SYMPOSIUM ON 'RECENT DEVELOPMENTS IN STATISTICAL GENETICS IN RELATION TO PLANT AND ANIMAL BREEDING'

A syposium on "Recent developments in Statistical Genetics in relation to Plant and Animal Breeding" was held during the 28th Annual Conference of the Indian Society of Agricultural Statistics at Haryana Agricultural University, Hissar, on January 1, 1975 under the Chairmanship of Dr. S. N. Kakar, Dean, College of Basic Sciences and Humanities, Haryana Agricultural University, Hissar. The convener for this syposium was Dr. Prem Narain, Senior Statistician, Institute of Agricultural Research Statistics, New Delhi. Eight papers were contributed to the symposium out of which only seven were actually presented. Relevant extracts from the papers read at symposium are given in the following paragraphs.

*Prem Narain**

On the theory of limits to artificial selection and average time taken to attain them

2. In any selection programme two kinds of forces affect the gene frequency. One of them is random sampling of gametes which introduces a random change from generation to generation in the frequency q of any gene. The average change is then zero and its variance is $q(1-q)/2N$ where N is the effective population size. The other is the steady change in gene frequency due to artificial selection which can be expressed as $sf(q)$ where s depends upon the relative selective advantages of the three genotypes at that locus and $f(q)$ is the function of the gene frequency depending on the type of gene action involved. The expected total change in gene frequency at the limit can then be expressed as $u(q)-q$ where $u(q)$ is the probability of fixation of the gene. This can be interpreted as the proportion of equivalent loci which would be expected to be fixed in any line or alternatively as the proportion of replicate selected lines in which an individual gene would be expected to be fixed. Converting the results in terms of the change in the character, it is found that the limits expressed in units of genetic standard deviation (L/σ_g) is a function of Nih (where h is the square-root of the heritability of

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character and i is the intensity of selection) and q, the initial frequency of the desirable allele assumed equal at all loci.

3. Considering a set of loci at a single chromosome with identical effects on the character and identical initial allele frequencies, it is found that the selection process can be adequately specified by 4 parameter combinations Nih, Nl, n and q where n is the number of loci and l is the length of the chromosome in cross-over units. It is further found that as n is increased, a limiting situation is reached in which the process is described by only 2 parameter combinations Nih and Nl. The effect of linkage on the limits is determined on the basis of a ratio between the limits expected with no crossing over (L_o) and the limits with free re-combinations (L_f). In the absence of crossing over, it is assumed that as n increases the initial distribution of chromosomal effects would be approximately normal. This would require initial frequencies of alleles not to be very much at extreme values. Under these conditions, (L_o/σ_g) is a function only of Nih. For small values of Nih, the slope of the standardised advance is 2 but as Nih increases, the standardised advance approaches a limit in the neighbourhood of 3. With independent segregation, it is known, from single locus theory that (L_f/σ_g) is a function of Nih, q and n with an initial slope of 2. The ratio (L_o/L_f) is then a function of Nih, n and q only. When Nih is less than 0.5, this ratio is near 1 and the linkage has little effect on the advance. As n increases, the ratio approaches a limiting value depending only on Nih and not on either n or q.

4. Assuming that the loci are evenly scattered along the chromosome, the amount of crossing over is expressed in terms of l, the chromosome length. In such a case, the effect of increasing the amount of recombination on the selection limit, expressed in terms of this limit with no crossing over (L/L_o) is found to be proportional to Nl only when Nl is small. The coefficient of proportionality is found to be almost independent of Nih and of the order of 1/3. With an equal spacing of loci along the chromosome, it is found that the selection limit could be expressed in terms of L_o, L_f and Nl only.

5. The duration of response to artificial selection in a finite population is expressed in terms of the probability distribution of time to fixation of a particular allele, disregarding the cases in which it is lost. In particular, one can talk of the average time taken for the attainment of limits to genetic improvement. The distribution of time until fixation of a gene is clearly distinct from the distribution of time until homozygosity i.e. either fixation or loss of the gene.

It is only when the chance of fixation of a gene is very near to 1 that the distribution of time until homozygosity approaches to that of time until fixation. With initial frequency q, this mean time is $\dfrac{-4N(1-q)}{q} \log_e (1-q)$. It tends to $4N$ when the initial gene frequency tends to zero. For higher values of Ns, transition matrix approach is used and results are obtained with the help of the computer. It is found that the average time until the limits are attained is a function of Ns and q. The mean time decreases as Ns increases in so far as an additive or recessive gene is concerned. But for a dominant gene, the mean time increases initially for small values of Ns and then decreases thereafter.

6. With several loci segregating independently and with no selection, if it is assumed that there are n loci each with two alleles and with identical effects as well as initial allele frequencies, then the average time taken for the fixation of a gamete having all the desirable alleles is found to be the same as that with single locus. With no crossing-over at all, the many-locus two allele situation is equivalent to a single locus with several alleles with the distribution of allelic effects approaching normality as the number of loci increases indefinitely. In such a case with no selection, the mean time until fixation of a given gamete is the same, as that for twoallele system. The effect of linkage on the mean time until fixation can, therefore, be described on the basis of a ratio between the mean time with no crossing over (M_o) and the mean time with free-recombination (M_f). In the absence of selection, the ratio (M_o/M_f) tends to unity. This result also holds true for small values of Nih. Linkage has therefore little effect on the mean time until fixation for small selective forces and identical effects as well as initial allele frequencies.

*V. Arunachalam**

The role of recent developments in Biometrical Genetics in practical Plant Breeding

7. The paper was presented by Dr. Prem Narain as desired by the author who could not attend the symposium due to unavoidable reasons.

8. Diallel mating is one of the popular systems of hybridisation. A slightly varied form is that of line x tester mating (LT), wherein a number of females are mated each to a number of males. The design LT makes it possible to estimate the covariance of full

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and of half sibs and hence the variances of general and specific combining ability. The presence of high g. c. a. variance coupled with a non-significant s.c.a. variance, for example, would indicate the possibility of selection for high yielding derivatives in the hybrid population. Then with the testing of the g.c.a. effects of the parents, one can choose parents for effecting prospective hybrid combinations to obtain productive derivatives. Defining in a similar way, the covariances of g.c.a. and s.c.a. between pairs of characters, one can estimate the matrix of g.c.a. and s.c.a. effects. An inspection of this matrix could throw light on the feasibility of selecting parents in order to effect simultaneous improvement for more than one character in their hybrid populations.

9. T) a limited extent, breeders use three-way and four-way crosses in their programmes. But if an experiment is conducted with single crosses as parents, say, as females and a line x tester mating system is adopted with improved varieties or productive single crosses as males, then one would have an opportunity to assess the productivity of three-way or doublecross hybrids from the angle of combining ability; in other words, one can assess the productivity of the double cross hybrid in terms of the combining ability effects of parents and grandparents. A comparison of different double crosses produced by a known mating system like LT should enable one to find ways of channelising the specific combining ability of single crosses into their double cross hybrids. Thus a breeder, in addition to formulating a hybrid release programme when the single cross hybrid is much superior to the parents, can now utilise such hydrids in higher hybrid combinations (multiple crosses) and look for getting variety derivatives from their progeny. For example, in double crosses in *triticale*, significant g.c.a. effects were noted for the grandparents for yield. The g.c.a. effects of the single cross parents, though not significant, were opposite in direction for yield. This High x Low cross revealed more heterosis for yield. In a similar way, the reasons for the presence or absence of heterosis in multiple crosses can be inferred once these crosses were the result of a proper mating system permitting inferences not only on the hybrid but on the parents as well as the grandparents.

10. Heritability and genetic correlation of quantitative traits cannot always be of use in practical plant breeding, since they are highly susceptible to environmental fluctuations. However, the inter-correlations should be assessed and utilised if one wishes to build a prediction criterion for yield. Such a problem presented itself in jute where the breeder would desire to use characters that

could easily be measured (before the small pod stage) and predict the fibre yield. Based on this, the breeder would decide to leave the plant for seed if the predicted yield was high; otherwise, he would chop the plant at small pod stage for extracting its fibre. Similar problems do exist in plantation crops where a decision to allow the growth of the crop has to be made at an intermediate stage on the basis of predicted yield. It would be uneconomical to grow all the coconut trees in an experimental farm for example, for many years in order to assess their final yield potential. On the other hand, prediction of yield with fair accuracy at an early stage, would enable one to retain only the productive populations at the cost of the sub-optimum ones.

11. In jute, a multiple regression analysis of about 20 important characters related to fibre yield revealed that plant height, base and middle diameters and fibre weights at these positions of a 5 sq. cm. sample bark, were adequate to predict the fibre yield. Using a hollow cone to describe the bark of a jute plant as a first approximation, the yields were derived using these characters. This yield formed the dependent variable y and the five characters mentioned above the independent variables x. A multiple regression was fitted using the measurements of the x's on the plants of the experimental population. This equation was utilised to predict the value of y, the fibre yield. The method thus allowed for the utilisation of the actual correlations between the characters important for prediction of fibre yield, in computing the predicted fibre yield. The predicted yield based on such a multiple regression was found to be superior to the geometric formulation of fibre yield. This technique would be a potent tool for selecting jute plants of populations based on a close estimate of their fibre yield.

*R. K. Singh**

New developments in the simultaneous selection theory with special reference to the control on individual trait means

12. Before a genotype is released and attains the status of a variety or a breed, it has to be made perfect in many ways. The breeder has to see that the genotype in question is suitably modelled to respond to the new agronomic practices and thus leading to high yield, to adopt well to the changing environmental conditions and thus providing stability in yield, to resist against the various diseases and pests, and also to meet the modern consumers demand in respect

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of quality matters and so on. Obviously, selection on several traits simultaneously should get more emphasis than selection on single-trait basis. While aiming to select on two or more characters simultaneously the breeder is, however, confronted with a number of additional problems which are otherwise non-existent in case of single-trait selection. For instance, the nature and degree of inter-relationship among the various characters needs to be given due importance in the selection model. Similarly, the relative importance, both genetic and economic, of these characters is another aspect which needs due consideration in simultaneons selection. The genetic significance of a character means its responsiveness towards selection which in turn depends on its heritability and its genetic association with other traits. The knowledge of functional relation-ship between various traits is equally important while constructing the selection model. Sometimes, the information available on its relatives may be used for constructing selection model. Similarly, in certain cases stage-wise information are available and therefore some indirect selection model is required to be constructed and so on.

13. Some of the important unsolved problems associated with the construction and application of selection indices are (i) the validity of selection indices due to lack of availability of precise and stable genetic and phenotypic parameters, (ii) the lack of generality of selection indices due to the very specific nature of genetic parameters which are the basis of selection index construction, (iii) the lack of objectivity in assigning the economic weights to the traits and their changing concept, (iv) tl e lack of control on the individual trait means during simultaneous selection. Only the fourth point would be discussed in detail here.

14. An index constructed in the usual manner is likely to bring about maximum aggregate genetic gain. But while doing so, the genetic means of individual characters included in the index construction are likely to move either in positive or negative direction. The extent of change will, however, depend upon the heritability of the character, the economic weight assigned to it and the magnitude and nature of genetic correlation with other traits. The breeder has thus no control on the changes occurring in the individual trait means and he has to be satisfied with whatever 'plant type' this index has chosen for him. Obviously no breeder would agree with this kind of selection procedure. On the contrary, he would like to have full control on his material and hence any change in the genetic mean of a character should be, if possible, according to his desire. Different

workers have attempted to solve this problem differently. Some considered the problem of complete restriction on some of the characters. There are, however, many situations where complete restriction is not required. The breeder rather wishes to change some of his characters up to certain optimum levels. Negative responses by certain characters during index selection has often been observed. In cases where traits are negatively correlated and have low heritabilities this is expected also. In such a case an index to improve one trait while putting restriction that changes in other traits be non-negative is constructed.

15. A solution to these several problems can be given by putting restrictions into one computational scheme, so that one computer programme is required to be written to handle all these problems. Such a solution is, however, valid only under certain assumptions. Besides, while putting restrictions simultaneously on an index weighing factors and solving for them, equations carrying restrictions are eliminated. There may however be certain advantages in retaining the equations of restrictions explicitly in the system. The method for achieving this is to augment the basic unrestricted equation by adding dummy variable to the index. In this way absolute restriction on a given trait is assured. If one wants to put partial restrictions, this can also be done in a similar way. If several simultaneous restrictions are required, they can be incorporated merely by augmenting the equations by a further dummy variable for each restriction.

16. Another way to control the individual trait means is simply by manipulating the economic coefficient vector during simultaneous selection. By Monte Carlo studies we investigated the effect of various combinations of arbitrarily selected economic weights on the genetic means of individual traits. We could notice that depression of genetic gain due to low heritability of a character and due to its negative association with other characters could be avoided by assigning higher economic weights to that character. We could further demonstrate that a balanced improvement in all the characters simultaneously selected could be achieved by choosing the appropriate combination of economic weights. A loss in the overall genetic gain was, however, observed with these restrictions.

*C. L. Arora, R. M. Acharya and S. C. Agarwal**
Immunogenetic distance as a measure of genetic divergence among populations

17. Taking cryptic polymorphic loci for haemoglobin and potassium types together, use of modified 'f' statistics based on the

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angular transformation, that could be used for di-allelic and multi-allelic loci to calculate an average value estimating the Wahlund's variance between two populations, to find out genetic similarity/ dissimilarity among different populations/breeds of Indian sheep was tried.

18. Wherever information on performance characteristics (polygenic) viz. body weights at different ages, wool yield and quality was available, testing similarity/dissimilarity was also made by the method of simple mean comparisons. It was observed according to mean comparison that Chokla and Nali form one group and Malpura and Sonadi form another group whereas on the basis of genogroup divergence Nali was more closer to Malpura and Sonadi along with Lochi and was quite distant from Chokla. Similar separation among these breeds could also be made from mean comparisons of performance traits. Marwari and Pugal were distinct populations whereas Chokla and Magra could be grouped together. Jaisalmeri was also observed to be more closer to Malpura and Sonadi group.

19. Results from the present study reveal that testing divergence among populations based on data on performance traits through simple mean comparisons is not appropriate as these traits (polygenic) are affected by a large number of tangible and non-tangible non-genetic factors. Divergence testing on the basis of immunogenetic phenogroups may be a more appropriate criterion for distinguishing groups on genetic basis.

*K.N. Ponnuswamy**

On certain recent developments in analysis of mating designs and on the construction of experimental designs useful for breeding experiments

20. On every relevant question which every practical breeder has to face before starting the experiment is to decide about the number of replications. Since, usually in breeding experiments, a large number of crosses are involved, it may be sufficient to have two or three replications only. Certain computer simulation experiments show that, for the estimation of heritability, it is inefficient to increase the number of replicates beyond two in the case of diallel cross, partial diallel cross and North Carolina designs I and II.

21. Another important question which arises in this context is which one of the numerous mating designs to use and how many

crosses should be made per parent, if the objective is to estimate one or more of the genetic parameters. In the case of North Carolina design I, the variance of the estimate of genetic components decreases with increasing sample size, but only slowly as the number of females per male increases beyond four. For estimation of the genetic parameters obtainable from diallel cross, half-diallel cross and North Carolina designs I and II, half diallel cross is the most useful design, followed by the two North Carolina designs. If epistatic effeets are present then an inflated estimate of dominance variance will result from North Carolina designs I and II, while a test for the presence of non-allelic interactions is possible for the data from a complete diallel. Partial diallel is found to be no better than North Carolina designs I and II in this regard.

22. Using the computer simulation technique, a comparison of the efficiencies of diallel, partial diallel and North Carolina designs I and II for the estimation of individual and family heritabilities shows that in the absence of epistasis, the partial diallel is the most efficient one followed in decreasing order of preference by North Carolina design II, the complete diallel and North Carolina design I. However, if the epistatic effects cannot be ignored then complete diallel is the best of the four designs considered.

23. For illustrating the role of epistasis in breeding experiments, cyclic single cross selection could be compared with reciprocal recurrent selection through computer simulation techniques. Considering three-epistatic and three non-epistatic models with 60 loci governing a single character, it was observed that the rate of advance over seven cycles was always greater for the former than for the latter on either a cycle or a generation basis. The advantages of the former breeding technique increases as the proportion of non-additive genetic variance increases. It is suggested that this technique should begin with divergent genetic populations and continue for three cycles with strong intensity of selection. Then final selection of superior single crosses would result when the lines are completely inbred.

24. The diallel analysis provides biased estimates for additive and dominance variances, in the presence of epistasis. Attempts should therefore be made to estimate not only the additive and dominance variances but also the epistatic components. Even though the double cross and three-way cross hybrids are in commercial production since 1930's, no attempt was made to evaluate the triallel, double cross and other higher order mating designs for the purpose of estimation of genetic parameters till early 1960's. Later

on, attempts were made for analysing complete and partial triallel crosses. These analyses show that triallel and double cross mating designs can be profitably used to provide unbiased estimates for additive, dominance, additive × additive, additive × dominance, dominance × dominance genetic variances in the absence of higher order epistasis.

25. Incomplete block designs useful lor laying out the diallel and triallel experiments in field were also studied. These incomplete block designs provide efficient estimates for the parameters of interest for the breeders. The constructions of these designs are very simple and can be easily understood by a practical worker.

Daya Singh Balaine, K. C. Abraham and S. S. Rathi[*]

Investigations on reproduction and production efficiency of different grades of Jersey and Red Sindhi with local Cattle of Kerala

26. Records of 211 animals belonging to six different genetic groups *viz.*, Locals, $\frac{1}{2}$Jersey+$\frac{1}{2}$Local, $\frac{1}{4}$Jersey+$\frac{3}{4}$Local, $\frac{3}{4}$Jersey+$\frac{1}{4}$Local, $\frac{1}{2}$Sindhi+$\frac{1}{2}$Local, and $\frac{3}{4}$Sindhi+$\frac{1}{4}$Local from Cattle Breeding Research Station, Thumbarmuzy (Kerala) were collected for conducting investigation on their reproduction and production efficiency. As the data were spread from 1960 to 1971, this duration was divided into 4 periods, each comprising of three consecutive years. Each year was sub-divided into two seasons: rainy (April to October) and non-rainy (November to March). Least Square technique was used to study the effects of genetic groups, periods and seasons. Significant differences, when present, were compared by multiple range test.

27. The overall means for reproduction and production efficiency were obtained as 66.08 ± 3.60 per cent and 1.25 ± 0.16 kg. per day of calving interval, respectively. The coefficient of variability ranged from 15.6 to 29.7 and 39.7 to 73.8 per cent in the same order. Genetic groups, periods and seasons had no significant effect on reproduction efficiency while the first two had significant effect on production efficiency. Genetic groups accounted for the presence of maximum variability in both the traits. The heritability of reproduction and production efficiency were estimated as 0.66 ± 0.54 and 0.59 ± 0.61, respectively. Genetic and phenotypic correlations of age at first calving were high positive with reproduction and production efficiency in both the genetic groups of half-breds. First service

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period and first calving interval had negative genetic and phenotypic correlations with both the traits in both the genetic groups except that the former trait had very low positive while the latter had high genetic association with production efficiency in Sindhi half-breds. Reproduction efficiency and production efficiency had negative phenotypic correlations in both the cross-breds, which is indicative of their mutual incompatability to a certain extent.

28.   These results indicate that locals with 50% Jersey inheritance were best out of all the grades from production efficiency point of view.   Because of the existence of desirable phenotypic and genetic association, it is possible to conclude that attempts at lowering first service period and first calving interval would also result in higher reproduction and production efficiency in Jersey half-breds and only higher reproduction efficiency in Sindhi half-breds.

S C. Chopra and R. M. Acharya***

Efficiency of adjustment of body weights of Magra Sheep

29.   In order to study the efficiency of data adjustment for significantly affecting non-genetic factors and its effect on heritability estimation, 1453 records of body weight at birth, weaning, 6 months and yearling age of Magra sheep, which were progeny of 40 sires, were analysed.   Since the sub-class frequencies were unequal and disproportionate, generalised least squares for the mixed statistical model was used.   Correction factors for the factors affecting significantly at 1 per cent probability level and having R^2 contribution more than 4 per cent were developed.   Data for these factors were adjusted and analysis of variance again conducted on the corrected records.   Efficiency of data adjustment was studied by comparing the mean squares of the various sources of variation on uncorrected and corrected data.   Heritability estimates on the two sets of data were calculated and compared.   On perusal of the results, it was observed that data adjustment by and large improved the heritabilities.

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30. Winding up the symposium, the Chairman, Dr. Kakar commented on the various papers presented and stressed that Geneticists and Statisticians have to work hand in hand to find answers to many unsolved problems of statistical genetics. He felt that, in a Symposium like this, more work on theoretical aspects rather than papers showing the application of already known techniques, were expected. However, the deliberations were useful from the practical point of view and papers were very well presented.