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Germ Plasm Utilization in Beef Cattle

Keith E. Gregory, Larry V. Cundiff, and Robert M. Koch¹

Introduction

Heterosis achieved through well-organized crossbreeding systems can be used to increase weight of calf weaned per cow exposed to breeding by about 20%. Comprehensive programs of breed characterization have revealed large differences among breeds for most biological traits of economic importance.

A high percentage of beef cattle in the U.S. and globally are in herds too small to use well organized crossbreeding systems on a self-contained basis. Further, there is wide fluctuation in breed composition between generations in rotational crossbreeding systems. Thus, there is need for experimental evaluation of the potential of composite populations as an alternative, or, as a supplement to continuous crossbreeding systems to use heterosis, and, as a procedure to use genetic differences among breeds to optimize such biological characters as growth rate and mature size, milk production level, leanto-fat ratio, and climatic adaptability. The primary objective of achieving and maintaining optimum breed composition is to synchronize cattle genetic resources with the production environment most favored by economic and technological factors and with market requirements.

The situation. More than 55% of the national beef breeding herd, involving 92% of the farms and ranches that have beef breeding cows, is represented by herds that have 100 or fewer cows. Organized crossbreeding systems favor herd size of 100 or more cows. The problem of achieving and maintaining the most optimum contribution by each breed used in rotational crossbreeding systems is reflected by the fact that in a two-breed rotation system, in each generation, 66.7% of the genes are from the breed of the sire and 33.3% of the genes are from the breed of the maternal grandsire at equilibrium (7 generations); and in a three-breed rotation system, in each generation, 57% of the genes are from the breed of the sire, 29% of the genes are from the breed of the maternal grandsire, and 14% of the genes are from the breed of the maternal great grandsire at equilibrium (7 generations). If the optimum contribution to achieve maximum adaptability to the production situation should be 25% for a specific breed, the optimum is approached infrequently in rotational crossbreeding systems.

Retention of initial heterozygosity following crossing (F_1) and subsequent random mating within the crosses (*inter se'*) is a function of the number of breeds and the proportion each breed contributes to a composite population. Retention of initial (F_1) heterozygosity is proportional to $1 - \frac{n}{2} P_i^2$, where P_i is the fraction of each of n breeds in the pedigree of a composite population; e.g., three-breed composite formed from 3/8 breed A, 3/8 breed B, and 1/4 breed C = $1 - [(3/8)^2 + (3/8)^2 + (1/4)^2] = .656$. Where the breeds contribute equally to the foundation of a composite population, retention of initial

heterozygosity following crossing can be computed $\frac{n+1}{n}$, where n is the number of breeds contributing equally to the foundation of a composite population; e.g., fourbreed composite formed from 1/4 breed A, 1/4 breed B, 1/4 breed C, and 1/4 breed D, $=\frac{n+1}{n}=3/4=.75$. The loss of heterozygosity occurs between the F_1 and F_2 generations in populations mated inter se'. Thus, for maternal traits, performance of F_2 generation dams is evaluated in their F_3 generation progeny.

Computations of heterozygosity retained in different mating types and estimates of the increase in weight of calf weaned per cow exposed to breeding as a result of heterosis are presented in Table 1. These estimates of heterosis are appropriate if retention of heterosis is proportional to retention of heterozygosity in composite populations. As indicated by Table 1, the percentage of F₁ generation heterozygosity retained in composite populations based on approximately equal contribution by either three or four breeds equals or exceeds the percentage of F₁ generation heterozygosity retained in a continuous two-breed rotational crossbreeding system after equilibrium is reached. A primary objective of this project is to determine experimentally if retention of heterosis in composite populations is proportional to retention of heterozygosity.

Research results from rotational crossbreeding systems have shown that retention of heterosis is approximately equal to retention of heterozygosity. Thus, production increases as a result of heterosis can be estimated with precision for different crossbreeding systems if the level of heterosis for the traits of interest

is known.

Research objectives. Specific research objectives of the Germ Plasm Utilization Project are: (1) Determine the percentage of initial heterosis (F1) that is retained in composite populations; i.e., to what extent is retention of heterosis proportional to retention of heterozygosity; (2) Determine the additive genetic variance, particularly for traits contributing to reproductive performance, in composite populations relative to parental purebred populations contributing to the composites; i.e., is selection for male and female reproductive traits more effective in composite populations than in the contributing purebreds; (3) Develop effective selection criteria and procedures to improve both male and female reproductive performance in beef cattle; (4) Determine the feasibility of developing new populations of beef cattle based on a multi-breed (composite) foundation as an alternative to rotational and other crossbreeding systems to utilize heterosis; and (5) Determine the feasibility of using genetic differences among breeds for making more rapid progress toward optimizing such biological characters as (a) climatic adaptability, (b) growth rate and mature size, (c) carcass composition, and (d) milk production.

The three combinations of breeds that contribute to the three composites (MARC I, MARC II, and MARC III) were identified with the intent of producing composite populations of different biological type (e.g., bioeconomic traits) using a series of breed combinations. Results obtained involving several breed combinations affects the inferences that can be made in application of the principles being investigated (i.e., research objectives) by the

experiment.

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Table 1—Heterozygosity of different mating types and estimated increase in performance as a result of heterosis

Mating type	Heterozygosity percent relative to F ₁	Est. increase in calf wt wnd per cow exposed ^a (%)
Pure breeds: Two-breed rotation at equilibrium Three-breed rotation at equilibrium Four-breed rotation at equilibrium	0 66.7 85.7 93.3	0 15.5 20.0 21.7
Two-breed composite: F ₃ - 1/2A, 1/2B F ₃ - 5/8A, 3/8B F ₃ - 3/4A, 1/4B	50.0 46.9 37.5	11.6 10.9 8.7
Three-breed composite: F ₃ - 1/2A, 1/4B, 1/4C F ₃ - 3/8A, 3/8B, 1/4C	62.5 65.6	14.6 15.3
Four-breed composite: F ₃ - 1/4A, 1/4B, 1/4C, 1/4D F ₃ - 3/8A, 3/8B, 1/8C, 1/8D F ₃ - 1/2A, 1/4B, 1/8C, 1/8D	75.0 68.8 65.6	17.5 16.0 15.3
Five-breed composite: F ₃ - 1/4A, 1/4B, 1/4C, 1/8D, 1/8E F ₃ - 1/2A, 1/8B, 1/8C, 1/8D, 1/8E	78.1 68.8	18.2 16.0
Six-breed composite: F ₃ - 1/4A, 1/4B, 1/8C, 1/8D, 1/8E, 1/8F	81.3	18.9
Seven-breed composite: F ₃ - 3/16A, 3/16B, 1/8C, 1/8D, 1/8E, 1/8F, 1/8G	85.2	19.8
Eight-breed composite: F ₃ - 1/8A, 1/8B, 1/8C, 1/8D, 1/8E, 1/8F, 1/8G, 1/8H	87.5	20.4

^aBased on heterosis effects of 8.5% for individual traits and 14.8% for maternal traits and assumes that retention of heterosis is proportional to retention of heterozygosity. These estimates of heterosis were obtained in a crossbreeding experiment involving the Angus, Hereford, and Shorthorn breeds that was started at the Fort Robinson Beef Research Station and completed at MARC.

Table 2—Germ Plasm Utilization Project - approximate number of calving females^a

			ear			
Breed group	1986	1987	1988	1989	1990	1991
MARC I-1/4C, 1/4B, 1/4L, 1/8H, 1/8/	Д					
F ₁	152	116	99	84	71	60
F ₂	132	110	100	100	100	111
F ₃	18	44	82	120	120	120
MARC II-1/4S, 1/4G, 1/4H, 1/4A						
F ₁	115	92	78	66	56	48
F ₂	120	110	100	80	79	87
F ₃	48	104	120	120	120	120
MARC III-1/4R, 1/4H, 1/4P, 1/4A						
F ₁	155	150	127	100	84	71
F ₂	76	128	120	120	120	120
F ₃		16	44	80	120	133
Composite total	816	870	870	870	870	870
Hereford (H)	110	90	90	90	90	90
Angus (A)	91	90	90	90	90	90
Limousin (L)	109	90	90	90	90	90
Brown Swiss (B)	91	90	90	90	90	90
Charolais (C)	103	90	90	90	90	90
Gelbvieh (G)	94	90	90	90	90	90
Simmental (S)	93	90	90	90	90	90
Red Poll (R)	91	90	90	90	90	90
Pinzgauer (P)	80	90	90	90	90	90
Purebred total	862	810	810	810	810	810
Grand total	1,678	1,680	1,680	1,680	1,680	1,680

^aFemales exposed to breeding will be 2,400; i.e., 1,680 calving females and 720 yearling heifers. After 1985 breeding season, open females have not been retained.

The calving schedule shown in Table 2 involving Composites (MARC I, MARC II, and MARC III) F_1 generation, F_2 generation, F_3 generation, and purebred females will provide the basic data essential for: (1) estimating linearity of association of heterosis with heterozygosity in composite populations; (2) estimating genetic and phenotypic parameters in order to determine selection response, particularly for traits contributing to fitness, in both composite and purebred populations; and (3) developing selection criteria and procedures for both male and female reproductive phenomena. As indicated by Table 2, F_1 generation, F_2 generation, F_3 generation, and contributing purebreds produce calves in the same seasons.

These contrasts provide the basis for estimating heterosis and for determining heterosis retention from the F_1 generation to the F_2 generation and to the F_3 generation for reproductive and maternal traits by comparing F_1 , F_2 , and F_3 generations and their F_2 , F_3 , and F_4 generation progeny with each other and with appropriate parental purebreds.

Composite populations were formed from the same genetic base that is represented in the contributing purebreds, i.e., males and females used to establish each composite population were used as foundation in the

contributing purebreds.

Matings through 1990 (Table 2) will be consistent with the procedures that have been followed in this project; i.e., yearling heifers are mated by natural service to yearling bulls for about 45 days and females 2 yr old and older have a breeding season of about 56 days; about one-half of the breeding season is by artificial insemination and one-half is by natural service in individual sire breeding pastures. All females born are retained for breeding and excess females in each population are removed based on nonperformance criteria; i.e., age, color, atypical anatomy, etc. Open females have not been retained subsequent to the 1985 breeding season.

The intent of the mating plan is to obtain 10-20 female progeny per sire for estimating genetic parameters for the characters of primary interest. Close matings are avoided in all populations to reduce rates of inbreeding.

In 1988, 1989, and 1990, male calves produced in the nine purebreds and the F₃ generation from each of the three composite populations (12 breed groups), except those needed for breeding, will be castrated at weaning and fed diets of two energy densities to two slaughter end points. There will be two pens for each breed group—one pen for each dietary energy density for each of the three yr. Feed consumption data will be recorded on a pen basis to permit estimation of feed efficiency for each breed group-energy density sub-class.

The right side of each carcass will be processed into boneless, closely trimmed (.3 in. outside fat) and further into boneless, fully trimmed (0 outside fat) product. Fat in a cross section of the longissimus muscle will be estimated by chemical analysis. Samples of cooked meat from the longissimus muscle will be used to obtain sensory evaluations (tenderness, flavor, and juiciness) and shear force values to estimate tenderness.

All female calves will be retained for breeding during this period, as has been done throughout the experiment, and all male calves will be left intact and fed in the stan-

dard mode again for the 1991 calf crop.

For calf crops born in 1989 and 1990, and, if needed in 1991, milk production/consumption will be recorded on 24, 3-, 4-, and 5-yr-old females in each yr from each of the nine purebreds, and from the F_2 generation of each of the three composite populations (12 breed groups). Three evaluations of milk production/consumption will be recorded in each yr on 24 cow/calf pairs using the weigh-nurse-weigh procedure. Milk production/consumption estimates will be made on the following schedule: (1) immediately before start of breeding season, about June 15, when calves avg about 2 mo of age, (2) end of breeding season, about August 15, when calves avg about 5 mo of age.

Table 3—Germ Plasm Utilization Project · Matings made to establish composites, retention of heterozygosity, and expected retention of heterosis

		Composites		
	MARC I	MARC II	MARC III	Mean
Matings to Produce F ₁ 's ^a	(C x LH) x (B x LA) or (C x LA) x (B x LH) Reciprocals	(GH) x (SA) or (GA) x (SH)	(PA) x (RH) or (PA) x (HR) Reciprocals	
Matings to produce F ₂ 's Matings to produce F ₃ 's	$F_1 \times F_1$ $F_2 \times F_2$	$F_1 \times F_1$ $F_2 \times F_2$	$F_1 \times F_1$ $F_2 \times F_2$	
Breed composition of F ₁ and subsequent generations	.25B,.25C,.25L,.125H,.125A	.25G,.25S,.25H,.25A	.25P,.25R,.25H,.25A	
F ₁ Heterozygosity ^b F ₂ Heterozygosity F ₃ Heterozygosity	.94 .78 .78	1 .75 .75	.75 .75	.98 .76 .76
F ₁ Heterosis ^c F ₂ Heterosis F ₃ Heterosis F ₄ Heterosis	.94 H ⁱ + 1 H ^m .78 H ⁱ + .94 H ^m .78 H ⁱ + .78 H ^m .78 H ⁱ + .78 H ^m	1 H ⁱ + 1 H ^m .75 H ⁱ + 1 H ^m .75 H ⁱ + .75 H ^m .75 H ⁱ + .75 H ^m	1 H ⁱ + 1 H ^m .75 H ⁱ + 1 H ^m .75 H ⁱ + .75 H ^m .75 H ⁱ + .75 H ^m	.98 H ⁱ + 1 H ^m .76 H ⁱ + .98 H ^m .76 H ⁱ + .76 H ^m .76 H ⁱ + .76 H ^m

^aComposites established from same animals used in purebred foundation where C = Charolais, L = Limousin, H = Hereford, B = Brown Swiss, A = Angus, G = Gelbvieh, S = Simmental, P = Pinzgauer, and R = Red Poll.

bln populations mated inter se', loss of heterozygosity occurs between the F₁ and F₂ generations and, if inbreeding is avoided, subsequent loss of heterozygosity does not occur.

°Hi denotes individual heterosis expressed by progeny and H^m denotes maternal heterosis expressed by dam of progeny and assumes retention of heterosis is proportional to retention of heterozygosity.

All females have been retained for breeding, and excess females have been removed from each population on nonperformance criteria. The same criteria have been used to identify males for use in all populations, e.g., color in composite populations and avoidance of extremes in all populations in regard to wt and skeletal and muscular anatomy. The same basic criteria have been used in all breed groups (purebred and composites) in identifying males to use and in the removal of females excess to the needs of the project.

The specific mating plan used to produce the F_1 , F_2 , and F₃ generations of the three composite populations and their breed composition is provided by Table 3. Heterozygosity for the F₁, F₂, and F₃ generations and expected heterosis for both individual and maternal traits is given in Table 3. Values given for heterosis for both individual (Hi) and maternal (Hm) traits assumes retention of heterosis proportional to retention of heterozygosity. Loss of heterozygosity in interse' mated populations occurs between the F₁ and F₂ generations and, if inbreeding is avoided, further loss of heterozygosity is not expected. Because heterosis for maternal traits is expressed in progeny, heterosis for maternal traits is expressed in F₃ generation progeny of F₂ generation dams (Table 3).

In Composite MARC I, the F₁ generation was produced from 1978 through 1983, the $\rm F_2$ generation was produced starting in 1980, and the $\rm F_3$ generation was produced starting in 1982. In Composite MARC II, the F₁ generation was produced from 1978 through 1982, the F₂ generation was produced starting in 1980, and the F3 generation was produced starting in 1982. In Composite MARC III, the F₁ generation was produced from 1980 through 1984, the F2 generation was produced starting in 1982, and the F₃ generation was produced starting in 1984. Purebred contemporaries have been maintained since 1978 for all except the Pinzgauer. For the Pinzgauer

breed, the first 3/4 Pinzgauer were produced in 1980, 7/8 Pinzgauer (purebred in females) were produced in 1982, and 15/16 Pinzgauer (purebred in males) have been produced since 1984. The Brown Swiss breed averages about 7/8 dual-purpose type from Europe (Braunvieh) and was established by using semen from nine Braunvieh sires from Switzerland and Germany (Bavaria), starting with a female foundation of typical dairy-type Brown Swiss females obtained as heifer calves in Wisconsin and Minnesota in 1967 and 1968. The grading toward the European dual-purpose type of Brown Swiss started in 1969.

The current phase of this experiment will be completed with the production and growing out through yearling age of the calf crop to be born in 1991.

Growth traits. Breed group means and standard errors for the nine purebreds and for the F₁, F₂, and F₃ generations of each of the three composite populations for birth, weaning, and yearling wt are presented in Tables 4 and 5 for bulls and heifers, respectively. These data were analyzed as individual traits. Differences are small among the Charolais, Simmental, Gelbvieh, Pinzgauer, and Brown Swiss breeds for these wt traits. The Limousin breed is intermediate in growth traits; the Angus and Red Poll breeds are similar to each other; and the Hereford breed is lightest in weaning and yearling wt. The three composite populations are closer in wt traits to the higher gaining purebred parents than they are to the lower gaining purebred parents.

Heterosis estimates for the F_1 , F_2 , and F_3 generations for each composite population and mean heterosis for the F_1 , F_2 , and F_3 generations for the three composite populations for birth, weaning, and yearling wt are presented in Tables 6 and 7 for bulls and heifers, respectively. The numbers on which these estimates are based are provided in Tables 4 and 5 for bulls and heifers,

Table 4—Breed group means and standard errors for birth, weaning, and yearling weight of bulls - Germ Plasm Utilization Project - 1978-1985

Breed	Na	Birth	O.F.b	200-day	C.F.	368-day	C.F.
group	IA	wt (lb)	SEb	wt (lb)	SE	wt (lb)	SE
Mean	5,086	93	.4	512	1.5	972	2.7
Red Poll (R)	348	84	.9	470	4.0	880	7.0
Brown Swiss (B)	367	100	.8	540	3.5	1,005	6.1
Hereford (H)	382	80	.9	406	4.0	831	7.1
Angus (A)	666	75	.7	436	2.9	866	5.1
Simmental (S)	364	97	.8	547	3.3	1,034	5.7
Limousin (L)	363	90	.8	470	3.7	902	6.4
Charolais (C)	324	103	.9	531	4.0	1,025	7.1
Gelbvieh (G)	284	97	1.0	558	4.1	1,021	7.2
Pinzgauer (P)	143	107	1.4	547	5.8	1,019	10.1
MARC I F1cd	238	94	1.1	522	4.6	1,001	8.1
F ₂	245	96	1.1	529	4.7	1,005	8.2
MARC I F ₁ ^{cd} F ₂ F ₃	55	98	1.8	520	8.0	986	13.8
MARC II F1cd	341	91	1.0	551	4.4	1,010	7.8
F ₂	365	93	1.0	525	4.1	1,005	7.3
MARC II F ₁ cd F ₂ F ₃	156	92	1.2	527	5.0	999	8.6
MARC III F1cd	237	91	1.2	505	5.0	961	8.8
	190	91	1.3	509	5.4	979	9.5
F ₂ F ₃	18	92	3.0	522	12.9	988	21.9

bSE = Standard Error.

BMARC I is 1/4B, 1/4L, 1/4C, 1/8H, 1/8A; MARC II is 1/4H, 1/4A, 1/4S, 1/4G; MARC III is 1/4R, 1/4H, 1/4A, 1/4P.

 $^{{}^{}d}F_{1}$, F_{2} , F_{3} is first, second, and third generation of matings to produce animals of the same breed composition, i.e., *interse'* mating.

Table 5—Breed group means and standard errors for birth, weaning, and yearling weight of heifers - Germ Plasm Utilization Project - 1978-1985

Breed		Birth		200-day		368-day	
group	Na	wt (lb)	SEb	wt (lb)	SE	wt (lb)	SE
Mean	5,090	87	.3	481	1.4	739	2.2
Red Poll (R)	349	79	.8	432	3.7	653	5.9
Brown Swiss (B)	353	93	.7	512	3.3	765	5.2
Hereford (H)	382	75	.8	379	3.9	608	6.2
Angus (A)	663	70	.6	412	2.8	666	4.4
Simmental (S)	379	90	.7	516	3.1	774	4.8
Limousin (L)	360	84	.7	441	3.5	686	5.4
Charolais (C)	373	96	.8	503	3.5	776	5.5
Gelbvieh (G)	303	92	.8	529	3.9	774	6.1
Pinzgauer (P)	148	98	1.2	522	5.6	772	8.8
MARC I F1cd	237	91	1.0	503	4.4	778	7.0
F ₂	203	91	1.0	505	4.6	783	7.3
F ₃	50	96	1.7	514	7.6	798	11.6
MARC II F1cd	332	84	.9	496	4.2	743	6.8
F ₂	372	86	.9	487	4.0	754	6.5
F ₃	126	86	1.1	498	5.0	763	7.6
MARC III F1cd	251	85	1.0	465	4.8	728	7.6
	185	84	1.1	476	5.2	739	8.1
F ₂ F ₃	24	84	2.3	472	10.4	739	15.7

N = Number observations.

**SE = Standard Error.

**MARC I is 1/4B, 1/4L, 1/4C, 1/8H, 1/8A; MARC II is 1/4H, 1/4A, 1/4S, 1/4G; MARC III is 1/4R, 1/4H, 1/4A, 1/4P, 1/4H, 1/4A, 1/4P, 1/4H, 1/4A, 1/4P, 1

^dF₁, F₂, F₃ is first, second, and third generation of matings to produce animals of the same breed composition, i.e., *inter*

Table 6-Heterosis for birth, weaning, and yearling weight of bullsa - Germ Plasm Utilization Project - 1978-1985

	Traits					
Contrast	Birth wt (lb)	200-day wt (lb)	368-day wt (lb)			
M	IARC I					
F ₁ minus Purebreds	1.5	31	55			
F ₂ minus Purebreds	2.9	37	62			
F ₃ minus Purebreds	5.7	29	40			
M	ARC II					
F ₁ minus Purebreds	3.5	62	73			
F ₂ minus Purebreds	5.7	37	66			
F ₃ minus Purebreds	4.8	40	62			
	RC III					
F ₁ minus Purebreds	4.4	40	62			
F ₂ minus Purebreds	4.2	44	82			
F ₃ minus Purebreds	5.5	57	88			
Mean	Heterosis					
F ₁ minus Purebreds	3.1	44	64			
F ₂ minus Purebreds	4.2	40	70			
F ₃ minus Purebreds	5.3	42	64			

See footnotes in Table 4.

respectively. Heterozygosity for F₁, F₂, and F₃ generations and expected heterosis for both individual and maternal traits for F_1 , F_2 , F_3 , and F_4 generations are presented in Table 3 for each composite population and for the mean of the three composite populations.

Because of limited numbers, the estimates of heterosis for the F₃ generation for these growth traits should be interpreted with some degree of caution. These early results for growth traits are based on data from calf crops born through 1985. The approximate additional numbers of F₂, F₃, and F₄ generation progeny out of F₁, F₂, and F₃ generation dams expected from 1986 through 1991 are given in Table 2. Even though additional numbers

Table 7—Heterosis for birth, weaning, and yearling weight of heifersa - Germ Plasm Utilization Project - 1978-1985

		Traits					
Contrast	Birth wt (lb)	200-day wt (lb)	368-day wt (lb)				
M	ARC I						
F ₁ minus Purebreds	4.6	40	62				
F ₂ minus Purebreds	4.8	40	66				
F ₃ minus Purebreds	10.4	48	82				
M	ARC II						
F ₁ minus Purebreds	2.2	35	37				
F ₂ minus Purebreds	4.4	29	48				
F ₃ minus Purebreds	4.4	40	57				
MAF	RC III						
F ₁ minus Purebreds	4.4	29	51				
F ₂ minus Purebreds	3.7	40	64				
F ₃ minus Purebreds	4.2	35	64				
· · · · · · · · · Mean	Heterosis						
F ₁ minus Purebreds	3.7	35	51				
F ₂ minus Purebreds	4.4	35	60				
F ₃ minus Purebreds	6.4	42	68				

aSee footnotes in Table 5.

of the F2 generation will be produced, the number (Tables 4 and 5) of the F2 generation on which these estimates of heterosis are based are sufficiently large to indicate that retention of heterosis is proportional to retention of heterozygosity for individual growth traits. The F2 generation is expected to reflect about threefourths of the F1 generation level of heterosis for individual traits and all of the F1 generation level of heterosis for maternal traits, whereas, the F₃ generation is expected to reflect about three-fourths of the F1 generation level of heterosis for both individual and maternal traits; i.e., further loss of heterosis is not expected (Table 3).

Based on these early results, we conclude that level of heterosis in the F₁ generation is high for birth, weaning, and yearling wt in all three composite populations, is reasonably uniform among the three composite populations, and, on a percentage basis, is greater in females than in males (Tables 6 and 7). The level of heterosis in the F₂ generation averages approximately the same as in the F₁ generation for birth, weaning, and yearling wt even though the F2 generation is expected to have less heterosis for individual traits than the F₁ generation because expected loss of heterozygosity has already occurred. The F3 generation reflects expected loss of heterosis for both individual and maternal traits (Table 3). The level of heterosis observed for birth, weaning, and yearling wt in the F₃ generation is approximately the same as observed for these traits in the F1 and F2 generations for both males and females (Tables 6 and 7), but, as stated previously, the heterosis estimates for the F₃ generation should be interpreted with some degree of caution because of limited numbers of F₃ generation included in these analyses (Tables 4 and 5).

Reproduction and maternal traits. Breed group means for the nine purebreds and for the F₁ and F₂ generations of composite populations for some reproduction traits and for some reproduction and maternal traits combined are presented in Tables 8 and 9, respectively. These data were analyzed as traits of the dam. The results presented in Tables 8, 9, 10, and 11 are based on analyses of observations of F_1 and F_2 generation females, and, when calf traits are involved, their F_2 and F_3 generation progeny. The production of F2 generation progeny by F1 generation dams is expected to reflect about threefourths of F₁ generation level of individual heterosis and all of the F₁ generation level of maternal heterosis, whereas, the production of F3 generation progeny by F2 generation dams is expected to reflect about threefourths of F1 generation level of both individual and maternal heterosis; i.e., further loss of heterosis is not expected (Table 3).

Large differences were observed among the purebreds for most reproduction traits. Composite populations generally were equal to, or exceeded, the superior contributing purebred parents for reproduction traits (Table 8). When reproduction and maternal traits are combined (e.g., 200-day wt per cow exposed or actual calf wt weaned per cow exposed), even larger differences among the purebreds were observed, and composite populations generally equalled or exceeded the superior contributing purebred parents (Table 9).

Heterosis estimates for the F₁ and F₂ generations for each composite population and mean heterosis for the F₁ and F₂ generations for the three composite populations are presented in Tables 10 and 11, respectively, for some reproduction traits and for some reproduction traits combined with maternal traits. The effects of heterosis were significant in both the F1 and F2 generations for all reproduction and maternal traits except calving difficulty (%) and calving difficulty score (Table 10). Even though the effects of heterosis on birth wt was about 5 lb, it did not result in increased calving difficulty (Tables 10 and

The numbers on which these estimates of heterosis are based are provided in Tables 8 and 9. Heterozygosity for F₁ and F₂ generation females producing F₂ and F₃ generation progeny and expectations for heterosis for both individual and maternal traits are presented in Table 3 for each composite population and for the mean of the three composite populations. Because these data were analyzed as traits of the dam when calf traits were involved (F2 and F3 generation progeny of F1 and F2 generation dams), the F₁ generation is expected to reflect about three-fourths of the F₁ generation level of heterosis for individual traits and all of the F₁ generation level of heterosis for maternal traits, whereas, the F2 generation is expected to reflect about three-fourths of the F₁ generation level of heterosis for both individual and maternal traits (Table 3).

Table 8—Breed group means for reproduction traits - Germ Plasm Utilization Project - 1979-1986

Breed group	Na	Puberty ^b (%)	Adjusted age at puberty ^b (days)	Concept. rate, yearling ^b (%)	Concept. rate, all ages (%)	Calf crop wnd, all ages ^c (%)	Calving diff.d (%)	Calving diff. score
Mean	17,402	89.8	376	78.3	85.7	76.9	17.2	1.6
Red Poll (R)	1,325	93.2	364	81.5	87.3	78.3	13.7	1.4
Brown Swiss (B)	1,333	95.7	343	82.2	84.5	73.8	27.0	2.0
Hereford (H)	1,396	67.6	435	61.6	77.9	72.7	13.5	1.4
Angus (A)	2,385	85.0	411	77.1	84.3	73.4	7.7	1.2
Simmental (S)	1,364	93.4	365	83.1	83.5	72.5	21.8	1.8
Limousin (L)	1,525	62.2	434	48.9	73.4	70.0	14.4	1.5
Charolais (C)	1,390	82.1	402	73.2	83.6	75.7	18.2	1.6
Gelbvieh (G)	991	96.0	347	86.1	85.5	78.6	20.3	1.7
Pinzgauer (P)	722	98.4	350	88.0	89.0	79.2	22.9	1.8
MARC I F ₁ fg	1,003	94.6	377	79.5	89.6	79.0	17.6	1.6
F ₂	485	97.8	368	85.6	91.1	80.5	17.2	1.6
MARC II F ₁ fg	1,447	92.9	349	73.8	87.0	79.7	17.9	1.6
F ₂	838	94.9	361	84.5	87.9	79.9	20.4	1.7
MARC III F ₁ fg	886	96.5	364	83.1	91.6	82.2	12.7	1.4
F ₂	312	97.5	372	86.1	88.7	77.4	12.8	1.4

^aN = Number observations for conception rate all ages

Gased on females of all ages exposed to breeding.
Galving difficulty = % requiring assistance.

MÁRC I is 1/4B, 1/4L, 1/4C, 1/8H, 1/8A; MARC II is 1/4H, 1/4A, 1/4S, 1/4G; MARC III is 1/4R, 1/4H, 1/4A, 1/4P. °F, and F, are females from the first and second generation of the same breed composition producing F, and F, progeny.

Number of heifers per breed group = 178 to 573, % reaching puberty by end of breeding season, and adjusted age at puberty includes heifers that had not reached puberty by end of breeding season

Calving difficulty score—1 = no assistance, 2 = minor hand assistance, 3 = little difficulty with calf jack, 4 = slight difficulty, 5 = moderate difficulty, 6 = major difficulty, 7 = caesarean birth.

Table 9—Breed group means for maternal traits and reproduction traits combined with maternal traits - Germ Plasm Utilization Project - 1979-1986

Breed group	Na	Birth wt (lb)	200-day wt (lb)	200-day calf wt per cow exposed (lb)	Actual calf wt wnd per cow exposed (lb)
Mean	13,347	90.8	495	384	356
Red Poll (R) Brown Swiss (B) Hereford (H) Angus (A) Simmental (S) Limousin (L) Charolais (C) Gelbvieh (G) Pinzgauer (P)	948	83.5	456	358	336
	988	98.2	527	390	356
	1,064	79.2	397	292	266
	1,680	74.3	428	317	300
	965	93.8	535	390	363
	1,126	86.4	457	325	292
	1,032	98.5	516	393	365
	790	95.1	540	427	391
	551	102.3	533	427	401
MARC I F ₁ bc	895	95.5	515	410	377
F ₂	407	94.9	503	409	381
MARC II F ₁ bc	1,235	91.1	505	406	378
F ₂	624	90.9	515	418	390
MARC III F ₁ bc	765	89.0	493	408	383
F ₂	277	88.8	491	382	357

aN = Number observations

 $^{\rm b} MARC$ I is 1/4B, 1/4L, 1/4C, 1/8H, 1/8A; MARC II is 1/4H, 1/4A, 1/4S, 1/4G; MARC III is 1/4H, 1/4H, 1/4A, 1/4P.

 $^{\rm c}{\rm F_1}$ and ${\rm F_2}$ are females from the first and second generations of the same breed composition producing ${\rm F_2}$ and ${\rm F_3}$ progeny.

These early results indicate that level of heterosis is high for most reproduction and maternal traits (Tables 10 and 11). The level of heterosis for most reproduction and maternal traits averages almost as great for the F_2 generation females as for the F_1 generation females (e.g., F_2 and F_3 generation progeny out of F_1 and F_2 generation dams for traits included in Tables 9 and 11). Because expected loss of heterosis has occurred in F_2 generation females, and in F_3 generation progeny produced by F_2 generation dams, these results indicate that loss of heterosis is not greater than loss of heterozygosity for reproduction and maternal traits in *inter se'* mated composite populations.

A note of interpretation is in order for the lack of heterosis observed for conception rate in F₁ generation yearling heifers for Composite MARC II (Table 10). The F₁ generation in Composite MARC II was produced by mating mature (6- to 12- yr-old) Simmental x Angus and Simmental x Hereford cross females to Gelbvieh x Hereford and Gelbvieh x Angus cross males, respectively (Table 3). Even though these records were adjusted as appropriate for the effects of differences in age of dam, these adjustments do not remove the negative association that exists for maternal effects between generations; i.e., a highly favorable maternal environment, as provided by mature crossbred cows, may result in physiological damage that may reduce level of performance in some reproductive and maternal traits in their daughters. We

think it is likely that the relatively low conception rate (73.8%) of the F_1 generation yearling heifers in Composite MARC II (Table 8) may be the result of the favorable maternal environment provided by their *mature* Simmental x Angus or Simmental x Hereford crossbred dams. There was a normal age distribution in the dams of the contributing purebred contemporaries to which they were compared. The relatively low conception rate of the F_1 generation Composite MARC II yearling heifers accounts for the lack of heterosis in this trait and is not consistent with the relatively high estimate of heterosis for conception rate observed in the F_2 generation of Composite MARC II yearling heifers (Table 10).

We do conclude, however, that, based on results obtained through 1986 breeding (1987 calving), heterosis retained in composite populations for reproduction and maternal traits is likely not less than retained heterozygosity of the F_2 generation relative to the F_1 generation. If inbreeding is avoided, further loss of heterozygosity does not occur subsequent to the F_2 generation. Collection of additional data on reproduction and maternal traits involving F_2 , F_3 , and F_4 generation progeny out of F_1 , F_2 , and F_3 generation dams (Tables 2 and 3) on calf crops to be born through 1991 will estimate more precisely the relationship between retained heterosis and retained heterozygosity in composite populations of cattle.

Table 10—Heterosis for reproduction traitsa - Germ Plasm Utilization Project - 1979-1986

Contrast	Puberty (%)	Adjusted age at puberty (days)	Concept. rate, yearling (%)	Concept. rate, all ages (%)	Calf crop wnd. (%)	Calving diff. (%)	Calving diff. score
			- MARC I -				
F ₁ minus Purebreds	15.6	-23	11.1	9.0	5.9	004	006
F ₂ minus Purebreds	18.7	-32	17.2	10.4	7.4	411	029
			- MARC II -				
F ₁ minus Purebreds	7.4	-41	-3.1	4.2	5.4	2.048	.062
F ₂ minus Purebreds	9.4	-29	7.5	5.1	5.6	4.568	.157
			- MARC III				
F ₁ minus Purebreds	10.4	-26	6.1	7.0	6.3	-1.756	085
F ₂ minus Purebreds	11.4	-18	9.0	4.1	1.6	-1.681	071
		M	ean Heteros	is			
F ₁ minus Purebreds	11.1	-30	4.7	6.7	5.9	.096	010
F ₂ minus Purebreds	13.2	-26	11.2	6.5	4.9	.825	.019

^aSee footnotes in Table 8.

Table 11—Heterosis for maternal traits and reproduction traits combined with maternal traits^a · Germ Plasm Utilization Project · 1979-1986

Contrast	Birth wt (lb)	200-day wt (lb)	200-day calf wt per cow exposed (lb)	Actual calf wt wnd per cow exposed (lb)
	MARC	1		
F ₁ minus Purebreds	5.5	37	56	53
F ₂ minus Purebreds	5.0	25	56	56
	MARC	C II		
F ₁ minus Purebreds	5.5	30	49	48
F ₂ minus Purebreds	5.3	40	61	60
	MARC	III		
F ₁ minus Purebreds	4.1	39	60	58
F ₂ minus Purebreds	3.9	38	33	31
	Mean He	terosis		
F ₁ minus Purebreds	5.0	35	55	53
F ₂ minus Purebreds	4.7	34	50	49

*See footnotes in Table 9.