SUMMARY

The paper describes the philosophy and methods of a company supplying genetic improvement to worldwide markets. The physical environment largely controls the type of sow needed, while market environment is the main influence on the type of boar. Breeding objectives have to be chosen from each of three areas: sow productivity, economy of gain, and carcass. The breeder then makes progress towards these by selection among available breeds and lines, by choice of an appropriate crossing system, and, in the longer term, by testing and selection within lines. Different production systems and carcass markets require quite different breeds and so a whole 'stable' of specialized lines is needed. While 'double-cross' hybrids \((C \times D) \times (A \times B)\) might seem optimum there are several reasons why they have not so far proved popular.

Traits which can be used as within-line selection criteria are limited, but can be weighted in different ways in order to achieve various objectives. Realized selection intensities, generation intervals and heterosis levels, and within-programme estimates of genetic parameters are compared with predicted values. The pyramid system of disseminating genetic improvement from Nucleus to commercial herds is illustrated quantitatively.

INTRODUCTION

This paper is written from the standpoint of a particular breeding company, engaged in the supply of genetic improvement to pig producers in many of the important markets worldwide. No attempt has been made to give a complete survey of all the products, and the methods used to create them. Instead the company's overall breeding philosophy is presented, as it has developed over the past 24 years, and illustrated with specific examples of breeding objectives, criteria, intensity and effectiveness of selection. Breeding programmes outside the company are only mentioned to bring out important general principles.

Any consideration of breeding strategies for hybrid pig production must start with the environment in which the pigs are going to produce. First the physical conditions in which the three different parts of the herd (sow herd, boar stud, finishing pigs) are expected to perform. Equally important however is the market environment into which the slaughter stock are sold. It is thus necessary to consider the relevant environmental features found in practice, as a background to the choice of breeding objectives.
Physical Environments

Sows

1) Degree of confinement: Individual pens (stalls, tethers) throughout the reproductive cycle; group penning inside; outside lots during mating/gestation; outside paddocks throughout the cycle including farrowing.

2) Diet: Entirely concentrate; major proportion of forage or other bulky feed.

3) Climate: Temperate; extreme heat for some part of year; exposure to strong sun.

Boars

1) Degree of confinement: Individual pens - collection of semen for artificial insemination; individual pens - handmating; group pens with sows; grouped in outside lots or paddocks.

2) Climate: Temperate; extreme heat for some part of the year.

Finishing pigs

1) Management system and technology including handling and transport systems: high; low.

Market Environment

Discrimination (with significant financial penalty) against:

- light or heavy carcass weight; skin colour; carcass length;
- conformation (degree of muscling) including loin eye shape and size;
- subcutaneous fat depth; muscle colour, texture, water holding capacity; fat colour, firmness, cohesion.

BREEDING OBJECTIVES

General

There are three classes of objectives which apply throughout all pig production systems.

a) High sow productivity - often assessed by piglets weaned (or sold) per sow per year. The importance of this is that it controls the quantity of output from the herd, and hence the share of the farm's fixed costs (including sow feed) carried by each pig sold.

b) Economy of gain - both growth rate and efficiency of conversion of feed to gain. Again these control the efficiency with which the farm's fixed costs (of finishing) and variable costs (feed) are used. While they are more commonly known in liveweight terms it is vital to convert them to a deadweight basis (using the killing out or dressing %) wherever pigs are paid for on carcass weight.
c) Suitability of carcass for available markets - in terms of weight, skin colour, length, muscling, fat depth, muscle and fat quality.

All three classes of objectives affect profits of the pig enterprise but the specific emphasis within each class will depend upon the prevailing conditions. The physical environment is the main factor controlling the type of sow needed; market environment then dictates the type of boar which will produce suitable offspring out of those sows.

In a totally integrated production and marketing system, where a single profit is taken from the pig produced, finished, slaughtered and sold to the housewife, by one organization, then the relative values of unit changes in all components of the objectives can be calculated. Such a system is not common and normally the chain involves many individual organizations (breeder - sow keeper - dealer - finisher - dealer - abattoir - wholesaler - processor - wholesaler - retailer - consumer). In this case the perceived values of many traits may change from the more 'rational' values calculated within the integrated system. For example, where the sow herd sells feeder pigs on for finishing then sow productivity may seem much more important to the piglet producer than any aspects of growth rate or carcass quality - and he is likely to make decisions on what kind of sows are kept.

Achievement of Objectives

There are many non-genetic methods of achieving the agreed objectives in order to improve the overall profitability of the pig enterprise. The producer may manipulate sex (castration), slaughter weight, nutrition (feed quantity and quality at various stages of growth), and disease levels. There are nearly always costs associated with such manipulations, and the costs need to be incurred afresh for each animal. By contrast many genetic solutions involve an initial cost, but then the improvements are maintained indefinitely in the absence of counter selection.

Genetic solutions are of three kinds. First the exploitation of existing between-line variation, involving choice among available breeds. Next the combination of breeds or lines into an optimum crossbreeding system to exploit both the strengths of each line and the heterosis expressed in some traits. Third the further improvement of the chosen lines by continuous within-population testing and selection procedures.

BETWEEN-LINE SELECTION

Several conflicts are apparent at the between-line level, even though these may not be reflected in within-line genetic correlations.

The most muscular breeds e.g. Pietrain, Belgian Landrace and Hampshire, tend to have poor female reproductive ability.

They also have lean tissue more likely to develop into PSE meat.

Short breeds tend to have higher killing out %.
Lines which have been selected for improved feed efficiency often have reduced voluntary feed intake. While this may be a desirable trait in a finishing pig it can lead to problems in the sow herd, since the demands of lactation drain the body reserves excessively and leave the sow unprepared for rapid re-breeding.

Those breeds with larger appetites for bulky feeds, and good maternal instincts, e.g. British Saddleback and some Chinese lines, have carcasses which may be too fat for today's markets.

These conflicts are a major reason why a policy of specialized sire and dam lines makes sense. While basic theory may not show large advantages in deliberately developing such specialized lines from a base population (Smith 1964), the fact is that some lines already exist which are superior in sow productivity traits, or in carcass traits, but not in both. Bennett, Tess, Dickerson and Johnson (1983) demonstrated greater profitability from utilizing United States' breeds in specific terminal crossing systems rather than as general purpose breeds. Hence most optimum solutions will include the more prolific breeds in the Parent sow. Just which breeds will depend upon the environment in which she is to live and reproduce.

For intensive single confinement systems the Large White and Scandinavian Landrace are well suited. For group systems still in full or partial confinement a more robust and aggressive Parent sow may be needed, and the Duroc breed may be added. For outdoor systems the need to survive and behave in a way which cuts down labour has encouraged the use of the British Saddleback in UK. Where the need is to consume a high proportion of bulky feed then one of the Chinese breeds may be included in future.

Breeds contributing to the Parent boar have so far been those with a carcass close to that traditionally demanded by the local market. Thus in Denmark and Britain, where the side-cured bacon market has predominated, then Scandinavian Landrace and Large White were preferred. In Italy where many pigs are taken to very heavy weights for the manufacture of salami and Parma ham, Large Whites are preferred because of their good muscle quality. In USA, a general purpose manufacturing pig is bought liveweight, and carcass parts diverted to fresh meat, ham and belly bacon. The Duroc and Hampshire breeds continue to be popular because of their traditional shape, and good yield and the absence of large discounts for fat. In Germany and Belgium, where the market demand has been for the most extreme muscular conformation, Parent boars have been well-muscled Landrace and Pietrain.

It is obvious that the hybrid breeder aiming to serve worldwide markets must retain a number of different lines in his 'stable'. Each may contribute to one or several different hybrid products, or may be in reserve, waiting for a role to develop in a new product.

CROSSBREEDING STRATEGIES

The chosen lines must then be put together in a crossbreeding system. If the Parent sow is an F1 between the two lines best fitted to give high production in the chosen environment it will provide the maximum maternal heterosis for these traits. If the Parent boar is an F1 between the two best carcass lines it will exhibit heterosis for libido and longevity and
compensate for the sow's lack of carcass development. For example in the United States market, for a full confinement unit with individual stalls, a Parent sow might be (Large White x British Landrace) and Parent boar (Duroc x Hampshire). Such simple "double-cross" hybrids are not yet very common, however, for several reasons.

In Britain, Scandinavia, the Netherlands and Italy, the most suitable sow lines have also had the best carcasses for the prevailing market demand. Hence a simple two-line back-crossing system has been popular (LW or LR^ x (LW x LR)\text{\textsubscript{f}}). The loss of half the individual heterosis (for survival and growth rate) has been accepted since no third line was available to improve the carcass.

In Germany, if the same prolific parent sow is to be used, then only the most extreme boar has been able to sire carcasses with sufficient muscling to achieve satisfactory grading. But a hybrid between Pietrain and Belgian Landrace, while meeting this requirement, often has poor fitness because the two breeds have been so intermingled, and because they both carry the halothane (stress) gene at high levels. A three-line cross boar (P\text{\textsubscript{f}} x (BL x LW)\text{\textsubscript{f}}) has therefore been preferred. The LW component gives the muscular boar a much needed increase in fitness, and the use of a crossbred grandparent sow (BL x LW) also lowers the boar production cost.

In Belgium, where the price differentials for heavily muscled carcasses are even more extreme, the extra output from prolific crossbred sows hardly compensates for the reduction in grading among their progeny. Hence a popular system continues to be a Pietrain Parent boar on a Belgian Landrace Parent sow, and more complex hybrid systems bringing in other lines have not had much impact.

The single-cross hybrid sow concept has been very widely accepted, with the F\textsubscript{1} (Large White x British Landrace) being used in confinement systems throughout Europe, N and S America and parts of Asia. For lower cost systems, where the sows live outdoors on the free draining soils of Southern England, the F\textsubscript{1} (Landrace x British Saddleback) sow has an important role. But while an F\textsubscript{1} crossbred parent female shows maximum maternal heterosis, and is simplest to produce, a three-way cross (C x (A x B)) Parent sow can show equal heterosis and possess other advantages. The use of an F\textsubscript{1} crossbred grandparent (A x B) sow cheapens the production cost of the Parent gilt. In addition, although the third line (C) may lower the potential prolificacy of the cross, it may also introduce traits beneficial to the survival and performance of the sow in its working environment. Thus a [Duroc x (Large White x Landrace)] sow is proving particularly well-suited to group housing situations throughout the USA and Mexico.

In all countries pig producers have traditionally bred their own replacement females, and not purchased them from outside. Today many of these are aware of the benefits from a hybrid sow but do not find it easy to maintain a small grandparent herd of purebred sows specifically to produce F\textsubscript{1} gilts. As a consequence there is a growing demand for purchased gilts, and breeding companies who have created the market are supplying it from specialist multiplier herds. In the USA this trend is not so far advanced, and many replacements are still produced in the commercial herd from some sort of rotational crossing system. With two or three types of purebred boars, of widely different characteristics, the mean genetic level in the herds
oscillates rather widely between generations. A system based upon two or three kinds of hybrid boars has been introduced to improve this aspect. Each boar is an F_{1} crossbred, thus improving working ability, and each is also a better balanced animal in its dual role of siring both slaughter progeny and replacement gilts.

Within-programme estimates of heterosis are not precise and unbiased, since purebred and crossbred performance has usually been measured in different herds. Nevertheless the levels observed in crosses between the British white breeds have been similar to those reported by Smith and King (1964), while crosses between these and United States' breeds have shown higher levels.

**WITHIN-LINE SELECTION**

Genetic improvement is frequently thought to result only from within-line selection, but it is hoped that the previous two sections have demonstrated that such selection logically takes third place - after a careful choice among lines and crossbreeding systems. Selection criteria need to be drawn up, so as to bring pressure on the chosen objectives. Again the choice is strongly influenced by the prevailing environment. For example the market environment in USA has not so far justified the same emphasis on reducing backfat as it has in UK, where strong price differentials have favoured the leaner carcass. Candidates are then assessed, by measurements on themselves or their close relatives, and a proportion selected as replacements.

It should be mentioned here that, unlike the purebred breeder who belongs to some herdbook association, the hybrid breeder can continue to exploit both between- and within-line variation. If he is convinced that faster progress towards a given objective can be achieved through immigration of progeny of selected animals from another 'breed', then he can do so. By contrast the purebred breeder is bound by his association's rules. These may approve such immigration from certain sources, or prohibit it altogether, and hence limit him to working only with the genes assembled from the breed's original crossbred base. Consequently, while breed names are used in this review for convenience, it must be realized that the lines in the hybrid breeder's 'stable' may be new synthetics, with only a majority of genes from the named breed.

**Selection criteria**

The number of traits which can be measured easily, cheaply and on large numbers of individuals within a line is quite limited (Table 1). At the start of hybrid programmes, major attention must be paid to the essentials which will help the organization grow and prosper. Hence selection criteria have been limited to rates of gain, ultrasonically measured fat depths, teats and physical soundness in gilts, plus daily feed intake and hence feed conversion in boars.
TABLE 1

Possible selection criteria to be measured on:

Candidate

Liveweight at birth and weaning
Rate of liveweight gain (from birth to a given age or from a start weight to an end weight)
Daily feed intake
Subcutaneous fat depth
Depth of longissimus dorsi
Conformation
Stress susceptibility
Teat number
Physical soundness
Age at sexual maturity (not easy)
Blood and tissue analyses (not cheap)

Candidate's relatives

Litter size
Rebreeding interval
Reproductive life
Male reproductive traits
Carcass traits - linear measurement
  killing out %
  classification/grading
  % composition
  fat and muscle quality

As the hybrid organization grows and aims at more objectives, then the complexity of the testing and assessment system has to grow. The increased costs can be spread over a larger product volume. Hence routine testing for stress susceptibility and dam's reproductive details can be included. In the future other more accurate indirect assessments of body composition could be used, and perhaps direct carcass evaluation on the candidates' relatives. But it is more important to achieve high selection pressure on a few simple criteria, rather than make the system too complex and expensive, or measure too few candidates.

Selection system

The choice of selection system partly dictates which criteria can be utilized - since, for example, if sibs are not to be routinely slaughtered and assessed then only indirect in vivo estimates of carcass composition are available. Most hybrid organizations were started at a time when performance testing had been shown to be theoretically more efficient than progeny testing. Hence performance testing, or combined testing using information on the candidate and his (or her) sibs, has been the preferred system. Complete combined selection, using data from relatives in both current and previous generations, only becomes practicable with a computerized database system, and may be adopted in future.
Linking criteria with objectives

Within a simple performance testing system, with no notice being taken of records from dams, aunts, full or half-sibs, the choice of criteria for selection is quite limited: on the one hand growth, feed efficiency and backfat; on the other the physical appearance of the animal—particularly legs and feet, teats, and muscle development. Nevertheless quite different selection results can be achieved depending on the relative weights given to these separate traits. The measured performance traits are usually weighted by means of selection index theory (Hazel 1943). Here all relevant selection objectives for the line in question are listed, and themselves weighted by the relative economic values of unit change in each. The weighted combination (usually a linear function) becomes the single objective of selection. All available measurements on the candidate are then listed and selection index weights, to be applied to these criteria, are derived as that set which maximizes the correlation between the criteria and the candidate's breeding value for the single selection objective. Fowler, Bichard and Pease (1976) described this as the economic model, and proposed an alternative 'biological' model in which an apparently simpler objective (lean tissue growth rate or lean tissue feed efficiency) was substituted. Candidates were then to be selected on their estimated performance in one of these objectives.

While the ensuing debate on these alternative approaches has done much to interest animal breeders in the biological consequences of their test environments and selection schemes, it has to be accepted that true objectives in pig production must take account of both speed of growth and efficiency of feed use for lean production. Furthermore the balance between them must be based on economic argument. In addition since the need is to improve the next generation, the information available should be weighted in a way which predicts the candidate's breeding value, and not its phenotypic value.

Thus Sire lines are selected by weighting the performance values in an Index calculated to give maximum economic response in the growth, efficiency and carcass traits for the future market where the line is expected to perform. In this way lean content has been very successfully increased without incurring problems of poor muscle quality or general stress susceptibility. For the most muscular lines, however, subjective scoring on the live animal seems to be an efficient method of selection to further improve total lean, lean to bone ratio, eye muscle area and killing out %—though at the expense of general fitness since such selection also increases the frequency of the halothane gene. Optimum methods of combining these two approaches have yet to be developed.

Specialized Dam lines have only recently emerged and the procedures for their selection have not yet stabilized. One method is to run cycles, where for say, two years, all selection pressure is on reproductive traits (Bichard and Seidel, 1982), and for the next five years all selection is for growth, efficiency and carcass traits. This has the advantage that the advances achieved in the reproductive traits can be assessed before they are accepted. The alternative strategy is to incorporate reproductive data into the selection index used each generation, alongside information on the performance traits, all suitably weighted. Avalos (1985) has calculated the contribution likely to be made by such inclusion under British conditions and concluded it would be worthwhile.
Intensity of selection

The proportion of tested candidates selected in a herd is largely controlled by the combined effect of the reproductive rate and the chosen rate of generation turnover. As a result, the intensity of selection realized in practice can only be properly assessed as the ratio \( i/t \) (where \( i = \) selection differential in standard deviation units; \( t = \) generation interval). Clearly \( i \) is affected by proportion selected, whether the selected individuals were chosen on the basis of their Index values and the variability of the Index. Figure 1 illustrates the way in which \( i \), \( t \) and their ratio are expected to vary in a 120-sow line with given reproductive performance. In PIC Nucleus herds the chosen generation interval has usually been between around 1.25 years. The actual values achieved in the early part of the programme (Swales 1975) and those in several countries in more recent years are shown in Table 2. The shortfall from theoretical predictions has a number of causes. It is impossible to base selection entirely on the Index criterion - some animals always have to be rejected because they are incapable of reproduction, or because their lack of fitness may have some genetic component.

FIGURE 1.

Selection intensity \((i)\), Generation interval \((t)\) and their ratio at several different replacement rates and at different numbers tested per sow per year in a 120 sow line.

\[
\begin{align*}
\text{Litters/ø} & \quad 1 & 2 & 3 & 4 \\
\text{Months ø kept} & \quad 3 & 6 & 9 & 12 \\
3.5/3.5 & = 3.5 \text{ ø and } 3.5 \text{ ø tested per year} \\
7/7 & = 7 \text{ ø and } 7 \text{ ø tested per sow per year}
\end{align*}
\]
TABLE 2

Selection intensity (i), Generation interval (t) and their ratio achieved in three nucleus herds

<table>
<thead>
<tr>
<th>Herd</th>
<th>i</th>
<th>t</th>
<th>i/t</th>
</tr>
</thead>
<tbody>
<tr>
<td>UK, 1966-69</td>
<td>1.12</td>
<td>1.38</td>
<td>0.81</td>
</tr>
<tr>
<td>Brazil, 1984</td>
<td>1.09</td>
<td>1.22</td>
<td>0.89</td>
</tr>
<tr>
<td>UK, 1985</td>
<td>1.36</td>
<td>1.22</td>
<td>1.11</td>
</tr>
<tr>
<td>USA, 1985</td>
<td>1.55</td>
<td>1.17</td>
<td>1.32</td>
</tr>
</tbody>
</table>

† Average of Large White and Landrace lines.

THE EFFECTIVENESS OF SELECTION

In order to predict response from the within-line selection component of the total system it is necessary to have relevant and accurate estimates of the genetic parameters - heritability and genetic correlation. Again, in the early years of development of a hybrid programme, it is impossible to derive such estimates from the data generated within the programme. Reliance must therefore be placed upon published estimates coming from similar populations. Support for this has recently come from analyses done by Avalos (1985) on data collected in a Nucleus herd over a 10-year period (1970-1980) covering nearly 12,000 purebred litters from two breeds. The estimates in Table 3 are fairly similar to those assumed to date (e.g. Strang and Smith 1979).

TABLE 3 (Source: Avalos 1985)

a) Heritabilities in Large White and Landrace Nucleus lines.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Daughter-dam regression</th>
<th>Paternal half-sib</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age at 90 kg</td>
<td>0.30 ± 0.04</td>
<td>0.49 ± 0.10</td>
</tr>
<tr>
<td>Ultrasonic backfat</td>
<td>0.41 ± 0.04</td>
<td>0.58 ± 0.11</td>
</tr>
<tr>
<td>Litter size</td>
<td>0.11 ± 0.01</td>
<td>0.08 ± 0.06</td>
</tr>
<tr>
<td>(all parities)</td>
<td></td>
<td>(1st parity)</td>
</tr>
</tbody>
</table>

b) Heritabilities, genetic (below diagonal) and phenotypic (above diagonal) correlations among different parities for litter size (daughter-dam regression) in Large White and Landrace Nucleus lines.

<table>
<thead>
<tr>
<th>Parity</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.11 ± 0.03</td>
<td>0.17</td>
<td>0.17</td>
<td>0.16</td>
</tr>
<tr>
<td>2</td>
<td>1.04 ± 0.20</td>
<td>0.10 ± 0.04</td>
<td>0.18</td>
<td>0.23</td>
</tr>
<tr>
<td>3</td>
<td>0.50 ± 0.22</td>
<td>1.29 ± 0.22</td>
<td>0.14 ± 0.06</td>
<td>0.23</td>
</tr>
<tr>
<td>4</td>
<td>0.46 ± 0.21</td>
<td>1.15 ± 0.19</td>
<td>1.06 ± 0.28</td>
<td>0.16 ± 0.11</td>
</tr>
</tbody>
</table>
It is not possible to be precise about the effectiveness of selection practised relative to predicted responses. No control lines were maintained, frequent environmental changes have been made, and analyses to estimate phenotypic trends free from the effects of these changes have not been attempted. Mitchell, Smith, Makower and Bird (1982) have estimated a rate of 1.8% annually in UK herds for an Index of six performance traits and their study included products of the programmes described in this paper. Smith (1984) calculated an annual rate of genetic change of 1.5% in litter size from these dam lines (LW and LR) by selection of hyperprolific females from a large recorded population, and this topic was recently reviewed by Bichard and David (1985). In future it is likely that better internal estimates of realized rates of genetic change will be needed, since many important decisions depend upon such knowledge.

PYRAMID STRUCTURE

The reason for the existence of the selection and crossbreeding systems is to improve the genetic potential of the animals kept at commercial level to produce pigmeat on the world’s farms. Because of the costs of creating genetic change a pig industry is often organized in a two-or-more-tier pyramid structure. A few specialized purebreeding (Nucleus) herds test and select to create this change, and pass the genetic improvement on to multiplication herds where line crossing takes place. These may in addition act as commercial production herds, if continuous, rotational or simple two-line crossing is practised. Otherwise a third or fourth tier of specialized production herds takes genetic material from herds in the tiers above and uses it as the basis for end products. These tiers may all be contained within a single complex breeding unit or may be separate in location and ownership.

Naturally if improvement is made in one herd, and transferred through one or more levels, there will be a time lag before it is expressed in the commercial (Parent) sows and their progeny. The size of this lag, measured as the difference in genetic merit between commercial and nucleus level, is affected by several factors (Bichard 1971, Guy and Smith 1981):

a) the rate of improvement being achieved at Nucleus level;
b) the method of transfer of genetic material - whether both sexes are moved, or only one;
c) the number of tiers in the pyramid, and whether some genetic material (e.g. boars or semen) moves down only one tier at a time, or bypasses one or more tiers;
d) the rate of turnover and hence generation interval at each level below the Nucleus;
e) the selection differentials achieved among replacements at each level below the Nucleus.

Methods of gene transfer are largely dictated by cost and health considerations. A typical system is illustrated in Figure 2.
It is not always appreciated that the only selection which has permanent and cumulative effects is that achieved in the Nucleus pure lines. All other selection differentials lower down the pyramid serve only to reduce the genetic lag by up to a fixed amount, and these effects disappear if the selection is relaxed. A selection differential can be generated at gilt-multiplier level, by only transferring a proportion of $F_1$ gilts with the highest test scores to commercial units. But since each parent gilt only produces some 60 progeny in her lifetime the costs of those gilts may easily be increased by more than the extra value of their progeny.

As a result it is normal policy to maximize selection differentials at Nucleus level, but then to concentrate upon efficiency of production of sound breeding stock in the lower tiers, and to transfer (sell) as many as possible into the multiplication and production herds. Typical numbers of end products which are produced from the multiplication system are also given in Figure 2.
REFERENCES


