction rate at young ages have prompted introduction and evaluation of other tropically adapted germplasm in cooperative research efforts involving the U.S. Meat Animal Research Center (MARC) and research stations in subtropical regions of the U.S. (i.e., Texas, Oklahoma, Florida, Georgia, and Louisiana). Recently a bulletin including 24 reports summarizing results from this cooperative research effort has been published (Southern Cooperative Series Bulletin 405).

Table 6. Sire Breed Means for Reproduction and Maternal Traits of F_1 Females Producing Their First Calves at 2 Years of Age (2001 and 2002)

Sire breed of female	No.	Calf crop born %	Calf crop wnd. %	Calving diff. score	Unassist. births %	Birth wt kg	200-d wt per calf kg
Hereford	80	92	70	1.9	74	37.0	187.4
Angus	84	83	76	2.0	72	36.2	192.2
Red Angus	104	86	76	2.2	68	35.5	188.1
Simmental	98	86	69	1.5	86	36.1	200.3
Gelbvieh	109	79	68	2.2	64	37.9	202.9
Limousin	109	85	73	2.0	68	36.4	194.7
Charolais	97	87	73	2.1	69	37.0	195.2
LSD < .05		14	15	.6	19	2.0	9.5

Tropically adapted breeds in the GPE Program. In Cycle V of the Germplasm Evaluation Program at MARC (Table 12), tropically adapted Tuli, Boran and Brahman sire breeds were evaluated relative to Hereford and Angus crosses (Cundiff et al., 2000). Semen from nine Tuli bulls and eight Boran bulls was imported from Australia for use in the experiment. Results for preweaning traits;

Table 7. Sire Breed Means for Reproduction and Maternal Traits of F_1 Females Producing Calves at 3-6 Years of Age (2002-2005)

Sire breed of female	No. rec.	Calf crop born %	Calf crop wnd. %	Calving diff. score	Unassist. births %	Birth wt kg	200-d wt calf kg
Hereford	244	94	91	1.16	96.9	43.0	233.1
Angus	241	95	89	1.03	98.4	41.2	239.0
Red Angus	288	89	85	1.19	96.4	40.7	234.8
Simmental	294	90	87	1.02	98.9	41.8	249.4
Gelbvieh	305	90	86	1.11	97.8	42.3	248.8
Limousin	303	95	91	1.06	98.7	42.3	240.1
Charolais	293	90	86	1.30	94.5	42.7	243.9
LSD < .05		7	8	.21	3.7	1.6	8.7

slaughter weight, carcass and meat traits; growth and puberty traits of heifers; and reproduction and maternal performance for F1 produced in Cycle V of the GPE Program are summarized in Tables 9, 10, 11, and 12, respectively. Performance of Nellore crosses, also shown in Tables 9, 10, 11, and 12 were estimated by adding the deviation of Nellore crosses from Hereford and Angus crosses produced in Cycle IV (Wheeler et al., 1996; Wheeler et al., 1997; Cundiff et al., 1998; Thallman et al., 1999) to the mean of Hereford and Angus crosses produced in Cycle V (The least significant differences between Nellore crosses and other breeds can be approximated by multiplying 1.5 times the least significant difference shown in Tables 9 through 12 for Cycle V contrasts).

Results indicate that Tuli sired steers had carcass (marbling) and meat (tenderness) characteristics more similar to progeny sired by British Bos taurus breeds (i.e., Hereford and Angus) than to progeny sired by Bos indicus breeds (i.e., Brahman or Boran). However, Tuli crosses had relatively low weaning weights (Table 9) and final slaughter weights compared to other breeds. Performance of Nellore crosses was comparable to that of current Brahman crosses for preweaning and postweaning growth rate, weight and percentage of retail product.

Tuli and Boran crosses were significantly younger at puberty and had higher percentages of calf crop weaned as 2-year-olds than Brahman crosses (Table 11). However, at three through seven years of age, percentages of calf crop weaned did not differ among Nellore, Brahman, Boran and Tuli sired females (Table 12). At all ages, maternal weaning weight (200 day weight per calf) was greater for Nellore and Brahman than Boran sired F1 cross females which were in turn greater than Tuli sired F1 cross females. Tuli germplasm may be useful to replace a portion of Bos indicus breeding and maintain tropical adaptation without detrimental effects on meat tenderness, provided they are crossed with other breeds that optimize size and growth rate.

Results from cooperative research efforts at research stations located in subtropical regions of the U.S. including Brooksville, Florida (Chase et al., 2005); McGregor, Texas (Sanders et al., 2005a); Uvalde, Texas (Holloway et al. 2005); and El Reno, Oklahoma (Phillips et al., 2005) for Tuli, Boran, and Brahman crosses have been similar to our results at MARC for growth traits, carcass and meat traits, and reproduction and maternal performance of F1 cross cows. Holloway et al. (2005) reported further that mature cow weights were significantly lighter for Tuli than Brahman crosses, and had greater efficiency of production as estimated by weight of calf weaned per unit of cow weight exposed to breeding.

In Cycle VIII of the GPE Program Brangus, Beefmaster, Bonsmara, and Romosinuano are being evaluated relative to Hereford and Angus crosses (Wheeler et al., 2006). Brangus and Beefmaster were included in Cycle VIII because they are prominent breeds used extensively in subtropical regions of the U.S., ranking 7th and 8th in registrations among beef breeds and 1st and 2nd among tropically adapted breeds in the U.S. (National Pedigreed Livestock Council, 2005-2006). Brangus is an American composite breed with 62.5% Angus and 37.5% Brahman inheritance. Beefmaster is an American composite with about 50% Brahman, 25% Hereford, and 25% Shorthorn inheritance. Bonsmara is a composite breed developed in South Africa with 50% Africaner (an African Sanga breed), 25% Hereford, and 25% Shorthorn inheritance. Semen was used from 19 Bonsmara bulls. The Romosinuano breed was developed primarily in Colombia and introduced into the U.S. from Venezuela at the Subtropical Agricultural Research Station (STARS), ARS, USDA and the University of Florida, Brooksville, FL. The Romosinuano is a Criollo (domestic) breed of Central America that traces back to Bos taurus cattle introduced from Europe about 400 to 500 years ago. Semen from 20 Romosinuano bulls was used. Estimates of sire breed means averaged over Angus and MARC III dams are shown in Table 13 for preweaning traits; Table 14 for slaughter weight, carcass and meat traits; Table 15 for female growth and puberty traits; and Table 16 for reproduction and maternal performance of cows.

Table 8. Sire breed least squares means for height, condition score, and weight of F_1 cows (adjusted for condition score) at 5 years of age

Breed	Number cows	Five-yr-old height, cm	Five-yr-old cond. sc.	Five-year-old Weight[a], kg	
Hereford	56	135.4	7.00	679	(677)
Angus	62	134.4	7.22	681	(673)
Red Angus	68	134.4	7.40	685	(672)
Simmental	70	137.4	6.98	669	(671)
Gelbvieh	68	135.0	6.77	627	(634)
Limousin	80	137.4	6.95	663	(665)
Charoalis	69	137.3	7.09	669	(667)
LSD < .05		0.8	.28	29	(26)

*P < 0.05. **P < 0.01.
[a] Estimates for Hereford, Angus, and Red Angus were adjusted to the level of heterosis expected in three-way F_1 crosses (estimate of 18.9 kg was added to five-year-old weight and 16.6 kg was added to five-year-old weight adjusted for condition score).

Birth weight did not differ significantly among progeny of Bonsmara, Brangus and Hereford sires, which were significantly heavier than progeny of Angus sires. Birth weights of Romosinuano sired progeny were significantly lighter than those of any other breed except Angus. Weaning weight at 205 days was significantly heavier for progeny of Beefmaster sires than for any other sire breed, followed by Brangus and Angus, which did not differ significantly. Brangus sired progeny were significantly heavier at weaning than Hereford sired progeny. Angus, Hereford and Bonsmara sire breeds did not differ significantly in weaning weight. Romosinuano sired progeny were significantly lighter at weaning than those of any other sire breed.

Beefmaster sired steers had significantly heavier final weights than all other breeds except Angus. Angus, Brangus, and Hereford sired steers were significantly heavier than Bonsmara sired steers at 426 days, which were in turn significantly heavier than Romosinuano sired steers. Romosinuano and Bonsmara sired steer carcasses had significantly higher percentages of retail product than Brangus, Hereford, Beefmaster and Angus sired steer carcasses. Angus sired steer carcasses had significantly lower percentages or retail product than those by any other sire breed. Estimates of weight of totally trimmed boneless retail product at 426 days of age were very similar for Beefmaster and Brangus sired steer carcasses and were significantly greater than estimates for Angus, Hereford, Bonsmara, and Romosinuano. Hereford, Angus, and Bonsmara did not differ significantly for weight of retail product. Steer progeny of Romosinuano sires had significantly lower retail product weights than those of all other sire breeds except Bonsmara.

Marbling score and percentage grading USDA Choice or higher were significantly greater for Angus than for any other sire breed. Carcasses from Hereford sired steers ranked second and had significantly greater marbling scores and a greater percentage grading USDA Choice or higher than those from Romosinuano, Bonsmara and Beefmaster sired steers. Brangus ranked

Table 9. Breed group means for preweaning traits of calves produced in Cycle V of the GPE Program (1992-1994 Calf Crops)

Sire breed of calf	No. calves born	Calvings unassist. %	Calving diff. score	Birth wt. kg	200-d wn. wt., kg
Hereford	334	97.0	1.17	42.7	241
Angus	313	98.3	1.06	41.0	240
Brahman					
original[a]	155	93.2	1.39	45.1	243
recent[b]	281	88.7	1.58	47.4	246
Boran	456	95.7	1.23	43.3	229
Tuli	451	97.4	1.19	38.9	225
Nellore[c]	196	96.8	---	44.4	247
LSD < .05		4.1	0.21	1.5	7

[a]Progeny of sires born in 1964-1975.
[b]Progeny of sires born in 1984-1989.
[c]Estimated by adding deviation for Nellore crosses from 1980's Hereford-Angus crosses produced in Cycle IV (Cundiff et al., 1998) to mean of Hereford-Angus crosses in Cycle V.

Table 10. Sire breed means for final weight and carcass traits of F_1 steers produced in Cycle V of the GPE Program (447 d)

Sire breed	No.	Final wt. kg	Retail product %	Retail product kg	Marbling score	USDA Choice %	14-d Shear kg
Hereford	106	576	61.9	204	520	70.3	4.8
Angus	101	580	62.2	206	556	84.6	4.0
Brahman							
Original	43	533	64.1	199	485	29.4	6.1
Recent	76	544	63.8	204	466	30.4	5.9
Boran	151	506	62.6	181	504	47.2	5.1
Tuli	162	503	63.4	184	525	63.8	4.6
Nellore	97	555	65.0	211	500	51.4	---
LSD < .05		22	1.7	8	30	22.2	.6

[a]Progeny of sires born in 1964-1975.
[b]Progeny of sires born in 1984-1989.
[c]Estimated by adding deviation for Nellore crosses from 1980's Hereford-Angus crosses produced in Cycle IV (Cundiff et al., 1998) to mean of Hereford-Angus crosses in Cycle V.

third in marbling and percentage grading USDA Choice or higher, but did not differ significantly from Hereford or from Romosinuano, Bonsmara, or Beefmaster.

Half of the Brangus, Beefmaster, Bonsmara, and Romsinuano females being produced at MARC were transferred at about 8 months of age from MARC to Louisiana State University to evaluate Genotype-environment interactions. Data summarizing growth and puberty characteristics of females (Tables 15 and 16), are only for the heifers that remained at MARC. The Brangus, Beefmaster, Brangus, and Romosinuano sired progeny represent only about 50% of the females being evaluated in the cooperative experiment. Results for growth of heifers are generally consistent with that of steers indicating that Beefmaster and Angus sired females had the greater growth rates to 400 days than all other sire breeds except Brangus. By 400 days, Brangus and Herefords did not differ significantly in body weight, but both were heavier than Bonsmara or Romosinuano sired females. By 18 months of age, after the summer grazing season, Beefmaster were significantly heavier than all other breeds except Brangus. Brangus sired heifers were significantly heavier at 18 months of age than Romosinuano sired females, but did not differ significantly from Hereford, Bonsmara or Angus sired females, which had similar 18-month weights. Brangus and Beefmaster sired heifers had significantly greater hip heights and frame scores at 18 months of age than Hereford, Bonsmara, Angus, or Romosinuano sired heifers. Hereford sired heifers ranked third in hip height and frame score and were significantly taller than Romsinuano sired heifers. Bonsmara, Angus and Romosinuano sired heifers did not differ in hip height or frame score at 18 months of age. Females by Angus sires reached puberty at a significantly younger age than those by any other sire breed. Females by Romosinuano sires reached puberty at significantly older ages than females by any other sire breed except Bonsmara.

Implications

The beef industry is challenged to 1) reduce costs of production to remain competitive with meat products from other species, especially poultry and swine, 2) match genetic potential with the climate and feed resources available in diverse environments, 3) reduce fat and increase leanness of products to gain greater acceptance of consumers,

Table 11. Sire breed means for growth and puberty traits of F_1 females produced in Cycle V of the GPE Program

Sire breed of female	No.	365-d wt. kg	18 month wt. kg	18 month ht. cm	Puberty age, days	Preg. rate %
Hereford	152	353	413	128.3	355	92.7
Angus	130	347	404	127.3	351	91.6
Brahman	212	328	398	132.0	426	84.2
Diff. (curr.[a]-orig.[b])		3	10**	2.9**	-6	15.0*
Boran	206	303	362	125.8	396	96.8
Tuli	244	302	357	125.5	371	90.2
Nellore	82	342	401	356	406	96.6
LSD < .05		6	6	1.6	13	11.0

[a]Progeny of sires born in 1964-1975.
[b]Progeny of sires born in 1984-1989.
[c]Estimated by adding deviation for Nellore crosses from 1980's Hereford-Angus crosses.

Table 12. Breed group means for reproduction and maternal trait of F_1 females in Cycle V of the GPE Program

Sire breed of female	No.	2-years of age: Calf crop weaned %	2-years of age: 200-day wt. per calf kg	2-years of age: 200-day wt. per cow exposed, kg	3 to 7 years of age: Calf crop wnd., %	3 to 7 years of age: 200-day wt. per calf kg	3 to 7 years of age: 200-day wt. per cow exposed, kg
Hereford	146	73.8	190.1	136.1	88.7	214.8	191.1
Angus	132	74.4	198.2	142.0	86.3	223.5	193.3
Brahman							
Original	69	54.3	206.8	108.0	85.9	231.9	199.6
Current	135	69.6	215.9	144.7	82.7	236.2	195.2
Boran	197	83.3	201.4	161.9	86.2	221.5	183.1
Tuli	235	74.6	187.3	134.3	84.1	213.7	191.1
Nellore	82	75.1	210.0	147.0	91.6	233.1	209.1
LSD < .05		13.9	8.2	28.1	6.7	6.3	16.1

[a]Progeny of sires born in 1964-1975.
[b]Progeny of sires born in 1984-1989.
[c]Estimated by adding deviation for Nellore crosses from 1980's Hereford-Angus crosses produced in Cycle IV (Cundiff et al., 1998) to mean of Hereford-Angus crosses in Cycle V.

Table 13. Breed group means for preweaning traits of calves produced in Cycle VIII of the GPE Program (2001 and 2002 calf crops)

Sire breed of calf	No. calves born	Calvings unassist. %	Calv. diff. score	Birth wt. kg	200-d wn. wt., kg
Hereford	212	94.4	1.33	41.3	242.4
Angus	208	97.2	1.19	39.5	245.6
Brangus	214	96.9	1.19	41.0	248.9
Beefmaster	222	95.6	1.23	43.3	254.0
Bonsmara	207	97.7	1.10	41.0	242.0
Romosinuano	207	99.2	1.05	38.4	230.1
LSD < 05		3.4	.20	1.4	4.9

and 4) improve palatability, tenderness, and consistency of beef products. Use of heterosis and breed differences through crossbreeding or use of composite populations, and selection of breeding stock to exploit genetic variation within breeds can all be used to help meet these challenges.

Effects of heterosis increase production per cow about 20 to 25 percent in Bos taurus breed crosses (e.g., Angus X Hereford) and at least 50 percent in Bos indicus X Bos taurus breed crosses (e.g., Brahman X Shorthorn). Significant levels of heterosis are maintained by rotational systems of crossbreeding and in composite populations. Rotational systems of crossbreeding provide for more effective use of heterosis than composite populations for any specific number of breeds. However, uniformity of cattle and greater consistency of end product can be provided for with greater precision by use of F1 seedstock or composite populations than by use of rotational crossing of pure breeds.

Results from the Germplasm Evaluation Program at MARC have provided a basis for classifying breeds into biological types (Table 17). In the table increasing X's indicate relatively greater growth rate and mature size, lean to fat ratios, marbling, beef tenderness, age at puberty of females, milk production, and tropical adaptation. Biological type classifications for growth rate and mature size are not the same today as they were 30 years ago. In the 1970's, Continental-European breeds had significantly faster growth rates and heavier body weight at weaning, yearling and mature ages. Recent results indicate that British breeds are comparable to Continental-European breeds for these traits. The advantage of Continental-European breeds over British breeds in retail product yield is about the same today as in the 1970's. However, British breeds, especially Angus, Red Angus, and Shorthorn's still excel in marbling relative to Continental-European breeds. No one breed excels in all traits of importance to beef production. Thus, crossing of two or more breeds can be used to optimize performance levels. In temperate environments, genetic potential for retail product and marbling are more nearly optimized in cattle with 50:50 ratios than in cattle with higher or lower ratios of Continental to British inheritance.

To limit costs of production and improve efficiency of production a strong influence of tropically adapted germplasm is needed in tropical and subtropical regions of the world. In hot and humid subtropical regions such as the U.S. Gulf Coast, cattle with 50:50 ratios of Bos indicus to Bos taurus inheritance may be optimal. A little further north (e.g., Southeastern Oklahoma, central Arkansas, Tennessee and parts of North Carolina), 25:75 ratios of Bos indicus: Bos taurus inheritance may be optimal in cow herds. In temperate climates (e.g., Nebraska), crosses with 50% or more Bos indicus inheritance suffer increased mortality when calves are born in colder seasons and reduced average daily gains in feedlots during winter months. Use of F1 Brahman cross cows, Nellore, or Boran F1 cross cows or rotational crossing of composite breeds such as Beefmaster, Brangus, Bonsmara, or Santa Gertrudis are especially appropriate in subtropical environments. In harsher tropical climates, it is possible that even more than 50% tropically adapted germplasm is required to provide for optimal performance. If replacement requirements for suitably adapted females are met and terminal crossing is feasible, then a Bos taurus breed can be used to optimize carcass and meat characteristics and increase market value of terminal cross slaughter progeny.

In developing composite populations with an overall level of 50% to 75% tropical adaptation, it may be appropriate to substitute a portion (e.g., 25%) of non Bos indicus germplasm for Bos indicus germplasm from such breeds as the Tuli, Romosinuano, or Senepole to maintain tropical adaptation and improve meat tenderness, provided they are crossed with other breeds that optimize size and growth rate. However, additional research is needed to determine optimum contributions of Bos indicus, British Bos taurus, Continental Bos taurus, tropically adapted Sanga breeds, and tropically adapted Criollo breeds from Central and South America for beef production in harsh tropical environments.

Experimental populations will be even more critical to the development of technology in the future than they have been in the past. It is very expensive and difficult to measure components of complex traits such as feed efficiency, meat tenderness and other quality attributes, disease

Table 14. Sire breed means for final weight and carcass traits of F_1 steers produced in Cycle VIII (426 days, 2001 and 2002 calf crops)

Sire breed	N	Final wt. kg	Retail product %	Retail product kg	Marb. score	USDA Choice %	W-B Shear kg
Hereford	102	564.9	61.8	211.5	515	52	3.67
Angus	103	582.0	60.0	212.8	548	71	3.44
Brangus	107	569.9	62.1	218.0	497	42	3.89
Beefmaster	103	587.9	61.2	218.8	483	35	4.08
Bonsmara	104	537.7	63.4	210.3	487	37	3.69
Romosinuano	102	521.4	64.4	205.2	488	37	3.78
LSD < .05		13.4	1.1	6.0	24	13	0.22

Table 15. Sire breed means for growth and puberty traits of F_1 females produced in Cycle VIII (2001 and 2002 calf crops)

Sire breed of female	N	400-d wt. kg	18 month wt kg	18 month ht cm	Frame score sc	Puberty age, days	Preg. rate %
Hereford	102	387.5	403.1	127.7	5.41	329	85
Angus	107	399.7	399.1	126.3	5.12	310	83
Brangus	47	394.8	410.1	129.3	5.74	341	92
Beefmaster	53	401.4	418.6	129.1	5.69	350	96
Bonsmara	51	377.2	403.4	126.7	5.20	352	84
Romosinuano	50	347.6	372.4	126.1	5.09	362	89
LSD < .05		11.8	11.5	1.2	.24	14	11

Table 16. Breed group means for reproduction and maternal traits of F_1 females in Cycle VIII of the GPE Program at MARC

		2-years of age			3 to 4 years of age		
		Calf crop	200-day wt.			200-day wt.	
Sire breed of female	No.	weaned %	per calf kg	per cow exposed, kg	Calf crop wnd., %	per calf kg	per cow exposed, kg
Hereford	101	76.5	205.2	156.8	91.7	238.2	218.3
Angus	104	69.0	215.0	147.5	91.9	248.4	228.5
Brangus	45	85.0	217.7	184.5	88.0	250.9	221.8
Beefmaster	51	86.1	220.5	188.9	94.3	244.5	231.5
Bonsmara	48	69.0	206.4	143.8	89.6	237.7	216.7
Romosinuano	50	79.2	188.4	148.6	97.0	217.6	212.7
LSD < .05		15.8	10.1	32.9	7.9	11.0	21.1

resistance, and age at puberty in industry herds. However, complex traits such as these can be measured in experimental populations. If the experimental populations are representative of those used in the industry, algorithms can be derived to compute EPDs based on DNA and phenotypic data obtained in experimental herds and only DNA data obtained in industry herds. Once sufficient markers are identified to account for significant genetic variation in seedstock populations, significant progress can be made from selection for traits that can only be measured in intensively managed experimental populations.

Literature Cited

Arango, J. A., L. V Cundiff, and L. D. Van Vleck. 2002a. J. Anim. Sci. 80:3123.

Arango, J. A., L. V Cundiff, and L. D. Van Vleck. 2002ba. J. Anim. Sci. 80:3133.

Arthur, P. F., H. Hearnshaw, P. D. Stephenson. 1999. Livestock Prod. Sci. 57:231.

BIF. 2002. Guidelines for uniform beef improvement programs. Beef Improvement Federation. www.beefimprovement.com.

Boston, A. C., M. Taylor, E. A. Icaza and T.O. McRae. 1969. Livestock Producers Day Report. Louisiana State University, Baton Rouge. LA 16:73.

Cartwright, T. C., G. F. Ellis, Jr., W. E. Kruse, and E. K. Crouch. 1964. Texas Agr.Exp. Sts. Tech. Monogr. 1.

Chase, C. C. Jr., D. G. Riley, T. A. Olson, and S. W. Coleman. 2005. Evaluation of Brahman and tropically adapted Bos taurus breeds in the humid subtropics. A Compilation of Research Results Involving Tropically Adapted Beef Cattle Breeds. Southern Coop. Ser. Bull. 405. pp.6-15. http://www.lsuagcenter.com/en/crops_livestock/livestock/beef_cattle/breeding_genetics/trpoical+breeds.htm

Crocket, J. R., M. Koger, and D. E. Franke. 1978. J. Anim. Sci. 46:1170.

Crouse, J. D., L. V. Cundiff, R. M. Koch, M. Koohmaraie, and S. C. Siedeman. 1989. J. Anim. Sci. 22:702.

Cundiff, L. V., K. E. Gregory, R. M. Koch. 1974. J. Anim. Sci. 38:711.

Cundiff, L. V., K. E. Gregory, R. M. Koch, and G. E. Dickerson. 1986. Proc. 3rd World Congress on Genetics Applied to Livestock Production. IX:271.

Cundiff, L. V., K. E. Gregory, R. M. Koch. 1998. J. Anim. Sci. 76:2528.

Cundiff, L. V., T. L. Wheeler, K. E. Gregory, S. D. Shackelford, M. Koohmaraie, H. C. Freetly, G. D. Snowder, and D. D. Lunstra. 2000. Germplasm Evaluation Program Progress Report No. 19. pp. 1-12. http://www.ars.usda.gov/Main/docs.htm?docid=6238

Cundiff, L. V., T. L. Wheeler, K. E. Gregory, S. D. Shackelford, M. Koohmaraie, R. M. Thallman, G. D. Snowder, and L. D. Van Vleck. 2004. Germplasm Evaluation Program Progress Report No. 22. pp. 1-15. http://www.ars.usda.gov/Main/docs.htm?docid=6238

Jenkins, T. G., L. V. Cundiff, and C. L. Ferrell. 1991. J.Anim. Sci. 69:2762.

Franke, D. E., O. F. Habet, L. C. Tawak, A. R. Williams, and S. M. De Rouen. 2001. J. Anim. Sci. 79:1713.

Frisch, J. E. and J. E. Vercoe. 1978. World Anim. Rev. 25:8.

Green, R. D., L. V. Cundiff, G. M. Smith, and R. M. Koch. 1991. J. Anim. Sci. 69:3156.

Gregory, K. E., and L. V. Cundiff. 1980. J. Anim. Sci. 51:1224.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1991. Breed effects and heterosis in advanced generations of composite populations for preweaning traits of beef cattle. J. Anim. Sci. 69:947.

Gregory, K. E., L. V. Cundiff, and R. M. Koch. 1999. Composite breeds to use heterosis and

TABLE 17. BREEDS GROUPED INTO BIOLOGICAL TYPES FOR SEVEN CRITERIA

Breed group	Growth rate and mature size	Lean to fat ratio	Marbling (Intra-muscular fat)	Tender-ness	Age at puberty	Milk production	Tropical adaptation
Jersey	X	X	XXXX	XXX	X	XXXXX	XX
Longhorn	X	XXX	XX	XX	XXX	XX	XX
Wagyu	X	XXX	XXXX	XXX	XX	XX	XX
Angus	XXXX	XX	XXXX	XXX	XX	XXX	X
Red Angus	XXXX	XX	XXXX	XXX	XX	XXX	X
Hereford	XXXX	XX	XXX	XXX	XXX	XX	X
Red Poll	XX	XX	XXX	XXX	XX	XXXX	X
Devon	XX	XX	XXX	XXX	XXX	XX	X
Shorthorn	XXXX	XX	XXXX	XXX	XX	XXX	X
Galloway	XX	XXX	XXX	XXX	XXX	XX	X
South Devon	XXX	XXX	XXXX	XXX	XX	XXX	X
Tarentaise	XXX	XXX	XX	XX	XX	XXX	X
Pinzgauer	XXXX	XXX	XXX	XXX	XX	XXX	X
Braunvieh	XXX	XXXX	XXX	XX	XX	XXXX	XX
Gelbvieh	XXXX	XXXX	X	XX	XX	XXXX	X
Holstein	XXXXX	XXXX	XXX	XX	XX	XXXXXX	X
Simmental	XXXXX	XXXX	XX	XX	XXX	XXXX	X
Maine Anjou	XXXXX	XXXX	XX	XX	XXX	XXX	X
Salers	XXXX	XXXX	XX	XX	XXX	XXX	X
Norwegian Red	XXXX	XXXX	XXX	XX	XX	XXXX	X
Swed. Red & White	XXXX	XXXX	XXX	XX	XX	XXXX	X
Friesian	XXXX	XXXX	XXX	XX	XX	XXXX	X
Piedmontese	XX	XXXXXX	X	XXX	XX	XX	XX
Belgian Blue	XXX	XXXXXX	X	XXX	XX	XX	X
Limousin	XXXX	XXXXX	X	XX	XXXX	X	X
Charolais	XXXXX	XXXXX	XX	XX	XXXX	XX	X
Chianina	XXXXX	XXXXX	XX	XX	XXXX	X	XX
Tuli	XX	XXX	XXX	XX	XXX	XXX	XXX
Romosinuano	X	XXX	XX	XX	XXX	XXX	XXX
Brangus	XXXX	XXX	XXX	XX	XXX	XXX	XXX
Beefmaster	XXXX	XXX	XX	XX	XXX	XXX	XXX
Bonsmara	XXX	XXX	XX	XX	XXX	XXX	XXX
Brahman	XXXX	XXXX	XX	X	XXXXX	XXXX	XXXX
Nellore	XXXX	XXXX	XX	X	XXXXX	XXX	XXXX
Sahiwal	XX	XXXX	XX	X	XXXX	XXXX	XXXX
Boran	XXX	XXX	XX	X	XXXX	XXX	XXXX

[a]Increasing numbers of X's indicate relatively higher value.

breed differences to improve efficiency of beef production. USDA, ARS, Technical Bulletin Number 1875. pp. 1-75.

Henderson, C. R. 1975. Biometrics 31:423.

Holloway, J. W., B. G. Warrington, D. W. Forrest, and R. D. Randel. 2005. Lifetime performance and efficiency of F1 tropically adapted beef cattle breeds X Angus in Semiarid rangeland. A Compilation of Research Results Involving Tropically Adapted Beef Cattle Breeds. Southern Coop. Ser. Bull. 405. pp.118-125. http://www.lsuagcenter.com/en/crops_livestock/livestock/beef_cattle/breeding_genetics/trpoical+breeds.htm

Koch, R. M., G. E. Dickerson, L. V. Cundiff, and K. E. Gregory. 1985. J.Anim. Sci. 60:1117.

Koch, R. M., L. V. Cundiff, K. E. Gregory, and L. D. Van Vleck. 2004. J.Anim. Sci. 82:668.

Koger, M., F. M. Peacock, W. G. Kirk, and J. R. Crocket. 1975. J.Anim. Sci. 40:826.

McDonald, R. P., and J. W. Turner. 1972. J. Anim. Sci. 35:1146.

National Pedigreed Livestock Council. 2005-2006. Annual Report, Directory & Career Opportunities. 177 Palermo Place, The Villages, FL 32159. USA. pp. 1-21.

Olson, T. A., K. Uuclides Filho, L. V. Cundiff, M. Koger, W. T. Butts, Jr., and K. E. Gregory. 1991. J. Anim. Sci. 69:104.

Peacock, F. M. and M. Koger. 1979. J. Anim. Sci.49: Suppl. 1.168.

Phillips, W. A., R. P. Wettemann, S. W. Coleman, and J. W. Holloway. 2005. Evaluation of Boran, Tuli Gelbvieh, and Brahman F1 crosses in Oklahoma. A Compilation of Research Results Involving Tropically Adapted Beef Cattle Breeds. Southern Coop. Ser. Bull. 405. pp. 6-15. http://www.lsuagcenter.com/en/crops_livestock/livestock/beef_cattle/breeding_genetics/trpoical+breeds.htm

Pollak, E. J. and R. L. Quaas. 1983. Prediction of Genetic Values for Beef Cattle. Workshop Proceedings. Beef Improvement Federation. Dec. 12-15, 1983. pp.58-69

Pollak, E. J., and R. L. Quaas. 2005. Multibreed genetic evaluations for beef cattle. Proc. Beef Improvement Federation 37th Annual Research Symposium and Annual Meeting. Billings, MT pp. 101-104. www.beefimprovement.com

Sanders, J. W., S. F. Cunningham, A. Ducoing, A. D. Herring, and D. K. Lunt. 2005a. Evaluation of the F1 crosses of Tulie, Boran, and Brahman with Herford and Angus for birth growth carcass, cow productivity, and longevity characteristics. A Compilation of Research Results Involving Tropically Adapted Beef Cattle Breeds. Southern Coop. Ser. Bull. 405. pp.126-130. http://www.lsuagcenter.com/en/crops_livestock/livestock/beef_cattle/breeding_genetics/trpoical+breeds.htm

Sanders, J. W., K. Key, D. Riley, and D. Lunt. 2005b. Evaluation of heterosis retention for cow productivity traits in Bos indicus/Bos taurus crosses. A Compilation of Research Results Involving Tropically Adapted Beef Cattle Breeds. Southern Coop. Ser. Bull. 405. pp.212-220. http://www.lsuagcenter.com/en/crops_livestock/livestock/beef_cattle/breeding_genetics/trpoical+breeds.htm

Southern Cooperative Series Bulletin. 405. A Compilation of Research Results Involving Tropically Adapted Beef Cattle Breeds. Southern Coop. Ser. Bull. 405. pp.1-227. http://www.lsuagcenter.com/en/crops_livestock/livestock/beef_cattle/breeding_genetics/trpoical+breeds.htm

Thallman, R. M., L. V. Cundiff, K. E. Gregory, and R. M. Koch. 1999. J. Anim. Sci. 77:2651.

Thrift, F. A. and T. A. Thrift. 2005. Rationale for evaluating alternative sources of subtropically adapted beef cattle germplasm. A Compilation of Research Results Involving Tropically Adapted Beef Cattle Breeds. Southern Coop. Ser. Bull. 405. pp.6-15. http://www.lsuagcenter.com/en/crops_livestock/livestock/beef_cattle/breeding_genetics/trpoical+breeds.htm

Turner, J. W., and R. P. McDonald. 1969. J. Anim. Sci. 29:389.

Utech, K. B. W., R. H. Wharton, and J. D. Kerr. 1978. Aust J. Agr. Res. 29:885.

Wheeler, T. L., L. V. Cundiff, R. M. Koch, and J. D. Crouse. 1996. J. Anim.Sci. 74:1023.

Wheeler, T. L., L. V. Cundiff, R. M. Koch, M. E. Dikeman, and J. D. Crouse. 1997. J. Anim.Sci. 75:2389.

Wheeler, T. L., L. V. Cundiff, L. D. Van Vleck, G. S. Snowder, M. D. Thallman, S. D. Shackelford, M. Koohmaraie. 2006. Germplasm Evaluation Program Progress Report No. 23. pp. 1-17. http://www.ars.usda.gov/Main/docs.htm?docid=6238