

PBG 509: (Breeding cereal crops) 3(2-1)

Session # 1: Tutorial

Importance of food cereals; wheat, rice, barley and oats

A cereal is any grass cultivated (grown) for the edible components of its grain (botanically, a type of fruit called a caryopsis), composed of the endosperm, germ, and bran. The term may also refer to the resulting grain itself (specifically "cereal grain"). Cereal grain crops are grown in greater quantities and provide more food energy worldwide than any other type of crop[1] and are therefore staple crops. Edible grains from other plant families, such as buckwheat (Polygonaceae), quinoa (Amaranthaceae) and chia (Lamiaceae), are referred to as pseudocereals.

In their natural, unprocessed, whole grain form, cereals are a rich source of vitamins, minerals, carbohydrates, fats, oils, and protein. When processed by the removal of the bran, and germ, the remaining endosperm is mostly carbohydrate. In some developing countries, grain in the form of rice, wheat, millet, or maize constitutes a majority of daily sustenance. In developed countries, cereal consumption is moderate and varied but still substantial.

The global importance of cereal crops to the human diet and moreover to the written history of man and agriculture cannot be over stated. Cereal grains are the fruit of plants belonging to the

grass family (Gramineae). The sustenance provided by cereals is frequently mentioned in the Bible, and they are by many other criteria the most important group of food crops produced in the world. Cereal crops are energy dense, containing 10 000-15 000 kJ/Kg, about 10-20 times more energy than most succulent fruits and vegetables. Nutritionally, they are important sources of dietary protein, carbohydrates, the B complex of vitamins, vitamin E, iron, trace minerals, and fiber. It has been estimated that global cereal consumption directly provides about 50 percent of protein and energy necessary for the human diet, with cereals providing an additional 25 percent of protein and energy via livestock intermediaries. Some cereals, notably wheat, contain proteins that form gluten, which is essential for making leavened bread. Although dried cereal grains constitute living cells that respire, when kept in an appropriate environment, whole grains can be stored for many years. In 1996, world cereal production amounted to more than two billion metric tons (Figure 1). Major cereal crops produced worldwide include wheat, rice, maize and barley (Figure 2). Other major cereal crops produced include sorghum, oats, millet and rye. Asia, America, and Europe produce more than 80 percent of the world's cereal grains. Wheat, rice, sorghum, and millet are produced in large quantities in Asia; corn and sorghum are principal crops in America, and barley, oats and rye are major crops in the former USSR and Europe (Chaven and Kadam, 1989).

Cereals have a variety of uses as food. Only two cereals, wheat and rye, are suited to the preparation of leavened bread. The most general usage of cereals is in cooking, either directly in the form of grain, flour, starch, or as semolina, etc. Another common usage of cereals is in

the preparation of alcoholic drinks such as whiskey and beer (barley; sorghum), vodka (wheat), American bourbon (rye), Japanese sake (rice), etc. A variety of unique, indigenous fermented foods, other than leavened breads and alcoholic beverages, are also produced in regions of the world that rely mainly on plant sources of protein and calories. In developed countries, that obtain most of their protein from animal products, cereals are increasingly used as animal feed. More than 70 percent of the cereal crop produced in developed countries is fed to livestock; whereas, in developing countries, 68-98 percent of the cereal crop is used for human consumption (Betschart 1982; Chaven and Kadam, 1989).

Session # 2 & 3: Laboratory

Development of genetic material using appropriate techniques

Crop improvement typically involves the transfer of genes from one source or genetic background to another, or combining genes from different sources that complement each other, with the hope that the new cultivar will combine the best of both parents, while being distinct from both. When a plant breeder has decided on the combination of traits that are to be incorporated in the new cultivar to be developed, the next crucial step is to find one or more sources of the appropriate gene(s) for such characters. In flowering species, the conventional method of gene transfer or gene combination is by crossing or sexual hybridization. This procedure causes genes from the two parents to be assembled into a new genetic matrix. It follows that if parents are not genetically compatible, gene transfer by sexual means cannot occur at all or, at best, may be fraught with complications. The product of hybridization is called a hybrid. Sexual hybridization can occur naturally through agents of pollination. Even though self-pollinating species may be casually viewed as “self-hybridizing”, the term hybridization is reserved for crossing between unidentical parents (the degree of divergence is variable). Artificial sexual hybridization is the most common conventional method of generating a segregating population for selection in breeding flowering species. In some breeding programs, the hybrid (F_1) is the final product of plant breeding (see hybrid breeding in Chapter 18). However, in most situations the F_1 is selfed (to give an F_2) to generate recombinants (as a result of recombination of the parental genomes) or a segregating population, in which selection is practiced. In clonally propagated crops, the F_1 usually segregates sufficiently and its clonally produced descendants will be submitted to selection without further crossing or selfing. The tools of modern biotechnology now enable the breeder to transfer genes by circumventing the sexual process (i.e., without crossing). More significantly, gene transfer can transcend natural reproductive or genetic barriers. Transfers can occur between unrelated plants and even between plants and animals.

Applications of crossing in plant breeding

Sometimes, crossing is done for specific purposes, within the general framework of generating variability. Hybridization precedes certain methods of selection in plant breeding to generate general variability. _ Gene transfer. Sometimes, only a specific gene (or a few) needs to be incorporated into an adapted cultivar. Crossing is used for the gene transfer process, followed by additional strategic crossing to retrieve the desirable genes of the adapted cultivar.

Recombination.

Genetically diverse parents may be crossed in order to recombine their desirable traits. The goal of recombination, which is a key basis of plant breeding, is to forge desirable linkage blocks. _ Break undesirable linkages. Whereas forging desirable linkage blocks is a primary goal of plant breeding, sometimes crossing is applied to provide opportunities for undesirable linkages to be broken. _ For heterosis. Hybrid vigor (heterosis) is the basis of hybrid seed development. Specially developed parents are crossed in a predetermined fashion to capitalize on the phenomenon of heterosis for cultivar development. _ For maintenance of parental lines. In hybrid seed development programs, crossing is needed to maintain special parents used in the breeding program (e.g., CMS lines, maintainer lines). _ For maintenance of diversity in a gene pool. Plant breeders may use a strategy of introgression (crossing and backcrossing selected entries with desired traits into adapted stocks) and incorporation to develop dynamic gene pools from which they can draw materials for crop improvement. _ For evaluation of parental lines. Inbred lines for hybrid seed development are evaluated by conducting planned

crosses to estimate combining abilities in order to select appropriate parents for used in hybrid seed development. _ For genetic analysis. Geneticists make planned crosses to study the inheritance and genetic behavior of traits of interest.

Artificial hybridization

Artificial hybridization is the deliberate crossing of selected parents (controlled pollination).

There are specific methods for crossing that depend on the species in which the cross is being made, which differ according to factors including floral morphology, floral biology, possible genetic barriers, and environmental factors. Methods for selected species are described later in this book. However, there are certain basic factors to consider in preparation for hybridization:

_ Parents should belong to the same or closely related plant species. In the case that they belong to different (related) plant species, all kinds of techniques may be required to obtain hybrid progeny. _ The parents, obviously, together should supply the critical genes needed to accomplish the breeding objective. _ One parent is usually designated as female. Whereas some breeding methods may not require this designation, breeders usually select one parent to be a female and the other a male (pollen source). This is especially so when hybridizing self-pollinated species. Whenever genetic markers are available (e.g., white flowers, white seeds), the female exhibits the recessive morphological trait. In some cases, selected parents of cross-pollinated species may be isolated and allowed to randomly cross-pollinate each other. _ The female parent usually needs some special preparation. In complete flowers (those having both male and female organs), the flowers of the parent selected to be female are prepared for

hybridization by removing the anthers, a tedious procedure called emasculation (discussed next). Emasculation is eliminated in some crossing programs by taking advantage of male sterility (renders pollen sterile) when it occurs in the species. _ Pollen is often physically or manually transferred. Artificial hybridization often includes artificial pollination, whereby the breeder physically deposits pollen from the male parent onto the female stigma. However, when hybridization is conducted on large scale (e.g., commercial hybrid seed development), hand pollination is rarely a feasible option.

7.4 Artificial pollination control techniques

As previously indicated, crossing is a major procedure employed in the transfer of genes from one parent to another in the breeding of sexual species. A critical aspect of crossing is pollination control to ensure that only the desired pollen is involved in the cross. In hybrid seed production, success depends on the presence of an efficient, reliable, practical, and economic pollination control system for large-scale pollination.

Pollination control may be accomplished in three general ways:

Mechanical control.

This approach entails manually removing anthers from bisexual flowers to prevent pollination, a technique called emasculation, or removing one sexual part (e.g., detasselling in corn), or excluding unwanted pollen by covering the female part. These methods are time consuming, expensive, and tedious, limiting the number of plants that can be crossed. It should be mentioned that in crops such as corn, mechanical detasselling is widely used in the industry to produce hybrid seed.

(ii) Chemical control.

A variety of chemicals called chemical hybridizing agents, or by other names (e.g., male gametocides, male sterilants, pollenocides, androcides), are used to temporally induce male sterility in some species. Examples of such chemicals include Dalapon₁, Estrone₁, Ethephon₁, Hybrex₁, and Generis₁. The application of these agents induces male sterility in plants, thereby enforcing cross pollination. The effectiveness is variable among products.

(iii) Genetical control.

Certain genes are known to impose constraints on sexual biology by incapacitating the sexual organ (as in male sterility) or inhibiting the union of normal gametes (as in self-incompatibility). The flower has a central role in hybridization. The success of a crossing program depends on the condition of the flower regarding its overall health, readiness or receptiveness to pollination, maturity, and other factors. The actual technique of crossing depends on floral biology (time of pollen shedding, complete or incomplete flower, self- or crosspollinated, size and shape of individual flowers and of the inflorescence).

Flower health and induction:

It is important that plants in a crossing block (or to be crossed) be in excellent health and be properly developed. This is especially so when flowers are to be manually emasculated. Once successfully crossed, an adequate amount of seed should be obtained for planting the first generation. The parents to be mated should receive proper lighting, moisture supply, temperature, nutrition, and protection from pests. Parents should be fertilized with the proper amounts of nitrogen, phosphorus, and potassium for vigorous plant growth to develop an adequate number of healthy flowers. Plants growing in the greenhouse should be provided with

the proper intensity and duration of light. If the species is photoperiod sensitive, the lighting should be adjusted accordingly. Proper temperature is required for proper plant growth and development. In some species, a special temperature treatment (vernalization, usually some period of low temperature) is required for flower induction. Furthermore, temperature affects pollen shed in flowers. Consequently, extreme temperatures may cause inadequate amounts of pollen to be shed for successful artificial pollination. Pollen quantity and quality are influenced by the relative humidity of the growing environment. Extreme moisture conditions should be avoided.

Synchronization of flowering

In artificial pollination, the breeder should be familiar with the species to know its flowering habits regarding time from planting to flowering, duration of flowering, mechanisms and timing of natural anther dehiscence and fertilization, and time of peak pollen production, in order to take advantage of the window of opportunity of anthesis (pollen shed) for best crossing outcomes. To ensure that parents in a crossing program will have flowers at the same time, the practice of staggered planting – to plant sets of parents at different times – is recommended. This way, a late-planted early flowering genotype may be pollinated by an early-planted late flowering genotype. When depending on natural pollination, interspersed planting on different dates will favor even pollen distribution. Photoperiod may be manipulated in photoperiod sensitive species to delay or advance flowering as appropriate, in order to synchronize flowering of the parents in a cross. Other techniques that have been used in specific cases

include manipulation of temperature and planting density, removal of older flowers to induce new flushes of flowers, and pinching (e.g., removal of plant apex to induce tillering or branching for additional flowers). In corn, the silk of an early flowering inbred parent may be cut back to delay the time to readiness for pollination.

Selecting female parents and suitable flowers:

After selecting lines to be parents in a cross, it is necessary in artificial crosses to designate one parent as female (as previously stated), as well as identify which type of flowers on the parent would be most desirable to cross. In crossing programs in which the CMS system is being used, it is critical to know which plants to use as females (these would be the male sterile genotypes, or A and B lines; Chapter 17). Because the pollen or male gamete is practically without cytoplasm, and because certain genes occur in the extranuclear genome (such as CMS), it is critical that parents selected as female plants be selected judiciously. Markers are important to plant breeding as was discussed previously. Some markers may be used to distinguish between selfed and hybrid seed on the female plant. For example, in sorghum, waxy endosperm is conditioned by a recessive allele while normal endosperm is under the control of the dominant allele. If a waxy female is crossed with a normal male, all F_1 seed with waxy endosperm would be products of selfing (undesirable) while normal seed would indicate a successful hybrid. Other markers, molecular and morphological, may be strategically included in a crossing program to allow the authentication of hybridity. In terms of flower characteristics, bigger flowers are easier to handle than tiny ones. Whenever possible, the

parent with bigger flowers should be used as female. Another critical aspect of flower physiology is the age of the flower when it is most receptive to pollination. The breeder usually determines the optimal stage of flower maturity by examining its physical appearance. Tell-tale signs depend on species. Usually, fully opened flowers would have already been pollinated by undesirable pollen. In most plant species flowers are emasculated in the bud stage just as the petals begin to show through the bud. Rice is ready in the boot stage, whereas wheat is best emasculated when florets are light green with well-developed but still green anthers and feathery stigmas that extend about a quarter of the length of the florets. Furthermore, flowers in the same inflorescence usually have different maturity levels. In species such as the broad bean (*Vicia faba*), the first inflorescence is more suitable for crossing than later ones. Also, flowers at the base and middle of inflorescences give better results than those at the top. Flowers in the inflorescence that are not used for crossing may be removed, while the ones that are used in crossing may be marked with a label or small clip or peg.

Emasculation

The process of making a bisexual flower female by removing the male parts or incapacitating them is called emasculation. It should be pointed out right away that emasculation is not a universal requirement for artificial crossing of plants. Species with fertility-regulating mechanisms (e.g., male sterility, self-incompatibility, protogyny, monoecy, dioecy) may be crossed without the often tedious and time consuming process of emasculation.

Factors to consider for success:

Apart from picking the right flowers, it is critical to know the duration of stigma receptivity and pollen viability. The maximum time between emasculation and pollination that can be tolerated varies among species. Since the anthers were removed before they were mature, the female parts often are not yet receptive at the moment of emasculation. This makes it necessary to pollinate at a later time, either during the same day or even later. The caution to observe is that prolonged delay between the two operations increases the chance of contamination from undesirable pollen. To reduce this risk, emasculated flowers may be covered with bags (e.g., glassine, paper or cloth bag). Pollen quality and quantity vary with the weather and time of day. For example, in chickpea, some breeders prefer to emasculate in the evening and pollinate in the morning. Because emasculation is done before anthers are mature in species such as wheat and barley, pollination is done 2–3 days later when the stigma is receptive. In extreme cases, such as in sugar beet, pollination may immediately follow emasculation or be delayed for up to 12 days.

Methods of emasculation

There are several techniques of emasculation used by plant breeders that include the use of instruments or chemicals. A pair of forceps or tweezers is one of the most widely used instruments in the emasculation of flowers. Different shapes and sizes are used according to the size and structure of the flower.

The methods of emasculation may be classified as direct or indirect.

Direct anther emasculation:

The technique of removing anthers from selected flowers is the most common procedure for emasculation of flowers (usually using a pair of forceps). When handling plants with inflorescence, it is important to firstly thin out the bunch by removing immature flowers as well as old ones. This improves the survival of the emasculated flowers. Breeders of various crops have developed convenient ways of removing the anthers. Sometimes, the sepals are first removed, followed by the petals before access is gained to the anthers. In soybean and sesame, a skilled person may be able to remove the petals and anthers in one attempt. In flowers such as soybean, the pedicel is easily broken as a result of physical handling of the delicate flower during emasculation. In wheat and barley, the florets are clipped with scissors.

Indirect anther emasculation:

In these methods, the anthers are incapacitated without being removed from the flower. Incapacitation is achieved in several ways: _ Thermal inactivation. The inflorescence is first thinned out to leave only flowers at the proper stage for emasculation. It is then immersed in hot water (e.g., held in a thermos bottle) to kill the pollen without injuring the pistil. The temperature and time of immersion are variable (e.g., 43 °C for 5 minutes in rice; 47–48 °C for 10 minutes in sorghum). The inflorescence is allowed to dry before pollinating about 30–60 minutes later. _ Alcohol emasculation. In species such as alfalfa the raceme is immersed in 57% ethanol for 10 seconds and then rinsed in water for a few seconds. _ Commercial gametocides. These are chemicals designed to kill the anthers (e.g., sodium methyl arsenate). If pollination is not to follow emasculation immediately, the flowers

should be covered to exclude contaminating pollen from elsewhere. Once properly pollinated, the flower should be tagged for identification.

Pollination :

Successful pollination depends on pollen maturity, quality (freshness), and timing of pollination, among other factors.

Collection and storage:

In some species (e.g., soybean) pollination immediately follows emasculation. In this case, there is no need for storage. Fresh pollen gives the best success of crossing. Good pollen flowers may be picked and placed in a Petri dish or some suitable container for use. In some species, mechanical vibrations may be used to collect pollen. Pollen is most copious at peak anthesis. Generally, pollen loses viability quickly. However, in some species, pollen may be stored at a cool temperature and an appropriate humidity for the species for an extended period.

Application of pollen:

Commonly, pollen is applied directly to the stigma by using a fine brush or dusting off the pollen onto the stigma directly from the flower of the pollen source (e.g., the staminal column may be used as brush). Sometimes, an object such as a cotton bulb or a tooth pick is used to deposit pollen on the stigma. In some flowers, pollen deposition is made without direct contact with the stigma. Instead, pollen may be injected or dusted into a sack covering the emasculated

inflorescence and agitated to distribute the pollen over the inflorescence. A key precaution against contamination during pollination is for the operators to disinfect their hands and tools between pollinations when different varieties are involved. It is critical to tag the pollinated flower for identification at the time of harvesting.

Tagging after pollination:

After depositing the desired pollen, it is critical to identify the flowers that were pollinated with an appropriate tag or label. The information on the label should include the date of emasculation, date of pollination, name of seed parent, and the name of pollen parent. The tag should be attached to the pedicel of the emasculated flower not the branch.

7.8 Number of F_1 crosses to make

There are practical factors to consider in deciding on the number of crosses to make for a breeding project. These include the ease of making the crosses from the standpoint of floral biology and the constraints of resources (labor, equipment, facilities, and funds). It will be easier to make more crosses in species in which emasculation is not needed (e.g., monoecious and dioecious species) than in bisexual species. Some breeders make a small number of carefully planned crosses, while others make thousands of cross combinations. Generally, a few hundred cross combinations per crop per year would be adequate for most purposes for species in which the F_1 is not the commercial product. More crosses may be needed for species in which hybrids are commonly produced, for the purpose of discovering heterotic combinations. As is discussed next, breeding programs that go beyond the F_1 usually require very large F_2 populations. Regarding the number of flowers per cross combination, there is

variation according to fecundity. Species such as tomato may need only one or two crosses, since each fruit contains over 100 seeds. Plants that tiller also produce large numbers of seed. Each crop species has its own reproduction rate, which may be huge (e.g., tobacco: 1000s of seeds produced per plant, 100s per bowl) or relatively small (e.g., pea: about 100 per plant, about 2–5 per pod).

Session # 4 & 5: Tutorial

Evolution, origin, and phenology of cereal crops

Cereals were the foundation of human civilization. Cereal frontiers coincided with civilizational frontiers. The term Fertile Crescent explicitly implies the spatial dependence of

civilization on cereals. The Great Wall of China and the Roman limes demarkated the same northern limit of the cereal cultivation. The Silk Road stretched along the cereal belt of Eurasia. Numerous Chinese imperial edicts stated: “Agriculture is the foundation of this empire,”[8] while the foundation of agriculture were the Five Grains.

Cereals determined how large and for how long an army could be mobilized. For this reason, Shang Yang called agriculture and war “the One.”[9] Guan Zhong, Chanakya (the author of Arthashastra)[10] and Hannibal[11] expressed similar concepts. At the dawn of history, the Sumerians believed that if agriculture of a state declines, Inanna, the goddess of war, leaves this state.[12] Several gods of antiquity combined the functions of what Shang Yang called “the One” – agriculture and war: the Hittite Sun goddess of Arinna, the Canaanite Lahmu and the Roman Janus. These were highly important gods in their time leaving their legacy until today. We still begin the year with the month of Janus (January). The Jews believe that Messiah will be born in the town of Lahmu (Bethlehem) and the Christians believe that he was already born there. Lahmu is the responsible why in Hebrew until today bread (lehem) and warfare (lehima) are of the same root. In fact, most persistent and flourishing empires throughout history in both hemispheres were centered in regions fertile for cereals.

Historian Max Ostrovsky argues that this historic pattern never changed, not even in the Industrial Age.[13] He stresses that all modern great powers have traditionally remained first and foremost great cereal powers. The “finest hour” of the Axis powers “ended precisely

the moment they threw themselves against the two largest cereal lebensraums” (the United States and the USSR).[14] The outcome of the Cold War followed the Soviet grave and long-lasting cereal crisis, exacerbated by the cereal embargo imposed on the USSR in 1980.[15] And, called “the grain basket of the world,” the most productive “cereal lebensraum” dominates the world ever since.[16]

Having analyzed the mechanism at work behind this pattern, Ostrovsky outlined that the cereal power determines the percentage of manpower available to non-agricultural sectors including the heavy industry vital for military power. He emphasized that chronologically the Industrial Revolution follows the modern Agricultural Revolution and spatially the world’s industrial regions are bound to cereal regions. Taken from space, map of the global illumination is said to indicate by its brightest parts the industrial regions.[17] These regions coincide with cereal regions. Ostrovsky formulized the universal indicator of national power which unambiguously demonstrates the unipolar international hierarchy of the present world order[18]:

The Green Revolution

During the second half of the 20th century there was a significant increase in the production of high-yield cereal crops worldwide, especially wheat and rice, due to an initiative known as the Green Revolution.[19] The strategies developed by the Green Revolution focused on fending off starvation and increasing yield-per-plant, and were very successful in raising

overall yields of cereal grains, but did not give sufficient relevance to nutritional quality.[20] These modern high yield-cereal crops tend have low quality proteins, with essential amino acid deficiencies, are high in carbohydrates, and lack balanced essential fatty acids, vitamins, minerals and other quality factors.[20] So-called ancient grains and heirloom varieties have seen an increase in popularity with the "organic" movements of the early 21st century, but there is a tradeoff in yield-per-plant, putting pressure on resource-poor areas as food crops are replaced with cash crops.[21]

Norman Ernest Borlaug: The man and his passion:

"For more than half a century, I have worked with the production of more and better wheat for feeding the hungry world, but wheat is merely a catalyst, a part of the picture. I am interested in the total development of human beings. Only by attacking the whole problem can we raise the standard of living for all people, in all communities, so that they will be able to live decent lives. This is something we want for all people on this planet".

Norman E. Borlaug.

Dr Norman E. Borlaug has been described in the literature in many ways, including as "the father of the Green Revolution", "the forgotten benefactor of humanity", "one of the greatest benefactors of human race in modern times", and "a distinguished scientist-philosopher". He has been presented before world leaders and received numerous prestigious academic honors from all over the world. He belongs to an exclusive league, with the likes of Henry Kissinger, Elie Wiesel, and President Jimmy Carter – all Nobel Peace laureates. Yet, Dr Borlaug is hardly a household name in the United States. But, this is not a case of a prophet being without honor

in his country. It might be more because this outstanding human being chooses to direct the spot light on his passion, rather than his person. As previously stated in his own words, Dr Borlaug has a passion for helping to achieve of a decent living status for the people of the world, starting with the alleviation of hunger. To this end, his theatre of operation is the developing countries, which are characterized by poverty, political instability, chronic food shortages, malnutrition, and prevalence of preventable diseases. These places are hardly priority sources for news for the first world media, unless an epidemic or catastrophe occurs.

Dr Borlaug was born on March 25, 1914, to Henry and Clara Borlaug, Norwegian immigrants in the city of Saude, near Cresco, Iowa. He holds a BS degree in Forestry, which he earned in 1937. He pursued an MS in Forest Pathology, and later earned a PhD in Pathology and Genetics in 1942 from the University of Minnesota. After a brief stint with the E.I. du Pont de Nemours in Delaware, Dr Borlaug joined the Rockefeller Foundation team in Mexico in 1944, a move that would set him on course to accomplish one of the most notable accomplishments in history.

He became the director of the Cooperative Wheat Research and Production Program in 1944, a program initiated to develop highyielding cultivars of wheat for producers in the area. In 1965, the Centro Internationale de Mejoramiento de Maiz y Trigo (CIMMYT) was established in Mexico, as the second of the currently 16 International Agricultural Research Centers (IARC) by the Consultative Group on International Agricultural Research (CGIAR). The purpose of the center was to undertake wheat and maize research to meet the production needs of developing countries. Dr Borlaug served as the director of the Wheat Program at CIMMYT

until 1979 when he retired from active research, but not until he had accomplished his landmark achievement, dubbed the Green Revolution. The key technological strategies employed by Dr Borlaug and his team were to develop high yielding varieties of wheat, and an appropriate agronomic package (fertilizer, irrigation, tillage, pest control) for optimizing the yield potential of the varieties. Adopting an interdisciplinary approach, the team assembled germplasm of wheat from all over the world. Key contributors to the efforts included Dr Burton Bayles and Dr Orville Vogel, both of the USDA, who provided the critical genotypes used in the breeding program. These genotypes were crossed with Mexican genotypes to develop lodging-resistant, semi-dwarf wheat varieties that were adapted to the Mexican production region. Using the improved varieties and appropriate agronomic package, wheat production in Mexico increased dramatically from its low 750 kg/ha to about 3200 kg/ha. The successful cultivars were introduced INTRODUCTION 13 into other part of the world, including Pakistan, India, and Turkey in 1966, with equally dramatic results. So successful was the effort in wheat that the model was duplicated in rice in the Philippines in 1960. In 1970, Dr Norman Borlaug was honored with the Nobel Peace Prize for contributing to curbing hunger in Asia and other parts of the world where his improved wheat varieties were introduced (Figure B1.2). Whereas the Green Revolution was a life-saver for countries in Asia and some Latin-American countries, another part of the world that is plagued by periodic food shortages, the sub-Saharan Africa, did not benefit from this event. After retiring from CIMMYT in 1979, Dr Borlaug focused his energies on alleviating hunger and promoting the general well-being of the people on the

continent of Africa. Unfortunately, this time around, he had to go without the support of these traditional allies, the Ford Foundation, the Rockefeller Foundation, and the World Bank. It appeared the activism of powerful environmental groups in the developed world had managed to persuade these donors from supporting what, in their view, was an environmentally intrusive practice advocated by people such as Dr Borlaug. These environmentalists promoted the notion that high yield agriculture for Africa, whereby the agronomic package included inorganic fertilizers, would be eco logically disastrous.

Variability in natural populations and its exploitation

Genetic variability:

Variability that can be attributed to genes that encode specific traits and can be transmitted from one generation to the next is described as genetic or heritable variation. Because genes are expressed in an environment, the degree of expression of a heritable trait is impacted by its environment, some more so than others (Figure 4.1). Heritable variability is indispensable to plant breeding. As previously noted, breeders seek to change the phenotype (trait) permanently and heritably by changing the genotype (genes) that encode it. Heritable variability is consistently expressed generation after generation. For example, a purple-flowered genotype will always produce purple flowers. However, a mutation can permanently alter an original

expression. For example, a purple-flowered plant may be altered by mutation to become a white-flowered plant. Genetic variation can be detected at the molecular as well as the gross morphological level. The availability of biotechnological tools (e.g., DNA markers) allows plant breeders to assess genetic diversity of their materials at the molecular level. Some genetic variation is manifested as visible variation in morphological traits (e.g., height, color, size), while compositional or chemical traits (e.g., protein content, sugar content of a plant part) require various tests or devices for evaluating them.

Origins of genetic variability:

There are three ways in which genetic or heritable variability originates in nature – gene recombination, modifications in chromosome number, and mutations. The significant fact to note is that, rather than wait for them to occur naturally, plant breeders use a variety of techniques and methods to manipulate and make these three phenomena more and more targeted, as they generate genetic variation for their breeding programs. With advances in science and technology (e.g., gene transfer, somaclonal variation), new sources of genetic variability have become available to the plant breeder. Variability generated from these sources is, however, so far limited.

Genetic recombination:

Genetic recombination applies only to sexually reproducing species and represents the primary source of variability for plant breeders in those species. As previously described, genetic

recombination occurs via the cellular process of meiosis. This phenomenon is responsible for the creation of non-parental types in the progeny of a cross, through the physical exchange of parts of homologous chromosomes (by breakagefusion). The cytological evidence of this event is the characteristic crossing (X-configuration or chiasma) of the adjacent homologous chromosome strands, as described in Chapter 3, allowing genes that were transmitted together (non-independent assortment) in the previous generation to become independent. Consequently, sexual reproduction brings about gene reshuffling and generation of new genetic combinations (recombinants). Unlike mutations that cause changes in genes themselves in order to generation variability, recombination generation variability by assembling new combinations of genes from different parents. In doing this, some gene associations are broken. Consider a cross between two parents of contrasting genotypes $AAbb$ and $aaBB$. A cross between them will produce an F_1 of genotype $AaBb$. In the F_2 segregating population, and according to Mendel's law, the gametes (AB , Ab , aB , and ab) will combine to generate variability, some of which will be old (like the parents – parental), while others will be new (unlike the parents – recombinants)

Ploidy modifications:

New variability may arise naturally through modifications in chromosome number as a result of hybridization (between unidentical genotypes), or abnormalities in the nuclear division processes (spindle malfunction). Failure of the spindle mechanism, during karyokinesis or even prior to that, can lead to errors in chromosome numbers transmitted to cells, such as polyploidy

(individuals with multiples of the basic set of chromosomes for the species in their cells) (Figure 9.3). Sometimes, instead of variations involving complete sets of chromosomes, plants may be produced with multiples of only certain chromosomes or deficiencies of others (called aneuploidy). Sometimes, plants are produced with half the number of chromosomes in the somatic cells (called haploids). Like genetic recombination, plant breeders are able to induce various kinds of chromosome modification

Mutation:

Mutation is the ultimate source of biological variation. Mutations are important in biological evolution as sources of heritable variation. They arise spontaneously in nature as a result of errors in cellular processes such as DNA replication (or duplication) and by chromosomal aberrations (deletion, duplication, inversion, translocation). The molecular basis of mutation may be described by mechanisms such as modification of the structure of DNA or a component base of DNA, substitution of one base for a different base, deletion or addition of one base in one DNA strand, deletion or addition in one or more base pairs in both DNA strands, and inversion of a sequence of nucleotide base pairs within the DNA molecule.

Transposable elements:

The phenomenon of transposable elements (genes with the capacity to relocate within the genome), creates new variability. Transposable genetic elements (transposable elements, transposons, or “jumping genes”) are known to be nearly universal in occurrence. These mobile

genetic units relocate within the genome by the process called transposition. The presence of transposable elements indicates that genetic information is not fixed within the genome of an organism. Barbara McClintock, working with corn in the 1940s, was the first to detect transposable elements, which she initially identified as controlling elements. This discovery was about 20 years ahead of the discovery of transposable elements in prokaryotes. Controlling elements may be grouped into families. The members of each family may be divided into two classes: autonomous elements or non-autonomous elements. Autonomous elements have the ability to transpose whereas the non-autonomous elements are stable (but can transpose with the aid of an autonomous element through trans-activation).

Biotechnology for creating genetic variability:

Gene transfer:

The rDNA technology is the state-of-the-art in gene transfer to generate genetic variability for plant breeding. With minor exceptions, the DNA is universal. Consequently, DNA from an animal may be transferred to a plant! The tools of biotechnology may be used to incorporate genes from distant sources into adapted cultivars. An increasing acreage of cotton, soybean, and maize are being sown to genetically modified (GM) cultivars, indicating the importance of this technology for creating variability for plant breeding. Economic gene transfers have been made from bacteria to plants to confer disease and herbicide resistance to plants. The most common GM products on the market are RoundupReady₁ cultivars (e.g., cotton, soybean) with herbicide tolerance, and Bt products (e.g., corn) with resistance to lepidopteran pests. The

technique of site-directed mutagenesis allows scientists to introduce mutations into specified genes, primarily for the purpose of studying gene function, and not for generating variability for breeding per se. Other tissue culture based techniques include protoplast fusion, cybrid formation, and use of transposons.

Somaclonal variation:

In vitro culture of plants is supposed to produce clones (genetically identical derivatives) from the parent material. However, the tissue culture environment has been known to cause heritable variation called somaclonal variation. The causes cited for these changes include karyotypic changes, cryptic chromosomal rearrangements, somatic crossing over and sister chromatid exchange, transposable elements, and gene amplification. Some of these variations have been stable and fertile enough to be included in breeding programs.

Session # 6 & 7: Tutorial

Objectives and application of breeding techniques

Plant breeding is an art and science, which tells us ways and means to change the genetic architecture of plants so as to attain a particular objective. Plant breeding can be accomplished through many different techniques ranging from simply selecting plants with desirable characteristics for propagation, to more complex molecular techniques. Plant breeding has been practiced for thousands of years, since near the beginning of human civilization. It is now

practiced worldwide by individuals such as gardeners and farmers, or by professional plant breeders employed by organizations such as government institutions, universities, crop-specific industry associations or research centers. International development agencies believe that breeding new crops is important for ensuring food security by developing new varieties that are higher-yielding, resistant to pests and diseases, drought-resistant or regionally adapted to different environments and growing conditions.

The objectives may be

- a) Crop improvement
- b) Improved agronomic characters
- c) Resistance against biotic and abiotic stress

1. Increased yield

Majority of our breeding programmes aims at increased yield. This is achieved by developing more efficient genotypes. The classical examples are utilization of Dee Gee Woo Gen in rice and Norin10 in wheat. Identification and utilization of male sterility

2. Improving the quality

Rice -milling, cooking quality, aroma and grain colour
wheat- milling and baking quality and gluten content.

4. Resistance against biotic and abiotic stresses

Biotic stress:

Evolving pests and diseases resistant varieties there by reducing cost of cultivation, environmental pollution and saving beneficial insects.

Abiotic stress: It is location specific problem. Soil factors and edaphic factors some times poses severe problems. Breeding resistant varieties is the easy way to combat abiotic stress.

5. Change in maturity duration – Evolution of early maturing varieties

6. Improved agronomic characters -Production of more tillers – E.g. Rice, Bajra,

7. Reducing the plant height to prevent lodging – Rice

8. Photoinsensitivity –sorghum

9

Scope of plant breeding

Since the cultivable land is shrinking and there is no scope for increasing the area under cultivation, the only solution to meet the food requirement is by increasing the crop yield through

genetic improvement of crop plants. There are two ways by which yield improvement is possible.

1. Enhancing the productivity of crops

This can be done

a) By the proper management of soil and crops involving suitable agronomic practices and harvesting physical resources.

b) By using high potential crop varieties created by appropriate genetic manipulation of crop plants.

2. Stabilizing the productivity achieved

This is done by using crop varieties that are bred especially for wide adaptation or for specific crop zones to offset the ill effects of unfavorable environmental conditions prevailing in the areas.

Session # 8 & 9: Tutorial

Development of commercial hybrids

They are the first generation from crosses between two pure lines, inbreds, open pollinated varieties of other populations that are genetically not similar.

Kinds of hybrids

1. Single cross hybrids

AxB

Crossing two inbreds or pure lines.

2. Three way cross hybrid

$(A \times B) \times C$

A cross between a single cross hybrid and an inbred.

3. Double cross hybrid

$(A \times B) \times (C \times D)$

cross between two F₁s.

4. Double Top Cross hybrid

Double Cross hybrid crossed with open pollinated variety.

Operation in production of hybrids.

In production of hybrids inbreds are preferred rather than open pollinated varieties

for the following reasons.

1. Inbreds can be maintained without a change in the genotype. Whereas open pollinated variety cannot be maintained pure. They may alter genotypically due to natural selection etc.
2. The hybrids derived from inbreds will be uniform where as it may not be in case, of open pollinated variety.
3. The inbreds are homogenous and their performance can be predicted where as open pollinated variety are heterogenous and their prediction in performance cannot be made.

Development of inbreds

1. By inbreeding, selfing etc.
2. Development of inbreds from haploids - rice, sorghum, maize.

Evaluation of inbreds

a) Phenotypic evaluation

Based on phenotypic performance. Highly suitable for characters with high heritability. .

b) Top cross test

Top cross test provides a reliable estimate of GCA. The selected inbreds will be crossed to a tester parent with wide genetic base i.e. open pollinated variety. The cross progenies will be evaluated in replicated progeny rows. Based on results better inbreds can be selected.

c) Single cross evaluation

The developed inbreds can be crossed and the single crosses can be estimated in replicated trial. Outstanding hybrids tested over years in different locations, then released.

d) Prediction of double cross performance

'The predicted performance of any double cross is the average performance of the four non parental single crosses involving the four parental inbreds'.

Inbreds : A, B, C, D.

6 possible single crosses = A x B, A x C, A x D, B x C, B x D, C x D.

From these 3 double crosses produced = (A x B) x (C x D)

(A x C) x (B x D)

(A x D) x (B x C)

The performance of these any one double cross can be predicted from performance of the four single crosses not involved in producing that particular hybrid.

$(A \times B) \times (C \times D)$

$A \times C$

$A \times D$

$B \times C$

$B \times D$

Average

Production of Hybrids

Methods

1. Hand emasculation and dusting – Wheat, rice

2. Use of male sterile lines

b) Genic male sterility - Redgram, Castor.

c) Cytoplasmic - genic male sterility Jowar, Bajra, Rice

Open pollination is allowed. The progeny obtained is Syn1. This is distributed as synthetic variety or it may be grown in isolation for one more season and Syn2 is distributed.

Merits

1. Less costly compared to hybrids.

2. Farmer can maintain his synthetic variety for more seasons which is not possible in hybrids.

3. Because of wider genetic base the synthetics are more stable over years and environments.

4. Seed production is more skilled operation in hybrids where as it is not so in synthetics.

Demerits

1. Performance is little bit lower compared to hybrids because synthetics exploit only

GCA while hybrids exploit both GCA and SCA.

2. The performance may not be good when lines having low GCA are used.

Composites

It is produced by mixing seeds of phenotypically outstanding lines and encouraging open

pollination to produce crosses in all possible combinations among mixed lines. The lines used

to produce a composite are rarely tested for combining' ability. So the yield of composite

varieties cannot be predicted easily. Like synthetics, composites are commercial varieties and

are maintained by open pollination.

Session # 9 & 10: Tutorial

Breeding methods in self- pollinated crops

Mass selection

In mass selection, seeds are collected from (usually a few dozen to a few hundred) desirable

appearing individuals in a population, and the next generation is sown from the stock of mixed

seed. This procedure, sometimes referred to as phenotypic selection, is based on how each

individual looks. Mass selection has been used widely to improve old “land” varieties, varieties

that have been passed down from one generation of farmers to the next over long periods.

An alternative approach that has no doubt been practiced for thousands of years is simply to eliminate undesirable types by destroying them in the field. The results are similar whether superior plants are saved or inferior plants are eliminated: seeds of the better plants become the planting stock for the next season.

A modern refinement of mass selection is to harvest the best plants separately and to grow and compare their progenies. The poorer progenies are destroyed and the seeds of the remainder are harvested. It should be noted that selection is now based not solely on the appearance of the parent plants but also on the appearance and performance of their progeny. Progeny selection is usually more effective than phenotypic selection when dealing with quantitative characters of low heritability. It should be noted, however, that progeny testing requires an extra generation; hence gain per cycle of selection must be double that of simple phenotypic selection to achieve the same rate of gain per unit time.

Mass selection, with or without progeny test, is perhaps the simplest and least expensive of plant-breeding procedures. It finds wide use in the breeding of certain forage species, which are not important enough economically to justify more detailed attention.

Pure-line selection

Pure-line selection generally involves three more or less distinct steps: (1) numerous superior appearing plants are selected from a genetically variable population; (2) progenies of the individual plant selections are grown and evaluated by simple observation, frequently over a period of several years; and (3) when selection can no longer be made on the basis of

observation alone, extensive trials are undertaken, involving careful measurements to determine whether the remaining selections are superior in yielding ability and other aspects of performance.

Any progeny superior to an existing variety is then released as a new “pure-line” variety. Much of the success of this method during the early 1900s depended on the existence of genetically variable land varieties that were waiting to be exploited. They provided a rich source of superior pure-line varieties, some of which are still represented among commercial varieties. In recent years the pure-line method as outlined above has decreased in importance in the breeding of major cultivated species; however, the method is still widely used with the less important species that have not yet been heavily selected.

A variation of the pure-line selection method that dates back centuries is the selection of single-chance variants, mutations or “sports” in the original variety. A very large number of varieties that differ from the original strain in characteristics such as colour, lack of thorns or barbs, dwarfness, and disease resistance have originated in this fashion.

Hybridization

During the 20th century planned hybridization between carefully selected parents has become dominant in the breeding of self-pollinated species. The object of hybridization is to combine desirable genes found in two or more different varieties and to produce pure-breeding progeny superior in many respects to the parental types.

Genes, however, are always in the company of other genes in a collection called a genotype. The plant breeder's problem is largely one of efficiently managing the enormous numbers of genotypes that occur in the generations following hybridization. As an example of the power of hybridization in creating variability, a cross between hypothetical wheat varieties differing by only 21 genes is capable of producing more than 10,000,000,000 different genotypes in the second generation. At spacing normally used by farmers, more than 50,000,000 acres would be required to grow a population large enough to permit every genotype to occur in its expected frequency. While the great majority of these second generation genotypes are hybrid (heterozygous) for one or more traits, it is statistically possible that 2,097,152 different pure-breeding (homozygous) genotypes can occur, each potentially a new pure-line variety. These numbers illustrate the importance of efficient techniques in managing hybrid populations, for which purpose the pedigree procedure is most widely used.

Pedigree breeding:

starts with the crossing of two genotypes, each of which have one or more desirable characters lacked by the other. If the two original parents do not provide all of the desired characters, a third parent can be included by crossing it to one of the hybrid progeny of the first generation (F1). In the pedigree method superior types are selected in successive generations, and a record is maintained of parent–progeny relationships.

The F2 generation (progeny of the crossing of two F1 individuals) affords the first opportunity for selection in pedigree programs. In this generation the emphasis is on the elimination of

individuals carrying undesirable major genes. In the succeeding generations the hybrid condition gives way to pure breeding as a result of natural self-pollination, and families derived from different F₂ plants begin to display their unique character. Usually one or two superior plants are selected within each superior family in these generations. By the F₅ generation the pure-breeding condition (homozygosity) is extensive, and emphasis shifts almost entirely to selection between families. The pedigree record is useful in making these eliminations. At this stage each selected family is usually harvested in mass to obtain the larger amounts of seed needed to evaluate families for quantitative characters. This evaluation is usually carried out in plots grown under conditions that simulate commercial planting practice as closely as possible. When the number of families has been reduced to manageable proportions by visual selection, usually by the F₇ or F₈ generation, precise evaluation for performance and quality begins. The final evaluation of promising strains involves (1) observation, usually in a number of years and locations, to detect weaknesses that may not have appeared previously; (2) precise yield testing; and (3) quality testing. Many plant breeders test for five years at five representative locations before releasing a new variety for commercial production.

The bulk-population method:

It differs from the pedigree method primarily in the handling of generations following hybridization. The F₂ generation is sown at normal commercial planting rates in a large plot. At maturity the crop is harvested in mass, and the seeds are used to establish the next generation in a similar plot. No record of ancestry is kept. During the period of bulk propagation natural

selection tends to eliminate plants having poor survival value. Two types of artificial selection also are often applied: (1) destruction of plants that carry undesirable major genes and (2) mass techniques such as harvesting when only part of the seeds are mature to select for early maturing plants or the use of screens to select for increased seed size. Single plant selections are then made and evaluated in the same way as in the pedigree method of breeding. The chief advantage of the bulk population method is that it allows the breeder to handle very large numbers of individuals inexpensively.

Often an outstanding variety can be improved by transferring to it some specific desirable character that it lacks. This can be accomplished by first crossing a plant of the superior variety to a plant of the donor variety, which carries the trait in question, and then mating the progeny back to a plant having the genotype of the superior parent. This process is called **backcrossing**. After five or six backcrosses the progeny will be hybrid for the character being transferred but like the superior parent for all other genes. Selfing the last backcross generation, coupled with selection, will give some progeny pure breeding for the genes being transferred. The advantages of the backcross method are its rapidity, the small number of plants required, and the predictability of the outcome. A serious disadvantage is that the procedure diminishes the occurrence of chance combinations of genes, which sometimes leads to striking improvements in performance.

Session # 11 & 12: Laboratory

Breeding methods in cross pollinated crops.

This article throws light upon the top three breeding methods used for cross-pollinated crops. The methods are:

1. Mass Pedigree Method

2. Inbreeding

3. Recurrent Selection.

1. Mass Pedigree Method:

In this method of breeding, the best individuals with desired characters are selected on the basis of phenotypic performance in a source population. Open-pollinated seeds of the selected

individual plants are divided into two halves. Second year replicated progeny row trial is conducted using one set of half seeds from each plant.

On the basis of the progeny performance, the best parental individuals are identified. The remnant half seeds from the superior parental plants are mixed and grown in isolation for random mating during the third year. This method of breeding is equivalent to ear-to-row selection in context of maize originally proposed by C.G. Hopkins at the Illinois Agricultural Experiment Station in 1896 to improve protein and oil content of maize. This method has been named as mass-pedigree method by S.S. Rajan in India. This very method is called line breeding when selection is based on progeny tests and a group of progeny lines is composited.

2. Inbreeding:

The mating of individuals more closely related than individuals mating at random is known as inbreeding. The lines produced by continued inbreeding are known as inbred lines. Self-fertilization is the most intense form of inbreeding.

In plant breeding nearly homozygous lines are produced by continued self-fertilization accompanied by selection for five to six generations. This can be used as the method of breeding only in those crops, which do not show any loss of vigour due to inbreeding, like cucurbits.

The three important uses of inbreeding in cross-pollinated crops are as follows:

- (i) To attain uniformity in plant characters.
- (ii) To improve yield etc. by individual plant selection as in cucurbits in which there is no inbreeding depression.
- (iii) To develop suitable inbred lines in production of hybrids and synthetics.

Synthetic Variety:

The term 'synthetic variety' has come to be used to designate a variety that is maintained from open pollinated seed following its synthesis by hybridization in all combinations among a number of selected genotypes, which have been tested for combining ability.

The components of a synthetic variety could be inbred (usually), clones, mass selected populations or various other materials. The component units are maintained so that the synthetic may be reconstituted at regular intervals.

The inbreeds to be used as component lines are chosen on the basis of combining ability tests.

The component inbred are crossed in all possible combinations. This inter-crossed seed is called as Syn 0.

Equal quantity of seed from all crosses is composited and the mixture is allowed open-pollination in isolation and seed is harvested. This becomes Syn 1 generation. In absence of reconstitution of a synthetic at regular intervals, the population becomes an open-pollinated variety.

The testing for combining ability is the decisive criterion for a synthetic variety by which it can be distinguished from a conventional variety of a cross-pollinating species, which originates in a continuous selection of individuals and subsequent progeny tests. The greater variability caused by crossing several components with high general combining ability makes the synthetic varieties more adaptable compared to conventional varieties.

Similar to hybrids, the yield of a synthetic variety generally also decreases after the Syn 2, until an equilibrium is reached which, in partially self-fertile species, depends on selfing rate and inbreeding (minimum depression), but also on the number of components used in the Syn 0.

Session # 13 & 14: Tutorial

Genetic improvement using novel techniques

.

The rDNA technology is the state-of-the-art in gene transfer to generate genetic variability for plant breeding. Mutation is non- conventional method of creating genetic variation. Mutations are important in biological evolution as sources of heritable variation. They arise spontaneously in nature as a result of errors in cellular processes such as DNA replication (or duplication) and by chromosomal aberrations (deletion, duplication, inversion, translocation). The molecular basis of mutation may be described by mechanisms such as modification of the structure of DNA or a component base of DNA, substitution of one base for a different base, deletion or

addition of one base in one DNA strand, deletion or addition in one or more base pairs in both DNA strands, and inversion of a sequence of nucleotide base pairs within the DNA molecule.

Gene transfer:

The rDNA technology is the state-of-the-art in gene transfer to generate genetic variability for plant breeding. With minor exceptions, the DNA is universal. Consequently, DNA from an animal may be transferred to a plant! The tools of biotechnology may be used to incorporate genes from distant sources into adapted cultivars. An increasing acreage of cotton, soybean, and maize are being sown to genetically modified (GM) cultivars, indicating the importance of this technology for creating variability for plant breeding. Economic gene transfers have been made from bacteria to plants to confer disease and herbicide resistance to plants. The most common GM products on the market are RoundupReady₁ cultivars (e.g., cotton, soybean) with herbicide tolerance, and Bt products (e.g., corn) with resistance to lepidopteran pests. The technique of site-directed mutagenesis allows scientists to introduce mutations into specified genes, primarily for the purpose of studying gene function, and not for generating variability for breeding per se. Other tissue culture based techniques include protoplast fusion, cybrid formation, and use of transposons.

Somaclonal variation:

In vitro culture of plants is supposed to produce clones (genetically identical derivatives) from the parent material. However, the tissue culture environment has been known to cause heritable

variation called somaclonal variation. The causes cited for these changes include karyotypic changes, cryptic chromosomal rearrangements, somatic crossing over and sister chromatid exchange, transposable elements, and gene amplification. Some of these variations have been stable and fertile enough to be included in breeding programs.

Session # 15:

Tutorial: Course/Discussion from session 1 to 14 (Mid Term Exam)