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The evolution of plant breeding techniques

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Abstract
Plant breeding is the science of changing the traits of plants in order to produce desired characteristics. To improve agronomic traits associated with various traits in crop plants, several conventional and molecular approaches have been used, including genetic selection, whole-genome sequence-based approaches, physical maps, and functional genomic tools. However, recent advances in genome editing technology using programmable nucleases, and CRISPR-associated (Cas) proteins have opened the door to a new plant breeding era. Therefore, to increase the efficiency of crop breeding, researchers around the world are using novel strategies such as speed breeding, genome editing tools, and high-throughput phenotyping. In this review, we summarize recent findings on several aspects of crop breeding to describe the evolution of plant breeding practices, from traditional to modern speed breeding.

Keywords: Deoxyribonucleic acid (DNA), ribonucleic acid (RNA) CRISPR, gene silencing, genome editing, reverse breeding

Introduction
Agriculture began around 10,000 years ago. Since then, humans have unknowingly selected plants to suit their needs. To begin with, only the best-performing plants that nature provided were selected and retained. Useful traits that had appeared spontaneously were bred into certain crops by human selection, often by going against natural selection; thereby practicing plant breeding without any scientific approach. The knowledge of Mendel's laws of inheritance was unknown by then. Towards the end of 19^{th} century, Mendel's laws were discovered, this accelerated plant modification. In 1953, Watson and Crick proposed the double helical model of DNA which increased the understanding of the genetic material substantially. This was a major plot twist to plant breeding as plant modifications targeting the DNA came to light, the first being mutation breeding in the 1960s and later the GM technology in the 1980s. Since then, the science of genetics has been taking leaps and bounds starting from different approaches of DNA analysis to Marker assisted selection. Although many different techniques have been discovered, they remain unique, each to suit a specific situation. The availability of several techniques gives plant breeders the 'tools' they require to come up with new varieties.

Why a non-terminating process?
"Plant breeding is a continuous process". Since ages, these words have not lost their sense. To meet the demands of the consumers, plant breeding plays an important role in food security and food safety. However, due to the exponential rise in the population, plant breeding is facing issues with food quality and quantity globally. In this era of fast forward lives, consumers prefer ready to eat food, where nutritional quality is compromised. Furthermore, changes in weather conditions caused by climate change are causing heat and drought stress; consequently, farmers around the world are facing significant yield losses. The world is expected to reach 10 billion by 2050. Keeping this in mind, new varieties are to be bred within the limited land available using the limited resources. Age old plant breeding practices, though have not lost their importance, do not alone suffice the current situation of food demand (Raza *et al.*, 2019) [21]. Also, plant breeding faces challenges its own challenges. It has the role to create novel allelic combinations, to fix the desirable alleles and to control the gene flow. Considering the mentioned criteria, plant breeding should remain an everlasting subject of interest and progress.

Plant Breeding, right from its conventional approaches to present day integration with modern biotechnological tools has evolved rapidly over the past years. During the course of time many improvements have been made in breeding plants for different purposes. Each advancement, though non replaceable, has expressed itself uniquely. In this article, an effort is made to incite the readers of the past, present and future trends and advancements in plant breeding.

The early plant breeding: selection and crossing.

The most basic form of plant breeding is selection. It is an art of discriminating the biological variants in a population to identify and pick desirable variants. It is the most primitive and age-old practice of plant breeding (Orton, 2020) [19]. Variabilities exploited were naturally occurring variants and wild relatives of crop species. During crossing, selective breeding is performed by applying pollen from one parent plant to the pistil of a flower of the other parent plant. Such selective crossing is very important in creation if variation as each product of crossing contains unique DNA combinations of its parents (Glenn *et al*., 2017) [10]. Many new varieties are developed by selection. Combining selection with cross-breeding will continue to benefit the plant breeding programmes (Louwaars, 2018) [16].

The hybrid technology

During the 1930s, the value of hybrids was realised. A hybrid is produced by crossing two inbred lines. Therefore, this technology combined both cross breeding and inbreeding. The base of hybrid technology lies in maize breeding. To obtain an F_1 hybrid, first inbred families are created by self pollination (Mette *et al*., 2015) [17]. Selfing leads to homogeneity among the genotypes. When the inbred families are formed, they are crossed with each other. The families are selected so as to have a variety of positive characteristics that complement each other. The F_1 hybrids are heterozygous and homogenous. As a result, F1-hybrids usually have hybrid vigour or heterosis. This is the effect where offspring perform better than the average of the two parents for one or more traits (Labroo *et al*., 2021) [15].

Commercial F1-hybrids display robust growth and give a higher yield. The performance of F_1-hybrids weakens in the successive generations and the heterosis effect completely disappears after a number of generations. This is because the offspring of F_1-hybrids are no longer uniform. They differ in their appearances and quality. As a result, growers need to buy new F_1 seeds every year if they want to maintain the same level of productivity. It goes without saying that this is clearly a profitable trait for breeders and seed companies (Bradshaw, 2017) [2].

The development of non crossables

The next step in the history of plant breeding was crossing among different species or different genera, also known as distant hybridization (Chen *et al*., 2018) [4]. There are many barriers in this method of crossing but it was possible to overcome these barriers through the advent of tissue culture technology in the middle of 20th century. The most classical example of this is that of a cross between wheat and rye. The idea here was to combine the high yielding ability and good grain quality of wheat with the hardiness of rye. By using different types of techniques, such as doubling the chromosomes using specific chemicals, a hybrid was nevertheless successfully obtained. The crop was named *triticale.* It is a crop that has been grown in the field since the 70s and is primarily used as animal feed (Gustafson, 1976) [12].

Mutation breeding technology

Through cross breeding it was possible to generate certain variations among the crop species but it could not suffice the purpose. Plant breeders always are in search of new variations. The greater the genetic variation within a species, the more possibilities there are to find traits of interest and combine them. Instead of depending on the naturally occurring variations alone, breeders had started to generate variations through external sources. The work on mutation breeding was started in the 1930s (Jankowicz-Cieslak *et al*., 2016) [13]. Scientists began to experiment with changing genetic material using X-rays first in *Drosophila* and later in crop plants (Calabrese, 2018) [3]. The variations created through artificial mutations were random, rapid and large. Initiatives were taken to expose the seeds to radiations in radioactive fields called gamma gardens and seeds have also been sent into outer space to expose them to cosmic radiation. Employing mutation breeding, more than three thousand crop varieties have been created during the past eighty years (Ahloowalia & Maluszynski, 2001) [1].

Marker assisted selection

Knowledge about how plant genes work and their role in plant growth and development increased, aiding in selecting the genes which control the traits. This is possible by detecting a specific DNA sequence, also known as a marker which is say linked to the trait like resistance (Jiang, 2013) [14]. DNA markers have enormous potential to improve the efficiency and precision of conventional plant breeding via marker-assisted selection (MAS) (Collard & Mackill, 2008) [5]. Through this technology, the character like disease resistance can be figured out during the early stages of the crop growth without having to infect the plants. In the present day, markers have become the first priority in any crop improvement programme, marker assisted selection being the most favourite of the breeders. Marker assisted selection has wide applicability in plant breeding. It facilitates assessment of material purity, parental selection and genetic diversity study, study of heterosis, identification of genomic regions governing the traits (Govindaraj *et al*., 2015) [11]. Thanks to this technology, a number of varieties have been released taking its due advantages.

Modification of genes

During the 1970s a technology was developed which allowed the insertion of genetic information into the plants without the need for crossing. In other words, the genes could be played with. Genes from any organism could be inserted into crop plants owing to this technology. This method was named, genetic engineering and the output called as genetically engineered organisms (Datta, 2013) [6]. The invention of this technology revolutionized plant breeding. Today, there are four major applications of GM: tolerance of herbicides, resistance to pests, resistance to viruses and drought resistance.

The first biological method of genetic modification was based on the ability of a soil bacterium *Agrobacterium* to transfer the DNA to crop plants. Along with infecting the host plants, it integrates a portion of its DNA along with the host DNA. This aspect was the break though for this technology (Gelvin, 2003) [9]. The portion of the bacterial DNA was replaced with the desirable genes for the crop plants. The first genetically modified plant was developed in 1982. It was a tobacco plant engineered to be resistant to herbicides (Shetty & Krishna, 2018) [22]. Later, many other mechanical methods of gene transfer were discovered. The most significant one being the particle bombardment method.

GM crops are promising to mitigate current and future problems in commercial agriculture. The GM seed market has changed drastically since 1996. To date, nearly 525 different transgenic events in 32 crops have been approved for cultivation in different parts of the world (Raman, 2017) [20].

The adoption of transgenic technology has been shown to increase crop yields, reduce pesticide and insecticide use, reduce CO2 emissions, and decrease the cost of crop production.

New plant breeding methods

GM technology does not mark the end of producing crops that suit our needs. New methods are continuous in process. They are otherwise called “New Breeding Technologies”.

New Plant-Breeding Techniques (NBTs) are methods which allow the development of new plant varieties with desired traits, by modifying the DNA of the seeds and plant cells. They are called ‘new’ because these techniques have only been developed in the last decade and have evolved rapidly in recent years (Enfissi *et al*., 2021) [8]. These New Plant-Breeding Techniques, which have emerged as the result of advances in scientific research, enable more precise and faster changes in the plant’s genome than conventional plant breeding techniques. An effort is made to present some of the aspects of these methods here.

Reverse breeding

The process of reverse breeding is converse to that of F_1 hybrid making process. The concept was given by Rob Dirks in 2009 (Dirks *et al*., 2009) [7]. The best performing hybrid lines are selected and their parental lines are re-generated. Thus, these newly created parents can produce hybrids in different combinations. The method is based on reducing genetic recombination in the selected heterozygote by eliminating meiotic crossing over.

Dirks *et al* (2009) [7] stated that one important application of reverse breeding is the production of complementary homozygous lines that can be used to generate specific F1 hybrids. When RB is applied to F1 heterozygotes, it is possible to generate chromosome substitution lines that allow targeted breeding on the single chromosome scale. Since the fixation of unknown heterozygous genotypes is impossible in traditional plant breeding, RB could fundamentally change future Plant Breeding.RB accelerates breeding process and increases number of available genetic combinations, allowing breeder to respond much quicker to the needs of farmers with better varieties. Facilitates selection of superior hybrid plants. Large population of plants can be generated and screened and well performing plants can be regenerated indefinitely without prior knowledge of their genetic constitutions.

Gene silencing technology

Traditional plant breeding is a time consuming process with limited genetic resources. RNA interference technology, also referred to as gene silencing is a promising new tool for plant breeding as it introduces small non coding RNA sequences into the genome. These non -coding sequences have the ability to switch-off the gene expression in a sequence specific manner. RNAi-mediated gene silencing techniques can provide plant researchers with the choice of suppressing genes in full or partially, in time and space, through proper choice of promoters and construct design (Mmeka *et al*., 2014) [18].

Recent plant transformation technologies have used RNAi as a tool to study gene expression by introducing dsRNA in a similar manner to sense and antisense RNAs, but with higher efficiency. It provides opportunity to the plant breeders to produce commercial crops, breeding for superior cultivars with disease resistance, stress tolerance, nutritional values, high yield, eliminated allergens, secondary metabolites and many other features that are impossible to obtain in one cultivar by conventional breeding.

Speed breeding - the time saving tool

Taking inspiration from NASA’s work in early 1980s, plant scientists at University of Queensland coined the term “speed breeding” in 2003 to develop and accelerate the growth of wheat crop. Speed breeding protocols are currently being developed for several crops. The principle behind speed breeding is to use optimum light intensity, temperature, and daytime length control (22 h light, 22 ◦C day/17 ◦C night, and high light intensity) to increase the rate of photosynthesis, which directly stimulates early flowering, coupled with annual seed harvesting to shorten the generation time. Intensity and wavelength of light plays a key role during flowering time (Watson *et al*., 2018) [25].

Until recently, speed breeding had been reported to shorten generation time by extending photoperiods in most of the crops, while certain crop species, such as radish, pepper, leafy vegetables such as Amaranth responded positively to increased day length. Speed breeding of short-day crops has been limited because of their flowering requirements. Nevertheless, recently, Lee Hickey and his research team worked on developing protocols for short-day crop like sorghum, millet and pigeon pea with the International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) as part of a project funded by the Bill and Melinda Gates Foundation.

Speed breeding allows researchers to rabidly mobilise the genetic variation found in wild relatives of crops and introduce it into elite varieties that can be grown by farmers. Generation time in most plant species represents a drawback in applied research programmes and breeding. Tackling this bottleneck means scientists can respond quicker to emerging diseases, changing climate and increased demand for certain traits.

Genome editing

Genome editing is the budding technology. It is the process of making precise, targeted sequence changes in the deoxyribonucleic acid of living cells and organisms. Recent advances have made genome editing widely applicable, offering the opportunity to rapidly advance basic and applied biology. Until 2013, the dominant genome editing tools were zinc finger nucleases and transcription activator-like effector nucleases (Wada *et al*., 2020) [24].

The latest ground-breaking technology for genome editing is based on RNA-guided engineered nucleases, which already hold great promise due to their simplicity, efficiency and versatility. The most widely used system is the type II clustered regularly interspaced short palindromic repeat (CRISPR)/Cas9 (CRISPR-associated) system (Song *et al*., 2016) [23]. CRISPR/Cas is a form of site-directed nuclease (SDN) technology. Nucleases are enzymes that cut DNA. The complex of cas 9 protein and guide RNA nicks the DNA at the desired genome location, which makes it possible to insert or delete sequences. Once this mechanism was deciphered by the scientists, they were not only able to apply in the model plants such as *Arabidopsis* and tobacco but also in crops such as wheat, corn, rice and tomatoes.

Because of their several attractive features such as simplicity, efficiency, high specificity, and amenability to multiplexing, genome editing technologies are revolutiozing the way crop breeding is done and paving the way for the next generation breeding.

Future outlook

To make our food production more effective, plant breeders are continuously making efforts. Adapting crops to suit our needs has always been the ulterior motive. The basic and primary breeding methods in modern agriculture are significant enough but do not alone suffice the current situation. They cannot satisfy the global food demand. To cope up with the challenges and improve the efficiency of crop breeding, marker-assisted breeding, and transgenic approaches have been adopted, generating desired traits and their transformation into elite varieties. The genome editing tools are excellent in providing rapid and efficient gene silencing. Crop breeding was revolutionized by the development of next-generation breeding techniques. These new breeding techniques have many advantages over traditional agricultural methods, given their simplicity, efficiency, high specificity, and amenability to multiplexing (Bradshaw, 2017) [2].

New techniques for working even more efficiently will continue to be developed and form part of the breeder's toolbox. Likewise, the transition of technology usually originates in developed countries, mostly in the private sector. It should be transferred to the public sector and into the developing world. In the future, we can expect a wide range of techniques to be developed using interdisciplinary principles to increase their benefits. In this review paper an effort was made to give an overview of different breeding methods that can be implemented for crop improvement. In addition to that, the chronology of the breeding methods from the traditional to the modern day has been presented. Being alert to new scientific technologies must be encouraged, this guarantees food and environmental safety.

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