Breed and crossbreeding effects on marbling

Heather Burrow

CRC for Cattle and Beef Quality, CSIRO Livestock Industries

Box 5545, Rockhampton Mail Centre, Qld 4702

Telephone 61-7-4923 8139; Facsimile 61-7-4923 8184; Email Heather.Burrow@li.csiro.au

Abstract. The literature is reviewed to determine the effects of breeds and crossbreeding on body composition traits, with a particular emphasis on marbling and retail beef yield percentage. Breeds that are superior for retail beef yield percentage produce carcasses with low levels of marbling and *vice versa*. For both traits, the between-breed variation is larger than the within-breed variation. Individual and maternal heterosis for marbling and retail beef yield percentage is low, meaning that if the focus of the breeding program is primarily or exclusively for one of these traits, then within-breed selection using a high marbling or high yielding breed would be a better option than crossbreeding to achieve the objective. However, significant gains can be achieved for traits like growth and female fertility through use of crossbreeding and as these traits are critical to every beef production enterprise, they should not be ignored in any breeding objective. As well, crossbreeding can potentially benefit an objective targeting both marbling and retail beef yield through complementary blending of breed characteristics to reduce problems associated with genetic antagonisms between the traits.

Introduction

Australia is currently the world's largest beef exporter, but to maintain or increase share of the world beef trade, it must continue to produce high quality, contaminant-free beef. Maximising beef production means matching the genotype (breed) to the particular environment being used for production. Some genotypes have attributes that make them better suited to particular environments. However, in every environment, there are factors that limit beef production, which basically means that no one breed is going to be "best" in all environments. Genetic variation in both quantity and quality of beef is evident through differences between breeds and crossbreeds and between sires within a breed.

Australian beef breeders are faced with the challenge of using vastly diverse production environments and systems to produce cattle that are both productive and profitable and beef products that satisfy consumer requirements. To do this, they need knowledge of genetic and non-genetic influences on beef production and quality. One of the most powerful tools available to them is the use of crossbreeding and composite populations. The purpose of this paper is to summarise research results from crossbred and composite populations from studies mainly in North America and Australia, with the aim of defining the effects of crossbreeding on body composition traits, with a particular emphasis on marbling and retail beef yield. For completeness, all carcass and beef quality attributes are summarised in this paper. Although the focus of the review will be on body composition traits, other traits such as growth, female fertility and adaptation should not be ignored as they are greatly influenced by crossbreeding effects and economically, are critical to every beef production enterprise.

Measurement of body composition traits

One of the major difficulties faced by scientists studying carcass and beef quality attributes is the lack of consistency between studies in the definition of attributes such as marbling and retail yield and the use of different measurements for the same trait. This means that in many cases, it is almost impossible to validly compare results from one experiment with those from other, very similar experiments. By way of example, in Australian abattoirs that use the AUSMEAT scheme, carcasses are weighed with all internal fat depots removed and with some subcutaneous fat trimming allowed. Consequently, yield based on data using a different definition of carcass weight (e.g. early Australian data or data from overseas studies) will have systematic errors. For the purpose of this paper, definitions and measurements of carcass composition traits reported in this review are summarised below.

Marbling score

Visual assessment of the amount of intramuscular fat in the *m. longissimus dorsi*. Scoring systems vary markedly (e.g. in Australia, AUSMEAT scores range from 1 to 7 and are scored at a site between the 12th and 13th ribs; the USA system has 11 marbling grades scored between the 12th and 13th ribs, with each grade scored over a 100 point scale; the Japanese system uses 12 marbling scores scored between the 6th and 7th ribs - these scores are then condensed into 5 marbling grades.)

Intramuscular fat percentage

Chemically extracted fat percentage from a sample of the *m. longissimus dorsi* between the 12th and 13th ribs, using either near infra-red spectroscopy or Soxhlet extraction.

Retail beef yield

Yield of saleable meat expressed either as a weight (kg) or as a proportion of carcass weight (%). The measurement depends on the amount of fat trim e.g. in Australia, carcasses are generally trimmed to 3 mm of subcutaneous fat, whereas in many USA studies, carcasses are trimmed to 0 mm of fat. Variations of this trait are sometimes referred to in the literature as 'cutability' or 'retail product yield'.

Between-breed variation

Production in a temperate environment

No single cattle breed has all attributes that are needed to produce beef efficiently in all environments and to meet the requirements of all markets. Great variation exists between breeds in performance for both productive and adaptive traits. Hence, appropriate use of systematic crossbreeding programs provides significant benefits to beef producers, particularly through improved growth and female fertility, in both temperate (e.g. Cundiff and Gregory 1999) and tropical (e.g. Frisch 1997) environments. Numerous reports are available on the effects of crossbreeding on carcass and beef quality attributes in *Bos taurus* breeds of cattle reared in temperate environments. Many of these reports also include tropically adapted breeds in their comparisons. However, there are relatively few reports of breed and heterotic effects on carcass and beef quality attributes of tropically adapted cattle grazed at pasture in the tropics and subtropics.

Possibly the largest experimental crossbreeding program ever undertaken in temperate environments has been ongoing at the US Meat Animal Research Centre (MARC) in Nebraska since 1970. Results from the Germplasm Evaluation Program (GPE) at MARC provide evidence that genetic variation between breeds is similar in magnitude to genetic variation within breeds for many bioeconomic traits (Cundiff and Gregory 1999). Figure 1 shows the range of differences between- and within-breeds for retail beef yield percentage and USA marbling score. For both traits, the between-breed variation was larger than the within-breed variation. When carcass and beef quality traits are considered, breeds that are

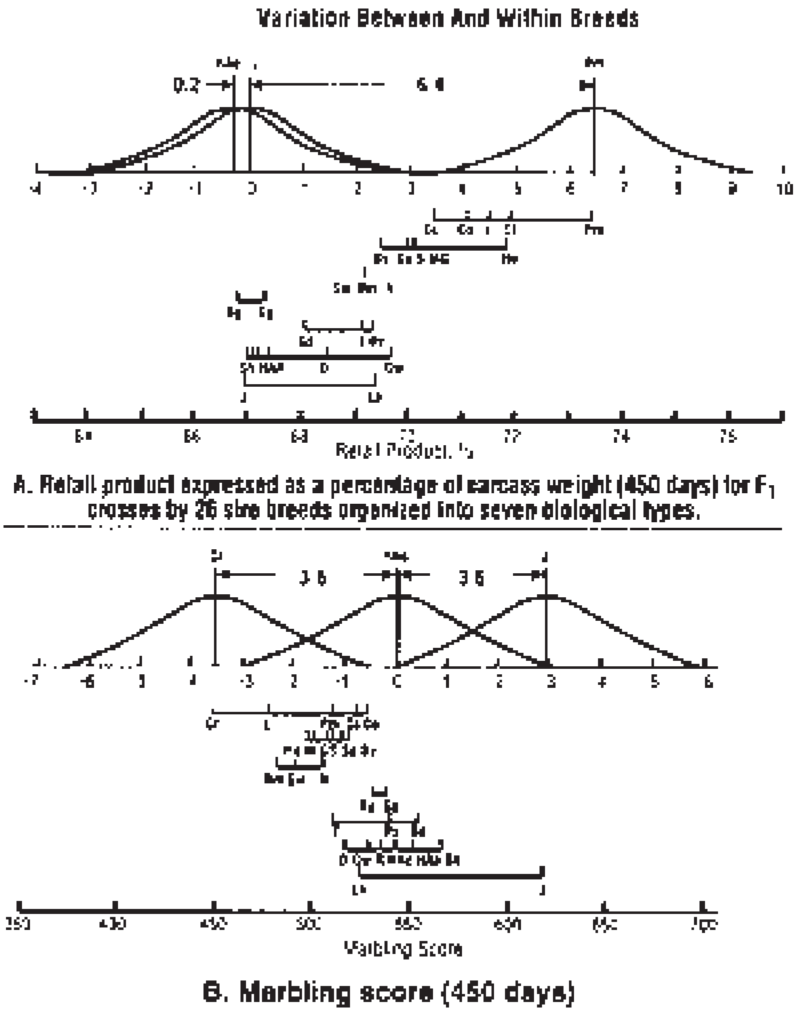

Figure 1. Variation between and within breeds for retail beef yield percentage and USA marbling score (for breed codes, see Table 1; source Cundiff and Gregory,

superior for retail beef yield percentage produce carcasses with low marbling scores.

Breed differences in body composition traits have been evaluated in numerous studies and were reviewed by Marshall (1994). Franke (1997) also reviewed carcass composition of subtropically adapted breeds in the USA. A schematic representation of breed differences in body composition and related traits from Cundiff and Gregory (1999) is presented as Table 1. Breed group rankings are shown for F_1 crosses grouped into 7 biological types based on relative growth rate and mature size, lean to fat ratio, age at puberty and milk production (Table 1).

Results for growth, carcass and beef quality attributes for steers produced in the Germplasm Utilisation Program (GPU) at MARC, as reported by Cundiff and Gregory (1999) are shown in Table 2. These data are for purebred steers produced contemporaneously over 4 calf crops between 1988 and 1991. Differences between breeds were significant and large for carcass and beef quality attributes. As expected, differences between pure breeds in the GPU program were about twice as great as differences between crosses in the GPE project that differ only in sire breed. Breed means for marbling were associated with breed means for tenderness, although this does not necessarily imply a cause and effect relationship. European breed steers excelled in retail product yield but had difficulty grading USDA Choice because of lower levels of marbling. British breeds excelled in USDA carcass quality grade due to their high levels of marbling, but had excessive fat thickness and percentage fat trim and reduced retail product yields.

Table 3 has been adapted from Cundiff and Gregory (1999) and Cundiff *et al.* (1999) and summarises results for sire breeds for crossbred progeny from Cycle 5 of the GPE project. Sire breed differences were large for final weight, carcass weight, fat thickness, marbling and beef yield traits (Tables 2 and 3). British breeds had significantly lower retail beef yield percentages than did the European breeds. Even though Limousin progeny had lower live weights than the average of Charolais, Simmental and Gelbvieh progeny, they did not differ from them in retail beef yield percentage because of their higher dressing percentage and lower carcass fat and bone percentages. Preliminary results indicate that Belgian Blue and Piedmontese had 5 to 9% higher retail yields than other sire

Table 1. Breeds grouped into biological types for four criteria (Source: Cundiff and Gregory, 1999; increasing number of +'s indicate relatively higher values)

Breed Group	Growth rate and mature size	Lean to fat ratio	Age at puberty	Milk production
Jersey (J)	+	+	+	+++++
Longhorn (Lh)	+	+++	+++	++
Hereford-Angus (HA)†	+++	++	+++	++
Red Poll (R)	++	++	++	+++
Devon (D)	++	++	+++	++
Shorthorn (Sh)	+++	++	+++	+++
Galloway (Gw)	++	+++	+++	++
South Devon (Sd)	+++	+++	++	+++
Tarentaise (T)	+++	+++	++	+++
Pinzgauer (P)	+++	+++	++	+++
Brangus (Bg)	+++	++	++++	++
Santa Gertrudis (Sg)	+++	++	++++	++
Sahiwal (Sw)	++	+++	+++++	+++
Brahman (Bm)	++++	+++	+++++	+++
Nellore (N)	++++	+++	+++++	+++
Braunvieh (B)	++++	++++	++	++++
Gelbvieh (G)	++++	++++	++	++++
Holstein (Ho)	++++	++++	++	+++++
Simmental (S)	+++++	++++	+++	++++
Maine Anjou (M)	+++++	++++	+++	+++
Salers (Sa)	+++++	++++	+++	+++
Piedmontese (Pm)	+++	++++++	++	+
Limousin (L)	+++	+++++	++++	+
Charolais (C)	+++++	+++++	++++	+
Chianina (Ci)	+++++	+++++	++++	+

AHA$_o$ denotes Hereford-Angus reciprocal crosses by original reference sires and HAc denotes Hereford-Angus reciprocal crosses by more current sires

Table 2. Means for weight, carcass and beef quality traits for steers of nine pure breed populations at the Meat Animal Research Centre, adjusted to average age of slaughter of 438 days (adapted from Cundiff and Gregory, 1999).

Breed	Number	Final weight (kg)	Carcass weight (kg)	Fat thick (mm)	Trimmed retail product: Retail yield (%)	Trimmed retail product: Fat trim (%)	Trimmed retail product: Bone (%)	Marbling score^A	USDA Choice (%)	Shear force (kg)	Sensory panel score^B: Tenderness	Sensory panel score^B: Juiciness	Sensory panel score^B: Flavour
Red Poll	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Hereford	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Angus	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Limousin	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Braunvieh	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Pinzgauer	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Gelbvieh	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Simmental	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Charolais	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

[A]Slight = 400-499, small = 500-599 etc.
[B]Scored: 1 = extremely tough, dry or bland to 8 = extremely tender, juicy or intense

breeds, with meat palatability similar to Angus and Hereford sire breeds (Table 3). However, <33% graded USDA Choice, due to their significantly reduced fat cover and marbling. Breed groups differed greatly in fat thickness and marbling score. British breeds were similar in marbling score and intramuscular fat percentage. Preliminary results indicate that tropically adapted Sanga (*Bos taurus sudafricanus*) cattle represented by the Tuli breed produce progeny with carcass and beef quality attributes more similar to progeny sired by British breeds (i.e. Hereford and Angus) than to progeny sired by *Bos indicus* breeds (i.e. Brahman and Boran). However, Tuli crosses had relatively low average daily weight gains. These results were subsequently confirmed in a separate experiment based in a southern USA

Table 3. Sire breed averages for final weight and carcass and beef quality attributes of steers representing Hereford, Angus and tropically adapted sire breeds in Cycle V of the germplasm evaluation at the Meat Animal Research Centre, adjusted to average age at slaughter of 447 days (adapted from Cundiff and Gregory 1999 and Cundiff *et al.* 1999).

Sire breed	Number	Final weight (kg)	Carcass weight (kg)	Fat thick (mm)	Dressing percent (%)	Marbling score^A	USDA Choice (%)	Number	Shear force (kg)	Sensory panel score^B: Tenderness	Sensory panel score^B: Juiciness	Sensory panel score^B: Flavour
Hereford	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Angus	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Average	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Brahman												
(Original)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
(Current)	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Average	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Boran	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Tuli	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Piedmontese	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
Belgian Blue	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]

[A]Slight = 400-499, small = 500-599 etc.
[B]Scored: 1 = extremely tough, dry or bland to 8 = extremely tender, juicy or intense

environment (Herring *et al.* 1996).

There were also significant differences between sire breeds for percentage of carcasses grading USDA Choice and for objective measures of tenderness (Warner Bratzler shear force) and sensory panel tenderness (Tables 2 and 3). In all cycles of the GPE project, breed differences for sensory juiciness and flavour were of little practical importance, but there were significant differences between breed types for tenderness. Cattle of high *Bos indicus* content had lower marbling scores at a given age and produced less tender and more variable steaks than *Bos taurus* breeds (Koch *et al.* 1982; Crouse *et al.* 1989; DeRouen *et al.* 1992; Wheeler *et al.* 1994; Barkhouse *et al.* 1996.) Some early breed comparison studies have been criticised on the basis of failure to control processing factors that may lead to cold shortening, which results in tougher meat, particularly in leaner and lighter breeds. However, studies that tightly controlled processing factors to ensure differential responses in cold shortening did not occur (e.g. Johnson *et al.* 1990) also reported that high *Bos indicus* content carcasses had tougher meat than *Bos taurus* and low *Bos indicus* content carcasses, indicating that genuine breed differences exist with respect to beef toughness.

A strong antagonism was evident between marbling score and beef yield percentage between the breed groups. Breed and biological type rankings that were developed for growth, carcass and beef quality attributes from the crossbreeding experiments at MARC also generally apply to results from elsewhere, based on similar breed types of cattle reared in other temperate environments throughout the world. Small differences occur in sire breed rankings, depending on the end point of production (age, weight, marbling, fat thickness and fat trim end points).

These results have been confirmed in recent Australian crossbreeding studies based in temperate environments. The "Southern Crossbreeding Project" was conducted at Struan Research Centre, Naracoorte, South Australia and various commercial feedlots (Pitchford *et al.* 2001). The aim of the project was to characterise between- and within-breed genetic variation for production, carcass and meat quality traits. Sires of 7 biologically diverse breed types were joined to Hereford females. Least squares means for a number of fatness traits are shown by sire breed in Table 4. A unique component of this study was the identification of the melting point of fat for the various sire breed groups. The melting point of fat is a reflection of the fatty acid composition and hence, affects flavour as well as the ease of trimming of the carcass. A lower melting point reflects a greater level of unsaturation of the fat and this is desirable. Highly marbled Jersey and Wagyu crossbred cattle had softer fat (6% lower melting point) than the other breeds (Pitchford *et al.* 2001). Angus crosses marbled like Jersey and Wagyu, but had harder fat similar to the very lean Belgian Blue.

Production in tropical and subtropical environments

Results from tropical and subtropical environments are less precise, partly due to the paucity of experimental evidence from these environments and from some breed types, but also because resistance of individuals to environmental stressors has a significant impact on growth rate and hence body composition, beef quantity and possibly beef quality. Genotype x environment (GxE) interactions are very important in tropical and subtropical environments, and have a major impact on breed and breed type rankings for some traits (for example, see Frisch and Vercoe 1984).

For most purposes in the tropics and subtropics, breeds can be categorised into several general groupings, as has been

Table 4. Least squares mean carcass weight, P8 rump fat depth, fat colour score, intramuscular fat percentage and fat melting point by sire breed, derived from the "Southern Crossbreeding Project" (Source: Pitchford *et al.* 2001).

Sire breed	Carcass wt (kg)	P8 fat depth (mm)	Fat colour (score)	Intramuscular fat (%)	Melting point (°C)
Jersey	236 ±3	10.7 ±0.4	1.0 ±0.1	4.8 ±0.2	37.1 ±0.3
Wagyu	244 ±3	11.8 ±0.4	0.5 ±0.1	4.5 ±0.1	37.8 ±0.3
Angus	283 ±3	14.3 ±0.6	0.5 ±0.1	4.6 ±0.2	39.4 ±0.4
Hereford	268 ±3	12.0 ±0.6	0.4 ±0.1	3.7 ±0.2	40.0 ±0.4
South Devon	284 ±3	9.8 ±0.4	0.5 ±0.1	3.8 ±0.2	40.3 ±0.3
Limousin	278 ±3	9.9 ±0.4	0.4 ±0.1	3.1 ±0.2	40.2 ±0.3
Belgian Blue	289 ±3	8.0 ±0.4	0.6 ±0.1	3.0 ±0.2	39.3 ±0.3

done for breeds in temperate areas. Even though in temperate areas there may be substantial differences in performance between breeds within the general groupings, in tropical and subtropical areas differences in performance tend to be masked, due to the effects of environmental stressors. The broad breed groupings are outlined in detail in MRC (1997) and performance attributes for the breed groupings, adapted from Frisch (1997) and MRC (1997), are shown here as Table 5. Representative breeds from the various breed groupings shown in Table 5 include Hereford, Angus and Shorthorn (British); Charolais, Simmental and Limousin (European); Africander, Tuli and Mashona (Sanga); Brahman, Sahiwal, Nellore (Indian zebu); and Boran (African zebu). In Table 5, relative performance for growth and fertility traits is compared within temperate and tropical environments.

From Table 5, British and European breed groups have the best growth and fertility rates of the pure breeds in temperate environments. In tropical environments though, they are unable to express the same levels of performance, due to their poor resistance to ticks, worms, disease, heat and drought (Table 5). Poor levels of adaptation to environmental stressors are also believed to be responsible for changes in breed rankings for meat tenderness in extreme environments, as reported by Pratchett *et al.* (1988). In that study, purebred Shorthorn steers had tougher beef than purebred Brahman steers, as rated by consumer taste panels on a scale of 1 = very tough to 6 = very tender (values = 2.94, 3.05, 3.21 and 3.60 for Shorthorn, Brahman, Brahman x Shorthorn and Africander x Shorthorn respectively). Because Shorthorn cattle were poorly adapted to the harsh dry tropical climate of the Kimberley region, their growth rates were substantially lower than those of the remaining breeds. Hence, it is likely that GxE interactions for growth rate, although unable to be tested by the experimental design, may have had a significant impact on meat quality. The results have serious implications for beef producers in northern Australia, as they very clearly demonstrate that to achieve eating quality specifications, cattle bred in these areas must not only be genetically able to meet market requirements but also need to be well adapted to environmental stressors. In most environments, the most productive breed group is the F_1 hybrid between *Bos indicus* and *Bos taurus*, indicating that significant production benefits accrue from crossbreeding.

Franke (1997) reviewed the literature to evaluate the Brahman and alternative subtropically adapted breeds to determine whether these breeds would be useful in improving the proportions of carcasses meeting market specifications with respect to yield grade and tenderness in the southern states of the USA. Several alternative sub-tropically adapted breeds seemed to have an advantage in one or two carcass traits over Brahman-sired steers when all were joined to Angus and Hereford dams, but no clear overall advantage was suggested. Brangus, Santa Gertrudis, Boran, Nellore and Tuli sire breeds had an advantage over Brahman sires for marbling. However, the Brahman-sired steers (F_1 *Bos indicus* x *Bos*

Table 5. Comparative rankings of different breed groups for productive traits in temperate and tropical environments and for adaptation to stressors of tropical environments (adapted from Frisch, 1997 and Meat Research Corporation, 1997; the higher the number of +'s the higher the value for the trait).

Breed group	Temperate area[A]		Tropical area[A]				Resistance to environmental stressors				
	Growth	Fertility	Growth	Fertility	Mature size	Meat quality[B]	Cattle ticks[C]	Worms[D]	Eye disease	Heat	Drought
Bos taurus											
British	++++	+++++	++	++	++++	+++++	+	+++	++	++	++
European[E]	+++++	++++	++	++	+++++	+++++	+	+++	+++	++	+
Sanga	+++	++++	+++	++++	+++	+++++	++++	+++	+++	+++++	+++++
Bos indicus											
Indian zebu	+++	+++	++++	+++	++++	+++	+++++	+++++	+++++	+++++	+++++
African zebu	++	++++	++	++++	+++	++++	+++++	++++	++++	+++++	+++++
F_1 *Bos indicus* x *Bos taurus*	++++	+++++	++++	+++++	++++	++++	++++	++++	++++	+++++	++++

[A]Temperate area environment is assumed to be an environment free of environmental stressors, whereas rankings shown for tropical environment apply to an environment where all environmental stressors are operating. Hence, whilst a score of +++++ for e.g. fertility in a tropical environment indicates that breed group would be expected to have the highest fertility in that environment, the actual level of fertility may be less than the actual level of fertility for breeds reared in a temperate area, due to the effect of environmental stressors that reduce performance.

[B] = Principally meat tenderness

[C] = *Boophilus microplus*

[D] = specifically, *Oesophagostomum, Haemonchus, Trichostrongylus* and *Cooperia* spp.

[E] = Data from purebred European breeds not available in tropical environments and responses predicted from the Tropical Beef Centre model *taurus*) were superior to most of these breeds for slaughter weight. The results of the review indicated that several alternative subtropically adapted breeds could be joined to British-breed dams to produce progeny whose carcasses would have increased marbling and higher carcass quality grades. However, those same carcasses would also weigh less at slaughter and have lower carcass weights. Thus, there seems to be a trade-off in choices of breeds that have some adaptation to subtropical environments, where environmental conditions are benign enough to allow use of British breed dams. The choice of breed or breeds should include an evaluation of other traits such as fertility and maternal ability, rather than carcass characteristics alone (Franke 1997).

In harsher tropical environments than those reviewed by Franke (1997), dam breeds must also have some degree of tropical adaptation. Hence, use of British breed dams is not feasible in those environments, from either a productive or an economic perspective. To achieve maximum heterosis in harsh tropical environments, use of *Bos indicus* dams joined to *Bos taurus* sire breeds to generate F_1 progeny is the preferred option. The CRC for the Cattle and Beef Industry (Meat Quality) established a terminal sire crossbreeding experiment in Central Queensland in 1995. The program was based on 1,000 high grade Brahman cows, joined to 7 sire breeds representing British (Hereford, Angus, Shorthorn), European (Charolais, Limousin), Brahman-derived (Santa Gertrudis, Charbray), Sanga-derived (Belmont Red) and purebred Brahman. Preliminary results were reported by Newman *et al.* (1999a,b) and are cited herein. Results of the most recent analyses of the CRC crossbreeding data will be presented at the Marbling Symposium.

Preliminary results showed there were significant breed of sire differences for all carcass and meat quality attributes except for ultimate pH in steers and heifers, for cooking loss in heifers and instron compression in steers and heifers. Table 6 shows the effects of sire breed on age at slaughter and carcass and meat yield attributes in steer and heifer progeny. In both steers and heifers, European breed sires (Charolais and Limousin) produced progeny that had heavier, leaner, higher-yielding carcasses than the remaining crosses. In steers, progeny of Santa Gertrudis and Angus sires had the highest subcutaneous fat cover and lowest yields. In heifers, progeny of Hereford sires had highest P8 fat depths and lowest yields, whilst progeny of Limousin sires had the lowest fat cover and highest yield of all the crosses. Over all steers, progeny of Charolais sires produced carcasses that were 21% heavier than purebred Brahman controls. There was a similar margin in carcass

Table 6. Effects of sire breed on age at slaughter and carcass and meat yield attributes in steers and heifers. Except for hot carcass weight, which is unadjusted, all means are adjusted to a common carcass weight within market endpoint (domestic, Korean or Japanese).

Sire Breed	No animals	Age at slaughter (days)	Carcass wt. (kg)	P8 fat depth (mm)	Eye muscle area (cm²)	Retail beef yield (%)	Retail primals (kg)
Steer Progeny							
Angus	23	714	295	11.8	75.3	66.1	66.5
Belmont Red	77	696	282	11.6	76.7	66.5	67.5
Brahman	78	705	250	10.8	76.3	66.6	67.2
Charolais	17	698	302	9.3	80.8	67.3	68.7
Hereford	20	717	290	10.5	76.2	66.8	67.8
Limousin	39	698	300	9.3	82.1	68.5	69.6
Santa Gertrudis	33	720	274	12.9	75.4	65.9	66.6
Shorthorn	15	702	289	10.8	79.3	66.0	66.5
Heifer Progeny							
Angus	22	671	266	15.7	71.0	65.3	58.2
Belmont Red	75	652	236	14.3	69.5	65.7	59.1
Brahman	93	670	214	14.5	68.6	65.7	59.3
Charolais	23	664	268	12.6	70.8	66.5	60.3
Hereford	26	658	271	15.9	65.7	64.6	58.0
Limousin	40	670	259	11.5	74.6	67.7	61.0
Santa Gertrudis	50	670	245	15.4	68.9	65.6	58.9
Shorthorn	18	671	260	15.6	69.2	65.5	58.6

weights of heifer progeny of both Hereford and Charolais sires relative to Brahman heifers. Differences between breeds in age at slaughter at younger ages partly reflect differences between AI and natural mate sires, as not all breeds were able to provide bulls for natural and backup mating following AI. Differences between ages at slaughter at different market endpoints also reflect differences in growth rate between for example, progeny of different sire breeds.

Table 7 shows the effects of sire breed on intramuscular fat percentage (marbling) and measures of meat tenderness in steers and heifers. Angus, Belmont Red and Shorthorn sires consistently produced progeny with the highest intramuscular fat percentages. Based on all indicators of meat toughness (cooking loss, ultimate pH, shear force and instron compression), purebred Brahman sires produced progeny with the toughest meat. Average shear force values in both steers and heifers were above the acceptable values for tenderness, indicating that consumers would deem a high proportion of Brahman carcasses unacceptably tough. Sire breed differences in instron compression were not as evident as in other indicators of toughness. Instron compression is believed to be a better indicator of toughness due to collagen content than shear force measures, suggesting that collagen content is not an issue with respect to toughness in these animals, although all animals in this dataset were less than 2.5 years of age at time of slaughter.

Implications of breed differences for commercial production systems

For traits with large breed differences, such as retail beef yield and marbling, selection of the proper breed should be done before selection within the breed. Breed effects were important in ranking for breeding value for most of the carcass and beef quality traits. Separate evaluations for breed or breed type, followed by within-breed selection may be an effective approach for genetic improvement in systematic crossbreeding

Table 7. Effect of sire breed on intramuscular fat percentage (IMF%), cooking loss, ultimate pH, shear force and instron compression in steer and heifer progeny. All means are adjusted to a common carcass weight within market endpoint (domestic, Korean or Japanese).

Sire breed	No. animals	IMF (%)	Cooking loss (%)	Ultimate pH	No. animals	Shear force (kg)	Instron compression (kg)
Steer Progeny							
Angus	23	2.66	22.5	5.57	14	4.58	1.72
Belmont Red	77	2.62	22.7	5.55	47	4.78	1.70
Brahman	78	1.95	23.7	5.55	50	5.89	1.81
Charolais	17	1.98	22.8	5.57	11	4.90	1.79
Hereford	20	2.41	22.0	5.58	11	4.64	1.84
Limousin	39	1.89	22.5	5.56	24	4.63	1.75
Santa Gertrudis	33	1.96	23.1	5.56	22	5.01	1.80
Shorthorn	15	2.62	21.3	5.59	10	4.76	1.73
Heifer Progeny							
Angus	22	3.35	21.9	5.56	21	4.54	1.77
Belmont Red	75	2.74	22.4	5.54	71	5.11	1.79
Brahman	93	2.16	22.8	5.57	85	5.90	1.86
Charolais	23	2.22	22.8	5.56	20	5.12	1.87
Hereford	26	2.52	22.6	5.55	25	4.53	1.78
Limousin	40	2.12	22.1	5.57	37	5.03	1.84
Santa Gertrudis	50	1.84	22.6	5.55	49	4.93	1.82
Shorthorn	18	3.23	21.9	5.55	18	4.83	1.72

programs. For many traits such as beef tenderness and palatability, between-breed differences may be more easily exploited than within-breed differences because exceptional breeds are easier to identify than exceptional animals. However, the effects of environmental factors on these traits must not be overlooked in any genetic improvement programs targeting beef quality.

Estimates of heterosis

Crossbreeding generates hybrid vigour or heterosis. Heterosis is defined as the difference between the average of reciprocal first crosses (for example, F_1 A x B and B x A) and the average of the two parental breeds (A and B) mated to produce the reciprocal crosses. Heterosis can be either favourable (e.g. increased calving rates of F_1 Brahman x British breed cows relative to the average calving rates of Brahman and British parental breeds) or unfavourable (e.g. increased calf mortalities that result directly from increased birth weights of F_1 Brahman x British calves out of British breed dams, compared to the average calf mortalities experienced by straightbred Brahman or British breed cows).

In general, heterosis and heritability (the degree to which a trait is under genetic control) are inversely related. Hence, greatest heterosis is achieved for traits that are the least heritable (e.g. female fertility, survival, longevity and for combinations of traits, such as weight of calf weaned per cow joined.) Heterosis can be defined as that due to the individual or that due to the effect of using crossbred dams. Heterosis is caused by nonadditive effects of genes such as dominance and epistasis and can be seen through individual animal and maternal effects on the trait. Complete dominance exists when one copy of an allele at a single location on paired chromosomes has a similar effect on performance as two copies. Epistasis results from similar interactions involving combinations of genes at two or more locations in the genome.

Estimates of heterosis averaged over diallel crossing experiments for a number of traits and from many studies throughout the USA were summarised by Cundiff and Gregory (1999). Heterosis effects were greatest for traits such as longevity, reproduction rate and lifetime production. Effects of heterosis on carcass and beef quality characteristics in all studies were relatively small (3% or less). In general, heterosis observed for carcass attributes was through heterotic effects on weight. When data were adjusted for differences in carcass weight, heterotic effects on carcass composition were not observed (Cundiff and Gregory 1999). Under subtropical conditions in the USA, and possibly under temperate conditions, *Bos indicus* x *Bos taurus* crosses had higher levels of heterosis than those reported for corresponding traits between *Bos taurus* crosses. Maternal effects were generally not important for carcass and beef quality attributes (Gregory *et al.* 1978; Johnston *et al.* 1992; Cundiff and Gregory 1999).

Estimates of individual and maternal heterosis for specific carcass and beef quality attributes were summarised by Marshall (1994) and are shown here as Table 8. The estimates were expressed as percentages of purebred means and were averaged across specific crosses within a study and then averaged across studies for a particular trait. Therefore, several of the values shown in Table 8 represent mean heterosis levels across many different breed crosses. The estimates were from studies where days fed or calf age was a slaughter end point or statistical covariate, meaning that the estimates retain some effects of carcass weight. Individual heterosis

Table 8. Individual and maternal heterosis estimates (% of straightbred mean) for carcass traits, averaged across breed-crosses and studies from crosses of *Bos taurus* x *Bos taurus* and *Bos taurus* x *Bos indicus* (age- or time-in-feedlot-constant basis; adapted from Marshall 1994; values are simple numerical unweighted averages).

Trait	Number of studies^	Individual heterosis (%)	Maternal heterosis (%)
Carcass weight	12 (4)	6.5	3.6
Marbling	7 (2)	3.8	-1.1
Fat depth	11 (4)	10.1	8.9
Longissimus muscle area	9 (3)	4.1	3.3
Retail product weight	2 (1)	6.6	2.2
Estimated retail product %	7 (1)	-0.6	-2.5
Fat trim %	1 (1)	6.3	12.7
Shear force	2 (1)	-6.7	0
Dressing percentage	3	-0.2	

Number in parentheses is for maternal heterosis (hm) estimates for carcass weight were consistently positive in all studies. Individual heterosis estimates were relatively large (average 10.1%) for fat thickness but tended to be relatively small in magnitude for most other carcass traits. Individual heterosis for marbling and retail beef yield percentage was 3.8% and -0.6% respectively, while maternal heterosis for the same traits was -1.1% and -2.5% respectively. Maternal heterosis estimates were generally positive and relatively large for fatness traits but tended to be small to moderate for other carcass traits (Marshall 1994).

Estimates of heterosis for fatness and other carcass attributes on a weight-constant basis tended to be much smaller than estimates of heterosis for the same characteristics on an age-constant basis (Gregory *et al.* 1978; Johnston *et al.* 1992), reflecting a faster maturing rate for crossbred animals. If cattle are marketed on a weight endpoint, then the contribution of individual heterosis to increased fatness or retail beef yield percentage is likely to be small.

There is only a single known study that estimated the effects of heterosis on carcass attributes in tropically adapted cattle reared in tropical environments. No studies have estimated these effects for meat quality attributes in cattle reared in the tropics. Thorpe *et al.* (1980) compared Africander, Angoni, Barotse and Boran breeds and reciprocal crosses of the latter three breeds in Zambia. For all carcass characters except those related to size, the Sanga breeds (Africander and Barotse) were very similar, as were the two zebu breeds (Angoni and Boran). Maternal effects were not important for carcass characters and the Angoni x Barotse and Angoni x Boran crosses showed no heterosis for any carcass attribute. Heterosis estimates in the Barotse x Boran crosses for slaughter and carcass weights and eye muscle area were between 8% and 9.5%, and for linear carcass measurements between 2% and 3%. These results indicate that heterosis for carcass attributes in tropically adapted cattle reared in the tropics may also be generally limited to carcass characters associated with weight, as is the case for cattle reared in temperate environments.

Although heterosis effects do not significantly improve carcass composition or beef quality, crossbreeding can potentially benefit these traits through increased growth rates and also through complementary blending of breed characteristics to reduce problems associated with genetic antagonisms between traits such as retail beef yield and marbling.

Relationship between breed means for marbling and tenderness

Marbling scores are regularly included in beef grading schemes as putative indicators of beef tenderness. The putative relationship between marbling and beef tenderness is reinforced by crossbreeding studies that clearly show that *Bos indicus* breeds, which have low marbling scores relative to British breeds, also tend to have tougher meat. However, Dikeman (1987) reviewed the literature to examine this relationship and reported that marbling accounted for only 5-10% of the variability in beef palatability. Since then, numerous studies have examined the relationships between marbling and tenderness, at both the genetic and phenotypic level, as part of an ongoing debate about the role of marbling in meat grading schemes.

Shackelford *et al.* (1994) conducted one of the largest studies on the relationship between marbling score and beef tenderness, based on 1,602 carcasses from 9 pure breeds and 3 composite populations finished on medium- and high-energy diets. Although their report indicated statistically significantly effects of marbling on objective and sensory tenderness scores, marbling score accounted for less than 10% of the variation in shear force value and sensory tenderness, juiciness and beef flavour intensity scores (simple correlation coefficients between these attributes being -0.32, 0.26, 0.26 and 0.10 respectively). It was concluded that, although degree of marbling accounted for only a low percentage of the variation in tenderness, it did provide a slight assurance of tenderness, juiciness and flavour.

Wheeler *et al.* (1994) reported small, positive associations between marbling score and palatability in beef from both *Bos taurus* and *Bos indicus* breeds. Shear force, taste panel tenderness rating and taste panel juiciness rating improved slightly and variation in shear force values decreased slightly as marbling increased in beef from both *Bos taurus* and *Bos indicus*. However, marbling explained at most, 5% of the variation in palatability traits. There was a large range in tenderness within each marbling score, indicating there could be a large amount of both tough and tender beef within each marbling score.

Future developments and recommendations

Differences between breeds for carcass and beef quality attributes are well documented in the scientific literature and, in general, there would be little justification for additional research in this area. An exception to this generality is an ongoing need to describe the carcass and beef quality attributes of some tropically adapted indigenous breeds in Africa and South America, to determine their potential role as partial or complete replacements for *Bos indicus* genotypes in harsh production environments where resistance of cattle to environmental stressors is paramount, but where market specifications demand tender and palatable beef and in future, are also likely to require an increased degree of marbling than is currently produced by the majority of tropically adapted breeds.

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