



Beef cattle genetic improvement research at the INIFAP: accomplishments, challenges and perspective



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Abstract:

The National Institute of Forestry, Agricultural and Livestock Research in Mexico has been active for decades in researching genetic improvement in beef cattle. This review uses master theses, congress papers and scientific articles published from 1987 to 2020 to summarize much of the relevant research, and addresses research challenges and outlook over the short-, medium- and long-term in this area. Research done over the last 34 yr has evaluated the productive and reproductive performance of *Bos indicus* and *Bos taurus* x *Bos indicus* beef cattle raised under tropical conditions. Multibreed genetic evaluations have been done for Simmental-Simbrah and Charolais-Charbray populations in Mexico. Analyses have

quantified the importance of maternal effects on growth traits, and estimated heritability and genetic correlations for growth and reproductive traits in male and female *Bos taurus* and *Bos indicus* animals. The genotype-environment interaction has been confirmed to influence expression of weaning weight in Simmental cattle. Age adjustment factors have been developed for maternal age for weights at birth and weaning, and prototypes of national genetic evaluation were developed for stayability and heifer fertility. Genetic diversity has been quantified for Simmental, Charolais and Simbrah populations, and SNPs identified that are associated with growth traits in Simmental and Simbrah populations. Short-term goals include development of selection indices and prediction of the genetic merit of carcass traits. Over the medium-term, emphasis is needed on genomic evaluations for tolerance to heat stress, residual feed intake and health traits, while in the long-term the goal is to make inter-breed genomic predictions.

Key words: Genomic association, Beef cattle, Genetic correlations, Crossbreeding, Genetic diversity, Heritability, Genetic improvement.

Received: 27/11/2020

Accepted: 29/03/2021

Introduction

In beef cattle production, crossbreeding is intended to utilize breed differences and heterosis effects to improve production outcomes. Heterosis in a crossbreeding program can increase cattle herd productivity by an estimated average of 26 % compared to a similar program using purebred animals. The greatest benefit occurs with the use of crossbred cows^(1,2,3). How much productivity increases from crossbreeding depends on the breeds involved. In the early 1980s, cattlemen in Mexico did not use crossbred cows to produce calves at weaning and the availability of specialized breed bulls was limited, especially in tropical regions. In 1978, the National Institute of Artificial Insemination and Animal Reproduction, of what was then the Ministry of Agriculture and Hydraulic Resources, a federal institution, made semen available from *Bos taurus* breeds specialized in beef production (Angus, Chianina, Charolais, Hereford, Limousin, Simmental and European Brown Swiss)⁽⁴⁾.

Genetic improvement of livestock involves selection of above-average animals to function as parents to subsequent generations. Identification of genetically superior animals as parents of the next generation requires breed associations to integrate their respective databases such that national-level genetic evaluations can be done. The first national genetic evaluation of

beef cattle was done in 2001 by a group of researchers from the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias (INIFAP; National Institute of Forestry, Agricultural and Livestock Research), using the database of the Asociación Mexicana Simmental-Simbrah (AMSS). The INIFAP has since entered into agreements with other associations to allow use of their databases for research purposes.

Evaluation of growth traits can usually be done using conventional genetic evaluations. However, measuring economically important traits such as reproductive performance, feed efficiency and carcass traits can be complex, difficult and/or expensive. Sequencing of the bovine genome has made evaluation of these traits more accessible. Arrays have been developed containing thousands of single nucleotide polymorphisms (SNPs), which allow research into prediction of genetic merit⁽⁵⁾.

The present review summarizes research done at the INIFAP on genetic improvement of beef cattle, as well as the challenges and research perspectives over the short-, medium- and long-term.

Results of *Bos taurus* x *Bos indicus* crosses at Las Margaritas Experimental Station, in a humid hot subtropical climate Af(c)

One study evaluated the reproductive performance to weaning of Zebu (Z) cows mated to sires from four *Bos taurus* (Bt) breeds [Angus (A), Charolais (Ch), Hereford (H) and Brown Swiss (S)], and two *Bos indicus* (Bi) breeds [Brahman (B) and Indubrasil (I)]. When mating was done in spring, weaning rate of cows mated to H (64.3%), B (60.7 %) and S sires (59.2 %) was highest, that of cows mated to A (56.1 %) and Ch sires (52.7 %) was intermediate, and that of cows mated to I sires (39.5 %) was lowest. When mating occurred in autumn, however, weaning rate of cows mated to H sires (72.4 %) was highest, that of cows mated to S sires (56.0%) was intermediate, and that of cows mated to Ch (55.9 %), I (49.8 %), A (44.9 %) and B sires (43.0 %) was lowest. In general, weaning rate of cows mated to B and I sires was 16.5 and 23.7 percentage units lower than that of cows mated to H sires. These results indicate that bull breed and mating season are important considerations when designing crossbreeding schemes for commercial production of weaned calves⁽⁶⁾.

Another study analyzed breeding data that included I and B cows, as well as F1 A x Z, H x Z, Ch x Z and S x Z cows. The F1 cows (except the Ch x Z) exhibited reproductive behavior from gestation to weaning that surpassed that of the I and B cows (Table 1). The weaning rate of F1 cows was 26 percentage units higher than that of Z cows, and calf weaning weight (WW) of F1 cows was 5.9 % higher than that of Z cows; in terms of kilograms of calf weaned

per cow exposed the overall advantage was 30.6 %. The F1 heifers also first calved at a younger age (17 mo on average) than the Bi heifers⁽⁷⁾.

Table 1: Least square means for productivity parameters in F1 *Bos taurus* x *Bos indicus* cows crossed with *Bos taurus* bulls, and Zebu cows crossed with *Bos indicus* bulls

Cow genetic group	PR[¥] (%)	CR[¥] (%)	WR[¥] (%)	LP* (kg)	WW210[‡] (kg)	TMP[‡] (kg)	ST2[▯] (%)	ST5[▯] (%)
Hereford x Zebu	82.0 ^a	81.0 ^a	73.0 ^a	738.8 ^{ab}	164.0 ^{bc}	1008 ^b	92.0 ^b	47.0 ^b
Brown Swiss x Zebu	79.0 ^a	76.0 ^{ab}	73.0 ^a	667.9 ^{bc}	185.0 ^{ab}	1256 ^a	75.0 ^{ac}	42.0 ^b
Charolais x Zebu	65.0 ^b	67.0 ^{abc}	61.0 ^{ab}	777.3 ^a	178.0 ^c	1012 ^b	92.0 ^b	55.0 ^{bc}
Angus x Zebu	85.0 ^a	80.0 ^a	74.0 ^a	871.8 ^a	191.0 ^a	1454 ^a	84.0 ^{ab}	62.0 ^c
Brahman	67.0 ^b	65.0 ^{bc}	56.0 ^b	521.1 ^c	113.0 ^d	902 ^b	66.0 ^a	32.0 ^a
Indubrasil	66.0 ^b	56.0 ^c	48.0 ^b	---	---	---	---	---

PR= Pregnancy rate; CR= Calving rate; WR= Weaning rate; LP= Lifetime productivity; WW210= Weaning weight adjusted to 210 d of age; TMP= Total milk production; ST2= Stayability at second parturition; ST5= Stayability at fifth parturition.

[¥]Cows were crossed with bulls of the same breed as cow's father (Ríos *et al*⁽⁷⁾).

*Vega *et al*⁽⁹⁾.

[‡]Quiroz-Valiente *et al*⁽¹¹⁾.

[▯]Vega *et al*⁽¹⁰⁾.

^{a,b,c,d} Different letter superscripts in the same column indicate difference ($P < 0.05$).

A study of the causes of culling and productive life found that Bi cows were culled at an average of 66.2 % due to infertility, which is much more than the 17.9 % in F1 cows. Clearly, F1 cows had longer productive life than Bi cows; the higher stayability of the F1 cows allowed them greater reproductive capacity since the differences in mortality and maternal ability were not notable. Overall, F1 cows lived 2.8 yr longer than purebred Bi cows⁽⁸⁾.

Other studies have evaluated lifetime productivity (LP) and stayability (ST) at different ages in B and F1 A x Z, S x Z, Ch x Z and H x Z cows^(9,10). Lifetime productivity was defined as cumulative weaning weight of calves weaned up to 9 yr of age per cow exposed, while ST was defined as the probability that a cow would have 2 (ST2), 3 (ST3), 4 (ST4) or 5 (ST5) calves, given that she had first calved before 3 yr of age. As part of these studies, B cows were mated to B bulls, while F1 cows were mated to Bi bulls from 1986 to 1989 and to Bt bulls from 1990 to 1994. In terms of LP, the F1 cows surpassed the B cows by 101.2 kg at 3 yr of age and by 242.9 kg at 9 yr of age; indeed, at 9 yr of age both the A x Z and Ch x Z cows had accumulated significantly more kilograms of weaned calf than the S x Z and B cows (Table 1)⁽⁹⁾. In relation with ST, important differences were found in ST2; average ST2 for Ch x Z and H x Z cows was 92 %, while that for B and S x Z cows was 65.5 %. Similarly, significant differences were also found in ST5; A x Z cows had greater ST5 than B cows (62

vs 32 %), with intermediate values for the Ch x Z, H x Z and S x Z cows (Table 1). The study showed that the F1 Bt x Bi cows were more likely to produce more calves than the B cows⁽¹⁰⁾. Both studies confirm F1 cows as an option for increased productivity to weaning in cow-calf systems in the tropics of Mexico. Another study evaluated milk production in B cows and four F1 Bt x Bi breed group cows and how it correlated to calf WW. Milk yield was measured using the calf weighing technique before and after suckling. A correlation coefficient of 0.61 was observed between total milk yield (TMY) and WW adjusted to 210 d of age (WW210), and A x Z and S x Z cows were found to have higher TMY and calves with higher WW210 than Ch x Z, H x Z and B cows (Table 1)⁽¹¹⁾.

Results of *Bos taurus* x *Bos indicus* crosses at the El Macho Experimental Station in a subhumid hot tropical climate Aw₁

One study evaluated the differences in productive performance of F1 Bt x Bi and Bi calves in terms of birth weight (BW), pre-weaning average daily weight gain (DWG) and WW adjusted to 232 d of age (WW232). The calves were the product of crosses between Z cows and Ch, Chianina (Ci), Limousin (L), Simmental (Sm), S and I bulls. Birth weight was generally 7 % higher in the F1 Bt x Bi calves than in the Bi calves (Table 2). The highest BW was observed in the Ch x Z calves, which was higher than that observed in the Ci x Z, Sm x Z, L x Z and S x Z calves, although these four crosses did not differ (Table 2). The lowest BW was in the I calves; BW was 13 % higher in the Ch x Z, 8 % in the Sm x Z, 6 % in the S x Z, 5 % in the L x Z and 4% in the Ci x Z. Among the six crosses, WW232 was highest in the Sm x Z and Ch x Z calves, which did not differ. These were followed by the remaining three crosses (S x Z, L x Z, Ci x Z) and I, which also did not differ. The Sm x Z and Ch x Z calves generally performed better in both traits compared to the I calves. Indeed they exhibited similar trends; in terms of WW232 the Sm x Z was 13 % heavier and the Ch x Z 12 % heavier than the I calves, while for BW the Sm x Z calves were 8% heavier and the Ch x Z 13 % heavier than the I calves⁽¹²⁾.

Table 2: Least square means for birth weight (BW), average daily weight gain (DWG) and weaning weight at 205 days (WW205) and 232 days (WW232) of age in *Bos indicus* and F1 *Bos taurus* x *Bos indicus* calves

Genetic group	BW (kg) [‡]	DWG (kg) [‡]	WW232 (kg) [‡]	BW (kg) [¶]	DWG (kg) [¶]	WW205 (kg) [¶]
Simmental x Zebu	31.70 ^b	0.713 ^b	197.3 ^b	30.80 ^{bc}	0.620 ^{bc}	157.80 ^c
Charolais x Zebu	33.08 ^c	0.693 ^b	193.7 ^b	31.58 ^b	0.634 ^b	159.45 ^c
Brown Swiss x Zebu	31.24 ^b	0.644 ^a	180.5 ^a	30.24 ^c	0.602 ^{bc}	154.44 ^{bc}
Limousin x Zebu	30.90 ^b	0.617 ^a	174.1 ^a	30.17 ^c	0.594 ^{cd}	151.15 ^{bc}
Chianina x Zebu	30.61 ^b	0.605 ^a	171.0 ^a	31.17 ^b	0.602 ^{bc}	154.56 ^{bc}
Indubrasil	30.34 ^a	0.610 ^a	171.3 ^a	30.08 ^c	0.564 ^d	148.91 ^b

^{a,b,c,d} Different letter superscripts in the same column indicate difference ($P < 0.05$).

[‡]Reynoso *et al*⁽¹²⁾. [¶]Martínez⁽¹³⁾.

Using a larger data set than in the previous study⁽¹²⁾, an analysis was done for BW, DWG and WW adjusted to 205 d (WW205)⁽¹³⁾. Birth weight was highest in the Ch x Z and Ci x Z calves, followed by the Sm x Z calves and finally the L x Z, S x Z and I calves (Table 2). Daily weight gain was highest in the Ch x Z calves and lowest in the L x Z and I calves, although the Sm x Z, Ci x Z and S x Z calves did not differ from the Ch x Z calves. Weaning weight adjusted to 205 d of age was highest in the Ch x Z and Sm x Z calves and lowest in the I calves, but the Ci x Z, S x Z and L x Z did not differ from the I calves. As occurred with BW, among the F1 crosses the Ch x Z exhibited the highest WW205 and the Ci x Z the lowest (Table 2). With these averages the direct additive genetic effects could be calculated for BW, DWG and WW205 (Table 3).

Table 3: Direct additive genetic effects^a for birth weight (BW), average pre-weaning daily weight gain (DWG) and weaning weight adjusted to 205 days of age (WW205) for four *Bos taurus* breeds and one *Bos indicus* breed

Breed	BW (kg)	DWG (kg)	WW205 (kg)
Indubrasil	1.65	51	17.9
Charolais	2.73	73	15.4
Simmental	1.22	47	12.3
Chianina	1.93	15	6.3
Brown Swiss	0.14	15	6.1

^a Expressed as deviation from the Limousin breed. Martínez⁽¹³⁾.

Overall, the results of the above studies suggest that the performance of Zebu calves is significantly surpassed by that of calves from terminal crosses of Z dams with Ch or Sm sires.

Genetic evaluations of *Bos taurus* and *Bos indicus* cattle

The Asociación Mexicana Simmental-Simbrah was the first breed association to carry out a national genetic evaluation (2001). Supported by the INIFAP, the AMSS currently publishes expected progeny differences for BW, WW, yearling weight (YW), scrotal circumference (SC), frame score (FS), ST and heifer fertility (HF) for the Simmental and Simbrah breeds. In genetic evaluations, and other research on these and other breeds (e.g. Charolais, Charbray, Red Brangus), HF is defined as the probability that a heifer calved before 1,281 d (42 mo) of age. Stayability, in turn, is defined as the probability that a cow has a second calf or more before six years of age given she had a calf at three years of age. Expected progeny differences are the product of a multibreed genetic evaluation in which, generally, the animal model includes the contemporary group (herd-year-season-calf sex), dam's age at calving (covariate), and the fixed effects of proportion of Simmental genes, heterozygosity, and recombination loss.

Simmental-Simbrah population. One multibreed genetic evaluation which compared different variants of the animal model found that the most appropriate model for estimating variance components for BW, WW and YW was one which included direct and maternal genetic effects as well as the maternal permanent environmental effect. Exclusion of maternal effects (genetic and permanent environment) or inclusion of the covariance between direct and maternal genetic effects caused an overestimation of additive genetic variance and, consequently, heritability. The estimated values of direct and maternal heritability generated with the most appropriate model were 0.17 (direct) and 0.01 (maternal) for BW, 0.14 (direct) and 0.02 (maternal) for WW, and 0.15 (direct) and 0.01 (maternal) for YW (Table 4)⁽¹⁴⁾. A separate multivariate analysis calculated genetic correlations of 0.26 for BW-WW, 0.26 for BW-YW and 0.62 for WW-YW, which suggest the presence of pleiotropic effects. However, given the magnitude of the estimated values, selection for higher WW can be expected to result in a higher correlated response in YW, compared to direct selection for lower BW, which is favorable to breeders⁽¹⁵⁾.

Table 4: Heritability (on the diagonal within each population) and genetic correlation estimates

Population		BW _d	BW _m	WW _d	WW _m	YW _d	YW _m	SC	FS	ST	HF
Simmental-Simbrah	BW _d	0.17		0.26		0.26					
	BW _m		0.01								
	WW _d			0.14	0	0.62					
	WW _m				0.02						
	YW _d					0.15		0.36	0.47		
	YW _m						0.01				
	SC							0.35	0.59	-0.24	-0.65
	FS								0.42		
	ST									-	0.47
HF										0.07	
Charolais-Charbray	BW _d	0.36									
	BW _m		0.13								
	WW _d			0.27	-0.81						
	WW _m				0.15						
	YW _d					0.30		0.37	0.42		
	YW _m						0.12				
	SC							0.21	0.15	0.76	-0.08
	FS								0.25		
	ST									0.26	0.57
HF										0.06	
Red Brangus	BW _d	0.40		0.41		-0.03		0.39	0.51		
	BW _m		0.22								
	WW _d			0.30	-0.15	0.68		0.88	0.50		
	WW _m				0.06						
	YW _d					0.30		0.88	0.81		
	YW _m						-				
	SC							0.18	0.97		
	FS								0.25		
	ST									-	
HF										0.06	
Limousin	BW _d	0.13		0.36		0.58					
	BW _m		0.15								
	WW _d			0.21	-0.69	0.42					
	WW _m				0.32						
Gelbvieh	YW _d					0.20					
	BW _d	0.30									
	BW _m		-								
	WW _d			0.21							
Santa Gertrudis	WW _m				-						
	YW _d					0.45					
	BW _d	0.06									
	BW _m		0.03								
Indubrasil	WW _d			0.32	-0.63						
	WW _m				0.07						
	YW _d					0.41					
	BW _d	0.27									
Indubrasil	BW _m		0.10								
	WW _d			0.11	-0.27						
	WW _m				0.09						
	YW _d					0.13					

BW_d= direct birth weight; BW_m= maternal birth weight; WW_d= direct weaning weight; WW_m= maternal weaning weight; YW_d= direct yearling weight; YW_m= maternal yearling weight; SC= scrotal circumference; FS= frame score; ST= stayability; HF= heifer fertility.

A subsequent multibreed genetic analysis of young Simmental and Simbrah bulls found estimated heritability values of 0.33 for YW, 0.35 for SC and 0.42 for FS, while those for the genetic correlations were 0.36 for YW-SC, 0.47 for YW-FS and 0.59 for SC-FS (Table 4). These results suggest the feasibility of employing YW, SC and FS in direct selection, although, direct selection to improve one of these three traits would cause a correlated response in the other two⁽¹⁶⁾. Breeders would therefore have to consider the wisdom of producing animals with higher YW or SC since FS of replacement females might not match with the resources available in the production system.

Multibreed genetic analysis of HF showed that, when comparing heritability in the logistic sire model with the linear models, this variable did not improve prediction of breeding values, and estimation of breeding values was unaffected by distribution of the adjusted variable. However, data quality and connectedness did impact prediction and animal ranking based on their breeding values⁽¹⁷⁾. When considering all the criteria used to compare the models, it was found that, for two basic reasons, genetic evaluation of HF is best done with a linear animal model. The first reason is that the database was large enough ($n=37,390$) since the number of animals with expected progeny differences was greater than in the sire models. Second, interpreting sire logistic model results is far more complicated. Heritability of HF was found to be low (0.07) in this study⁽¹⁷⁾, however, the observed ranges of expected progeny differences (-5.79 to 8.72 for Simmental; -9.56 to 8.84 for Simbrah) indicate that genetic change in HF may occur in response to selection⁽¹⁸⁾.

Two other studies addressed the association between reproductive traits of females and males. In one, estimated genetic correlation between SC and HF (-0.65; Table 4) suggests that sire selection based on SC breeding values can lead to improvement in HF. Moreover, the genetic correlation between ST and HF (0.47) suggests that cows' ST can be increased when they are selected as replacement heifers based on HF breeding values⁽¹⁹⁾. In the other study, age at first calving (AFC), calving interval (CI) and cumulative WW at second calving (CWW) were found to significantly correlate: 0.42 for AFC-CI, 0.63 for AFC-CWW, and 0.97 for CI-CWW. Direct response to selection for CI and CWW was predicted to be greater than the expected correlated response with selection for AFC, independent of calf number per sire. Indirect selection was superior to direct selection by 42 % in the AFC-CI and by 63 % in the AFC-CWW⁽²⁰⁾.

A more recent study analyzed WW as a different trait in three different regions of Mexico⁽²¹⁾. Differences between regions were observed in the estimated values for direct heritability (0.10 to 0.54), maternal heritability (0.44 to 0.71), the correlation between direct effects (0.35 to 0.69) and the correlation between maternal effects (-0.76 to 0.16). These differences suggest the presence of genotype-environment interaction since a genetic correlation of less than 0.80 is reported to indicate the existence of this interaction⁽²²⁾. Consequently, genetic evaluations of the Simmental breed need to consider this factor. These results also highlight

the importance of knowing a selected sire's environmental conditions, and emphasize the need to prioritize superior genotypes in production systems similar to those of the country or region where a sire was bred.

Another study compared additive dam age adjustment factors for BW and WW generated using AMSS data to those recommended by the U.S. Beef Improvement Federation (BIF) and those generated by the American Simmental Association (ASA). For unadjusted BW, the sum of squares (SOS) associated with dam's age was 8,812 kg², but when applying the respective correction factors it was 4,595 kg² with the BIF factor, 1,151 kg² with the ASA and 184 kg² with the AMSS. For unadjusted WW, the SOS associated with dam's age was 110.138 kg², but when the correction factors were applied it was 32.0733 kg² with the BIF, 241.840 kg² with the ASA and 11.245 kg² with the AMSS. The error mean square for unadjusted BW was 881 kg² and that for WW was 11,014 kg², although after applying the estimated correction factors they were 18 and 1,124 kg², respectively. These results show that use of the adjustment factors estimated for Simmental cattle under Mexican environmental conditions is recommended. Use of the adjustment factors for dam's age recommended by the BIF and ASA could bias estimation of breeding values because they are based on the environmental conditions of the United States of America, which differ markedly from those of Mexico. The adjustment factors for Mexican Simmental cattle are: BW, daughters of cows 2, 3, 4, 5-11 and 12 yr of age= 1.95, 1.12, 0.41, 0.00 and 0.48 kg, respectively; BW, sons of cows 2, 3, 4, 5-11 and 12 yr of age= 2.30, 1.21, 0.36, 0.00 and 0.61 kg, respectively; WW, daughters of cows 2, 3, 4, 5-7 and 8-12 yr of age= 9.30, 5.86, 1.08, 0.00 and 3.04 kg, respectively; WW, sons of cows of 2, 3, 4-8 and 9-12 yr of age= 10.20, 5.55, 0.00 and 3.56 kg, respectively⁽²³⁾.

In one study, expression of the *HSP60* gene was evaluated in Simbrah cattle in four tropical locations in Mexico (Coahuayana, Compostela, Tamazula, Puerto Vallarta) at two times: in the early morning (AM), when environmental temperature was not high; and in the afternoon (PM), when temperature was high. Mean $2\text{-}\Delta\Delta\text{Ct}$ values differed between times at Compostela (3.12 in AM and 5.16 in PM) and Tamazula (1.94 in AM and 2.93 in PM), but not at Coahuayana (2.02 in AM and 1.91 in PM) or Puerto Vallarta (0.21 in AM and 0.47 in PM). The results highlight the possible identification of heat-tolerant animals in the Simbrah breed which could be incorporated into genetic improvement programs⁽²⁴⁾.

Charolais-Charbray population. The Charolais-Charbray Herd Book de México currently publishes expected progeny differences for the same traits assessed by the AMSS, which are also estimated using a multibreed animal model. The first study done in the Charolais-Charbray population found that the most appropriate animal model for estimating genetic parameters for BW, WW and YW included the direct additive genetic effect, the maternal additive genetic effect, the covariance between the direct and maternal genetic effects, and the maternal permanent environmental effect. Compared to five other models, this model

substantially reduced the $-2[\text{logarithm of the likelihood}]$, providing the best fit for all three traits. Using the most appropriate model, the estimated values of direct heritability, maternal heritability and variance of the permanent maternal environment as a proportion of the phenotypic variance were 0.36, 0.13 and 0.042 for BW, respectively; 0.27, 0.15 and 0.060 for WW, respectively; and 0.30, 0.12 and 0.045 for YW, respectively (Table 4). In the analysis of each trait, and in comparison to the more complex model, the simplest animal model, composed only of the direct additive genetic effect, was found to underestimate direct additive genetic variance but overestimate residual variance⁽²⁵⁾.

In a later study analyzing data from young Charolais and Charbray bulls, SC, FS and YW showed to be moderately heritable with values of 0.21, 0.25 y 0.30, respectively (Table 4)⁽²⁶⁾. Also, the genetic correlations of YW-SC (0.37) and YW-FS (0.42) were found to be moderately strong, which means that some of the genes that control YW also control SC and FS (pleiotropic effect). Young bulls that excel in terms of YW can therefore also be expected to excel in terms of SC and FS. In contrast, these latter two traits were only weakly correlated (0.15). Estimated direct response to selection based on five half-sib offspring per bull was 0.38 cm for SC, 0.18 units for FS and 8.30 kg for YW. If selection is focused on higher YW, the expected correlated response in the next generation is 0.16 cm for SC and 0.08 units for FS. It follows, therefore, that indirect selection of SC and FS based on YW would not be as effective as direct selection to improve SC and FS. Finally, the direct and correlated responses to selection based on 500 half-sib offspring per bull were almost two times higher than those based on only five offspring.

In an effort to genetically improve female reproduction, a national genetic evaluation prototype was developed for HF in Charolais and Charbray, which is equivalent to that developed for HF in Simmental and Simbrah. Using this prototype, estimated HF heritability was 0.06 (Table 4). The range for the expected progeny differences was -7.94 to 8.22 for Charolais and -7.29 to 6.14 for Charbray, each indicating the feasibility of identifying bulls outstanding in HF. The genetic trends estimated with this prototype indicated that HF had exhibited a favorable genetic change in both breeds during the 2007-2011 period⁽¹⁸⁾.

One of the most recent studies of these two breeds evaluated the association between male and female reproductive traits. A strong genetic correlation was identified between SC and ST (0.76; Table 4), suggesting that selection of bulls based on expected progeny differences for SC could induce a favorable genetic change in ST. An important genetic relationship was also found between ST and HF (0.57), highlighting the possibility of increasing a cow's probability of remaining in a herd if, at an early age, she is selected as a replacement heifer because she has a high expected progeny difference for HF. Estimated heritability values were 0.18 cm for SC, 0.26 % for ST and 0.11% for HF, while those for direct response to selection, assuming five half-sib offspring per bull, were 0.15 cm for SC, 0.04 percentage units for ST and 0.15 percentage units for HF. If bulls are selected based on their expected

progeny differences for SC, and assuming the same number of offspring, a correlated response to selection of 0.20 percentage units in ST can be expected, but no correlated response is expected in HF. However, when the estimates of the direct response to selection are based on ten offspring, the values are higher for SC (42.3 %), HF (50.0 %) and ST (40.0 %)⁽²⁷⁾.

Red Brangus population. As has been done with the Simmental, Simbrah, Charolais and Charbray breeds, a large number of traits have been incorporated into genetic evaluations of the Red Brangus breed, although ST is not among them. A recent multivariate analysis found a moderately heritable direct additive genetic effect for BW (40 %), WW (30 %), YW (30 %) and FS (25 %) (Table 4), but poor heritability for SC (18 %). The maternal additive genetic effect for BW was moderately heritable (22 %), but that of WW was lowly heritable (6 %). When analyzing the relationship between traits it was found that selection for higher WW can result in a considerable correlated response in BW, YW, SC and FS. This was due to the high values of the genetic correlation estimates of WW with BW (0.41), YW (0.68), SC (0.88) and FS (0.50). There were also strong correlations between YW and SC (0.88), YW and FS (0.81), and SC and FS (0.97) (Table 4)⁽²⁸⁾. A univariate analysis with a linear animal model showed that in Red Brangus HF heritability is low (0.06)⁽²⁹⁾, as reported for the Simmental, Simbrah, Charolais and Charbray populations.

Limousin population. Genetic evaluations of the Limousin breed have included BW, WW, YW and SC. One study found that the most suitable animal model for BW and WW included the direct and maternal genetic effects plus their covariance, whereas for YW it only included the direct genetic effect. When the BW and WW models did not consider the maternal effects they overestimated genetic variance and heritability. The direct and maternal genetic effects of WW (0.21 and 0.32, respectively) were found to be more heritable than those of BW (0.13 and 0.15, respectively) (Table 4), while the direct genetic effects of WW (0.21) and YW (0.20) exhibited similar heritability (Table 4)⁽³⁰⁾. In another study, a trivariate analysis found BW, WW and YW to be moderately correlated: 0.36 (BW-WW), 0.58 (BW-YW) and 0.42 (WW-YW) (Table 4). When selecting any of these traits a correlated response can therefore be expected in the other two⁽³¹⁾.

Gelbvieh and Santa Gertrudis populations. Genetic evaluations implemented by the Asociación Mexicana de Criadores de Ganado Santa Gertrudis (Mexican Association of Santa Gertrudis Cattle Breeders) and the Asociación de Criadores de Ganado Gelbvieh de la República Mexicana (Gelbvieh Cattle Breeders Association of the Mexican Republic) have calculated expected progeny differences for BW, WW and YW. One study using BW, WW and YW data to compare models for genetic evaluation of the Gelbvieh breed considered six random effects in the models: direct genetic (D), maternal genetic (M), the covariance (C) between D and M, maternal permanent environment (P) and the residual. No significant differences between the models (i.e. D, DP, DM, DMP, DMC and DMCP) were identified

for any of the variables. Inclusion of C in the model underestimated direct heritability for BW and overestimated it for WW. Considering this and the importance of maternal genetic effects on both traits, the DMP model appeared to be the most suitable model for genetic evaluation of BW and WW. However, for YW the D model was more suitable given the low importance of M and P for this trait. When using the respective most suitable model the estimated values for direct heritability were 0.30 for BW, 0.21 for WW and 0.45 for YW (Table 4)⁽³²⁾. In a later study using data only for the Santa Gertrudis breed, it was observed that the estimates of direct additive genetic variance, as a proportion of phenotypic variance, indicated little direct additive genetic variability for BW (direct heritability= 0.06), but clear variability estimated for WW (0.32) and YW (0.41). The estimated values for maternal heritability suggest that very little of the variability in BW and WW was due to maternal genetic effects⁽³³⁾.

Indubrasil experimental population. A study done using data from an experimental Indubrasil herd at INIFAP kept in a humid tropical climate found that for BW and WW the direct genetic effect was more important than the maternal genetic effect. In addition, the maternal permanent environmental effect did not influence expression of WW. Estimated values of direct heritability were 0.27 for BW, 0.11 for WW and 0.13 for YW, while those of maternal heritability were 0.10 for BW and 0.09 for WW (Table 4)⁽³⁴⁾. A different study which analyzed the female reproductive traits of CI, age at first service and AFC found considerable genetic variation and moderate to high heritability values (0.13 for CI, 0.31 for age at first service and 0.39 for AFC). In contrast, gestation length, days open and services per conception exhibited little genetic variation and therefore low heritability (0.08 for gestation length, 0.03 for days open and 0.03 for number of services per conception)⁽³⁵⁾.

Estimation of genetic diversity in *Bos taurus* and *Bos taurus* x *Bos indicus* cattle using genealogical data

A population's genetic diversity can be studied by analyzing pedigree data. These genealogical data, together with statistics based on probabilities of gene origin, provide valuable information for the study of populations that have been under selection for several years⁽³⁶⁾. An analysis of registered Simmental cattle in Mexico included animals born between 1985 and 2014; 1985 is when the first Simmental animals born in Mexico were registered. The population has had a low inbreeding coefficient, varying from 0.68 % for animals born in 2014 to 1.65 % for those born in 1997. When considering five-year subpopulations beginning in 1985, the effective population size increased from 134.7 in 1985-1989 to 186.6 in 2010-2014. The effective numbers of founders, ancestors, and founder genomes increased from 1985 to 2004, but decreased from 2005 to 2014. For animals born

in the periods 2005-2009 and 2010-2014, the ratio of the effective number of ancestors to the effective number of founders suggests loss of diversity due to bottlenecks in both periods. For the same animals, the ratio of the effective number of founder genomes relative to the effective number of ancestors suggests genetic drift in both periods. Finally, for animals born in 2010-2014 one ancestor explained 3.4% of total genetic variability and 15 ancestors explained 20 % of said variability; the marginal genetic contribution of each of these 15 ancestors was similar⁽³⁷⁾.

An analysis of the genetic diversity of registered Simbrah cattle in Mexico used animals born between 1990 and 2014. The inbreeding coefficient was low, with a clear tendency to decrease over time; it varied from 0.14 % for animals born in 1990 to 0.03 % for those born in 2014. When analyzing five-year subpopulations beginning in 1990, effective population size decreased from 79.3 in 1990-1994 to 36.4 in 2010-2014. The effective numbers of founders, ancestors, and founder genomes increased from 1990 to 2009, but decreased dramatically from 2005 to 2014. For animals born in the period 2010-2014, the ratio of the effective number of ancestors to the effective number of founders suggests loss of diversity due to bottlenecks. For the same animals, the ratio of the effective number of founder genomes relative to the effective number of ancestors suggests genetic drift. For animals born from 2010-2014, one ancestor explained 0.21 % of total genetic variability and 10 ancestors explained 1.4 % of said variability⁽³⁸⁾.

For registered Charolais cattle in Mexico, analysis of the evolution of its genetic diversity was done using data for animals born between 1984 and 2018. The inbreeding coefficient remained between 2.1 and 1.3 % throughout the 35-yr study period. Effective population size gradually increased from 105.0 in 1984 to 237.1 in 2013, then decreased slightly to 233.2 in 2018. An increase in the effective number of ancestors was observed from 1984 to 2008, followed by a decrease in the following decade. The effective number of founder genomes increased from 1984 (130.1) to 2003 (143.7), but decreased over the next 15 yr (127.7), resulting in allele loss from 2004 to 2018. The ratio of the effective number of ancestors to the effective number of founders suggests that the loss of genetic diversity in the period 1999 to 2018 was due, in part, to formation of pedigree bottlenecks. The ratio of the effective number of founder genomes to the effective number of ancestors suggests loss of founder alleles due to genetic drift⁽³⁹⁾.

Genome-wide association studies for growth traits in *Bos taurus* cattle

Analyses of association have been done using the whole genome (Gn) and by chromosome (Chr) in registered Simmental⁽⁴⁰⁾ and Simbrah⁽⁴¹⁾ cattle to identify SNPs associated with growth traits. The genotypes and phenotypes of 967 animals (473 Simmental and 494 Simbrah) were used. The phenotypes used were the deregressed breeding values of BW, direct WW (DWW), maternal WW (MWW) and YW. Genotyping was done with high-density panels. After quality control, 105,129 autosomal SNPs were obtained. In the Simmental animals, 22 SNPs were found to be associated with BW, 25 with DWW, 28 with MWW and 42 with YW. For BW, 18 SNPs were identified in the Gn and 8 in the Chr, while for DWW, 15 SNPs were isolated in the Gn and 15 in the Chr. For MWW, 21 SNPs were found in the Gn and 8 in the Chr, while for YW, 18 SNPs were found in the Gn and 34 in the Chr. Overlap between Gn and Chr analyses was 4 SNPs for BW, 5 for DWW, 1 for MWW and 10 for YW⁽⁴⁰⁾. In the Simbrah animals, a total of 50 SNPs were associated with BW, 29 with DWW, 18 with MWW, and 19 with YW. For BW, 24 SNPs were significant in the Gn analysis and 38 in the Chr analysis; for DWW, 25 SNPs were found in the Gn and 9 in the Chr analysis. For MWW there were 16 SNPs in the Gn and 5 in the Chr, while for YW there were 14 in the Gn and 12 in the Chr. Overlap between the Gn and Chr analyses was 12 SNPs for BW, 5 for DWW, 3 for MWW and 7 for YW⁽⁴¹⁾.

Research challenges and perspective

The objectives of modern genetic improvement have evolved towards development of better evaluation methods. These have made it possible to increase the accuracy of breeding value estimates, shorten generational interval and produce more efficient crossbred animals⁽⁴²⁾. For the past 20 yr, genetic evaluations have been done for different beef cattle breeds in Mexico, but genetic improvement still faces new challenges in terms of pace and direction. Little or no progress has been made for some traits because they are expensive to measure (residual feed intake, methane production, tolerance to heat stress), their genetic variation is low (fertility), and/or genetic correlation is unfavorable between some of these traits⁽⁴³⁾.

Selection in beef cattle is currently done using a large number of traits for which genetic predictions can be made and which are available to farmers. In the short-term, selection needs to be done based on traits of interest by applying selection indices, such as maternal or terminal indices⁽⁴⁴⁾. Greater emphasis needs to be placed on carcass traits. Some breed associations in Mexico began measuring phenotypes for these traits in 2016 and predictions

of genetic merit for these traits should be available shortly. Using the traits measured currently, estimates are needed of the genetic correlations between them and their correlated response to selection. The structure of phenotypic data (i.e. greater number of progeny per sire) can be improved in a way that allows an increase in or establishment of reference populations, which will support genomic selection over the medium-term⁽⁴⁵⁾. In this same time frame it is also important to consider new phenotypes (although they can be expensive and difficult to measure) that contribute to production efficiency; these can include methane production, tolerance to heat stress, residual feed intake, and health traits that improve animal welfare. Periodic genomic evaluations of these traits are then needed to track them.

There is great interest in developing methods that allow comparison between individuals of different breeds because it provides potential commercial opportunities. Research is needed over the medium- and long-term on crossbreed genomic prediction. This will be much more challenging because different breeds can exhibit different QTLs, dominance or epistasis may occur and allele frequencies can vary between populations⁽⁵⁾.

In beef production, genetic improvement is focused on identifying individuals that can efficiently provide high quality protein while considering environmental equilibrium, greenhouse gas emissions and growing consumer consciousness of animal welfare and food safety. The beef production strategies currently under development in Mexico are inefficient. The genetic improvement tools now available for selection and crossbreeding need to be focused on identifying animals with greater productive and biological efficiency and a reduced environmental footprint, while guaranteeing the highest standards of animal welfare and food safety.

Conclusions

By using increasingly larger databases for the various beef cattle breeds used in Mexico (Bt, Bi and Bt x Bi), genetic improvement practices and research have attained many milestones. For Bi and Bt x Bi animals under tropical conditions, characterization was done for productive (growth, milk production, longevity, lifetime productivity) and reproductive traits (age at first calving, pregnancy rate, calving rate, weaning rate, kilograms calf weaned per cow exposed). A multibreed genetic evaluation model has been developed for the registered Simmental-Simbrah and Charolais-Charbray populations. The importance of maternal effects (genetic and permanent environment) for growth traits has been quantified, which has allowed identification of the most suitable animal model for genetic evaluation of BW, WW and YW. The magnitude of heritability and genetic correlation was estimated for growth and reproductive traits (including AFC, CI and CWW) in males and females, which allows

prediction of the direct and correlated responses to selection based on different numbers of offspring per bull in these traits. The genotype-environment interaction has been proven to be an important factor in WW expression in the Simmental breed, suggesting that it needs to be incorporated into national-level genetic evaluations. Dam age adjustment factors for BW and WW have been developed, thus avoiding use of adjustment factors generated in other countries, which can result in biased breeding value estimates. National-level genetic evaluation prototypes have been developed for ST and HF based on the environmental and management conditions of Mexico. Expression of the *HSP60* gene in Simbrah cattle exposed to heat stress in the tropics of Mexico has been evaluated. Estimates of genetic diversity in the registered Simmental, Charolais and Simbrah populations have been obtained, and, finally, SNPs associated with growth traits have been identified in the Simmental and Simbrah breeds.

Impacts

In the early 1980s, when most cattlemen in the Mexican tropics used Zebu cows in cow-calf systems, a project was begun (described herein) that proved the advantages of using Bt x Bi cows to produce calves. Almost forty years later, an estimated 50 % of beef cattle production units in Mexico use Bt x Bi cows. Once the first national genetic evaluation of beef cattle was done by INIFAP researchers in 2001 using AMSS data, other beef breed associations began their own national genetic evaluations. The INIFAP currently does genetic evaluations for breeders of Simmental-Simbrah-Simangus, Charolais-Charbray, Red Brangus, Santa Gertrudis, Braford and Italian cattle. These evaluations provide breeders the tools to genetically improve beef cattle in Mexico through the approximately 14,000 bulls sold annually to commercial and registered producers.

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