INTRODUCTION

One of the many constraints on milk production in the tropics is the poor genetic potential of the indigenous animals. Tropical cattle are mostly of zebu (*Bos indicus*) type. These cattle are well adapted to the conditions prevailing in the tropics. Natural selection over hundreds of generations has provided them with a high degree of heat tolerance, some resistance to many tropical diseases and the ability to survive long periods of feed and water shortage. However, their dairy potential is poor; they have low milk yield, they are late maturing and usually do not let down milk unless stimulated by the sucking of the calf.

Genetic improvement alone might not result in drastic increases of milk production in the tropics, but it is a prerequisite for such increases. Genetically more productive animals are also the best incentive to improved feeding and management.

GENOTYPE AND ENVIRONMENT

The performance of an animal is the result of the joint action of its genotype and the non-genetic effects to which it is exposed. The non-genetic factors are often collectively termed the "environment".

The genotype is often conceived as a frame which restricts the performance to a given level. Below this level, the performance is determined by the environment. This concept is visualized in Figure 1a. Two genotypes, A and B, are considered. The superiority of the better genotype, A, is expressed only if the environment is more favourable than that which is necessary to exploit fully the potential of the poorer genotype, B. When the environment is worse than this, both genotypes would perform similarly and genetic improvement beyond the level of B would be of no use. According to this model both genotype and environment can act as bottlenecks which restrict performance. Although this might seem reasonable, the available evidence indicates that the concept is in general not providing an appropriate description of the interaction between genotype and environment.

The model illustrated in Figure 1b is much more likely to be correct in most cases. Here the superiority of the better genotype, A, is realized, regardless of the environmental conditions, but the
Figure 1. Different models of genotype x environment interaction. For explanation, see text.
difference between the two genotypes increases as the environment improves. This means that genotype A responds more to improved conditions than genotype B (indicated by the steeper slope of the line), but the genetic difference is expressed also under poor conditions. Most research on genotype – environment interaction in dairy cattle supports this model (review by Syrstad, 1976). In studies on field data, progenies of various bulls have been found to rank very similarly over a wide range of production levels. The same was true when progenies of the same bull in Mexico and U.S./Canada were considered (McDowell et al., 1975). A recent review of dairy cattle crossbreeding in the tropics (Syrstad, 1989) suggests that the relative merits of two genetic groups (1/2 vs. 3/4 exotic inheritance) is independent of production level.

Figure 1c describes a situation in which the different responses of the two genotypes to environmental improvement results in reversed ranking. Genotype A is the better under good conditions, while B is superior when the environment falls below a given level. This might occur in cases when the environment varies over a very wide range. An example from beef cattle is presented by Hearnshaw & Barlow (1982). Crosses of Hereford with Friesian, Simmental and Brahman (American Zebu) were compared under good, intermediate and poor pasture conditions. The Friesian and Simmental crosses were the best on good pasture, while Brahman crosses were superior on poor pasture. In dairy cattle, Buvanendran & Petersen (1980) found almost no relationship between the performance of daughters of the same bull in Denmark and Sri Lanka. However, the number of daughters in Sri Lanka was small, and the lack of association might be incidental.

Model (b) suggests that the best breeding strategy is to select breeding animals on their performance in a good environment, as this is when the genetic differences between animals is most clearly expressed. But this would be dangerous if model (c) should be correct. The safest, and usually the most efficient, approach is to base selection on the merits of the animals as expressed under environmental conditions similar to those which their progenies will be exposed to.

METHODS FOR GENETIC IMPROVEMENT

a) Selection within the local population

Cattle indigenous to the tropics have, except in very few cases, been subjected to only little artificial selection for increased milk production. In view of the impressive results achieved by selection in many temperate dairy breeds there should be good prospects for improving the dairy potential of tropical cattle by the same method.

Genetic improvement per generation from selection depends on the variability of the traits considered, their heritability (i.e. the
proportion of total variation which can be ascribed to genetic differences), and the intensity of selection. Variability, in terms of the coefficient of variation, is usually greater in tropical than in temperate cattle, but the variation in actual units is less. Studies of heritability based on sufficiently large amounts of data are few, but estimates reported fall within the same range as those from temperate countries. Intensity of selection is restricted by the reproductive rate, and is further reduced by early mortality, which often is high under tropical conditions.

Many dairy cattle breeding programmes claim a genetic improvement in milk yield of one to two percent per year. Of this improvement, 60 to 70 percent is derived from the selection of bulls on the basis of the performance of their daughters (progeny testing). This is achieved by a combination of accurate progeny testing (i.e. many daughters per bull) and intensive selection (many bulls tested per year). These conditions can be fulfilled only in large populations, comprising tens (if not hundreds) of thousands of females, artificial insemination, and widespread milk recording.

In most tropical countries such populations do not exist, and are not likely to be available in the foreseeable future. Instead a breeding programme might have to be established in a single herd or a few cooperating herds. In order to make progeny testing worthwhile, even strictly on genetic grounds, several hundred females would be needed. Still, the high costs involved might not make such a programme attractive. But if the herd serves as a nucleus herd, also providing bulls for breeding outside the herd, the benefit of genetic progress will in turn be transmitted to a much larger number of animals, and it might be justified to maximize genetic progress in spite of high costs. Thus a rather small breeding scheme can have tremendous impact if organized and operated properly.

b) Introduction of improved tropical breeds

Some breeds of tropical cattle, e.g. Sahiwal and Red Sindhi, have been selected for increased milk yield over a long time and have reached a much higher dairy potential than most cattle in the tropics. This is a genetic resource which should be exploited for upgrading of unimproved stock. After a few generations of back-crossing to bulls of the improved breed, the inheritance of the local cattle has been almost completely replaced by the improved inheritance. The risk of losing adaptability to local conditions by this method is small, a breed like Sahiwal has shown to adapt well to conditions in four different continents. An improvement which would require ten generations of intensive selection could be obtained in two or three generations of upgrading with an improved breed. Unfortunately the number of animals of improved tropical breeds is small, and breeding stock of high quality are not easily available.
c) **Introduction of temperate breeds**

Reports on the high milk yields in some temperate countries have spread the belief that the importation of European-type dairy breeds is the solution to the problem of low production levels in the tropics. In some cases introduction of temperate breeds has been successful but much more often the experience has been disappointing and sometimes almost disastrous. Diseases, high mortality rates and low fertility have been frequent problems among the imported animals and their progenies, and animals which have survived have failed to reach the expected production levels. Offspring born in the tropical country have often produced much less than their dams, which were imported as heifers. The lack of adaptation to tropical conditions has been obvious. On the basis of experience up to this time, purebred European-type dairy cattle can be recommended in the tropics only if climatic stress is moderate, health services are easily available and reasonably good feeding is practised.

d) **Crossbreeding with European type cattle**

Crossbreeding of tropical cattle with cattle of European-type breeds has occurred for more than one hundred years, and a large number of reports has been published. In most cases, females of local stock have been mated to bulls of the imported breed or by the use of imported semen.

In almost all cases, crossbreeding with a European breed led to a dramatic increase in milk yield in the first crossbred generation (F1), compared with the local stock. The crossbred females calved at a much younger age than native animals, produced two to three times more milk and had longer lactations, shorter dry periods and shorter calving intervals. Mortality and susceptibility to disease were only slightly higher than in native cattle.

These favourable results were, naturally, ascribed to the superiority of the exotic inheritance, and it was tempting to introduce more of it by backcrossing to exotic bulls. But the expected further improvement did often not occur and in many cases a decline in performance was observed. Problems of high mortality and reduced fertility increased as the level of exotic inheritance increased towards 100 per cent.

When it had been found that upgrading towards the European breed was not advisable under most conditions, the next step was to try to stabilize the level of exotic inheritance by mating F1 males and females together. But again the results were often disappointing. In almost all projects the performance of the second half-bred generation, F2, has been much below that of F1. Age at first calving and calving intervals have increased considerably and milk yield has dropped by up to 30 per cent.
A summary of results from 54 sets of data reported from cross-breeding experiments in various regions of the tropics is presented in Table 1. The good performance of the first crossbred generation (F1) and the deterioration in the next generation (F2) are clearly demonstrated. The most obvious explanation is the presence of hybrid vigour (heterosis); this effect is maximized in the F1 but half of it is expected to disappear in the F2 and forward generations. In addition other genetic mechanisms might also be involved.

The great effect of hybrid vigour in crosses of zebu x European-type cattle might be expected because of the wide genetic distance between the two types (Cunningham and Syrstad, 1987). Furthermore it has been suggested that hybrid vigour is more important under stressful than under favourable environmental conditions (review by Barlow, 1981). The breeding strategy for dairy cattle in the tropics should therefore also aim at exploiting hybrid vigour. Exactly how this can be done under various conditions is still a question for discussion, and more research is needed.

Table 1. Performance of zebu cattle, European type cattle, and their crosses in the tropics. Summary of 54 sets of data. Source: Syrstad (1988).

<table>
<thead>
<tr>
<th>Proportion</th>
<th>Age at first calving, months</th>
<th>Milk yield, kg</th>
<th>Calving interval, days</th>
</tr>
</thead>
<tbody>
<tr>
<td>0 (i.e. zebu)</td>
<td>43.6</td>
<td>1052</td>
<td>459</td>
</tr>
<tr>
<td>1/8</td>
<td>40.1</td>
<td>1371</td>
<td>450</td>
</tr>
<tr>
<td>1/2 (F1)</td>
<td>32.4</td>
<td>2039</td>
<td>429</td>
</tr>
<tr>
<td>5/8</td>
<td>33.8</td>
<td>1984</td>
<td>432</td>
</tr>
<tr>
<td>3/4</td>
<td>33.9</td>
<td>2091</td>
<td>450</td>
</tr>
<tr>
<td>7/8</td>
<td>34.4</td>
<td>2086</td>
<td>459</td>
</tr>
<tr>
<td>1 (i.e. European)</td>
<td>31.6</td>
<td>2162</td>
<td>460</td>
</tr>
<tr>
<td>1/2 (F2, from F1xF1)</td>
<td>33.7</td>
<td>1523</td>
<td>449</td>
</tr>
</tbody>
</table>
Table 2. Comparison of F1 and backcrosses (1/2 and 3/4 European inheritance) at low, intermediate and high production levels. Summary of 30 sets of data. Source: Syrstad (1989).

<table>
<thead>
<tr>
<th>Production level</th>
<th>Average milk yield, kg</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F1</td>
</tr>
<tr>
<td>Low (&lt;2000 kg)</td>
<td>1487</td>
</tr>
<tr>
<td>Intermediate (2000-2405 kg)</td>
<td>2175</td>
</tr>
<tr>
<td>High (&gt;2405 kg)</td>
<td>2798</td>
</tr>
</tbody>
</table>

REFERENCES

Barlow, R. Experimental evidence for interaction between heterosis and environment in animals. Animal Breeding Abstracts 49: 715-737.


Syrstad, O. Dairy cattle crossbreeding in the tropics: The importance of genotype x environment interaction. Submitted for publication in *Livestock Production Science*. 