Graziers are all aware of genotype-environment interactions but may not know them as such. It is evident from the distribution of sheep in Australia that there is a segregation of certain types of sheep according to climate, pastures, proximity to market and other factors that make up the environment. Obviously, certain types of sheep are better suited to particular areas, and it is not possible to make a general statement that a particular breed, strain or line of sheep is the most profitable in all parts of the continent.

The greater the difference in genotypes and/or environment, the more likely it is that GxE will be important. Evolution has resulted in a diversity of genotypes that have developed as a result of 'survival of the fittest' in different environments. Different environments require different components of fitness, and desirable attributes in one environment are not necessarily an advantage in other environments, particularly when the environments are markedly different. This paper will briefly discuss the available evidence for GxE in sheep relevant to Australian conditions and the likely implications. Discussion will be restricted to situations where environmental differences are large and measurable.

**Breed x environment**

There is ample evidence that when two environments differ widely, breed rankings can change. However, when environments are less diverse, the relative performance of breeds should be more predictable. Daly and Carter (1955) studied Lincoln, Corriedale, Polworth and finewool Merinos at two nutritional levels and concluded that with few exceptions, the relative positions of the breeds for the characters measured were generally maintained as intakes were reduced; although the body weight of Merinos tended to be more sensitive to changes in nutritional level than that of other breeds.

For disease incidence, breed x E can often be important. With a moderate challenge from the foot-rot bacteria, Emery et al. (1984) found that British breeds were more resistant than Merinos to the development of severe symptoms. However, with more severe challenges, all breeds were equally susceptible. Similar interactions could be expected with other diseases, such as flystrike.
Evaluations of dam breeds for prime lamb production in Australia have been remarkably consistent in the conclusion that Border Leicester-Merino cross ewes are the most profitable. However, when out-of-season lambs are required, or when the breeding programme is accelerated, Dorset-based crosses can be more productive (Woolaston 1975). High fecundity breeds and strains are also being developed, based largely on the Booroola. It is likely that the full benefits of these genotypes will only be realised in favorable conditions, as handicaps due to multiple births are less pronounced in favorable conditions, both in terms of survival and growth rates. Woolaston (1975) and Cotterill (1976) were unable to detect any important sire breed x nutrition (pens versus pasture and between-season) effects on growth or carcase characteristics of lambs sired by Suffolk, Poll Dorset and Lincoln rams. For carcase composition and conformation, breed x E has not been shown to be important when comparisons are made at an equal stage of maturity. The choice of dam breed for prime lamb production then, will depend very much on the circumstances under which the sheep will be run, whereas the preferred sire breed will be governed more by overall breed performance (bearing in mind likely heterosis), and the type of lamb required by the market.

The economic environment can influence the choice of sheep via cost differentials, even though GxE may be unimportant with respect to quantitative traits. For example, prime lambs are produced mainly in areas close to large markets, where transport is less of a problem. Another example is that price penalties for faults in wool (eg. vegetable fault) tend to more severe for finer wools, and this can contribute to the geographical distribution of Merino strains. Some producers capitalise on this interaction by housing fine-wool sheep and receiving a premium for their product.

Heterosis-environment interaction can be considered as a form of breed x E, and this subject has been extensively reviewed by Barlow (1981). His conclusion was that interaction is "the expectation rather than the exception". That is, the degree of heterosis expressed in a particular cross is largely a function of the environment.

Strain x Environment

The distribution of the Merino in Australia is such that strong wool types are found predominately in the pastoral areas and superfine strains are mainly found in high rainfall areas. In the more arid regions where sheep need to walk long distances for food and water, large-framed sheep with longer legs are considered by graziers to be most suitable. Such sheep are associated with stronger wool which resists dust penetration. In wetter regions where fleece-rot is more of a problem, finer woolled sheep are better suited. Moule (1946) also cited work by his colleagues that lends some support to the notion that fine-wool sheep require better quality feed for maintenance.

The most striking experimental evidence for the existence of strain x E is in the differential susceptibility to fleece rot by Merino strains (Dunlop and Hayman 1957). This can also be reflected in strain x year interaction for fly-strike incidence (Atkins et al. 1980). Although there is no difference between strains in fleece rot incidence in dry climates (and dry years), distinct differences become apparent under conditions of high rainfall. Here strong-wool strains appear to be the
most susceptible, and fine non-Peppin the least susceptible. In WA, where dermatophilosis is the main predisposing factor for fly-strike, studies have shown that the relationship between the incidence of this disease and fibre diameter is less clear. Merino strains also differ in their ability to produce wool and these differences increase with plane of nutrition (Dunlop 1962). However, the efficiency of conversion of feed to wool doesn't appear to be affected by strain x nutrition interaction (Saville and Robards 1972).

The classic strain x location study in Australia was made by Dunlop (1962, 1963) who studied five strains of Merino run together at Cunnamulla, Armidale and Deniliquin. Dunlop was able to measure the degree of adaptation (GxE) in both the foundation ewes and station-born ewe progeny, for a variety of traits. Real interactions were found for most of the traits, but except for fleece rot incidence, interactions were generally small and accounted for only a small part of the variation. Most of the variation could be explained by the main effects of strain and location. Of all the quantitative traits studied by Dunlop, clean fleece weight was the most consistently affected by GxE. In general, this was a consequence of scale effects, where differences between strains tended to be accentuated when the general levels of production were high. There are specific comparisons within Dunlop's data, however, that suggest that care should be taken when extrapolating from main effects. For example, the clean wool production of the fine wool strain at Deniliquin was 0.9 kg less than would be expected from a knowledge of fine-wool versus strong-wool differences at Armidale, and the overall differences in wool cut between Deniliquin and Armidale. When translated into dollars to the producer, this represents a considerable financial error (around five dollars per head at current prices). In this instance, some compensation would be made by the fact that fibre diameter interactions were in the same direction. Nevertheless, it does illustrate the need to replicate strain comparisons in several environments.

Although de Haas and Dunlop (1969) did not detect important GxE effects on the components of fertility, there is some evidence that the genotype of Merinos can adapt when the environment imposes constraints on reproduction. In WA, progeny of ewes with a successful reproductive history whilst grazing oestrogenic pastures were compared with random contemporaries whose dams had grazed non-oestrogenic pastures in sub-clover evaluation trials (K. Croker, unpublished). On oat pastures, there was little difference between the two groups in percentage of ewes lambing, but on oestrogenic pastures the "resistant" flock was much less affected. Dun et al. (1966) reported an interaction between strain and season of joining which they attributed to a long history of spring joining in the South Australian Merino parent flock. With autumn joining, Peppin ewes had higher fertility and fecundity than South Australian Merinos, whereas the ranking was reversed with spring joining. There is also a suggestion in the data of Robinson et al. (1970) that Merinos may adapt over a period of time to spring joining; although in this instance, it is not certain whether the adaptation was due to genetic or early environmental effects. (On this point, it is worth mentioning that Dunlop (1962) also suspected early environmental effects as a cause of the lower degree of GxE in ewes born on the test station than in imported foundation ewes. If this effect is real, GxE studies involving a confounding of genotype and early environment must be interpreted with a certain amount of caution.)
Effect of GxE on selection for wool production

One of the features of long-term selection experiments with Merinos is that differences in wool production between selected and control flocks appear to be related to the level of performance of the control flocks. This GxE led to early speculation that response in the Trangie and CSIRO selection flocks had plateaued after two generations of selection, whereas analysis of experiments over a longer period indicates that response is continuing (McGuirk 1983).

In studies of flocks selected for high and low fleece weights, made at various levels of nutrition, significant flock x nutrition interactions effects have been demonstrated for wool growth and efficiency of conversion, both in pens (Williams 1966) and at pasture (Hamilton and Langlands 1969). In the studies of Saville and Robards (1972), the efficiency of selected sheep relative to unselected sheep increased with increasing intake, then decreased again at high intakes. This GxE did not result in a change in ranking of selected and unselected flocks, merely a change in the magnitude of their difference. At very low intakes however, when body weights are declining, the rankings may change (Piper and Dolling 1969). The availability of sulphur-containing amino acids appears to be limiting the production of sheep selected for increased fleece weight, and nutritional management may have to be modified to remove this limitation (see McGuirk 1983).

Genotype x age interactions have not received much attention, but there is evidence that the genetic correlation between yearling and later fleece weights is significantly less than unity in some breeds (Eikje 1975, Lever et al. 1979). If similar interaction is found to occur in Australian Merinos then optimal selection procedures for improving lifetime production may need to be reviewed.

Sire x environment

The question of sire x E is potentially one of the most important in Merino breeding but about which least is known. Stud breeders frequently select sires based on performance under favorable conditions while their progeny are expected to perform under commercial conditions. The efficiency of this practice is determined by the heritability of the trait in the two environments and the degree to which the same genes are involved in both environments.

It is often the case that the variance of a trait increases as the mean level of performance increases. It would therefore seem logical that genetic differences will be magnified under more favorable conditions. However, experimental evidence shows that genes required for maximum performance in favorable environments are not necessarily the same as those required in less favorable environments, and this could diminish or even negate any increase in heritability that may arise through selection in the better conditions.

By exposing groups of half-sibs to two different nutritional treatments, Morley (1956) was able to examine sire x nutrition effects on a range of fleece and body characters. Interactions were not found to be important for any fleece characteristics or early body weight. However, body weights at 12 and 17 months were affected by large and highly
significant interactions. It appeared as if the heritability was the same in both treatments, so in this instance it would be more efficient to select for hogget body weight under the nutritional level at which the genotypes are expected to perform. This finding was supported by Chopra (1978) who examined sire x stocking rate interactions in the New Zealand Romney. Interactions for fleece characteristics tended to be small and unimportant, but for hogget live weight the interaction was large and highly significant. His estimate of the intra-trait genetic correlation was significantly less than one ($r_C = 0.58 \pm 0.20$), indicating that different genes are involved at each stocking rate. Expected gains under direct selection at the target stocking rate were calculated to be 13-28 per cent. higher than under indirect selection at the alternate stocking rate.

Dunlop and Young (1966) estimated the effect of sire x E on clean wool weight in data generated by Dunlop's (1962) strain x location study. These workers concluded that sire x location interactions were at times of sufficient magnitude to hinder selection, although on average, the expected gains would be reduced by about five per cent, by selecting at a different location. The data sets of Dunlop and Young (1966) were much smaller the minimum size suggested by Robertson (1959) and it can be shown that even if sire x location interactions were quite large and of biological significance, one would not expect the analyses of Dunlop and Young to be effective in detecting them. By comparison, Morley (1956) was able to overcome the problem of insufficient numbers to a degree by deliberately increasing the between-sire variance. It would therefore seem that the question of sire x location and sire x year interactions on wool production under Australian conditions remains somewhat open.

Effect of sire x environment interaction on the Merino Industry

Most of the published estimates of heritability obtained by the paternal half-sib method are based on sire effects nested within years. In the presence of sire x year interaction, this would have the effect of inflating heritability estimates, and response to selection will be less than expected.

If sire x E is important, it is likely to become evident over a period of time in sire-referencing schemes. Two approaches will be possible. Firstly, test flocks could be categorised according to specified environmental criteria, and superior sires selected for each category. A more efficient alternative would be to use the technique developed by James (1961), where the performance of progeny in each environment is entered into an index for overall gain. This method can produce greater overall gain than separate selection, but it relies on accurate estimates of genetic parameters and has the problem that home sires are only tested in one environment.

In the hierarchical structure of the Merino stud industry, the flow of genes is essentially in one direction only, from parent stud to daughter and general studs and then to commercial flocks. If sire x E is important, then genetic gains realised at the commercial level will be less than they could be, unless stud breeders are able to identify and select for all of the characteristics that are desirable under commercial conditions. It is probably fair to say that there is a certain level of belief in the industry that some stud masters do possess such skills,
evidenced by the relatively large number of sires that cross State and climatic boundaries every year.

In nucleus breeding systems where there is a two-way flow of genes, the impact of sire x E will depend upon the magnitude of environmental differences between flocks on the various levels. When there is considerable variation in the plane of nutrition under which flocks in the system are run, and when hogget live weight is the main selection criterion, GxE will probably negate any advantage that may accrue by having a two-way flow of genes. When wool production is the main selection criterion, as is usually the case, GxE should be less of a problem. When environmental differences encompass more than just plane of nutrition effects, the importance of GxE is less certain and conclusions must await further evidence.

REFERENCES