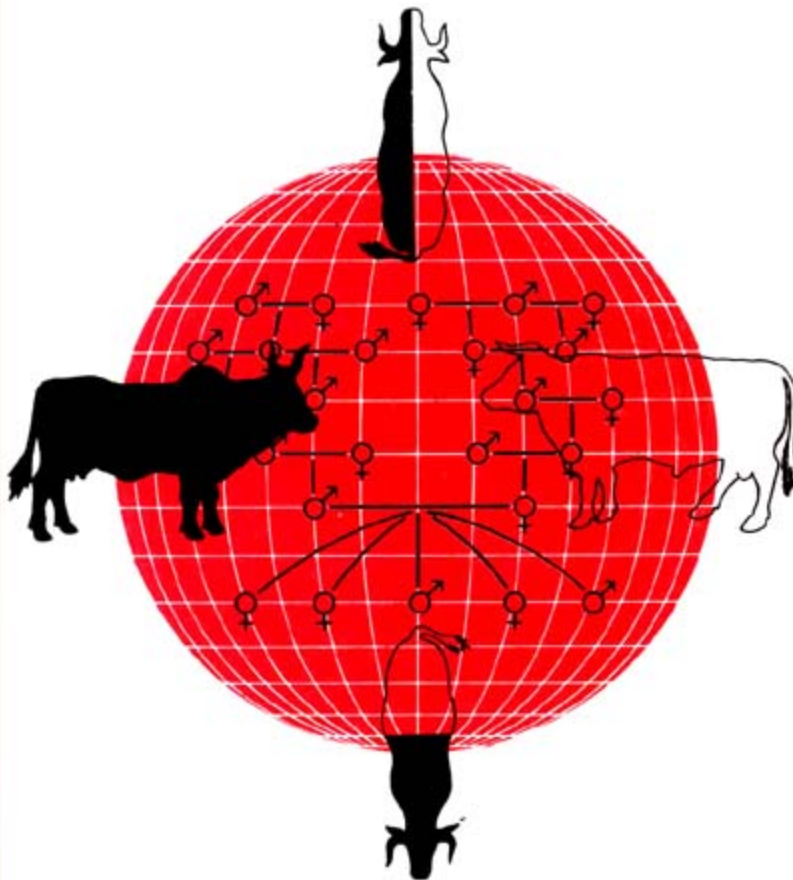


Crossbreeding *bos indicus* and *bos taurus* for milk production in the tropics

FAO
ANIMAL
PRODUCTION
AND HEALTH
PAPER

68



FOOD
AND
AGRICULTURE
ORGANIZATION
OF THE
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Crossbreeding
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and bos taurus
for milk production
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by
E.P. Cunningham
O. Syrstad

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Rome, 1987**

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PREFACE

In recent decades there have been many attempts to improve the productivity of indigenous dairy cattle in developing countries by crossing them with temperate breeds. Results have been variable with well-known examples of both success and failure. During this process much has been learned about the percentage of temperate breed genes which can be successfully introduced and also about lost adaptation of the crossbreds if the percentage of indigenous breed genes is too low. It is now clear that under most lowland tropical conditions the most productive dairy animal is a crossbred between *Bos indicus* and *Bos taurus*.

This presents animal breeders with the task of formulating a structured crossbreeding programme to create, maintain and improve the crossbred population, and thereby it raises questions about the relative importance of additive and heterotic effects and their interactions with different environmental and management levels.

FAO recently became convinced that the large number of documented crossbreeding projects between *Bos indicus* and *Bos taurus* dairy cattle in the tropics now offers the chance to develop a coherent and logical approach to this important subject. We were fortunate to be able to enlist the interests in such a publication of two researchers having both developing and developed country experience, who were already thinking and writing about this topic. This new publication offers a valuable synthesis of published data which has been integrated and reinterpreted on a global scale. In addition, theoretical models have been developed and tested against the data thus offering a rational genetic explanation for what has been experienced in practice. This provides a sound basis for the future planning of dairy cattle breeding in the tropics. The publication also develops some guidelines for planning new research in the most efficient way.

This publication will be of value and interest to all concerned with animal breeding and genetics of dairy cattle in both developing and developed countries. Clearly, when *Bos indicus* and *Bos taurus* are brought together in a systematic and orderly breeding programme, they are able to contribute effectively to increased milk production from cattle in the tropics.

ABSTRACT

This publication on the genetics and breeding of dairy cattle in the tropics is concerned with the crossing of *Bos indicus* and *Bos taurus*. It contains a re-evaluation of published papers on the subject from all parts of the tropics. It integrates and reinterprets the results globally and draws conclusions on the ideal combination of indigenous with temperate genes. It examines genetic models of the additive-dominance type. It evaluates the contributions of additive and heterotic effects and their interactions with levels of management and environment. Suggestions are made on the most efficient design of future research on this topic and breeding plans for project development are proposed.

KEY WORDS

Dairy Cattle, *Bos indicus*, *Bos taurus*, crossbreeding, adaptation, milk production, additive genetic variance, heterosis, rotational crossing, additive-dominance model, synthetic breeds, grading up, zebu cattle types, temperate cattle types, efficient design of crossbreeding experiments.

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CHAPTER 1

INTRODUCTION

The world population, now approaching 5.0 billion people, has doubled since 1950. According to present predictions it is expected to double again by the year 2025, and to stabilise at some higher level by the year 2100. Population growth is already stabilising in the developed countries. Almost all of the future expansion in numbers will therefore take place in the countries of the developing world.

The challenge to the world's cattle population in servicing human needs for milk (and also for meat and work) therefore lies overwhelmingly in developing countries. The huge expansion in demand for milk which will follow from population growth is superimposed on a milk supply position which is already inadequate. Typical annual milk consumption figures for large sectors of the developing world are around 25 kg. per head per year. This contrasts with the 300 kg. per year which is normal in the countries of the developed world.

World cattle numbers are currently 1.2 billion, giving a ratio of approximately four humans to one bovine. Broadly speaking, the developed world has one-third of the cattle, 23% of the people and produces over 80% of the milk. The countries of the developing world (Latin America, Africa and Asia) have three-quarters of the human population, two-thirds of all the cattle stocks, and produce less than 20% of the milk (Table 1.1). There are some obvious reasons for these great disparities: climate, feed resources, cattle types, degree of economic development. These factors are reflected in productivity levels per cow on the one hand, and consumption patterns per person on the other (Table 1.2).

TABLE 1.1.
PERCENT OF WORLD CATTLE, PEOPLE AND MILK PRODUCTION IN DIFFERENT
REGIONS (FAO, 1982).

	PERCENT OF WORLD		
	Cattle	People	Milk
N. America	10	6	16
W. Europe	8	8	33
E. Europe/USSR	12	8	29
Oceania	3	1	3
Lat. America	23	8	8
Africa	14	9	2
Asia:	30	58	9
Near East	5	5	2
India	15	16	3
China	5	22	1

There is a 10 fold range in milk output per cow, from approximately 500 kg. per annum in Africa and India to over 5000 kg. in North America and Europe. Milk available per person per year varies from less than 10 kg. in China to about 25 kg. in India and Africa, nearly 100 kg. in Latin America, and 300 kg. or more in most developed countries. The world average is 95 kg. per person.

At a world level there are estimated to be somewhat over 200 million dairy cows representing 17% of total cattle stocks. The definition of what is a dairy cow is a rather elastic one, and includes many animals which are only marginally involved in milk

production. Throughout the developed world, the total numbers of dairy cows are declining, though total milk production is being maintained. In the developing world, on the other hand, dairy cow numbers have been increasing, at about 3% per annum in Latin America and the Near East, and somewhat more slowly in Asia and Africa. Continued growth in numbers is expected in these areas.

TABLE 1.2.
SOME STATISTICS ON WORLD CATTLE AND DAIRY COW NUMBERS AND MILK OUTPUT (FAO, 1982).

	Total Cattle m.	Dairy Cows m.	Dairy Cows As % cattle %	Total Milk mt.	Milk/Cow kg.	Total People m.	Milk/Person kg.
N. America	128	13	10	70	5285	256	272
USA	116	11	9	62	5637	232	266
L. America	277	36	13	35	975	382	91
Brazil	93	15	16	11	738	128	84
W. Europe	100	37	37	143	3838	375	381
E. Eur/USSR.	149	57	44	128	2248	383	335
USSR	116	44	38	90	2052	269	333
Asia	366	58	16	40	699	2672	15
Near East	56	15	27	10	975	224	44
India	182	26	14	14	531	712	19
China	55	9	16	6	699	1021	6
Africa	173	22	13	10	473	401	26
Oceania	33	4	12	12	3027	18	656
World	1226	209	17	438	1935	4591	95

In parallel with these broad differences in numbers and productivity of dairy cows between the developed and developing worlds, there is also a major difference in cattle types: *Bos taurus* breeds being exclusively used in temperate and developed areas, while *Bos indicus* types predominate numerically throughout most of the developing world (Figure 1.1). The origins of these two broad cattle types predate modern organised breeding programs. The physical, physiological and behavioural differences between the two types arise from the different selection pressures exercised over long periods by the very different physical environments to which they were exposed. These differences have been accentuated within the past century by accelerated selection for high level specialised dairy production in some *Bos taurus* populations. Within *Bos taurus*, this has led to the emergence of a few dominant breeds, with an increasing global dominance of Holstein-Friesian types. This process of highly effective selection for dairy function, coupled with increasing concentration on fewer breed types, is continuing.

As various countries in the developing world tackle the challenge of increasing the productivity of their dairy cow populations, it is immediately apparent that the substantial genetic difference in milk production potential between *Bos indicus* breeds and improved *Bos taurus* breeds is too large to be ignored. To put this difference in perspective, we could say that the *Bos taurus* dairy cattle appear to have a genetic potential for milk production 100% higher than that of *Bos indicus* (see table 5.7.1.3). At the same time, efficient dairy selection schemes produce rates of genetic change of approximately 1% per year. The genetic difference between *taurus* and *indicus* types therefore is roughly equivalent to the gain achievable from 100 years of sustained and highly efficient selection within a population.

The most obvious way to exploit this difference would be to simply import *Bos taurus* cattle to tropical areas. This has been tried on many occasions in the past, generally with unsatisfactory results. *Bos taurus* types usually fail to produce adequately, and often even to survive, in the face of the multiple challenges of climatic stress, new diseases and parasites, and nutritional insufficiency. In recent decades, some successes have been achieved, particularly in the dry tropics, where great efforts have been made to control disease, improve nutrition, and reduce climatic impact. Nevertheless, the early failures led to considerable disillusionment with *Bos taurus* types in tropical areas. The result was, particularly in India, the adoption of policies of reliance on development of local breeds.

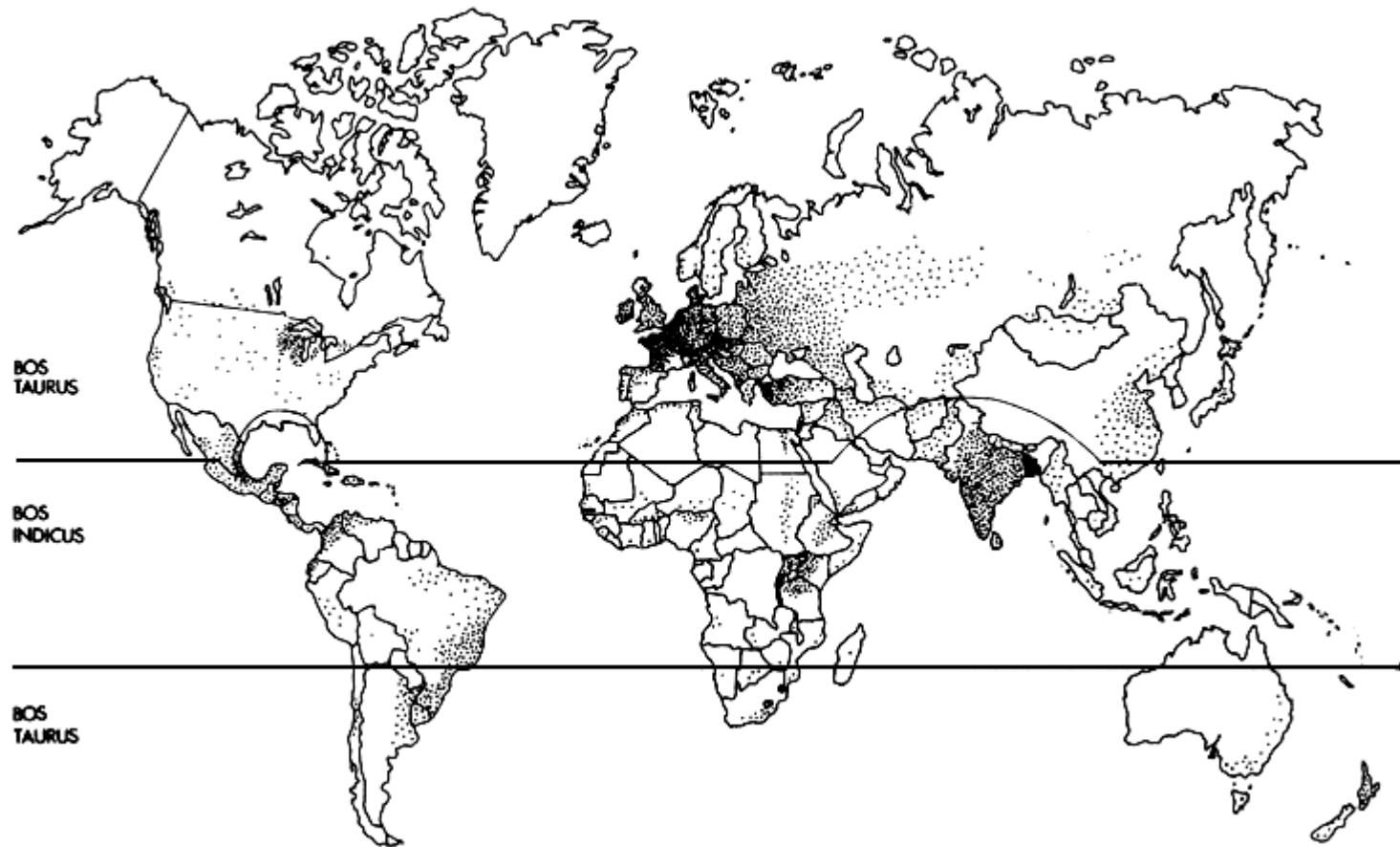


Figure 1.1 World distribution of dairy cows, showing the approximate limits of Bos Taurus and Bos Indicus predominance.

In the last three decades, the accumulation of new knowledge and new techniques has led to a further shift in opinion on these matters. The availability of artificial insemination has made crossbreeding between *Bos taurus* and *Bos indicus* populations very widely possible. The conclusions from a substantial number of crossbreeding trials, summarised later in this report, indicate substantial advantages, even in stressful conditions, for crossbreds between the two types. These questions have been most systematically addressed in India, where the accumulated information has led to a change in national policy, which now is aimed at producing crossbreds between *Bos taurus* and local *Bos indicus* breeds on a very large scale (20 million). This strategy is being emulated on a smaller scale in many other countries whose native populations are of *Bos indicus* type.

The scale of commitment of resources to these large crossbreeding schemes is very great. It is also a commitment which has to be sustained for many decades into the future. Furthermore, it is essential that these programs are successful, if the challenge of real nutritional need in the developing countries is to be met. All of these considerations serve to emphasise the necessity for soundly based decision making in the planning stages of these crossbreeding programs. This requires both the generation and correct interpretation of appropriate experimental and pilot scale data. It also requires a rational planning framework on which to develop practical breeding schemes.

CHAPTER 2

GENETIC ASPECTS OF CROSSBREEDING

The purpose in the discussion which follows is to establish a sound basis, both in terms of genetic theory and in the light of experimental evidence, for a rational choice of breeding or crossbreeding strategy in any particular case.

First, however, it is useful to set crossbreeding options in context with selection alternatives. Selection within populations is based on a simple additive model of gene action. In practice it generally delivers genetic gains in line with theoretical expectations (Smith, 1984).

Crossbreeding is often regarded as an alternative to selection. It therefore needs to be stressed that these are not mutually exclusive strategies, and that any of the crossbreeding options discussed here requires a supporting selection program, either in the contributing pure breeds, or in the resulting synthetic. The relationship between possible selection and crossbreeding strategies in a typical local dairy cattle population where crossing with an exotic breed is being contemplated is illustrated in Figure 2.1

2.1 GENETIC MODELS

The average performance of a group of animals is determined by their genetic capacity and by the environmental conditions in which they are kept. Sometimes the genetic and environmental components interact, e.g., when genetic differences between animals are larger in one environment than in another.

The genetic component is the aggregate effect of the actions of innumerable genes acting individually and in concert with other genes or groups of genes in the System. The bovine genotype has of the order of three million such genes. Many are no doubt functionless as far as any particular trait is concerned. Much is known about the biochemical structure and function of some genes. For most, however, we have no such information. Since there is little evidence that individual genes have major effects on most economic traits, it would in any case be difficult to use such information for the purposes of genetic improvement.

The genetic models from which we develop working procedures for breeding programs therefore begin at the level of the gene. Since genes occur in pairs, and are also grouped in chromosomes, it is convenient to consider gene effects at three levels:

- Additive effects: the effects due to single genes acting independently of the remainder of the genotype.
- Dominance effects: the effects due to the joint action of gene pairs within loci.
- Epistatic effects: the effects due to the joint action of two or more genes at two or more loci.

Selection theory is based on the accumulation of favourable additive effects from generation to generation. Crossbreeding theory is largely (though not exclusively) based on the arrangement of favourable dominance effects in each generation. These dominance effects are not cumulative from one generation to the next, though they can be enhanced by appropriate selection (e.g., Rich and Bell, 1980; Orozco, 1976). Epistatic effects can take an infinite number of forms involving any number of genes and any number of loci. It is therefore impossible to build any general consideration of epistatic effects into either selection or crossbreeding models.

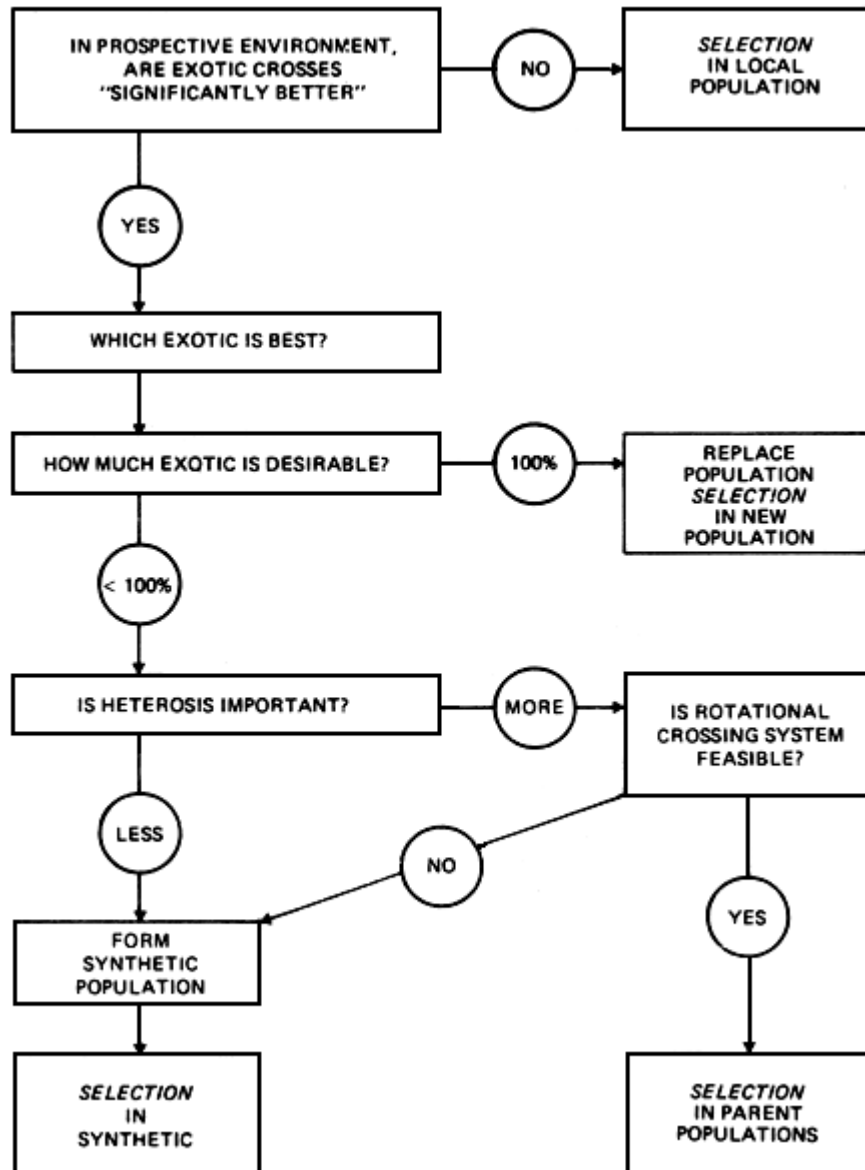


Figure 2.1 Strategic options involving crossbreeding and selection.

In the discussion which follows, the main emphasis is on the development of models for crossbreeding based solely on additive and dominance effects. In many cases, these are a fully adequate basis for breeding decisions.

The main factors which can render these models inadequate in certain cases are (1) the presence of epistatic effects (2) the presence of maternal effects (3) interaction of genotypic effects with environmental factors. These factors are discussed separately.

2.2 THE ADDITIVE-DOMINANCE MODEL (GENE LEVEL)

This is the name used for a model which includes only additive and dominance effects. In the case of an individual (or group) produced by combining two separate genetic strains through some crossing system, the additive component is proportional to the gene contribution from each strain. For example, in a first cross (F_1) between two strains (P_1 and P_2) the additive value is $1/2 (P_1 + P_2)$. The additive value of a backcross to strain 1 ($B_1 = P_1 \times F_1$) is $3/4 P_1 + 1/4 P_2$.

The dominance value is somewhat more complex. Since it is made up of the aggregate of dominance effects at many separate loci, it can be explained best by considering it first at one locus. Assume that for any particular locus, there are two alleles, A_1 and A_2 with frequencies p and q . Define the present genotypic mean, determined by all other loci except this one, as μ . Let the value of the genotype $A_1 A_1$ then be $\mu + a$, that of the genotype $A_2 A_2$ be $\mu - a$ and that of the heterozygous genotype $A_1 A_2$ be $\mu + d$. This situation is illustrated in Figure 2.2 for four different degrees of the dominance effect, d .

It is clear that d is simply the deviation of the heterozygote $A_1 A_2$ from the average of the two homozygotes $A_1 A_1$ and $A_2 A_2$. For reasons which are discussed below, it has generally been found that these dominance effects are positive. The mean genotype is then the average of the three genotypic values, which is obtained by multiplying each of them by its frequency and summing these products:

$$\begin{aligned} \text{Mean} &= p^2(\mu + a) + 2pq(\mu + d) + q^2(\mu - a) \\ &= \mu + (p - q)a + 2pqd \end{aligned}$$

In the absence of selection, efforts to increase or decrease the level of heterozygosity in a population do not of themselves change gene frequencies - they merely change the relative proportions of homozygotes and heterozygotes. The first two terms in this equation are therefore not affected by increasing or decreasing heterozygosity. The third term is simply the product of the frequency of heterozygotes and the dominance effect at that locus. Given that there is some dominance, the mean genotypic value is then a linear function of the proportion of heterozygotes.

This model relates to a single locus. Extended to N independent loci, it says that the mean genotypic value in the population is a linear function of the average heterozygosity at all loci at which some dominance exists. The nature of the dominance effect does not need to be specified - there may be partial, complete or overdominance at any or all of these loci.

Fisher (1931) developed the argument that evolution will tend to have produced dominance of favourable genes, and recessiveness of deleterious genes. He suggested that this is brought about by the effect of selection acting on genes (at other loci) which modify the value of the heterozygote. Wright (1977) and Kacser and Burns (1981) have shown that the evolution of dominance is more likely to be a consequence of the way enzymes interact in metabolic pathways. Most experimental evidence confirms that

disadvantageous mutants tend to be recessive. The widespread occurrence of dominance (partial, complete or over-dominance) of favourable alleles provides the basis for the general expectation that at any particular locus the heterozygote will be better than the mean of the two corresponding homozygotes. Carried through to N loci, this leads in turn to the expectation that the mean genotypic value of the population should increase linearly as heterozygosity increases.

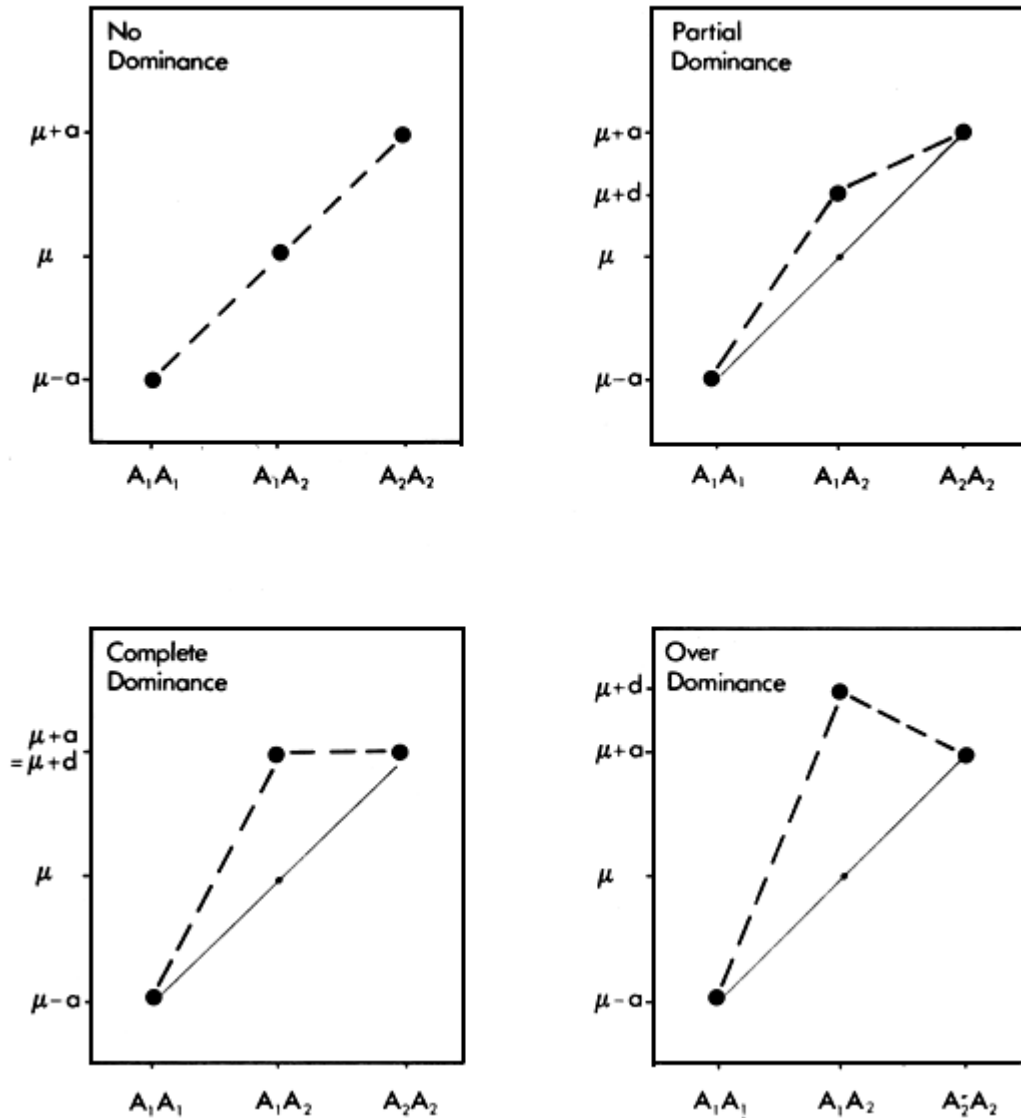


Figure 2.2 Different degrees of single locus dominance.

2.3 THE ADDITIVE-DOMINANCE MODEL (POPULATION LEVEL)

The sum of all positive or beneficial dominance effects at individual loci is the basis of the broader concept of heterosis. Heterosis is defined as the deviation (positive or negative) of an individual or group from the mean of its parents. Because heterosis is almost exclusively the aggregate of all single locus dominance effects, and because these are usually positive or beneficial, heterosis can be expected also to be usually in a favourable direction. This has generally been found to be the case.

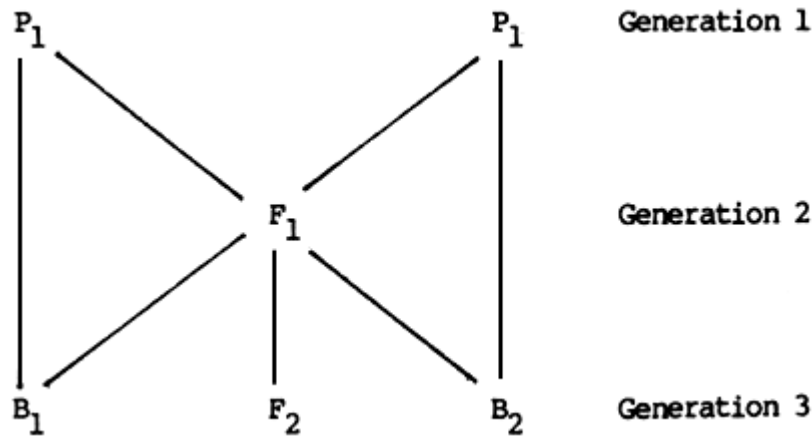
Arising from the single locus model, the heterosis effect is also expected to be a linear function of the level of heterozygosity. Extending the Additive-Dominance model from its single-locus version to the level of a multi-locus trait, we can say that the expected average performance of any group of individuals produced by combining the genetic resources of two parental strains through some form of crossbreeding will be

$$\mu + X_1 A + X_2 H$$

In this model, μ is the overall mean value in the population, A is the additive difference between the two parental strains, and H is the heterosis displayed by their F_1 offspring. Note that A is the sum of the additive gene effects for which the parental strains differ, and H is the sum of the dominance effects created when the two strains are crossed. The weighting factor X_1 , measures the proportion of genes contributed by the two strains, and X_2 measures the level of heterozygosity. If the additive difference A is defined as $P_2 - P_1$, then μ can arbitrarily be set equal to P_1 and X_1 will simply be the proportion of genes contributed by the second parent, P_2 . From the mating System that is used to produce any particular crossbred group, the value of X_2 , the expected heterozygosity level, can readily be calculated.

In order to predict the genetic value of a crossbred group therefore, we need to know four quantities: A , H , X_1 and X_2 . The two weighting factors X_1 and X_2 can be deduced from the mating or breeding structure. The values of A and H need to be estimated from actual data. The real purpose of experiments intended to clarify crossbreeding options is therefore the estimation of A and H .

The use of this model to describe or predict the genetic value of a group can be illustrated by applying it to the first four types of crossbreds which can be produced from two parental breeds or strains. These types or groups are



P_1 and P_2 are the parental strains, e.g., Sahiwal and Holstein breeds. F_1 is the first crossbred generation, produced by mating Sahiwal cows to Holstein bulls (or vice versa). F_2 is the second crossbred generation, produced by mating F_1 bulls to F_1 cows. B_1 and B_2 are backcrosses to Sahiwal (P_1) and Holstein (P_2) respectively, produced most conveniently by mating Sahiwal and Holstein bulls to F_1 females. In each case, the reciprocal crosses (i.e., F_1 bulls mated to Sahiwal and Holstein cows) could also be used to produce the same genotypes.

The difference between the parental breeds is $P_2 - P_1 = A$. The heterosis shown by the F_1 is $F_1 - (P_1 + P_2)/2 = H$. The expected value of each group is then as follows.

$$\begin{aligned}
P_1 &= \mu \\
P_2 &= \mu + (1)A \\
F_1 &= \mu + (1/2)A + (1)H \\
F_2 &= \mu + (1/2)A + (1/2)H \\
B_1 &= \mu + (1/4)A + (1/2)H \\
B_2 &= \mu + (3/4)A + (1/2)H
\end{aligned}$$

The relationships between these six genetic groups are illustrated in Figure 2.3.

Since the expected performance of each group is a function of two factors, A and H, it can be displayed by superimposing the heterosis effect H on the additive effect A. The result is a diagram which has some resemblance to the front elevation of a classical Greek temple, and is therefore called the Greek Temple Model (Cunningham, 1987).

It is clear that, provided this Additive-Dominance model is appropriate, the expected value of any group resulting from a crossbreeding scheme can be predicted if we know the values of A + H and can state (i) the proportion of genes from the two parental strains and (ii) the proportion of maximum heterozygosity. In the following section, a number of crossbreeding Systems are considered using the framework provided by this model.

2.4 SYNTHETIC BREEDS

A synthetic population can be formed by inter se mating from any crossbred group. The simplest form of synthetic, with two parental breeds, is formed from the F_1 generation. The performance of the F_2 and subsequent generations can be readily predicted. On average, they contain a 50% gene contribution from each parental breed, and therefore have half of the additive effect. They also, on average, retain 50% of the heterozygosity of the F_1 generation, and therefore should display half of the heterosis effect.

Synthetics may also be formed from any other crossbred group, for example, a backcross to the superior breed. This will have three-quarters of the additive effect, and should have 37.5% of the heterosis effect. In general, the proportion of maximum heterozygosity, and hence of heterosis, retained in synthetic populations is (Dickerson, 1973)

$$1 - \sum p_i^2$$

where P_i is the proportion of genes contributed to the synthetic by the i th source breed. Thus, a synthetic started from a backcross will have .75 of its genes from one breed and .25 from the other. The proportion of heterozygosity retained is then

$$1 - .75^2 - .25^2 = .375$$

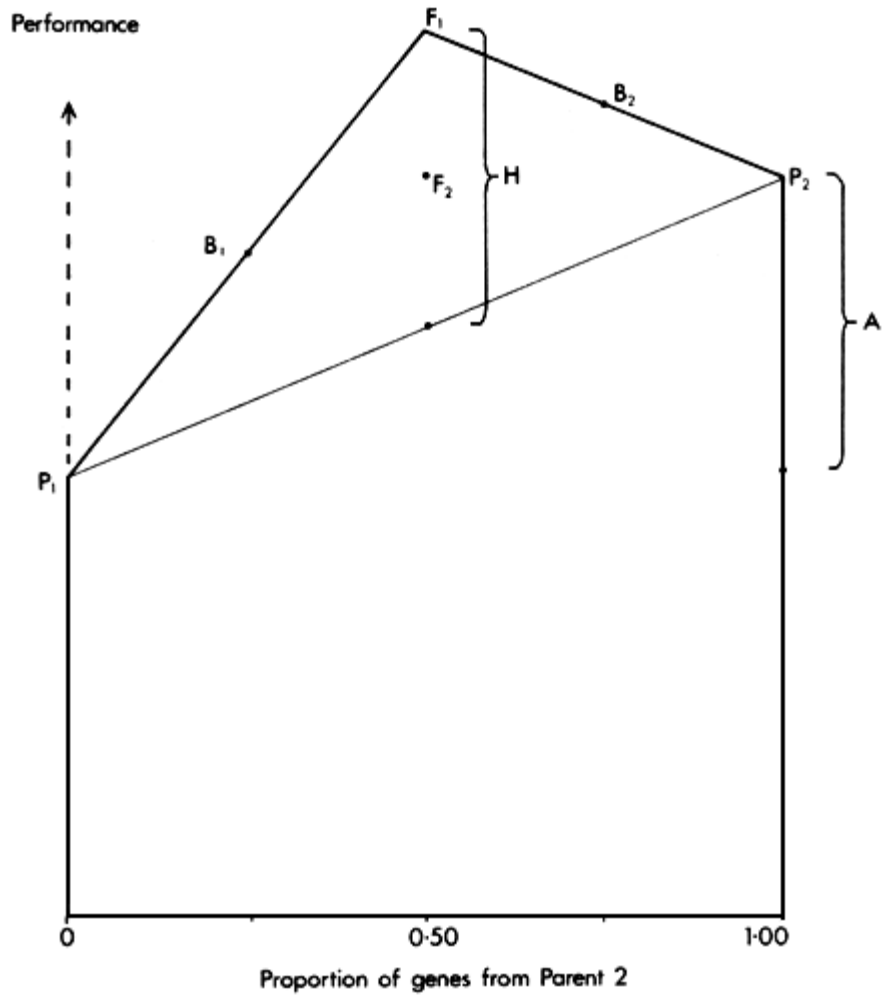


Figure 2.3 The Greek Temple Model, showing the expected performance of parental (P^1 and P^2), F^1 , F^2 and backcross (B^1 and B^2) groups as functions of Additive (A) and Heterosis (H) effects.

In the context of crossbreeding between *Bos taurus* and *Bos indicus*, we are usually dealing with two breeds only - one from each type. Where a third breed is involved it is usually a second *Bos taurus* type. Heterosis between *Bos taurus* breeds is usually very low by comparison with that found for taurus-indicus crosses. In considering such three breed synthetics therefore we are usually concerned only to measure how much of this taurus-indicus heterosis is retained. This can be calculated simply by considering the two *Bos taurus* contributing breeds as if they were one.

The proportion of heterosis retained in synthetics formed with various proportions of *Bos taurus* and *Bos indicus* is then as follows:

PROPORTION OF GENES FROM		PROPORTION OF HETEROSIS RETAINED IN SYNTHETIC
TAURUS	INDICUS	
.125	.875	.22
.25	.75	.375
.375	.625	.47
.5	.5	.5
.625	.375	.47
.75	.25	.375
.875	.125	.22

Since a synthetic can be formed by inter se mating of individuals with any level of gene proportions from the two parental breeds, the expected performance of synthetics then forms a continuous curve on the Greek Temple diagram (Figure 2.4). For any given gene proportion, the synthetic is always inferior to the original cross from which it was formed.

2.5 ROTATIONAL CROSSING

A rotational cross between two breeds is established by using pure bred males of each breed in alternate generations. The first generation is clearly an F_1 , but after a few generations the population has a two-third gene complement from one parental breed, and one-third from the other. In each following generation, the two parental breeds still contribute two-third and one-third of the gene complement, but the position of the two breeds is reversed. In each generation, the breed contributing two-thirds of the gene complement is the breed which most recently provided the males to the mating system.

In each generation, the proportion of maximum heterozygosity retained is two-thirds, and therefore the expected performance includes two-thirds of the heterosis effect.

The performance of animals in two successive generations of a two breed rotation is thus

$$\mu + 1/3A + 2/3H \text{ and}$$

$$\mu + 2/3A + 1/3H.$$

If A is large, then these two generations may differ substantially in performance. With overlapping generations, the population would then contain animals of quite variable type and production levels, and this can be a serious disadvantage.

Figure 2.4 shows the two positions occupied by alternate generations of a two breed rotation relative to the parental breeds, F_1 , backcrosses and synthetics.

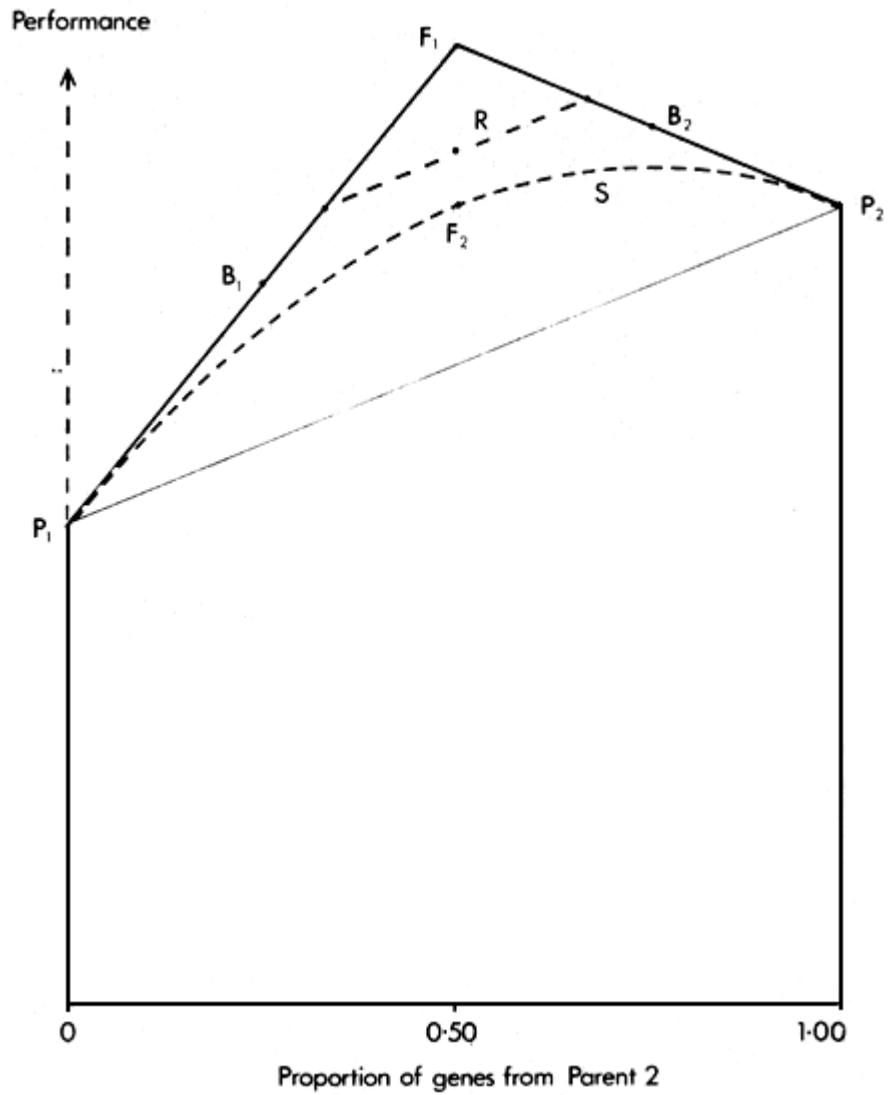


Figure 2.4 The Greek Temple Model, showing the expected performance in Rotational (R) and Synthetic (S) breeding systems

2.6 DEVIATIONS FROM THE ADDITIVE-DOMINANCE MODEL

The previous discussions have all been based entirely on the additive-dominance model. The following are the three main factors which can, in some circumstances, render this model inadequate.

Epistatic effects. The term epistasis is used to describe all multiple gene effects which involve more than one locus. The simplest such effect is the joint effect of two genes at two separate loci. This specific kind of epistatic effect is an additive by additive effect. The joint effect of a single gene at one locus and a gene pair at a second locus is another form of epistasis, called an additive by dominance effect. If we limit consideration to two loci, there are possible four such additive by additive effects, four additive by dominance effects and one dominance by dominance effect, or a total of nine specific types of epistatic effect. These may be positive or negative. Cockerham (1954) has written a general model to accommodate these effects. It is, however, difficult to measure the effects in practice.

Using differing specifications of the effects, Dickerson (1973), Kinghorn (1980), Hill (1982) and Sheridan (1981) have given the expected performance of different types of crosses, taking account of two locus epistasis. Koch et al (1985) discuss the relationships between the first three of these formulations of epistasis. In all cases, the loss of beneficial epistatic effects in F_2 and backcross generations, and in rotational and synthetic populations led to the expectation of lower performance in these cases than would be predicted solely from the additive-dominance model.

If consideration is extended to three or more loci, then the number and kind of possible epistatic effects increases rapidly, and genetic models are of purely theoretical interest. Attempts to interpret deviations from the additive-dominance model in terms of epistasis have therefore largely been limited to consideration of two locus epistasis.

What evidence is there of the existence of significant epistatic effects? Cunningham (1982) concluded that the great majority of analyses reported in mice, dogs, corn and beef cattle supported the adequacy of the additive-dominance model. Sheridan (1981) presented evidence in poultry, showing that this model was insufficient. In particular, his data showed performance in the F_2 substantially below expectation. The data from *Bos taurus* - *Bos indicus* crossbreeding trials, summarised by Syrstad (See Section 5.7), suggest that a similar situation may obtain for first lactation milk production, though for other traits the additive-dominance model seems adequate.

In the context of planning dairy cattle crossbreeding in the tropics, therefore, it seems reasonable at the present state of knowledge to develop the plans using the additive-dominance model. However, a particular aim of future crossbreeding experiments should be to further test the validity of this model.

Maternal effects. Some traits are substantially affected by the maternal environment. This is particularly the case where the offspring are reared on the dam, as in most sheep, beef cattle and pig production systems. In such cases, the maternal effect, like other effects with a genetic component, can have both additive and dominance components. Under the same assumptions as before, these lead to additive and heterosis effects which are proportional to the gene complement in the dam, and to the fraction of maximum heterozygosity in the dam. Where necessary, these elements can be added to the model, and can be estimated from appropriate analyses. The models are discussed in Dickerson (1973) and a good example involving beef cattle is given by Koch et al. (1985).

In the context of dairy cattle crossbreeding in the tropics, maternal effects can generally be ignored. The reasons for this are first that the calves are generally reared artificially from birth, and secondly that the traits of most interest are recorded after a long interval of separation between dam and offspring. Maternal effects are therefore not taken into account in the models elaborated here.

Genotype by environment interaction. Both additive and heterosis effects can vary with environmental level. Additive by environment interactions are well documented. There is less evidence for interaction of heterosis by environment interaction. However, the review by Barlow (1981) concluded that it was more often the rule than the exception.

These interactions are of obvious importance in predicting the consequences of different crossbreeding Systems. Since the predictions in all cases depend on the estimated level of additive and heterosis effects, the accuracy of the predictions depends on the validity of these estimates in the environment in which the crossbreeding system is implemented. The existence of interactions will also mean that the crossbreeding Systems appropriate, with a particular pair of breeds, in one location may not be appropriate in another environmental situation.

Figure 2.5 illustrates a range of situations in which the absolute and relative sizes of the additive and heterosis effects vary. Three levels of the additive effect are included ($A = 80\%$, 40% and 20% of mid-parent value). Likewise, three levels of heterosis effect are used ($H = 40\%$, 20% and 10% of mid-parent value). It can be seen, by reference to Figure 2.4, that the expected performance levels of the parents, F_1 , F_{2-} , backcrosses, rotation and synthetic groups relative to each other will all depend on the absolute and relative levels of both A and H . These in turn may, for a given pair of breeds, depend on the environment.

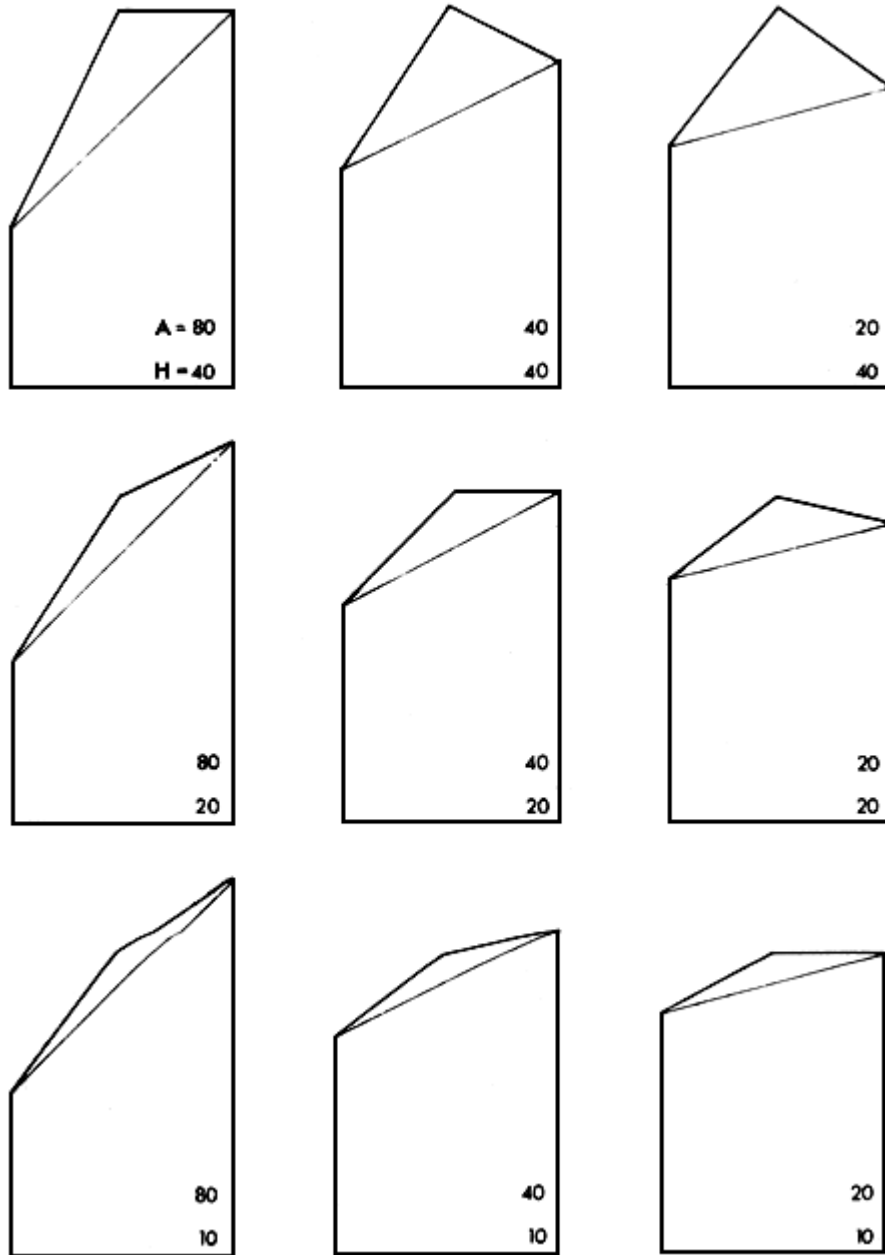


Figure 2.5 Greek Temple Models illustrating nine combinations of levels of A (80, 40 and 20%) and H (40, 20 and 10%)

CHARTER 3

DIFFERENT CROSSBREEDING SYSTEMS

Crossbreeding strategies can be classified into the following three broad categories:

- Breed replacement strategies
- Establishment of stable crossbreeding Systems
- Formation of synthetic populations

In the context of dairy cattle crossbreeding alternatives, there are some practical limitations to the range of possibilities which can be considered. In most cases, attention is limited to two breeds, one a local Zebu population and the other an exotic, usually a *Bos taurus* breed. The advantages of involving a third breed are seldom substantial. Continuing access to an exotic breed through artificial insemination makes grading up schemes a relatively easy option. The establishment of a synthetic is often operationally easier than the organisation of a rotational breeding structure.

In order to consider any of these breeding strategies it is necessary to balance these questions of operational convenience and cost against the estimated genetic benefits resulting. These in turn depend on the extent of the additive and heterotic effects to be exploited. The scale of these may depend on the environment. The proportions of these effects which are in fact utilised will depend on the fraction of maximum heterozygosity and on the balance of genes between the contributing breeds. The first element in the examination of any particular strategy must therefore be to quantify additive and heterotic effects.

3.1 GRADING UP TO EXOTIC.

This is probably the most widely practiced of all crossbreeding Systems. It is in fact a population replacement strategy, replacing more than 90% of the genotype of the local population within four generations.

The breeding structure is shown in Figure 3.1, where E stands for the exotic breed, and L for the local. Figure 3.1 also shows the rate at which gene replacement takes place in the local population, and the extent to which maximum heterozygosity is lost as the generations proceed. After the first two or three generations, the amount of heterosis contributing to performance becomes negligible. This strategy therefore depends almost entirely on the size of the additive difference between the two breeds. It also depends on this additive difference being large relative to any heterosis effects.

3.2 GRADING UP TO 50% EXOTIC

In many instances, it is clear that less than 100% replacement of the genes of the local population by exotic *Bos taurus* genes is desirable. One crossbreeding strategy in these circumstances which has both operational and genetic advantages is to grade up to 50% exotic bulls. The breeding structure, and the way in which heterozygosity is maintained and exotic genes are introduced to the population is shown in Figures 3.2 and 3.3. Bulls from the exotic breed (E) are mated to selected cows of the local population (L_1). The F₁ bulls produced by these matings are then used for general crossing on the main local population (L).

In each generation, 50% of the maximum heterosis effect is maintained. The first crossbred generation in the local population has 25% of exotic genes, but this proportion

rapidly approaches a stable value of 50%. The System therefore exploits half of the heterosis effect and half of the additive difference between the local and exotic breeds. The expected performance level is that of the F_2 or 50% synthetic (Figure 2.3). Depending on the relative sizes of the heterosis and additive effects, this combination could therefore give close to optimum performance.

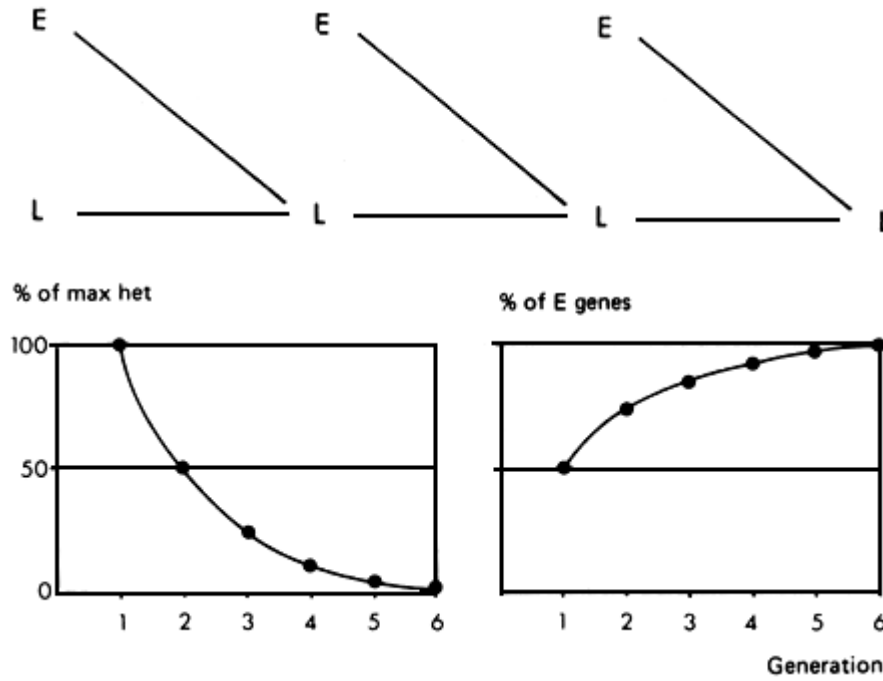


Figure 3.1 Grading up to exotic: breeding structure, rate of retention of heterosis and rate of infusion of exotic genes.

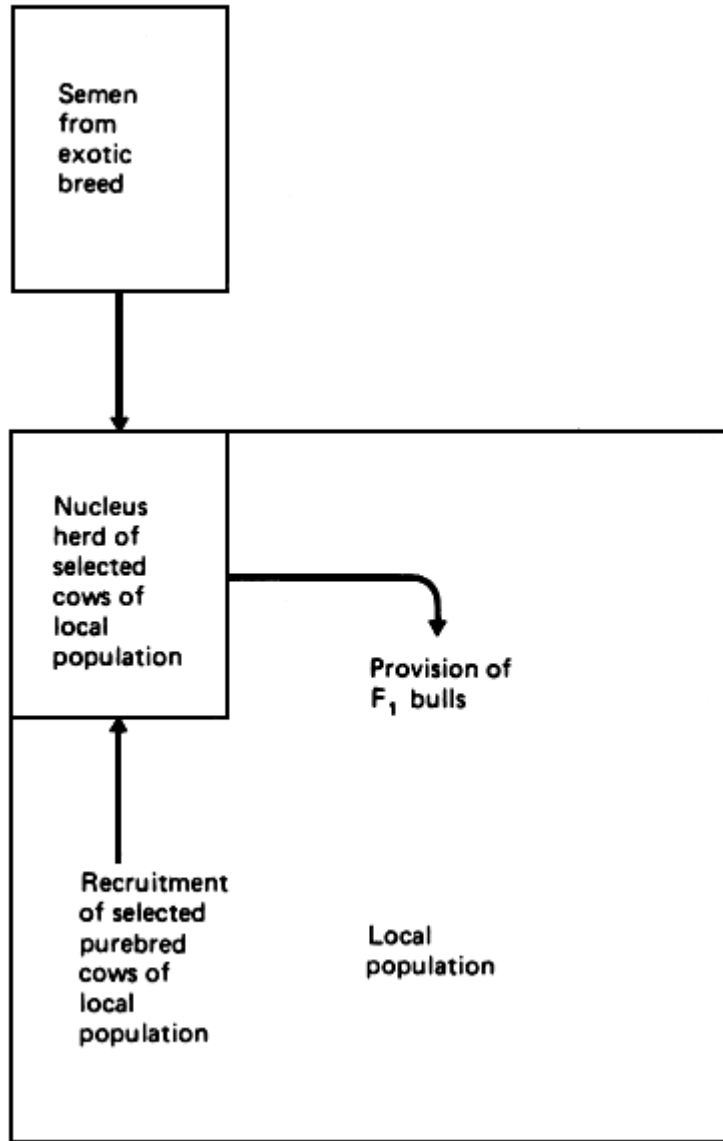


Figure 3.2 Grading up to 50% exotic: breeding structure.

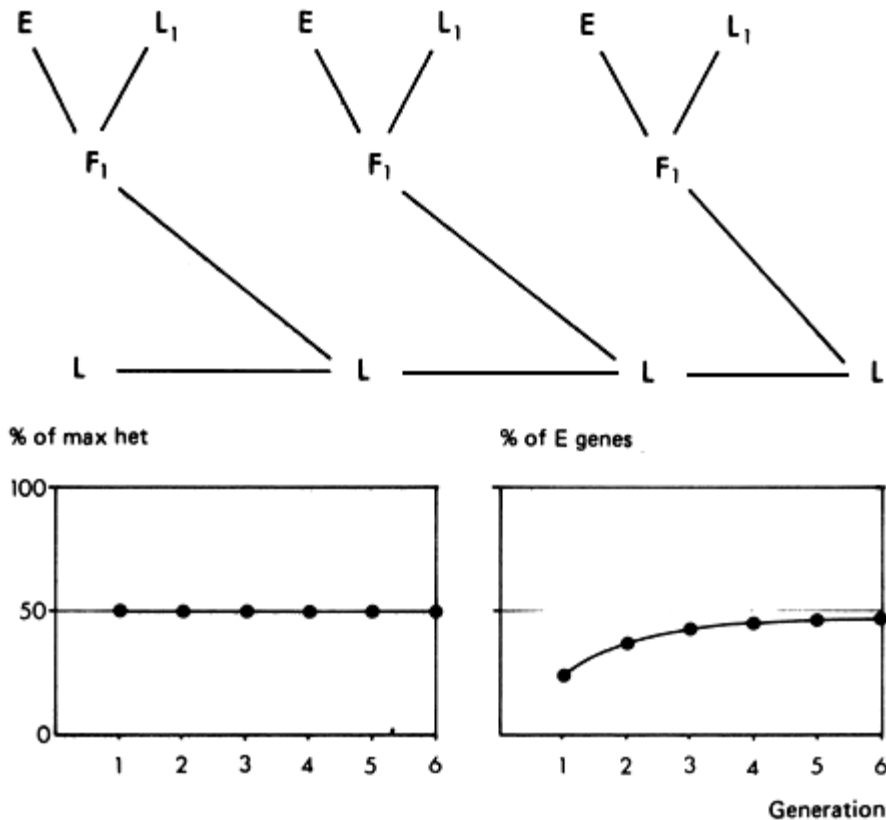


Figure 3.3 Grading up to 50% exotic: breeding structure, rate of retention of heterosis and rate of infusion of exotic genes.

The operational advantages of the scheme are as follows. In many local populations, it is difficult to organise any kind of breeding intervention other than the provision of bulls. On the other hand, it may well be possible to organise an effective nucleus herd of selected females from the local population. These females could then be mated with semen imported from the chosen exotic, and the resulting F₁ bulls could be used either in natural service or artificial insemination to breed the local cow population. In addition to achieving a planned exploitation of both heterosis and additive differences, therefore, the structure would also permit exploitation of any selection gains achieved in assembling the nucleus herd. It would also permit continuous exploitation of any genetic improvement in the exotic population.

The overall advantages are that the desired intermediate genotype is rapidly achieved; a significant proportion of maximum heterozygosity is retained; no organised activity is required in the commercial population, other than the acceptance of F₁ males; if the selection of B₁ females as dams of F₁ males is effectively done, then the benefits of improved local genes are recirculated to the population; and finally, the continuing benefits of any selection program in the exotic population are carried through rapidly, and continuously, into the local population.

3.3 GRADING UP TO 75% EXOTIC

If a higher degree of exotic genes is required in the crossbred population, but still short of 100%, one possibility is to grade up to three-quarter exotic bulls. This structure is illustrated in Figures 3.4 and 3.5. As in the preceding structure, exotic bulls are first

mated to selected females of the local population to produce an F_1 generation. These are backcrossed to the exotic to produce three-quarter bred males, which are then used on the local population. This procedure could be repeated in each generation, thus exploiting the opportunity of using whatever genetic improvement was taking place in the exotic population. Alternatively, a synthetic population could be formed by mating the backcross bulls to females of the same genetic constitution, and this nucleus synthetic group could be a continuing source of three-quarter bred bulls for use in the local population.

This breeding System brings the local population up to three-quarters exotic genes within about four generations. On the other hand, the proportion of maximum heterosis, which begins at 75% in the first generation, drops to a level of 37.5%. The expected performance level is that of a synthetic population with 3/4 exotic genes.

As can be seen from the different situations shown in Figure 2.4, the relative performance of populations obtained by grading up to 50% or 75% exotic bulls will depend on the relative sizes of the additive and heterosis effects. For example, the data summarised elsewhere in this report suggest that the additive difference between *Bos taurus* and *Bos indicus* breeds is of the order of 100% (of mid-parent mean), while the heterosis effect is about 25%. With these values, the 3/4 exotic population will have a performance about 13% higher than the 50% exotic. If additive and heterosis effects are each equal to 50% of mid-parent mean, then the advantage is only 4%. If heterosis is high, say 50% of mid-parent mean, while the additive difference is low, say 20%, then the 3/4 exotic has an expected performance 1% below that of the 50% exotic population.

3.4 CONTINUOUS F_1 PRODUCTION

This is in some ways the simplest crossbreeding System of all. Bulls of the exotic breed are used on females of the local population to produce F_1 offspring which form the commercial population. The two pure breeds are used in each generation to repeat this process. The main disadvantage in a cattle context is that a large population of the local genotype would need to be maintained in pure form as a source of these crossbred offspring. The system is widely used in pigs and in poultry where, because of the high reproductive rate, a small nucleus of purebred females can provide all the replacements for the commercial population.

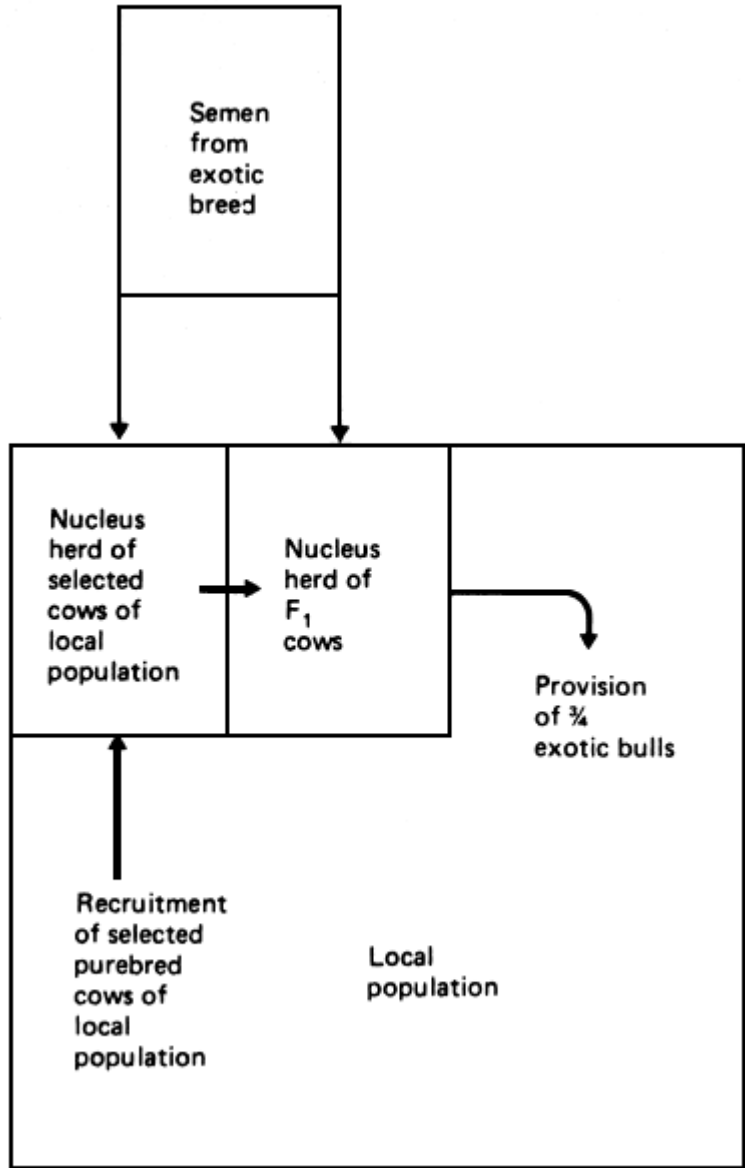
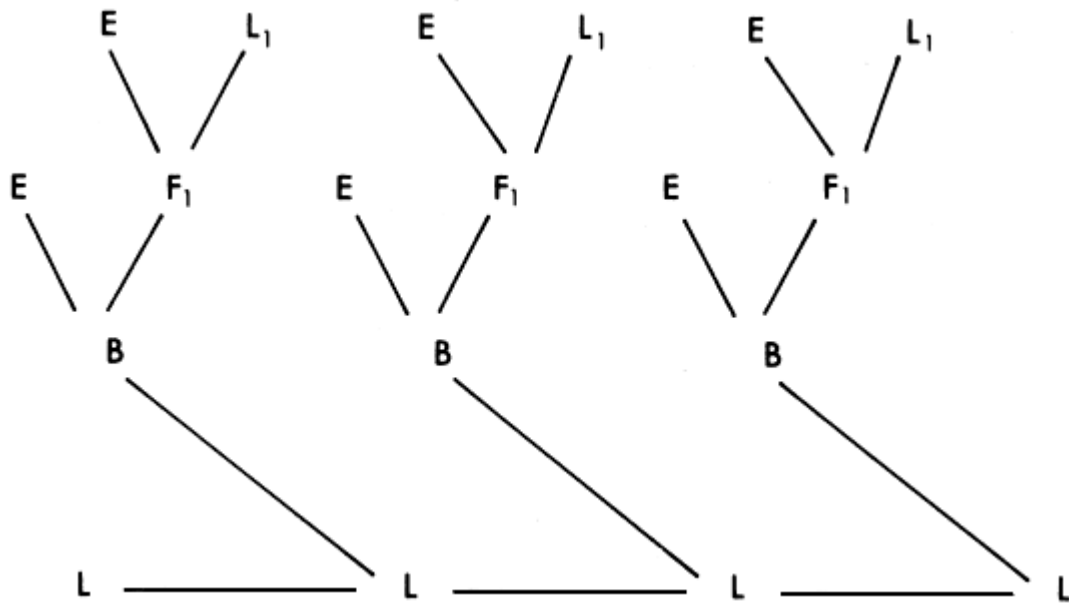
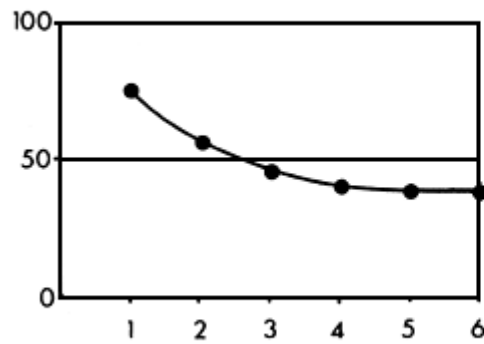


Figure 3.4 Grading up to 75% exotic: breeding structure.



% of max het



% of E genes

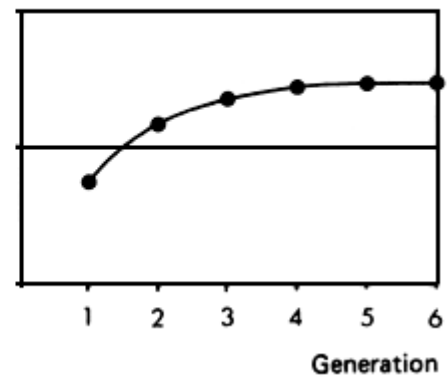


Figure 3.5 Grading up to 75% exotic: breeding structure, rate of retention of heterosis and rate of infusion of exotic genes.

The breeding structure and its consequences for maintenance of heterozygosity and proportions of genes from the two sources is illustrated in Figure 3.6. The biggest advantage of this System is that it maintains the full extent of heterozygosity, and thus of heterosis in all generations. If heterosis is very important relative to the size of the additive difference, then the System could be worth considering. Despite the fact that the production of F_1 offspring is usually the first step in any exotic crossing program in a Zebu population, the continued use of the System beyond the first generation is operationally difficult, and is unlikely to be justified by the relative sizes of the additive and heterosis effects.

3.5 TWO BREED ROTATION

This system (also known as crisscross or reciprocal backcross), which appears to be more frequently advocated than practiced, has some operational advantages. The mating pattern is illustrated in Figure 3.7.

The system gives 100% of achievable heterozygosity in the first generation, 50% in the second, 75% in the third, and gradually settles down to a consistent 67% in succeeding generations. The percent of genes from the two parent strains fluctuates, and for any one of the strains, alternates from 33% to 67% in alternate generations. This is no disadvantage in cases where the two types of crosses are very similar. However, in crosses between European and tropical cattle, these two types might perform quite differently. The System has the advantage that, since purebred males are used in each generation, very small pure bred nuclei are needed to service a quite large commercial population. This advantage is enhanced if artificial insemination is used, and the system should therefore have some potential in cattle populations.

The expected performance level fluctuates between two points (Figure 2.4). The difference between these two points amounts to $1/3$ of the additive effect. In the case of *Bos taurus* by *Bos indicus* crosses, it could therefore be of the order of 33% of the mid-parent mean, which is rather bigger than the maximum heterosis effect. The average expected performance level is better than that of the F_2 or 50% synthetic by an amount equal to 17% of the heterosis effect. With an additive effect of 100% (of mid-parent mean) and a heterosis effect of 25%, then the average performance value of a two breed rotation would be 3% better than that of a synthetic.

3.6 THREE BREED ROTATION

The principles of operation are similar to those in a two breed rotation, and the mating pattern is shown in Figure 3.8. Each of the three breeds is used in turn in pure form as a sire breed. We assume in this case that there is one local population, and that two exotic breeds (E_1 and E_2) are used. Each breed is used in pure form as a sire breed. The rotation begins with the use of the first exotic breed on the local population, to produce an F_1 population. These are mated to the second exotic breed, to produce a population which has 75% exotic genes. These are then mated to bulls of the local breed, to produce a population with 37.5% exotic genes. This completes one cycle of the rotation.

The consequences of this breeding pattern for the maintenance of maximum heterozygosity, and for the percent of exotic genes in the population is also shown in Figure 3.8. In practice, little heterosis is expected when genes of the two exotic breeds are brought together. In contrast, substantial heterosis is expected whenever exotic genes of either are brought together with genes of the local population. The illustration therefore distinguishes between the expected heterosis effect if all breed combinations

gave equal heterosis ($\frac{1}{2}$) and the more relevant expected heterosis arising only from exotic by local heterozygosity (...). The former situation has some relevance in, for example, three-breed rotational crossing of pigs or beef cattle as practiced in North America. It can be seen that a high proportion of maximum heterozygosity is maintained. However, if only $E \times L$ heterozygosity is of value, the proportion of maximum heterosis expected in each generation then fluctuates very widely from one generation to the next. In *Bos taurus*-*Bos indicus* crosses, where heterosis is important, this is an undesirable feature.

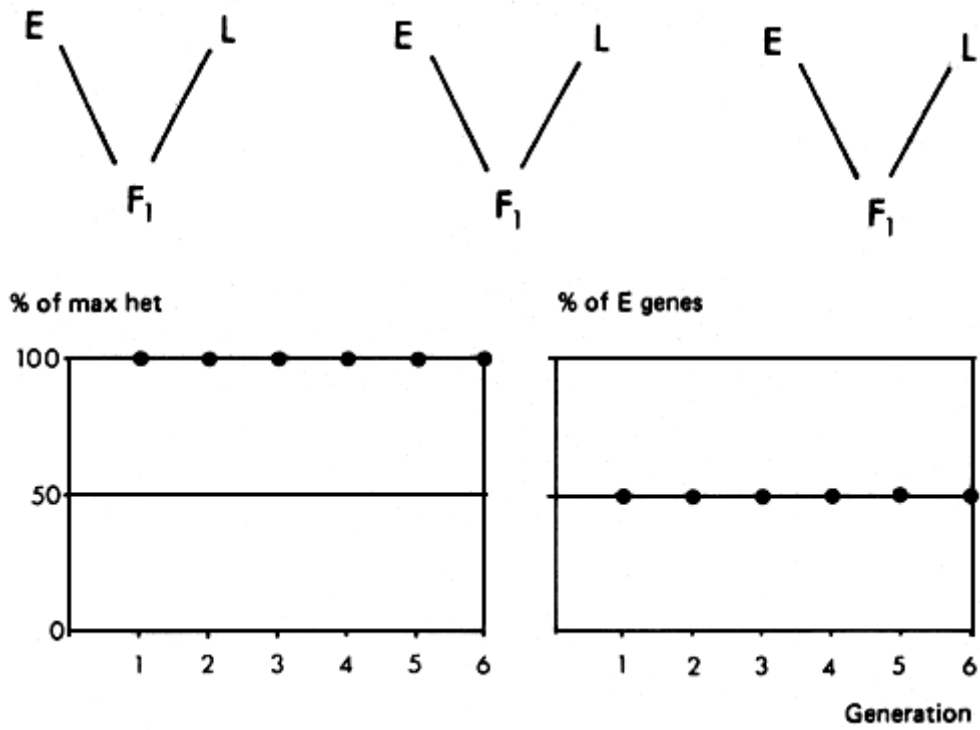


Figure 3.6 Continuous F₁ production: breeding structure, rate of retention of heterosis and rate of infusion of exotic genes.

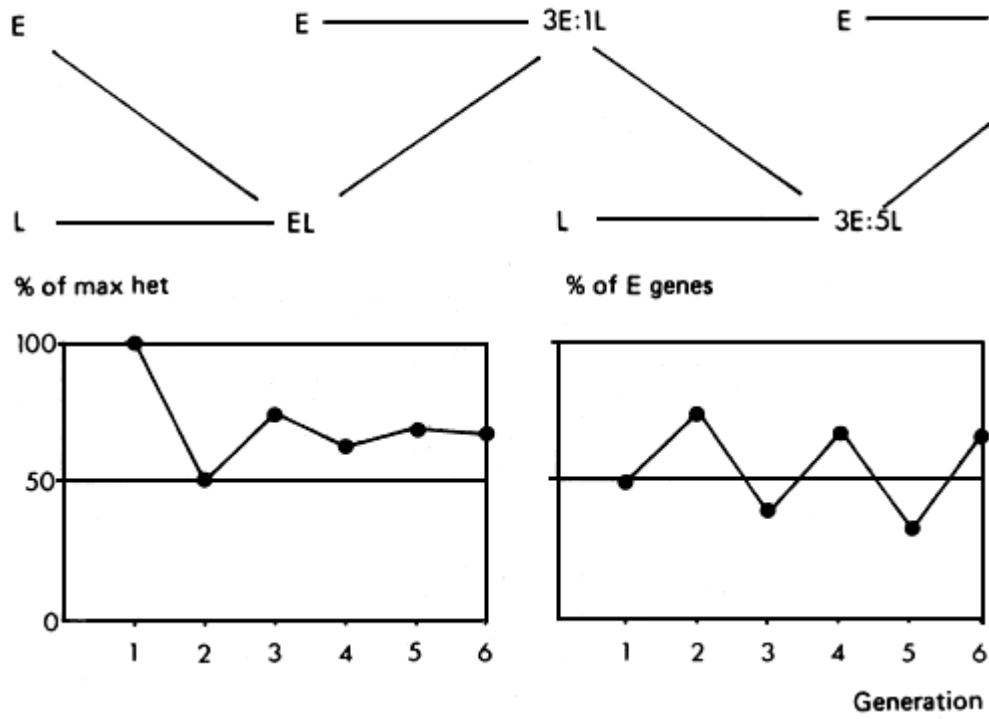


Figure 3.7 Two breed rotation: breeding structure, rate of retention of heterosis and pattern of infusion of exotic genes.

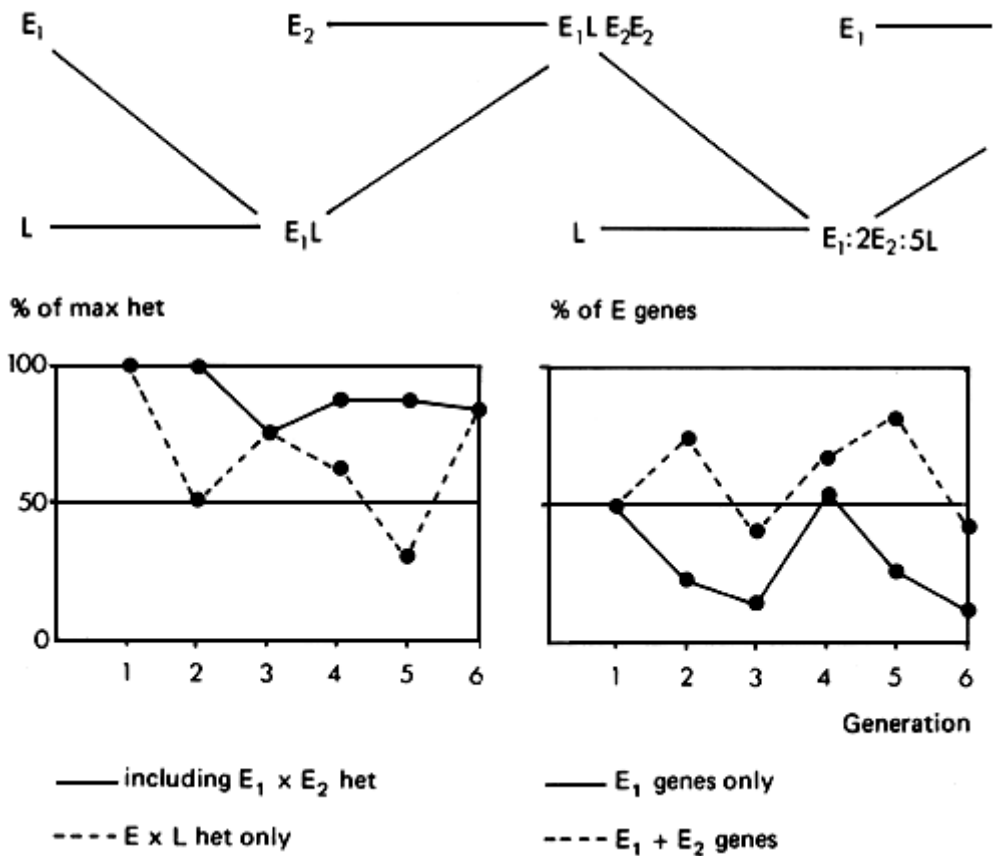


Figure 3.8 Three breed rotation: breeding structure, rate of retention of heterosis and pattern of infusion of exotic genes.

The breed composition as measured by the percent of genes from, say, the E_1 strain fluctuates considerably, and eventually settles down to a pattern with repeats every three generations, with proportions of 4/7, 2/7 and 1/7 of E_1 genes in each of the three generations (—). It is probably of more interest to follow the proportion of total exotic genes ($E_1 + E_2$). This proportion is maintained at a higher level, but also fluctuates widely from one generation to the next (...).

The expected performance of the different generations in such a three breed rotation can be followed, given the expected size of the additive and heterosis effects. The great variability in performance expected over the generations is a disadvantage. The System also has the disadvantage of operational complexity, requiring records of the breed identity of the each cow, as well as the provision of pure bred bulls of all three breeds. In practice, there could also be difficulties in obtaining acceptance for the use of bulls of the local population once a crossbreeding program has been established.

The expected performance level, as before, depends on the scale of the additive and heterosis effects. In all cases, the average performance level will be somewhat below that of a comparable two breed rotation (by 17% of the heterosis effect).

Synthetic populations are most effected by the loss of any epistasis. If epistatic effects can be ignored, then the two breed synthetic has the same expected performance as a population produced by grading up to F_1 bulls. In the latter System, a proportion of any epistatic effects present in the exotic breed will be preserved, while in the synthetic these will be largely dissipated. The importance of this consideration, of course, depends on the kind of epistatic effects postulated, and on the size of their contribution to performance.

3.7 TWO BREED SYNTHETIC

The formation of synthetic populations has considerable advantages in terms of operational simplicity over rotational crossbreeding Systems, each of which requires the maintenance of separate nucleus populations. The simplest synthetic is one derived from two parent strains. These are crossed to produce an F_1 generation, in which inter-se mating of selected individuals produces an F_2 generation, in which selection and mating again takes place. The process is repeated in subsequent generations. The pattern is illustrated in Figure 3.9.

The system gives 100% of possible heterozygosity in the F_1 generation, and this declines to 50% in the F_2 and subsequent generations. The percent of genes from the E strain is exactly 50% in the first generation, and should also be 50% in subsequent generations, though individuals will vary in the proportions of E genes which they carry, while the concurrent selection exercised may simultaneously raise or lower the average proportion of E genes.

3.8 THREE BREED SYNTHETIC

More complex synthetics may be put together in a variety of ways. In the context of exotic and local crossbreeding in the tropics, perhaps the most relevant System would be one involving two exotic breeds and one local, to produce a synthetic with 25% local genes, 25% genes from one of the exotics (E_1), and the remaining 50% from the second exotic (E_2). Such a System is illustrated in Figure 3.10.

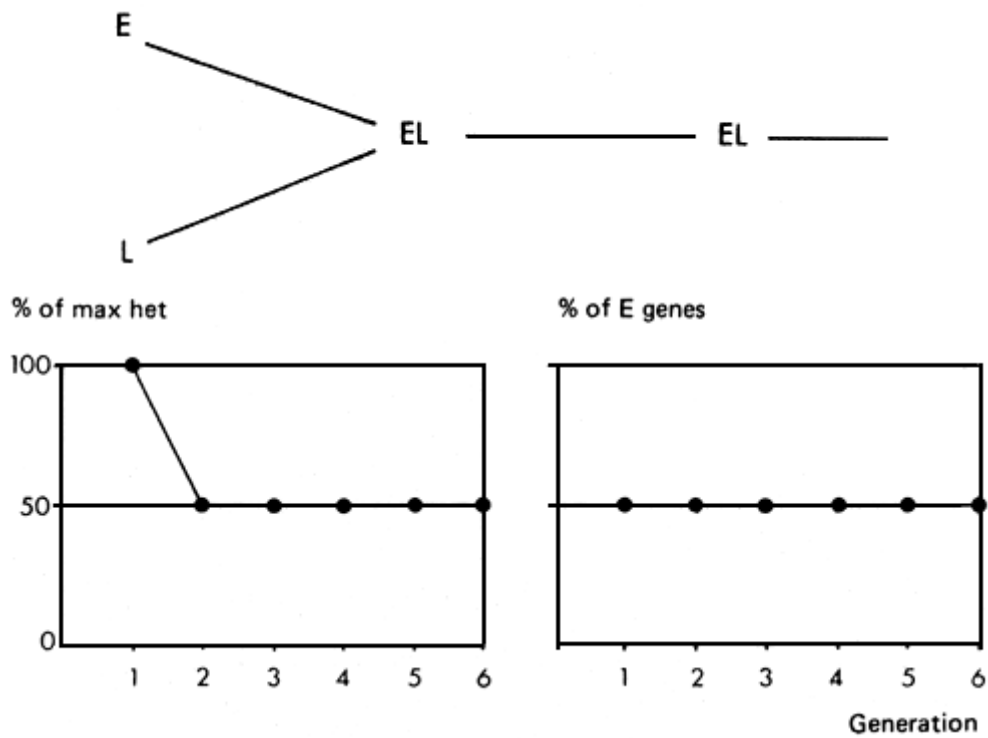


Figure 3.9 Two breed synthetic: breeding structure, rate of retention of heterosis and rate of infusion of exotic genes.

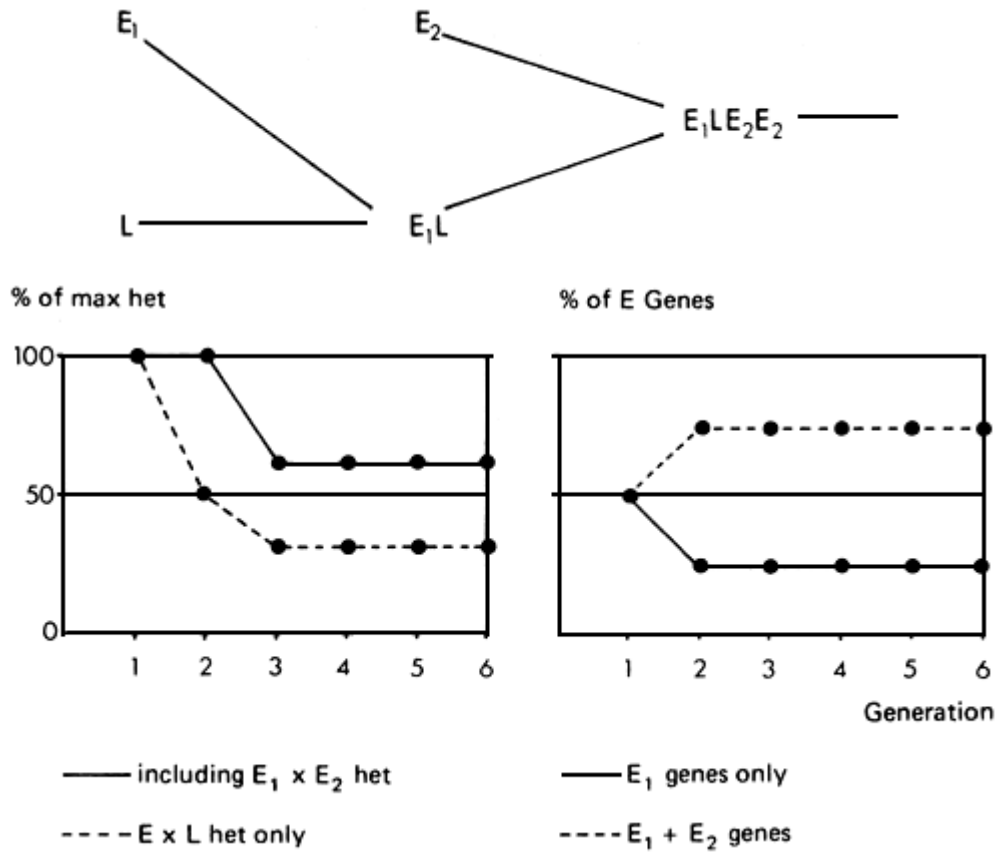


Figure 3.10 Three breed synthetic: breeding structure, rate of retention of heterosis and rate of infusion of exotic genes.

In the first generation, an F_1 is produced by E_1 and L. These are mated to bulls of the E_2 breed, to produce a second generation, which is the foundation for the synthetic population.

As in the three breed rotation, the main interest may lie in maintenance of $E \times L$ heterosis. It can be seen (...) that this drops in the third generation to 37.5%, and is maintained at that level in subsequent generations. The proportion of heterozygosity between all three breeds is maintained at a higher level (\square). The proportions of genes from the two exotic breeds are maintained at 25% and 50%, giving a 75% exotic gene complement in the synthetic. The expected performance level can again be calculated as a function of the expected heterosis and additive effects, but will in all cases be slightly below the average performance of a comparable three breed rotation. The latter, however, has the disadvantage of great variability from generation to generation. As in the two breed synthetic, so in the three breed synthetic any loss of epistasis could be of somewhat more consequence than in a comparable rotational cross.

CHAPTER 4

TYPES AND BREEDS OF TROPICAL AND TEMPERATE CATTLE

Domesticated cattle are usually classified into two major groups, zebu (*Bos indicus*) and European (*Bos taurus*) cattle. These groups are considered to constitute two different species, although they are believed to descend from the same wild species, the aurox (Epstein & Mason, 1984). They have the same number of chromosomes, but differ in the morphology of the Y chromosome. There are also substantial physical and physiological differences between the two groups. Nevertheless they can readily be interbred, and produce fertile offspring of both sexes.

4.1 ZEBU CATTLE

Most of the cattle indigenous to the tropics belong to the zebu species. The external trait which most clearly separates zebu from European type cattle is the hump over the shoulders or the posterior part of the neck. The term humped cattle is frequently used as a synonym to zebu cattle. The hump consists of muscle, connective tissue, and variable amounts of fat. The size and shape of the hump vary by breed, sex, and age of the animal. The function of the hump is not clearly understood. The earlier assumption that the hump was important as a store of fat for use during periods of feed scarcity has now been rejected.

Other conformation traits which are common to most zebu cattle are a narrow body, a sloping rump, and rather long legs. The hide is thin, loosely attached, and the brisket and dewlap are usually well developed, particularly in males. Size of the animals varies over a wide range, and breed averages from below 200 to above 400 kg for mature cows have been reported.

Zebu cattle are well adapted to the tropical environments, mainly because of the following attributes:

a) A high degree of heat tolerance, derived partly from low heat production and partly from a large ability to dissipate heat. A high density of efficient sweat glands increases the loss of heat through evaporation, and the short, sleek coat facilitates the convection to the surrounding air. It has also been maintained that the small body size contributes to the heat tolerance, as small animals have a higher surface to body mass ratio. However, the heat production at maintenance is proportional to metabolic weight rather than to actual weight, and the ratio of body surface to metabolic weight is almost independent of size.

b) Partial resistance to ticks, and thus to the many tickborne diseases occurring in tropical countries. Zebu animals have the ability to repel ticks by movements of the skin, but this is only part of the explanation of their larger resistance. It has been demonstrated that when animals are infested with tick larvae, fewer larvae develop into ticks in zebu than in European type cattle (Utech et. al. 1978). Zebu cattle are often claimed to possess a certain degree of resistance also to many other tropical diseases. To what extent this is a genetic property or has been acquired by immunization due to exposure in early life is questionable (Ansell, 1985).

c) Low nutritional requirements, because of small size, low metabolic rate, and possibly also more efficient digestion at low feeding levels.

The potential for milk production is poorly developed in most zebu cattle. The milk yield is low, often not much more than needed to feed the calf properly. The cows usually do not let down milk unless stimulated by the sucking of the calf, and adapt

poorly to modern milking routines. Failure to let down milk when milked by hand or machine without the presence of the calf usually leads to complete cessation of milk secretion and consequently to short lactations. Zebu animals are late maturing, both physiologically and sexually, and heat symptoms are weaker than in European cattle. The fat and solids-not-fat content of milk is higher in zebu cattle than in most European dairy breeds.

Zebu cattle can, somewhat arbitrarily, be classified into a number of subgroups according to external traits, such as coat colour, size and shape of horns etc. A more useful classification might be on the basis of utility. A large number of zebu breeds have been described, but few of them have gained any importance outside their home region.

Sahiwal and Red Sindhi are the most widely used dairy breeds of zebu cattle. Both breeds originate from present day Pakistan, and are rather similar in external traits. They are usually greyish red or brown in colour, have short horns and a characteristic convex profile of the forehead. Records collected at the Indian National Dairy Research Institute indicate that the two breeds also perform similarly. Body weight of mature cows was 300 to 350 kg, and average milk yield about 2000 kg per lactation with 5 per cent fat (Bhatnagar et al. 1979 b). Individual cows of both breeds have produced more than 4000 kg of milk in a lactation. Both Sahiwal and Red Sindhi are rather small in numbers, but have been widely used for upgrading of local cattle in many countries, both in South-east Asia and in other continents. A collaborative programme for preservation and improvement of the Sahiwal breed in India has been established (Nagarckenkar, 1983). Eight institutional herds with altogether about 750 breedable females are included, and the programme is based on use of deep frozen semen in combination with progeny testing. In Kenya, a National Sahiwal Stud was established in 1962, and Sahiwal is used both as a pure breed, for grading of unimproved cattle, and for crossbreeding with European breeds (Meyn & Wilkins, 1974). Sahiwal has also made important contributions to most of the new breeds of mixed zebu - European ancestry.

Tharparkar is a third breed originating from Pakistan. Animals of this breed are usually white or light grey, and slightly larger than the two breeds described above, but have similar milk yields (Bhatnagar et al. 1979 a).

Most of the many Indian breeds are bred for both milk and draught. Kankrej (Guzerat) and Gir, both from the western regions of the country, combine good draught ability with acceptable milk yields, and have also a high potential for meat production. The same can be said about Ongole (Nellore), a breed originating from Southern India. Kankrej, Gir and Ongole have all been exported to Central and South America, and have played an important role in the beef and dairy industry of that region.

Hariana is the predominant breed of Northern India. The bullock is highly recognized for its vigour and persistency for draught, and the cows produce up to about 1000 kg of milk per lactation. Hariana has been the local counterpart in many cross breeding programmes.

Most zebu breeds of African origin have been bred mainly for beef production. Boran has gained a good reputation as a dual-purpose breed. The home region of the Boran is the dry areas in Southern Ethiopia/Northern Kenya, and the breed has been widely used in improvement programmes all over Eastern Africa, mainly for beef. The most promising dairy breeds of African zebu are probably Kenana and Butana, both originating from Central Sudan. Average milk yields of about 1500 kg per lactation have been reported for large herds of these breeds (Cunningham, 1983). The White Fulani

cattle of the pastoral people of West Africa have also a fairly high potential for milk production.

4.2 TROPICAL CATTLE OF EUROPEAN TYPE

The only major populations of humpless cattle native to the tropics are found in West Africa and in Latin America. The West African types consist of several breeds of small, shorthorned cattle. The most well known representative is the N'Dama, found in Guinea and adjoining countries. N'Dama is a triple-purpose breed, kept for milk, beef and draught. The animals are small in size (body weight of mature cows about 200 kg) but very hardy. N'Dama and some other breeds of the same group are found to be highly resistant to bovine trypanosomiasis, and are regarded as an important genetic resource for this characteristic.

America had no cattle when the continent was discovered by the Europeans. The descendants of the cattle brought by the conquistadors in the 16th and 17th centuries are therefore considered to be the indigenous cattle of Central and South America. These cattle, the criollo, are essentially of European type, but have evidently developed some adaptation to the tropical environment. A considerable number of different breeds has been developed, mainly for beef production. Among the more important dairy breeds are the Central American Milking Criollo and the Limonero cattle of Venezuela, which is derived from partly the same base. These cattle are claimed to have low early mortality, good fertility, and high fat and protein content in the milk. A major problem is the high frequency of failure to let-down milk unless the calf is present (Alba, 1978). A somewhat similar breed is the Costeno con Cuernos in Columbia. In recent years criollo cattle have to a large extent been replaced by zebu breeds, particularly Kankrej and Gir, and also by specialized European type breeds.

4.3 INTERMEDIATE TYPES.

In some regions of the tropics the indigenous cattle can not easily be classified as *Bos taurus* or *Bos indicus*, but exhibit a mosaic of the traits typical for the two groups.

Sanga cattle, predominant in Southern Africa, are usually classified as a zebu type. The hump in Sanga cattle is less prominent than in zebu, and located at the posterior part of the neck (cervico-thoracic hump). Sanga breeds are kept mainly for beef production, and the milk yield is low. Recent research suggests that Sanga cattle have part of their inheritance in common with European cattle, e.g. the Y-chromosome is of the same shape as in European breeds (Meyer, 1984).

Intermediate types are also common on the frontiers between *Bos indicus* and *Bos taurus* territories, and along major routes of migration. An example is the Near East, where the native cattle, e.g. the Damietta in Egypt and the Damascus cow in Syria, obviously have been influenced by both groups.

4.4 TEMPERATE DAIRY BREEDS

Since the establishment of the first herd books in the late 1700's, most European dairy cattle populations have developed into clearly defined breed types. Selection for specialised dairy or dual purpose function has been accompanied by an increase in uniformity of colour and other external characteristics within each breed. In recent decades, the number of breeds has declined substantially. More than half of the dairy cows in Europe and North America now belong to one breed type, the Holstein Friesian.

Many of the temperate breeds have been used in crossbreeding in tropical countries. The more important among these are described below.

HOLSTEIN FRIESIAN. The origins of this breed are in the area running from the province of Schleswig-Holstein on the Danish-German border to the province of Friesland in the northern part of the Netherlands. The original cattle populations of these areas varied considerably in colour, but by the middle of the nineteenth century the characteristic black and white colour pattern was predominant. Substantial exports from the Netherlands from 1860 onwards established the breed in a number of European countries, and in North America. Rapid expansion has taken place in this century, to the point where there are about 70 m. Holstein Friesian type cows, accounting for one-third of all dairy cows in the world. It is the dominant dairy breed in Europe, where it is known as Friesian or Black-and-White, and in North America, where it is known as Holstein-Friesian or Holstein.

In this century, significant differences have developed between the separate national populations of Holstein Friesian. These differences have been measured systematically in a large FAO-sponsored study in Poland (Stolzman et al., 1981). The trial indicated that North American types exceeded European Friesians in milk producing ability by about 15%, though with lower butterfat and protein levels; that North American types had higher mature body weights by about 6%; that European type Friesians had better beef potential, as measured by carcass conformation and meat/bone ratio; and that New Zealand Friesians, at lower body weights than North American types, had higher fat percentage and somewhat lower milk yield, giving an equivalent fat yield per lactation. Within the past ten years, most European Friesian populations have been making extensive use of North American genetic material, with the result that these inter-population differences have now largely disappeared.

Because it is the predominant breed in most developed countries, the Holstein Friesian benefits from the large scale investment in testing and selection being made, and in many countries annual average rates of genetic improvement for milk production are close to 1%.

BROWN SWISS. The breed known internationally as Brown Swiss has its origins in the Alpine regions of several European countries. In Switzerland, Austria and Southern Germany, the breed is known as Braunvieh, while in Italy it is known as Bruna Alpina, and in France as Brune des Alpes. In North America, it is known as Brown Swiss.

Internationally, the breed is much less numerous than the Holstein Friesian, numbering perhaps 4 m. cows, or 2% of world dairy cattle.

Trials within the last decade have confirmed that the divergence between the North American and European strains has paralleled that in Holstein Friesian, with the North American type having higher milk production, lower butterfat, and less suitability for beef production. As in the Holstein Friesian situation, the European brown populations have been using North American genetic material in a systematic way for about ten years. In addition, the Brown Swiss has been chosen as the source from which to broaden the genetic base of the Red Dane population.

While critical comparisons are lacking, large scale milk recording results in several countries suggest that Brown Swiss are somewhat below Holstein Friesians in milk capacity, though somewhat higher in butterfat percentage, and slightly better in beef merit.

JERSEY. The origins of the Jersey breed are on the island of Jersey in the English channel. The local cattle population, now numbering about 5,000 cows, has been closed to importation for over two centuries. Based on stock exported from the island,

significant populations now exist in New Zealand, Denmark, Great Britain, and the USA, with smaller nuclei of the breed in many other countries. In Australia it has been used as the basis for the development of the AMZ, a synthetic Zebu × Taurus dairy breed. Likewise, it is a major contributor to the Jamaica Hope. Total numbers of Jersey cows worldwide amount to perhaps 2 m., or 1% of the world population.

The characteristics of the breed are its small mature body size (mature body weight equals 60% of Holstein Friesian); early sexual maturity; high butterfat levels; poor beef capacity.

OTHER TEMPERATE BREEDS. Other temperate breeds which have in the past been used in crossbreeding on Zebu populations include the following:

DAIRY SHORTHORN. This breed, once dominant in Britain and Ireland, and highly influential in other countries, is now a small minority breed where it occurs, and is generally declining in numbers.

AYRSHIRE. A specialist dairy breed of Scottish origin, it is now mainly represented by the Finnish population, though the breed is also found in Canada, USA, Britain and a number of other countries.

RED DANE. This breed, which some decades ago was frequently used as an improving cross in other European Red populations, now represents 20% of the Danish cow population, and is involved in a systematic crossbreeding program with American Brown Swiss.

FLECKVIEH OR SIMMENTAL. This strongly dual purpose breed predominates in southern Germany. Substantial populations are also found in Switzerland, Austria, France, Italy and some countries in Eastern Europe. It has been used as a specialised beef breed for crossing on other beef breeds in the United States and elsewhere. Some European populations, particularly the Swiss, have been using genetic material from North American Red Holstein sources.

NORMANDE. This strongly dual purpose population predominates in the Normandy region of northern France.

GUERNSEY. A specialised dairy breed, originating in the island of Guernsey in the English Channel. It is somewhat larger than the Jersey, though with many common characteristics. It is more numerous than Jersey in the USA.

MRY. This is a strongly dual purpose breed, which makes up one-third of the Netherlands cow population. The breed is red and white in colour, and has slightly lower milk potential than Friesian, but better beef merit.