Diallel cross in swine production: A review

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ABSTRACT

A review of diallel cross and its influence on different genetic and crossbreeding parameters derived in swine production is attempted following its application by various researchers. With different genetic models developed by different researchers from the 1950’s till date, diallel cross methodology and its application in animal breeding, particularly in swine improvement has experienced many modifications and technical innovations derived and developed. The genetic gains derived from diallel cross have two major sources viz: additive (direct and maternal) and dominance genetic effects. The practical importance of these two sources is evaluated, through estimates of average direct genetic, average maternal genetic, general combining ability, specific combining ability, reciprocal, direct heterotic and maternal heterotic effects. In the case of significant reciprocal effect; sex-linked and autosomal effects can be estimated. This review paper tries to cover the different approaches used in optimization of diallel crossing between different available pig breeds in terms of the crossing parameters, as well as the findings of various studies using diallel cross aimed at swine production and improvement.

Key words: Animal breeding, Cross, Crossbreeding, Heterosis, Maternal effects.

Diallel cross is a crossbreeding scheme applied in plant and animal production aimed at investigating the genetic underpinnings of quantitative traits with a set of parents producing offspring from all possible mating pairs. It has been applied in swine production by various researchers with the aim of estimating crossbreeding parameters which is the tool needed to identify an efficient crossbreeding scheme (Ibáñez-Escriche et al. 2014). It has been widely used by breeders to study the efficient use of genetic resources in crossbreeding and the parameters include among others average direct genetic, average maternal genetic, general combining ability, specific combining ability, reciprocal, line and specific direct heterotic and maternal heterotic effects. The genetic models for generating these parameters are based on direct and maternal additive and dominance genetic effects as would be expected in animal species (Eisen et al. 1983). Although dialled design is used to investigate the genetic underpinnings of quantitative traits of lines and breeds in all possible crossing combinations (Eisen et al. 1983, Crusio et al. 1984, Hallauer and Miranda 1988), it was focused mainly on identifying the most productive genetic combinations (Comerford and Benyshek 1988, Orengo et al. 2009). However several authors has attempted the use of diallel cross, defined in different models aimed at estimating the effects on crossbreeding parameters, which originated in animal and plant breeding as an extension of the idea that, from a breeding perspective, you should judge the value of an individual by the phenotypes of its offspring (Christie and Shutte, 1992).

Several reproductive traits such as litter traits (measured in terms of number of piglets born alive (NBA), total number of piglets born (TB), litter birth weight etc), milk production traits, sow weight changes etc has been improved using diallel cross (Baas et al. 1992, Hanenberg et al. 2001, García-Casco et al. 2012). Growth traits such as body weight at birth to maturity, 420 days, morphometric traits, rate of daily growth, average daily gain (ADG) has also been reported using diallel cross.(Fernández et al. 2002, García-Casco et al. 2012, Okoro 2012, Ibáñez-Escriche et al. 2014).

Jakubec et al. (1987) suggested that the major reason for diallel crossing in animal breeding is among others; the estimation of genetic effects and the breeding potential of populations by means of crossbreeding parameters (reciprocal or residual reciprocal effects, general and specific combining ability, direct and maternal effects, specific heterosis and line heterosis). Similarly, in swine breeding, many authors have attempted the use of diallel crossing to estimate genetic effects aimed at identifying the most productive combination of the breeds in terms of the given traits (Irgang et al. 1994; Perez-Enciso and Gianola 1992; Cassady et al. 2002; Jungst and Kuhlers 1984; Okoro 2012; Almeida et al. 1996). This review will attempt to look at the methods of estimation applied in swine production, the various genetic effects that are estimated

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using diallel cross, and finally give a breakdown of the various recent outputs that touch on these genetic effects, estimated in relation to growth and reproductive traits in swine production.

**Estimation of genetic effects from diallel cross**

**Brief history of diallel designs:** Diallel cross was originally defined as the set of all possible \( F \) pairwise crosses between two parents, and was later introduced into the genetics literature by Jinks and Hayman, (1953). Later, the diallel, whose definition quickly broadened to encompass any set of \( F \) (first filial generation) crosses between \( J \geq 2 \) parents, caught the attention of an active group of quantitative geneticists who went on to develop a series of elaborations of the design and its analysis. Among the most popular analytic decompositions is that of (Griffing 1956). If \( Y_{jk} \) is the mean phenotype or predicted value for the cross of parent \( j \) with parent \( k \), then the parental effects can be modeled as

\[
Y_{jk} = \mu + g_j + g_k + s_{jk}
\]

where \( \mu \) is the intercept, \( g_j \) is the main effect of parent \( j \), and \( s_{jk} \) is the statistical interaction of \( j \) and \( k \), that is, the deviation from the combined main effects induced by the specific pairing of parents \( j \) and \( k \). Following the terminology introduced by (Sprague and Tatum 1942) and used throughout diallel literature, \( g \) is the generalized combining ability (GCA) of parent \( j \) whereas \( s \) is the specific combining ability (SCA) of the parents \( j \) and \( k \). GCA captures aggregate effects of additive genetics whereas SCA reflects aggregate genetic effects that lead to departures from additivity, such as dominance and epistasis. Numerous extensions to Griffing’s model have been proposed to extract more subtle effects from the diallel. These include decomposing SCA into dominance, heterosis, and epistasis components; later into reciprocal effects; their further decomposition into maternal and paternal effects (Cockerham and Weir 1977, Zhu and Weir 1996), and sex-linked variants thereof (Carbonell et al. 1983). Conversely, interest in obtaining GCAs with fewer than \( F \) crosses has motivated variants of the design such as the half-diallel (Griffing 1956) and the partial diallel (Kempthorne and Curnow 1961), among others (Christie and Shattuck 1992, Lynch and Walsh 1998), which have themselves led to technical innovations.

**Modifications in the estimation of crossbreeding parameters in a diallel cross:** Modifications of these diallel cross designs have been developed by several authors to realize different types of diallel cross: reciprocal crosses are sometimes omitted if maternal (or paternal) influences are assumed to be absent (half-diallel); or only a part of all possible crosses is raised (partial diallel) (Crusio et al. 1984). Sometimes only one replication is bred, and in such cases, one may encounter problems in estimating the error component. Since several models had been developed for the evaluation of the diallel experiments for crossbreeding parameters, recent studies developed these models further in order to understand the interdependencies between parameters in two different models, easily. Komender, (1988) developed a general method of comparing models to estimate crossbreeding parameters with its application to diallel crossbreeding experiment. This has made the test for reliability of models easier. Also Komender and Hoeschele, (1989) developed the mixed-model methodology which is different from the usual least-squares in use, which reduces the true standard errors of the estimates of crossbreeding parameters, and also remove biases caused by the confounding of certain animals and crossbreeding groups by selection. This has also increased the reliability and underestimates the standard errors of crossbreeding parameters, which improves estimation of parameters. Greenberg et al., (2010), also developed the hierarchical Bayesian model for partial diallel crossing design, aimed at assessing accurately and precisely quantitative genetic parameters such as heritability, dominance and genetic correlations in the face of complex and unbalanced designs. Lenarcic et al., (2012) also developed a Bayesian model for analyzing diallel data on dioecious diploid sexed and inbred parents, which cleanly decomposes the observed patterns of variation into biologically intuitive components, simultaneously models and accommodates outliers, and provides shrinkage estimates of effects that automatically incorporate uncertainty due to imbalance, missing data, and small sample size. All these models can be applied to swine production as swine is diploid specie. Most of the theory of optimal diallel cross designs is based on standard linear model assumptions where the general combining ability effects are taken as fixed and the primary interest lies in comparing the lines with respect to their general combining ability effects. Under such a model, among others, (Gupta and Kageyama 1994, Dey and Midha 1996, Mukerjee 1997, Das et al. 1998, Ghosh and Das 2004) have characterized and obtained optimal completely randomised designs and incomplete block designs for diallel crosses. Jakubec et al., (1987) most importantly developed and evaluated three models for the analysis of complete (full) diallel crosses in animal breeding, derived from (Gardner and Eberhart 1966), (Harvey 1960) and (Griffing 1956) models, which is advantageous when the parental population is small and most efficient as it gives detailed information about crossbreeding parameters. However, the disadvantage is that the costs and the demands on testing capacities increase very rapidly with the growing number of tested parental populations. Hence Wolf et al., (1991) developed the methodologies for the analysis of partial dials with two sets of parental populations, which handles a reduced number of parent and crossbred populations. This methodology is appropriate for such crosses that may be done between any two sets of populations with different gene frequencies, such as local and exotic breeds, beef and dairy cattle, specialized sire and
Blup prediction of genetic effects from diallel cross: Best Linear Unbiased Prediction (BLUP) and Adjusted Unbiased Prediction (AUP) predictors are estimators of choice in diallel design because they give extremely low bias for predicted mean genetic effects; hence they are unbiased for random genetic effects like crossbreeding parameters (Zhu and Weir 1996). The variances of predicted random genetic effects are always smaller than the true variances for both BLUP and “BLUP” methods. This is shown by Monte Carlo simulations that these two methods yield predictions with unbiased means but under-estimates variances for all the random effects as well as restricted maximum likelihood (REML) method. In plants and animal breeding, ‘BLUP’ is mostly used by breeders for evaluating breeding values of genetic materials. However Jakubec et al., (1987) was of the opinion that direct derivation of the earlier expressions for analyzing diallel cross using ANOVA and least squares estimators provides unbiased means of crossbreeding parameters. Therefore it can be concluded that as BLUP and AUP can be used for predicting genetic effects and standard errors of predictors, which can be obtained by the jack-knife procedure as in the case of estimating variances and covariances; and a t-test used for detecting significance of specific genetic effects.

Reciprocal effects estimates in swine production: A common assumption underlying most analyses of the diallel cross is the absence of any reciprocal differences, which are primarily caused by sex-linkage and maternal effects which are non-additive genetic effects. Although the effects of such differences on the analysis of diallel crosses have been examined by Mather and Jinks, (1982), they were primarily concerned with testing the significance of possible effects and with determining the probable cause of reciprocal effects. Estimating the reciprocal effects will help to identify superior nicking genetic group/groups for improvement (Iraqi et al. 2007) through the knowledge of the nature and magnitude of genetic variation in genetic groups. Several authors had reported that reciprocal effects in pigs are not significant particularly on growth traits; however (Okoro 2012) reported significant reciprocal effects at 2 – 9 weeks and 12 - 18 weeks bodyweight in a partial diallel cross involving indigenous, Landrace and Large white pigs. In another study, Duroc et al., (2015) also reported a significant reciprocal effect on body weight and some morphometric traits from a full diallel cross involving indigenous, Large White and Landrace breeds of pigs. Also Almeida et al., (1996), estimated reciprocal effects on bodyweight at birth, 21, 35, and 77 days in crosses involving Duroc, Landrace, Yorkshire and Large White with a non-significant reciprocal effect at birth, 21 days and 35 days of age. In another vein, Garcia-Casco et al., (2012) reported a very low, non-significant reciprocal effect for both body weights at 420 days and rate of daily growth in crosses of 4 Iberian pig strains using Bayesian procedures. However, the significant reciprocal effect in body weight and some morphometric traits indicates maternal and sex-linked effect at the affected ages, implying that significant reciprocal cross may be used to attain high performance for the growth traits in the progeny.

In similar studies involving reproductive traits, a non-significant reciprocal effects were reported for litter size and weight from birth to maturity; mortality, number of piglets at birth, weaning and 140 days; in Iberian, Duroc, Landrace, Yorkshire, Large white and Nigerian Indigenous pigs (Almeida et al., 1996, Garcia-casco 2012, Okoro, 2012). This goes to support the findings of Hutchens et al. (1982), that there are no significant reciprocal effects among any of the reproductive traits of swine, including age or weight at puberty in a diallel crossing involving Duroc, Yorkshire, Spotted and Landrace breeds of pigs.

General combining ability and specific combining ability estimates in swine: Diallel mating designs are important tools in animal breeding programs needed to obtain information on inheritance, such as general combining ability (GCA) and specific combining ability (SCA), of quantitative or complexly inherited traits (Zhang et al. 2005, Saadey et al. 2008). GCA is an estimate of the average performance of a genotype in hybrid combinations, and is related to the proportion of additive genetic variability. GCA for a particular genotype is measured as the deviation of its progeny mean from the mean of all the lines used. Meanwhile, SCA estimates how progeny from a specific cross perform in relation to what would be expected based on the average performance of the genotypes involved (Murphy et al. 2008). The GCA is due to the genetic additive effects and to the epistatic effects that include only additive combinations. The SCA depends on the dominance effects and the epistatic effects that include dominance combinations (Hill et al. 2012, Balaguer 2014). In partial diallel studies involving Duroc, Yorkshire and Landrace breeds of pigs Kurnianto et al., (2010) estimated GCA for birth weight, average daily gain (ADG), post weaning ADG and body weight at 42 days and found it to be significantly in favour of Duroc breed, with the highest value. Meanwhile the estimates of SCA were significantly in favour of Yorkshire x Landrace breed cross for all the growth traits studied. Similarly, Bereskin and Hetzer (1986) reported a significant GCA effect for average pig weight at birth and at 56 days of age in a full diallel cross involving 4 lines of Duroc and Yorkshire breeds of pigs. Duro et al., (2015) estimated GCA and SCA from a full diallel cross involving indigenous, Large White and
Landrace breeds of pigs and there was no significant GCA effect (P>0.05) on all the traits measured, but SCA was significant (P<0.01) for all morphometric traits and body weight. (Kurnianto et al. 2010) also estimated the GCA and SCA for reproductive traits such as litter size, the number of nipples, and the number of piglets at weaning from a partial diallel cross involving Duroc, Yorkshire and Landrace breeds of pigs. His findings were that the GCA of Duroc was higher than that of Yorkshire and Landrace on all the reproductive traits measured. SCA was significantly highest for number of nipples in the crossing of male Duroc x female Yorkshire, while the crossing of male Yorkshire x female Landrace was the highest SCA on litter size and the number of piglets at weaning. Bereskin and Hetzer, (1986) reported a significant GCA effect involving 4 lines of Duroc and Yorkshire breeds of pigs. Duroc high-fat line was highest in GCA but lowest in maternal ability for litter size at any age with Duroc evidencing more GCA than Yorkshires for litter weight through 56 days. Also Wheat et al., (1981) reported significant specific combining ability (SCA) for litter weight at 21 and 56 days for male Yorkshire x female Duroc cross while inter-breed crosses of similarly-selected lines evidenced most SCA in ranking above inter-breed crosses and inter-breed crosses of oppositely-selected lines in all traits except litter size at birth. Landrace displayed a consistent advantage in GCA. The Landrace-Duroc cross seemed to produce faster growing pigs, with better feed efficiency, and carcasses with less fat, but there were fewer pigs per litter. However, the genetic underpinnings of these findings might not be different as reported, as other undeveloped breeds needs to be subjected to this test to identify the nicking effects of the genes responsible for the variations in these reproductive traits.

Maternal effects estimates in swine: The growth of a pig is determined by the piglet as well as its dam, respectively through effects termed direct and maternal effects (Alves et al. 2015). The trait, as measured, is the phenotypic value of the offspring, but it is composed of at least two components: offspring growth and a maternal effect contributed by the dam. In mammals, the female provides an environment for her offspring to survive and grow, mainly by the dam’s milk production and mothering ability (Meyer 2004). Females vary in their ability to provide a good environment for their offspring, and this variability has a genetic basis. Large breed differences in direct and maternal genetic effects are evident for most economically-important traits in swine (Johnson 1981). With large-scale use of strain and breed crossing in swine production, it is important to identify superior cross combinations using diallel crossing. Thus, in order to plan a sound breeding programme, it is necessary to know the kind of gene action (additive or non-additive) and the maternal contribution to the performance of the offspring (Dillard et al. 1980, Jungst and Kuhlers 1984). Lo et al., (1992) reported a significant maternal effect on Landrace breeds for Average Daily Gain (ADG), while Almeida et al., (1996), estimated the maternal effects on bodyweight at birth, 21, 35, and 77 days in Duroc, Landrace, Yorkshire and Large White pigs and reported a significant maternal effect at birth, 21 days and 35 days of age. Also Bereskin and Hetzer, (1986) reported that maternal effects on pig body weights appeared to be positive from weaning to 154 days in Yorkshire breed dams, while Duroc dams seemed not to express maternal effects. The positive influence of Yorkshire gilts on pig size was somewhat unexpected in view of the fact that Yorkshire gilts also had the largest crossbred litters. Thus, Yorkshire gilts not only raised slightly larger litters but also weaned heavier pigs and their advantage carried through to 154-day weight (Bereskin and Hetzer 1986). Okoro, (2012) reported a significant maternal effect on body weight and morphometric traits from birth to 9 weeks in partial diallel cross involving Indigenous, Landrace and Large white breeds of pigs, particularly on the Landrace dams.

García-Casco et al., (2012) reported significant maternal effects on litter sizes at first and second parities, but not in the third and fourth parities. There were no differences between Number born alive (NBA) and Total number of piglets born (TB). Baas and Christian, (1992) reported that Landrace females were superior to Hampshire females for number born (NB), number born alive (NBA), litter birth weight (LBW), adjusted 21-d litter weight (ALW), and milk production at d 10 of litter age (WT10). However, Hampshires were superior to Landrace for percentages of protein in milk (PCPR) at d 10 of litter age and percentage of solids-not-fat (PCSN) at day 10 and 20 of litter age. Also maternal heterosis effects were significant for LBW. Almeida et al., (1996) also reported non-significant difference for maternal effects for reproductive traits such as total number of piglets at birth (TNPB), number of piglets at birth (NPAB) at 21 days, at weaning (35 days) and at end of growth period. Also maternal effects were not significant on mortality rate from birth to the end of the growth period in the four different breeds of pigs. Bereskin and Hetzer, (1986) and Schneider, (1978) also reported significant higher maternal effect in Large White breed than in Duroc breed. Wheat et al., (1981) reported a significant maternal effect on TNPB, with the Yorkshire-Landrace cross being the most prolific, while the Duroc boar x Landrace gilt cross had the best rate of gain, but the reciprocal cross was inferior because of poor mothering ability of Duroc gilts.

Heterotic effects in swine: Studies have shown that crossbred animals were superior to purebred animals for heterosis particularly in number of live piglets, vigour of the animals at birth, survival from birth to weaning and litter weight at weaning. These genetic differences can lead to large economic differences among various crossing systems,
differences that depend on breeds involved and the percentage of heterosis utilized by the system (Johnson 1981). Garcia-Casco et al., (2012) reported a significant heterotic effect on weight at 420 days of age for the different crosses of Iberian pigs, while a non-significant heterotic effect for daily growth rate was inferred in the first 5 combinations, with the remaining combinations having significant heterosis (+66g/d). Wheat et al., (1981) reported that offspring from Duroc boars were most efficient in feed utilization, and the superior cross was the Duroc-Landrace in a diallel cross involving 3 lines of pigs. They also reported heterotic gains of weights at birth, 21, 56 and 154 days and age at 95.3 kg of 0.1,5, 3.1, 16.2 and 9.4% heterosis, respectively for cross among Yorkshire, Duroc and Landrace diallel cross. These results are in general agreement with an earlier report (Johnson 1981) in which birth weights of crossbreds were intermediate to those of the parental breeds, but weights of crossbreds at weaning and at later ages exceeded parental breed averages by 8 to 10% heterosis. Crossbreeding programmes must be systematic and well-planned to take full advantage of heterosis and breed differences and diallel cross which is one of the methods employed, is to enables the producer to take advantage of heterosis and to combine desirable characteristics of different breeds. The exploitation of heterosis is the major reason for crossbreeding (Ibe 1998). McLaren et al., (1987) reported a highly significant individual heterosis estimates for post-weaning performance traits and reasonably consistent trend in a diallel crosses involving Duroc, Yorkshire, Landrace and Spotted pig breeds. Meanwhile, reported experimental estimates of individual heterosis for carcass traits have in general been non-significant (Johnson 1981, Wheat et al. 1981). Johnson (1980) reported average heterosis of 9.4 and 2.5% for Average Daily Gain (ADG) (age at 56 days) and Carcass Average Back fat Thickness (CABT), respectively in a diallel cross involving Large white, Duroc and Yorkshire pig breeds.

Garcia-Casco et al., (2012) reported a negligible progeny specific heterotic effects on litter size traits in early parities, but highly significant at third and later parities. Baas and Christian, (1992) reported a significant heterosis effect for Number born alive (NBA) and litter birth weight (LBW). However, heterosis and recombination effects were not significant for milk production or milk composition. According to Johnson, (1981), heterotic estimates for litter weight at 21 days were highly variable but part of this variation was because similar crosses produced different estimates in independent experiments. Heterosis is evidenced only in the presence of directional dominance effects at the loci affecting the trait and difference in gene frequencies between the lines, being crossed (Falconer and Mackay 1996).

CONCLUSION

With diallel cross design being used to investigate the genetic underpinnings of quantitative traits of lines and breeds in all possible crossing combinations in both plants and animals; in animals focus is placed mainly on identifying the most productive genetic combinations. Most of the breeds found in this investigation are the highly developed and prolific ones, found in the hands of major commercial breeders, sold as hybrids and used in upgrading of lowly unproductive indigenous breeds. Therefore, further studies using diallel crossing methodology in pigs will be more effective on undeveloped breeds which have not been subjected to this methodology, and are few in their natural environment. This method will be useful in identifying the most productive genetic combinations that will be viable in the natural habitat of the breeds, as it will have more impact on pig production. This is necessary as Assis et al., (2004); Dickerson, (1993); Ghosh and Das, (2004) agree that diallel cross is an effective method to evaluate the genetic and heterotic potential of the breeds or lines involved in genetic improvement programs.

REFERENCES


