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# Cross-breeding cattle for milk production in the tropics: achievements, challenges and opportunities

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**Summary**

This paper reviews experiences with cross-breeding for milk production in the tropics. Data were compiled from 23 different studies evaluating the performance of different grades of cross-bred animals as well as local breeds. Relative performance of indigenous breeds compared with different grades of cross-breeds was calculated for three climatic zones. Traits considered were milk yield per lactation, age at first calving, services per conception, lifetime milk yield and total number of lactations completed. At 50 percent *Bos taurus* blood, lactation milk yields were 2.6, 2.4 and 2.2 times higher than those of local cattle in the highland, tropical wet and dry, and semi-arid climatic zones, respectively; lactation lengths increased by 1.2, 1.2 and 1.9 months in the above-mentioned climatic zones, respectively; there was a reduction in calving interval by 0.8 times and in age at first calving by 0.9 times. Similarly, cross-breds with 50 percent *B. taurus* genes had 1.8 times higher lifetime milk yields and a 1.2 times higher number of total lactations. Although cross-breeding faces a number of challenges such as better infrastructure, higher demand for health care, there are many advantages of using it. These are higher production per animal, higher income for the families and provision of high-value food. It is therefore likely to continue to be an important livestock improvement tool in the tropics in the future, where farmers can provide sufficient management for maintaining animals with higher input requirements and access to the milk market can be secured.

**Keywords:** *Cattle, cross-breeding, milk production, tropics*

**Resumen**

Este artículo hace un repaso por las experiencias obtenidas con el cruzamiento de razas para la producción de leche en los trópicos. Se recopilaron datos de 23 estudios diferentes que evaluaron los rendimientos de animales con distinto grado de cruce así como de animales de razas autóctonas. Se compararon los rendimientos de las razas autóctonas con los de animales con distinto grado de cruce para tres zonas climáticas. Las características consideradas fueron el rendimiento lechero por lactación, la edad al primer parto, el número de servicios por concepción, la producción lechera total a lo largo de la vida del animal y el número total de lactaciones completadas. Con un 50 por ciento de sangre Bos taurus, los rendimientos lecheros por lactación fueron 2,6, 2,4 y 2,2 veces mayores que los del ganado bovino autóctono en las zonas climáticas de las Tierras Altas, Tropical Húmeda y Seca y Semiárida, respectivamente; la duración de la lactación se incrementó en 1,2, 1,2 y 1,9 meses en las zonas climáticas anteriormente mencionadas, respectivamente; el intervalo entre partos y la edad al primer parto se redujeron, respectivamente, 0,8 y 0,9 veces. Asimismo, los animales cruzados con una genética 50 por ciento Bos taurus tuvieron rendimientos lecheros, para la totalidad de su vida productiva, 1,8 veces mayores y un número total de lactaciones 1,2 veces mayor. Si bien el cruzamiento implica afrontar una serie de retos como una mejor infraestructura o una mayor demanda de atención sanitaria, su uso presenta múltiples ventajas como son una mayor productividad por animal, mayores ingresos para las familias y el aprovisionamiento en alimentos de alto valor. Por ello, el cruzamiento seguirá seguramente siendo una importante herramienta de mejora del ganado en los Trópicos, donde los ganaderos pueden aportar las condiciones adecuadas de manejo para mantener animales con elevadas necesidades, garantizándose así el acceso al mercado de la leche.

**Palabras clave:** *Ganado bovino, cruzamiento, producción lechera, trópicos*

**Résumé**

Ce travail de synthèse fait le point des expériences obtenues avec le croisement de races pour la production laitière sous les tropiques. Les données de 23 études différentes ayant évalué les performances d'animaux avec différent degré de croisement ainsi que ceux d'animaux de races indigènes ont été compilées. Les performances des races indigènes ont été comparées à celles d'animaux avec différent degré de croisement pour trois zones climatiques. Les caractères considérés ont été la production laitière par lactation, l'âge au premier vêlage, le nombre de services par conception, la production laitière sur la durée de la vie de l'animal et le nombre total de lactations complétées. Avec un 50 pour cent de sang Bos taurus, les productions laitières par lactation ont été 2,6, 2,4 et 2,2 fois plus élevées que celles des bovins indigènes dans les zones climatiques des Hauts-Plateaux, Tropicale Humide et Sèche et Semi-aride, respectivement; la durée de la lactation a augmenté de 1,2, 1,2 et 1,9 mois dans les susdites zones climatiques, respectivement; l'intervalle entre mises bas et l'âge au premier vêlage ont été, respectivement, 0,8 et 0,9 fois plus bas. De même, les animaux croisés à 50 pour cent de sang Bos

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taurus ont eu des productions laitières, sur la durée de leur vie, et un nombre total de lactations 1,8 et 1,2 fois plus élevés, respectivement. Bien que le croisement suppose affronter des défis tels qu'une meilleure infrastructure ou une plus grande demande en soins sanitaires, son usage comporte de nombreux avantages, parmi lesquels une majeure productivité par animal, un revenu plus élevé pour les familles et l'approvisionnement en aliments de grande valeur. Ainsi, le croisement continuera certainement à être un outil important d'amélioration du bétail sous les Tropiques, où les éleveurs peuvent fournir les conditions adéquates d'élevage pour maintenir des animaux à forts besoins et s'assurer ainsi l'accès au marché du lait.

**Mots-clés:** *Bovins, croisement, production laitière, tropiques*

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## Introduction

Cross-breeding native cattle, often of *Bos indicus* type, with exotic *Bos taurus* cattle is now a widely used method of improving reproduction and production of cattle in the tropics (VanRaden and Sanders, 2003). Although indigenous cattle are well adapted to local production conditions, they usually mature late and have poor growth rates and low milk yields (Syrstad, 1988).

Reports on cross-breeding in the tropics date back to 1875 (Gaur, Garg and Singh, 2005), when shorthorn bulls were crossed to native cows in India. Other reports (Buvanendran and Mahadevan, 1975) indicate that livestock improvement in the tropics using this method began more than 300 years ago when exotic cattle were introduced into what is today Sri Lanka. Results on the performance of such crosses in well-designed experiments have, however, only been available since 1930 and a great number of reports have been published since then. It has now become clear from studies carried out by Amble and Jain (1967); Mason (1974); Katpatal (1977); Kimenye (1978); Rege (1998); Demeke, Neser and Schoeman (2004a) and Gaur, Garg and Singh (2005) that where cattle management is good, the performance of cross-breds increases with the number of *B. taurus* genes, and that the breeds that have 50 or 75 percent of these genes perform better than all other levels of exotic inheritance. Animals with these levels of *B. taurus* blood calve earlier than the indigenous stock, produce more milk, and have longer lactations and shorter calving intervals (CIs). Cross-breeding is therefore a very attractive short-term livestock improvement tool as improvements can be made in a population within a single generation. However, despite the impressive results and high demand for milk in the tropics, well-organized and successful cross-breeding programmes remain few (McDowell, Wilk and Talbott, 1996). For example, in India only 12 percent of its 187 million head of cattle are cross-breeds (Ahlawat and Singh, 2005); similarly, in Bangladesh cross-bred cattle account for only 2 percent of all milking cows (Miazi, Hossain and Hassan, 2007). Reasons for this include (1) lack of strategies and policies to take advantages of crosses in most parts of the tropics (Rege, 1998); (2) gaps in knowledge as to what the appropriate levels of exotic inheritance should be for a particular production system (Kahi, 2002); (3) lack of in-depth analysis of the socio-economic and cultural values of livestock in the different production systems or production environments, which leads to wrong breeding objectives (Chagunda, 2002) and (4) small herd sizes that do not allow maintaining sufficiently large breeding stock for cross-breeding and often unknown exotic blood level.

This paper reviews the achievements that have been made in cross-breeding for milk production in the different climatic zones (climatic zones) in the tropics, and discusses the challenges and opportunities for its use in the future.

## Cross-breeding: the genetic background and types of cross-breeding

### Genetic background

The genetic basis of cross-breeding can be broadly divided into two components: additive and non-additive. The additive component is because of the average effect of the strains involved (breeds or parental lines), weighted according to the level of each parental breed in the cross-bred genotype. The non-additive component of cross-breeding is heterosis (Swan and Kinghorn, 1992). Heterosis is defined as the difference between the increase in cross-breeds' performance from the additive component based on the mean performance of the pure-bred parental lines. The levels of heterosis are presented as percentage values and can be used to calculate the expected performance of cross-bred individuals (Bourdon, 2000). Heterosis is caused by dominance (interactions within loci) and epistasis (interactions between loci) effects of genes. The positive effects of dominance are the result of increased levels of heterozygosity, which allow an individual to react to environmental challenges in different ways (Swan and Kinghorn, 1992). Epistasis interactions can have a negative effect because of a breakdown of favourable interactions between loci in pure-bred animals, which prior to cross-breeding developed by both natural and artificial selection within breeds (Roso *et al.*, 2005). These effects have been observed in cross-breeding studies for milk production in the tropics. Syrstad (1989) reviews results obtained from

F1 and F2 *B. indicus* and *B. taurus* crosses for milk production. In his article, a deterioration in performance because of the breakdown of epistatic gene effects was found to occur between the F1 and F2 for all traits studied (age at first calving (AFC), calving interval (CI), milk yields and lactation lengths (LLs)).

## Types of cross-breeding

Cross-breeding can be grouped into three types. They are grading up, rotational crossing or criss-crossing and formation of synthetic or composite populations (Cunningham and Syrstad, 1987).

### Grading up

This is a common cross-breeding strategy employed in most parts of the tropics. Usually an indigenous female animal is mated with an exotic male. The first cross generation (F1) performs very well in productive and reproductive traits: it has higher milk yields, shorter CIs and the animals calve at a younger age than the indigenous stock. Further upgrading, however, usually leads to mixed results (McDowell, 1985; Rege, 1998). These results are because of a reduction in heterozygosity as the generations proceed (Cunningham and Syrstad, 1987). Although the average performance of the F1 usually exceeds that of the indigenous breeds in milk yields, performance of the cross-breds can be variable. This could be because of the large variation in the environmental conditions that exist in the tropics, and a result of the two genotypes involved (Cunningham, 1981; McDowell, 1985; Dhara, Ray and Sinha, 2006).

### Rotational crossing

Rotational crossing is used or widely advocated in different parts of the tropics as a strategy to maintain high levels of heterozygosity and at the same time achieve specific proportions of the domestic and exotic strains (Cunningham, 1981; Gregory and Trail, 1981). Madalena (1981) describes four forms of this method. In the first, two bulls (one exotic and one indigenous) are used in alternate generations; the exotic bull is bred to the indigenous cow, then the indigenous bull is bred to the resulting cross-bred cows, and so on. Within a few generations, the system stabilizes at two types of grades (2/3 and 1/3), which coexist on one farm at the same time. The second form also involves two breeds: one exotic and one indigenous bull. In this system, the indigenous bulls are only mated to cows with more than 75 percent exotic blood. This leads to a herd that is composed of three coexisting grades (3/7, 5/7 and 6/7). In other words, the exotic bull is used on two generations and followed by an indigenous bull for one generation. The third form is similar to the first one, but instead of an indigenous bull, a cross-bred bull is used. In the fourth form, three breeds are used: two exotic bulls and one indigenous bull. In the first stage, the exotic breed is mated with the indigenous breed to produce the F1 population. This new breed is mated to the second exotic breed to produce offspring with 75 percent exotic genes. To complete the cycle, these are mated to the local breed to produce offspring with 37.5 percent exotic genes.

Rotational cross-breeding also has some limitations. First, in the two-breed rotational system the genes contributed by the two breeds fluctuate between 1/3 and 2/3 between generations. This makes it difficult to harmonize adaptability and performance characteristics to appropriately match the management level or the prevailing natural environment. Second, regular cross-breeding as described in the previous section is expensive to maintain.

### Synthetic breeds

Synthetic breeds are made up of two or more component breeds, and are designed to benefit from hybrid vigour without crossing with other breeds (Bourdon, 2000). Synthetic breeds can be formed in many ways. Cunningham and Syrstad (1987) describe two methods: the simplest form involves two parental breeds which are crossed to produce the F1 generation. Selected F1 individuals are then *inter se* mated to produce the F2 generation. This process is repeated in subsequent generations. Figure 1 shows a summary of the cross-breeding programme that is followed in the development of the Australian milking Zebu (AMZ), a Sahiwal:Jersey synthetic. There are also other methods of forming synthetic breeds. A programme using three breeds, for instance, could produce a synthetic with 25 percent local genes (*B. indicus*), 25 percent from one of the *B. taurus* breeds and 50 percent *B. taurus* genes from a second exotic animal.

## Materials and methods

The relative performance of different grades of crosses with the indigenous genotypes from different climatic zones in the tropics was compared. The data used in the study were obtained from published records for different parts of the tropics, and grouped into climatic zones according to the classification used by World Book (2009). Data were compiled from several studies on cross-breeding for dairy production in the tropics (the complete data set is provided in Supplementary Tables S1–S3). From these, a subset of studies was extracted that evaluated the performance of different grades of cross-breeds in comparison with local breeds (*B. indicus*). Reports that did not have local breeds in their design were excluded. At the end of the process, 23 studies were obtained, as can be seen in Table 1. Data were further clustered into three production environment groups according to whether the study was conducted on stations or on farms, and according to the climatic zone in which the study was undertaken. Studies undertaken on large commercial farms are marked on-farm 1, and studies conducted on small-scale farms on-farm 2. The final data set comprised data obtained from three climatic zones:

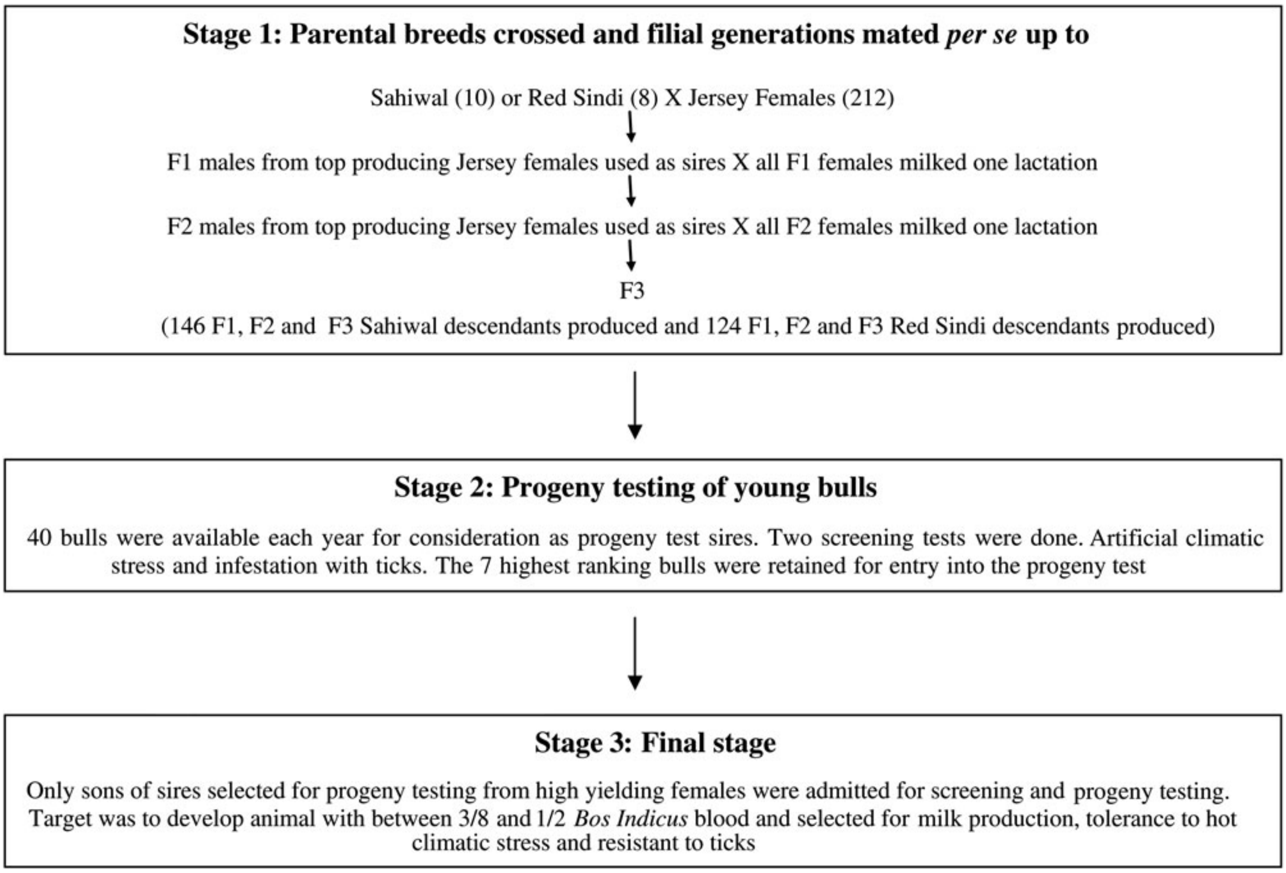


**Figure 1.** Summary of the breeding programme used to develop the Australian Milking Zebu. Source: Developed from Hayman (1974).

highlands, tropical wet and dry and semi-arid. Owing to the small differences between the tropical wet and dry climatic zones, and because of the small amount of data obtained from the tropical wet zone, the data from these two zones were merged into one tropical wet and dry zone. Traits compared in the study were milk yield per lactation (MYL), lactation length (LL), CI, AFC, services per conception (SPC), lifetime milk yield (LMY) and total number of lactations completed (TLC). Some of the studies used did not evaluate all these traits; in that case only the traits reported were considered. Relative performance of the different grade crosses was compared with that of local breeds by dividing the least squares mean (LSM) of a given trait in the different cattle grades by the LSM of the same trait in the local breeds. Finally, means and standard deviations of the relative performance ratios for the different grade crosses for a given climatic zone were computed. The ratios obtained for every study under analysis are given in Supplementary Tables S4 and S5.

Most available cross-breeding studies are based on single lactation records, and therefore do not account for lifetime productivity of cows, which is an important measure of overall profitability of dairy cattle (Matharu and Gill, 1981). For the purpose of this paper, reports on LMY and lactations completed (LC) were compiled (Supplementary Table S4) for indigenous cattle and the different grades of crosses. Unlike for the other traits, results from the different climatic zones were analysed together because of the low number of available studies.

## Results

### Grading up

In all climatic zones, cross-breds had higher milk yields, increased LL, shorter CIs and lower AFC compared with the local breeds (Tables 2 and 3). In the highland climatic zone, it was observed that the mean MYL for cows with 50 percent *B. taurus* genes was 2.6 times higher than that of the indigenous cows. Cows at the next level of exotic inheritance with 75 percent *B. taurus* genes showed a similar performance, with an MYL 2.7 times higher than that of local cows. In the tropical wet and dry climatic zone, increasing the percentage of *B. taurus* genes beyond 75 percent resulted in lower milk yields than that observed in the 50 percent crosses. The F2 in this climatic zone performed significantly lower than the F1. In the semi-arid region, MYL increased by 2.2 times at the 50 percent *B. taurus* level. In all climatic zones, all cross-breds with the exception of the 25 percent cross in the tropical wet and dry climatic zone had longer LLs. The overall range of change for MYL was between 1.1 and 4.5. In the tropical wet and dry climatic zone, and in the

**Table 1.** Summary of data from 23 different studies used in the analysis.

| No. | *Bos indicus* | *Bos taurus* | climatic zone | Country | Location | Production environment | Source |
|---|---|---|---|---|---|---|---|
| 1 | Boran | HF | Highlands | Ethiopia | Holeta station | On station | Demeke, Neser and Schoeman (2004a) |
| | Boran | Jersey | Highlands | Ethiopia | Holeta station | On station | Demeke, Neser and Schoeman (2004a) |
| | Boran | HF | Highlands | Ethiopia | Holeta station | On station | Demeke Neser and Schoeman (2004b) |
| | Boran | Jersey | Highlands | Ethiopia | Holeta station | On station | Demeke Neser and Schoeman (2004b) |
| 2 | Arsi | HF | Highlands | Ethiopia | Aresela region | On station | Kiwuwa *et al.* (1983) |
| | Arsi | Jersey | Highlands | Ethiopia | Aresela region | On station | Kiwuwa *et al.* (1983) |
| | Zebu | HF | Highlands | Ethiopia | Aresela region | On station | Kiwuwa *et al.* (1983) |
| 3 | Barca | HF | Highlands | Ethiopia | Aresela region | On station | Tadesse and Dessie (2003) |
| 4 | Sahiwal | Ayrshire | Highlands | Kenya | Nanyuki | On farm1 | Gregory and Trail (1981) |
| | Sahiwal_S | Ayrshire | Highlands | Kenya | Nanyuki | On farm1 | Gregory and Trail (1981) |
| 5 | Sahiwal | Ayrshire | Highlands | Kenya | Ngong | On station | Kimenye (1978) |
| | Sahiwal_S | Ayrshire | Highlands | Kenya | Ngong | On station | Kimenye (1978) |
| 6 | White Fulani | HF | Tropical WD | Nigeria | Vom | On station | Knudsen and Sohael (1970) |
| 7 | White Fulani | HF | Tropical WD | Nigeria | Vom | On station | Sohael (1984) |
| 8 | White Fulani | HF | Tropical WD | Nigeria | Vom | On farm1 | Olutogun, Yode-Owolade and Abdullah (2006) |
| 9 | Sahiwal | HF | Tropical WD | India | Ambala | On station | Amble & Jain (1967) |
| | Sahiwal | HF | Tropical WD | India | Meerut | On station | Amble & Jain (1967) |
| 10 | Sahiwal | Brown Swiss | Semi-arid | India | Karnal OS | On station | Bala and Nagarcenkar (1981) |
| | Deshi | HF | Tropical WD | India | Haringhata | On station | Bala and Nagarcenkar (1981) |
| | Hariana | HF | Tropical WD | India | Haringhata | On station | Bala and Nagarcenkar (1981) |
| | Hariana | Brown Swiss | Tropical WD | India | Haringhata | On station | Bala and Nagarcenkar (1981) |
| 11 | Deshi | Jersey | Tropical WD | Srilanka | Karagoda -Uyan. | On station | Buvanendran (1974) |
| 12 | Sinhala | HF | Tropical WD | Srilanka | Karagoda -Uyan. | On station | Wijerante (1970) |
| 13 | Sindi | Jersey | Tropical WD | Srilanka | Undugoda | On station | Buvanendran and Mahadevan (1975) |
| | Sihala | HF | Tropical WD | Srilanka | Karagoda-Uyangoda | On station | Buvanendran and Mahadevan (1975) |
| 14 | Criollo | Jersey | Tropical WD | Costa Rica | Turrialba | On station | Alba and Kennedy (1985) |
| 15 | Local | Jersey | Tropical WD | India | Chalakudy | On station | Katpatal (1977) |
| | Local | Jersey | Tropical WD | India | Vikas Nagar | On station | Katpatal (1977) |
| | Local | Jersey | Tropical WD | India | Visakhapatnam | On station | Katpatal (1977) |
| 16 | Local | HF | Tropical WD | Bangladesh | Comilla | On farm2 | Miazi, Hossain and Hassan, 2007 |
| | Local | Jersey | Tropical WD | Bangladesh | Comilla | On farm2 | Miazi, Hossain and Hassan, 2007 |
| | Local | HF | Tropical WD | Bangladesh | Khulna | On farm2 | Ashraf *et al.* (2000) |
| 17 | Local | HF | Tropical WD | Bangladesh | Dhaka | On station | Majid, Talukder and Zahiruddin (1996) |
| 18 | Local | Jersey | Tropical WD | Bangladesh | Dhaka | On station | Majid, Talukder and Zahiruddin (1996) |
| | Sahiwal | HF | Tropical WD | Bangladesh | Dhaka | On station | Majid, Talukder and Zahiruddin (1996) |
| | Local | Jersey | Tropical WD | Bangladesh | Dhaka | On station | Rahman, Islam and Rahman (2007) |
| 19 | Local | HF | Tropical WD | Bangladesh | Dhaka | On station | Rahman, Islam and Rahman (2007) |
| | Local | HF | Tropical WD | Bangladesh | Barisal/Patuakahli | On station | Al-Amin and Nahar (2007) |
| 20 | Sahiwal | HF | Semi-arid | Pakistan | Bahadurnagar | On station | McDowell, Wilk and Talbott (1996) |
| 21 | Sahiwal | HF | | India | | On farm1 | Matharu and Gill (1981) |
| 22 | Ratini | Red Dane | Semi-arid | India | Bikaner | On farm1 | Singh (2005) |
| 23 | Ongole | Jersey | | India | Visakhapatnam | On farm1 | Singh (2005) |

*Note:* Tropical WD = tropical wet and dry.

**Table 2.** Relative performance of breed groups (F1 1/4 exotic; F1 1/2 exotic; F1 1/3 exotic; F2) in two selected production traits in different climatic zones.

| climatic zone | Milk yield per lactation | | | | Laction length | | | |
|---|---|---|---|---|---|---|---|---|
| | Breed group | | | | Breed group | | | |
| | 1/4 | 1/2 | 3/4 | F2 | 1/4 | 1/2 | 3/4 | F2 |
| **Highlands (*n* = 10)** | | | | | | | | |
| Mean | n.a. | 2.6 | 2.7 | 3.4 | 1.2 | 1.2 | 1.3 | n.a. |
| SD | n.a. | 1 | 1 | 0.4 | 0.2 | 0.2 | 0.2 | n.a. |
| Range | n.a. | 1.4–4.5 | 1.8–4.5 | 3–3.6 | 1–1.3 | 1–1.5 | 1.2–1.5 | n.a. |
| **Tropical wet and dry (*n* = 27)** | | | | | | | | |
| Mean | 1.7 | 2.4 | 1.8 | 1.9 | 1 | 1.2 | 1.1 | 1.1 |
| SD | 0.4 | 0.8 | 0.6 | 0.6 | 0.01 | 0.2 | 0.1 | 0.1 |
| Range | 1.1–2 | 1.2–3.9 | 1.4–2.8 | 1.2–2.9 | 1.05–1.07 | 1–1.7 | 0.9–1.3 | 1–1.3 |
| **Semi-arid (*n* = 4)** | | | | | | | | |
| Mean | 1.4 | 2.2 | 1.5 | 1.4 | n.a. | 1.9 | n.a. | n.a. |
| SD | 0.5 | 0.4 | 0.5 | 0.5 | n.a. | 0.6 | n.a. | n.a. |
| Range | 1.1–1.7 | 1.8–2.6 | n.a. | 1.2–1.5 | n.a. | 1.2–2 | n.a. | n.a. |

*Note:* n.a = not available.

semi-arid climatic zone, the F2 had lower MYL as compared with the 50 percent. With the exception of the semi-arid climatic zone, where LL increased by 1.87, mean LL ranged between 1 and 1.3 times in all the other climatic zones.

There were also some unexpected results: for example, MYL of the F2 in the highlands zone was higher than that of the F1. This observation is in contrast with findings from other studies (Syrstad, 1989; Rege, 1998), and could be because of the small amount of data used, and the fact that no correction was made for the different breed combinations used in the different studies. The widest mean range (1.4–4.5) for relative performance was observed in MYL for the F1 and 75 percent crosses in the highlands. This could be the result of the large differences in management between farms, or because of the different *B. taurus* and *B. indicus* breeds used in the various cross-breeding programmes providing the data. For example, in the highlands of Ethiopia a MYL of 529 litres was observed for Boran cattle, as compared with the 809 litres obtained from the Arsi breed in the same area (Kiwuwa *et al.*, 1983; Demeke Neser and Schoeman, 2004b). Holstein–Friesian (HF) crosses had the highest relative performance for MYL, followed by Jersey and Ayrshire crosses. Similar effects of *B. taurus* blood on performance (MYL and AFC) have been reported in other earlier studies. Cunningham and Syrstad (1987) compared production traits in different projects in which two or more *B. taurus* breeds were used simultaneously. The study included HF, Brown Swiss and Jersey cows. Jersey crosses were the youngest and Brown Swiss crosses the oldest at first calving, both differing significantly from Friesian crosses. Friesian crosses had the highest and Jersey crosses

**Table 3.** Relative performance of breed groups (F1 1/4 exotic; F1 1/2 exotic; F1 3/4 exotic; F2) in three selected reproduction traits in different climatic zones.

| climatic zone | Calving interval | | | | Age at first calving | | | Service/conception | |
|---|---|---|---|---|---|---|---|---|---|
| | Breed group | | | | Breed group | | | Breed group | |
| | 1/4 | 1/2 | 3/4 | F2 | 1/2 | 3/4 | F2 | 1/2 | F2 |
| **Highlands (*n* = 7)** | | | | | | | | | |
| Mean | n.a. | 0.9 | 1 | 0.9 | 0.8 | 0.8 | 0.9 | 0.8 | 0.89 |
| SD | n.a. | 0.1 | 0.1 | 0.01 | 0.01 | 0.01 | 0.01 | 0.1 | 0.1 |
| Range | n.a. | 0.8–1 | 0.9–1 | 0.91–0.92 | 0.8–1 | 0.8–0.9 | 0.92–0.93 | 0.7–0.8 | 0.8–0.9 |
| **Tropical wet and dry (*n* = 16)** | | | | | | | | | |
| Mean | n.a. | 0.92 | 1 | 1 | 0.8 | 0.9 | 0.9 | 1 | n.a. |
| SD | n.a. | 0.1 | 0.2 | 0.1 | 0.1 | 0.1 | 0.01 | 0.17 | n.a. |
| Range | n.a. | 0.8–1 | 0.8–1.3 | 0.9–1.1 | 0.6–1 | 0.8–1 | 0.84–0.85 | 0.8–1.2 | n.a. |
| **Semi-arid (*n* = 4)** | | | | | | | | | |
| Mean | n.a. | 0.9 | 1.01 | 1 | 0.83 | 0.7 | 0.8 | n.a. | n.a. |
| SD | n.a. | 0.01 | 0.06 | n.a. | 0.1 | 0.03 | 0.02 | n.a. | n.a. |
| Range | n.a. | n.a. | 0.9–1.0 | n.a. | 0.7–0.9 | 0.7–0.8 | 0.8–0.84 | n.a. | n.a. |

*Note:* n.a. = not available.

the lowest milk yields, and the differences between them were significant.

Cross-bred animals with 50 percent *B. taurus* genes had between 1.4–2.6 times higher LMY and 1.2 times more LC than the indigenous cattle. An increase in LMY and LC among cross-breds is also reported by Singh (2005), who reviewed lifetime parameters on two and three-breed crosses from different studies conducted on government and research farms in various parts of India involving several local and exotic breeds. HF crosses of 50 to 62.5 percent *B. taurus* genes had higher LMY and more LC than those above these levels of crossing (75 or 87.5 percent). These results were confirmed by a later study carried out by Goshu (2005), who compared lifetime performance of different grades of crosses of HFs with Ethiopian Boran cattle under an intensive grazing system with supplementation at Chefa farm in Ethiopia. The level of crossing significantly affected herd life and LMY. The 50 and 75 percent *B. taurus* cross-breeds had significantly higher LMY and longer herd life than animals with higher levels of exotic inheritance (87.5 or 93.7 percent).

To enable proper overall comparison of the different genotypes, some studies on upgrading have focused on economic performance in different production environments. Madalena *et al.* (1990) undertook a study involving 65 commercial cooperative farms in the states of Minas Gerais, São Paulo, Rio de Janeiro and Espírito Santo, and two research centres (Santa Monica and USEPA São Carlos) in Brazil. Six red and white HF × Guzera crosses (25, 50, 62.5, 75 and 87.5 percent crosses and pure HF) kept under two types of management systems were compared, one with high and the other with low-level management and inputs. The F1 had a longer herd life, and better productive and reproductive performance than the other groups, and therefore yielded higher profits. The superiority of the F1 over all HF backcrosses was more pronounced at low levels of management.

In a more recent study, Haile *et al.* (2007) conducted an economic comparison of Ethiopian Boran animals and their crosses of 50, 75 and 87.5 percent HF inheritance, which were all reared in an intensive, stall-feeding system in the central highlands of Ethiopia. The study covers one calendar year (2003) and collected its data from cattle kept on the Debre Zeit Research Station in Ethiopia. Returns per day and per cow were calculated from dung and milk production. Results showed that the cost of producing 1 litre of milk was significantly higher for the Ethiopian Borans than for the crosses. The 87.5 percent crosses returned a significantly higher profit per day per cow and profit per year per cow than the 50 percent crosses. The crosses of 75 percent, however, did not yield a significantly higher profit per day per cow and profit per year per cow than the 50 or 87.5 percent crosses. It was concluded that intensive dairy production with indigenous tropical breeds is not economically viable.

Variations in economic performance between crosses of different breeds have also been observed. Hemalatha, Prashanth and Reddy (2003) compiled reports in which Friesian crosses, Jersey crosses and local cattle kept in different parts of India were compared. These reports showed that the cross-breds produced higher profits per kilogram of milk produced than the indigenous Zebu animals. It was also observed, however, that maintenance costs were highest for Friesian crosses, followed by Jersey crosses and lowest for local cattle. The economic impact of cross-bred cows in smallholder farming systems has been demonstrated in a number of studies. Some of these studies (Patil and Udo, 1997; Bhowmik, Sirohi and Dhaka, 2006; Policy Note, 2007) reported that in areas where cross-bred animals can be maintained, farmers incorporating them into their production systems had higher household incomes than those with pure indigenous breeds.

## Rotational cross-breeding

One well-documented rotational cross-breeding programme is the one conducted at Kilifi Plantations in the humid lowlands of Kenya. The rotational cross-breeding programme on this farm dates back as far as 1939. Gregory and Trail (1981) analysed data from two groups of cattle produced on this farm in a two-breed continuous rotational cross-breeding system. Group 1 consisted of 67 percent Sahiwal and 33 percent Ayrshire genes, whereas group 2 consisted of 67 percent Ayrshire and 33 percent Sahiwal genes. The records analysed were collected between 1972 and 1978. With regard to milk production, group 2 (463 observations) performed significantly better than group 1 in the following traits: AFC (1019 versus 1042 days), MYL (2843 versus 2662 kg) and annual lactation yield (2616 versus 2503 kg), but had significantly longer CIs (398 versus 390 days) than group 1. In a follow-up study, Thorpe, Morris and Kang'ethe (1994) analysed lifetime performance of the two groups and of the cross between them (interbreeds). LMY was 48 percent higher for group 2 (67 percent Ayrshire and 33 percent Sahiwal genes group) than for group 1. The interbreeds yielded 34 percent less than the average rotational cross (groups 1 and 2). This decline is thought to be because of recombination loss, which results from the breakdown of favourable epistatic interactions between genes in different loci (Table 4).

Later, two more breeds (Brown Swiss and HFs) were introduced into the breeding programme. Mackinnon, Thorpe and Barker (1996) analysed data from a three-breed rotation programme consisting of Brown Swiss, Ayrshire and Sahiwal cattle in various combinations. The data contained 8447 observations. MYL for the herd was 3268 kg, and the LL and CI were 322 and 398 days, respectively. The improvement in performance of the three-breed crosses as compared with the two-breed crosses was attributed to the large amount of heterosis from crossing Sahiwal and the two *B. taurus* genomes. In a more recent study (Kahi

**Table 4.** Relative performance of F1 with 50 percent exotic blood level in life time production traits summarized across all studies ($n = 6$) in which these traits have been assessed.

| | Life time milk yield ($n = 6$) | Total lactations completed ($n = 6$) |
|---|---|---|
| **Value** | **F1 (50%)** | **F1 (50%)** |
| Mean | 1.8 | 1.2 |
| SD | 0.5 | 0.03 |
| Range | 1.4–2.6 | 1.21–1.26 |

*et al.*, 2000), performance of the herd was analysed after the introduction of HFs. The data set contained 25 cross-breed combinations of HF, Ayrshire, Brown Swiss and Sahiwal cattle. Overall herd MYL, CI and LL were 3446 kg, 402 and 326 days, respectively. Crosses with 50 percent HF genes had significantly higher MYL, longer LL and shorter CI than those with 50 percent Brown Swiss genes. It was concluded that, as farm management had not changed, the improvement in MYL for the herd relative to the earlier study (Mackinnon, Thorpe and Barker, 1996) was because of the introduction of the HFs.

## Formation of synthetic populations

Several attempts have been made to form synthetic groups: Hayman (1974), Katyega (1987), Gaur, Garg and Singh (2005), Singh (2005) and Cerutti, Alvarez and Rizzi (2006) give accounts of 13 synthetic breeds at varying levels of development from different parts of the tropics. McDowell (1985) compared data of five of these groups and found that performance of each group was superior to that of the native breeds. Table 5 shows a summary of some of the traits that were compared. For comparison, the performance of the native breeds used is indicated in the same table. It should be noted that the figures given for the native breeds were selected from a few studies only to enable quick comparison. Performances of the same native breeds observed in different studies are summarized in Supplementary Table S1.

The Australian Friesian Sahiwal (AFS) is one of the successful synthetic breeds: the 50:50 Sahiwal:Friesian is a well-documented synthetic developed by the government of Queensland, Australia, from 1960 until 1994, when the programme was sold to a private company. The programme is now under the management of the AFS Association of Australia, which continues breed development, genetic management and progeny testing for AFS Bulls (Meat and Livestock Australia, 2006). The AFS was bred for milk letdown, tick resistance and milk yield. Under extensive grazing on tropical pastures, the AFS averaged 2556 litres of milk and 105 kg of fat, which compares favourably with the HF performance of 2291 litres of milk and 82 kg of fat (Alexander, 1986). Another equally successful synthetic is the Girolando, a 62.5:37.5 HF:Gir synthetic developed in Brazil. The Girolando produces 80 percent of the milk in Brazil and is characterized by an average of 3600 kg of milk with 4 percent fat content, and has a CI of 410 days (Girolando Associação Brasileira Dos Criadores de Girolando, 2005). In some parts of the tropics, where synthetic breeds have been successfully developed and reared by farmers, major increments in overall milk yields have been recorded. For instance, the Sunandini cattle have contributed greatly to the dairy economy of Kerala State in India. It

**Table 5.** Description of origin and composition of selected synthetic breeds and overview of performance parameters of selected synthetic and indigenous breeds.

| | Description of synthetic breed | | | | |
|---|---|---|---|---|---|
| | **Jamaica Hope** | **Pitanguei-Ras** | **Australian milking Zebu** | **Karan-Swiss** | **Sibovey** |
| Origin | Jamica | Brazil | Australia | India | Cuba |
| Composition | Jersey × Sahiwal | Red Poll × Zebu | Jersey × Sahiwal/Red Sindi | Brown Swiss × Sahiwal/Red Sindi | Holstein × Zebu |
| **Performance of sythetic breeds** | | | | | |
| AFC (months) | 34.5 | 34.7 | 31 | 36.3 | 31.3 |
| MYL (kg) | 2930 | 2780 | 1987 | 2519 | 2897 |
| LL (days) | 282 | 281 | 244 | 324 | 298 |
| CI (days) | 439 | 414 | 422 | 415 | 405 |
| **Performance of the indigenous breeds used in establishment of synthetic breeds above** | | | | | |
| | **Sahiwal[2]** | **Red Sindi** | **Zebu[5]** | | |
| AFC (months) | 37.4 | 40.5[3] | | | |
| MYL (kg) | 1891 | 1270[4] | 929 | | |
| CI (days) | 439 | 414 | 422 | 415 | 405 |
| **Performance of the indigenous breeds used in establishment of synthetic breeds above** | | | | | |
| | **Sahiwal[2]** | **Red Sindi** | **Zebu[5]** | | |
| AFC (months) | 37.4 | 40.5[3] | | | |
| MYL (kg) | 1891 | 1270[4] | 929 | | |
| LL (days) | 305 | | 303 | | |
| CI (days) | 392 | 535[3] | 451 | | |

Source: [1]McDowell (1985), [2]Amble and Jain (1967), [3]Stonaker (1953), [4]Acharya (1970), [5]Kiwuwa *et al.* (1983).
Note: AFC = age at first calving; MYL = milk yield per lactation; CL = calving interval; LL = lactation length

is a synthetic breed developed by crossing nondescript local cows of Kerala State with Jersey, Brown Swiss and HF cows. It is estimated that through the active involvement of farmers in the breeding programme, milk production increased from 0.164 million tonnes in 1966 to 19.3 million tonnes in 1993 (Chacko, 2005).

## Breeding strategies of smallholder farmers

A study of Ethiopian smallholder farmers keeping cross-breds has shown that farmers make informed decisions about the blood level they keep on their farm. Above 85 percent of all respondents ($n = 62$) prefer cross-bred cows with an exotic blood level between 50 and 75 percent. Main reasons for their preference are good level of income, adaptation of animals to environment and acceptable management level. A similar number of farmers (80 percent) also prefer their bulls/artificial insemination (AI) semen between 50 and 75 percent of exotic blood. However, 47 percent of farmers prefer their bulls/AI semen to have even more than 75 percent exotic blood. The percentages do not sum up to 100 percent, because farmers were allowed to give more than one exotic blood-level group. They like having a choice of more than one blood levels to be able to use higher grade bulls/AI for mating with local and low-grade cross-bred cows and lower-grade bulls/AI for mating with high-grade cross-bred cows (Roschinsky *et al.*, 2012). Madalena, Peixoto and Gibson (2012) also report that farmers with smaller herd sizes use bulls from different breeds in an often disorganized way in order to sustain their cross-bred herds.

Most farmers (88.7 percent) would advice other farmers to start with cross-breeding given proper management and accessible markets.

# Challenges

In spite of the great potential of cross-breeding as a livestock improvement method, it has not led to a wide-spread increase in milk production in the tropics (Bayemi *et al.*, 2005). Owing to several challenges, cross-breeding has yet to be successfully and sustainably adopted and practised in the region (Rege, 1998; Kumar, Birthal and Joshi, 2003; Miazi, Hossain and Hassan, 2007). These include (1) limitations of cross-breeding methods; (2) mismatches between genotypes and production system, (3) intermittent funding of programmes and lack of appropriate policies and (4) lack of or limited involvement of farmers in the design of the interventions.

## Limitations of cross-breeding methods

The many impressive results of grading up on record were mostly achieved at research stations and commercial farms, where the level of management and nutrition of stock is good (e.g. Katpatal, 1977; Thorpe, Morris and Kang'ethe, 1994; Tadesse and Dessie, 2003; Demeke, Neser and Schoeman, 2004a; Tadesse *et al.*, 2006). The smallholder sector in the tropics, which constitutes the majority of farmers, is at times unable to raise the levels of management and nutrition in line with the requirements of the new genotypes (Kahi, 2002). This often leads to low productivity and high mortality among the animals (Chagunda, 2002; Philipsson, Rege and Okeyo, 2006).

Although results from rotational cross-breeding have shown a marked improvement in animal productivity, this improvement method can only be used on large-scale operations, where management is good. The programmes associated with it are not practical for small-scale farmers, whose herd sizes may not justify keeping more than one bull. In the two-breed rotation system, there is great variability in genotypic composition from generation to generation, depending on the sire breed used. This is not practical for small-scale operations (Trail and Gregory, 1981; Syrstad, 1989; Madalena, Peixoto and Gibson, 2012). The most widely reported success, the Kilifi Plantation rotation programme (Mackinnon, Thorpe and Barker, 1996; Kahi *et al.*, 2000), has never been expanded beyond the single ranch programme or replicated elsewhere. Thus, this programme has had only limited impact as a source of improved genetics to the wider dairy farming community in the hot and humid coastal region of Kenya.

The development of synthetic populations has its drawbacks, too. First, it takes many years to develop a synthetic population, during which the production environment could change. Second, the development can be expensive. For example, the development of the AFS started in the 1960s and the costs amounted to $30 million Australian dollars. The breeding programme was later sold off to a private company, which has continued commercial development since 1994 (Chambers, 2006; Meat and Livestock Australia, 2006). During the development period of the AFS, there were drastic changes in Australia's infrastructure. As a result, milk production systems changed and the synthetic could not compete with breeds such as HF or Jersey under the new intensive production systems. It is now estimated that only 250 pure-bred AFS cattle remain in Australia, but exports of AFS cattle continues to many tropical countries including Mexico, Brunei, Thailand, India and Malaysia (Chambers, 2006). However, as will be later discussed in the section 'Opportunities', the innovative combination of emerging assisted reproductive technologies (ART), genomics and dense single nucleotide polymorphism (SNP) marker technologies can significantly speed up the development of synthetics.

## Production environment and production system

Poor infrastructure and market access are major obstacles to the successful implementation of cross-breeding programmes, especially in rural areas with lower agricultural potential. In addition, pricing policies for milk in some countries are often poor. Prices paid to the farmers are low and cannot support the purchase of feeds or investment in the necessary infrastructure, all of which are necessary to make the production system economically viable (McDowell, 1985). The failure to recognize the different needs of different production systems has also affected the success rate of cross-breeding programmes. In many tropical countries, past, and, in some cases, ongoing cross-breeding programmes have often been based on a one-genotype-combination-fits-all premise, with HFs being the preferred improver breed even in the hot and humid tropics and under production systems such as stall feeding (zero grazing), where other breeds might be better suited (King *et al.*, 2006). Such genotype × production system mismatches that ignore the important genotype-by-environment interaction effects are partly responsible for the largely disappointing and poor performance of cross-bred cattle in the tropics and their often insignificant impact (McDowell, 1985; King *et al.*, 2006; Philipsson, Rege and Okeyo, 2006). The assumption that production systems can easily be changed and adapted to fit the needs of cross-bred animals seems in many circumstances wrong. In these cases the genetic improvement of local breeds should be considered a more realistic approach.

The choice of *B. taurus* breeds and the level of crossing for different production systems should not only be based on the genetic potential for milk yield, but also on farmers' ability to follow adequate husbandry practices as well as on the available healthcare services and markets. In addition, the availability of adequate, good-quality feeds and water needs to be taken into account, too. Increasing the genetic potential of the animals alone is not enough, the above factors must be considered as well for the full beneficial heterotic effects to be realized (Ansell, 1985; Chantalakhana, 1998).

### Intermittent funding of programmes and lack of appropriate policies

A well-planned cross-breeding programme requires adequate funding (Kumar, Birthal and Joshi, 2003). However, funds in the required amount are not always available, which has caused the interruption of many programmes (Shem and Mdoe, 2003; Cardoso and Vercesi Filho, 2006; Shem, 2007). In addition, a lack of supportive national breeding policies and appropriate strategies has contributed greatly to the failure of many programmes. Rege (1998) and Chantalakhana (1998) observed that there is hardly a country in the tropics that has developed appropriate policies to take advantage of cross-breeding. This issue is of major concern to both farmers and technical personnel who are constantly seeking answers on how to maintain the appropriate level of crossing or determine which level of crossing is appropriate for a given production environment (Ansell, 1985; Chantalakhana, 1998). The lack of proper guidelines has led to undesirable consequences, especially at smallholder units where indigenous breeds are upgraded to higher exotic grades without following a defined cross-breeding programme (Kahi, 2002).

### Participation of farmers

Ownership of farmers of any breeding programme, either for improving local breeds or cross-breeding with exotic breeds, is a crucial point for the success for any livestock improvement intervention. Farmers must have the right to express their opinion and should be involved in decision-making processes. This can ensure that new procedures such as data recording can be easily implemented, and that animals that better fit to the management of the individual farmers are bred.

## Opportunities

Certain advantages exist to assist in addressing the challenges discussed in the previous section. These include: (1) availability of a large base population of indigenous tropical cattle; (2) advancements in ART; (3) availability of alternative recording methods; and (4) advances in genomic technology. Well-planned programmes using all or a combination of the existing advantages may lead to a large number of productive cross-bred animals in the tropics. In this section, the potential and impact of the advantages given above are discussed.

### Availability of large base populations

A considerable number of cattle are found in the tropics. It is estimated that of the 1.4 billion cattle in the world, more than two-third are found in the tropics (Wint and Robinson, 2007). Most of these are indigenous cattle and belong to the Zebu type. The Zebu can be classified into a number of subgroups according to external traits, such as size, origin or utility. It has been proposed that improvement in tropical cattle should be made by selective breeding within the *B. indicus* race. This has however been shown to be a slow way to meet the fast-growing need for production (Ansell, 1985). The large number of existing animals with unique qualities provides an opportunity to make rapid improvements over a short period, if breeding programmes that cross-breed large numbers of animals with *B. taurus* milk breeds can be successfully implemented.

### Assisted reproductive technologies

Recent developments in ART provide an opportunity for rapid multiplication of cross-bred populations. ART are defined as techniques that manipulate reproductive-related events and/or structures to achieve pregnancy with the final goal of producing healthy offspring in bovine females (Velazquez, 2008). ART began with the development of AI about 50 years ago. Widespread use of AI has been greatly enhanced by the possibility to freeze semen. In well-structured cross-breeding programmes in the tropics, AI has the potential of increasing the rate at which genetic change happens in the local population by increasing the reproductive rates of the bulls (Cunningham, 1999). Through AI it has been possible to transfer exotic genes to the tropics through imported semen. In some parts of the tropics, the persistent use of AI has yielded impressive results. In India, a well-planned cross-breeding programme resulted in the formation of the Sunandini synthetic breed. By 1993, Sunandini cattle had contributed greatly to the increase in milk production in Kerala State, India (Chacko, 2005).

A successful example for the use of AI for cross-breeding in the tropics is the dairy husbandry programme of the non-governmental organization (NGO) BAIF Development Research Foundation in India. Established in the 1970s in Maharashtra, India, with support from various international development agencies and the government of India, BAIF has built up a successful AI programme. BAIF's programme has served over 4.4 million families by establishing over 3500 cattle development centres across most states of India. The centres provide doorstep AI services to farmers accompanied by training and support concerning all aspects of dairy cattle farming (BAIF, 2011b). Farmers buy high-quality semen collected at BAIFs own bull station which houses 300 bulls of various exotic and indigenous breeds (BAIF, 2011a). The joint efforts of an NGO, the government of India, private sponsors and farmers benefitting from and recognizing the value of this ART have led to a successful, sustainable cross-breeding programme.

Following the success of AI, other methods of recovering, storing and implanting embryos, for instance multiple ovulation and embryo transfer (MOET), were developed. This opened up new possibilities for genetic improvement. It has been shown in some studies (e.g. Mapletoft and Hasler, 2005) that well-organized MOET programmes can result in increased selection intensity and reduced generation intervals, which eventually lead to higher genetic gains. It is for example estimated that if nucleus herds are established and heifers subjected to juvenile MOET (before first breeding), genetic gains twice than those obtained through traditional progeny testing programmes can be achieved. Since the middle of the 1990s, another important technique has been developed: ovum pick-up followed by *in vitro* embryo production (OPU-IVP). In this method, oocytes are harvested from females and fertilized *in vitro* (Cunningham, 1999; Van der Werf and Marshall, 2003). Through OPU-IVP, reproductive rates in females can be increased. For example, if two OPU-IVP sessions are carried out per week, up to 150 embryos and 70 calves per donor can be produced every year. There are two benefits for cross-breeding programmes: The number of females required in the programme is significantly reduced, and it is possible to multiply the number of animals with the required qualities rapidly (Cunningham, 1999). If sexed semen is used for *in vitro* fertilization, the sex of the offspring can be predetermined. This opens up additional opportunities for repeatedly and rapidly producing cross-breds of specific breed combinations and preferred sex (Wheeler *et al.*, 2006). It has also been proposed (Rutledge, 2001) that OPU-IVP be used widely as a method for continuous production of F1s by using oocysts from spent dairy cows and semen from adapted breeds. In this method, lactation in F1 cows can be initiated by transfer of F1 *in vitro* produced embryos. This strategy eliminates the loss of the heterosis effect and increases the phenotypic variation that results when F1 cattle are bred to either a pure-bred or cross-bred sire (Hansen, 2006). Wide-scale use of the technologies mentioned above (MOET, OPU-IVP and AI) is, however, not possible in the tropics at the moment because of the high costs involved, the poor infrastructure in many countries and the shortage of technical personnel (Kahi *et al.*, 2000). Madalena, Peixoto and Gibson (2012) report that there is one large cooperative in Brazil that offers to members F1 heifers pregnant with F1 or other female embryos.

## Alternative recording methods

It has been pointed out (Cunningham, 1981) that any cross-breeding programme adopted for a population requires at some point in the programme an indigenous selection operation. A serious constraint on this is that performance records are not readily available in the tropics. The sort of extensive milk recording programmes which support dairy breeding in the temperate regions are virtually non-existent in the tropics (Syrstad and Ruane, 1998; Kahi *et al.*, 2000; Kosgey, Kahi and Van Arendonk, 2005). The reasons for this have been outlined by different authors (Ansell, 1985; Islam, Rahman and Faruque, 2002; Singh, 2005) and include: small herd sizes, scattered herds, poor communication, low level of farmer education, lack of incentives for farmers to record data, poor facilities for collecting and processing data and great diversity in feeding and management regimes. Mason and Buvanendran (1982) argue that recording systems in the tropics do not have to be as elaborate as in the temperate regions. They propose the following approaches, which are simpler, cheaper and easier to adopt for the farmers, but would still allow progeny testing to be done: (1) bi-monthly recording: in this system, the recorder visits the farm every alternate month and records the milk yield obtained during a 24-hour period; (2) AM–PM sampling: in this method, the morning milk is weighed one month, and the evening milk the next month. It maintains monthly visits but is cheaper; and (3) sampling at particular stages of lactation: sampling during early, mid or late lactation. This system is difficult to adopt for herds calving all year as the cows will always be at different stages of lactation.

Another approach that could be employed to reduce sampling costs is to contract selected herds in a given region to produce the desired cross-breeds. In this approach, detailed recording would only take place for the contracted herds. Farmers could be familiarized with these recording systems through community-based organizations for general improvement of livestock (CBOGIL), which have been established by several groups of farmers. Kahi *et al.* (2000) define CBOGIL as organizations owned by farmers in a community with the objective of improving livestock production through use of animal genetic resources. Other authors (Sölkner, Nakimbugwe and Valle-Zarate, 1998; Wurzinger *et al.*, 2008) refer to this livestock improvement approach as village breeding programmes. CBOGIL ensure effective participation of the local communities and other stakeholders, which can lead to the establishment of successful recording systems and breeding programmes, either for pure or cross-breeding programmes (Kahi *et al.*, 2000).

### Genomic technology: current and future opportunities

Recent development in molecular genetics and the powerful new tool genomic selection are profoundly changing dairy cattle breeding in developed countries. Genomic selection refers to selection decisions based on genomic estimated breeding values (GEBV) or genomic breeding values (Hayes *et al.*, 2009). GEBV are the sum of the effects of dense genetic markers or the haplotypes of these markers across the genome (Hayes *et al.*, 2009). Genomic selection is now becoming feasible because of the availability of large numbers of SNP markers. In the case of cross-breeding, pure-breds can be selected for performance of cross-breds by estimating the effects of SNPs on cross-bred performance using phenotypes and SNP genotypes evaluated on cross-breds, and applying the results estimates to SNP genotypes obtained on pure-breeds (Dekkers, 2007). This is a major achievement because *B. taurus* breeds used in most cross-breeding programmes in the tropics are selected in the temperate regions under different management conditions. Owing to genetic differences between pure-breds and cross-breds, and the environmental differences between the two production systems, the performance of pure-bred parents is not a good predictor for that of their cross-bred descendants. This development now makes it possible to identify pure-breed parents whose descendants will perform best as cross-breds. Other benefits of genomic selection for cross-breeding include: (1) it does not require pedigree information on cross-breds; (2) once estimates of the SNP effects have been made, the genotype and phenotypic data can be used for several generations, and (3) it reduces the rate of inbreeding (Ibáñez-Escriche *et al.*, 2009).

The availability of large numbers of SNP makers has other benefits as well. It is, for example, possible to use certain techniques to accurately determine the breed composition of cross-bred animals without prior pedigree information. This is important because recording systems in the tropics are rare, and as a result many cross-bred populations exist whose breed compositions are unknown. Determining the breed composition of an animal enables inclusion of animals of unknown genotypes into breeding programmes and allows farmers to find out the accurate breed composition of the animals they wish to buy or sell.

The use of genomic technology in combination with ART opens up new possibilities of speeding up the formation of synthetic breed populations by taking advantage of reduced generation intervals and thereby multiplying the animals of the required breed combination (e.g. synthetic breeds) faster than is currently possible. The costs of these new technologies must, however, come down before they can be used on a wide scale.

## General discussion

Results from over 60 years of research confirm that cross-breeding is the fastest way to improve milk production, but not necessarily to long-lasting genetic improvement of livestock, with the exception of the formation of synthetic breeds. However, results obtained at the various research centres have not been widely transferred to the farming community. This review has provided some reasons for this failure and proposed solutions for overcoming the still widespread problems. Results from a study point to the fact that the milk production performance of the F1 could be close to being the optimum, but other factors such as reproductive performance also need to be considered to give recommendations on the right combination of exotic inheritance for a particular production system. Maintaining the suitable breed inheritance through grading up and rotational breeding still remains a challenge. Implementing the proposal of continuous production of F1s (Rutledge, 2001) as described in subsection 'Assisted reproductive technologies' can only be guaranteed if technical and financial issues limiting the use of ART are addressed. Another way to acquire animals of the required breed combination could be through special contracts with rotational breeders who supply smallholder farmers at an agreed price. The impact of such a move, however, would be limited, as there are only a few large-scale rotational breeders in the tropics. What is more, this approach cannot guard against genetic variation when offspring are mated to animals of different breed composition. It appears, therefore, that maintaining the suitable breed combination from generation to generation will be best achieved through developing synthetic breeds for the different production environments. This approach ensures the creation of a self-replacing population. It also ensures that the farmers deal with one kind of animal, which makes management easier, especially in harsh production environments. The combination of ART with advanced molecular genetics plus the availability of simple recording schemes provide great opportunities for developing and multiplying synthetic breeds at a much faster rate than in previously conducted breeding programmes. Success of this kind of programme requires farmer involvement already at the development stage and long-term financial commitment of governments and funding bodies in the tropics. Innovative ways should be found to help deal with the high costs associated with ART and the use of genomic technology. The newly developed methods could, for example, initially be targeted at farmers that have established a community-based breeding programme in which recording and breeding information is shared. This approach also enables efficient use of technical personnel and equipment as it is available in a single place.

More and more exhaustive studies on the various merits of indigenous tropical genotypes still need to be undertaken. The findings of these studies will help determine which combinations of exotic and indigenous breeds to use, and the level of exotic blood to maintain in the new genotypes. The conservation of indigenous breeds should not only not be ignored but become part of national breeding programmes as this group of animals possesses qualities that make them a valuable resource for present and future generations.

## Conclusion

Cross-breeding remains an attractive option for livestock improvement in the tropics because of the quick results that can be obtained by its use and the potential benefits it has for farmers. Nevertheless, careful assessment should be made on whether or not appropriate intervention strategies need to be put in place for each individual case. The required infrastructure for improved management and market access has to be secured. In most cases, the F1 crosses perform better than other genotypes, but the continuous production of F1s and animals of required genetic combinations for the different production environment still remains a big challenge. Production and multiplication of synthetic breeds is perhaps a solution to this problem. The success of any strategy followed to improve results obtained from cross-breeding depends greatly on long-term financial commitment of governments, active involvement of the beneficiary farming communities in the design as well as operationalization of the breeding programmes, and on the successful combination of advances in ART and molecular genetics in breeding programmes.

## Supplementary material

Supplementary online material is available at http://cambridge.journals.org/agr.

## References

**Acharya, R.M.** 1970. Cross-breeding of Zebu cattle with exotic breeds for milk production. *Indian J. Anim. Sci*. 40: 110–119.

**Ahlawat, S.P.S. & Singh, P.K.** 2005. Conservation and improvement of Indian cattle breeds. *VIII National Conference on Animal Genetics and Breeding, Indian Society of Animal Genetics and Animal Breeding*, Mathrua, India, 8–10 March 2005.

**Al-Amin, M. & Nahar, A.** 2007. Productive and reproductive performance of non-descript (local) and crossbred dairy cows in coastal area of Bangladesh. *Asian J. Anim. Vet. Adv*. 2(1): 46–49.

**Alba, J. & Kennedy, B.W.** 1985. Milk production in the Latin American milking Criollo and its crosses with the Jersey. *Anim. Prod*. 41: 143–150.

**Alexander, G.I.** 1986. Australia's tropical dairy breed. *Ag China Conference*, Guangzhou, China, 1986, P. 402–406.

**Amble, V.N. & Jain, J.P.** 1967. Comparative performance of different grades of crossbred cows on military farms in India. *J. Dairy Sci*. 50(10): 1695–1702.

**Ansell, R.H.** 1985. Cattle breeding in the tropics. *Wild Anim. Rev*. 54: 30–38.

**Ashraf, A., Islam, S.S., Islam, A.B.M.M. & Ali, S.Z.** 2000. A study of some economic traits of indigenous cattle and their crossbreeds in southern Bangladesh. *Asian-Aust. J. Anim. Sci*. 13(9): 1189–1192.

**BAIF.** 2011a. *Central Research Station: technologies for small farmers*. BAIF fact sheet 2/2011. BAIF, Pune, India.

**BAIF.** 2011b. *Dairy husbandry for sustainable livelihood*. BAIF fact sheet 3/2011. BAIF, Pune, India.

**Bala, A.K. & Nagarcenkar, R.** 1981. Evaluation of different cattle breed groups in hot humid tropics. Karnal, India, NDRI. Cited in Cunningham, E.P. and Syrstad, O., 1987 (Ph.D. project).

**Bayemi, P.H., Bryant, M.J., Perera, B.M.A.O., Mbanya, J.N., Cavestany, D. & Webb, E.C.** 2005. Milk production in Cameroon: a review. Livestock Research for Rural Development. Vol. 17, *Art. #60*. Retrieved 18 January 2010 (available at http://www.lrrd.org/lrrd17/6/baye17060.htm).

**Bhowmik, P., Sirohi, S. & Dhaka, J.P.** 2006. Gains from crossbreeding of dairy cattle in the North East: micro evidence from Tripura. *Indian J. Agr. Econ*. 61(3): 305–313.

**Bourdon, R.** 2000. *Understanding animal breeding*, 2nd edition. Prentice-Hall Inc., Upper Saddle Valley River, New Jersey.

**Buvanendran, V.** 1974. Crossbreeding experiments of Jersey with Indian Zebu breeds. *XIXth International Dairy Congress, New Delhi*, Vol. I. E. 55. Cited in Cunningham, E.P. and Syrstad, O., 1987.

**Buvanendran, V. & Mahadevan, P.** 1975. Crossbreeding for milk production in Sri Lanka. *Wild Anim. Rev*. 15: 7–13.

**Cardoso, V.L. & Vercesi Filho, A.E.** 2006. Alternative crossbreeding strategies for dairy cattle production in tropical circumstances. *Proceedings of 8th World Congress on Genetics Applied to Livestock Production*, 13–18 August 2006, Belo Horizonte, Brazil.

**Cerutti, F., Alvarez, J.C. & Rizzi, R.** 2006. Development of the Carora breed. *Proceedings of 8th World Congress on Genetics Applied to Livestock Production*, 13–18 August 2006, Belo Horizonte, Brazil.

**Chacko, C.T.** 2005. Development of the Sunandini cattle breed in India. In J.M. Ojango, B. Malmfors and A.M. Okeyo, eds. *Animal genetics training Resource, Version 2, 2006*. International Livestock Research Institute, Nairobi, Kenya and Swedish University of Agricultural Sciences, Uppsala, Sweden.

**Chagunda, M.G.G.** 2002. The importance of a national breeding policy – case for the Malawian dairy industry. In J.M. Ojango, B. Malmfors and A.M. Okeyo, eds. *Animal genetics training resource, Version 2, 2006*. International Livestock Research Institute, Nairobi, Kenya and Swedish University of Agricultural Sciences, Uppsala, Sweden.

**Chambers, F.** 2006. Status of Rare Breeds of Domestic Farm Livestock in Australia. Official Publication of Rare Breeds Trust of Australia (available at http://www.rbta.org/Pdf%20Files/RBTA%20%20Breeds%20Status%20Report%202006.pdf).

**Chantalakhana, C.** 1998. Role of exotic breeds in dairy and beef improvement in Asia. *Proceedings of 6th World Congress on Genetics Applied to Livestock Production*, 11–16 January 1998, Volume 25, 213–222, Armidale, Australia.

**Cunningham, E.P.** 1981. Selection and crossbreeding strategies in adverse environments. FAO Anim. Prod. Health Paper No. 24, 284–293, Rome, Italy.

**Cunningham, E.P.** 1999. Recent developments in biotechnology as they relate to animal genetic resources for food and agriculture. FAO Background Study Paper No. 10, Rome, Italy.

**Cunningham, E.P. & Syrstad, O.** 1987. Crossbreeding *Bos indicus* and *Bos taurus* for milk production in the tropics. FAO Anim. Prod. Health Paper No. 68, Rome, Italy.

**Dekkers, J.C.M.** 2007. Marker-assisted selection for commercial crossbred performance. *J. Anim. Sci*. 85: 2104–2114.

**Demeke, S., Neser, F.W.C., Schoeman, S.J.** 2004a. Estimates of genetic parameters for Boran, Friesian, and crosses of Friesian and Jersey with the Boran cattle in the tropical highlands of Ethiopia: reproduction traits. *J. Anim. Breed. Genet*. 121: 57–65.

**Demeke, S., Neser, F.W.C., Schoeman, S.J.** 2004b. Estimates of genetic parameters for Boran, Friesian, and crosses of Friesian and Jersey with the Boran cattle in the tropical highlands of Ethiopia: milk production traits and cow weight. *J. Anim. Breed. Genet*. 121: 163–175.

**Dhara, K.C., Ray, N. & Sinha, R.** 2006. Factors affecting production of F1 crossbred dairy cattle in West Bengal. Livestock Research for Rural Development. Volume 18, Article #51. Retrieved 18 January 2010 (available at http://www.lrrd.org/lrrd18/4/dhar18051.htm).

**Gaur, G.K., Garg, R.C. & Singh, K.** 2005. Experiences of crossbreeding cattle in India. *VIII National Conference on Animal Genetics and Breeding, Indian Society of Animal Genetics and Animal Breeding*, Mathrua, India, 8–10 March 2005.

**Girolando Associação Brasileira Dos Criadores de Girolando.** 2005. Performance (available at http://www.girolando.com.br/site/ogirolando/performance.php).

**Goshu, G.** 2005. Breeding efficiency, lifetime lactation and calving performance of Friesian-Boran crossbred cows at Cheffa farm, Ethiopia. Livestock Research for Rural Development. Volume 17, Article #73. Retrieved 18 January 2010 (available at http://www.lrrd.org/lrrd17/7/gosh17073.htm).

**Gregory, K.E. & Trail, J.C.M.** 1981. Rotation crossbreeding with Sahiwal and Ayrshire cattle in the tropics. *J. Dairy Sci*. 64: 1978–1984.

**Haile, A., Joshi, B.K., Ayalew, W., Tegegne, A. & Singh, A.** 2007. Economic comparison of Ethiopian Boran cattle and their crosses with Holstein Friesian in central Ethiopia. *Ethiopian J. Anim. Prod*. 7(1): 77–87.

**Hansen, P.J.** 2006. Realizing the promise of IVF in cattle – an overview. *Theriogenology* 65: 119–125.

**Hayes, B.J., Bowman, P.J., Chamberlain, A.J. & Goddard, M.E.** 2009. Invited review: genomic selection in dairy cattle: progress and challenges. *J. Dairy Sci*. 92: 433–443.

**Hayman, R.H.** 1974. The development of the Australian milking Zebu. *Wild Anim. Rev*. 11: 31–35.

**Hemalatha, B., Prashanth, V.R.N. & Reddy, Y.V.R.** 2003. Economics of milk production of different breeds of bovines in Ahmednagar district of Maharashtra. Quoted in Singh, A., 2005.

**Ibáñez-Escriche, N., Fernando, R.L., Toosi, A. & Dekkers, J.C.M.** 2009. Genomic selection of purebreds for crossbred performance. *Genet. Sel. Evol*. 41: 12.

**Islam, N.M., Rahman, M.M. & Faruque, S.** 2002. Reproductive performance of different crossbred and indigenous dairy cattle under small holder farming condition in Bangladesh. *Online J. Biol. Sci*. 2 (4): 205–207.

**Kahi, A.K.** 2002. Choice of genetic types for specific production environments and production systems. In J.M. Ojango, B. Malmfors & A. M. Okeyo, eds. *Animal genetics training resource, Version 2, 2006*. International Livestock Research Institute, Nairobi, Kenya and Swedish University of Agricultural Sciences, Uppsala, Sweden.

**Kahi, A.K., Nitter, G., Thorpe, W. & Gall, C.F.** 2000. Crossbreeding for dairy production in the lowland tropics of Kenya: II. Prediction of performance of alternative crossbreeding strategies. *Livest. Prod. Sci*. 63: 55–63.

**Katpatal, B.G.** 1977. Dairy cattle crossbreeding in India. *Wild Anim. Rev*. 22: 15–21.

**Katyega, P.M.J.** 1987. Mpwapwa cattle of Tanzania. *FAO/UNDP Anim. Genet. Resour. Inform. Bull*. 6: 23–26.

**Kimenye, D.** 1978. Milk production of Ayrshire and its crossbreds with Sahiwal at Machakos and Ngong Veterinary Farms, Kenya. *Egerton Coll. Agric. Bull*. 2(2): 44–47.

**King, J.M., Parsons, D.J., Turnpenny, J.R., Nyangaga, J., Bakari, P. & Wathes, C.M.** 2006. Modelling energy metabolism of Friesians in Kenya smallholdings shows how heat stress and energy deficit constrain milk yield and cow replacement rate. *Anim. Sci*. 82: 705–716.

**Kiwuwa, G.H., Trail, J.C.M., Kurtu, M.Y., Worku, G., Anderson, F. & Durkin, J.** 1983. *Crossbred dairy cattle productivity in Arsi Region, Ethiopia*. ILCA Research Report 11, International Livestock Centre for Africa.

**Knudsen, P.P. & Sohael, A.S.** 1970. The Vom herd: a study of the performance of a mixed Friesian/Zebu herd in a tropical environment. *Trop. Agric*. (Trinidad) 47: 189–203.

**Kosgey, I.S., Kahi, A.K. & Van Arendonk, J.A.M.** 2005. Evaluation of closed adult nucleus multiple ovulation and embryo transfer and conventional progeny testing breeding schemes for milk production in tropical crossbred cattle. *J. Dairy Sci*. 88: 1582–1594.

**Kumar, A., Birthal, P.S. & Joshi, P.K.** 2003. Research on crossbreeding in cattle: an analysis of its economic and social impact in India. *Agric. Econ. Res. Rev*. 16(2): 91–102.

**Mackinnon, M.J., Thorpe, W. & Barker, R.L.** 1996. Sources of genetic variation for milk production in a crossbred herd in the tropics. *Anim. Sci*. 62: 5–16.

**Madalena, F.E.** 1981. Crossbreeding strategies for dairy cattle in Brazil. *Wild Anim. Rev*. 38: 23–30.

**Madalena, F.E., Lemos, A.M., Teodoro, R.L., Barbosa, R.T. & Monteiro, J.B.** 1990. Dairy production and reproduction in Holstein-Friesian and Guzera crosses. *J. Dairy Sci*. 73: 1872–1886.

**Madalena, F.E., Peixoto, M.G.C.D. & Gibson, J.** 2012. Dairy cattle genetics and its applications in Brazil. Livestock Research for Rural Development. Volume 24, Article #97. Retrieved 10 August 2012 (available at http://www.lrrd.org/lrrd24/6/made24097.htm).

**Majid, M.A., Talukder, A.I. & Zahiruddin, M.** 1996. Productive performance of pure breeds, F1, F2 and F3 generations cows raised on the Central Cattle Breeding and Dairy farm of Bangladesh. *Asian-Aust. J. Anim. Sci*. 9: 461–464.

**Mapletoft, R.J. & Hasler, J.F.** 2005. Assisted reproductive technologies in cattle: a review. *Rev. Sci. Tech. Off. Int. Epiz*. 24(1): 393–403.

**Mason, I.L.** 1974. Maintaining crossbred populations of dairy cattle in the tropics. *Wild Anim. Rev*. 11: 36–43.

**Mason, I.L. & Buvanendran, V.** 1982. Breeding plans for ruminant livestock in the tropics. FAO Animal Production and Health Paper 34, Rome, Italy.

**Matharu, R.S. & Gill, G.S.** 1981. Evaluation of different grades of Holstein-Friesian × Sahiwal crosses on the basis of lifetime production and reproduction efficiency. *Indian J. Dairy Sci*. 24: 16–20.

**McDowell, R.E.** 1985. Crossbreeding in tropical areas with emphasis on milk, health, and fitness. *J. Dairy Sci*. 68: 2418–2435.

**McDowell, R.E., Wilk, J.C. & Talbott, C.W.** 1996. Economic viability of crosses of *Bos taurus* and *Bos indicus* for dairying in warm climates. *J. Dairy Sci*. 79: 1291–1303.

**Meat and Livestock Australia** 2006. *Handbook of Australian livestock*, 5th edition. Meat and Livestock Australia Limited (available at http://www.mla.com.au/NR/rdonlyres/DC211937-3533-4EC8-98C3-5D2836A89C3B/0/HandbookofAustraianlivestock.pdf).

**Miazi, O.F., Hossain, E. & Hassan, M.M.** 2007. Productive and reproductive performance of crossbred and indigenous dairy cows under rural conditions in Comilla, Bangladesh. *Univ. J. Zool. Rajshahi Univ*. 26: 67–70.

**Olutogun, O., Yode-Owolade, A. & Abdullah, A.R.** 2006. Comparative analysis of lactation traits of Holstein-Friesian White-Fulani Zebu and their F1 crossbred cows in Nigeria. *Proceedings of 8th World Congress on Genetics Applied to Livestock Production*, 13–18 August 2006, Belo Horizonte, Brazil.

**Patil, B.R. & Udo, H.M.J.** 1997. The impact of crossbred cows at farm level in mixed farming systems in Gujarat, India. *Asian-Aust. J. Anim. Sci*. 10(6): 621–628.

**Philipsson, J., Rege, J.E.O. & Okeyo, A.M.** 2006. Sustainable breeding programs for tropical farming systemsin. *In* J.M. Ojango, B. Malmfors and A.M. Okeyo, eds. *Animal genetics training resource, Version 2, 2006*. International Livestock Research Institute, Nairobi, Kenya and Swedish University of Agricultural Sciences, Uppsala, Sweden.

**Policy Note.** 2007. Dairy Sector Development in Sub-saharan Africa. Retrieved from www.alive-online.org

**Rahman, M., Islam, R. & Rahman, M.M.** 2007. Estimation of genetic Parameters for Economic Traits in Dairy Cattle of Bangladesh. *Asian J. Anim. Med. Adv*., 2(1): 9–14.

**Rege, J.E.O.** 1998. Utilization of exotic germplasm for milk production in the tropics. In: *Proceedings of the 6th World Congress on Genetics Applied to Livestock Production*, 11–16 January 1998, Armidale, NSW, Australia.

**Roschinsky, R., Sölkner, J., Puskur, R., Wurzinger, M.** 2012. Crossbreeding as innovation for dairy stock keepers in the tropics – case study Amhara Region, Ethiopia. *Poster published at symposium: "Festsymposium 140 Jahre Universität für Bodenkultur Wien. Quo vadis, Universitäten?"*, Vienna, *2012*.

**Roso, V.M., Schenkel, F.S., Miller, S.P. & Wilton, J.W.** 2005. Additive, dominance, and epistatic loss effects on preweaning weight gain of crossbred beef cattle from different *Bos taurus* breeds. *J. Anim. Sci*. 83: 1780–1787.

**Rutledge, J.J.** 2001. Greek temples, tropical kine and recombination load. *Livest. Prod. Sci*. 68: 171–179.

**Shem, M.N.** 2007. The dairy industry development in Tanzania: Lessons from the past for a better tomorrow. *In*: *5th National dairy development conference, building sustainable dairy chains in Tanzania*, Arusha, Tanzania.

**Shem, M.N. & Mdoe, N.S.Y.** 2003. Dairy production and poverty alleviation in Tanzania: A historical perspective. *Paper presented during the Annual Conference of Society for Animal Science*, December 2003, Arusha, Tanzania.

**Singh, A.** 2005. Crossbreeding of cattle for increasing milk production in India: a review. *Indian J. Anim. Sci*. 75(3): 383–390.

**Sohael, A.S.** 1984. Milk production potential of cattle on the Jos Plateau. *Nigeria Livest. Earner* 4(3): 13–14.

**Sölkner, J., Nakimbugwe, H. & Valle-Zarate, A.** 1998. Analysis of determinants for success and failure of village breeding programs. In: *Proceedings of the 6th World Congress on Genetics Applied to Livestock Production*, vol. 25, 11–16 January 1998, Armidale, NSW, Australia, pp. 273–280.

**Stonaker, H.H.** 1953. Estimates of genetic changes in an Indian herd of red Sindhi dairy cattle. *J. Dairy Sci*. 36: 688–697.

**Swan, A.A. & Kinghorn, B.P.** 1992. Evaluation and exploitation of crossbreeding in dairy cattle. *J. Dairy Sci*. 75: 624–639.

**Syrstad, O.** 1987. Dairy cattle crossbreeding in the tropics: choice of crossbreeding ctrategy. *Trop. Anim. Health and Prod*. 28: 223–229.

**Syrstad, O.** 1988. Crossbreeding for increased milk production in the tropics. *Norw. Agric. Sci*. 2: 179–185.

**Syrstad, O.** 1989. Dairy cattle cross-breeding in the tropics: performance of secondary cross-bred populations. *Livest. Prod. Sci.* 23: 97–106.

**Syrstad, O. & Ruane, J.** 1998. Prospects and strategies for genetic improvement of the dairy potential of tropical cattle by selection. *Trop. Anim. Health Prod*. 30: 257–268.

**Tadesse, M. & Dessie, T.** 2003. Milk production performance of Zebu, Holstein Friesian and their crosses in Ethiopia. Livestock Research for Rural Development 3 (15) (available at http://www.lrrd.org/lrrd15/3/Tade153.htm).

**Tadesse, M., Dessie, T., Tessema, G., Degefa, T. & Gojam, Y.** 2006. Study on age at first calving, calving interval and breeding efficiency of *Bos taurus, Bos indicus* and their crosses in the highlands of Ethiopia. *Ethiopian J. Anim. Prod*. 6(2): 1–16.

**Thorpe, W., Morris, C.A. & Kang'ethe, P.** 1994. Crossbreeding of Ayrshire, Brown Swiss, and Sahiwal Cattle for annual and lifetime milk yield in the lowland tropics of Kenya. *J. Dairy Sci*. 77: 2415–2427.

**Trail, J.C.M. & Gregory, K.E.** 1981. Sahiwal cattle. An evaluation of their potential contribution to milk and beef production in Africa. ILCA Monograph 3, International Livestock Centre for Africa.

**Van der Werf, J. & Marshall, K.** 2003. Combining gene-based methods and reproductive technologies to enhance genetic improvement of livestock in developing countries. *Book for Extended Synopses. FAO/IAEA International symposium on application of gene based technologies for improving animal production and health in developing countries, 6–10 October 2003*, Vienna, Austria.

**VanRaden, P.M. & Sanders, A.H.** 2003. Economic merit of crossbred and purebred US dairy cattle. *J. Dairy Sci*., 86: 1036–1044.

**Velazquez, M.A.** 2008. Assisted reproductive technologies in cattle: applications in livestock production, biomedical research and conservation biology. *Annu. Rev. Biomed. Sci*. 10: 36–62.

**Wheeler, M.B., Rutledge, J.J., Fischer-Brown, A., VanEtten, T., Malusky, S. & Beebe, D.J.** 2006. Application of sexed semen technology to *in vitro* embryo production in cattle. *Theriogenology* 65: 219–227.

**Wint, W. & Robinson, T.** 2007. *Gridded Livestock of the World*. FAO, Rome, Italy (available at http://www.fao.org/docrep/010/a1259e/a1259e00.htm).

**World Book, Encyclopedia and Learning Resources.** 2009. Available at http://www.worldbook.com/wb/Students?content_spotlight/climates/about_climates

**Wurzinger, M., Willam, A., Delgado, J., Nürnberg, M., Valle Zarate, A., Stemmer, A., Ugarte, G. & Sölkner, J.** 2008. Design of a village breeding programme for a llama population in the High Andes of Bolivia. *Anim. Breed. Genet. 125*, 5: 311–319.