

# CONSIDERATIONS IN THE DEVELOPMENT OF FUTURE PIG BREEDING PROGRAMS

— Review —

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## Summary

Pig breeding programs have been very successful in the improvement of animals by the simple expedient of focusing on a few traits of economic importance, particularly growth efficiency and leanness. Further reductions in leanness may become more difficult to achieve, due to reduced genetic variation, and less desirable, due to adverse correlated effects on meat and eating quality. Best linear unbiased prediction (BLUP) of breeding values makes possible the incorporation of data from many sources and increases the value of including traits such as sow performance in the breeding objective. Advances in technology, such as electronic animal identification, electronic feeders, improved ultrasonic scanners and automated data capture at slaughter houses, increase the number of sources of information that can be included in breeding value predictions. Breeding program structures will evolve to reflect these changes and a common structure is likely to be several or many breeding farms genetically linked by A.I., with data collected on a number of traits from many sources and integrated into a single breeding value prediction using BLUP. Future developments will include the production of a porcine gene map which may make it possible to identify genes controlling economically valuable traits, such as those for litter size in the Meishan, and introgress them into nucleus populations. Genes identified from the gene map or from other sources will provide insight into the genetic basis of performance and may provide the raw material from which transgenic programs will channel additional genetic variance into nucleus populations undergoing selection.

(Key Words: Pigs, Breeding, Genetics)

## Introduction

It is now virtually axiomatic that an efficient animal breeding program consists of the definition of breeding objectives, the selection of the best breeds with the optimum crossbreeding structure, followed by effective within breed improvement by selection. Over the past 20 to 30 years most countries have changed from producing slaughter pigs from purebred lines to the use of some form of crossbreeding. A system commonly used world-wide is a hybrid F1 female, usually Large White (Yorkshire) × Landrace crossed back to a Large White sire or a sire of a third breed, for example, Duroc. The slaughter pigs are thus either a backcross or a three breed cross. Such systems are effective because they utilize both the complementarity of maternal and production

characteristics of different breeds and the heterosis found in breed crosses. The use of F1 females is particularly important, because heterosis is largest for maternal reproduction traits (Sellier, 1976).

The development of crossbreeding programs has been complemented by relatively simple but effective selection schemes within breeds. These have focused selection efforts largely on the efficiency of lean growth, and in the U.K. it has been estimated that this had led to rates of genetic improvement of up to 2% per annum in this trait (Mitchell et al., 1982). The improvement of the efficiency of lean growth has been achieved largely by improved partitioning of energy intake away from fat deposition towards lean deposition, resulting in an improved lean content of carcasses. Relatively little selection effort has been expended on other important traits, such as litter size and meat quality. This is because the relative difficulties of obtaining accurate estimates of breeding values for these traits has meant that overall economic efficiency

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can be enhanced only slightly by their inclusion in the selection objective (Clarke and Smith, 1979).

Several developments have combined to produce a reappraisal of breeding programs. In Britain and Europe the success of selection programs in the public and private sector has greatly reduced the fat content of pig carcasses. This leads to the possibility that the improvement of lean growth efficiency by the re-partitioning of energy away from fat towards lean may become more difficult to achieve in the future. Furthermore, the reduction of carcass fat content can have adverse effects on meat and eating quality, suggesting that it may be possible to reach an optimum level of fat content at which further reductions are detrimental. These factors make improvement of other traits more economically attractive. At the same time, the estimation of breeding values for traits such as litter size is becoming less difficult. The main reason for this latter development is the statistical mixed model methodology, Best Linear Unbiased Prediction (BLUP), which can enhance genetic progress particularly for traits of low heritability and traits which are only expressed in one sex (i.e. traits which are sex-limited), such as litter size. The application of BLUP technology is facilitated by improved genetic links between herds which can be achieved by an increased use of artificial insemination. Other technologies which contribute to improved breeding value estimation include methods for better estimation of body composition, such as real-time ultrasonic scanning (Molenaar, 1984) and X-ray computer tomography (Vangen, 1984; Sehested and Vangen, 1989) and the use of indirect measures of genetic merit, such as may be provided by ovulation rate and pre-natal survival (Johnson et al., 1985).

In the near future, further developments are likely to stem from the recognition that breeds other than the relatively few, already widely exploited, breeds of Western origin contain genes of value. Chief amongst these are the Chinese Taihu breeds, particularly the Meishan, which have genes of value for traits such as prolificacy, early puberty, docility and possibly other traits. The Meishan has much to offer in terms of research, but in addition, it is likely that genes from this breed will be used in practical breeding programs.

In general the selection of a few genes of value from one breed and their transfer to a second may be problematic. In future this is likely to be facilitated by marker assisted selection. Marker assisted selection requires the development of a complete genetic map of the pig on which valuable genes for quantitative traits can be located and then selected by use of linked markers.

One final development will be the use of direct manipulation of the porcine genome via 'transgenesis'. There is much to be learnt on the targeting of genetic manipulations, on the control of expression of 'transgenes', and on which genes to manipulate. None the less, this technique has great potential in breeding programs of the future.

The focus of this survey of possibilities will remain largely on more intensive production systems. However, opportunities for a diversification of production systems will increase, and are likely to lead to some diversification of breeding objectives. Such diversification may include 'free-range' systems, systems based on forage or other low cost diets, systems based on organic production and systems producing product for the gourmet market, for example based on Wild Boar crosses (Booth et al., 1988). None the less, it is in the more intensive systems, capable of producing pork at 'value for money' prices, that the majority of pigs are likely to be produced for many years to come.

### Current Possibilities

#### *Breeding objectives for production traits*

**Performance testing**—The focus of selection over the last 20-30 years has been largely on efficiency of growth due to its economic value, its relative ease of measurement and its moderate to high heritability. This focus has resulted in rapid and highly cost-effective improvements in economic efficiency (Mitchell et al., 1982). In addition carcass fat content has been reduced, making pork a more attractive product for the consumer. The ability to improve growth efficiency by the re-partitioning of energy away from fat towards lean is likely to continue for some time. However, as subcutaneous fat levels decrease it may become more difficult to improve pigs by the same route. There could be little genetic variation in the

efficiency of growth in the absence of genetic variation for energy partitioning, as the extent of genetic variation in the efficiency of energy conversion into lean tissue, in maintenance energy requirements and in other processes underlying the overall efficiency of growth is uncertain. Thus it may become increasingly difficult to improve the efficiency of growth by selection. Additionally there are indications that the declining fat content of the carcass is accompanied by some reduction in meat quality (Wood et al., 1986). Both of these factors are likely to reduce the emphasis of improvement efforts on the efficiency of lean growth and increase the emphasis on the rate of lean growth, carcass and meat quality traits and reproduction traits (Webb, 1988).

One aspect of the change in breeding objectives will be an increased use of performance testing under *ad lib*, as opposed to restricted, feeding conditions. This will both allow effective selection for growth rate and for voluntary food intake. Concern has been expressed that a decline in voluntary food intake has occurred which may both jeopardise prospects for long term improvement and compromise performance at several stages of the life cycle (Webb, 1988; Ollivier et al., 1990). Additionally, the clear eating quality advantages associated with *ad lib* feeding (Meat and Livestock Commission, 1989) may increase the emphasis on production systems based on *ad lib* feeding. In this latter case, performance testing under an *ad lib* feeding regime should reduce the potential for genotype  $\times$  environment interactions (see below) which could threaten the dissemination of genetic progress from breeder to producer.

The ability to carry out performance testing under *ad lib* feeding conditions has been greatly enhanced by the development of electronic feeders which allow group penning of animals with individual feeding and recording of feed consumed and, in some cases, of weights of animals at feeding. This new technology has the potential to offer accurate measures of food intake and growth efficiency with relative ease for the first time under *ad lib* feeding conditions. With animal weights recorded it also offers the prospect of selection directly on the growth curves of animals, and not just on the mean growth rate over a period of time. Electronic feeders are already being adopted by breeding companies in order

to enhance their selection programmes (Brown and Van der Steen, 1990).

**Carcass composition**—Carcass composition (the distribution of cuts) and meat quality are likely to receive increased attention in future. Methods for the measurement of carcass composition have become increasingly more sophisticated, with greater accuracy of measurement of lean content (Allen and Vangen, 1989). Ultrasonic methods used in pig breeding programs were originally pulse-echo techniques, which gave a simple measure of fat depth. More sophisticated real-time scanners give representations of cross sections and allow some measurement of areas of fat and lean (figure 1). The accuracy of prediction of lean content by the use of real-time, as opposed to pulse-echo, ultrasonic techniques can be markedly increased (Molenaar, 1984).

A further technique, X-ray computer tomography, produces a 2-dimensional cross-section through the whole body and different tissue types in the cross-section can be identified accurately. The use of X-ray computer tomography appears capable of increasing the accuracy of prediction of lean content over the best ultrasonic techniques. (Vangen, 1984; Allen and Vangen, 1989). Vangen's (1984) results suggest a further advantage, that is, that the accuracy of prediction does not fall off at low depths of fat (mean of 10.2 mm) using X-ray computer tomography in the way that it does when using ultrasonic measurement of fat depth. X-ray computer tomography can also give some measures of the chemical composition of tissue, and in the long run it may be possible to use it for obtaining measures of meat quality. The disadvantages of X-ray computer tomography are the immense equipment costs (around  $\pounds 5 \times 10^5$  compared to  $\pounds 5 \times 10^5$  for a real-time ultrasonic scanner) and running costs and also the length of time it takes to measure individual animals compared to ultrasonic methods. Further techniques which are still experimental as far as *in vivo* carcass assessment are concerned including nuclear magnetic resonance (which may be as accurate or more accurate than X-ray computer tomography, but is also very expensive and slow) and electrical conductivity (for which experimental results are so far mixed) (Allen and Vangen, 1989).

Undoubtedly techniques such as X-ray com-

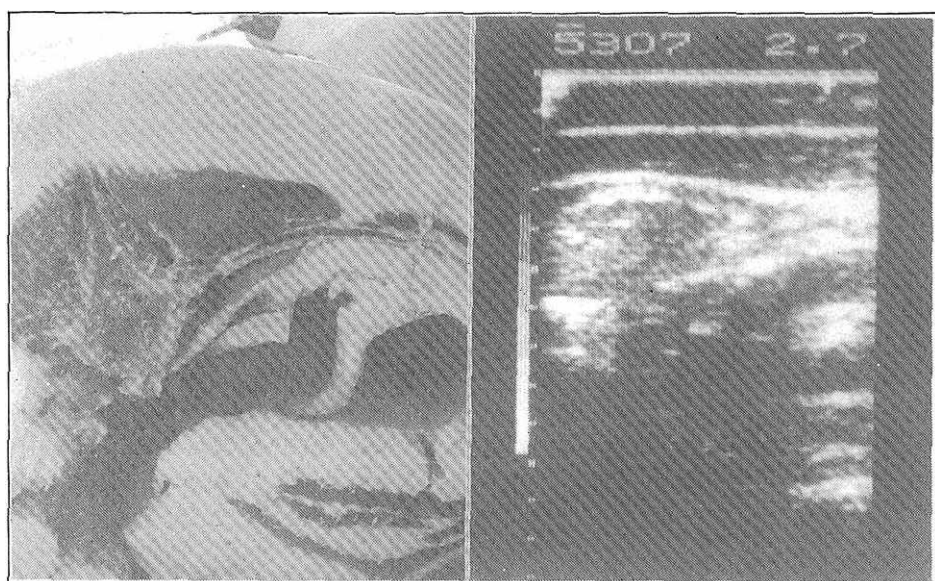


Figure 1. A section through a mature purebred Meishan sow at the last rib position, together with the same cross-section recorded by a real-time ultrasonic scanner on the live animal just prior to slaughter. The fat layers and the eye muscle can be clearly seen. Better scanners than the one used to obtain this picture are now in use.

puter tomography show great promise, and their cost may be justified in large improvement programs, for example for the final selection of boars for use at A.I. after preliminary selection based on cheaper methods. Real-time ultrasonic scanning is already seeing more widespread use, and as predictions based on it become more fully developed it should enhance selection for carcass composition.

It is possible that as slaughter houses become increasingly sophisticated, the need for *in vivo* carcass assessment will be reduced. Carcass assessment methods at the slaughter house are being automated and becoming increasingly accurate (Walstra, 1989). This fact in itself is likely to put increasing financial dividends on improvements in carcass conformation and lean content. The information collected at the slaughter house is of little direct use to the breeder whilst it cannot be connected with individual animal identities. However, micro-miniaturization of animal identification systems, for example the implantation of miniaturized transponders, makes the automated collection and return of information on carcass and meat quality to the breeder a future possibility. This information can be incorporated in the evaluation of relatives of slaughtered

animals. Alternatively, with collection of semen prior to slaughter of boars, it could be used to select animals to use as sires after potential candidates had been slaughtered.

**Meat and eating quality**—The improvements in carcass lean content that have been achieved in Europe may have been accompanied by some slight decline in meat quality as measured by objective indices (Christensen et al., 1986; Ollivier, 1986). In leaner genotypes subcutaneous fat tends to be softer, with a greater tendency to separate and with a higher proportion of unsaturated fat (Wood and Enser, 1989). Whilst fat from lean pigs may be healthier, it may be unappealing to the consumer both in appearance and in handling qualities. Lean meat from lean carcasses is detectably less juicy than lean meat from fatter carcasses, but this may not be reflected in the overall acceptability of the meat as judged by consumers or taste-panelists (Kempster et al., 1986; Wood et al., 1986). The amount of fat within the lean meat in the form of marbling does appear to vary independently of overall fatness, but a clear association between this and measures of eating quality has yet to be established (Wood and Enser, 1989).

Measures of meat quality are included amongst the objectives in a number of breeding programs in Europe (Lundström et al., 1989). BLUP methodology provides a means of including measures of meat quality in breeding programs and new methods of assessment are being utilized (Lundström et al., 1989). With the points listed in the previous paragraph in mind, it is clear that further research is required to clarify exactly what constitutes good meat and eating quality and how this is genetically related to measures of growth and carcass composition. It is not yet clear what weight should be given to measures of meat and eating quality in present and future breeding programs. However, the minimum should perhaps be to monitor and possibly eliminate genes with a known major deleterious effect on meat quality. Two of these are known, the halothane gene (Webb et al., 1982) and the gene affecting 'Napole' yield, which may be at a high frequency in the Hampshire breed (Sellier, 1988).

Whilst it may not yet be clear what emphasis to place upon meat and eating quality in breeding programmes, it is apparent that some aspects at least are amenable to environmental manipulation, both via treatment around slaughter and via factors such as the diet (Wood and Enser, 1989; Meat and Livestock Commission, 1989). As noted earlier, the ability to improve meat and eating quality via the use of *ad lib* feeding could emphasize the use of this feeding regimen in performance testing programmes.

#### Specialized maternal lines

Until recently, specialized dam line selection objectives have not been utilized, and little selection pressure has been put on maternal traits. One reason for this has been that the low heritability for litter traits (for example, 10% for litter size, Haley et al., 1988) meant that predicted rates of improvement were slow using traditional techniques. Additionally, the relatively high economic values and heritabilities of growth and carcass traits led to very little increase in the overall rate of economic improvement when maternal traits were included in the selection objectives. However, now it may become more difficult to improve leanness and growth efficiency in some of the very lean modern lines which may be reaching optimum fat levels (Hill and Webb,

1982). Also, new selection techniques have been developed which mean that litter size can be increased more rapidly. Taken together, these new developments mean that the value of including maternal traits, particularly litter size, in the selection objective is increased, as is the value of developing specialized dam lines.

The selection method adopted depends upon the improvement scheme into which they have to be incorporated (for example, central nucleus herd or progeny testing scheme), but several basic schemes have been suggested:

**Family selection**—In the simplest of schemes for improving litter size, replacement boars and gilts are selected based upon the farrowing performance of their dam. However, in every herd, all individuals have many relatives, and the accuracy of selection of replacement boars and gilts can be increased by combining information on the litter sizes of relatives of the sire and dam in a selection index. For example, with three gilts per litter every sow has two female full-sibs and every boar three female full-sibs and if each boar sires 10 litters, every individual has 27 female half-sibs (although some of these may be farrowing in multiplier herds). Theoretically combining this information in a selection index can almost double the rate of increase in litter size to nearly half a piglet per litter per year (table 1), although this assumes that there is no selection for other traits. Simulation studies suggest that these predictions may be over-optimistic, particularly in small populations, due to the reduction in genetic variance caused by selection and the correlated family structure not accounted for in the theoretical predictions (Toro et al., 1988). Another problem may be inbreeding, which increase with selection on a family index and may be 2 to 3 times that predicted assuming no selection (Toro et al., 1988). However, although inbreeding may depress performance in the nucleus herd, as commercial sows and slaughter pigs are crossbred, inbreeding is of limited practical importance.

An alternative source of family information is from progeny, and Skjervold (1983) and Leukunen (1984) have considered the use of progeny testing with nucleus herds for litter size improvement. The system requires extensive use of A.I. combined with recording of sow performance. Males are selected by progeny test on the national

TABLE 1. PREDICTED ANNUAL INCREASE IN LITTER SIZE USING SELECTION BASED ON FARROWING RECORDS OF RELATIVES (AVALOS AND SMITH, 1987) AND SIMULATED RESPONSES IN A 100 SOW NUCLEUS POPULATION (TORO ET AL., 1988)

| Relatives included            | Annual genetic change<br>(pigs/litter/year) |           |
|-------------------------------|---|-----------|
|                               | Predicted                                   | Simulated |
| Dam's record only             | 0.27  | 0.25      |
| Dam and dam's family          | 0.35  | 0.31      |
| Dam and dam and sire families | 0.46  | 0.34      |

sow population. Females are selected in the nucleus herd using a family index of farrowing records from their female relatives. The genetic merit of the national sow population would follow that of the nucleus population due to the use of nucleus boars via A.I. Avalos and Smith (1987) have investigated theoretically the rates of progress possible when selecting only for litter size using progeny testing and they predict that these rates would be similar to those possible using records from sibs and half-sibs.

**Hyperprolific selection**—Large scale sow recording schemes allow the identification of sows from large populations which have repeated high performance for litter size (e.g. sows with an average litter size over 4 farrowings of at least 14). Such sows may represent the top 1 or 2% of the population and after selection may be mated to sons of other such 'hyperprolific' sows to start a 'hyperprolific' line (Legault and Gruand, 1976). This selection has been used successfully several times, for example, in both France and Britain (Legault, 1985; Bichard et al., 1985). Litter size increases of almost 1 pig per litter have been recorded, which is at the level predicted (Avalos, 1985) from a heritability of 10%.

Searching a population for hyperprolific sows can provide a useful lift for the initiation of a dam line. However, as many as seven years are needed to re-populate the national herd and accumulate sufficient records on sows to allow another round of hyperprolific selection. This means that the predicted annual rate of improvement is quite low, varying between 0.05 and

0.22 piglets per litter (Avalos and Smith, 1987).

**Economics of selection for maternal traits**—There is no general answer to the question of how much selection effort should be put into the improvement of reproductive performance at the expense of other traits. The balance is affected by the costs and returns of pig production, the usage of the improved lines (i.e. general purpose, maternal or sire lines) and the expected rate of genetic response.

It has been demonstrated that selection for specialized sire and dam lines is always at least as efficient as selection of a single generalized line and specialized sire and dam lines are often more efficient (Smith, 1964). However, at the time of Smith's (1964) study the advantages of specialized sire and dam lines were not large enough to support the cost of setting up specialized sire and dam lines. However, with the new techniques for breeding value estimation, there are substantial advantages to setting up specialized lines. Avalos and Smith (1987) estimated that, under British economic conditions, the economic advantages of including a family index of litter size in the selection objectives were 2 to 5% in general lines, but as much as 10 to 18% in specialized dam lines. This was when compared to selection for just growth and carcass traits in general purpose lines.

The benefits may be even greater if it is assumed that making improvements in growth and carcass traits may become more difficult. If no further improvement in lean growth was either possible or desirable, the increase in the economic response obtained from selecting sire and dam lines rather than general purpose lines could be as high as 22% (Webb and Bampton, 1988).

**Physiological indicators of reproductive performance**—It would be possible to increase rates of response to selection if an individual's genetic merit for reproduction traits could be measured more accurately. Walkley and Smith (1980) have demonstrated how the use of physiological indicators of reproductive performance can be used in this way to enhance selection responses. The value of the components of litter size; the number of eggs shed (ovulation rate) and the proportion that survive to be born as piglets (prenatal survival), as indirect indicators has been explored

by Johnson et al. (1984). Selection for ovulation rate on its own is largely ineffective at increasing litter size, due to a negative genetic correlation between this trait and prenatal survival. This correlation means that prenatal survival declines as ovulation rate increases, resulting in no significant increase in litter size with an increase in ovulation rate. However, an index combining ovulation rate and prenatal survival measured at day 50 of pregnancy was predicted to be more effective at increasing litter size than selection for litter size itself (Johnson et al., 1984). This prediction rests on the assumption that the genetic correlation between the number of fetuses measured at day 50 and litter size is high. A recent re-assessment suggests that this may not be the case, and the responses in litter size may be less than originally predicted, although putting optimum emphasis on the components of litter size may still be more effective than direct selection (Johnson and Neal, 1988).

The development of BLUP methodologies that incorporate information from many relatives can potentially enhance selection responses and thus reduce the relative benefits of using physiological predictors of litter size by comparison. However, in such a scheme physiological predictors will allow more accurate evaluation of an individual's genetic merit. This will tend to reduce the emphasis placed on information from relatives which will help alleviate inbreeding. Thus the search for usable indicators of genetic merit for reproduction remains worthwhile. One possibility is that an understanding of the mechanisms by which some Chinese breeds achieve their prolificacy will lead to physiological indicators that can be used within European breeds.

**Prolific Chinese breeds**—The Chinese breeds which have attracted attention in the West in recent years are the 'Taihu' breeds, which have an average number of piglets born alive of over 14 in later parities (Bidanel et al., 1989; Haley and Lee, 1990). Individual sows have recorded exceptionally over 22 piglets born alive on average over nine parities and up to 40 piglets born alive in one litter. Another feature of Taihu breeds is their early sexual maturity. Both sexes reach puberty at around 3 months of age, some 3 months before Western breeds. With a similar gestation length to Western breeds, Taihu breeds

are capable of farrowing at seven months of age. However, Taihu breeds are relatively slow growing, inefficient and fat when compared with European breeds.

Research on Chinese pigs in Europe has been performed in France on two Taihu breeds, the Meishan and the Jiaxing and 32 Meishan pigs have also been imported into Britain for research purposes. There are four ways in which the prolific Chinese breeds may be of benefit to pig breeding programs; (1) through the information they provide on the genetics of litter size and other traits; (2) by the provision of one or more major genes; (3) in crossbreeding programs; (4) in a 'synthetic' line.

**Providing information for the improvement of European breeds**—Research in Britain is designed to show how the Meishan achieves its high litter size. Comparative study of the Meishan and less prolific European breeds may indicate traits which can be developed as physiological predictors of litter size for use in selection programs in European pigs. If the genes in the biochemical pathways which are responsible can be identified, there is a real possibility that this knowledge could be used to increase litter size in European breeds. With the development of modern molecular genetic techniques it is possible that the changes necessary could be engineered directly in the genome of European pigs, avoiding the problem of the fat carcass and slow growth of the Meishan.

Studies in the UK on the causes of prolificacy in the Meishan are in their early stages. The Meishan appears to have a similar relationship between ovulation rate and prenatal survival as European pigs, with prenatal survival declining as ovulation rate increases. However, the mean prenatal survival at a given ovulation rate is higher in the Meishan than it is in the Large White (figure 2) and this difference is due to genes which are acting in the mother and not in the embryo (Haley and Lee, 1990). The immediate cause of this difference is not yet apparent, but is actively being investigated (Wilmot et al., 1990a).

**Using a major gene**—A possible explanation for the high litter size in Taihu breeds is that they differ by a single major gene for litter size

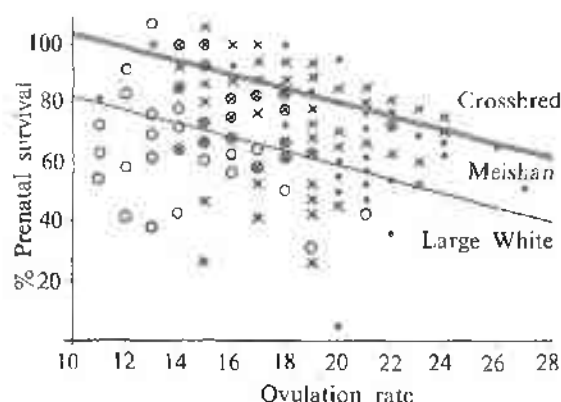


Figure 2. Prenatal survival and ovulation rate in Meishan (•) and Large White (Yorkshire) (○) pigs and the F1 cross (×) between them. In all three genotypes prenatal survival decreases at the same rate as ovulation rate increases, but the mean level of prenatal survival for a given ovulation rate is higher in the Meishan and the F1 cross. This difference between genotypes is caused by genes acting in the mother of a litter, not in the piglets themselves.

from other breeds, a situation found in the prolific Booroola sheep. If this gene exists, the crossbreeding results suggest that it is a dominant gene acting in the mother, not in the litter (Bidanel et al., 1989; Haley and Lee, 1990). In this case, it would be expected that the gene would segregate in backcross females produced by crossing, for example, F1 (Large White × Meishan) animals to purebred Large White. Thus half backcross females of this type would be heterozygotes carrying the gene and have high litter sizes and half would be homozygotes not carrying the gene and have normal litter sizes. Due to the large amount of variation in litter size which is normally found, it is likely to be difficult to discriminate between females carrying the gene and those which do not just by looking at litter size. Thus, in our research, we will be looking at not only litter size, but also at both the number of eggs produced and the proportion which survive, as well as at any reproductive hormones which differ between the breeds. Even with the aid of such physiological traits it may be difficult to detect the segregation of a major

gene, but the task will be greatly facilitated by the use of marker genotypes in a gene map as discussed later.

If a major gene is discovered it could be backcrossed into European breeds to increase their litter size. Backcross females of the type described above only contain 25% Meishan genes. If carriers are identified and crossed again to Large White sires, their progeny only contain 12.5% of Meishan genes. Each time this procedure is repeated the proportion of Meishan genes is halved. In this way a line could be produced which was as prolific as the Meishan, but had growth efficiency and carcass qualities almost as good as European breeds. As shown below (figure 5), markers flanking a prolificacy gene could be used to enhance its introgression into a European breed.

**Crossbreeding.** Possible systems include the crossing of the Meishan to a reasonably prolific European breed to produce a maternal F1, which would in turn be crossed to a lean terminal sire breed to produce the slaughter pigs (figure 3a). Such a system utilizes the high level of heterosis for both reproduction and growth traits in crosses between the Meishan and European breeds (Bidanel, 1988; Bidanel et al., 1989; D'Agaro et al., 1990; Haley and Lee, 1990). However, for long term use, it requires a nucleus of purebred Meishan pigs which are selected on a maternal index, which will be costly because of the poor economic performance of the Meishan as a purebred. The relative benefits of such a system compared to the traditional system will vary between countries depending upon the performance of local breeds, the relative value of fat and lean and the overheads of pig production. Much of the work in France has looked at the use of the Taihu breeds, especially the Meishan, in crossbreeding (Bidanel, 1988). The prolificacy of F1 (Meishan × European breed) females is largely offset by the poorer lean growth of their progeny (table 2).

In summarizing the results from France, Bidanel (1988, 1989) concluded that there was little advantage in using the Meishan at present, but that if a pure Meishan line were selected for growth and carcass traits the advantages on a 15 year time scale would be great. However, it is not known how much genetic variation exists



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in the Meishan for growth and carcass traits and there may be problems performance testing such a sexually precocious breed which make selection

TABLE 2. THE PERFORMANCE OF F1 (MEISHAN X EUROPEAN BREED) FEMALES AND THEIR 75% MEISHAN OFFSPRING COMPARED TO STANDARD CONTROL CROSSES (BRUEL ET AL., 1986)

| Trait                     | F1 (Meishan x European dam) | Control dam |
|---------------------------|-----------------------------|-------------|
| Number of litters (total) | 322                         |             |
| Number born alive         | 13.3                        | 10.4        |
| Number weaned             | 11.0                        | 9.0         |
| Number of animals         | 76                          | 77          |
| Daily gain (g)            | 836                         | 858         |
| Feed conversion ratio     | 3.07                        | 3.00        |
| Killing out (%)           | 77.1                        | 77.8        |
| Carcass lean (%)          | 49.4                        | 53.6        |

difficult (Sellier and Legault, 1986).

In countries where there is little premium paid for lean meat, as is the case in the USA at present, the use of the Meishan in crossbreeding programs may be more immediately attractive. Several options have been explored by McLaren (1990) by simulation using the genetic parameter estimates currently available and under the economic conditions of the midwestern USA. McLaren (1990) concluded that the best crossbreeding system which utilized genes from unimproved Meishan pigs outperformed the best system not utilizing Meishan genes by about 6%. This conclusion must be regarded as tentative until estimates of genetic parameters obtained under US conditions are available.

**Synthetic lines**—One possible use of the Taihu breeds would be as a component of a synthetic line which also contained genes from Western breeds. This maternal line would be selected on a maternal index including both growth and

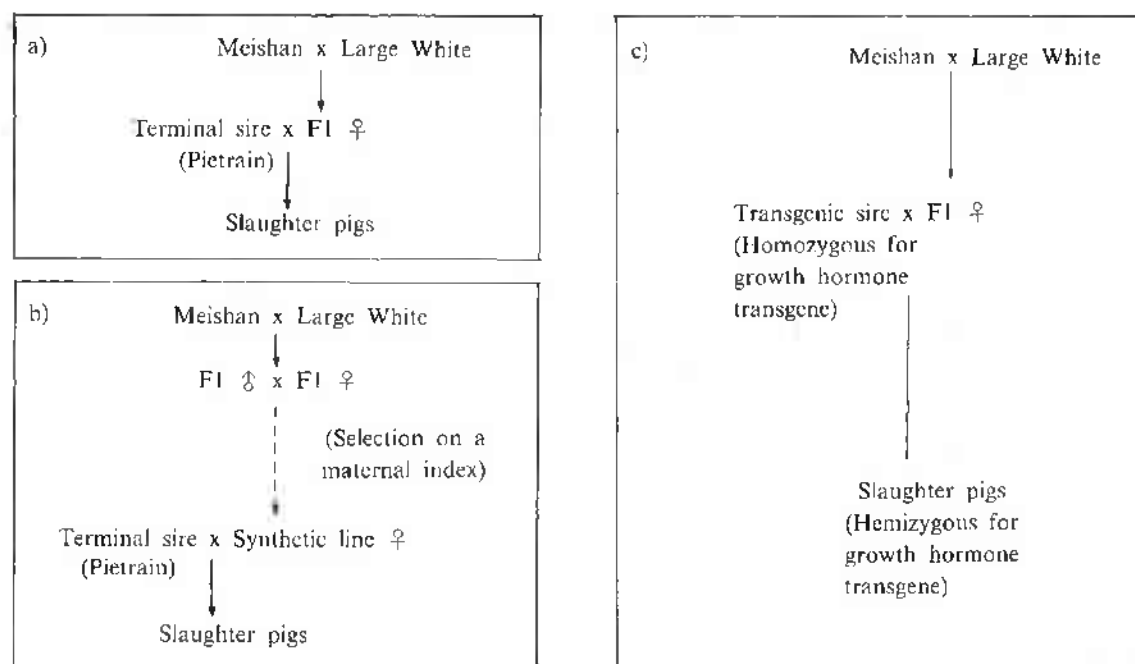


Figure 3. Possible crossing programs for the utilization of the Meishan pig. a) As one half of a maternal F1 crossed to a lean terminal sire to produce slaughter pigs. b) As a component of a synthetic line selected on a maternal selection index and crossed to lean terminal sire to produce slaughter pigs. c) As part of a maternal line (an F1 is shown here, but a synthetic line would be an alternative) crossed to a sire homozygous for a growth hormone transgene to produce slaughter pigs hemizygous for the transgene.

carcass and maternal traits. The slaughter pigs would be produced by crossing the maternal line to a lean terminal sire (figure 3b). The advantages of a synthetic line over a purebred Meishan line would be that it would be less costly to maintain and select and there would be no shortage of genetic variation, and possibly more than in either purebred line. The preliminary estimates from France and the U.K. suggest that a synthetic line containing 50% Meishan genes and 50% European genes would be expected to maintain about 75% of the litter size advantage of the Meishan (i.e. have a litter size equal to that of 75% of that of the Meishan plus 25% of that of the other breed in the synthetic population). The carcass composition is likely to be intermediate between that of the synthetic line and that of the terminal sire, but some heterosis for growth rate is expected. Bidanel (1988, 1989) concluded that the creation of such a line is the best solution in the medium term and it is known that synthetic lines incorporating Meishan genes are being produced in France (Krapoth, 1990; Looft et al., 1990; Naveau, 1990).

#### Genotype $\times$ environment interaction

Of increasing concern in recent years has been the possibility of the existence of genotype  $\times$  environment interactions and their implication for breeding programs (Webb and Curran, 1986). In the presence of genotype  $\times$  environment interactions the relative genetic merit of animals may vary depending upon the environment in which they are performing, and thus the genetic correlation between the performance of the same genotypes in different environments is low. Hence animals selected in a nucleus herd or at a central testing facility may not provide genes which are the best possible for the commercial environment, and genetic progress made in the nucleus herd may not be seen in commercial herds. Possible causes of genotype  $\times$  environment interaction include differences between test and commercial environment in feeding level (*ad lib* versus restricted), diet (energy and protein content), numbers in a pen (individual versus group housing), disease status and ages at measurement.

Whatever the causes of genotype  $\times$  environment interaction, the magnitude of the problem has yet to be resolved. Earlier data reviewed by

Webb and Curran (1986) reports some low genetic correlations between test and commercial environments, but often such studies were small and used less good statistical methodology than is now available. Recent studies in large populations have produced contrasting results. Merks (1989a) found that, for daily gain, the genetic correlation between animals tested centrally and on farm was only low to moderate (0.30 to 0.65), and that between animals tested centrally and animals commercially fattened was very low or zero (-0.48 to 0.17). For depth of back-fat Merks (1989a) found low to moderate genetic correlations between central and on-farm tested animals (0.3 to 0.7) and moderate genetic correlations (0.57 to 0.64) for carcass characteristics measured in central test and under commercial fattening. On the other hand, Van Diepen and Kennedy (1989) estimated correlations between central test and on-farm test of above 0.85 for backfat depth and of 0.74 for growth rate. These latter correlations were estimated using the latest statistical technology with a large amount of data and provide the best estimates to date. Crump et al. (1990) used similar statistical techniques and estimated the genetic correlations between males and females reared in different environments for measures of growth rate and ultrasonic fat depth. All the estimates of between-sex genetic correlations within a trait were very high, averaging 0.9 for measures of fat depth and 0.91 for growth rate, providing little evidence for the importance of genotype  $\times$  environment interaction.

The consequence of genotype  $\times$  environment interactions for pig breeding programs depends upon their magnitude. If genetic correlations between central testing and the commercial environment are high, as estimated by Van Diepen and Kennedy (1989) then they are of little consequence, and breeding programs based around centrally tested pigs or nucleus populations will be effective for the improvement of commercial pigs. Alternatively, if the genetic correlations are only moderate or low, as estimated by Merks (1989a), then breeding programs will require to be redesigned to make them more effective. The consequences of genotype  $\times$  environment interaction for the structure of breeding programs have been considered by Brascamp et al. (1985) and Merks (1989b). Merks (1989b) concluded that, with the magnitude of genotype  $\times$  environment

interaction he estimated, supplementing centrally tested boars with paternal half-sibs tested on-farm could make approaching three times more genetic progress than the use of central testing alone. With a single nucleus population, as in a breeding company, large genotype  $\times$  environment interactions would make the use of A.I. from nucleus boars on commercial farms, with collection of performance data on-farm, worthwhile. It is fortunate that BLUP technology makes the integration of information from these several sources feasible, at least in principle, although, to the author's knowledge, no programs of this type have been initiated as yet. Finally, as discussed below, large genotype  $\times$  environment interactions would increase the relative worth of integrated selection and production systems. Whether genotype  $\times$  environment interactions are of sufficient magnitude to merit the redesign of breeding programs will have to await the results of further population and experimental studies, such as that currently under way in the UK (Webb and Curran, 1986; Cameron et al., 1988).

#### Breeding program structure

Population structures in current use vary quite widely. Breeding companies typically have a single nucleus for each breed, in which performance testing, selection and breeding takes place in a single environment. This nucleus provides genetically improved stock to the producer via one or more multiplier herds (Webb and Bampton, 1988, figure 4a). National schemes vary, but usually animals from several or many breeding herds are evaluated at central testing facilities, with selected males often used on the national herd by A.I. (Christensen et al., 1986, figure 4b).

Several studies have demonstrated the additional improvement that can be gained by use of BLUP breeding value estimation, both in closed nucleus herds (Belonsky and Kennedy, 1988; Wray, 1988) and in the context of a national program (Sorensen, 1988). These benefits derive from: (1) improved use of information from relatives; (2) improved elimination of bias due to environmental effects and genetic progress when making comparisons between animals and (3) optimization of replacement strategies (i.e. replacement of breeding animals when animals of

improved genetic merit become available). The predicted rate of genetic improvement using BLUP compared to selection indices could be increased by up to 25% for traits of low heritability (Sorensen, 1988; Wray, 1988; Rohe et al., 1990). However, in an already well designed breeding program the increased genetic progress obtained by the use of BLUP may be no more than 5 to 10%.

BLUP allows improved rates of genetic improvement within current breeding programs, but it also permits a wider range of structures to be feasible (Webb and Bampton, 1988). With connections between different herds provided by genetic links, for example by A.I., BLUP allows unbiased comparison of animals from different herds and genetic information to be accumulated over herds. In a breeding company, this allows the nucleus to be expanded to a 'group nucleus', incorporating several herds and including what were formerly multiplier herds (Webb and Bampton, 1988). This large nucleus of around 1000 sows now provides sufficient information from relatives for accurate evaluation of traits of low heritability, such as litter size or sow longevity. At the same time, group nucleus herds are of sufficient size to reduce problems of inbreeding which might otherwise accompany the use of large amounts of family information. This makes possible the adoption of selection schemes as suggested by Avalos and Smith (1987) and thus facilitates the development of specialized dam lines.

In a national breeding program BLUP could make the traditional role of central testing stations obsolete (Sorensen, 1988; Webb and Bampton, 1988). With adequate links between producers' farms by A.I., BLUP makes possible unbiased selection following on-farm performance testing and sow performance recording. This may allow an increase in the rate of genetic progress of around 20% (Sorensen, 1988). Additional advantages will accrue if genotype  $\times$  environment interaction is important, as integration of on-farm data will enhance the prediction of breeding values for the farm environment (Merks, 1989b). Whether central test facilities would have a role in such a scheme, for example to provide more accurate measures of carcass conformation or to link herds together more firmly, is uncertain. However, as BLUP and electronic identification

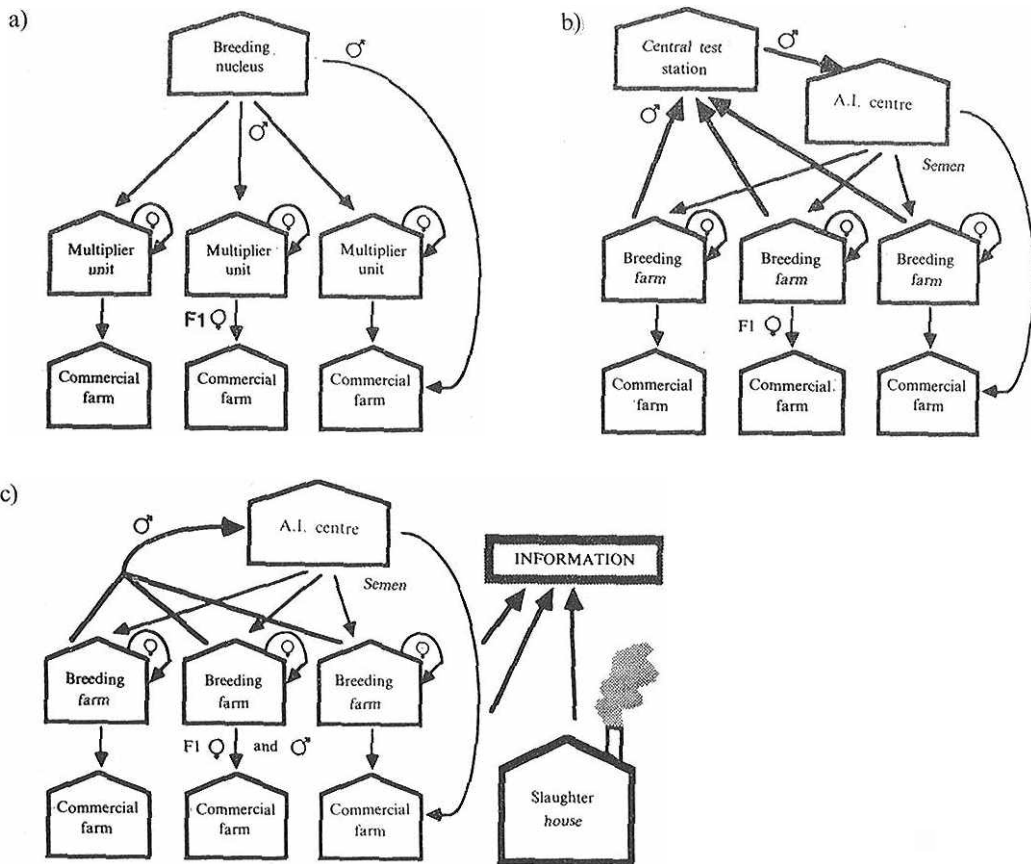


Figure 4. Current and future structures of a pig breeding program. a) Typical breeding company structure with a single nucleus population for each line where performance testing and selection takes place and several multiplier herds producing purebred and crossbred animals for sale to commercial farmers. b) An example of a national breeding program with a number of breeding farms for each line which produce purebred animals (and possibly crossbred females) for commercial farmers. The breeding farms select their own female replacements and provide males to central testing stations. Males selected after central testing provide genes to the breeding and commercial farms via A.I. c) A potential future structure for both breeding companies and national breeding programs with a number of breeding farms for each line providing purebred males and crossbred females to commercial farmers. The breeding farms are genetically linked through selected males used at an A.I. centre and this centre may also provide genes to the commercial farmer. Selection of females within breeding farms and males across breeding farms is by BLUP, with information on all aspects of performance being collected from all levels of the structure including the slaughter house.

and recording systems become further advanced the role of central test facilities may become further marginalised, with carcass and meat quality data being automatically collected at the slaughter house and integrated into breeding value prediction.

Ultimately, the structure of national and

company breeding programs could converge. Both might consist of a number of herds genetically linked by A.I. in which selection takes place and which produce breeding stock for commercial farmers. Breeding value prediction for a given line will take place centrally with data from a number of sources (electronically recorded per-

formance test and *in vivo* carcass assessment from the breeding farm, slaughter house carcass and meat quality data, data on reproductive performance, data from commercial farms, etc.) being incorporated as appropriate for the line in question (i.e. maternal component or sire line) using BLUP (figure 4c). National and company programmes will still differ in scale, in the stimulus they receive from outside competition, their ability to respond to changed circumstances, the degree of control they can exercise over the breeding programme and the extent to which they are answerable to the commercial farmer and the consumer. Although national schemes may have the potential to out perform company schemes in consequence of their sheer scale, whether they ever have the stimulus and flexibility to do so is uncertain.

A further structure outside that of national or breeding company is that of self-contained farms where selection takes place in house (Hargreaves, 1984; McPhee, 1984). The advantages of such a system include lower costs of replacement stock and less potential risk of disease as no animals are bought in. A further advantage may be that as animals are selected in the same environment as that in which the slaughter pigs are produced, problems of genotype  $\times$  environment interactions are minimized (see above). However, the selection objectives may be limited by the difficulty of measuring traits and the cost of setting up and supporting such a scheme may be prohibitive for the smaller producer lacking specialized breeding knowledge. In the smaller herd it is not possible to maintain and select more than a single breed and two-breed synthetics may be used and then some loss of heterosis is experienced. In a farm with several hundred or thousands of sows these limitations do not apply and turnover is likely to be sufficient to support selection in two breeds allowing the use of F1 sows and backcross slaughter pigs.

The spread of BLUP and electronic recording technology may make the integrated breeding and production farm more widespread. Computerized herd recording schemes are already common place and records of sow performance in these Combined with simple performance recording would provide the data for an effective improvement program. Electronic feeders are already finding their way onto farms and further developments

on these are under way to make them capable of recording feed intake and weights of individual animals, providing information on both growth rate and feed conversion efficiency. This could be further enhanced by the use of ultrasonic fat measures. As slaughter houses become more advanced, further information on carcass conformation and meat quality is being collected. With effective animal identification this information can be returned to the farmer and incorporated into a breeding value prediction program. Therefore the information will be available to produce effective improvement programs on-farm and BLUP technology will be capable of integrating this information in the most effective way. Furthermore, within a given structure (i.e. population size, boar to sow ratio etc.) BLUP can automatically optimize progress by dictating replacement of breeding animals when others of higher breeding value become available. Thus the combination of electronic recording and BLUP may mean that farms of a reasonable size can run their own breeding programs without a great deal of specialized knowledge.

### Future Possibilities

#### Genome mapping

A genetic map would be made up of linked polymorphic marker loci approximately evenly distributed through the genome and is made possible by the availability of large numbers of genetic markers based on DNA polymorphisms (e.g. RFLPs and VNTRs). There are several very good reasons for the production of a genetic map of the pig, the potential benefits include:

- It can be used to help us understand the causes of genetic variation in economically important quantitative traits and the contributions and interactions of individual genes. This could lead to improved methods of selecting animals.
- It can be used to improve breeding stock by the manipulation of identified quantitative trait loci (QTLs) within and between breeds using marker assisted selection (i.e. by selection of markers linked to valuable genes rather than by direct selection of the genes or of the phenotype they produce).
- It may be possible to use the map position of QTLs and other genes as a starting point from

which to clone these genes using 'reverse genetics'. This will enable study of the action of these genes and provide the raw material for future transgenic programs.

— The map will allow the study of the comparative genome organization of the pig and other mammals to be studied and evolutionary relationships to be investigated. It may also allow the development of porcine models of human disease which will ultimately benefit the treatment of these diseases.

It is expected that the genetic map length of the pig will be found to be about 30 Morgans (i.e. similar to that of man) and thus 150–200 polymorphic molecular genetic markers will ultimately be needed for a map with 20 centimorgans between markers. In addition to DNA polymorphisms, all other polymorphic loci (e.g. blood groups or proteins) could be mapped, many for the first time. As the map is being constructed, or at a later date, individuals are measured for a variety of performance traits (e.g. growth rate, litter size, disease resistance, etc.) which enables identification of QTLs linked to the marker loci. Physical mapping, using hybrid cell lines and *in situ* hybridization, is used to place detected linkage groups on particular chromosomes or chromosomal regions.

Our understanding of the genetic architecture of variation for economically important traits is very poor. Present techniques are not capable of showing whether appropriate models should be based on a few genes or a few tens of genes. Using the genetic map and statistical techniques currently being developed (Lander and Botstein, 1989) it will be possible to detect and map QTLs of moderate or large effect. This will show for the first time the extent to which genes of this size contribute to genetic variation in economically important traits and will also tell us the genomic organization of the loci involved. At first the techniques will be applied to the study of the large genetic differences which exist between breeds. As the genetic map and techniques become more refined, it will also be possible to study the causes of genetic variation within breeds or lines and show whether this is controlled by the same loci as between breed variation.

The identification and measurement of linkage relationships between QTLs and marker loci allows the use of marker assisted selection

(Soller and Beckmann, 1987). Animals are selected on their genotypes at marker loci as well as on their phenotypes. Marker loci could be used to delimit those portions of the genome that are required to be transferred from one breed to another. This method might be used to transfer genes for litter size or early puberty from the Meishan breed into leaner Western breeds, or genes for disease resistance, etc. from other breeds. The method used would be to identify markers flanking the QTL of interest and then backcross the QTL allele into the nucleus population. Selection on the markers is used to select the section of chromosome containing the QTL allele of interest whilst at the same time maintaining the majority of the genome from the nucleus population (figure 5). This is much more effective than relying on phenotypic selection to maintain the frequency of the QTL allele (Soller and Beckmann, 1987). The technique is already finding use in plant breeding, for example, a RFLP based genetic map has been produced for tomatoes and has been used to map QTLs of commercial importance with a view to producing a commercial variety by combining the best alleles from two species (Paterson et al., 1989). The potential value of this technique is large, for example if the genetic map enables genes controlling half the additional prolificacy of the Meishan to be transferred into European pigs (i.e. increasing the size of their litters by 2 pigs), this would reduce pig production costs by over £30 × 10<sup>6</sup> per annum in the U.K. and by over £200 × 10<sup>6</sup> per annum in the countries of the EEC. As techniques improve, marker assisted selection could be applied within breeds, potentially leading to significant improvements in selection responses.

In the longer term, it may be possible to isolate and clone QTLs known only by their map position. Such 'reverse genetics' has been successfully applied to clone disease loci in man (e.g. as has been done for cystic fibrosis, Riordan et al., 1989). Once cloned, the structure, expression and function of the loci can be studied. This technique will reveal some of the genes which have yet to be located (estimated to be more than 95% of all genes) and provides potential material for other developments, such as transgenic programs. Additionally, the alignment of the porcine and human maps will allow the development of

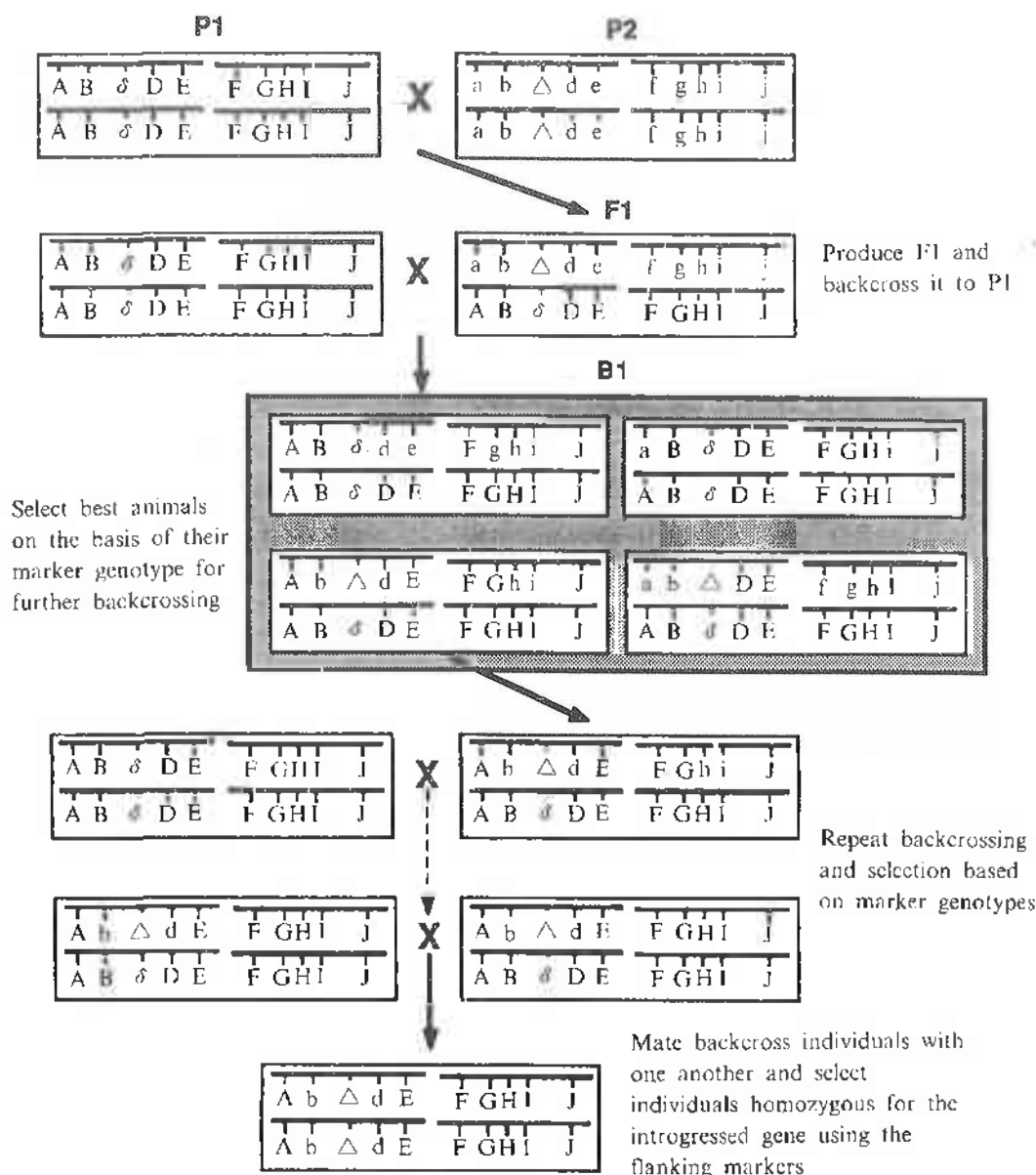


Figure 5. The introgression of a valuable quantitative trait locus (QTL) using marker assisted selection. A genetic map of markers (A, B, D, E, F, G, H, I, J) has been produced. The QTL ( $\Delta$ ,  $\delta$ ) has been located between the B and D marker loci (e. g., by study of a large F<sub>2</sub> population, note that individuals can not be genotyped for the QTL directly). The QTL has an allele of value ( $\Delta$ ) in the P<sub>2</sub> line, which needs to be introgressed into the P<sub>1</sub> line. Repeated backcrossing with selection on alleles from the P<sub>1</sub> line for all markers except those flanking the QTL achieves this efficiently.

models of human disease which can be experimentally manipulated, as is already happening with malignant hyperthermia (halothane sensitivity/PSE in pigs).

Producing a genetic map of the pig-A preliminary RFLP map of man has been produced (Donis-Keller et al., 1987). This provides a foundation upon which to build genetic maps of

other mammalian species as human DNA probes are likely to detect homologous DNA sequences in other mammals, but the proportion that detect RFLPs has yet to be determined. Conservation of linkage relationships between man and other mammals (Nadeau, 1989) enables human DNA probes to be selected which are distributed evenly across the genome. However, mapping other mammalian genomes will be a major project requiring collaboration between laboratories in several countries.

The pig has several advantages for gene mapping such as a short generation interval and large full-sib family size. Unlike cattle, sheep and poultry, the pig has a well defined and easily determined karyotype with high resolution banding, making physical mapping more tractable, especially by *in situ* hybridization (Yerle et al., 1986; Chowdray et al., 1989). Finally, the forward looking pig breeding organizations in Europe mean that advanced techniques, such as marker assisted selection, are likely to be exploited in future.

An ideal tool for the production of a genetic map is a cross between two diverse strains which differ in allele frequencies at individual marker loci. This increases the number of animals which provide information on linkage in the F<sub>2</sub> (at the extreme, when the two strains are fixed for different alleles at a marker locus, all F<sub>1</sub> matings are informative). Additionally, a large phenotypic strain difference means that QTLs segregating in the F<sub>2</sub> cross between strains can be mapped.

Three diverse pig stocks are the Chinese Meishan, European commercial lines and the European Wild Boar. Insufficient information is available to compare the 3 stocks directly, but the genetic distance between the Meishan and European breeds is large (Oishi et al., 1989). At the phenotypic level, the Meishan differs from European breeds for many traits (40% greater litter size, with advantages in ovulation rate and prenatal survival, puberty at less than half the age, resistance to stress and K88 *E. coli*, docile temperament, slow growth rate and twice the subcutaneous fat thickness, Bidanel et al., 1989), and the European Wild Boar is different again for traits including litter size and seasonality (Spitz, 1986). Therefore crosses between pairs of these breeds will provide a good foundation for the production of a marker map and the mapping

of QTLs. Ultimately, there is the possibility of studying the function of individual QTLs or of using marker assisted selection to cross potentially valuable Meishan or Wild Boar QTLs into European breeds (or vice versa).

The European PiGMap project—Researchers in 16 laboratories in Europe are just initiating a collaborative project to produce a gene map of the pig (Haley et al., 1990). An outline and timetable of the Pig Gene Mapping Project (PiGMap) is shown in figure 6.

For genetic mapping the first priority is the accumulation of cloned DNA sequences (probes) detecting RFLPs between the foundation breeds. These probes would be a mixture of porcine coding sequences and heterologous sequences, the former would be isolated using standard techniques (Schumm et al., 1988; Bowden et al., 1989) and the latter would be largely from man and which had already been placed on the human map. The markers detected would largely be di-allelic, but their human map position and assumed human/pig syntenic conservation would enable them to be selected so as to be approximately evenly spread through the pig genome. These markers would be used to assess the degree of genetic divergence between the foundation breeds (European commercial stocks, European Wild Boar and Chinese Meishan). This would determine the most useful crosses and the degree of complementarity between the various crosses.

Ultimately, the genetic map should be composed of highly polymorphic loci in order to make it informative for work within breeds as well as between breeds. VNTRs, either based on minisatellite or microsatellite sequences, provide such loci. Minisatellite sequences would be used to screen pig genomic libraries to provide locus specific probes for the detection of RFLPs on Southern blots (Jeffreys et al., 1985; Nakamura et al., 1987). VNTR loci based on simple oligonucleotide sequences (microsatellite sequences) are also highly polymorphic and may have a more random distribution than minisatellite sequences, are amenable to PCR typing and are found in many species (Litt and Luty, 1989; Weber and May, 1989; Tautz, 1989).

Di allelic and VNTR markers would be assessed on F<sub>2</sub> reference families (50-100 F<sub>2</sub> individuals per group) to confirm monogenic segre-



# FUTURE PIG BREEDING PROGRAMS

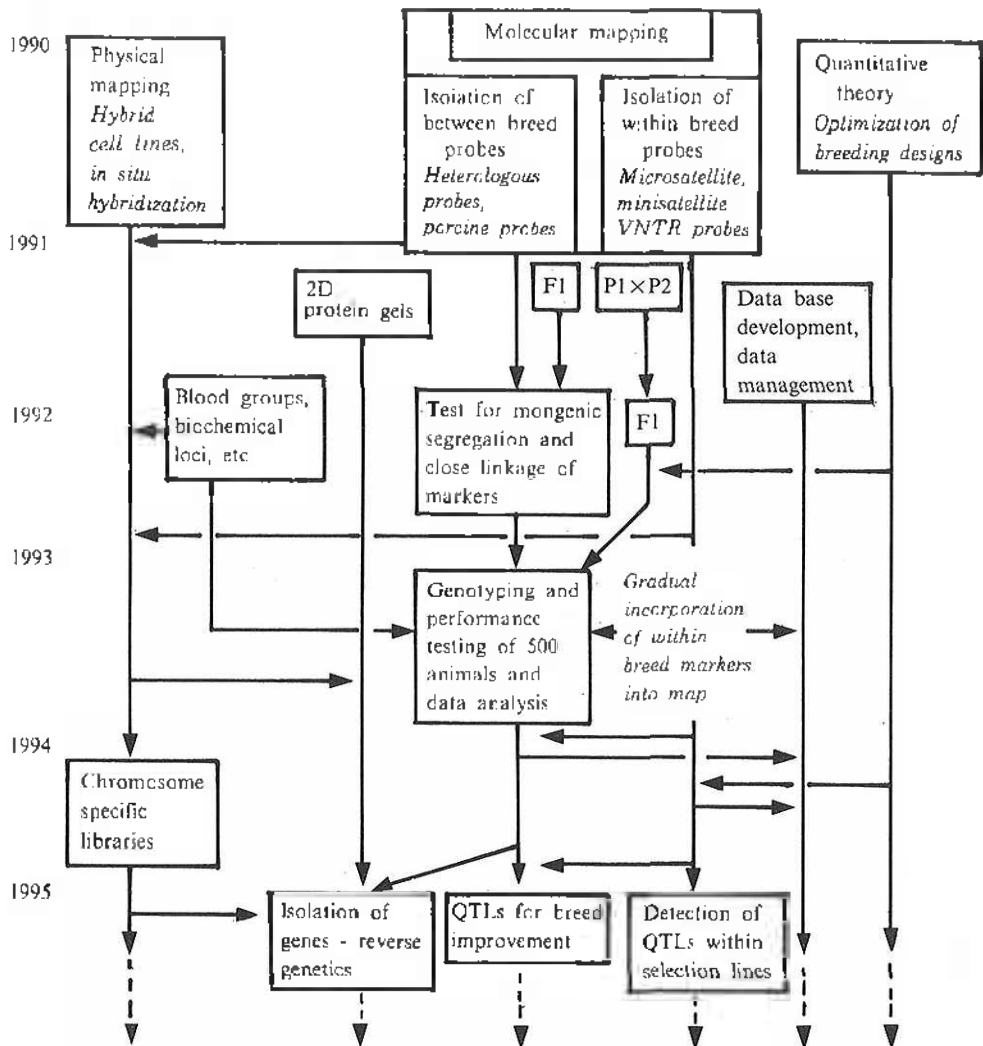


Figure 6. The proposed timetable for the European Pig Gene Mapping Project (PiGMap). The project involves the production of a low resolution genetic and physical map of the porcine genome followed by the location of quantitative trait loci in crosses between diverse strains (e.g. Meishan and Large White).

gation of the markers and to detect close linkage or allelism between markers. Polymorphic markers would be exchanged between collaborating groups and linkage information accumulated over all groups of reference families. This would provide a powerful test for linkage and allow comparison of distances in different types of crosses (e.g. Meishan  $\times$  Large White versus Wild Boar  $\times$  Large White) to provide further information on comparative genomic organization.

Physical mapping will be performed using two techniques. *In situ* hybridization of cloned genes

on metaphase or prometaphase chromosomes allows precise localization of cloned genes within chromosomal regions. The rationalization of the panels of hybrid cell lines which contain different combinations of porcine chromosomes makes it possible to rapidly assign cloned sequences to chromosomes. The availability of porcine cell lines and animals carrying chromosomal translocations will be particularly useful.

The porcine karyotype is particularly suited to FACS chromosome sorting (Grunwald et al., 1989) and a dual laser FACS sorted flow kar-

yotype will be developed within the project. This will enable the distribution of filters carrying FACS sorted chromosomes to participants to allow rapid assignment of cloned sequences to chromosomes. The isolation of chromosome specific markers and future attempts to isolate coding sequences associated with QTLs will be greatly aided by chromosome specific libraries, and the production of these for selected chromosomes will also be undertaken.

The final part of the project will be the initiation of the experiments required to map QTLs. This involves the development of the computer technology, the coordination of the traits to be measured at participating centres and the initiation of the crosses. It is anticipated that the genotyping and performance testing of the animals in this part of the project and the mapping of QTLs will be undertaken in the years 1993 to 1995.

### Transgenesis

The impact of direct manipulation of the genome by molecular genetic means of animal breeding programs could be large in the longer term (Pursel et al., 1989; Clark, 1990). At present techniques in farm animals are limited to the addition of extra genes to the germ line. This is achieved by direct injection of several hundred copies of a gene construct directly into the nucleus of an early embryo. The percentage of injected embryos which survive to become 'transgenic' offspring is low, making the technique expensive, and expression of the inserted gene is variable. Research is being pursued to overcome the limitations of the techniques available for farm animals (Wilmut and Clark, 1990). In future the techniques are likely to become more effective and it may become possible to more precisely target changes, to turn off or downregulate endogenous genes and to regulate expression of transgenes.

The techniques for genetic engineering are gradually becoming available, but as yet there are very few genes that are potential targets for manipulation. Most of the work in pigs so far has followed the lead provided by the demonstration of the dramatic effects on growth of additional copies of the growth hormone gene in mice. Thus constructs used have largely been based on growth hormone or growth hormone

releasing factor (Pursel et al., 1989). Pigs expressing growth hormone transgenes have been found to grow up to 15% faster, be up to 18% more efficient, and have markedly reduced levels of subcutaneous fat compared to litter mate controls. However, at the same time these animals have depressed appetites and a marked decline in general fitness (Pursel et al., 1989).

The effects of growth hormone transgenes are similar in magnitude to the effects of injections of exogenous growth hormone (Evock et al., 1988). The improvements in efficiency achieved by additional growth hormone are probably due largely to improved partitioning of energy from fat to lean deposition and benefits may be less in the leaner genotypes used in Europe than they are in the U.S.A. However, the benefits of exogenous growth hormone are at least as great in pigs containing a proportion of genes from indigenous Chinese breeds as they are in U.S. breeds, with increases in feed efficiency of up to 30% and no significant decrease in feed intake (McLaughlin et al., 1988). This suggests that an effective route to the utilization of prolific Chinese breeds could be their combination with growth hormone transgenics. For example, an F1 maternal cross of which one component is the Meishan pig could be complemented by a transgenic sire line, with piglets produced in large litters with low overhead costs but growing rapidly and efficiently (figure 3c).

Other prospects for the use of transgenesis in pig breeding programs are available. Disease resistance may be amenable to genetic manipulation, and a gene for resistance to influenza type A has been isolated from mice. This strain of influenza also infects pigs, causing growth retardation and, rarely, mortality. Attempts are now being made to produce pigs transgenic for the mouse resistance gene which are themselves resistant to the virus (Brem et al., 1988; Brenig et al., 1990).

Another possibility may be the enhancement of the pigs digestive capabilities to enable it to digest lower quality feeds and waste products more efficiently. Pigs are monogastric and digest cellulose poorly, however, genes for the enzyme cellulase, which breaks down cellulose to simpler polysaccharides, have been isolated from bacteria. Attempts are now being made at our institute to produce transgenic mice which produce cellu-

lase specifically in the pancreas for secretion into the small intestine. If this proves successful, it could be a route to enhancing digestive efficiency in pigs (Hazlewood, 1989).

Prospects for the improvement of porcine reproduction via transgenesis are currently distant. Although it can be envisaged that ovulation rate might be increased by molecular genetic manipulation, this is unlikely to increase litter size because, as discussed earlier, prenatal survival is the main limiting factor in pigs. Research has indicated some areas of promise, in particular, the profiles of estradiol and progesterone may be associated with the recognition of pregnancy and prenatal survival, additionally, genes of major effect on prenatal survival linked to the porcine major histocompatibility complex may exist (Wilmut et al., 1990b). However, all of these areas require further research before target genes for transgenic programs can be identified.

**Integration of transgenics in breeding programs.** At present it is only possible to envisage limited goals for transgenic programs. It is likely that molecular genetic techniques will be used to tackle specific problems, whilst at the same time selection utilizing the latest statistical and computing technology will be used to improve the remainder of the genome. This in itself will require some agility by animal breeders, as potentially large changes to single traits may radically change selection objectives in the remainder of traits and may even alter genetic parameters and genetic relationships between traits (Smith et al., 1987). If growth hormone transgenics prove viable in breeding programs, selection effort is likely to shift away from lean growth efficiency towards improvements in reproduction, meat quality and general health.

The introgression of transgenes into a nucleus population already under selection will need to be done with care. Until transgenic technology has been radically improved, each transgenic animal is unique, with the effects of the transgene depending upon insertion site, expression and copy number. Several different transgenic founder animals may be produced with the same gene construct and the effects of the particular transgene will require to be tested and compared in both their hemizygous and homozygous form in descendants of the founder animals (Smith,

1988). The selected transgene can be backcrossed into the nucleus population, but this will require several generations in order to recombine the transgene from its background genotype and avoid inbreeding.

Smith et al. (1987) consider that, with rates of genetic improvement in the nucleus of 1-3% per annum achievable by selection and several generations required to test a transgene and introgress it into the nucleus, an economic improvement of at least 5-10% due to the transgene is required before its use is worthwhile. This may be too pessimistic, for the backcrossing phase will reduce the genetic lag between the transgenic stock and the nucleus population (figure 7). During the period of introgression, selection would be continuing in the nucleus population and the intensely selected males used in the nucleus population would be crossed to hemizygous transgenic females and the backcrossing repeated with their daughters. Producing transgenic animals in stock from the nucleus population reduces the number of rounds of backcrossing required, but transgenes contained in less advanced stock can be introgressed in a similar manner by several rounds of backcrossing to nucleus males. After the backcrossing phase a final round of *inter se* mating is required to produce homozygous animals, in this generation, selection opportunities will be absent in females and limited in males. Nonetheless, the total genetic lag is likely to amount to less than two generations whether the transgene was originally present in nucleus stock or in less genetically advanced stock. With economic merit increasing by the order of 1.8% per annum (generation) in the UK (Mitchell et al., 1982), transgenes which improve economic merit by the order of 5% would be viable. Additionally, when a porcine genetic map is available, polymorphic markers flanking the site of insertion of the transgene can be used to aid the recombination of the transgene from the genetic background of the founder animal in order to further minimize genetic lag and speed the introgression of the transgene into the nucleus population.

## Conclusions

The main focus in pig selection programs has been on the efficiency of lean growth. This has

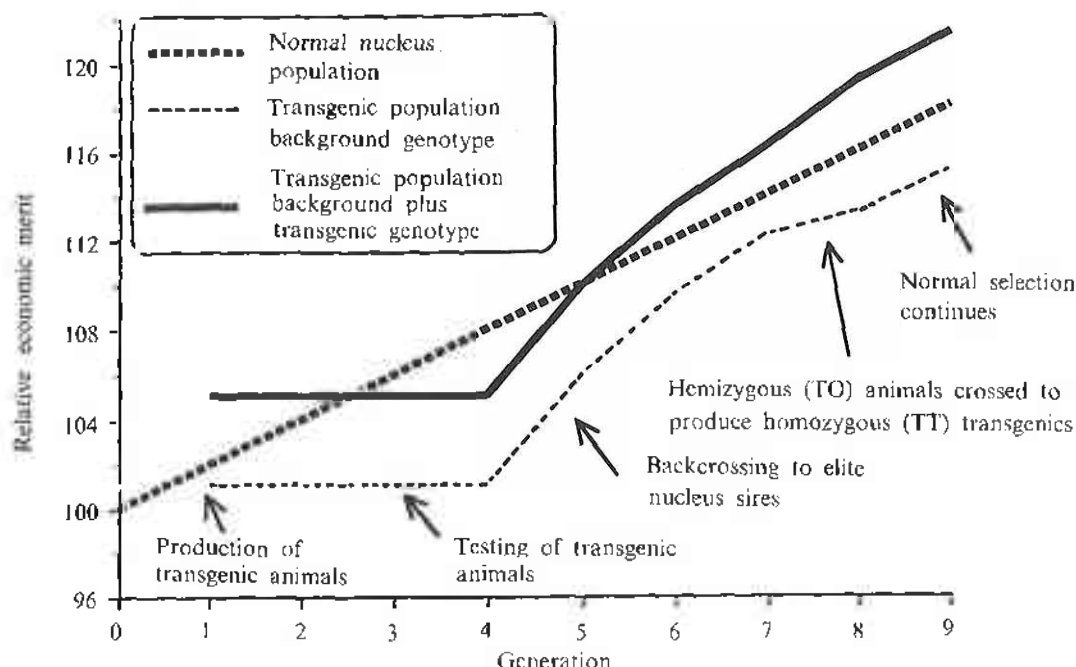


Figure 7. The introgression of a transgene in a pig nucleus population. Economic merit in the normal nucleus population is increasing at 2% per annum. The first transgenic animals are born in generation 1 and are progeny of elite sires and dams from the nucleus population. In generations 2 to 4, transgenic animals are performance tested in hemizygous and homozygous form and a transgene of net economic benefit 4% in hemizygous form and 6% in homozygous form is selected. In generation 4, transgenic females are backcrossed to elite sires, their transgenic female offspring selected and the process repeated up to generation 7. In generation 7, hemizygous males and females are selected and mated, and homozygous transgenic offspring used to produce the new transgenic nucleus in which selection continues. In this example backcrossing occurs after the testing of transgenic animals, but it would be possible to perform the two processes simultaneously in generations 2 to 4. Although this would not reduce the ultimate genetic lag between the nucleus population and the background genotype of the transgenic animals, the time taken for the introgression process would be reduced.

resulted in pigs which convert feed more efficiently and thus produce cheaper pork, which is also leaner and more attractive to the consumer. The advent of new technology is having the effect of broadening the objectives in breeding programs. Chief amongst these new technologies is best linear unbiased prediction (BLUP) of breeding values, which in principle allows information to be incorporated from many sources in an optimum way. BLUP is now beginning to be incorporated into pig breeding programs. Specialized sire and dam lines are being developed and BLUP facilitates the incorporation of litter size and other

reproduction traits in the objectives for dam lines. Genes from prolific Chinese pigs such as the Meishan are likely to be incorporated into dam lines to further enhance their performance. Techniques for carcass assessment are becoming more refined, and it is likely that carcass, meat and eating quality will become increasingly important objectives in breeding programs. This trend will be further stimulated by increased automation of carcass grading in slaughter houses, with identification of individual carcasses and payment to the producer based on quality.

BLUP combined with genetic links achieved

through A.I. increases flexibility in the design of breeding programs. This will be fortunate if further research proves that genotype x environment interactions are a major problem, as incorporation of performance data from several tiers of the breeding pyramid may be required to effectively predict the breeding value of nucleus animals.

Future developments are likely to include the use of marker assisted selection and the incorporation of transgenics into breeding programs. Marker assisted selection has the ability to facilitate the introgression of genes of value from one breed into another, but requires the development of a gene map of the pig. Several laboratories around the world are working on a porcine gene map, and its completion on a five year time scale can be envisaged. Few genes are currently available for use in transgenic programs, but several possibilities are being explored. Growth hormone transgenics have increased efficiency and reduced fat content. If it proves possible to control expression, growth hormone transgenics, possibly combined in a system with prolific Meishan pigs could prove to be a practical system. However, testing and evaluation of systems involving transgenic animals will require to be carefully carried out and only transgenes providing reasonable overall improvements in economic returns will be viable.

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