THEORETICAL ASPECTS OF CROSSBREEDING*

W. G. HILL

Institute of Animal Genetics, Edinburgh EH9 3JN, Scotland

SUMMARY

Methods of utilising breeds and breed crosses in animal production are discussed, taking account of both genetical and economic aspects. The theoretical principles for breed and breed cross comparison are analysed, but most emphasis is given to methods of improvement of existing crosses. A new synthetic breed is likely to have higher genetic variation, and reach a higher selection limit than the pure breeds from which it originates. However, it may take many years for the synthetic to surpass the best available purebred under continuous selection. Returns obtained in early years have more monetary benefit than those obtained later, for they can earn interest and incur a smaller risk element, so that a synthetic of use only in later years is unlikely to be cost-effective. Despite the flexibility in maintaining several alternative breeds, these need to be continually selected if they are to remain competitive, so better returns may be obtained by exerting more pressure on the best available present material. It is unlikely on theoretical grounds that cross testing schemes such as reciprocal recurrent selection have much to offer for breed cross improvement in large animals where growth and carcase traits are important.

INTRODUCTION

Crossbreeding has been an established practice for centuries in the domesticated animal species. Breeders have had many objectives: crosses have been made every generation to obtain any benefits there may be from heterosis or from the particular merits of the individual breeds as maternal or paternal parents. Alternatively the crosses have been used to form new populations with desirable characters from each of the parental breeds with, perhaps, increased variability to enable more rapid progress from later selection. The theoretical basis of crossbreeding has been studied extensively to enable us both to understand the genetic mechanism underlying heterosis and to design breeding programmes to utilise it.

There are two essentially separate aspects of crossbreeding, although they can not be considered entirely independently of each other. The first includes the choice of breeds and method of utilising them in crosses, if necessary, in order to maximise *present* economic performance. For example, we may wish to know whether breed cross A × B is superior to A × C or to A as a single breed, when all productive and maternal traits are considered. The second area of breed utilisation is concerned with improvement over a period of a few generations. We would like to know which breeds or crosses to choose now and use in a selection programme so as to maximise economic merit over the next 10 or 20 years. The extreme examples occur with corn or poultry breeding, using a cross of inbred lines. The breeder may have the best two-way cross on the market at present, but could find difficulty improving it. There is some suggestion that breeding programmes in corn are moving back from an inbreeding and crossing scheme towards programmes in which selection is practised every generation. In the large animal context we are more concerned with whether to form new breeds with, perhaps, enhanced variation, or whether to use the best available at present.

In a recent review DICKERSON (1969) discussed the experimental information required for a rational choice of breeds, but was primarily concerned with immediate performance. Although I shall briefly discuss the theoretical framework on which such decisions should be made, I will give more emphasis to the problem of maximisation of future performance which has not, I believe, been investigated adequately in the context of breed utilisation. Unfortunately the analysis is bound to be somewhat speculative, for we generally lack adequate information on genetic parameters within different breeds and crosses in most practical situations. However it is possible to set out some of the conditions under which new cross populations might respond faster and further than their parent breeds. The analysis has not been taken very far, but hopefully it will provide a few pointers, and I shall give more attention to the arguments on which decisions should be based, rather than to conclusions in any specific instance.

For the purpose of this discussion the term *breed* will refer to any closed population from which members can be identified by phenotype or pedigree. A breed may have been kept distinct from other breeds under consideration for only a few generations, so that, for example, Canadian and Dutch Holstein cattle may be viewed as separate breeds for this purpose. I shall also make considerable reference to *productive* and *maternal* traits. In the class of productive traits are included growth and carcase characters of animals for slaughter for meat and milk production in a dairy breed. Maternal traits include litter number, conception rates, milk production in suckler herds and perhaps even adult body size, in so far as it affects breeding costs. In effect, the genes for productive traits are contributed by both parents in a cross, those for maternal traits are expressed only in the dam. The other term to be defined is *synthetic*, which will be used for any new breed cross which is maintained as a new population, breed or " gene pool ".

CROSSBREEDING AND PRESENT PERFORMANCE

In principle, the utilisation of crossbreds to obtain maximum performance at the present is simple. It is necessary only to find the most efficient purebred or crossbred combination, taking account of both productive and maternal traits. There may, however, be considerable difficulties in actually finding the best cross combination, especially when there are specific heterotic relationships between pairs of breeds and when there are important genotype by environment interactions. In these situations it may be necessary to test a large number of combinations. Otherwise good predictions of merit may be possible from pure line performance in some standard environment. MOAV (1966) discussed criteria for evaluating crossbreds. He defines a non-linear relation between maternal performance and economic merit, but we shall simplify this here to linearity. Consider a cross of breeds A (sire) and B (dam) with productive performance P_A, P_B and heterosis P_{AB}, and for the dam breed a maternal performance R_B. The economic merit, E, is

$$E = K + x \left(\frac{1}{2} P_A + \frac{1}{2} P_B + P_{AB} \right) + y R_B$$

or in a three-way cross A × (B × C) it is, approximately,

$$E = K + x \left(\frac{1}{2} P_A + \frac{1}{4} P_B + \frac{1}{4} P_C + \frac{1}{2} P_{AC} + \frac{1}{2} P_{BC} \right)$$
$$+ y \left(\frac{1}{2} R_B + \frac{1}{2} R_C + R_{BC} \right)$$

Here K, x and y are appropriate constants. Of these K includes fixed costs and does not affect comparisons between breeds. Examples of the values of x and y are given by MOAV (1966) for pigs, and these can be modified to correspond with the formulation used here. Let E be the excess of returns over variable costs, measured in pounds sterling per pig of 100 kg live weight marketed. Letting P be the feed conversion efficiency (kg feed per kg gain) then $x = 3.1$, and letting R be the number of pigs marketed per sow per year then $y = 0.21$, where R has a mean of about 16. These figures are for integrated operations, and they may not reflect present economic conditions, but should serve as an example.

These formulae illustrate some important, if somewhat obvious, points. Unless there is a large amount of interaction, P_{AB}, *specific* to particular breed combinations, the sire breed with highest performance on productive traits should be used, for we are assuming here that many dams are mated per sire, or that AI is used, so that the sire breed contributes a very small proportion of total maintenance costs. In the dam breed both productive and maternal traits have to be considered, and the weightings x and y determine how much should be given to each. These same weightings can be used for calculating indices for selection within breeds. We see that the fixed crossing scheme takes full advantage of any heterosis for productive traits in a two-way cross, and for maternal traits also in the three-way cross.

In cattle or sheep a high proportion of animals may have to be bred pure to provide replacements in the dam breed. If a proportion, q, of the animals marketed are pure breds of the dam breed, and $1 - q$ are crosses, the average merit becomes

$$E = K + x \left[\left(\frac{1-q}{2} \right) P_A + \left(\frac{1+q}{2} \right) P_B + (1-q) P_{AB} \right] + y R_B$$

so that productive performance in the dam breed becomes relatively more important. If a new synthetic breed is made from the cross of the A and B breeds the overall merit becomes

$$E = K + x \left(\frac{1}{2} P_A + \frac{1}{2} P_B + \frac{1}{2} P_{AB} \right) + y \left(\frac{1}{2} R_A + \frac{1}{2} R_B + \frac{1}{2} R_{AB} \right)$$

There is a loss of half the heterozygosity for productive traits, but a gain in the maternal traits. With a rotational crossing scheme on two breeds the average merit, taken over successive crosses, includes $2/3$ of the heterosis between the breeds for productive and maternal traits, but is otherwise the same as for the synthetic.

This discussion will not be carried further here. Reference should be made to the papers of DICKERSON (1969), MOAV (1966) and FEWSON and JAKUBEC (1970).

CROSSBREEDING AND FUTURE PERFORMANCE

In making decisions about breed or breed cross improvement in future years we face problems at two levels. We have to estimate the potential genetic progress and compare these rates of progress with alternative schemes. In addition we should consider the costs of these schemes and relate these to their potential economic benefits. Most geneticists have occupied themselves with measurement of response, considering economics only when designing a selection index to give optimum weight to the traits. I feel we need to go further than this and will attempt to do so after some discussion of the relevant genetic theory.

Imagine that on the basis of our breed and breed cross testing programme we find that the breed cross $A_1 \times B_1$ is most efficient. Therefore, unless there are specific interactions between these breeds, A_1 is the best available for productive traits and B_1 is good for both productive and maternal characters. We now have several options open for improving the cross, although some of them may not seem very promising. These are: (a) form a synthetic from the $A_1 \times B_1$ cross; (b) select solely within the breeds A_1 and B_1; (c) initiate rotational crossbreeding between A_1 and B_1; (d) form a synthetic sire or dam breed; and (e) maintain alternative sire or dam lines. The options are not mutually exclusive not do they cover the whole range of possible programmes, but they give some indication of the main direction of selection effort. We shall consider them in turn.

A. — *Form synthetic from $A_1 \times B_1$ cross.*

A new breed could be formed and maintained and marketed as a pure breed but this is unlikely to be useful. There is an initial loss of half the heterosis between the breeds for productive traits, which later increases as the synthetic becomes inbred, and a loss of half the maternal advantage of breed B_1 over A_1. Secondly, it has been shown by SMITH (1964) and MOAV and HILL (1966) that greater progress for overall merit is made if separate sire and dam lines are maintained, with selection in the sire line (or breed) made solely for productive traits and in the dam line for an index of productive and maternal traits. This advantage may be small in species such as pigs in which important maternal traits all have low heritability so that little pressure should be imposed on them.

In a dual purpose beef and dairy cattle system there may be considerable advantages in maintaining separate breeds. In the dam, or dairy breed, most selection effort has to be applied to milk production, and selection for beef characteristics can only be undertaken with minor weighting in the milk progeny test, or by performance testing prior to the progeny test. In either case the rate of response for traits relevant to beef production is much smaller than could be achieved in a beef breed used solely as a sire in crosses. In the beef breed intense selection can be practised on a performance test, using a short generation interval. Imagine, for example, that a pure Holstein could currently outperform any cross with the Holstein on some intensive management systems. Yet after a few years of selection either in a beef breed or in a separate strain of Holsteins, crosses to this breed or strain could be superior for beef traits, so that cross matings in excess of requirements for dairy breed replacement should be made.

There may be an increase in variability in the $A_1 \times B_1$ cross relative to the parent lines so that response is enhanced. However there are more appropriate means of forming synthetics with the aim of increasing variation, and these are discussed later.

B. — *Select within A_1 and B_1 breeds.*

In this way we retain, at least in the short term, the heterosis and other desirable properties of the cross combination. The main issue in this scheme is the mode by which selection should be practised: whether it should be based on pure line or on cross performance using some scheme such as reciprocal recurrent selection. For traits determined primarily by additive or completely dominant genes it has been shown theoretically that the rate of improvement in the cross and the selection limit are approximately the same in pure line and reciprocal recurrent selection schemes, *providing* that the same intensity of selection is practised in each system (HILL, 1970). But it is unlikely that any improvement scheme using cross testing could be operated in large animals with the same intensity and generation interval as in schemes for within breed selection, except perhaps

in programmes to improve milk production using progeny testing. If there is overdominance faster rates and higher limits can, of course, be achieved with reciprocal recurrent selection. An indication of whether this might be possible can be obtained from the genetic correlation of pure and cross performance. If this is close to unity there will be no advantage in the short term in selecting for cross performance directly. However, it is conceivable, in theory at least, that an initial programme of pure line selection would reduce later gains with reciprocal recurrent selection when both breeds have approximately the same gene frequency so that there is selection towards the equilibrium frequency. In large animals the traits of major importance include growth rate (and feed conversion efficiency), carcase quality (or simply degree of fatness), milk yield and milk quality, and reproductive traits. Of these carcase and milk quality typically show little heterosis, growth rate and milk production moderate heterosis, and the reproductive traits exhibit rather more. One can conjecture therefore that at most only a small proportion of the variance for all these traits, with the possible exception of fertility and litter size, for example, are contributed by overdominant genes. Breeding programmes with selection on pure line performance can therefore be continued with safety.

Whilst there appears to be little place for selection programmes based on cross performance in a two way cross structure they could be more relevant for improving the reproductive performance of the B × C mother in the three-way cross A × (B × C). But although each breed in the dam side of the cross contributes only $1/4$ of the genes for the productive traits in the final crossbred animals it also contributes only $1/2$ to the maternal performance of B × C. The relative index weightings which should be applied to maternal and productive traits in these breeds B and C are therefore almost the same as should be used in the single dam breed of a two way cross. In pigs the economic weightings for food conversion efficiency and carcase quality are so high, and the heritability of litter size is so low that most selection pressure should be devoted to these productive traits in the dam breeds. Thus even in a three-way cross a reciprocal recurrent selection programme would seem unjustified. Similarly, inbreeding schemes used to generate between line variation within the chosen breeds can not be effective relative to programmes utilising constant selection for the highly heritable traits.

C. — Rotational crossbreeding of A_1 and B_1.

In a rotational crossbreeding scheme each breed contributes to the cross to the same extent on average, both as a sire breed and as part of the dam combination. Therefore selection pressure has to be put on the same traits, both productive and maternal, in each of the two (or more) parent breeds, so that specialised sire and dam lines can not be developed. We must then expect to make less selection progress in the rotational crossbred than in a fixed crossing scheme such as $A_1 × B_1$, where different programmes can be used for the two breeds.

D. — *Form synthetic sire or dam breed.*

If we have available other breeds A_2, A_3 etc. which are only slightly poorer than A_1 as sire breeds, these could be crossed with A_1 to form a synthetic and yet retain general heterosis in the cross. Similarly other dam breeds B_2, B_3 could be crossed with B_1 to form a synthetic sire line. These are likely to be more attractive alternatives than making a synthetic from the cross $A_1 \times B_1$. The new synthetic breeds could be useful if they show greater genetic variation thanthe pure breeds, so that after a few years of selection their merit will reach and then surpass that of A_1 or B_1, and could then be substituted in the cross. JAMES (1966) has discussed procedures for selecting animals from among several populations, but only in the context of maximising the present performance of the synthetic.

If there is information available on heritabilities in the breed A_1 and the synthetic $A_{1 \times 2}$, say, it is simple to predict the time needed before it surpasses A_1. However this could be many years in a practical situation. For example, assume that in beef breeds the trait, weight to 400 days, has a standard deviation of 40 kg and that A_1 exceeds $A_{1 \times 2}$ by 10 kg (in breeding value since heterosis within the sire line is not of interest). In an efficient breeding programme with selection only on males and rapid replacement of females an annual response of 16 h^2 kg per year can be made. So if the heritability in the synthetic was, say, 50 % and in the pure breed it was 40 % and both were continuously selected, it would take 10 /(16 $\times$ 0.1) or at least six years for the new breed to catch up. Some years would also be needed to establish and multiply the synthetic and obtain the necessary estimates of genetic parameters.

It is usually difficult or expensive to obtain accurate estimates of heritability, and it is unlikely in many situations that estimates of *differences* in heritability between synthetics and pure breeds could be obtained with sufficient precision that practical decisions could be taken using them. It is possible to make some theoretical predictions of differences in genetic variance, but these too suffer from severe limitations. The simplest situation is where breeds A_1 and A_2, say, are essentially randomly selected but distant by several generations from a common base. Assume there is additive gene action, and the additive variance in the synthetic (or in the foundation population) is σ_G^2. If the populations have been inbred by an amount F, the expected within-population variance is $(1 - F)\sigma_G^2$, and the variance between populations is $2F\sigma_G^2$. In a sample of size two from a normal distribution the first ranking individual is, on average, 0.56 standard deviations superior to the mean of the two. If h^2 is the heritability in the foundation or in the synthetic population, and the phenotypic variance is assumed to be altered, the synthetic will take about $0.56\sqrt{2F}/iFh$ generations to reach the better pure line when both are under continued selection. For example, if F = 0.2, i = 1.0 (averaged over sexes) and h^2 = 0.4, the synthetic is expected to take 2.8 generations to reach the better pure line, or 7 years for our beef cattle example with the 2,5 year generation interval. After that period, assuming

there had been no change in variance through selection or further inbreeding, the synthetic would gradually become increasingly superior.

In other cases predictions of variance in the synthetic are essentially speculative, although one or two useful relationships are known. Let q_1 and q_2 be the frequency of some gene in lines A_1 and A_2, and $\bar{q}$ be the mean frequency. Then

$$\bar{q}(1 - \bar{q}) = \frac{1}{2} q_1(1 - q_1) + \frac{1}{2} q_2(1 - q_2) + \frac{1}{4}(q_1 - q_2)^2$$

so the mean heterozygosity at this locus and variance if the genes act additively is at least as high in the synthetic as in the average of the two parental lines. More generally, JACKSON and JAMES (1970) have shown that, with additive effects, the variance within the synthetic is given by $\frac{1}{2}\sigma^2_B + \sigma^2_W$, where σ^2_B is the genetic variance between populations and σ^2_W the genetic variance within populations, assumed to be the same in each. At loci showing complete dominance the additive variance is higher in the synthetic when the mean frequency of the recessive allele is greater than 0.5, otherwise it is less (LERNER, 1954). But at such loci most additive variance is expressed when the recessive frequency is high, so that averaged over all loci the synthetic will probably have higher variance. If the parent lines and synthetic are selected in closed populations of the same size for a long period of time the selection limit is expected to be higher for the synthetic than for the mean of the two pure lines. This relationship holds for both additive and completely dominant genes at all frequencies but the effects of linkage and epistasis are being ignored. However we are making the basic assumption that the traits under selection are influenced by a large number of loci, so there are only small differences in mean gene frequencies between the alternative populations. If there are wide differences in mean initial frequency the synthetic could have higher initial variance than the best line, yet never catch up with it under continued selection. But this would seem unlikely, especially as one population may have genes segregating which are absent from another. In general however, we lack concrete evidence and have an unsound basis for making practical decisions.

In the Institute of Animal Genetics in Edinburgh a relevant experiment with *Drosophila melanogaster* has been started by LOPEZ-FANJUL. Response to selection for sternopleural bristle number is being measured in two populations (Kaduna and Pacific) from different locations which have been maintained in cages in the laboratory for many years, and in synthetics formed from crosses between them. The initial performance of the two populations is almost exactly the same, but Pacific shows rather higher genetic variance and has responded somewhat more rapidly to selection. The cross shows no significant heterosis. With selection started from the F1 generation the synthetic has advanced at a rate intermediate between that of the parent lines. After allowing six generations of random mating without selection after the cross the heritability was estimated in another sample of the synthetic. Although a higher heritability value was obtained from the offspring-parent regression at this time, the subsequent selec-

tion response was no faster than in the parent lines. This result is rather hard to interpret, for one would expect an increase in genetic variance in F2 and later generations if there was negative linkage disequilibrium between the populations making the cross, but this should be accompanied by greater subsequent response. These results are as yet preliminary and the experiments are small. Nevertheless it is clear that the synthetic has little or no more additive genetic variance than the parent lines, which suggests that essentially the same loci are segregating in the two populations. More definitive conclusions will be possible when selection limits are reached. Unlike our domestic species these populations have no history of selection, so we should be cautious about making inferences from the *Drosophila* work.

E. — *Maintain alternative sire or dam lines.*

In addition to selecting in our chosen breeds A_1 and B_1, selection could be continued alongside in other populations, although their merit may be less at present. Of course the synthetic could be one of these. If rather different criteria were chosen for selection in these populations the programme would be much more flexible in that alternative breeds could be substituted as market demand and economic conditions change. The main disadvantage of this kind of scheme is that these potential substitute breeds have to be selected at almost the same rate as the ones already used, or they will gradually lag behind for the major traits and can never be utilised. Thus the breeding programme becomes much larger and more expensive. The same requirement has to be met for any breed which may be crossed into A_1 or B_1 in future years because it has some particularly valuable feature. Unless these breeds have performance near that of A_1 or B_1 the new synthetic A or B will be inferior. However there could be benefits from forming new synthetics if reproductive performance in A_1 or B_1 had deteriorated with inbreeding.

If our objective is to maximise gain over a long period of time, yet our facilities for maintaining animals under selection are limited, we have two distinct options. A synthetic can be formed immediately and selected as a single population. Alternatively the separate populations can be maintained as smaller populations, and each selected for a period before crossing and reselecting as a single larger population. ROBERTSON (1960) and MARUYAMA (1970) have shown that the same limit is obtained in either case. However the average rate of response will be higher if the synthetic is made initially since the subpopulations will become inbred more rapidly. But in the short term, in generations at least, our best strategy is probably to select in the highest ranking available breed or population.

ECONOMIC ASPECTS

Attempts have been made recently to evaluate breeding programmes in monetary terms using, in effect, the discounted cash flow procedure commonly employed in management accounting. The principles of the technique were first used in a genetic context by POUTOUS and VISSAC (1962) and subsequently by SOLLER, BAR-ANAN and PASTERNAK (1966). I shall give these in outline, and discuss their implications on alternative breed and cross bred improvement programmes.

Returns and costs incurred in any year are discounted back to some base, perhaps the year at which a decision is made to build a new testing station, or perhaps merely to the year at which a selection decision is made. For example, with an interest rate of 8 %, £ 100 invested now would realise £ 108 next year, £ 100 × (1.08)² the following year and so on. Thus £ 108 earned next year is equivalent to having only £ 100 now, or £ 1 obtained next year is worth £ 1/1.08 = £ 0.926 now, and £ 1 earned 5, 10 or 20 years later is equivalent to £ 0.68, £ 0.46 and £ 0.21 earned now. With such an approach we can compute the aggregate benefits of selection response which are both permanent (at least in terms of changes in the traits) and cumulative. We can calculate either an overall ,, profit '' or the investment yield, which is the interest rate at which the scheme would just break even. Widely different programmes can be compared, or the returns from minor changes in selection procedure, involving relatively small extra expenditure, can be evaluated. Of course many simplifying assumptions need to be made, and it is difficult or impossible to take account of unforeseen changes in economic conditions. Such risks can be hedged to some extent by adopting discount rates considerably in excess of current interest rates. For example an estimated yield of 20 % evaluated over a period of only 15 years might be considered necessary before undertaking a programme. Especially when high discount rates are used the returns made in early years are weighted very heavily; it is this property of the procedure which has most relevance to our discussion of crossbreeding, for with large animals any programmes undertaken are likely to be of a long-term nature.

Consider the merit of maintaining synthetics or other substitute breeds of lower initial performance, but with the hope that they will eventually surpass the present superior population. No returns are obtained from this synthetic until the nucleus herd has reached the level of that of the superior breed, itself under selection, and until the population has been multiplied and progeny marketed. We considered earlier an example with beef cattle where the synthetic would require 6 years to catch up. We have to add to this, say, 2 years for bulls to mature and have progeny by A.I. and another 2 years before progeny are slaughtered, making a total of 10 years in all. At 10 years the discount factor is 0.46 if the rate is 8 %, and 0.16 if it is 20 %. Further, the extra returns after this period come only from the *increased* gain of the synthetic over the original breed, although only one selected population, the synthetic, now has to be maintained.

Using the same arguments it becomes difficult to justify maintaining several pure breeds or strains as potential substitutes. These must be selected at rates near those of the current commercial populations if they are ever likely to be competitive, whether or not the objectives in the schemes are exactly the same. The costs of maintaining and selecting these populations will inevitably be considerable. Our rather simplified arguments lead us, therefore, to the conclusion that almost all our attention should be devoted to improving the breeds or crosses which are currently best. However a breeding organisation or country committing itself to such a scheme is vulnerable to a change in consumer demand or an exhaustion of genetic variance. But no scheme runs entirely in isolation, for there are competitors or other countries running similar programmes. These offer the best potential source of new variation!

LIMITATIONS

In conclusion a few comments should be made about the limitations of the analysis. In the first place it has been idealistic, and has by-passed many practical difficulties and limitations imposed by existing breeding systems, and by breeders' and farmers' prejudices. For example there may be resistance to use of what is clearly the best breed, or there may be legislation, as in Britain, to prevent the use of crossbred bulls. Even within the theoretical framework many simplifying assumptions have been made. In particular, interactions have been ignored both at the genetic level, between loci, and at the applied level, between environments. Nor has any general solution been given, but this is not possible with our current state of knowledge. There is clearly considerable need for greater understanding of the genetics of the major quantitative traits in our domestic species.

RÉSUMÉ

ASPECTS THÉORIQUES DU CROISEMENT

Une discussion des méthodes d'utilisation des races de bovins et ses croisements, tenant compte des aspects génétiques et économiques, est présentée. L'essentiel de la théorie des comparaisons entre les races et leurs croisements est analysé mais, surtout, on a développé l'amélioration des croisements actuels.

Sans doute, une « population synthétique » aura plus de variabilité génétique et les limites de la sélection seront portées plus loin que celles des races qui la composent. Cependant, il s'écoulera souvent plusieurs années avant que cette « population synthétique » ne surpasse la meilleure race sous sélection continue. Pour cette raison les résultats économiques d'un tel procédé restent douteux.

En dépit de la marge de manœuvre que l'on a, en conservant plusieurs races, il faut les sélectionner continuellement si on veut qu'elles restent compétitives. Ainsi on peut attendre de meilleurs résultats par une sélection plus intensive des meilleures races existantes. Théoriquement, des schémas de sélection, basés sur les croisements, comme la sélection récurrente réciproque, ne permettent guère de faire progresser la sélection des gros animaux où les qualités de croissance et de carcasse sont importantes.

REFERENCES

DICKERSON G. E., 1969. Experimental approaches in utilising breed resources. *Anim. Breed. Abstr.*, **37**, 191-202.

FEWSON F., JAKUBEC V., 1971. Gewinnfunktionen-ein Hilfsmittel für die Planung von Gebrauchskreuzungen beim Schwein. *Ann. Génét. Sél. Anim.*, **3**, 000.

HILL W. G., 1970. Theory of limits to selection with line-crossing. In Kojima, K., *Mathematical topics in population genetics*, 210-245. Springer, Heidelburg.

JACKSON N., JAMES J. W. Comparison of three Australian Merino strains for wool and body weight. II. Estimates of between stud parameters. *Aust. J. Agric. Res.* (in press).

JAMES J. W., 1966. Selection from one or several populations. *Aust. J. Agric. Res.*, **17**, 583-589.

LERNER M., 1954. *Genetic homeostasis*. Oliver and Boyd, Edinburgh.

MARUYAMA T., 1970. On the fixation probability of mutant genes in a subdivided population. *Genet. Res.*, **15**, 221-225.

MOAV R., 1966. Specialised sire and dam lines. *Anim. Prod.*, **8**, 193-202, 203-211, 365-374.

MOAV R., HILL W. G., 1966. Specialised sire and dam lines. IV. Selections within lines. *Anim. Prod.*, **8**, 375-390.

POUTOUS M., VISSAC B., 1962. Recherche théorique des conditions de rentabilité maximum de l'épreuve de descendance des taureaux d'insémination artificielle. *Ann. Zootech.*, **11**, 233-256.

ROBERTSON A., 1960. A theory of limits in artificial selection. *Proc. Roy. Soc. Lond.*, B, **153**, 234-249.

SMITH C., 1964. The use of specialised sire and dam lines in selection for meat production. *Anim. Prod.*, **6**, 337-344.

SOLLER M., BAR-ANAN R., PASTERNAK M., 1966. Selection of dairy cattle for growth and milk production. *Anim. Prod.*, **8**, 109-120.