COURSE CODE:	PBS 505
COURSE TITLE:	**GENETIC METHODS IN PLANT BREEDING**
NUMBER OF UNITS:	2 Units
COURSE DURATION:	**Three hours a week**

COURSE DETAILS:

Course Coordinator: Prof. D.K Ojo B.Sc, M.Sc, Ph.D
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Office Location: Room 246 and 234
Other Lecturers: Dr. J.B.O Porbeni B.Sc, M.Sc, Ph.D

COURSE CONTENT:

Definition of plant breeding, Sources of genetic variability Significance of genetic variability. Selection methods (SM). Factors affecting (SM). Heterosis & examples Hybridization crossing methods –inbreeding/ outcrossing. Convergent breeding, Divergent breeding. Evaluation of inbred lines by: Single crosses; 3-way crosses, Performing top crosses, Diallel analysis. Combining ability. General & specific. Diallel analysis example. Testing of means: Phenotype & components of phenotypic variability. Probability in Plant Breeding. T-test, expectation of MS

COURSE REQUIREMENTS:

This is a compulsory course for all 500Level students of the Department of Plant Breeding and Seed Technology. In view of this, students are expected to participate in all the course activities and have a minimum of 75% attendance to be able to write the final examination.

READING LIST:

1. Allard, R.W. (1960). Principles of planting breeding. John Wiley and Sons. N.Y.
2. Christiansen, F.B. (1984). The definition and measurement of fitness. In: *Evolutionary ecology* (ed. Shorrocks B) pp65–79. Blackwell Scientific, Oxford by adding survival selection in the reproductive phase.
3. Darwin C (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* John Murray, London; modern reprint Charles Darwin, Julian Huxley (2003). *On The Origin of Species*. Signet Classics. ISBN 0-451-52906-5. Published online at The complete work of

Charles Darwin online: On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life .

4. FAOSTAT, (2006): Breeding has led to increases in crop yield worldwide: wheat 1961- 2005.
5. http://www.Wikipedia, (20011). Diallel cross.
6. http://www.Wikipedia, (20011). Heterosis.
7. http:// www. Encyclopedia Britannica, (2011). Heterosis.
8. Klug, W.S., and M.R. Cummings (2003). Concepts of Genetics. Pearson Education Inc., Upper Saddle river, N.Y.
9. Paul, S. A and Denys, N. W. (2008). *Thinking about Life: The History and Philosophy of Biology and Other Sciences*. *Springer*. p. 43.
10. McGinley, M., and J. Emmett Duffy, (2008). "Genetic variation." *In*: Encyclopedia of Earth. (Eds.) Cutler J. Cleveland (Washington, D.C.: Environmental Information Coalition, National Council for Science and the Environment). http://www.eoearth.org/article/Genetic_variation.
11. Rose. H., Rose, S. P.R. and Jencks, C. (2000). *Alas, Poor Darwin: Arguments Against Evolutionary Psychology*.

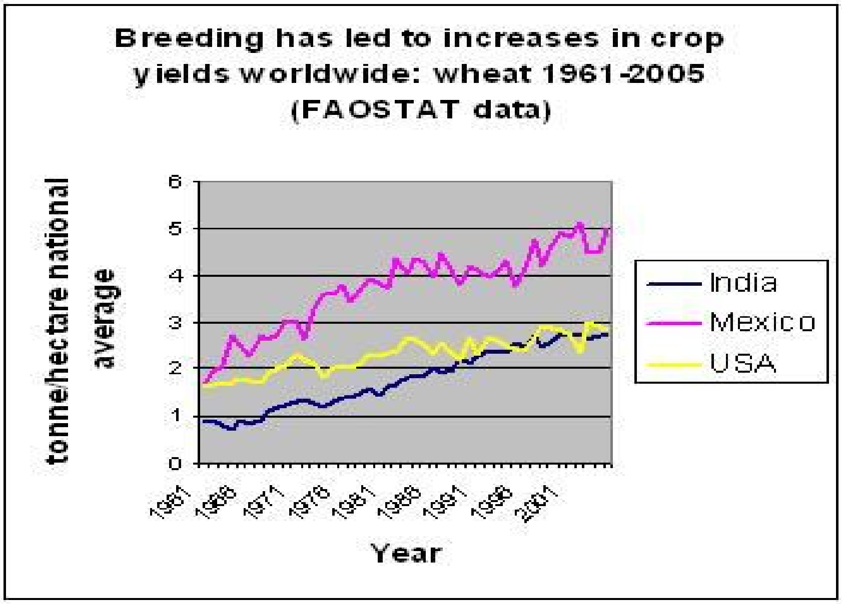
LECTURE NOTES

Plant breeding

Plant breeding is the purposeful manipulation of plant species in order to create desired genotypes and phenotypes for particular purposes, such as food production, forestry, and horticulture. Breeders have tried to introduce, into crop plants, traits that will increase the quality and yield of the crop; enhance their ability to tolerate harsh environmental conditions including salinity, high temperatures, and water shortage; enhance their ability to resist infection by viruses, fungi and bacteria, and enhance their ability to withstand insect pests and to tolerate herbicides.

Plant breeding is an artificial version of natural evolution, involving artificial selection of desired plant characteristics and artificial generation of genetic variation; it complements other farming innovations (such as introduction of new crops, grafting, changed crop rotations and tillage practices, irrigation, and integrated pest management) for improving crop productivity and land stewardship. Since 1930, crop breeding, in concert with these other innovations, has led to spectacular increases in crop yields especially with cereal grains. Plant breeding has been practiced since the beginning of human civilization, but rapid advances since 1900 have been driven by concepts and techniques developed in the science of genetics. This scientific plant breeding has contributed about 50% of the improvement in crop yield seen in the major cereal crops since 1930.

Plant breeding is practised by both government institutions and commercial enterprises. International development agencies believe that breeding new crops is important for ensuring food security and for developing sustainable agriculture by developing crops that minimize agriculture's impact on the environment.



FAOSTAT data December 2006

Domestication of plants is an artificial selection process conducted by farmers to produce plants with fewer undesirable traits than wild plants, and which makes them dependent on artificial (usually enhanced) environments for their continued existence. Many crops in present-day cultivation are the result of domestication in ancient times, about 5,000 years ago in the Old World and 3,000 years ago in the New World. In the Neolithic period, domestication took at least 1,000 years and possibly as much as 7,000 years. Today, all of our principal food crops come from domesticated varieties.

A bowl of indica (white, long grains) and japonica (brown, short grains) rice. From: 'Rice genome approaches completion'

A cultivated crop species that has evolved from wild populations due to selective pressures from traditional farmers is called a landrace. Landraces, which can be the result of natural forces or domestication, are plants (or animals) that are ideally suited to a particular region or environment. An example are the landraces of rice, *Oryza sativa* subspecies *indica*, which was developed in South Asia, and *Oryza sativa* subspecies *japonica*, which was developed in China.

Genetics and crop breeding intertwined

Plant breeders created the earliest artificial hybrids between different species (such as the feed cereal Triticale) in the 19th century, and progress in the science of genetics has been intertwined with crop breeding ever since. In 1903, W. L. Johannsen defined the heritable component of biological variability in experiments with a self-pollinated bean. In 1908, US plant breeder G. H. Scull discovered substantial crop yield improvements in interspecies hybrids of maize (now called 'hybrid vigor' or heterosis) with dramatic consequences for the development of a successful commercial corn-seed breeding industry, first in the USA and later elsewhere. Plant geneticists subsequently realized that hybridization can allow fuller exploitation of genetic diversity available in a plant population, and developed widely used interspecies hybrids for pearl millet, sorghum, rice and rapeseed (canola) crops.

Barbara McClintock developed fundamental concepts about chromosome behavior and cytogenetics with maize in the 1930s. Chromosome and genome relationships both within and between crops species have been the conceptual keystones to much successful crop breeding. It is now realized that most crops have undergone duplication of the minimal diploid set of chromosome at some stage, either as ancient duplications (as in the case of maize), or by hybridization between different species (as in allopolyploids such as wheat)

Protecting major crops against disease has rested on alien gene transfer into the crop variety using chromosomal engineering. This technique relies on manipulation of chromosome pairing at meiosis. In 1956, chromosomal engineering enabled Ernest Sears to translocate a segment of goatgrass (*Agilops umbellulata* Zhuk) chromosome that conferred resistance to leaf rust onto wheat chromosome 6B, and this achievement was followed by numerous successes in transfers of alien genes to crop plants by chromosome manipulation (the so-called wide-crosses)

Chromosomal engineering is facilitated by using X-ray radiation to promote chromosome breakage, plant tissue culture, and mutants such as *Ph-1* of wheat that relax normal strict pairing of homologous chromosomes in meiosis. It can be valuable to artificially promote doubling of chromosome number using colchicine in inter-species and inter-generic cross hybrid lines as a step to enable transfer of alien chromosome segments into crop germplasm.

The expansion of biotechnology after 1980 led to many advances in genetics which are accelerating the usually slow process of plant breeding and leading to important discoveries that improve plant breeding, such as molecular markers, plant genomics, RNA interference, and numerous gene characterizations such as the genes affecting abiotic stress responses and pest and pathogen tolerance.

Strategies for scientific plant breeding

The starting point for plant breeding is the identification of novel, useful traits in populations of parental organisms. The use of chemically or radiation induced mutation can also exploited to increase the range of useful genetic variability, and plant breeding exploits genetic recombination to generate novel combinations of traits. The end-result of lengthy selective breeding programs using these methods is "elite" varieties of high performing germplasm for major crops that are used widely in broad-acre farming.

Plant breeding strategies used by the International Maize and Wheat Improvement Center (CIMMYT) encapulate the way in which modern plant breeding should be pursued. CIMMYT wheat breeding strategies aim to achieve an optimal combination of the best genotypes, in the right environments, under appropriate crop management, and appropriate to the needs of the people who must implement and manage them.

Useful traits

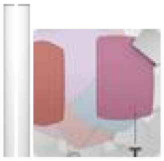
Techniques for increasing the available heritable variation in the initial population include introduction of new germplasm from distant geographical regions or from seed-bank collections, cross-pollination, either within the species, or between related species and genera

- including wide-crosses using wild relatives of domesticated plants to introduce pest resistant traits needed in domesticated varieties, and creation of mutations by irradiation or chemical treatment.

Variation: differences between parents and their offspring or among individuals in a population. It is an important aspect of breeding, for if all organism look alike there will be no bases for breeding work. Variation in a population or among a group of individual therefore is important to the breeder.

CELLS

DNA TO PROTEIN



PROTEIN SYNTHESIS,

HEREDITY & TRAITS (pass from one generation to the next)

VARIATION DOES EXIST EVEN IN ANIMAL OF THE SAME SPECIES.

Genetic variability is a measure of the tendency of individual genotypes in a population to vary from one another. Variability is different from genetic diversity, which is the amount of variation seen in a particular population. The variability of a trait describes how much that trait tends to vary in response to environmental and genetic influences.[1] Genetic variability in a population is important for biodiversity, because without variability, it becomes difficult for a population to adapt to environmental changes and therefore makes it more prone to extinction.

Variability is an important factor in evolution as it affects an individual's response to environmental stress and thus can lead to differential survival of organisms within a population due to natural selection of the most fit variants. Genetic variability also underlies the differential susceptibility of organisms to diseases and sensitivity to toxins or drugs — a fact that has driven increased interest in personalized medicine given the rise of the human genome project and efforts to map the extent of human genetic variation such as the HapMap project.

Causes

There are many sources of genetic variability in a population:

- Homologous recombination is a significant source of variability. During meiosis in sexual organisms, two homologous chromosomes from the male and female parents cross over one another and exchange genetic material. The chromosomes then split apart and are ready to form an offspring. Chromosomal crossover is random and is governed by its own set of genes that code for where crossovers can occur (in cis) and for the mechanism behind the exchange of DNA chunks (in trans). Being controlled by genes means that recombination is also variable in frequency, location, thus it can be selected to increase fitness by nature, because the more recombination the more variability and the more variability the easier it is for the population to handle changes

- Immigration, emigration, and translocation – each of these is the movement of an individual into or out of a population. When an individual comes from a previously genetically isolated population into a new one it will increase the genetic variability of the next generation if it reproduces.

- Polyploidy – having more than two homologous chromosomes allows for even more recombination during meiosis allowing for even more genetic variability in one's offspring.

- Diffuse centromeres – in asexual organisms where the offspring is an exact genetic copy of the parent, there are limited sources of genetic variability. One thing that increased variability, however, is having diffused instead of localized centromeres. Being diffused allows the chromatids to split apart in many different ways allowing for chromosome fragmentation and polyploidy creating more variability.

- Genetic mutations – contribute to the genetic variability within a population and can have positive, negative, or neutral effects on a fitness. This variability can be easily propagated throughout a population by natural selection if the mutation increases the affected individual's fitness and its effects will be minimized/ hidden if the mutation is deleterious. However, the smaller a population and its genetic variability are, the more likely the recessive/hidden deleterious mutations will show up causing genetic drift.

Sources of Variability/ Variation.

- Immigration of genes
- Mutation

Mutation—natural or spontaneous mutation
- induced mutation

Induced mutation: (a) use of chemicals e.g EMS, mustard gas, ethydiumbromide (b) Radiation e.g X-ray, UV, infrared ray.

Virtually every organism show individual differences in nature, these differences could be continuous or discontinuous.

i. Qualitative or discontinuous characteristics: possess only a few distinct phenotypes and can be grouped into distinct phenotypic classes. They are usually inherited in a Mendelian ratio e.g flower, pod and seed coat colour, seed coat texture- plant.

ii. Qualitative or continuous characteristics: these arise from 2 phenomena

(b) Many are polygenic i.e they are influenced by genes at many loci, and therefore many genotype are possible each producing a slightly different phenotype.

(c) When environmental factors affect the phenotype because environmental differences result in a single genotype producing a range of phenotype.

Examples of qualitative traits; height, yield, days to flowering or maturity, pod length etc (agronomic traits).

- Recombination
- Crossing Over

SELECTION

Natural selection is the nonrandom process by which biologic traits become more or less common in a population as a function of differential reproduction of their bearers. It is a key mechanism of evolution.

The genetic variation within a population of organisms may cause some individuals to survive and reproduce more successfully than others. Factors which affect reproductive success are also important, an issue which Charles Darwin developed in his ideas on sexual selection.

Natural selection acts on the phenotype, or the observable characteristics of an organism, but the genetic (heritable) basis of any phenotype which gives a reproductive advantage will become more common in a population (see allele frequency). Over time, this process can result in adaptations that specialize populations for particular ecological niches and may eventually result in the emergence of new species. In other words, natural selection is an important process (though not the only process) by which evolution takes place within a population of organisms. As opposed to artificial selection, in which humans favor specific traits, in natural selection the environment acts as a sieve through which only certain variations can pass.

Natural selection is one of the cornerstones of modern biology. The term was introduced by Darwin in his influential 1859 book *On the Origin of Species*,[1] in which natural selection was described as analogous to artificial selection, a process by which animals and plants with traits considered desirable by human breeders are systematically favored for reproduction. The concept of natural selection was originally developed in the absence of a valid theory of heredity; at the time of Darwin's writing, nothing was known of modern genetics. The union of traditional Darwinian evolution with subsequent discoveries in classical and molecular genetics is termed the *modern evolutionary synthesis*. Natural selection remains the primary explanation for adaptive evolution.

General principles

Typica and *carbonaria* morphs resting on the same tree. The light-colored *typica* (below the bark's scar) is hard to see on this pollution-free tree, camouflaging it from predators such as Great Tits.

Natural variation occurs among the individuals of any population of organisms. Many of these differences do not affect survival (such as differences in eye color in humans), but some differences may improve the chances of survival of a particular individual. A rabbit that runs faster than others may be more likely to escape from predators, and algae that are more efficient at extracting energy from sunlight will grow faster. Something that increases an animal's survival will often also include its reproductive rate; however, sometimes there is a trade-off between survival and current reproduction. Ultimately, what matters is total lifetime reproduction of the animal.

If the traits that give these individuals a reproductive advantage are also heritable, that is, passed from parent to child, then there will be a slightly higher proportion of fast rabbits or efficient algae in the next generation. This is known as *differential reproduction*. Even if the reproductive advantage is very slight, over many generations any heritable advantage will become dominant in the population. In this way the natural environment of an organism "selects" for traits that confer a reproductive advantage, causing gradual changes or evolution of life. This effect was first described and named by Charles Darwin.

The concept of natural selection predates the understanding of genetics, the mechanism of heredity for all known life forms. In modern terms, selection acts on an organism's phenotype, or observable characteristics, but it is the organism's genetic make-up or genotype that is inherited. The phenotype is the result of the genotype and the environment in which the organism lives Genotype-phenotype distinction).

This is the link between natural selection and genetics, as described in the modern evolutionary synthesis. Although a complete theory of evolution also requires an account of how genetic variation arises in the first place (such as by mutation and sexual reproduction) and includes other evolutionary mechanisms (such as genetic drift and gene flow), natural selection appears to be the most important mechanism for creating complex adaptations in nature.

Types of selection

Natural selection can act on any heritable phenotypic trait, and selective pressure can be produced by any aspect of the environment, including sexual selection and competition with members of the same or other species. However, this does not imply that natural selection is always directional and results in adaptive evolution; natural selection often results in the maintenance of the status quo by eliminating less fit variants.

The unit of selection can be the individual or it can be another level within the hierarchy of biological organization, such as genes, cells, and kin groups. There is still debate about whether natural selection acts at the level of groups or species to produce adaptations that benefit a larger, non-kin group. Likewise, there is debate as to whether selection at the molecular level prior to gene mutations and fertilization of the zygote should be ascribed to conventional natural selection because traditionally natural selection is an environmental and exterior force that acts upon a phenotype typically after birth. Some science journalists distinguish natural selection from gene selection by informally referencing selection of mutations as "pre-selection."

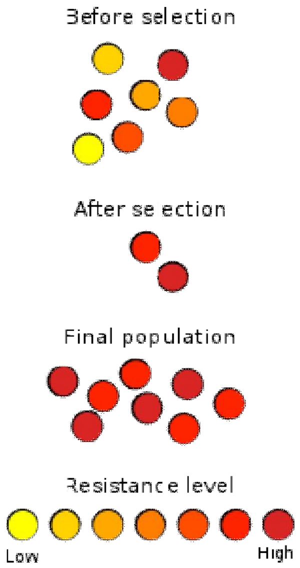
Selection at a different level such as the gene can result in an increase in fitness for that gene, while at the same time reducing the fitness of the individuals carrying that gene, in a process called intragenomic conflict. Overall, the combined effect of all selection pressures at various levels determines the overall fitness of an individual, and hence the outcome of natural selection.

The life cycle of a sexually reproducing organism. Various components of natural selection are indicated for each life stage.

Natural selection occurs at every life stage of an individual. An individual organism must survive until adulthood before it can reproduce, and selection of those that reach this stage is called *viability selection*. In many species, adults must compete with each other for mates via sexual selection, and success in this competition determines who will parent the next generation. When individuals can reproduce more than once, a longer survival in the reproductive phase increases the number of offspring, called *survival selection*.

The fecundity of both females and males (for example, giant sperm in certain species of *Drosophila*) can be limited via "fecundity selection". The viability of produced gametes can differ, while intragenomic conflicts such as meiotic drive between the haploid gametes can result in gametic or "genic selection". Finally, the union of some combinations of eggs and sperm might be more compatible than others; this is termed *compatibility selection*.

Examples of natural selection



Resistance to antibiotics is increased though the survival of individuals which are immune to the effects of the antibiotic, whose offspring then inherit the resistance, creating a new population of resistant bacteria.

A well-known example of natural selection in action is the development of antibiotic resistance in microorganisms. Since the discovery of penicillin in 1928 by Alexander Fleming, antibiotics have been used to fight bacterial diseases. Natural populations of bacteria contain, among their vast numbers of individual members, considerable variation in their genetic material, primarily as the result of mutations. When exposed to antibiotics, most bacteria die quickly, but some may have mutations that make them slightly less susceptible. If the exposure to antibiotics is short, these individuals will survive the treatment. This selective elimination of maladapted individuals from a population is natural selection.

These surviving bacteria will then reproduce again, producing the next generation. Due to the elimination of the maladapted individuals in the past generation, this population contains more bacteria that have some resistance against the antibiotic. At the same time, new mutations occur, contributing new genetic variation to the existing genetic variation. Spontaneous mutations are very rare, and advantageous mutations are even rarer. However, populations of bacteria are large enough that a few individuals will have beneficial mutations. If a new mutation reduces their susceptibility to an antibiotic, these individuals are more likely to survive when next confronted with that antibiotic.

Given enough time, and repeated exposure to the antibiotic, a population of antibiotic-resistant bacteria will emerge. This new changed population of antibiotic-resistant bacteria is optimally adapted to the context it evolved in. At the same time, it is not necessarily optimally adapted any more to the old antibiotic free environment. The end result of natural selection is two populations that are both optimally adapted to their specific environment, while both perform substandard in the other environment.

The widespread use and misuse of antibiotics has resulted in increased microbial resistance to antibiotics in clinical use, to the point that the methicillin-resistant *Staphylococcus aureus* (MRSA) has been described as a "superbug" because of the threat it poses to health and its relative invulnerability to existing drugs. Response strategies typically include the use of different, stronger antibiotics; however, new strains of MRSA have recently emerged that are resistant even to these drugs.[

This is an example of what is known as an evolutionary arms race, in which bacteria continue to develop strains that are less susceptible to antibiotics, while medical researchers continue to develop new antibiotics that can kill them. A similar situation occurs with pesticide resistance in plants and insects. Arms races are not necessarily induced by man; a well-documented example involves the spread of a gene in the butterfly Hypolimnas bolina suppressing male-killing activity by Wolbachia bacteria parasites on the island of Samoa, where the spread of the gene is known to have occurred over a period of just five years

Evolution by means of natural selection

A prerequisite for natural selection to result in adaptive evolution, novel traits and speciation, is the presence of heritable genetic variation that results in fitness differences. Genetic variation is the result of mutations, recombinations and alterations in the karyotype (the number, shape, size and internal arrangement of the chromosomes). Any of these changes might have an effect that is highly advantageous or highly disadvantageous, but large effects are very rare. In the past, most changes in the genetic material were considered neutral or close to neutral because they occurred in noncoding DNA or resulted in a synonymous substitution. However, recent research suggests that many mutations in non-coding DNA do have slight deleterious effects. Although both mutation rates and average fitness effects of mutations are dependent on the organism, estimates from data in humans have found that a majority of mutations are slightly deleterious.

The exuberant tail of the peacock is thought to be the result of sexual selection by females. This peacock is an albino; selection against albinos in nature is intense because they are easily spotted by predators or are unsuccessful in competition for mates.

By the definition of fitness, individuals with greater fitness are more likely to contribute offspring to the next generation, while individuals with lesser fitness are more likely to die early or fail to reproduce. As a result, alleles which on average result in greater fitness become more abundant in the next generation, while alleles which generally reduce fitness become rarer. If the selection forces remain the same for many generations, beneficial alleles become more and more abundant, until they dominate the population, while alleles with a lesser fitness disappear. In every generation, new mutations and re-combinations arise spontaneously, producing a new spectrum of phenotypes. Therefore, each new generation will be enriched by the increasing abundance of alleles that contribute to those traits that were favored by selection, enhancing these traits over successive generations.

Established traits are not immutable; traits that have high fitness in one environmental context may be much less fit if environmental conditions change. In the absence of natural selection to preserve such a trait, it will become more variable and deteriorate over time, possibly resulting in a vestigial manifestation of the trait, also called evolutionary baggage. In many circumstances, the apparently vestigial structure may retain a limited functionality, or may be co-opted for other advantageous traits in a phenomenon known as preadaptation. A famous example of a vestigial structure, the eye of the blind mole rat, is believed to retain function in photoperiod perception.

Speciation

Speciation requires selective mating, which result in a reduced gene flow. Selective mating can be the result of 1. Geographic isolation, 2. Behavioral isolation, or 3. Temporal isolation. For example, a change in the physical environment (geographic isolation by an extrinsic barrier) would follow number 1, a change in camouflage for number 2 or a shift in mating times (i.e., one species of deer shifts location and therefore changes its "rut") for number 3.

Over time, these subgroups might diverge radically to become different species, either because of differences in selection pressures on the different subgroups, or because different mutations arise spontaneously in the different populations, or because of founder effects – some potentially beneficial alleles may, by chance, be present in only one or other of two subgroups when they first become separated. A lesser-known mechanism of speciation occurs via hybridization, well-documented in plants and occasionally observed in species-rich groups of animals such as cichlid fishes. Such mechanisms of rapid speciation can reflect a mechanism of evolutionary change known as punctuated equilibrium, which suggests that evolutionary change and particularly speciation typically happens quickly after interrupting long periods of stasis.

Genetic changes within groups result in increasing incompatibility between the genomes of the two subgroups, thus reducing gene flow between the groups. Gene flow will effectively cease when the distinctive mutations characterizing each subgroup become fixed. As few as two mutations can result in speciation: if each mutation has a neutral or positive effect on fitness when they occur separately, but a negative effect when they occur together, then fixation of these genes in the respective subgroups will lead to two reproductively isolated populations. According to the biological species concept, these will be two different species.

Historical development

The modern theory of natural selection derives from the work of Charles Darwin in the nineteenth century.

Pre-Darwinian theories

Several ancient philosophers expressed the idea that nature produces a huge variety of creatures, apparently randomly, and that only those creatures survive that manage to provide for themselves and reproduce successfully; well-known examples include Empedocles and his intellectual successor, Lucretius, while related ideas were later refined by Aristotle. The struggle for existence was later described by Al-Jahiz, who argued that environmental factors influence animals to develop new characteristics to ensure survival

Abu Rayhan Biruni described the idea of artificial selection and argued that nature works in much the same way. Such classical arguments were reintroduced in the 18th century by Pierre Louis Maupertuis and others, including Charles Darwin's grandfather Erasmus Darwin. While these forerunners had an influence on Darwinism, they later had little influence on the trajectory of evolutionary thought after Charles Darwin.

Until the early 19th century, the prevailing view in Western societies was that differences between individuals of a species were uninteresting departures from their Platonic idealism (or typus) of created kinds. However, the theory of **uniformitarianism** in geology promoted the idea that simple, weak forces could act continuously over long periods of time to produce radical changes in the Earth's landscape. The success of this theory raised awareness of the vast scale of geological time and made plausible the idea that tiny, virtually imperceptible changes in successive generations could produce consequences on the scale of differences between species.

Early 19th century evolutionists such as Jean Baptiste Lamarck suggested the inheritance of acquired characteristics as a mechanism for evolutionary change; adaptive traits acquired by an organism during its lifetime could be inherited by that organism's progeny, eventually causing transmutation of species. This theory has come to be known as Lamarckism and was an influence on the anti-genetic ideas of the Stalinist Soviet biologist Trofim Lysenko.

Darwin's theory

In 1859, Charles Darwin set out his theory of evolution by natural selection as an explanation for adaptation and speciation. He defined natural selection as the "principle by which each slight variation [of a trait], if useful, is preserved". The concept was simple but powerful:

individuals best adapted to their environments are more likely to survive and reproduce. As long as there is some variation between them, there will be an inevitable selection of individuals with the most advantageous variations. If the variations are inherited, then differential reproductive success will lead to a progressive evolution of particular populations of a species, and populations that evolve to be sufficiently different eventually become different species.

Darwin's ideas were inspired by the observations that he had made on the *Beagle* voyage, and by the work of a political economist, the Reverend Thomas Malthus, who in *An Essay on the Principle of Population*, noted that population (if unchecked) increases exponentially whereas the food supply grows only arithmetically; thus inevitable limitations of resources would have demographic implications, leading to a "struggle for existence". When Darwin read Malthus in 1838 he was already primed by his work as a naturalist to appreciate the "struggle for existence" in nature and it struck him that as population outgrew resources, "favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The result of this would be the formation of new species."

Here is Darwin's own summary of the idea, which can be found in the fourth chapter of the *Origin*:

> If during the long course of ages and under varying conditions of life, organic beings vary at all in the several parts of their organization, and I think this cannot be disputed; if there be, owing to the high geometrical powers of increase of each species, at some age, season, or year, a severe struggle for life, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of existence, causing an infinite diversity in structure, constitution, and habits, to be advantageous to them, I think it would be a most extraordinary fact if no variation ever had occurred useful to each being's own welfare, in the same way as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance they will tend to produce offspring similarly characterized. This principle of preservation, I have called, for the sake of brevity, Natural Selection.

Once he had his theory "by which to work", Darwin was meticulous about gathering and refining evidence as his "prime hobby" before making his idea public. He was in the process of writing his "big book" to present his researches when the naturalist Alfred Russel Wallace independently conceived of the principle and described it in an essay he sent to Darwin to forward to Charles Lyell. Lyell and Joseph Dalton Hooker decided (without Wallace's knowledge) to present his essay together with unpublished writings which Darwin had sent to fellow naturalists, and *On the Tendency of Species to form Varieties; and on the Perpetuation of Varieties and Species by Natural Means of Selection* was read to the Linnean Society announcing co-discovery of the principle in July 1858. Darwin published a detailed account of his evidence and conclusions in *On the Origin of Species* in 1859. In the 3rd edition of 1861 Darwin acknowledged that others — notably William Charles Wells in 1813, and Patrick Matthew in 1831 — had proposed similar ideas, but had neither developed them nor presented them in notable scientific publications.

Darwin thought of natural selection by analogy to how farmers select crops or livestock for breeding, which he called "artificial selection"; in his early manuscripts he referred to a 'Nature' which would do the selection. At the time, other mechanisms of evolution such as evolution by genetic drift were not yet explicitly formulated, and Darwin believed that selection was likely only part of the story. For Darwin and his contemporaries, natural selection was essentially synonymous with evolution by natural selection. After the publication of *On the Origin of Species*, educated people generally accepted that evolution had occurred in some form. However, natural selection remained controversial as a mechanism, partly because it was perceived to be too weak to explain the range of observed characteristics of living organisms, and partly because even supporters of evolution balked at its "unguided" and non-progressive nature, a response that has been characterized as the single most significant impediment to the idea's acceptance.

However, some thinkers enthusiastically embraced natural selection; after reading Darwin, Herbert Spencer introduced the term *survival of the fittest*, which became a popular summary of the theory. The fifth edition of *On the Origin of Species* published in 1869 included Spencer's phrase as an alternative to natural selection, with credit given: "But the expression often used by Mr. Herbert Spencer, of the Survival of the Fittest, is more accurate, and is sometimes equally convenient." Although the phrase is still often used by non-biologists, modern biologists avoid it because it is tautological if "fittest" is read to mean "functionally superior" and is applied to individuals rather than considered as an averaged quantity over populations.

Modern evolutionary synthesis

Natural selection relies crucially on the idea of heredity, but it was developed long before the basic concepts of genetics. Although the Austrian monk Gregor Mendel, the father of modern genetics, was a contemporary of Darwin's, his work would lie in obscurity until the early 20th century. Only after the integration of Darwin's theory of evolution with a complex statistical appreciation of Gregor Mendel's 're-discovered' laws of inheritance did natural selection become generally accepted by scientists.

Methods of Selection

The choice of a selection method will determine the effectiveness of reaching a given goal in breeding. Plant Breeding is the conscious human effort needed to improve and develop new varieties of crop in order to satisfy the demands for human food and animal feed.

Objectives

(i) To discuss the genetic concepts that may help breeders to choose appropriate breeding strategies for different situations.
(ii) To discuss the different forms of plant material available and their possible uses in breeding progammes.
(iii) To describe and compare different selection plans for developing useful cultivars

A breeder strategy is a breeding program set up to improve certain characteristics in a crop plant. It is very important to analyse specific crop problems in depth before starting a breeding programme in order to minimize the risk of wrong choices and unexpected results. Characteristics of a breeding strategy such a breeding strategy should:

(1) Make an impact on the agricultural development of a region e.g increase yield, insect/disease resistance.
(2) Make economic, social and environmental impact on the people e.g better mechanization and commercialization of a crop, better growing conditions, smaller and cheap input and labour.
(3) Have realistic objective - not abstract.

(4) Be handled by a team of well-trained personnel

Selection and genetic variation

A portion of all genetic variation is functionally neutral in that it produces no phenotypic effect or significant difference in fitness; the hypothesis that this variation accounts for a large fraction of observed genetic diversity is known as the neutral theory of molecular evolution and was originated by Motoo Kimura. When genetic variation does not result in differences in fitness, selection cannot *directly* affect the frequency of such variation. As a result, the genetic variation at those sites will be higher than at sites where variation does influence fitness. However, after a period with no new mutation, the genetic variation at these sites will be eliminated due to genetic drift.

Mutation selection balance

Natural selection results in the reduction of genetic variation through the elimination of maladapted individuals and consequently of the mutations that caused the maladaptation. At the same time, new mutations occur, resulting in a mutation-selection balance. The exact outcome of the two processes depends both on the rate at which new mutations occur and on the strength of the natural selection, which is a function of how unfavorable the mutation proves to be. Consequently, changes in the mutation rate or the selection pressure will result in a different mutation-selection balance.

Genetic linkage

Genetic linkage occurs when the loci of two alleles are *linked*, or in close proximity to each other on the chromosome. During the formation of gametes, recombination of the genetic material results in reshuffling of the alleles. However, the chance that such a reshuffle occurs between two alleles depends on the distance between those alleles; the closer the alleles are to each other, the less likely it is that such a reshuffle will occur. Consequently, when selection targets one allele, this automatically results in selection of the other allele as well; through this mechanism, selection can have a strong influence on patterns of variation in the genome.

Selective sweeps occur when an allele becomes more common in a population as a result of positive selection. As the prevalence of one allele increases, linked alleles can also become more common, whether they are neutral or even slightly deleterious. This is called *genetic hitchhiking*. A strong selective sweep results in a region of the genome where the positively selected haplotype (the allele and its neighbours) are essentially the only ones that exist in the population.

Whether a selective sweep has occurred or not can be investigated by measuring linkage disequilibrium, or whether a given haplotype is overrepresented in the population. Normally, genetic recombination results in a reshuffling of the different alleles within a haplotype, and none of the haplotypes will dominate the population. However, during a selective sweep, selection for a specific allele will also result in selection of neighbouring alleles. Therefore, the presence of a block of strong linkage disequilibrium might indicate that there has been a 'recent' selective sweep near the center of the block, and this can be used to identify sites recently under selection.

Background selection is the opposite of a selective sweep. If a specific site experiences strong and persistent purifying selection, linked variation will tend to be weeded out along with it, producing a region in the genome of low overall variability. Because background selection is a result of deleterious new mutations, which can occur randomly in any haplotype, it does not produce clear blocks of linkage disequilibrium, although with low recombination it can still lead to slightly negative linkage disequilibrium overall.

Factors affecting Selection Methods

(a) Reproductive system of the plant

Self pollinating (autogamous) Vs Crossers (allogamous). Autogamous plants cannot be easily outcrossed to other plants due to functional or morphological barriers which have to be overcome by artificial techniques e.g emasculation. However, hybrids can be produced in certain self pollinating crops e.g. wheat, tomato, tobacco, cotton. Autogamous plants are homozygous.

It is easy to cross most allogamous plants by hand or by exposing female plant to desired pollen due to their hetrozygosity nature e.g maize.

(b) Heterosis

Heterosis has been used in the development of hybrid maize as high production costs are easily compensated for by higher yields in hybrids.

(c) Cytogenetic structure

The ploidy level of a crop can influence the expression of a particular character of that crop e.g

- *Tetraploidy:-* four (4) sets of genome is used to increase dry matter yield in forage crops.
- *Alloploidy:-* Multiples of different set of genomes is useful for creating new crop species such as triticale (wheat xrye)
- It is also used to transfer genes from the wild to cultivated crop genotypes manifestations of Heterosis.
  - (a) Increased size and productiveness
  - (b) Earlier maturity than either parents
  - (c) Greater resistance to disease, insect and environmental factors
  - (e) Increase number of leaves, nodes in the F_1

(d) Qualitative Vs. Quantitative Traits

Qualitative traits show simple Mendelian inheritance, controlled by one or 2 genes. Phenotypes in the F_2 have close resemblance with the parents. They are easily measured e.g flower, shape, specific resistance. Quantitative traits are continuous in their phenotypic expression and segregants in the F_2 are diverse cannot be grouped into distinct classes e.g response to light, temperature and water etc which are morpho/physiological; grain yield, total dry matter, protein and oil content, general disease resistance such traits are agronomic and have a complex inheritance and are controlled by many (major genes) with environment segregant in the F_2 diversed. These traits are improved by Recurrent Selection which leads to small but steady genetic gain to the trait in each selection cycle. Therefore, selection is faster when dealing with qualitative traits because unfavourable alleles are easily eliminated.

(e) Gene action

There are 3 possible genotypes in the Fn when a pair of gene is in a single locus involved Heterozygote (Hn) and the two homozygous (HH and h) (2Hh)

Additive gene action: absence of DOMINANCE in case of single locus i.e ∂^2_A = 100% ∂^2_G = 0%. There can be <u>additive gene action</u>. HH and hh similar can be substituted or dominance gene action all HH or Hh

HHHh and hh are genotypes
A d -a genotypic values (Falconer, 1981)
H is favourable allele (it adds to trait value)
H is unfavourable allele (it substracts from
a is additive effect
d is Dominance effect
Where gene action is additive d = 0
Alleles at a given locus act in an additive manner:∂^2_A = 66.62%
Where there is dominance gene$_2$ actions ∂^2_G = 33.33%
d is the different from zero and ∂^2_G large α sig GCA is warrant of additive gene action. The more the deviation from zero, the more important the dominant gene action will be.

Therefore, the breeding procedure chosen for a crop genotype will depend on the prevalence of gene action e.g additive gene action will be effective in accumulating favourable alleles in breeding materials especially in self-pollinating crops e.g Additive models accounted for almost the whole genetic variability in soyabeans which is autogamous with additive effects, unfavourable alleles can be eliminated at Hh & hh state.

Whole genetic variability in soyabeans which is autogamous hybrid varieties will show the highest performance. Dominance gene action is employed in hybrid seed production. This the most appropriate selection methods will be those that take advantage of heterosis and general & specific combining abilities. Recessive unfavourable alleles can be eliminated if they manifest at homozygous (hh) state. Therefore, selfing which increases homozygosity 9hh) alternated with crossing that recovers heterozygosity is the ideal breeding strategy under this condition.

(f) Heritability

Phenotype = Genotype + environment

$$h^2 = \frac{\partial^2_A}{\partial^2_P}$$

Where

$$S^2_P = S^2_G + \frac{\partial^2_{G\,x\,E}}{e} + \frac{\partial^2_E}{rxe}$$

∂^2_A = genetic variance

$\partial^2_{G\,x\,E}$ = genetic x environmental variance

∂^2_E = environmental variance = experimental error

e = number of environment

r = number of replication

From the above, it means that only the additive part of the variance is transmitted to the offspring.

h^2 will improve if we can reduce the environmental error and the genetic x environment component of the phenotypic variance i.e

- increase the number of replications (r)
- increase the number of sites (e) in a selection experiment to reduce ∂^2_E

Note

Replication is possible only if selection units are families (not if individual plants) or unless individual plants are clonally propagated.

Thus

Heritability of a trait (h^2) can be improved only if selection is made on a family basis. Improved genetic gain.

(g) Conventional Vs Special Methods

- Selection, testing, crossing, selfing, polyploidy, mutation breeding are all conventional methods.
- Tissue culture, genetic engineering, (genetic marker) methods are special methods.

A combination of both methods is the most likely avenue for future plant breeding. The choice depends on availability of time, facilities & expertise (trained & experienced personnel)

SOURCES OF GENETIC VARIABILITY

What is Plant Breeding – Give or explain 2 definitions of Plant Breeding

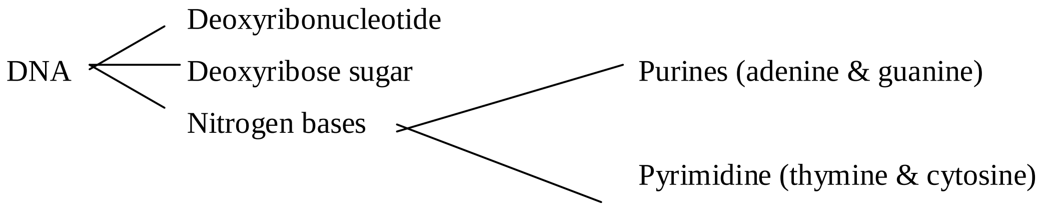
List the sources of Genetic var. needed in Plant Breeding Explain 2

Success in Plant Breeding depends on the genetic variability in the source population as plant breeding is a selection made, possible by the existence of variability. Selection acts on the existing variability but does not creation variability sources include

(a) Gene mutations
(b) Gene recombinations
(c) Direct gene manipulation or gene transfer
(d) Somaclonal variation
(e) Plant hybridization
(f) Plant introduction

Gene mutation & recombination occur naturally; gene transfer is made possible by the use of recombinant DNA techniques while somaclonal variations involve the application of tissue and cell culture techniques.

Gene mutation:- Sudden heritable change in genes structure. This occurs at random in nature or can occur due to environment effects.



(a) Accidental mutation may take place after a tautomeric shift of the (H) hydrogen atom which prevents the pairing of the bases in DNA

Normal pairing

A	T	C	G	A	T
I	I	I	I	I	I
T	A	G	C	T	A

A = T double

C = T triple

Abnormal

A - Adenine pairs
I - with guanine
G

As a result, different amino acids are bound resulting in the synthesis of different proteins. Chromosomal aberration (deletion, duplication inversion & translocation) also cause mutations.

In Micro organisms which have high reproductive rate, the number of mutation that occur in a single reproduction cycle is very large.

(b) Induced mutation also cause gene mutation x-rays, (irradiation) chemical mutages, fomaldehyler plenol, mustard gas, pyrimidine nitrous acid physical treatments are examples of mutagens. Note that many induced mutations are detrimental and disadvantageous to their carrier. Such mutation can be eliminated by natural or artificial selection.

(2) Gene recombination

This mans combination of genes from different parents that results in genetic variability. Assume that two parents differ in two pairs of allelic gene which are not linked, one is dominant over the other,

P_1 AAbb x aaBB P_2
F_1 AaBb

AaBb x AaBb
F_2 AABB – a new genotype
AAbb -
aaBB- Parental genotype
aabb – a new genotype

With intra or inter-allelic gene interactions, it is possible to obtain genotypes with traits that are not possessed by either parent. However, "transgression" is another source of genetic variability leading to segregation of traits in one or both directions with regards to the parental traits. It leads to the progenies in the F_2 populations either earlier than earlier parent, shorter than the parent or superior in food content than the better parent. A level of heterosis is thereby exhibited.

Note that planned hybridization of genetically diverse individuals after selection is the richest source of new genetic variability needed for plant breeding.

(3) Gene Transfer

It is now possible, with modern technology to isolate individual genes from an organism, clone them, transfer to a vector and incorporate them into another organisms. Efforts have been made to transfer gene by recombinant. DNA from one organisms to another in order to provoke an increased production of proteins used in chemical industry and pharmacy.

At inception, viruses or plasmids were mostly used as vectors of desirable genes. However, recent studies have shown that gene transfer is possible by direct injection of genes into the cell (protoplast) or into organelles by genetic engineering.

The application of the recombinant DNA technique has helped in

(a) Successful production of human insulin
(b) Successful production of human growth hormone used in the therapy of human dwarfs.
(c) Production of interferone used in the therapy against cancer and viral infection
(d) Increased production of proteins used in pharmacy and chemical industry

(4) Somaclonal variation (S.V.)

Variability observed in single-gene traits (colour, shape, size) as well as multi-gene traits (height, branching etc) as a result of the effects of genotype and environment on a plant is called S.V. It involves the application of tissue and cell culture techniques.

Plants that are grown from in vitro culture, normally give plants that are phenotypically and genotypicaly identical to the materials from which the tissues or cells have been taken. However, the culture medium, the age of tissues or cells in culture, genotype and effects of water, light and temperature, may bring about a large variability called somaclonal variability. The new plants so formed are called somaclones. The longer the tissue culture cycle, the more is the variation found especially when undifferentiated callus (calli) or cell suspensions or protoplasts are used in culture. Meristem and shoot tip cultures do not give much culture variation.

It has been suggested that the cell culture is a kind of “mutagenic treatment” because new mutations occur continuously in cell cultures.

(5) Plant Hybridization

Sexual crossing between plant parents that are genetically dissimilar. This involves making crosses within and between various plant species after careful selection merits of hybridization are that it comes out with new and desirable gene recombinations. It also allows for the vegetative use of the F_1 generation which frequently contains the best combination f genes of two parents. Hybridization results in gene recombination particularly when many parents are involved. It is the richest source of genetic diversity needed for crop improvement.

G_s = genetic advance under selection = grain from selection
depends on K, ∂_P and H

Such that

$G_s = K\partial_P H$

Where

Genetic advance under selection = gain from selection

(GS) = mean genetic value of source population

Mean genetic value of selected lines

Gs depends on K, ∂_p and H such that

$G_s = K\partial_p H$

K = selection differential taking into consideration the mean phenotypic value of selected (q) and original source (n) lines; the selection intensity and the phenotypic standard deviation (∂_P) k is expressed in standard deviation units, it is fairly stable and estimated as 2.06 for 5% selection in large samples from a normally distributed population.

For 1,2,5 and 10% selections intensity k = 2.64, 2.42, 2.06 and 1.76 respectively ∂_p = standard deviation which is the square root of phenotypic variance and H is the heritability in percentage.

Thus Gs is expressed in the unit of the character under measurement whereas GA is expressed as percentage (%) of the mean.

If phenotypic variance of seed yield in g/plot = 6355.48g

and heritability of seed yield = 39.0

$Gs = 2.06 \times \sqrt{6355.48} \times 0.39 = 64$g/plot

If mean yield per plot is 900g/plot

GA = 64/900 = 7.1%

Significant genetic variability can exist within local crop cultivars due to agricultural practices

(1) Absence of artificial selection

(2) Lack of seed quality control

(3) Use of mixed varieties for planting deliberate/accidental

(4) Natural cross-pollination and

(5) Spontaneous mutation

Advantage

Suitability of many local cultivars for individual and pedigree selection.

How to Evaluate Variability

Study variations in yield, yield components and other morphological characters of given local cultivars, number of branches, number of leaves, 100 seed weight, seed yield, number of pods/plant, number of seed/pod, pod length.

Observed and Expected gain per Selection Cycle

Note which of the components present the highest expected gain through selection per selection cycle.

Analyze the genetic variability of named character from chosen cultivars through individual plant selection form original population (S_0) and evaluate their progenies (S_1).

Heterosis

Heterosis, or **hybrid vigor**, or **outbreeding enhancement**, is the improved or increased function of any biological quality in a hybrid offspring. It is the occurrence of a genetically superior offspring from mixing the genes of its parents.

A mixed-breed dog

Heterosis (hybrid vigor): accelerated growth and increased dimensions, endurance, and fertility of various first-generation animal and plant hybrids. Heterosis is usually attenuated in the second and later generations. True heterosis, which is the ability of hybrids to leave a large number of fertile descendants, is distinguished from gigantism, which is the enlargement of the entire hybrid organism or of its individual parts. Heterosis is found in various multicellular animals and plants, including self-pollinating ones. Phenomena resembling heterosis are also observed in the sexual processes of some unicellular organisms. Heterosis often results in a considerable increase in the productivity and yield of agricultural animals and crops.

Heterosis and its converse, inbred depression, were already known to the ancient Greeks, particularly Aristotle. The first scientific studies of heterosis in plants were carried out by the German botanist J. Kölreuter (1760). Darwin generalized observations on the use of hybridizations (1876), thus greatly influencing the work of I. V. Michurin and many other breeders. The term “heterosis” was proposed in 1914 by the American geneticist G. Shull, who was the first to obtain double interlinear corn hybrids. In 1917, D. Jones developed the principles of a method of industrial cultivation of these hybrids. The application of hybridization in agriculture has increased over the years, stimulating theoretical investigation of heterosis. Species with marked heterosis have advantages in natural selection; thus, the phenomenon of heterosis increases and contributes to increased genetic variability. Often, stable genetic systems arise, ensuring predominant survival of heterozygotes by numerous genes.

Aside from the usual study of morphological traits, investigation of heterosis requires the application of physiological and biochemical methods, making it possible to detect fine differences between hybrids and the original forms. Heterosis has also begun to be studied at the molecular level. In particular, the structures of specific protein molecules of many hybrids (for example, enzymes and antigens) are being studied.

According to Darwin, heterosis depends on the conjunction of diverse hereditary tendencies in the fertilized egg. On the basis of this, two main hypotheses regarding the mechanism of heterosis were established. The hypothesis of heterozygosis (overdominance or single-gene heterosis) was proposed by the American researchers E. East and G. Shull. When they combine in the heterozygote, two states (two alleles) of one and the same gene reinforce each other in their action on the organism. Each gene controls the synthesis of a particular polypeptide. In heterozygotes a few different protein chains are synthesized instead of one, and often heteropolymers—that is, hybrid molecules—are formed. This process may be advantageous for the heterozygotes. The hypothesis of dominance (summation of dominant genes) was formulated by a number of American biologists, including A. V. Bruce (1910) and D. Jones (1917). Mutations (changes) of genes are, on the whole, harmful. A defense against them is increased dominance of normal genes for a population of genes (evolution of dominance). Combination in a hybrid of favorable dominant genes of two parents results in heterosis.

The two hypotheses on heterosis can be combined in the concept of genetic balance, which was developed by the American scientist D. Jones, the English scientist K. Mather, and the Russian geneticist N. V. Turbin. Obviously, heterosis is based on the interaction of both allelic and nonallelic genes; however, in all cases heterosis is associated with enhanced heterozygosity of the hybrid and with its biochemical enrichment, which also depends on an increase in the rate of metabolism.

Of particular practical and theoretical interest is the problem of the stabilization of heterosis. It can be solved by doubling sets of chromosomes, creating stable heterozygous structures, and using every possible form of apomixis, as well as by vegetative reproduction of hybrids. The effect of heterosis may also be fixed by doubling individual genes or small parts of chromosomes. The role of such duplications in evolution is very great; therefore, heterosis is considered an important stage in evolutionary progress.

Heterosis in agriculture. In the cultivation of plants, heterosis is an important way to increase productivity. Crops from heterotic hybrids are 10-30 percent greater than from ordinary varieties. In order to use heterosis in production, economically profitable means have been developed of obtaining hybrid seeds of corn, tomatoes, eggplants, peppers, onions, cucumbers, watermelons, gourds, sugar beets, sorghum, rye, lucerne, and other agricultural plants. A special position is occupied by a group of vegetatively reproducing plants—for example, a variety of potatoes and fruit and berry crops obtained from hybrid seeds—in which it is possible to fix heterosis in the descendants. To use heterosis for a practical purpose, intervarietal crossing of homozygous varieties of self-pollinating plants, intervarietal (interpopulation) crossing of self-pollinated lines of cross-pollinated plants (conjugate, trilinear, bilinear, quadrilinear, and multilinear ones), and strain-line crosses are done. The advantage of certain types of crossing for each agricultural crop is established on a basis of economic evaluation. Elimination of difficulties in obtaining hybrid seeds can be facilitated by the use of cytoplasmic male sterility, the property of incompatibility in some cross-pollinated plants, and other hereditary peculiarities in the structure of the flower and raceme, excluding large expenditures on castration. In choosing parental forms to obtain heterotic hybrids, their combination capacity is assessed. Originally, selection in this direction led to separation of the genotypes with better combination value from the population of free-pollinating varieties on the basis of inbreeding by forced self-pollination. Methods have been developed to evaluate and increase the combination capacity of lines and other groups of plants that are used for crossing.

The maximum effect in the application of heterosis is obtained with corn. The creation and introduction into production of corn hybrids made it possible to increase by 20-30 percent the total harvests of grain on the enormous areas occupied by that crop in various countries of the world. Corn hybrids have been created that combine high yield and good seed quality, drought resistance, and immunity to various diseases. Heterotic sorghum hybrids (Early 1 hybrid, Rise hybrid) and heterotic intervarietal sugar beet hybrids, of which the Ialtushkovskii hybrid has become most widespread, have been zoned. A line of sugar beet with a sterile pollen is being used increasingly to obtain heterotic forms. The phenomena of heterosis are also established with many vegetable and oil-yielding crops. First results have been obtained in studying heterosis in first-generation wheat hybrids, and sterile analogues and fertility reducers produced from sources of cytoplasmic male sterility in wheat have been discovered.

In livestock breeding the phenomena of heterosis are observed in hybridization—intervarietal and intravarietal (interlinear) crossing. Heterosis causes a notable increase in the productivity of agricultural animals, and it has become most widely used in industrial crossing. In poultry farming, when egg-producing varieties of chickens are crossed—for example, leghorns with Australops or Rhode Islands—the egg production of first-generation crosses increases by 20-25 eggs per year. The crossing of meat breeds with meat-egg breeds of chickens improves meat quality. According to a complex of traits, heterosis is obtained when crossing closely related lines of fowls of one breed or by intervarietal crossing. In pig, sheep, and cattle raising, industrial crossing is used to obtain heterosis for meat productivity, which is manifested in earlier maturation, increased live eights, increased dressing percentage, and improved quality of the carcass. Meat-lard (combined) breeds of pigs are crossed with meat varieties of boars. Local breeds of small, low-productivity sheep are crossed with meat-wool sheep, and fine wool parents are crossed with early maturing meat or semifine wool breeds. To raise meat productivity, milk cows, milk-meat, and local meat breeds are crossed with specialized meat breeds of bulls

Genetic basis of heterosis

Two competing hypotheses, not necessarily mutually exclusive, have been developed to explain hybrid vigor. The **dominance hypothesis** attributes the superiority of hybrids to the suppression of undesirable (deleterious) recessive alleles from one parent by dominant alleles from the other. It attributes the poor performance of inbred strains to the loss of genetic diversity, with the strains becoming purely homozygous deleterious alleles at many loci. The **overdominance hypothesis** states that some combinations of alleles (which can be obtained by crossing two inbred strains) are especially advantageous when paired in a heterozygous individual. The concept of heterozygote advantage/overdominance is not restricted to hybrid lineages. This hypothesis is commonly invoked to explain the persistence of many alleles (most famously the erythrocyte-sickling allele) that are harmful in homozygotes; in normal circumstances, such harmful alleles would be removed from a population through the process of natural selection. Like the dominance hypothesis, it attributes the poor performance of many inbred strains to a high frequency of these harmful recessive alleles and the associated high frequency of homozygous-recessive genotypes.

Hybrid corn

Nearly all field corn (maize) grown in most developed nations exhibits heterosis. Modern corn hybrids substantially out yield conventional cultivars and respond better to fertilizer.

Corn heterosis was famously demonstrated in the early 20th century by George H. Shull and Edward M. East after hybrid corn was invented by Dr. William James Beal of Michigan State University based on work begun in 1879 at the urging of Charles Darwin. Dr. Beal's work led to the first published account of a field experiment demonstrating hybrid vigor in corn, by Eugene Davenport and Perry Holden, 1881. These various pioneers of botany and related fields showed that crosses of inbred lines made from a Southern dent and a Northern flint, respectively, showed substantial heterosis and outyielded conventional cultivars of that era. However, at that time such hybrids could not be economically made on a large scale for use by farmers. Donald F. Jones at the Connecticut Agricultural Experiment Station, New Haven invented the first practical method of producing a high-yielding hybrid maize in 1914-1917. Jones' method produced a double-cross hybrid, which requires two crossing steps working from four distinct original inbred lines. Later work by corn breeders produced inbred lines with sufficient vigor for practical production of a commercial hybrid in a single step, the single-cross hybrids. Single-cross hybrids are made from just two original parent inbreds. They are generally more vigorous and also more uniform than the earlier double-cross hybrids. The process of creating these hybrids often involves detasseling.

Hybrid livestock

The concept of heterosis is also applied in the production of commercial livestock. In cattle, hybrids between Black Angus and Hereford produce a hybrid known as a "Black Baldy". In swine, "blue butts" are produced by the cross of Hampshire and Yorkshire. Other, more exotic hybrids such as "beefalo" are also used for specialty markets.

Within poultry, sex-linked genes have been used to create hybrids in which males and females can be sorted at one day old by color. Specific genes used for this are genes for barring and wing feather growth. Crosses of this sort create what are sold as Black Sex-links, Red Sex-links, and various other crosses that are known by trade names.

Commercial broilers are produced by crossing different strains of White Rocks and White Cornish, the Cornish providing a large frame and the Rocks providing the fast rate of gain. The hybrid vigor produced allows the production of uniform birds with a marketable carcass at 6–9 weeks of age.

Hybridization

The crossing of organisms differing in heredity—that is, in one or more pairs of alleles (conditions of genes) and consequently in one or more pairs of traits and properties. The crossing of individuals belonging to different species or even to less closely related taxonomic categories is called distant hybridization. The crossing of subspecies, varieties, or breeds is called intraspecific hybridization. The process of hybridization—especially natural hybridization— was observed in very ancient times. Hybrid animals (for example, mules) existed as early as the second millennium B.C.. The possibility of producing hybrids artificially was first suggested by the German scientist R. Camerarius (1694). The first to carry out artificial hybridization was the English horticulturist T. Fairchild, who crossed different species of pinks in 1717. The founder of teaching on sex and hybridization in plants is thought to be J. G. Kolreuter, who obtained hybrids of two tobacco species—*Nicotiana paniculata* and *N. rustica* (1760). G. Mendel's experiments on the hybridization of peas laid the scientific foundation of genetics, and Darwin performed an enormous number of experiments on hybridization.

The essence of hybridization is the fusion during fertilization of genotypically different sex cells and the development from the zygote of a new organism that combines the hereditary disposition of the parents. Copulation in unicellular organisms is also included among the phenomena of hybridization. The first generation of hybrids is often characterized by heterosis, which is manifested in better capacity for adaptation and greater fertility and viability of organisms. Hybridization as well as mutations are the main sources of hereditary variation, which is one of the main factors in evolution.

In natural hybridization and in artificial hybridization that is carried out by man for breeding and other purposes, flowers of the maternal form are pollinated with pollen from another species (variety) of plant, or animals of different species (subspecies, breeds) are mated. The sexual process guarantees the combining of genomes and results in the union of the nuclei of gametes—karyogamy. Therefore, it is impossible to obtain so-called vegetative hybrids. The "vegetative" hybrids described by some investigators are simply tissue chimeras.

In livestock breeding, intraspecific hybridization is a method of industrial breeding by which individuals of different breeds or strains are mated. Distant hybridization in animals is the obtaining of hybrids between varieties, species, and genera—for example, the crossing of fine-wooled sheep and Pamir argalis or cattle and zebus. This is difficult to accomplish, and the hybrids are generally sterile.

In 1935 the Soviet geneticist G. D. Karpechenko made a distinction between congruent crossings, or hybridization, and incongruent crossings in plants. Congruent crossings are intraspecific and sometimes interspecific crossings in which parental pairs with homologous chromosomes are crossed and the offspring are fertile. Incongruent crossings are generally distant crossings—that is, crossings of two individuals with structurally incompatible chromosomes and differences in the chromosome number or cytoplasm. The offspring are partly or completely sterile and the nature of the segregation is complex.

Crossings may be direct or reciprocal. For example, the hybrids ♂ A × ♀B and ♀B + ♂ A are reciprocal. If a hybridis crossed with one of the parental forms, the crossing is called a backcross. A testcross involves backcrossing a hybrid with a parent that is recessive for the trait under study. This is done to establish the hybrid's heterozygosity, linkage groups, or the frequency of crossing over between linked genes. Repeated backcrossing of a hybrid with one of the parents is called saturation. It is used to introduce into genotype A the traits of genotype B or to transfer the genome to the cytoplasm of another variety, subspecies, or species. There are also complex crossings called convergent crossings. First the parental varieties are crossed in pairs. The hybrids are then crossed with each other, and the newly produced hybrids are crossed with each other. In such cases individual hybrids often have valuable combinations of properties and traits.

Hybridization is widely used in breeding. Depending on the purpose of hybridization, there may be "combination" breeding to combine the desirable traits of the parental forms and "transgressive" breeding to obtain and select genotypes that are superior to parents in the bred trait.

Hybridization: It is the crossing of two plants differing from each other in one or more characters to get offsprings with new desirable characters, as a result of genetic recombinations. In hybridization, it is possible to combine all good characters present in different varieties in a single variety. The hybrid formed is superior over either parent in one or more characters. It is known as hybrid vigour or heterosis. The term heterosis was coined by ShuII (1914)

Based on the taxonomic relationship of the parental plants involved in a cross hybridization may be

i. Intravarietal ii. Intervarietal iii. Interspecific or iv. Intergeneric

• **Intravarietal hybridization** : This is a cross between two plants of the same variety but with different genotype. This method is helpful for the improvement of self pollinated crops.

• **Intervarietal hybridization :** It is also called intraspecific hybridization where the cross in between plants of two different varieties of same species. This is used in the improvement of self pollinated as well as some cross pollinated crops. Some improved varieties obtained through intervarietal hybridization are

i. Wheat: NP 52 x NP 165 NP 710 V '

ii. Cotton : Malvi 8 x Jarlia —» Maljari

iii. Tomato : Sioux x Meeruti —» Pusarubi planted to produce high yeilding double cross seeds.

• **Interspecific hybridization :** This is a cross between plants of different species belong to the same genus. This type of cross is mainly used to produce varieties resistant to disease, drought, pest and salinity. Genes for resistance present in wild species are brought into a hybrid by repeated crossing between the local species and wild species. Resistant varieties of wheat, potato, tomato, sugarcane etc. have been obtained by this method :

i. Cotton: *Gossypium hirsutum* x *G. arborium —» Deviraj. G. hirsutum* x *G. herbaceum —> Devitej*

ii. Potato : (*Solatium curtilobum* x *Solatium tuberosum)* x *Solatium andigena —> Kufri Kuber*

iii. Tomato: *Lycopersicum esculentum* x *L. pimpinellifolium —> Pusa red plum*

iv. Sugar cane: All the sugarcane varieties now in cultivation have been developed from complex crosses between *Saccharum officinarum, S. barberi, S. robustum* and *S.*

spontaneum. S. spontaneum has been used to combine- its hardiness and disease resistance with the high sugar content and high yielding ability of *S. officinarum.*

- **Intergeneric hybridization :** This is a cross between plants of different genera belonging to the same family. It is the most difficult of all types of crosses. Hybrids produced by this method are both scientifically as well as agriculturally significant. Hybrids produced by this method are:

i. Wheat x Rye Triticale

ii. Raphanus (Radish) x Brassica (Cabbage) Raphanobrassica (Rabbage)

iii. Brinjal x Tomato —> Bromato

iv. Sugarcane x Sorghum —> Sugarcane Sorghum

Technique of Hybridization

Hybridization can be done only by skilled persons. The technique of hybridization comprises the following steps : i. selection and isolation of parents; ii. emasculation ; iii. bagging, iv. collection of pollen grains,-v. crossing, vi. Tagging, vii. Harvesting hybrid seed and raising F_1 generation plants, viii. production of F_2 generation; ix. Trials, multiplication and distribution.

For this purpose a breeder must have the following appliances in his Kit:

a. Forceps, b. Scissors, c. Needles, d. Scalpel, e. Hair brush (f) Alcohol bottle and (g.) Labels

- **Selection and isolation of parents:** Two healthy locally available plants with desirable characters are selected. Then these parent plants are grown separately on isolated plots to avoid cross pollination. These plants are self pollinated for 6 - 8 generations till the majority of plants become homozygous and true breeding. The last generations of both the parents are used for further steps of hybridization.

- **Emasculation:** It is the removal of stamens from one of the parents (if bisexual) before they release their pollen grains. Emasculation may be done by removing

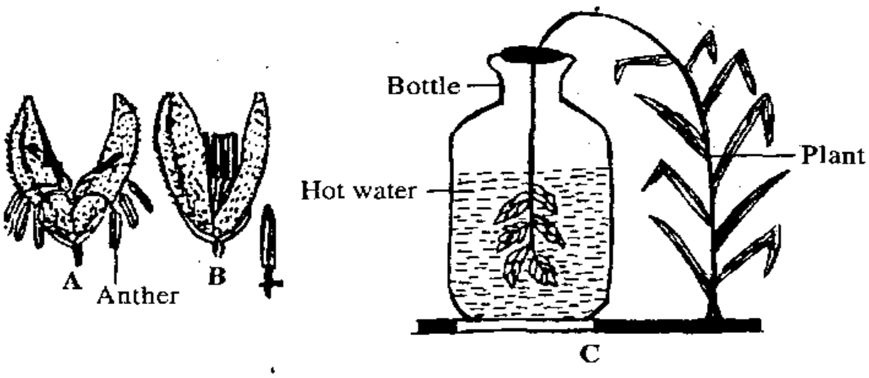


Fig. 2.5.1 : Emasculation technique. Removal of anthers by forceps in rice spikelet. **A.** Spikelet **B.** After opening the flower to removal of anthers by forceps **C.** Emasculation by hot water treatment.

anthers with the help of forceps in plants with large flowers; or by dipping the flower buds in hot water (4 - 53°C) or in ethyl alcohol for about 3-10 minutes in plants with small flowers. (Fig. 2.5.1).

Emasculation of stamens in bisexual flowers prevents the process of self pollination.

- **Bagging:** Soon after emasculation, the flowers are covered by polythene bags to prevent cross pollination by undesired pollen grains. The polythene bags are tied at the base of flower or inflorescence by threads or copper wires. (Fig. 2.5.2)

- **Crossing:** Pollen grains are collected from the flowers of other parent plant. When the stigma of emasculated flowers matures, the polythene bag is removed and the stigma is rusted with pollen grains collected. The flowers are again bagged immediately. It is advisable to perform crossing early in the morning as in most of the crops stigma become receptive at different times in the morning.

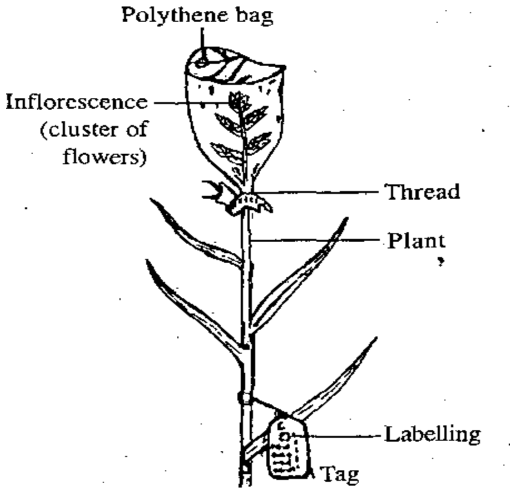


Fig. 2.5.2 : Bagging and tagging at the time of hybridization

- **Tagging:** The flowers thus crossed are suitably labelled. A tag (label) with relevant information is attached to the plant. The tag should contain :(i.) date of crossing, (ii.) note about female plant, (iii.) note about the male plant, (iv.) serial number in the record book : and (v.) remarks, if any.

- **Harvesting hybrid seed and raising Fn generation:** When the seeds mature, the polythene bags are removed. Seeds are harvested, dried, cleaned and stored properly along with its label. In the next season, the seeds are sown in the field to raise F, generation plants. Traits in these hybrid plants are studied.

- **Production of F_2 generation plants:** F, generation plants are selfed to get F_2 generation plants. F_2 plants with desirable characters are carefully identified and developed further.

- **Trials, multiplication and distribution:** F_2 plants with desirable characters are cultivated selected generation are distributed to the farmers. Different crop plants have been developed by the hybridization techniques. Some of them are

i. Wheat : NP 165, NP 710 etc.

ii. Rice : Jaya, Padma, Sabarmati, Krishna

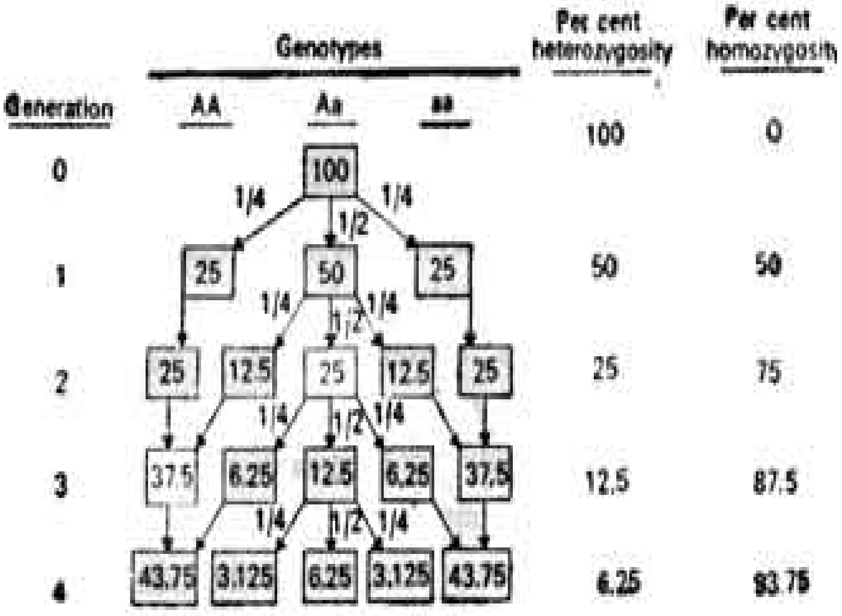
iii. Maize : Deccan, Sweet maize, Ganga etc

iv. Tomato : Pusa ruby, Pusa red plum etc.

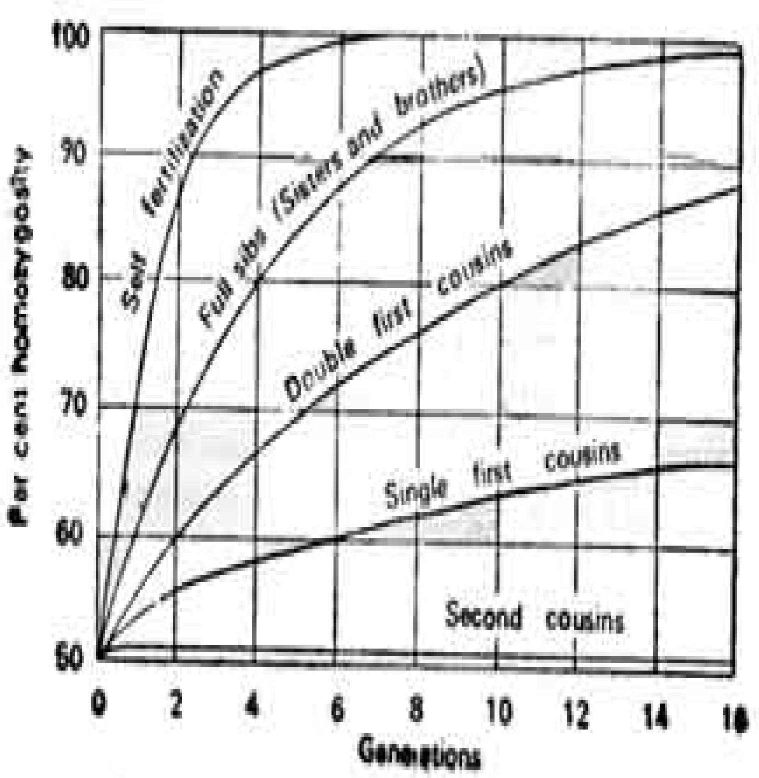
v. Cotton : Deviraj, Devitej, Laxmi etc.

Genetic Effects of Inbreeding

The continuous inbreeding results, genetically, in homozygosity. It produces homozygous stocks of dominant or recessive genes and eliminate heterozygosity from the inbreed population. For example, if we start with a population containing 100 heterozygous individuals (Aa) as shown in figure, the expected number of homozygous genotypes is increased by 50% due to selfing or inbreeding in each generation.



Thus, due to inbreeding in each generation the heterozygosity is reduced by 50% and after10 generations we can expect the total elimination of heterozygosity from the inbred line and production of two homozygous or pure lines. But, because a heterozygous individual possesses several heterozygous allelic pairs, therefore, we can conclude that inbreeding will operate on all gene loci to produce totally pure or homozygous offsprings. In man if inbreeding continued over a number of generations it results in increasing homozygosity, but somewhat slowly. The different types of inbreedings and their corresponding increase in homozygosity have been graphically illustrated as follows:



Cross Breeding

Mating of individuals from entirely different races or even different species is called cross breeding. This represents the most extreme form of out breeding that is possible among animals. Cross breeding produces sterile hybrids in comparison to normal outbreedings.

Example- The mule is a heterotic individual which had been produced by cross breeding of a male donkey (*Equus asimus*, 2n=62) with the female horse (*Equus caballus*, 2n=64). It displays a conspicuous vigorosity and because of this it has served mankind as a patient beast of burden since time immemorial.

Genetical Basis of Heterosis

The genetical basis of heterosis is still a subject of controversy and following two theories have been propounded to explain it:

1. Over dominance theory of heterosis-The over dominance theory or physiologic stimulation hypothesis of Shull (1874-1954) considers heterozygosity to have stimulating effect on the heterosis of hybrid individual. Heterozygosity itself was thus considered to be the controlling factor.

Example-If we suppose that four gene loci are contributing to a quantitative trait, homozygous recessive genotype contribute 1 unit to the phenotype, heterozygous genotype contribute 2 units to the phenotype and homozygous dominant genotypes contribute Ii units. Then, the results can be represented as follows:

2. Dominance theory of heterosis- The dominance theory of heterosis holds that increased vigour and size in a hybrid is due to combination of favourable growth genes by crossing two inbred races. In other words, the hybrid vigour is a result of action and interaction of dominant or fitness factors or cumulative (polygenic) effect of dominant genes. Example- If we suppose that a quantitative trait is governed by four genes. Each recessive genotype contributes on unit to the phenotype and each dominant genotype contributes two units to the phenotype. An out cross (out breeding) between two inbred lines can produce more heterotic F1, individuals than the parents. in the following manner:

Parents:	AABBccdd	X	aabbCCDD
Phenotypic value:	11/2+11/2+1+1=5	↓	1+1+11/2+11/2=5
F_1		AaBbCcDd 2+2+2+2=8	
Parents:	AAbbCCdd	X	aaBBccDD
Phenotypic value:	2+1+2+1=6	↓	1+2+1+2=6
F_1		AaBbCcDd 2+2+2+2=8	

Crossing Methods:

Convergent breeding (crossing):- Used for the improvement of a single trait or a couple of traits in an otherwise good cultivar taking cognizance of the other positive traits of that cultivar also called backcross method.

Initial crossing	A	x	B
	Recurrent parent		donor
1st backcross (50% genes from A	F_1 x A		
2nd backcross (75% A)		BC_1F_1 x A	
3rd backcross (87.5%A)		BC_2F_1 x A	
4th backcross (93.7% A)		BC_3F_1 x A	
5th backcross (96.9% A)		BC_4F_1 x A	
6th backcross (98.4% A)		BC_5F_1 x A	

Used to incorporate a resistance into a recurrent parent without changing its original trait. The above is a complete backcrossing because the current parent has been reconstituted – used when the donor parent posses a large number of negative traits but with one highly valued positive trait.

However incomplete backcrossing is recommended i.e one or two backcrosses with the recurrent parent when the donor parent posses a number of other positive traits.

Divergent Method (breeding):- Used in the evaluating of inbred lines also known as recombination because it makes use of genetically diverse parents in order to recombine their desirable traits.

(i) the single cross method A x B

(ii) three-way cross (A x B) x C

↓

F_1 x C

(iii) Successive cross [(AxB)xC]xD

(iv) Double cross (AxB) x (C xD)

(iv) Diallel crosses

A x B

↓

F1x C

↓

F1x D

↓

selection

Used to pinpoint parents (from a large bulk) capable of producing heterotic F_1 hybrids or those capable of producing large number of superior progencies.

One may have 6 new parents A,B,C,D,E,F.

AxB
AxC BxC 15 cross combinations
AxD BxD CxD
AxE BxE CxE DxE
AxF BxF CxF DxF ExF
6C2 = 6x5½ = 15
n – (n-1)/2

Method of diallel cross is used exclusively for genetic studies because it gives information on the effect of a number of genes, combining ability and gene interaction.

* It is not used in the breeding of self pollinated plants

(a) Genetics = science of heredity and variation (Bateson, 1906)

(b) Gene = unit of heredity e.g gene A or a

(c) Allele = (formally allelomorph meaning ‘other) is one of the two or more forms of a gene. Alternative form of a gene A, a are both alleles of the ‘A’ gene.

(d) Genotype = genetic constitution (or hereditary makeup) of an organism e.g AA, Aa, aa are genotypes

(e) Phenotype = the physical appearance of the organism in terms of colour, weight, height.

(f) Homozygousity = situation when ‘both genes in an individual are the same e.g Genotype AA have both genes the same also SS, aa etc.

(g) Heterozygousity = both genes different as Aa, Ss.

Reciprocal cross does not produce different F_1 genotypes from the main cross except that a trait is inherited through the female i.e unless there is cytoplasmic inheritance e.g

$$\left.\begin{array}{lllll} AA & x & aa & = & Aa = F_1 \\ aa & x & AA & = & Aa = F_{1(R)} \end{array}\right\} \begin{array}{l}\text{similar} \\ \text{genotypes}\end{array}$$

Both F1 and $F_{1(R)}$ are similar except the gene contributions are made by different species. Maternal influence if F_1 in main cross differs from the F_1 in the reciprocal cross.

*The cytoplasmic content of the egg is determined by the female parent content is temporary. Phenotypic expression of homozygous, recessive condition is delayed by one generation though the genotype is expressed in the present generation; its effect are temporary.

Phenotype is not consistent with the genotype in which case, the genetic control is in the nucleus but the cytoplasm has temporary influence.

No maternal influence, no reciprocal difference if the 2 F_1s are similar.

Normal transmission (or inheritance) of character is through the sperm which contributes little or no cytoplasm, but rather through the nucleus i.e it is the nucleus that determines the genotype.

*Additive gene action = absence of dominance in the case of single locus i.e the effect of substituting gene A for a.

Both AA and Aa are dominant genotypes.

Crop Improvement by Breeding

Introduction of alien variation

An increase in the precision of selection

An increase in the speed of selection

Modification of the breeding system

A decrease in the generation time

A more precise definition of breeding objective

Hybrid Varieties

These are varieties or F_1 population obtained by crossing (hybridizing) populations [such as inbreds, clones or open-pollinated varieties] that are genetically diverse. Hybrid varieties are F_1 populations used for commercial planting because of their higher hybrid vigour (heterosis).

These can be obtained from

(a) Single cross (AxB)
(b) 3-way cross (AxB)xC
(c) Double cross (AxB) x (CxD)

In open-pollinated crop like maize Inbred lines are used (lines that are self-pollinated over a long generation i.e over generations of inbreeding). *Homozygosity is attained after 5 or 6 generations. Inbreds are never better than their parents but early testing of inbred lines for combining is used to eliminate lines that may not produce superior progenies upon further inbreeding.

To obtain inbred lines:

(1) Select plant parents
    (a) that the vigorous (good vigour)
    (b) that are free from diseases
    (c) that have desirable characters e.g
        (i) increased seed size or productiveness
        (ii) earlier maturity than either parent
        (iii) greater resistance to diseases, pests or environmental stress
        (iv) increased number of nodes, leaves, pods in F1
(2) Self the selected plants to produce homozygous inbred lines A,B,C,D,E,F etc
(3) Cross AxB, AxC, CxD single double 3-way

Evaluation of Inbreds

(a) as single crosses early testing of inbred lines for combining ability is used to eliminate lines that my not produce superior progenies upon further inbreeding with every n line developed evaluate. Detassel inbred Aa(n-1)/2 or single crosses over tassel A with a tassel bag. Also cover the ear of inbred B to prevent self pollination.

(b) by 3-way crosses

(c) by performing top-crosses crossing inbred with a tester to test general combining ability of the top-cross is cross between a clone, an inbred selection or line and a common pollen parent. ○ +

Topcrosses	Line selection	x	tester
	Inbred	x	tester
	Clone	x	tester

Tester may be a variety line or hybrid that has a large number of positive traits on a wide genetic base. It is used to test for general combination ability.

Common pollen parent = tester

(d) by diallel analyses - to measure the GCA and SCA of inbreds $^6C_2$

$$= \frac{6x5x4\cancel{x3x2x1}}{2x4\cancel{x3x2x1}}$$

$$= 15$$

Success of selecting inbred lines for yield depends on the diversity of the original parents. However, early testing of inbred lines for GCA will help to eliminate lines that may not produce inbreds upon further inbreeding

<u>Note:-</u>

- Hybrid varieties make use of heterosis to a great extent: unrelated parents give high heterosis
- Hybrid varieties from inbred crosses are highly uniform
- Hybrid varieties have narrower genetic base
- The yield ability of hybrids lack consistent superiority from year to year. i.e performance reduces with years of continuous cultivation.
- Hybrid varieties are costlier to produce.

Combining Ability In Crops Plants

Good combining ability implies the ability of a parent plant to produce superior progenies when combined with another parent.

During the process of recurrent selection- building up of minor genes, test crosses are used to measure combining ability.

The tester used here (open-pollinated parent-line, variety, single cross hybrid e.t.c) must have broad genetic base so that variations in their performance among testcrosses will be due to differences in their general combining ability (GCA).

*GCA is the average performance of a line in hybrid combination. $GCA_1 = 59.8$

Average mean performance.

Diallel cross

A **diallel cross** is a mating scheme used by plant and animal breeders, as well as geneticists, to investigate the genetic underpinnings of quantitative traits.

In a full diallel, all parents are crossed to make hybrids in all possible combinations. Variations include half diallels with and without parents, omitting reciprocal crosses. Full diallels require twice as many crosses and entries in experiments, but allow for testing for maternal and paternal effects. If such "reciprocal" effects are assumed to be negligible, then a half diallel without reciprocals can be effective.

Common analysis methods utilize general linear models to identify heterotic groups, estimate general or specific combining ability, interactions with testing environments and years, or estimates of additive, dominant, and epistatic genetic effects and genetic correlations.

There are four main types of diallel mating design:

1. Full diallel in which parents and reciprocal crosses are involved along with F1
2. Full diallel without inclusion of parents
3. Half diallel with parent and without reciprocal crosses
4. Half diallel without parents or reciprocal crosses

Diallel mating designs: when the same parents are used as females and males in breeding, the mating design is called **diallel.** Here are some commonly used diallel mating designs in forestry:

Half diallel - Each parent is mated with every other parent, excluding selfs and reciprocals.

F/M	1	2	3	4	5	6
1	-	*	*	*	*	*
2		-	*	*	*	*
3			-	*	*	*
4				-	*	*
5					-	*
6						-

Smart diallel - Parents are sorted for their breeding values from the best to the poorest and most crosses are made among the best.

F/M	1	2	3	4	5	6
1	-	*	-	*	-	*
2		-	*	-	*	-

3			-	*	-	-
4				-	-	-
5					-	-
6						-

Advantages and disadvantages of diallel mating designs

Diallel designs provide good evaluation of parents and full-sib families,

Provide estimates of both additive and dominance genetic effects,

Provide estimates of genetic gains from both additive and non-additive genetic variance,

When the number of parents mated increases, the number of crosses increases by 2N, where N is the number of parents and the design can be costly

Using the same parents as males and females make the mating design a little bit complicated to analyze.

Diallel analysis of 5 inbreds

	Lines						
	1	**2**	**3**	**4**	**5**	**Mean**	**$\overline{X}$**
1	-	41.7	62.2	70.8	64.4	59.8	239.1
2	41.7	-	65.7	72.1	64.4	61.0	243.9
3	62.2	65.7	-	64.2	60.4	63.1	252.5
4	70.8	72.1	64.2	-	59.6	66.7	266.7
5	64.4	64.4	60.4	59.6	-	62.2	248.8
Mean	59.8	61.0	63.1	66.7	62.2	-	
	$5C2 = \frac{5x4x3x2}{3x2x2} =$ 10 single crosses						

Specific Combining Ability (SCA)

*SCA is the performance (behavior) of parent (X) when crossed with another parent (Y)

y= a tester i.e the performance of the line when compared with a tester.

A line with high heterosis when compared with the tester is said to have good SCA.

Mean performance of line 1 and line 4 above is given as

$M_{1,4} = GCA_1 + GCA_4 + SCA_{1,4}$

$= 59.8 + 66.7 + 70.8 = 197.3$

$M_{2,4} = GCA_2 + GCA_4 + SCA_{2,4}$

61.0 + 66.7 + 72.1 = 199.8

$SCA_{2,4}$ = $Mean_{2,4}$ + GCA_2 + GCA_4

= 61.0 + 66.7 + 72.1 = 72.1

(xi+xii) = total value for rows + mean value of parents

From the table line 4 has the highest GCA of 66.7. It also has good SCA with line 1 and 2.

Therefore,

If the mean performance of lines in hybrid combination is known, then the SCA which is either higher or lower than the mean can be calculated as

SCAxy = Meanxy - GCAx - GCA y

When carrying out selection for specific combining ability (SCA), we normally use testers with narrow genetic base.

Combining ability should therefore be examined always when we want to develop superior progenies i.e when heterosis is practically exploited or when hybridization is used to develop new cultivars.

Diallel crossing method is used when we want to test whether a line is a good or poor combiner. Hybridization is made between pans a non of selected genotypes in all possible combinations.

The number of crosses taking into consideration the reciprocal ones is n(n-1) i.e

With a set of 10 lines, it is necessary to make a 10(10-1) = 90 cross combinations. If there is no reciprocal n(n-1)/2.

*When the number of crosses to be made is practically impossible, the GCA is evaluated by testing all lines against a common parent i.e a tester – performing topcrosses.

A best hybrid or a standard variety can be used as a tester in the case of maize. The lines that perform well with the tester are selected for diallel crossing for SCA.

GCA is considered to be a result of additive gene action while SCA, is as a result of non-additive variance i.e dominance and **Epistasis.**

Epistasis (interallelic gene interaction)

Dominance (intraallelic gene interaction)

(a) Significant MS of GCA & SCA shows that the cultivars included in diallel crosses had significant differences i.e they are highly variable.

(b) Large MS for GCA compared with MS for SCA means that additive gene action played a more important role in the inheritance of a trait than non-additive gene action (dominance and epistasis)

Phenotype and Components of Phenotype Variability

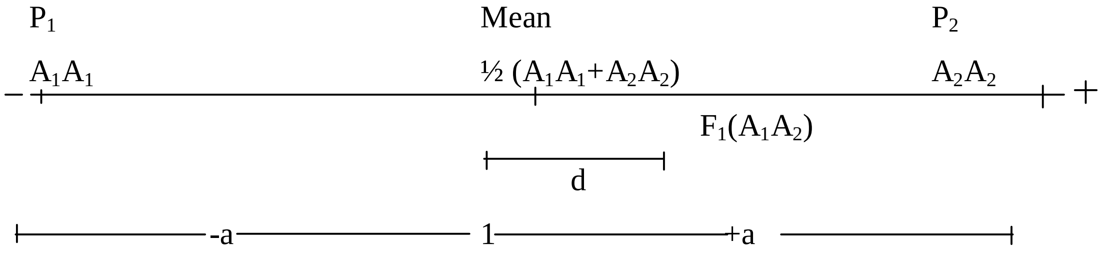
P (phenotype) = G(genotype) + E(environmental effect)

Individuals differ in phenotypic values i.e in outward or physical appearance as a result of genetic differences among the individuals, environmental factors and interaction between the genotype and the environment. Thus the phenotypic value of individuals is made up of components that can be determined by the analysis of variance. From the above statements.

$V_p = V_a + V_E + V_{GE}$

Where;

V_p = Phenotypic variance, V_G = genotype variance and V_E = environmental variance.



If A_1A_1 = 6cm and A_1A_2 = 7cm

It implies that

The presence of A_2 in the F_1 causes a change of 7cm compared with meaning that the gene expression above is additive. If dominance A_2 will be recessive. If there is epistasis, there will be interaction among different gene loci e.g AA x BB. A_1A_1 expresses an additive effect when it occurs with another gene B_1B_1 but a dominant effect when it occurs with the recessive allele b_1b_1.

Therefore,

$V_G = V_A + V_D + V_I$

V_A = Variance with additive gene effect

V_D = Variance with dominance gene effect

V_I = Variance as a result of interaction between genes

Hence

$V_P = V_A + V_D + V_I + V_E + V_{GE}$

V_E = is the environmental variance as a result of factors of the environment

$V_E = V_{P1}+V_{P2} + V_{F1}/3$ because the three are a measure of environment variance

Let us look at the genotypic variance via F_2 and the backcross B_1 and B_2

$A_1A_1 \text{ x } A_2A_2 \qquad F_2 = A_1A_2 \text{ x } A_1A_2$

$A_1A_2 = F_1 \qquad F_2 = A_1A_1+2A_1A_2+A_2A_2$

Three genotypes; four phenotypes 1:2:1

$A_1A_1 = ¼;\ A_1A_2 = ½ ;\ A_2A_2 = {}^1/_4$

From the table or diagram above

(P_1)	(F_1)	(P_2)
$A_1A_1 = -a$	$A_1A_2 = d$	$A_2A_2 = +a$

Which are deviations from the parent mean

$F_2 = ¼\ A_1A_1 + ½\ A_1A_2 + ¼\ A_2A_2$

$= ¼\,(-a) + ½d + ¼a = ½d$ (F_2) deviation

Variance $(V_G) = f(x-x)^2$

$V_G = (-a-½)^2 + ½(d-½d)^2 + ¼(a-½)^2$

$= ¼(a^2+ad+¼d^2) + ½({}^1/_4 d^2) + ¼\,(a^2- ad +¼d^2)$

$= ½a^2 + ¼d^2$

$V_G = ½a^2 +¼\, d^2 \qquad$ if $a^2 = A$

$V_G = ½A + ¼D \qquad d^2 = D$

$V_{F2} = V_G + V_E = ½A + ¼D + E$ (Total variance)

Note that from the cross above

$B_1 = A_1A_2 \overset{\downarrow}{x} A_1A$

$A_1A_1 + A_1A_2 = ½(-a) + ½d$

$½(-a – ½d)^2 + ½(d- ½d)^2 = ¼a^2 + ¼d^2$

$= ¼a^2 + ¼d^2$

Like the above

$B_1 = ¼A + ¼D$

$V_{B1} = ¼A + ¼D + E$ because $VB_1 = V_G + V_E$

Also,

$V_{B1} = ¼A + ¼D + E$

$V_{B1}+V_{B2} = ½A + ½D + 2E$

V_{P1} = E

V_{P2} = E E = $(V_{P1}+V_{P2}+V_{F1})/3$

V_{F1} = E

Mean values ($\bar{x}$) and variance (∂^2) of seed germination in the parent and hybrid generations of two soybean genotypes.

E = (25.2 + 5.5 + 27.6)/3 = 19.4

FV_2 = 137.2 = ½A + ¼ D+E E = 19.4

½A + ¼D = 137.2 – 19.4

½A + ¼D = 117.8 …………….(i)

= $\partial^2 g$

B_1+B_2 = ½A + ½D + 2E

= ½A + ½D + 38.8 = 206.7

= ½A + ½D = 167.9 ……………………(ii)

Parent & hybrids	No of plants analysed	Percent Germination	
		$\bar{X}$	∂^2
P_1 TGX 1448-2E	20	94.5	25.2
P_2 TGX 737p	20	98.0	5.5
F_1 (P_1 x P_2)	20	94.7	27.6
B_1 (F_1 x P_1)	10	95.0	161.1
B_2 (F_1 x P_2)	10	97.0	45.6
F_2 (F_1 x F_1)	126	94.9	137.2

½A + ¼D = 117.8

½A + ½D = 167.9

2A + D = 471.2 ……………………………………….(iii)

2A + 2D = 671.6 ……………………………………….(iv)

Equations 4 minus equation 3

D = 200.4

2A + 200.4 = 471.6

2A = 271.2

A = 135.6

From F_2 variance

V_{F2} = $\frac{1}{2}A + \frac{1}{4}D + E$

$137.2 = \frac{1}{2}(135.6) + \frac{1}{4}(200.4) + 19.4$

$137.2 = 67.8 + 50.1 + 19.4$

Express as a %

$100\% = 49.4 + 36.5 + 14.1$ in V_{F2}

$V_A = 49.4\%$

$V_D = 36.5\%$

$V_E = 14.1\%$

$H_B = 85.9\%$

$H_N = 49.4\%$

From the analysis, the F_2 generation that has total variance is shown to have very high genetic variability for seed viability (49.4 + 36.5%) = 85% than environmental variance (14.1%).

This suggest that there is big genetic differences between TGX 1448-2E and 737p. About 57.5% of genetic variance is due to the additive gene action and 42.5% was due to the dominance gene action.

The above shows the simplest way of calculating the components of genetic variance but note that the variances due to epistasis (interallelic interactions) which are frequently associated with quantitative traits are omitted. This is because, such calculations call for more complex formulae of biometrical genetics using the models of Mather and Jinks (1971); Falconer (1981) and others.

Calculations from diallel crosses using the methods of Jinks (1954); Haymann (1954) and Mather and Jinks (1971) may also be used. Mean and variances of six generations for height from a maize trial with completely randomized individual is presented in the table.

Generation	**No of individuals**	**(cm) mean**	**Variance**
P_1	50	69.6a	48.6
P_2	50	68.4a	40.1
F_1	100	89.6c	53.0
F_2	200	79.5b	97.3
B_1	200	77.4b	66.5
B_2	200	78.3b	84.6

P_1 & P_2 have similar means (69.6, 68.4)

F_1 mean is considerably high (89.6)

F_2 is in-between P_1P_2 and F_1 values (79.5)

P_1, P_2 and F_1 have similar variance (48.7 on average)

F_2 variance is much larger (97.3)

Environmental variance $\partial^2 e = 48.7 = VE = E$

MP height = 69.0cm

F_1 mean height = 89.6

$$\text{Heterosis} = \frac{89.6 - 69.0}{69.0} = \frac{20.6}{69.0} = 29.9\%$$

If variance in the F_2 $(V_{F2}) = 1/2A + ¼D+E$

$V_{B1} = V_{B2} = ¼A + ¼A + E$

Where

A = Additive gene action

D = Dominance gene action

(a) Solve or estimate the values of A & D and hence determine whether plant height in maize is controlled by additive or dominance gene effects

(b) What effect does environment have on plant height in maize

(c) Estimate Heterosis for plant height

Q2 ANOVA of seed yield of 6 genotypes of cowpea in a particular tropical environment.\

Source	Df	Ms	Expected ms	F-ratio
Total	Rt-1			
Rep	r-1	192.0		*24.68
Treatment	t-1	69.8	$\partial^2 e + r\partial^2 t$	8.97**
Error	(t-1) (r-1)	7.78	$\partial^2 e$	

$\partial^2 e = 7.78$

$r\partial^2 t = 69.8 - 7.78 = 62.02$

$\partial^2 t = 62.02/4 = 15.51$

$\partial^2 p = \partial^2 e + \partial^2 t = 23.29$

$Hb = \partial^2 t/\partial^2 p = 66.57$

$= 66.60\%$

(a) Recopy the table if 5 treatments was planted in 4 reps in randomized complete block.

(b) What type of design is used here and why?

Testing for Means of Difference

Significant mean squares is an indication that variability exists among the sources under consideration. For instance, significant mean squares for genotype indicates that the genotypes are quite diverse or there is genotypic variability causing the genotypes to perform differently under similar environmental conditions.

Differences between two means can be tested using

(i) Fisher's Least Significant Difference (FLSD)
(ii) Bayer's Least Significant Difference (BLSD)
(iii) Honest Least Significant Difference (HLSD)
(iv) Duncan's Multiple Range Test (Duncan separation)

Any of the above is used when F-test has been shown to be significant

Steps

1. Perform a preliminary F-test
2. Calculate (Sd) Standard error of difference between 2 treatment means from the variances of the means (error mean squares)
3. Obtain 't' value at error df at 5% probability level

⟹ Error variance = $\partial^2 e$

With "r" replications OR n = no of observation

⟹ Variance of the mean = $\frac{\partial^2 e}{r}$ or $\partial^2/r = \partial^2 \bar{x}$

⟹ Standard error of a mean = $\sqrt{\text{variances of mean}}$

$\sqrt{\partial^2 \bar{x}}$ = $\sqrt{\partial^2/r} = \sqrt{\partial^2/n}$

⟹ Variance of 2 treatment means

$\partial^2_1 - \partial^2_2 = \partial^2_{\bar{x}1} - \partial^2_{\bar{x}2} = \partial^2_{\bar{x}1 - \bar{x}2}$

⟹ Standard error of 2 treatment means.

$\backslash\ \partial^2/r - \partial^2/r \quad = \quad \backslash\ \partial^2 x_1 - \overline{x_2} \quad = \quad \partial\overline{x_1} - \overline{x_2} = 2d^2/r$

$\partial\overline{x_1}-\overline{x_2} \quad = \quad \sqrt{2}\partial^2/r \quad = \quad \partial\sqrt{2}/r$

$= \quad \partial\overline{d}$

Assume $\partial^2 e \quad = \quad 1.78$ and $r = 4$

$\partial\overline{x} \quad = \partial^2 e/r = \quad 1.78/4 = \quad 0.45$

$\partial\overline{x_1}-\overline{x_2} \quad = \quad \sqrt{2}\partial^2/r \quad = \quad \frac{\sqrt{2x\ 1.78}}{4} \quad = \quad \sqrt{0.89} = 0.94$

See t-test and Lsd defined on loose sheet

If error df = 12 and probability level is 5%

$t_{5\%}df_{12} \quad = \quad 2.179$

$Lsd_{5\%} \quad = \quad t_{5\%}df_{12} \times \partial \quad = \quad 0.94 \times 2.179$

DMRT see loose sheet $\quad = \quad 2.05$

Statistical Tests

1. t-tests (Lsd) test of significant for paired observations
2. F-tests (ANOVA tests)
3. Duncan Multiple range test
4. Test of association – Correlation

   - Regression

   Path Coefficient Analysis
5. Stability tests
6. Scaling tests – test of adequacy of the additive-dominance model in the backcrosses, F_2 and F_3 populations.

$A \quad = \quad 2\overline{B}_1 - \overline{F}_1 - \overline{P}_1$

$B \quad = \quad 2\overline{B}_2 - \overline{F}_1 - \overline{P}_2$

$C \quad = \quad 4\overline{F}_2 - 2\overline{F}_1 - \overline{P}_1 - \overline{P}_2$

OR

$C \quad = \quad 2\overline{F}_2 - \overline{B}_1 - \overline{B}_2$ to test non-allelic interaction

$D \quad = \quad 8\overline{F}_3 - 3\overline{P}_1 - 3\overline{P}_2 - 2\overline{F}_1$

Test for reciprocal difference (maternal effects)

e.g $\overline{F}_1 - \overline{F}_{1(R)} \quad = \quad 96.0 - 94.7 \quad = \quad (1.3)$ observed

t-test: to test for significance in paired observations e.g two mean values

$$t \quad = \quad \frac{\overline{x}_1 - \overline{x}_2}{Sx} \quad = \quad \overline{F}_1 - \overline{F}_{1(R)} \quad = \quad \frac{1.3}{S\overline{x}}$$

$S\bar{x}$ = Standard error of the mean = $\sqrt{\partial^2/n} = \partial/\sqrt{n}$

n = no of observations, ∂^2 = variance of the means

$$Sx = \sqrt{\frac{27.6}{20}} = 1.17$$

$$t = \frac{1.30}{1.17} = 1.10 \text{ cal (expected)}$$

A df_{19}5% (i.e $\frac{0.05}{2}$ = 0.025)= 2.093 (tab)

cal < tab

No significant difference between 1.3 and 1.10
No reciprocal difference, no maternal effect.

From Question

$M = \frac{1}{2}(\overline{P_1} + \overline{P_2}) = 69.0$

$[d] = \frac{1}{2}(\overline{P_1} - \overline{P_2}) = 0.60$

$[h] = \overline{F_1} - M = 20.60$

Dominance ratio (h/d) measures the degree of dominance of the allele at a locus

h/d = 1 A completely dominant to a

h/d = -1 a completely dominant to A

h/d = 0 no dominance (co dominance)

D = 87.08

H = 20.42

F = 18.1

Ew = 47.23 = Environmental variation within families

= $(VP_2 + VP_2 + VF_1)/3$

Eb = Environ. Variation between families

Variances have to be homogeneous.

*If heterogeneous, heterogeneity (though small) is caused by the fact that variances are positively correlated with the means.

Variance at F_2 = 97.3 i.e phenotypic variance

Genetic variance = 97.3 – 47.23 = 50.07

h_B = 50.07/97.3

= 51.4% = 0.51

i.e 51% of variation was due to genes and 49% was due to environment.

Mathematically: $\partial^2 g = ½ d2 + ¼ h2$

$= ½D + ¼ H$

$\partial^2 p = ½D + ¼H + Ew$

F= 18.1 is additional term contained in the two backcrosses

H's sign depends on the direction of dominance or dominant allele

F = (∑dh)

If P_1 has dominant alleles, F will be positive and thus variance within B_1 will be less than that within B_2.

If F = 0, then both parents carry the same number of dominant alleles.

F = B_2 Variance - B_1 Variance

= 84.6 – 66.5

= 18.1