Germ Plasm Evaluation Programmes

The presumed purpose of animal evaluation programmes is to provide accurate and relevant information about the usefulness of alternative breeding stocks and breeding systems for defined breed roles and production-marketing environments. The two levels of animal germplasm evaluation programmes to be considered here are 1) Direct comparisons of genetic stocks and 2) Crossbreeding experiments. Programmes for genetic evaluation of individuals within breeds are considered only as they may contribute to comparisons among breeds.

General.

Direct comparisons of genetic stocks include a wide range of usefulness, from only growth efficiency of young males to total input/output efficiency of herds or flocks. Usefulness depends on both accuracy and completeness of information obtained. Accuracy is affected by method of sampling the stocks and by the design and scale of performance recording. Inaccurate or incomplete descriptive data can be not only inadequate but even misleading to those using the information to guide choice of breeding stock for a commercial animal production system. Crossbreeding experiments are planned matings to estimate not only mean performance differences among straightbred animals of different breeds or strains of livestock, but also to measure the parameters of breed, heterosis and gene-recombination effects in crosses that will allow prediction of relative efficiency for alternative breeds and systems of breeding. Examples of these two levels of germplasm evaluation programmes will be discussed for major species of livestock.

Poultry.

The "on farm" improvement and record of performance plans are useful primarily for selection within a breeder's own flocks. Both the possible selection of birds enrolled and environmental differences among breeders flocks limit the usefulness of published records for comparisons among genetic stocks. The early publicly operated central tests compared performance for samples of adult birds from different stocks under a common environment (Warren, 1958). However, the weaknesses of small and selected samples from each stock soon led to development of so-called Random Sample Performance Tests (Dickerson 1965). The avowed purpose of Random Sample Tests has been "to provide a reliable guide for commercial producers, hatcheries and breeders concerning the potential performance of commercial chicks or poults offered for sale by hatchery outlets".

For egg production stocks, random samples are obtained from commercial hatchery sources, preferably as hatching eggs rather than chicks. Performance is compared under a commercial egg production environment. Pens of each entry are replicated within a test location. Preferably, each stock is entered in a large number of different test locations, thereby increasing the reliability of the stock rankings based on data from all locations. Records of mortality, age at onset of lay, body size, egg production, egg size, shell strength, blood and meat spots and albumen quality are used to calculate egg and meat output value from each entry. Records of feed consumption and chick cost constitute input. Economic comparisons are made in terms of income over feed and chick cost per pullet housed (net income).

Feed per unit weight of eggs produced provides a measure of biological efficiency, but one which ignores output of salvage chicken meat at the end of the laying period. A measure of economic efficiency influenced less by stock differences in body size would be total input cost per unit of output value.

Two-year combined summaries of results from all Random Sample Egg Production Tests in U.S.A. and Canada provided overall estimates of breeding values, with 5% confidence limits, for each performance trait of each stock (e.g., see ARS, 1966). Information also was included for each trait concerning the average within-test correlation of the same stocks among replicates and between years, as well as the repeatability of the same stock between test locations in the same and different years. Because measures of some traits are much more accurate than others as indicators of their breeding values (i.e., more highly heritable), an index weighting of component traits was shown to be a better predictor of net income in future tests and years than net income itself (Kinney et al., 1969). This analysis also showed that future net income could be predicted nearly as accurately without including the measures of feed intake, using only age at first egg, eggs per hen housed, egg weights, laying mortality and hen body weight. Use of the same unselected control stock at all test locations over years permitted estimation of genetic changes over time for the genetic stocks entered in the tests.

Such analysis of test results helps users to realize the limited accuracy of results from a single year and test location (e.g., repeatability of .4 to .5 for net income) and the value of entering each stock at many test locations each year. However, even estimates of net income based on entries at many locations are far from perfectly accurate (e.g., $1.93 ± .10 per pullet housed for a stock with 80 pens at 32 locations). Even this accuracy is low enough that small changes in overall ranking of a stock can occur unpredictably from year to year, and is a reason for breeders to avoid relying too heavily on results of Random Sample Tests for their sales promotion.

In Random Sample Tests of chicken and turkey meat production stocks, maternal effects of parent flock health, age and egg size on chick size, mortality and later broiler weights make unbiased sampling of eggs for each entry difficult (Goodwin, 1961). Ideally samples for each stock entered should come from several parent-stock flocks of the same standard age. Primary emphasis has been placed on feed conversion or feed intake per unit weight of market birds. This measure ignores any differences in dressing percentage, or carcass composition, and in cost of chicks or poults, as affected by parent flock body size, egg production, fertility and hatchability of eggs. Factors affecting cost of broiler chicks or turkey poults presumably should be reflected in their price to growers. Evaluation of carcasses is increasingly important but more difficult, requiring direct or indirect measures of body fat and scores for conformation.

Random sample testing of poultry stocks can be useful both to the industry and to breeders, especially when there are many stocks to be compared and many independent growers. Properly conducted, such public evaluations of the available stocks direct industry attention to the real merit of the alternative breeding stocks. However, continued usefulness of such public testing to the poultry industry depends upon the accuracy and relevance of test information not obtainable more directly by individual producers and breeders.

At an earlier period, there were many breeds of both egg, meat and dual purpose chickens. Since then, there has been much Random Sample Testing and experimental evaluation of breeds and their crosses, leading to development of the present specialized egg and meat production stocks (Warren, 1942, 1958). In the meat stocks, specialized maternal and terminal sire lines have been developed to maximize efficiency in production of market meat birds. Parallel developments have occurred in meat turkeys. The extremely high reproductive rate of poultry, the intensive mass-production management systems and the intense competition in the poultry, egg and meat industry, have now led to sharply reduced numbers of surviving breeders in much of the world. Strain-crosses of Leghorn or part Leghorn composites have become the dominant egg producing stocks. Strain-crosses, with white feathers and skin for market acceptance, now dominate the chicken and turkey meat industry.

Diallel or partial diallel designs (Table 1) are generally used in crossbreeding evaluation of poultry breeds or strains (see review by Jacobec et al., 1987) because of their high reproductive rate and intensive management. Generally, first cross-heterosis is important for sexual maturity, rate of lay, viability and total egg mass per pullet housed. However, experiments extended to include F_2 or later generation progeny from inter se mating within the

F_1 cross have shown more loss of F_1 heterosis than the 50% expected from the reduced heterozygosity in the F_2 generation (review by Sheridan, 1981). This experience, and the very small proportion of pure line populations necessary to produce the parents of commercial chicks, logically have led to use of specific crosses by commercial producers. If composite lines are developed, it is done to obtain a desired blend of characteristics in a new line intended for later use as the male or female parent in some specific F_1 commercial cross.

Pigs.

Organized central performance testing of swine stocks began in Denmark in the early 1900's (Clausen and Gerwig, 1958). Typically, four slaughter pigs from each litter entered were fed together under standard conditions from about 20 to 90 kg to measure rate of gain, feed conversion and carcass traits. The purpose was to improve accuracy in comparing the genetic merit of breeder stock by testing all samples under a single uniform environment. This approach largely removed herd environmental differences from the comparisons and facilitated the uniform recording of feed consumption and of carcass traits. It also permitted valuable analyses of genetic variation in performance traits (Lush, 1936). However, the limited total capacity of the central testing facilities allowed only small and potentially selected (unrepresentative) samples of each breeder's stock for use as a sib or progeny test.

Similar central testing of samples from breeders spread to the U.S.A. and other countries in the 1920's (Craft, 1958). Then in the 1950's, testing samples of full or half-sib sets of boars alone, or of boars and sib-sets of barrows and gilts for slaughter was initiated in many states of U.S.A. and other countries (King, 1955). Boars with the better records are offered for sale to breeders. Such programmes allow comparison between boars from different breeders or even breeds, but the limited proportion of all boars that can be accommodated limits their accuracy in estimating differences among breeds or breeders. It also means that most selection by breeders still must be based on their own records.

A more complete central testing procedure was developed in Britain (MLC, 1977) and the Netherlands (Schoonoord, 1981) to compare commercial cross combinations offered by large breeders or breeding companies, using entries of both boars and gilts to measure whole litter growing performance and carcass traits (MLC, 1977). In Denmark (Jonsson, 1975), facilities have been expanded to allow growth and carcass testing of a set of four litter mates at one of twenty testing stations from each of one-half of all approved breeding sows. Participating breeders also record measures of age, weight and ultra-sonic sidefat, eye-muscle and fat areas. Thus breeders and producers have rather adequate summaries of both central test and on farm records to use in selecting replacement breeders and for choices among the breeds and breed crosses evaluated.

More recently "on-farm" recording of reproduction, growth and backfat performance in purebred herds of major US breeds (Stewart et al., 1991; Harris et al., 1989) has been organized to provide estimates of breeding values intended primarily for use in selection within breeds. However, such complete herd records are also highly useful for comparisons between breeds within a common regional production system. The main limitation of such comparisons is the lack of direct feed conversion records and incomplete carcass evaluation. These limitations can be overcome by joint use of the more limited central-test comparisons along with predictions from the "on-farm" body weights and backfat measures on live animals. The New Zealand Voluntary Improvement Plan (VIP, 1979) is an example of central boar testing combined with comprehensive on-farm performance recording. Clearly, the information necessary to characterize differences among pure breeds of swine can be obtained from both central test and on farm recording of performance or a combination of these approaches. Central testing can provide more complete information, but usually is handicapped by problems of cost and of small, potentially selected, samples. Error in breed comparisons from environmental variation among herds in on-farm performance recording can be largely overcome by averaging unselected records from many herds and very large numbers for each breed within a region. However, the primary focus of "on-farm" recording must be its use for within-herd selection, to avoid potential errors from environmental competition among herds.

The important improvements in viability and growth of market pigs and in productivity of sows from crossing pure breeds have been demonstrated in extensive crossbreeding experiments beginning in the early 1900's (Winters et al., 1937; Lush et al., 1939; reviews by Jonsson, 1975; Sellier, 1976; Johnson. 1981). Complete or partial diallel mating designs have been used, including three-way crosses to measure breed and heterosis effects on reproductive performance of the F, crossbred sows (as in Table 2). Some of these experiments also have compared F_1 with purebred boars of the same breeds and found significant heterosis in F_1 male reproductive performance, but negligible effects on performance of progeny.

Generally, crossbreeding results have indicated that maximum industry efficiency in pork production can be realized by mating females of an F_1, cross chosen for superiority in reproductive, growth and carcass traits with boars of the breed or F_1, cross with best transmitted viability, growth, carcass traits and superior male reproductive performance (Bennett et al., 1983). If deviations of heterosis from degree of heterozygosity are not importantly negative, composites of 3 or 4 maternal breeds or irregular "periodic" rotations of sire breeds would retain 2/3 to 3/4 of the average F_1 heterosis without requiring continued F_1 replacements from purebred populations (Dickerson, 1973; Bennett, 1987).

A design that would be useful in evaluating optimum fraction of an introduced breed in a composite (e.g., Young, 1991) is comparison of reciprocal backcrosses (1/4 *vs* 3/4 or 1/8 *vs* 7/8) relative to a common control and the F_2. Here backcross comparisons can be made within the same level of retained heterozygosity (Table 4).

A recent experiment (Young et al., 1989) has compared parental, F_1, F_2 and F_3 generations of crosses among two sets of four breeds each, chosen either for market pig traits or for sow performance and pig traits, to see how well F_3 composite performance agrees with prediction from parental and F_1 performance. The F_3 of the maternal breed cross was above prediction for number weaned, but later in puberty and lower in loin eye area. The F_3 of the paternal breed crosses was slightly above prediction for pig weight at weaning, earlier in puberty but lower in loin eye area. These minor deviations of performance from predictions based on only additive and dominant gene effects, along with the very small proportion of purebred matings required to produce replacements, have encouraged swine industry use of specific crossbreeding systems based upon estimates of the breed-average and F_1 heterosis effects for pig and sow performance traits.

Sheep and Goats.

Evaluation of sheep and goat germplasm covers a broad spectrum, from summaries of on-farm or field performance records to central testing of breed samples, to designed crossbreeding experiments measuring average breed heterosis, and non-allelic gene interaction effects. Performance traits studied vary with the major objective (meat, wool and/or milk) and with the production environment (temperate, tropical, intensive, extensive).

Organized on-farm field recording of information on unselected animals for reproductive rate, mortality, body weights and wool yields can provide initial characterization of differences among breeds maintained under similar regional management conditions. Of course, large total numbers are required to reduce the errors from environmental variation among the flocks sampled from each breed. More precise breed comparisons of growth rate, feed conversion, carcass composition, wool yield and quality, as well as milk production can be obtained by comparing samples from each pure breed under a uniform central test environment, provided that adequate numbers of representative samples are obtained from each breed (Turner, 1969). Central tests have been widely used to compare only the growth potential of rams from terminal sire breeds (Waldron et al., 1989), as a means of identifying the better sources of replacement rams. Addition of feed consumption records would increase the value of such ram testing. Central tests also could be used to compare sire progenies from several meat breeds for growth, feed conversion and carcass characters of ewe and wether lambs. Usefulness of such central test comparisons of breeds and breeders is heavily dependent upon adequate and representative sampling.

Experimental comparison of breeds for maternal (ewe) performance in market lamb production can be done most efficiently by mating representative ewes of each candidate breed to the same rams of one or more meat-type breeds. This experimental design minimizes sampling error from random sire effects on progeny in direct comparison of ewe breeds (e.g., Fimland et al., 1969).

When adequate numbers of ewes from the candidate breed are not available, representative rams of each maternal breed can be mated to ewes of one or more "native" breeds to produce the F_1 females, which, in turn are evaluated in subsequent matings with sires of the meat-type breeds (e.g., Jacobec and Drizik, in EEAP, 1988). This indirect design is approximately one-fourth as efficient because it measures only one-half of the maternal breed differences (Figure 1). However, there is no difference in the efficiency of comparisons among the meat-type sire breeds. Records needed for a comprehensive evaluation include not only those of ewe lifetime reproductive performance but also the viability, growth and carcass traits of the market lambs produced (Dickerson, 1977).

When the objective is to determine the optimum proportion of an exotic breed in composite populations derived from crossing with adapted native breeds, a mating design comparing ewes of the F_2 (i.e., from F_1 x F_1) generation with those of the 1/4 and 3/4 exotic backcrosses (as in Oltenacu et al., 1981) is efficient, because the proportion of maximum F_1, heterosis retained is expected to be equal (50%) for these three levels of exotic breed contribution (Table 4). A prime example is the worldwide experimental evaluation of Finnsheep and other prolific breeds to increase net productivity under environments ranging from temperate to subtropical and from intensive to extensive range management (EEAP, 1988). Some of these experiments compared F_1, with the less heterozygous backcrosses, but the estimated fractional breed effects for litter size born were relatively unbiased because heterosis was slight. A Canadian experiment compared levels from 1/8 to 7/8 and purebred Finnsheep ewes (Fahmy, 1990). The reviews by Baker and others in an EEAP symposium (EEAP, 1988) provide a comprehensive summary of experiments evaluating potential usefulness of Finnsheep crossbreeding under diverse managements. Experiments comparing Finnsheep with Romanov, Booroola and other prolific breeds also are discussed.

Choices between systematic crossbreeding and the optimum composite require estimates of the average heterosis in overall performance realized for the two systems, including the dilution of average heterosis from the proportion of purebreds required to sustain each system. Such a comparison requires prediction of performance and over-all efficiency for the complete crossbreeding system, and for the F_2 or later generation of the inter se mated composite, using deviations from weighted means for the pure breeds involved, as in Young et al. (1986). For meat production in sheep, comparisons likely would include maternal composite or maternal crossbred ewes, when both are mated to meat-breed rams, and a straightbred general-purpose composite. Such comparisons should include all important traits and the relative values of wool and lamb that influence lifetime ewe productivity under the intended production-marketing system (Ercanbrack and Knight, 1989). Breed differences for each breed role in crossbreeding could be based on input costs per unit of output value in the experiment and compared with expected breed differences in unit costs based on prior estimates of the economic weightings for each trait (e.g., Wang et. al., 1991).

Because of the large differences among sheep breeds in prolificacy *vs* growth-carcass merit, industry breeding systems for market lamb production generally use superior large growth-carcass breeds to sire lambs from ewes of smaller, more prolific breeds, breed-crosses or composites. Choice of the ewe-breeds depends partly upon the feasability of production environments in which nutrition, matings and care at lambing can be controlled. Heterosis retained in prolific part-Finnsheep composites (Young et al., 1986) has been encouraging for their use in crossing with terminal sire breeds, thus simplifying matings required for production of replacement ewes. However, there has been considerable variation among sheep crossbreeding experiments from linear association of heterosis retained with level of increased heterozygosity expected, possibly related to interaction with production environments. Thus experimental evaluation of promising composite breed combinations seems justified before recommending their adaption for industry use.

Beef Cattle.

The various types of on-farm "record of performance" programmes are intended primarily for use in selection within a pure breed (Gregory et al., 1961). However, when averaged across many herds of each breed, they can provide much useful information about differences among breeds that exist within the same geographical and livestock management region. Their value depends on accurate measurement and reporting of the important performance traits for unselected animals. It is not usually feasible to include on-farm records of feed consumption or of carcass composition. Central Testing Stations can be used to compare samples from different breeds under a common environment for some of the important performance traits, such as growth, feed conversion, conformation and live fat measures of young bulls (Olson, 1989) or these traits plus carcass traits of steers. However, the small number of potentially selected animals and traits measured tend to limit both the accuracy and completeness of breed comparisons based on information from Central Tests.

The major potential advantages of planned beef cattle crossbreeding experiments are 1) the measurement of both breed average and crossbreeding heterosis effects, 2) minimizing environmental sources of error and 3) more complete measurement of traits affecting production efficiency. The production objective may be meat production only or a combination of meat and milk production. In some cases, it may be desirable to include more than one environment or management system in the experiment, although this multiplies the necessary scale of the experiment (e.g., Olson et al., 1991).

When the objective is to evaluate several introduced or exotic breeds, the more feasible crossbreeding design is one comparing a representative sample of sires from each introduced breed in matings with one or more "native" breeds to improve performance potential or adaptation to a difficult environment (Figure 1, Table 4 as in Gregory et al., 1985; Trail et al., 1985, or Paschal et al., 1991). The first generation allows comparison among introduced breeds for the combination of transmitted (g^I) and heterosis (h^I) effects of each breed of sire. Adding information from the F_2 and the two backcross generation matings would allow separate estimation of breed differences in transmitted individual (g^I), heterosis (h^I), and recombination effects (r^I). It also would allow evaluation of the optimum fraction of each introduced breed from 1/4 to 3/4 at the same proportion of F_1 increase in heterozygosity (Table 4).

Estimation of maternal breed (g^M), heterosis (h^M) and recombination (r^M) effects requires third generation matings of generation-two females with sires of an unrelated breed (Table 4), and combining these results with information from generations one and two. See Cundiff et al., (1986) and references cited for partial examples of this approach. A summary of information from these breed and crossbreeding evaluation experiments, as applied to the choices among alternative crossbreeding systems, is given by Gregory and Cundiff (1980).

When adequate samples of females as well as males are available from each breed to be evaluated, the complete diallel design (Table 1, as in Gregory et al., 1980; Baker et al., 1989; or Comerford et al., 1991) is more efficient for estimating breed individual (g^I) and maternal (g^M) and individual heterosis (h^I) effects. It can be extended to measure maternal heterosis (h^M) by including the three-way crosses (Table 2). However, measurement of individual recombination effect (r^I) deviations from linear association with average changes in heterozygosity (i.e., from the additive plus dominance expectations) would require comparison of F_2 with mean of reciprocal backcrosses (Table 4).

Possible non-allelic gene interaction deviations from linear association with expected heterozygosity (r^I, r^M, r^p) could be measured most completely by comparing deviations from purebred means for each four-way cross with those for the mean of the corresponding four F_3 generation two-way crosses (Table 3). If paternal effects (g^p, h^p, r^p) are negligible, similar comparisons for each three-way cross with those for the mean F_3 generation of the two corresponding two-way crosses (Table 3) would provide similar estimates for r^I and r^M deviations, e.g.,

$$\frac{1}{4}(CA^3+CB^3+DA^3+DB^3-C-D-A-B)-\frac{1}{2}(CDxAB)+\frac{1}{8}(C+D+A+B)$$

$$=\frac{1}{8}r^I_{gg}+\frac{1}{4}(r^I_{dd}+r^M_{gg})+\frac{1}{2}r^M_{dd}\text{, and}$$

$$\frac{1}{2}(CA^3+CB^3)-\frac{C}{2}-\frac{A}{4}-\frac{B}{4}-\frac{1}{2}(CxAB)+\frac{C}{4}+\frac{A}{8}+\frac{B}{8}$$

$$=\frac{3}{16}r^I_{gg}+\frac{3}{8}r^I_{dd}+\frac{1}{4}r^M_{gg}+\frac{1}{2}r^M_{dd}$$

Several large scale studies of heterosis retention in beef cattle (Gregory and Cundiff, 1980; Koch et al., 1985; Gregory et al., 1991a,b) under favorable temperate environments have not detected important deviations from additive-dominance expectations in advanced generations of composite populations. If these results are representative of cattle in general, most breed and crossbreeding evaluation studies need not extend beyond the three-way crosses needed to evaluate heterosis in maternal performance. However, crossbreeding results with dairy cattle (Madalena, 1989; Madalena et al., 1990a) have indicated important recombination losses in composites under difficult tropical environments.

Dairy Cattle.

The trait of primary importance in dairy cattle obviously is milk production, qualified by fat, protein and total solids content. However, efficiency of milk production can be also greatly affected by fertility, mortality and culling as they affect herd life and replacement costs, as well as by fixed and maintenance costs related to health care and cow size (Blake et al., 1986a; Schmidt and Pritchard, 1988, Holman et al., 1990). Resistance to disease and parasites and the tolerance of heat and of marginal feed intake are especially important under some tropical, low-input production systems. Adjustments should be avoided for such gene-influenced components of milk production as age at first calving or lactation length under stressful environments (Madalena et al., 1989).

Within-herd recording of milk, fat and now protein production is the longest, most systematic and best utilized system of performance recording for domestic animals. Although the DHIA system of performance recording is intended for use in within-breed selection, breed averages across herds under similar management clearly are good measures of breed differences in performance, and can be used for comparing genetic evaluations between countries as well (Philipsson, 1987). Within-herd records of milk, fat and protein production, supplemented by body weights and reproductive performance of pedigreed cattle could even be used to estimate breed differences in the economic efficiency of milk production, under ranges of relative prices for milk components, feedstuffs and other inputs (Blake et al., 1986a; Schmidt and Pritchard, 1988). Properly controlled, such field comparisons could even be used to compare breeds of dairy cattle with crosses between breeds (Fimland, 1975; Ericson, 1987; Ahlborn-Bruer and Hohenboken, 1991). Thus, designed breed evaluation experiments are needed mainly for the comprehensive evaluation of breeds in crossbreeding, including crossing of native with exotic breeds to improve performance in difficult environments (Simpson and Wilcox, 1982; Blake et al., 1986b; Cunningham and Syrstad, 1987; Syrstad, 1988; Cunningham, 1989; Tewolde et al., 1990).

The most informative crossing design is a complete diallel extended to include the three-way crosses of females from each F_1 and contemporary purebreds by the same sires (Tables 1 and 2). The USDA diallel crossing of Holstein, Ayrshire and Swiss breeds (McDowell and McDaniel, 1968) included these matings plus the first generation of a three-breed rotation. Heterosis for fat corrected milk production was 8 to 10% in F_1 crosses with Ayrshire and Brown Swiss but negligible for Ayrshire x Swiss F_1. Heterosis in milk yield was even greater for the three-way crosses. However, only the Ayrshire x Holstein, Swiss x Holstein and Holstein x (Ayrshire - Swiss) exceeded purebred Holstein in first lactation net return, after adjusting for differences in health, mortality and calving interval.

The Holstein x Guernsey crossbreeding experiment at the University of Illinois (Touchberry, 1970, 1992) attempted to include all outputs and inputs affecting efficiency of dairy production (e.g., milk solids yield, viability, reproduction, body weights, veterinary service, mastitis, etc.). Breeding groups compared were purebred Holstein and Guernsey, and reciprocal F_1 crosses, from the same sire within a year and the same dams in different years. The second generation compared the two pure breeds with 1/4 and 3/4 Holstein backcrosses, using the same Holstein or Guernsey bulls to sire each pair of purebred and backcross progenies and allowing each F_1 female to be mated for both backcrosses in different years. The third generation included the two pure breeds plus the 3/8 and 5/8 backcrosses, from matings of the same sires to produce either pure and 5/8 Holstein or pure and 5/8 Guernsey progeny. The next two generations were from crisscross matings of Holstein sires with pure and 3/8 Holstein and Guernsey sires with pure and 3/8 Guernsey females followed by the reverse backcross, to produce 5/16, 11/16, 11/32 and 21/36 and 100% Holstein and Guernsey progeny, approaching the equilibrium 1/3 to 2/3 of a two-breed rotation. Effects of breed additive and crossbreeding heterozygosity were estimated from partial regressions on fractional breed of sire or dam and heterozygosity. The F_1 heterosis was about 7% for total milk solids, but nearer 22% in terms of net return after adjustment for reproductive, health and other traits. However, the pure Holsteins used still exceeded the F_1 crosses by about 10%, because the pure Holsteins exceeded Guernsey's used by over 100% in estimated income over input costs. Thus, the potential advantage from crossbreeding would be much greater between breeds of more nearly equivalent performance, as for Jerseys and Holsteins under the seasonal-pasture, milk-solids production system of New Zealand (Ahlborn-Breur and Hohenboken, 1991). There, Jersey-Holstein rotation crossbreeding apparently would slightly exceed pure Holstein fat production before taking into account crossbred advantages in reproduction, viability, and other performance.

Because of the general superiority of the Holstein-Friesian breed for milk production, especially in temperate climates, interest has focussed on differences among Friesian strains from different countries. The FAO sponsored comparison in Poland of 10 strains of Friesian cattle (Stolzman et al., 1988; Jasiorowski et al., 1988a,b) compared the F_1 and the 3/4 and 1/4 backcrosses of nine other strains with Polish Friesian. Differences among the nine F_1 crosses with the Polish Friesians would include $1/2\ g^I + h^I$ effects for each strain. Those among the nine breed of sire 3/4 backcrosses would contain $3/4\ g^I + 1/2\ h^I + 1/8\ r^I + 1/2\ g^M + h^M$ effects for each strain. Comparisons of 3/4 with 1/4 backcrosses would contain only the $1/2\ g^I$ effect of each strain, and this would indirectly permit estimation of differences in h^I from the combination of F_1 and backcross information. Use of estimates for g^I and h^I differences between strains would then permit estimates of differences in $1/2\ g^M + h^M + 1/8\ r^I$. If contemporary purebred Polish Friesians had been included, the experiment would have been much more efficient for estimating both individual and maternal heterosis (h^I and h^M). Inclusion of the F_2 generation of each cross would have allowed estimation of epistatic recombination effects as well (Table 4).

Another important question concerns the role of high producing dairy breeds from temperate climates in the crossbreeding improvement of milk production in more difficult tropical environments (Simpson and Wilcox, 1982; Cunningham and Syrstad, 1987a; Cunningham, 1989; Tewolde et al., 1990) or role of Zebu cattle crossbreeding in semitropical environments (Blake et al., 1986b). This question can be approached from analysis of well planned experiments on cooperator farms as in Madalena et al. (1989; 1990a), being careful to avoid adjustment for gene-influenced components of milk production, such as lactation length and age at first calving. Partial regressions on fractions for breed composition and on relative crossbreeding increase in heterozygosity (Robison et al., 1981) can be used. When inter se matings of crossbreds are included along with levels of backcrossing to both exotic and adapted native breeds (as in Madalena et al., 1989; 1990a), epistatic recombination deviations from additive breed and dominance effects can be detected (Table 3). For example, performance of the 5/8 inter se in this analysis was markedly below the additive plus dominance expectations, relative to those for the 1/4 to 31/32 Holstein crosses with Guzera. Madalena et al. (1990b) also compared profit/day of herd life for the F_1, 3/4 Holstein, 5/8 inter se, rotational cross and modified 2 Holstein: 1 Guzera rotation, under high and low management levels. Results emphasized the greater advantage of F_1 over 3/4 Holstein for low than for high management. Also results from the 2 Holstein: 1 Guzera (2H:1G) rotation relative to F_1 were good (75%) under high management, while the 1H:1G rotation was 60% of F_1 and better than the 2H:1G rotation under low management. However, Syrstad's (1990) summary analysis of many studies comparing F_1 and 3/4 backcross milk yields of first parity Holstein and Jersey crosses indicated that the increased exotic breed effect at least compensated for the reduced heterozygosity of the 3/4 backcross over a wide range of herd production levels. Also, the ratio of Jersey to Holstein F_I, crosses was similar from low to high herd production levels. Perhaps, more evidence for interaction of heterosis or breed effects with herd production level would have been detected if viability, lactation length and age at first calving could have been examined.

These results suggest caution in assuming linear association of heterosis with heterozygosity retained in breed composite populations until further experimental evidence is obtained for the full array of important component traits, especially under difficult production environments.