Genetic and genomic technologies from A-Z

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Summary

For many years, genetic improvement in swine herds was traditionally made by small breeders. Beginning in the last half of the 20th century, following the lead of corn hybrid companies, breeding companies and larger seedstock breeders moved to improve swine by employing stringent selection methods, developing specialized sire and dam lines and then synthetic lines to be sold to customers as commercial products. Fat reduction and increased growth rates were significant but gains in reproduction and feed efficiency were more limiting and meat quality generally declined. Beginning in the early 1990s advances in the fields of molecular genetics began to provide additional tools for further improvements. Several recent quantitative trait loci (QTL) scans and candidate gene analyses have identified important chromosomal regions and individual genes associated with traits of economic interest including growth and fat levels, meat quality traits, reproduction and disease resistance. Commercial genetic companies are actively using this information combined with traditional performance information to improve pig production by marker assisted selection (MAS). Completion of the sequencing of the pig genome, coupled with development of large single nucleotide polymorphism (SNP) panels offers the possibility of whole genome association trials and genomic selection which is likely to provide the ability to select animals for traits previously difficult to improve. Such genetic improvement will improve production characteristics and provide healthier food products worldwide. The purpose of this paper is to help breeders understand the technologies and see how they fit in their programs.[1]

Introduction

Genetic improvement of swine first began with domestication. Such domestication is likely to have occurred at least 5,000 years ago and perhaps as long as 10,000 years. Development of specific strains or so-called breeds occurred as individual small breeders applied the use of inbreeding (mating of related individuals), and selection to find characteristics that would later help define strains and breeds. Such processes were confined to small breeders of herds at the beginning of the 20th century when Mendel's discoveries initiated the field later to be known as genetics.

While small breeders were certainly the rule in the early 1900s the advent of corn breeding companies and the successful development of inbred lines and crosses paved the way for the development of breeding companies who began to control swine breeding. In the beginning, a number of pig breeding and family seedstock companies existed. Market pressures, superior business approaches and changes in the marketplace have reduced the numbers of individual family breeders to a very small share of the marketplace. In the swine breeding business very few companies (less than ten) now actively compete worldwide: in the US the top two companies likely make up 65 to 70% of market-share.

[1] Many of the terms used from A to Z are listed in the glossary at the end of this paper

In pigs the primary selection for the past nearly 60 years has been devoted to faster and leaner growth. Such selection has had clear and decisive outcomes. From 1930s phenotypic measures of back fat have been reduced from 45 mm to closer to 15 -16 mm, with growth rates increasing in some cases by more than 50% faster growth. This was done while increasing markets weights from 80 kg to 125 kg. Feed conversion has also nearly halved with the best commercial herds having efficiency ratios of 2.5 to 2.6 kg feed consumed to kg gained over the lifetime of the pig. Even in more recent years genetic improvement has continued with reductions in age to market weight of -0.4 days/yr in genetic trend. Some industry analysts believe fat levels have now reached a minimum. Unfortunately these changes have been accompanied with reductions in marbling and pH and meat quality has suffered. In terms of number born alive genetic rates of improvement of 0.2 pigs per litter per generation appear to be the norm.

Genetic maps, gene discovery and the molecular age

Molecular genetic analysis has revolutionized how geneticists examine genetic differences that exist within pigs. Beginning about 1991, the PiGMap consortium was formed to develop genetic linkage maps (Archibald *et al*., 1995). In the first 10 years, efforts were directed toward the development of useful genetic linkage maps consisting of anonymous genetic markers and a limited number of known genes. In addition, comparative genome maps were developed which have aided greatly in our search for interesting and potentially useful genes in the pig.

The coverage on these genetic maps soon became sufficient to allow researchers to search for causative genes by conducting quantitative trait loci (QTL) linkage analyses. These QTL linkage analyses involved employing a genome scan where generally F2 or backcross families were used and genotypes are obtained for many (>100) markers relatively evenly spaced across the genome. Many such experiments in pigs were completed and can be reviewed in the Pig QTL database (http://www.animalgenome.org/QTLdb/pig.html). There are nearly 6000 pig QTL in the database from 268 publications representing many different pig traits. Most deal with traits such as backfat and meat quality (4000+), production (600+), health (580+), exterior (370+) and reproduction (270+). These QTL discoveries usually encompassed chromosomal regions of 10 to 20 cM though on occasion regions of the chromosomes which are much larger.

Candidate gene analyses (Rothschild and Soller, 1997) are undertaken when a gene is chosen based on the physiology of the trait. This is supplemented by comparative gene analysis that allows researchers to find “positional candidate genes” in the regions associated with possible QTL. These approaches have been successful in identifying major genes affecting several traits. Significant effects of major genes and candidate genes have been reported (see Bidanel and Rothschild, 2002). For example, the MC4R (melanocortin 4 receptor) gene was found to significantly affect growth rate by 7 to 9% by influencing feed intake. The MC4R gene maps to chromosome 1 close to a significant QTL. Due to the MC4R effect on feed intake, variation in this gene is also significantly associated with 5 to 8% differences in backfat and relates to one QTL for backfat thickness on chromosome 1 (Kim *et al*., 2000). Other regions with backfat QTL include the region carrying the IGF-2 locus at the end of the short arm of chromosome 2. IGF2 significantly affects growth and muscle quantity in pigs and acts as a major gene locus (Van Laere *et al*., 2003). Many QTL with significant effects on backfat thickness were also obtained (Figure 1) in many other regions (Malek *et al*., 2001a). Two of them were detected in different regions of chromosome 6 near HFABP and LEPR. One QTL for backfat was also found on chromosome 13, near PIT1.

Major genes for meat quality include the HAL or RYR1 gene (Fujii *et al*., 1991) and RN^- (Milan *et al*., 2000). Genetic tests for these are now available and are used worldwide by small breeders and commercial companies alike to remove the deleterious effects of these genes. The QTL located on chromosome 15 had significant effects on meat ultimate pH in Berkshire x Yorkshire F2 pigs (Malek *et*

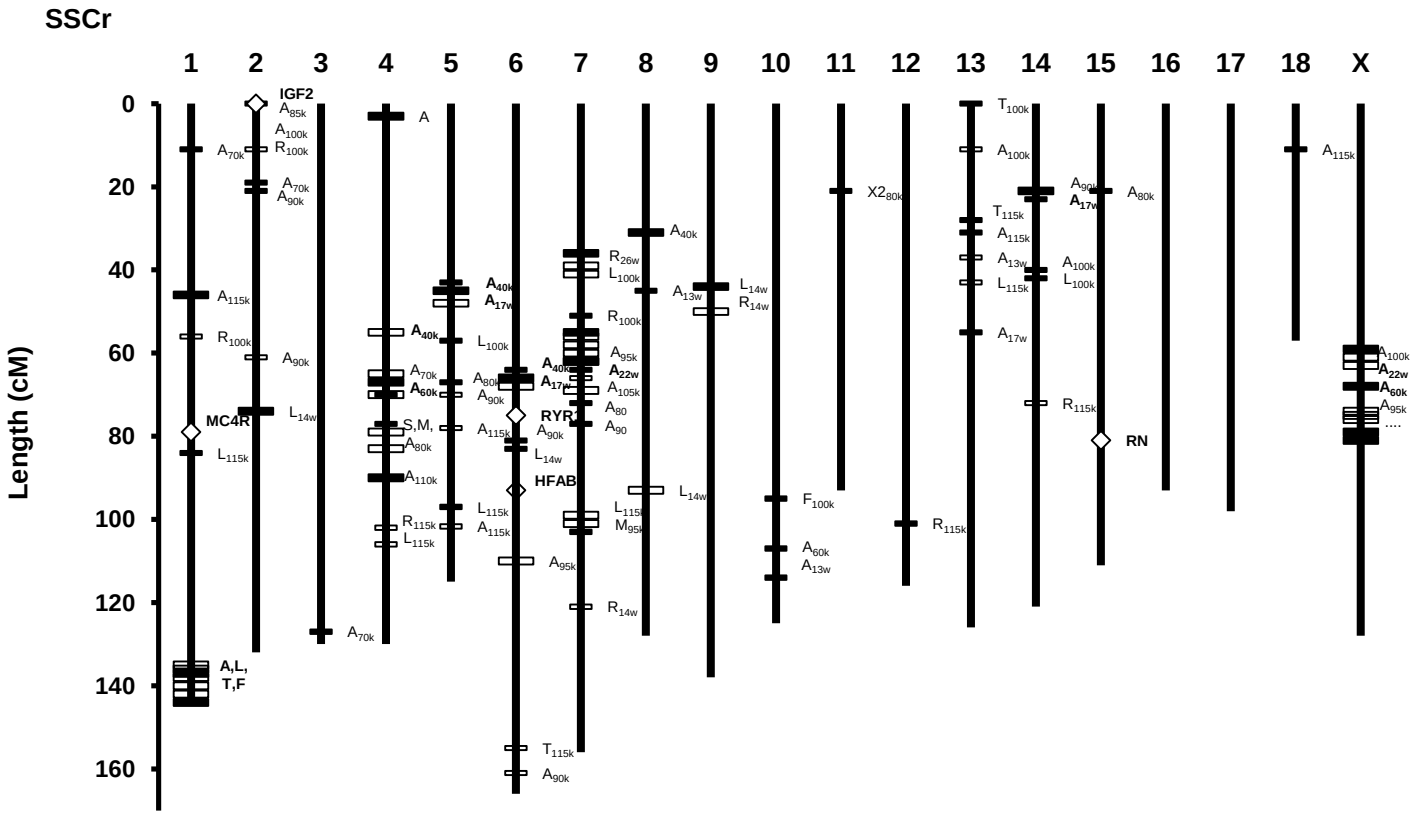

Figure 1. Candidate genes and quantitative trait loci detected for backfat thickness.

Symbols = A (average), L (lumbar), R (last rib), T (tenth-rib), S (shoulder), M (mid-back), F (first-rib) backfat thickness at xx kg (k) or xx weeks (w) of age; Locus names (in bold characters) : MC4R = melanocortin-4 receptor locus; IGF2 = insulin growth factor 2; RYR1 = ryanodine receptor locus ; HFAB = heart fatty acid binding protein locus; PIT1 = regulatory factor locus; RN = “acid meat” locus.

al., 2001b). The chromosome 15 QTL explains 4-6% of ultimate pH variance and presents favorable, but partly recessive Berkshire alleles. This muscle glycolytic potential QTL is localized in the same region as the RN locus. The original RN^- mutation (Milan *et al*., 2000) was not present in the population studied. The observed effects were due to three additional mutations inside the gene containing the RN locus (Ciobanu *et al*., 2001). Further study has demonstrated that the three mutations when combined into haplotypes (linked markers) they produced differences in pH that may be as high as 0.1 pH unit in all breeds except Berkshires in which the differences may exceed 0.2 units. Unlike the RN^- mutation, which is essentially only in Hampshire pigs, these three new mutations are in all breeds and this makes them extremely important economically.

Suggestive QTL were obtained for sensory traits also in some experiments but they correlated well with more objective measures like pH or instron measures of tenderness. In addition, a small but distinct QTL for tenderness was detected in the middle of chromosome 2 (Malek *et al*., 2001b). Further investigation revealed that Calpastatin (CAST), mapped under the QTL, is a specific inhibitor of calpains, a Ca^{2+}-activated protease family and considered to be the major cause of initiation of myofibrillar protein degradation. Extensive analysis of the CAST gene revealed several polymorphisms that altered the protein and these had large effect on tenderness (Ciobanu *et al*., 2004). Candidate gene analysis for reproduction has also shown considerable merit. Results have clearly demonstrated that the estrogen receptor (ESR) is significantly associated with litter size (Rothschild *et al*., 1996). Estimates of allelic effects vary between 1.15 pigs/litter in Meishan synthetics and 0.42 pigs/litter in Large White lines. The ESR marker was incorporated successfully into the selection indices for some commercial Large White based dam lines, resulting in an increase in the rate of genetic response in its nucleus herds. Other researchers have shown that another gene involved in reproduction,EPOR, is also associated with significant liter size effects.

The existence of a gene responsible for resistance to K88 *E. coli* diarrhea has been known for many years. The gene coding for the K88 *E. coli* receptor in the pig is on chromosome 13 and candidate gene analysis of the region is underway in many labs. Resistance to edema disease caused by F18 *E. coli* has also been reported and was mapped to chromosome 6. The work confirmed that a polymorphism in the FUT1 gene (Meijerink *et al*., 2000) is probably the causative mutation for adhesion resistant animals in these breeds.

Potential of DNA markers and their use in selection in the swine industry

Information at the DNA level can help producers, breeders and veterinarians to select for a specific major mutation such as FUT1 resistance or against negative mutations like the negative Halothane allele or RN^- allele in the pig. The DNA information can also be used to assist in the selection of quantitative traits, called Marker Assisted Selection or MAS (e.g., using ESR B to increase litter size and MC4R to reduce feed intake). Molecular information can increase the accuracy of selection, allow for selection for sex limited traits and allow for selection for traits like meat quality. These approaches have led to a number of genes and markers being used in the swine industry (Table 1). Many of these genetic tests were made recently available to all breeding companies and they are available from genotyping service companies for smaller breeding companies and seedstock producers. Their use has been limited, in part due to cost and in part due to lack of clear knowledge to their availability and use. Recommendations include using ESR in Large White lines to select for increased litter size, MC4R for increased feed efficiency in all lines but those with Hampshire and use of CAST and PRKAG3 for improved meat quality, especially in sire lines.

Table 1. Molecular Genetic Tests Used by the Swine Industries

Swine Gene or test	Industry Use
Parentage tests	exclusive use within some companies, commercially available
HAL	meat quality, commercially available
ESR, EPOR	litter size, commercially available
KIT	white color - exclusive use
MC1R	red/black color, use unknown
MC4R	growth and fatness, commercially available
FUT1	edema E. coli F18, exclusive use
RN	meat quality, commercially available
AFABP, HFABP	intramuscular fat, use unknown
PRKAG3	meat quality, commercially available
CAST	tenderness, commercially available
IGF2	carcass composition, commercially available
Trade secret tests	several traits – many companies

Sequencing the genome and whole genome association trials and genomic selection

Sequencing is the unraveling of the DNA to understand the genetic code. It is equivalent to breaking down books into individual sentences and even specific letters in these sentences and words. The letters in the genetic code (A, T, G, C) are combined into "words" and these words are the genes that control traits or contribute to phenotypes of the animal like rate of growth, level of fat, reproductive performance and disease susceptibility. Knowing the genetic code requires that we apply modern molecular biology or laboratory methods to break up the code into smaller pieces and then "read" the code.

Sequencing the pig genome sequencing began in part when a Danish-Chinese project was initiated several years ago. This project produced limited genome coverage. To have excellent sequence, a 6X copy of sequence is needed which means that there should be at least 6 copies of each segment that are each sequenced for accuracy. A new international effort was initiated in 2006 by the US, UK and other countries. Sequencing is nearly completed. Funding to sequence the pig genome is an international effort provided by the USDA, National Pork Board, Iowa Pork Producers Association, University of Illinois, Iowa State University, North Carolina Pork Council, North Carolina State University, the Wellcome Trust Sanger Institute, UK and a number of research institutions from around the world including those from China, Denmark, France, Japan, Korea, Scotland and the U.K.

Sequencing is but the first step. Further gene discovery and associations will be made possible by development of new tools like the SNP (Single Nucleotide Polymorphism) chips. These chips are designed to genotype animals for 60,000 SNPs or more at one time for a cost of about $150 US dollars per animal. Such SNP genotyping will allow for "whole genome association trials" and discovery of many significant associations. The pig SNP chip has just been recently produced (Ramos *et al*., 2009).

Once found these SNP associations can then be used to perform genomic selection. Genomic selection (Meuwissen *et al*., 2001) can be described as the prediction of an animal's breeding value using 1000s of SNP associations. Such predictions offer many opportunities to advance genetic improvement. First and foremost they offer a real look at the relatedness of animals from a DNA basis instead of predicting it on average from pedigrees. Second, genomic selection would allow the ability to predicting trait values for animals which do not have the trait. For instance we could

predict a breeding value for litter size on boars without ever progeny testing. Finally, for some traits that have been difficult to measure on the live animal, like meat quality or disease resistance, such associations will likely give breeders real opportunities to make noticeable genetic improvement (see Figure 2). Such opportunities with genomic selection should make it possible to develop specialized lines for niche markets and unusual environmental conditions. These developments may be years away.

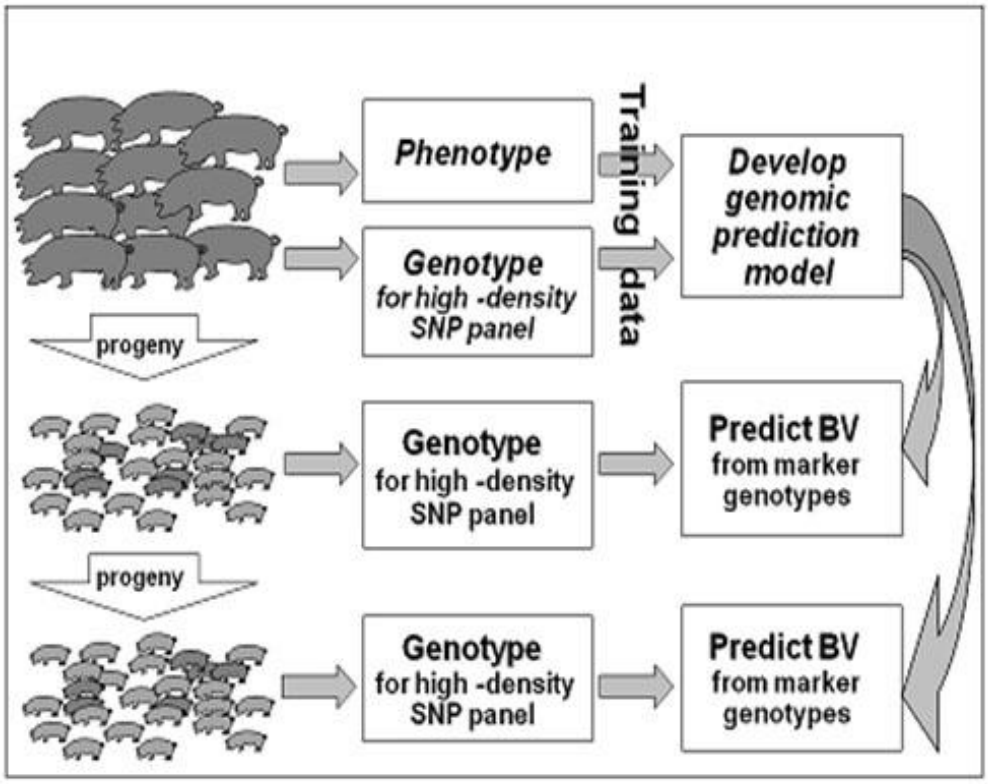

Figure 2. Steps in Genomic Selection (Dekkers *et al*., 2011)

Conclusions

Genetic improvement in the 20th century in pigs was considerable using the tools of measurement, selection and crossbreeding. In the 21st century many gene markers were identified and available for marker assisted selection. Breeders have not uniformly used this technology, in some part due to their lack of understanding and because of unsure cost benefit concerns. Now genome sequencing has been nearly completed in the pig. Results of these efforts are already being used to develop SNP chip technologies to examine who genome associations. Use of genomic selection may take place in pigs in the next few years but such approaches are likely only by the biggest companies unless costs are reduced greatly. Breeders, producers and consumers will all benefit from using individual markers in the near future and turn to other strategies as they are commercially cost effective. These advances in genomics and the resulting genetic improvement will be considerable.

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Genetic glossary (Hu *et al*., 2011)

Bold words are glossary entries. *Italicized words* are concepts that may be independent glossary entries as well.

Adaptation traits — Adaptation traits contribute to individual fitness and to the evolution of animal genetic resources. By definition, these traits are also important to the ability of the animal genetic resource to be sustained in the production environment.

Additive genetic effects — The effect of an allele on animal performance, independent of the effect of the other allele at a locus. These effects of the two alleles at a locus add up (thus "additive"). Alleles at a locus may have other effects (*dominance*, *epistasis*), so that there are not genes that have just "additive" effects and other genes with only "dominance" effects. Additive genetic effects can be inherited; other genetic effects such as dominance and epistasis are the result of allele combinations that are lost between generations. The additive genetic effect that an animal has for a trait is equal to its breeding value.

Allele — One of a pair, or series of alternative forms of a gene that can occur at a given locus on homologous chromosomes.

Amino acids — Any one of a class of organic compounds containing the amino (NH_2) group and the carboxyl (COOH) group. Amino acids are combined to form proteins.

Animal model — A system for genetic evaluations that estimates breeding values of individual animals (males, females) at the same time. The system uses production data on all known relatives in calculating a genetic evaluation.

Ancestor — Any individual from which an animal is descended

Assortative mating — Assigning animals as mates based on phenotypic or genetic likeness. *Positive assortative mating* is mating animals that are more similar than average. *Negative assortative mating* is mating animals that are less similar than average.

Autosome — Any chromosome that is not a sex chromosome.

Backcross — The cross produced by mating a first-cross animal back to one of its parent lines or breeds.

Best linear unbiased prediction (BLUP) — A method of genetic prediction (with the properties of smallest variance, linear and unbiasedness) that is particularly appropriate when performance data come from genetically diverse contemporary groups.

Breed — Either a sub-specific group of domestic livestock with definable and identifiable external characteristics that enable it to be separated by visual appraisal from other similarly defined groups within the same species, or a group for which geographical and/or cultural separation from phenotypically similar groups has led to acceptance of its separate identity.

Breeding value — The mean genetic value of an individual as a parent. It can be estimated as the average superiority of an individual's progeny relative to all other progeny under conditions of random mating.

Categorical trait — Scores are given usually in a few categories up to several categories (i.e. scores 1-5 for leg movement).

Centromere — Spindle-fiber attachment region of a chromosome.

Chromosome — Microscopically observable linear arrangement of DNA in the nucleus of a cell. Chromosomes carry the genes responsible for the determination and transmission of hereditary characteristics.

Co-dominant alleles — Alleles, each of which produces an independent effect in *heterozygotes*.

Combining ability — The mean performance of a line when involved in a *cross-breeding* system. General combining ability is the average performance when a breed or line is crossed with two or more other breeds or lines. Specific combining ability is the degree to which the performance of a specific cross deviates from the average general combining ability of two lines.

Composite (synthetic) breed — A hybrid with at least two and typically more breeds in its background. Composites are expected to be bred to their own kind, retaining a level of hybrid vigor normally associated with traditional cross-breeding systems.

Control line — A line that is randomly selected and randomly mated. Usually used in selection experiments to monitor environment effects in order to estimate genetic change in a selected line.

Correlation coefficient — A measure of the interdependence of two random variables that ranges in value from −1 to +1, indicating perfect negative correlation at −1, absence of correlation at zero, and perfect positive correlation at +1. It determines the degree to which two variables' movements are associated. No cause and effect is implied.

Covariance — The degree to which two measurements vary together. A positive covariance is when two measurements tend to increase together. A negative covariance is when one measurement increases and the other measurement tends to decrease.

Crossbreeding — Matings between animals of different breeds or lines.

Crossover — The process during meiosis when chromosomal segments from different members of a *homologous* pair of chromosomes break, and part of one will join a part of the other, so that two gametes form possessing new combinations of *genes*. The frequency of crossover between two *loci* is proportional to the physical distance between them.

Crossover unit — Each unit is equal to a one percent frequency of crossover *gametes*.

Cytoplasm — The protoplasm outside a cell *nucleus*.

Descendant — An individual descended from other individuals.

Diallel cross — When both males and females from each breed (or line) in a set of breeds (or lines) are mated to males and females of each breed (or line) in the set including their own breed (or line).

DNA — Deoxyribonucleic acid, the chemical material which carries information to code for a gene.

Dominant — Applied to one member of an allelic pair of genes, which has the ability to express itself wholly or largely at the exclusion of the expression of the other allele.

Dominance genetic effects — The effect that an allele has on animal performance, which depends upon the genotype at the locus. For example, the "a" allele may have a different effect on animal performance in "aa" animals than in "Aa" animals. See *additive genetic effects*.

Economic trait loci — Loci that have effects on traits of economic importance.

Economic value — A measure of the contribution an individual trait makes to the overall economic value of an animal.

Environment — The aggregate of all the external conditions and influences affecting the life and development of the organism.

Environmental correlation — When two traits tend to change in association with each other as a result of environmental effects.

Environmental variance — Variation in phenotype which results from variation in environmental effects.

Estimated breeding value — A prediction of a breeding value. See *breeding value*.

Epistasis — When the gene at one locus affect the expression of the gene at another locus.

F_1 — Animals resulting from crossing parents from different lines or breeds.

F_2 — Animals resulting from matings among F_1 parents.

F_3 — Animals resulting from matings among F_2 parents.

Family size — The mean number of offspring per parent that successfully reproduce.

Full sibs — Individuals having the same male and female parents.

Gamete — A sperm or egg cell containing the haploid (1n) number of chromosomes.

Gene — A functional hereditary unit that occupies a fixed location on a chromosome, has a specific influence on phenotype, and is capable of mutation to various allelic forms.

Generation interval — The average age of the parents when the progeny that will replace them are born.

Genetic correlation — When two traits tend to change in the same or opposite directions as a result of genetic effects.

Genetic distances — A measure of gene differences between populations (hence genetic relationships among them) described by some numerical quantity; usually refer to the gene differences as measured by a function of gene frequencies.

Genetic drift — Changes in gene frequency in small breeding populations due to chance fluctuations.

Genetic gain — The amount of increase in performance that is achieved through genetic selection after one generation of selection.

Genetic maps — See *linkage map.*

Genetic marker — A gene or DNA sequence having a known location on a chromosome and associated with a particular gene or trait; a gene phenotypically associated with a particular, easily identified trait and used to identify an individual or cell carrying that gene.

Genetic variance — Variation in phenotype which results from variations in genetic composition among individuals.

Genome — The complete set of *genes* and *non-coding* sequences present in each cell of an organism, or the genes in a complete haploid set of *chromosomes* of a particular organism.

Genomics – The study of all the gene (DNA) in each cell or organism

Genotype — The genetic constitution of one or a few *gene*(s) or *locus* (*loci*), or total genetic make-up (genes) of an individual organism.

Genotype-environment interaction — When the difference in performance between two genotypes differs, depending upon the environment in which performance is measured. This may be a change in the magnitude of the difference or a change in rank of the genotypes.

Germplasm — The germinal material or physical basis of heredity; the sum total of the genes.

Grade-up — The process of repeated backcrossing to one parental line to produce a population that is nearly purebred.

Half sibs — Individuals that share only one common parent.

Haplotype — A set of alleles at a closely linked group of loci, so closely linked that the allelic set behaves almost as one allele in terms of inheritance.

Hardy-Weinberg law — A population is in *genotypic equilibrium* if p and q are the frequencies of *alleles* A and a, respectively, and p^2, 2pq and q^2 are the *genotypic frequencies* of AA, Aa, and aa under the condition of *random mating*.

Heritability — Degree to which a given trait is controlled by inheritance; proportion of total phenotypic variation that is attributable to *genetic variation* (in contrast to environment-caused variation).

Heterosis — The degree to which the performance of a crossbred animal is better or worse than the average performance of the parents.

Heterozygote, adj. heterozygous — An organism with unlike members of any given pair or series of alleles, which consequently produces unlike gametes.

Homologous chromosomes — Chromosomes which occur in pairs and are similar in size and shape, one having come from the male and one from the female parent.

Homozygote, adj. homozygous — An organism whose chromosomes carry identical members of a given pair of genes. The gametes are therefore all alike with respect to this locus.

Inbreeding — Matings among related individuals, which results in progeny that have less heterozygosity and hence more *homozygous* gene pairs than the average of the population.

Inbreeding coefficient — A measurement of the increase in *homozygosity*; each unit is equal to a 1% increase in *homozygosity* relative to the average *homozygosity* in the base population.

Inbreeding depression — The decreased performance normally associated with accumulation of *inbreeding*. Many recessive genes result in undesired traits or decreased performance when they are expressed. Inbred animals have more recessive genes in the *homozygous* condition that are expressed and result in reduced performance or undesired traits.

Independent culling — When animals are culled if they do not meet all of the minimum levels of performance for a set of traits.

Introgression — A breeding strategy for transferring specific favorable alleles from a donor population to a recipient population. This would, for example, be of great interest for genes responsible for disease resistance, which could be *introgressed* into a susceptible but otherwise economically superior breed.

Karyotype — The appearance of the metaphase chromosomes of an individual or species, which shows the comparative size, shape, and morphology of the different chromosomes.

Lethal gene — A gene that results in the death of the animal.

Liability — Both internal (e.g., genetic merit) and external (e.g., nutrition, disease, exposure) forces that influence the expression of a threshold character (e.g., disease, conception, abnormalities, etc.).

Line-breeding — Mating of selected individuals from successive generations to produce animals with a high relationship to one or more selected ancestors. It is a mild form of *inbreeding*.

Linkage — Association of genes physically located on the same *chromosome*. A group of linked genes is called a *linkage group*.

Linkage map — A linear map of an experimental population that shows the position of its known genes and/or genetic markers relative to each other in terms of *recombination frequency*.

Locus, pl. loci — A fixed position on a *chromosome* occupied by a given *gene* or one of its *alleles*.

Major gene — A gene that has an easily recognizable and measurable effect on a characteristic.

Marker — Specific and identifiable sequences of the DNA molecule. These markers may or may not be functional genes.

Marker—assisted selection (MAS) — Selection for specific alleles using genetic markers.

Maternal heterosis — The advantage of the *crossbred* mother over the average of *purebred* mothers.

Mating systems — The rules which describe how selected breeds and/or individuals will be paired at mating.

Meiosis — The process by which the chromosome number of a reproductive cell becomes reduced to half the *diploid* (2n) or somatic number and results in the formation of eggs or sperm.

Migration — Movement of animals, and consequently genes, from one population to another.

Mitochondria — Small bodies in the cytoplasm of most plant and animal cells responsible for energy production.

Mitosis — Cell division process in which there is first a duplication of *chromosomes,* followed by migration of *chromosomes* to the ends of the spindle and a dividing of the *cytoplasm,* resulting in the formation of two *cells* with diploid (2n) number of *chromosomes*.

Molecular genetics — The branch of genetic studies that deals with hereditary transmission and variation on the molecular level. It deals with the *expression of genes* by studying the *DNA* sequences of *chromosomes*.

Multiple alleles — Three or more alternative forms of a *gene* representing the same locus in a given pair of *chromosomes*.

Mutation — A sudden change in the *genotype* of an organism. The term is most often used in reference to **point mutations** (changes in base sequence within a gene), but can refer to *chromosomal changes*.

Natural selection — Natural processes favoring reproduction by individuals that are better adapted, and tending to eliminate those less adapted to their environment.

Nucleus — Part of a *cell* containing *chromosomes* and surrounded by *cytoplasm*.

Outcrossing — Mating of individuals that are less closely related than the average of the population.

Overdominance — A form of *dominance* where the performance of the *heterozygote* exceeds that of the best *homozygote*.

Partial dominance — A form of *dominance* where the performance of the *heterozygote* is intermediate between the two *homozygotes*, but more closely resembles the performance of the *homozygous dominant* type.

Pedigree — Usually refers to *pedigree chart* or what a pedigree chart represents in genetics. It is a document to record the ancestry of an individual. A pedigree can also be used to illustrate the family structure or breeding scheme.

Penetrance — The proportion of the individuals with a particular gene combination that express the corresponding *trait*.

Permanent environmental effects — Environmental effects that result in permanent effects on the phenotypic expression of a trait. For example, severe mastitis during lactation may have a permanent effect on milk production and litter weaning weight for an animal in subsequent litters.

Phenotype — Actual exhibit of observable *traits*. Normally, it refers to characteristics of an individual such as size, shape, color, or performance.

Phenotypic correlation — When two traits tend to change in the same or different direction as a net result of genetic and environmental effects.

Phenotypic value — A performance record; a measure of an animal's performance for a trait.

Phenotypic variation — Variation in phenotype which results from variation in genetic and environmental effects on the individuals.

Pleiotropy — The property of a gene whereby it affects two or more characters, so that if the gene is segregating, it causes simultaneous variation in the characters it affects.

Polymorphism — Where *DNA* or *genes* have more than two forms or *alleles* in the population.

Population — Entire group of organisms of a kind that interbreed.

Population genetics — The branch of genetics which deals with frequencies of *alleles* in groups of individuals.

Progeny — Offspring or individuals resulting from specific matings.

Progeny test — A test used to help predict an individual's breeding values, involving multiple matings of that individual and evaluation of its offspring.

Protein — Any of a group of complex nitrogenous organic compounds that contain *amino acids* as their basic structural units, occur in all living matter, and are essential for the growth and repair of animal tissue.

Qualitative trait — A trait that can generally be classified into a limited number of categories, and the animal can be said to "possess" the quality or not. Examples include hair color, skin color, and ear stature.

Quantitative trait — A trait that is represented by an almost continuous distribution of measurements. Examples include average daily gain, backfat thickness, and height.

Quantitative trait locus (QTL) — A *locus* that affects a *quantitative trait*.

Random mating — A mating system in which animals are assigned as breeding pairs at random, without regard to genetic relationship or performance.

Recessive — Applies to one member of an *allelic pair* which lacks the ability to manifest itself when the other, *dominant,* member is present.

Reciprocal cross — A breeding scheme where males of breed A are mated to females of breed B and males of breed B are mated females of breed A.

Reciprocal recurrent selection — A method of selection for combining ability or heterosis. Selection within two lines is based on the performance of crossbred progeny produced by crossing the two lines.

Recombination — The observed new combinations of *DNA* segments, or *loci*, or *traits*, which are different from those combinations exhibited by the parents.

Recurrent selection — A method of selection for combining ability or *heterosis*. Selection within one line is based on performance of crossbred progeny from matings with a "tester" line.

Repeatability — The proportion of total phenotypic variation that is attributable to variations caused by genetic and permanent *environmental effects*. It is a measure of the degree to which early measures of a trait can predict later records of the same trait.

RNA — Ribonucleic acid, involved in the transcription of genetic information from DNA.

Segregation — The separation of paired *alleles* at *loci* during *germ cell* formation.

Selection — Any natural or artificial process favoring the survival and propagation of certain individuals in a population.

Selection criteria — The character(s) upon which selection decisions are based, with the intent of changing the character(s) in the *selection objective*.

Selection differential — The difference in mean performance of the selected group of animals relative to the mean performance of all animals available for *selection*.

Selection index — The combining of measurements from several sources into an estimate of genetic value; when more than one measurement on a trait, and/or measurements of the trait on relatives, and/or measurements of more than one trait are combined into a single estimate of overall genetic value.

Selection intensity — The proportion of animals selected to be parents relative to the total number available for selection. The smaller the proportion selected, the higher the selection intensity.

Selection objective — The character(s) which are intended to be modified by selection.

Sex chromosomes — The X or Y chromosomes.

Sex-influenced — Traits for which the expression depends on the sex of the individual.

Sex-limited — A trait that can be expressed only in one sex, such as milk production.

Sex linked — Genes that are located on the sex (X or Y) *chromosomes*.

Synthetic breed — See *composite breed*.

Zygote — The cell produced by the union of mature *gametes* (egg and sperm) in reproduction.