2 History of plant breeding

Purpose and expected outcomes

Agriculture is a human invention that continues to impact society and the environment. The players on this stage advanced the industry with innovation, technology, and knowledge available to them during their era. The tools and methods used by plant breeders have been developed and advanced through the years. There are milestones in plant breeding technology as well as accomplishments by plant breeders over the years. In this chapter, individuals (or groups of people) whose contributions to knowledge, theoretical or practical, have impacted on what has become known in the modern era as plant breeding will be spotlighted. After studying this chapter, the student should be able to:

1. List and describe the contributions of some of the people through history whose discoveries laid the foundation for modern plant breeding.
2. Describe the contributions of Mendel to modern plant breeding.
3. Discuss the advances in plant breeding technologies.

2.1 Origins of agriculture and plant breeding

In its primitive form, plant breeding started after the invention of agriculture, when people of primitive cultures switched from a lifestyle of hunter–gatherers to sedentary producers of selected plants and animals. Views of agricultural origins range from the mythological to ecological. The Fertile Crescent in the Middle East is believed to be the cradle of agriculture, where deliberate tilling of the soil, seeding and harvesting occurred over 10 000 years ago. This lifestyle change did not occur overnight but was a gradual process during which plants were transformed from being independent, wild progenitors, to fully dependent (on humans) and domesticated varieties. Agriculture is generally viewed as an invention and discovery. During this period humans also discovered the time-honored and most basic plant breeding technique – **selection**, the art of discriminating among biological variation in a population to identify and pick desirable variants. Selection implies the existence of variability.

In the beginnings of plant breeding, the variability exploited was the naturally occurring variants and wild relatives of crop species. Furthermore, selection

Principles of Plant Genetics and Breeding, Second Edition. George Acquaah.

was based solely on the intuition, skill, and judgment of the operator. Needless to say that this form of selection is practiced to date by farmers in poorer economies, where they save seed from the best-looking plants or the most desirable fruit for planting the next season. These days, scientific techniques are used in addition to the aforementioned qualities to make the selection process more precise and efficient. Even though the activities described in this section are akin to some of those practiced by modern plant breeders, it is not being suggested that primitive crop producers were necessarily conscious of the fact that they were manipulating the genetics of their crops.

2.2 The "Unknown Breeder"

Two distinct kinds or groups of people continue to impact plant improvement in significant ways, but with recognition that cannot be personalized.

2.2.1 The "farmer-breeder"

The term "breeder" is a modern day reference to professionals who knowingly manipulate the nature of plants to improve their appearance and performance in predetermined ways. These professionals operate with formal knowledge from the discipline of plant biology and allied disciplines. They are preceded by people who unknowingly and indirectly manipulated the nature of plants to their advantage. This category of "breeders" (to use the term very loosely), or "farmer-breeders", continues to impact world crop production today. Of course, the image of the farmer today is variable from one part of the world to another. In developing countries, many farmers still produce crops with primitive technologies, while high-tech defines the farmer of today in technologically advanced countries.

The age-old practice is for farmers to save seed from the current year's crop to plant the next season's crop. In doing so, farmers depend on their instincts, intuition, experience and keen observation to save seed from selected plants for planting the next crop. Performance and appeal are two key factors in the decision making process. For example, seeds from a plant without blemish among a plot of others with disease symptoms would be saved because it obviously had "something" that makes it ward off diseases. This may be described as primitive or rudimentary "breeding" for disease resistance. Similarly, farmers may save seed on the basis of other agronomic features of their preference, such as seed or fruit size, seed or fruit color, plant stature, and maturity, and in the process manipulate plant genetics without knowing it. I call this "unconscious breeding".

Over time, farmers create varieties of crops that are adapted to their cultural environments, the sole technique being the art of discrimination among variability, or selection as it is called in modern crop improvement. These creations are called **farmer-selected** varieties and sometimes **landraces**. The practice prevails in areas of subsistence agriculture, which represent many parts of the developing world. These varieties are highly adapted to local regions and can be depended upon by farmers who produce their crops with limited resources. Farmer-selected seed continues to sustain agricultural production in these parts of the world while the commercial seed supply system is being developed.

Farmer-selected varieties or landraces are an important source of breeding material for modern breeders. This primitive or exotic germplasm is heterogeneous and is useful for initiating some plant breeding programs.

2.2.2 The "no name" breeder

One of the common practices or traditions in modern plant breeding is to refer to germplasm whose source, name or breeding history is unknown as simply "No Name". This casual acknowledgement appears to absolve the breeder of any deliberate and willful infringement on intellectual property. These nameless products are modern day examples of cultivars that have fallen victim to improper record keeping.

2.3 Plant manipulation efforts by early civilizations

Archeological and historical records from early civilizations indicate that some of these communities engaged in rudimentary plant manipulations, albeit in the dark, without knowledge of plant heredity. Whereas it would not be far-fetched to assume that, just like farmers of the early civilizations who domesticated crops species would have also continued their

selection practices to produce farmer-selected varieties, evidence of deliberate plant manipulation for the purposes of improvement are few. Archeological findings occasionally reveal some ancient practices which indicate that plant manipulation beyond phenotypic selection among natural variability occurred. Babylonians are said to have perceived the role of pollen in successful fruit production and applied it to the pistils of female date palms to produce fruit. The Assyrians did likewise in about 870 BC, artificially pollinating date palms.

2.4 Early pioneers of the theories and practices of modern plant breeding

Plant breeding as we know it today began in earnest in the nineteenth century. Prior to this era, a number of groundbreaking discoveries and innovations paved the way for scientific plant manipulation. Some of the early pioneers of plant breeding include the following:

Rudolph Camerarius (1665–1721). Rudolph Camerarius was a professor of philosophy at the University of Tubingen in Germany. He conducted research that contributed to establishing sexual differentiation, defining the male and female reproductive parts of the plant. His seminal work, *De sexu plantarum* (On the sex of plants), was published in 1694 in a letter to a colleague. Camerarius's work also described the functions of the reproductive parts in fertilization and showed that pollen is required for this key process in heredity.

Joseph Gottlieb Koelreuter (1733–1806). German botanist, J.G. Koelreuter became professor of natural history and director of the botanical gardens in Karlsruhe in 1764. He was a pioneer in the application of the discovery of sex in plants as a vehicle for their genetic manipulation. He observed that the hybrid offspring generally resembled the parent that supplied the pollen as closely as the parent on which seed was borne. Koelreuter conducted the first systematic experiments in plant hybridization, using the tobacco plant as subject. He recognized the role of insects and wind in pollination of flowers, and also conducted experiments to study artificial fertilization and development in tobacco plants. The golden rain tree genus (*Koelreuteria*) is named in his honor.

Louis de Vilmorin (1902–1969). Louis de Vilmorin was a noted French seedsman. His experiments in heredity contributed to our understanding of the cause of variation. Vilmorin conducted studies in plant improvement in vegetables using a method called genealogical selection, which is the modern breeding equivalent of progeny testing. He recognized that new varieties of plants could be developed by selecting certain characteristics, which would then be transmitted through genealogy to the progeny. In 1856, he published his "Note on the Creation of a New Race of Beetroot and Considerations on Heredity in Plants", which laid the theoretical groundwork for the modern seed breeding industry. The modern day company Vilmorin is a major player in the global seed industry; along with its international subsidiaries it is ranked among the top five largest seed companies in the world. The company is also credited with producing the first seed catalog for farmers and academics, among other significant publications.

Thomas Andrew Knight (1759–1838). This British horticulturalist and botanist conducted basic research in plant physiology that led to the discovery of the phenomenon of geotropism, the effects of gravity on seedlings. He also showed how decay in fruit trees was transmitted through grafting. In terms of practical crop improvement, Knight conducted research in the breeding of horticultural plants, including strawberries, cabbages, peas, apples and pears. The "Downton" strawberry that he developed is noted in the pedigree of most of the important modern strawberries. He is credited with pioneering work in the science of fruit breeding. In 1797 he published a *Treatise on the culture of apple and pear.* Knight is also said to have demonstrated segregation for seed characters of the garden pea but, unfortunately did not offer an explanation for the event as Mendel eventually did.

Carl Linnaeus (1707–1778). A Swedish botanist, physician, and zoologist, Carl Linnaeus is most noted for his work in plant taxonomy, which led to the development of his enduring conventions for naming living organisms, the universally accepted **binomial nomenclature**, also called Linnaean taxonomy or the scientific classification of organisms. The binomial nomenclature classifies nature within a hierarchy, assigning a two-part name to an individual, a *genus* and a *species* (specific epithet). His work was published in his most noted publication *Species Plantarum*. There are specific rules and

guidelines for writing scientific names, which are in Latin, the genus beginning with a capital letter while the species does not; being non-English, the name is italicized (or underlined), for example, *Zea mays* (corn). Further, the genus can stand alone, but not the species (e.g., *Zea, Zea sp, or Z. mays*).

Charles Darwin (1809–1882). Charles Robert Darwin was an English naturalist with one of the most recognizable names of all times, because of his work that led to one of the most enduring theories ever, the **theory of evolution**. He proposed what is sometimes called the unifying theory of life sciences that all species of life have evolved over time from a common ancestor. The process of evolution is extremely slow, requiring thousands or even millions of years to bring about the gradual changes which incrementally result in the divergence or diversity of life that is now seen. The primary mechanism of evolution, he reckoned, is natural selection, the arbiter in deciding which individuals survive to contribute to the subsequent generations (survival of the fittest). Genetic mutations are the ultimate source of variation, but natural selection decides which modifications are advantageous and contribute to the survival of individuals. The survival or extinction of an organism depends on its ability to adapt to its changing environment. He published his seminal work in his 1859 book, *On the origin of species.*

For all intents and purposes, modern plant breeding is evolution happening in real time. Instead of thousands or millions of years to bring about a new variety, plant breeders achieve their goal in about ten years, depending upon the method used, among other factors. Random mutations may be used to create variation, but other more efficient methods are preferred today. Once generated, breeders use artificial selection (not natural selection) to discriminate among the variability to decide which individual plants to advance to the next step in the breeding program.

Gregor Mendel (1822–1844). Born in 1822, Gregor Mendel, an Augustinian monk, is known for his scientific research that led to the foundations of modern transmission genetics. Of German ethnicity, his nationality was Austrian–Hungarian. Even though several researchers in his time and prior to that time had conducted research or made observations similar to what he did, it was Mendel who was credited with being first to provide empirical evidence about the nature of heredity, the underpinnings of traits and how genes that condition them are transmitted from parents to offspring. He made his ground-breaking findings from making and studying *Pisum* (pea) hybrids. His paper *Experiments with hybrid plants* was published in 1866 to reveal what became known as the **laws of Mendel** – the laws of dominance, segregation, and independent assortment, which are the foundations of modern genetics. In fact, Mendel is often referred to as the father of modern genetics. In addition to the laws he established, Mendel also made two other significant contributions to the field of genetics – the development of pure lines, and good record keeping for use in statistical analysis that led to his discoveries (he counted plant variants).

Luther Burbank (1849–1926). An American botanist and horticulturalist, Burbank is known to have developed numerous varieties of fruits, flowers, grains, grasses and vegetables. One of his most remarkable creations is the **Russet Burbank potato**, which has a russet-colored skin and which is used worldwide today. This natural variant was isolated and propagated by Burbank.

It is significant to note that some of the most widely used plant breeding methods of selection were developed prior to the nineteenth century, preceding Mendel! These methods include mass selection, pedigree selection, and bulk breeding.

2.5 Later pioneers and trailblazers

Since the beginning of the nineteenth century, there has been an explosion of knowledge in plant breeding and its allied disciplines. Discussing each one would simply overwhelm this chapter. Consequently, only a sample of the key innovations or discoveries with direct and significant implication on plant breeding is discussed briefly. Some of these innovations or discoveries pertain to breeding schemes or methods and other applications that are discussed in detail later in the book and therefore are only introduced briefly.

M.M Rhoades and D.N. Duvick,. Cytoplasmic male sterility(CMS) was discovered as a breeding technique by Marcus Rhoades in 1933. Duvick was a major player in the discovery of various aspects of this technology. In 1965, he published a summary of work done in this area.

Nikolai I. Vavilov. Vavilov identified eight areas of the world which he designated **centers of diversity**

of crop species or centers of origin of crops. He distinguished between primary centers, where the crop was first domesticated, and secondary centers, which developed from plants migrating from the primary center. He also established the **law of homologous series** in heritable variation, showing the existence of parallelism in variability among related species. This law allows plant explorers to predict, within limits, forms that are yet to be described. Germplasm banks explore and collect germplasm from these centers to be classified and preserved for use by researchers.

E.R. Sears and C.M. Ricks. Sears and Ricks were first to apply their knowledge of cytogenetics to plant breeding of wheat and tomato, respectively. Their efforts showed how researchers could transfer genes and chromosomes from alien species to cultivated crop species. This achievement aided the use of cytogenetics in the evolutionary study of plant species.

H.J. Muller. The pioneering experiments by Muller (1927) showed that it is possible to alter the effect of genes. Using X-rays, he demonstrated that the physiology and genetics of an organism could be altered upon exposure to this radiation. Mutagenesis or mutation breeding became possible because of this discovery. In 1928, Stadler described the mutagenic effects of X-rays on barley.

Wilhelm Johannsen. The work of Johannsen pioneered the **single plant selection** method. He was the first to distinguish between **genotype** and **phenotype**. Working with the field bean, a self-pollinated species, he selected extreme individuals each generation and observed that improvement only occurred in the first generation (i.e., heritable variation did not extend beyond the first generation). Variation observed in the second and subsequent generations was environmental (not heritable). Repeated selfing, after some time, is unresponsive to selection because of lack of genetic variation. Prolonged selfing leads to an individual with extreme homozygosity. He called such products pure lines. This became the **pure line theory** in 1903.

H.H. Hardy and W. Weinberg. The work in 1908 of Hardy, an Englishman, and Weinberg, a German, laid the foundation for modern day breeding of cross-pollinated species. They independently demonstrated that in a large random-mating population, both gene and genotypic frequencies remained unchanged from one generation to the next, in the absence of change agents like mutation, migration and selection. This later became known as the **Hardy–Weinberg equilibrium** or law. This concept is foundational to the breeding strategies employed for breeding cross-pollinated species.

Nilsson-Ehle. Nilsson-Ehle is credited with being the leader of the first scientific wheat breeding program, which was started by the Swedish Seed Association at Svalof. It was there, in 1912, that he developed the method of plant breeding called **bulk breeding** to cope with the large number of crosses, generations, and plants involved is his breeding program. His breeding program centered on the winter hardiness of wheat. He space-planted the F_1 and bulk-harvested the F_2.

H.V Harlan and M.N. Pope. Harlan and Pope first applied the **backcross breeding** scheme to plants in 1922, after observing its success with animal breeding. Unable to observe desired recombinants in the segregating population of a cross between the commercial cultivar, "Manchuria", a rough-awned wheat, and a smooth-awned exotic parent (donor parent), they resorted to a repeated crossing of the F_1 to the commercial or adapted parent (recurrent parent).

C.H. Goulden. Goulden developed the **single seed decent** (rapid generation advance) selection scheme in 1941 as a means of speeding up the attainment of homozygosity. This was later modified by Brim in 1966.

E.M. East and D.F. Jones. The concept of **recurrent selection** was independently proposed by Hayes and Garber in 1919, and East and Jones in 1920. Hayes and Garber also proposed the method of **synthetic breeding** in 1919.

F.H. Hull. Hull coined the term **recurrent selection** in 1945. His work included recurrent selection for combining ability.

F.E Comstock, H.F. Robinson, and P.H. Harvey. These breeders proposed the method of **reciprocal recurrent selection** in 1949.

C.M. Donald. An Australian biologist, Donald proposed the **ideotype breeding** concept as a way of managing plant breeding programs by modeling plant architecture. Breeding based on a plant model (archetype) meant that breeders paid more attention to their breeding goals and strategies. They could introgress exotic germplasm and expand genetic diversity in their program, following judicious strategies. Even though it did not attain prominence in plant breeding, notable applications were made by Wayne Adams (the major graduate advisor of the author of this book) at Michigan

State University, and by Rasmussen at the University of Minnesota.

H.H. Flor. Flor proposed the **gene-for-gene hypothesis** in 1956 to postulate that both host and parasite genetics were significant in determining whether or not a disease resistance reaction would be observed. The expression of resistance by the host was dominant while the expression of avirulence by the parasite was dominant. In other words, there was a single gene in the host that interacted with a single gene for the parasite.

G.H. Shull. George Shull coined the term **"heterosis"** for the phenomenon of **hybrid vigor**. His research on crossing corn, an open pollinated species, led to the observation of hybrid vigor. This observation had also been made by East and Yates and other researchers, but it was Shull who gave the correct interpretation of heterosis in 1908. Hybrid vigor is the reason why hybrid seed is a huge commercial success.

W.J. Beal. Beal was one of the pioneers in the development of hybrid corn. He is also noted for the oldest and continuously operated botanical garden (The W.J. Beal Botanical Garden) in the United States, located at Michigan State University. His noted publications include the *The New Botany*, *Grasses of North America*, and *History of Michigan Agricultural College*. In 1879, Beal started one of the longest running experiments in botany, designed to determine how long seed can remain viable. The experiment, which includes periodic retrieval and germination testing of the buried seeds, is scheduled to be completed in 2100.

Ronald Fisher. Though not a plant breeder, this biologist made major contributions to the field of statistics and genetics. He introduced the concept of **randomization** and the **analysis of variance** procedure that are indispensable to plant breeding research and evaluation. The concept of **likelihood** (maximum likelihood) is his original idea. His contributions to quantitative genetics aided breeders in the understanding and manipulation of quantitative traits.

C.C. Cockerham. Cockerham's contribution to the role of statistics in plant breeding was summarized in his seminal paper of 1961. It connected statistics to genetics by shedding light on sources of variation and variance components, and covariance among relatives in genetic analysis. There are other names that are associated with this effort, including Mather and Jinks, and Eberhardt and Comstock.

Murashige and Skoog. Tissue culture technology is vital to plant breeding. Many applications, such as embryo rescue, anther culture, micropropagation, *in vitro* selection, and somaclonal variation, depend on tissue culture. The development in 1962 of the Murashige–Skoog media (MS media). Modern methods of genetic engineering depend on tissue culture systems for key steps such as transformation and regeneration.

Watson and Crick. The understanding of heredity that underlies the ability of plant breeders to effectively manipulate plants at the molecular level to develop new cultivars, depends on the seminal work of Watson and Crick. Their discovery of the **double helical structure of the DNA molecule** laid the foundation for the understanding of the chemical basis of heredity.

Norman Borlaug. In the modern era of agriculture, Norman Borlaug deserves mention, not so much for his contribution to science as much as application of scientific principles to address world food and hunger, according to a methodology driven by his personal philosophy. This philosophy, dubbed the "Borlaug Hypothesis" by some economists, proposes to increase the productivity of agriculture on the best farmland to help curb deforestation by reducing demand for new farmland. His signature accomplishment, for which his name is synonymous, and for which he received the prestigious Nobel Prize (for Peace) in 1970 – the first agriculturalist to be so recognized – was the **Green Revolution**. While the award signified an acknowledgment of the positive impact of this work, the Green Revolution received criticism from a broad spectrum of sources. Undeterred by his detractors, Borlaug continued his advocacy for the poor and those plagued by perpetual hunger, working hard until his death in 2009 to alleviate world hunger.

Herb Boyer, Stanley Cohen, and Paul Berg. In 1973, Herb Boyer, Stanley Cohen, and Paul Berg lead the way into the brave new world of genetic manipulation in which DNA from one organism could be transferred into another, by achieving the feat with bacteria. Called **recombinant DNA technology,** the researchers successfully transferred foreign DNA into a bacterium cell. This began the era of **genetic engineering**. Currently, this is one of the major technologies in modern plant breeding, albeit controversial.

Industry highlights

Barley breeding in the United Kingdom

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Targets

Barley breeding in the United Kingdom aims to produce new cultivars that offer an improvement in one or more of the key traits for the region (Table B2.1). New cultivars must have a good yield, preferably in excess of the currently established cultivars if targeted solely at the feed market. To be accepted for malting use, a new cultivar must offer improvement in one or more key facets of malting quality, primarily hot water extract, with no major defects in, for example, processability traits. Additionally, new cultivars must have minimum levels of disease resistance, which equates to being no worse than moderately susceptible, to the key diseases listed in Table B2.1.

Crossing to commercialization

Barley breeders therefore design crosses in which the parents complement each other for these target traits and attempt to select out recombinants that offer a better balanced overall phenotype. Whilst a wide cross may offer a better chance of producing superior recombinants, most barley breeders in the United Kingdom concentrate on narrow crosses between elite cultivars. The main reason for doing so is that a narrow cross between elite lines is more likely to produce a high mid-parental value for any one trait, so the proportion of desirable recombinants is thus far greater in the narrow cross than in the wide (Figure B2.1). Thus, the chances of finding a desirable recombinant for a complex trait such as yield in the wide cross is low and the chances of combining it with optimum expression for all the other traits is remote. As breeders are still making progress using such a narrow crossing strategy, it is possible that there is still an adequate level of genetic diversity with the elite barley gene pool in the United Kingdom. A similar phenomenon has been observed in barley breeding in the USA, where progress has been maintained despite a narrow crossing strategy (Rasmusson and Phillips, 1997). Rae *et al.* (2005) genotyped three spring barley cultivars (Cocktail, Doyen and Troon) on the 2005 United Kingdom recommended list with 35 Simple Sequence Repeat (SSR) markers and found sufficient allelic diversity to produce over 21 million different genotypes. It would appear, therefore, that the breeding challenge is not so much to generate variation as to identify the best recombinants.

Table B2.1 Traits listed in the current UK recommended lists of barley (www.hgca.com).

Trait	Spring Barley	Winter Barley
Yield (overall and regional with fungicide)	Yes	Yes
Yield without fungicide	Yes	Yes
Height	Yes	Yes
Lodging resistance	Yes	Yes
Brackling resistance	Yes	
Maturity	Yes	Yes
Winter hardiness		Yes
Powdery Mildew resistance	Yes	Yes
Rhynchosporium resistance	Yes	Yes
Yellow rust resistance	Yes	Yes
Brown rust resistance	Yes	Yes
Net blotch resistance		Yes
BaYMV complex resistance		Yes
BYDV resistance	Yes	
Grain nitrogen content	Yes	Yes
Hot water extract	Yes	Yes
Screenings (2.25 and 2.5 mm)	Yes	Yes
Specific weight	Yes	Yes

The progress of a potential new barley cultivar in the United Kingdom, in common with that of the other cereals, proceeds through a series of filtration tests (Figure B2.2) and the time taken to pass through all but the first is strictly defined. The opportunity to reduce the time taken for breeders' selections is fairly limited given that multiplication of material for and conducting single and multisite trials takes at least three years, irrespective of whether out of season nurseries are used for shuttle breeding for the spring crop or doubled haploidy (DH) or Single Seed Descent (SSD) for the winter crop. The length of the breeding cycle is thus fairly well defined, with occasional reduction by a year when a cultivar from a highly promising cross is speculatively advanced by a breeder. A breeder may also delay submitting a line for official trials for an extra season's data but breeders now aim to submit the majority of their lines to official trials within 4–5 years of making a cross.

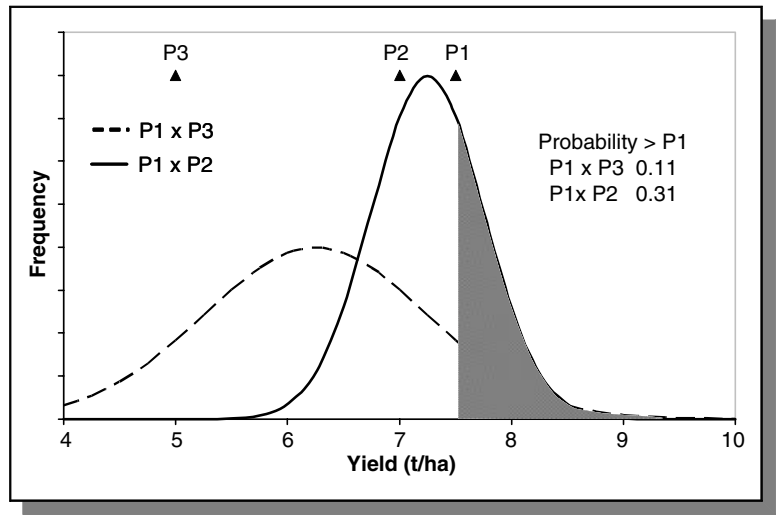

Figure B2.1 Frequency distribution of two crosses with a common parent (P1) and alternative second parents (P2 and P3). P2 is a slightly lower yielding parent, thus progeny from the cross will have a high mid-parent and small variation. P3 is a comparatively high yielding unadapted parent and the cross has a lower mid-parent but much greater variance. Areas under the shaded portion of both curves represent the fraction selected for high yield potential (>P1). Thus, whilst the extreme recombinant of P1 × P3 has a greater yield potential than that of P1 × P2, the probability of identifying superior lines for just this one trait is far greater for the latter. Figure courtesy of W.T.B Thomas.

Given that many breeders would have begun re-crossing such selections by this stage of their development, the approximate time for the breeding cycle in the United Kingdom is four years.

During the two years of National List Trials (NLT), potential cultivars are tested for Distinctness, Uniformity and Stability (DUS) using established botanical descriptors. A submission therefore has to be distinct from any other line on the National List and not have more than a permitted level of "off-types", currently equivalent to a maximum of 3 in 100 ear rows. Lines are tested over more than one year to ensure that they are genetically stable and do not segregate in a subsequent generation. DUS tests are carried out by detailed examination of 100 ear rows and three bulk plots (approximately 400 plants in total) submitted by the breeder. Thirty-three traits are examined routinely and there are three special and 59 approved additional traits. At the same time plot trials are carried out to establish whether the submission has Value for Cultivation and Use (VCU), and the VCU and DUS submissions are checked to verify that they are the same. Occasionally, a submission may fail DUS in NLT1, in which case the breeder has the option of submitting a new stock for a further two years of testing. Generally, the VCU results are allowed to stand and a cultivar can be entered into RLT before it has passed DUS in the anticipation that it will have succeeded by the time a recommendation decision has to be made. Full details can be obtained from www.defra.gov.uk/planth/pvs/VCU_DUS.htm.

The UK barley breeding community

The Plant Varieties and Seeds act of 1964, which enabled plant breeders to earn royalties on the certified seed produced for their cultivars, led to a dramatic increase in breeding activity in the United Kingdom. Formerly, it was largely the province of state funded improvement programs, such as that of the Plant Breeding Institute (PBI), of Cambridge, UK, that had produced the highly successful spring cultivar Proctor. The increase in breeding activity in the 1970s and early 1980s was largely as a result of dramatic expansion in the commercial sector, initially led by Miln Marsters, of Chester, UK, who produced Golden Promise, which dominated Scottish spring barley production for almost two decades. The two sectors co-existed until the privatization of the breeding activity at PBI and the state marketing arm, the National Seed Development Organisation, together with a change in government policy led to the withdrawal of the public sector from barley breeding. Barley breeding in the commercial sector in the United Kingdom is highly competitive with currently five UK-based crossing and selection programs. A number of other companies have their own selection programs based in the United Kingdom and many continental breeders have agency agreements for the testing and potential marketing of their products. For example, 41 spring and 34 winter barley lines were submitted for NLT1 for harvest 2004 and these were derived from 16 different breeders.

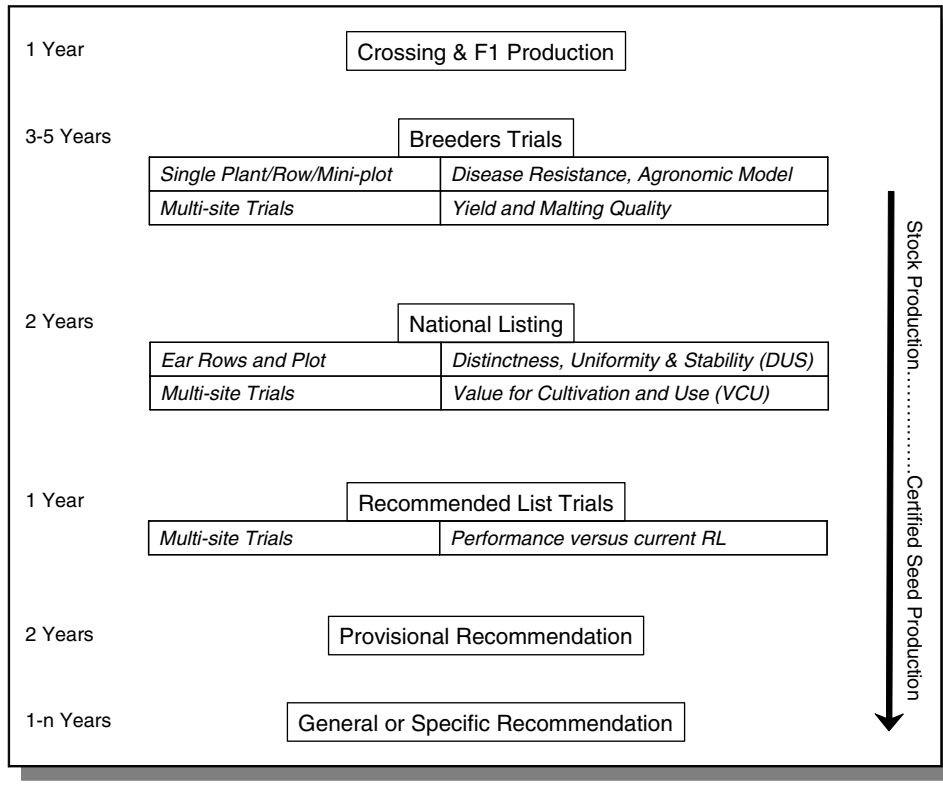

Figure B2.2 The phases in the development of a successful new cultivar from crossing to commercialization with the timescale for each. The exact nature of the scheme adopted in breeder's trials varies according to breeder and crop type but is either based upon a version of the pedigree or doubled haploid system. A cultivar may persist on the recommended list for *n* years, where *n* is the number of years where there is a significant demand for it. Figure courtesy of W.T.B Thomas.

The amount of certified seed produced for each cereal variety in the United Kingdom is published by the National Institute of Agricultural Botany. The total annual production of certified barley seed has been in decline since its peak of over 250 000 t in 1987 and has declined by 43% since 1995, with most due to a reduction in winter barley seed (Figure B2.3). There are a number of potential reasons, such as an increase in farm-saved seed, but the principal feature has been a marked decrease in winter barley cropping over the period whereas spring barley has remained fairly static and winter wheat has increased. Over this period, certified seed production has exceeded 100 000 metric tons for two spring (Optic and Chariot) and two winter (Regina and Pearl) barley cultivars; these can be considered notable market successes. There has been substantial production for a number of others but total production exceeded 25 000 tonnes for only six and seven spring and winter barley cultivars, respectively. When it is considered that over 830 lines were submitted for NLT over this period, the overall success rate is 1.6%. Nevertheless, real breeding progress is being made. Using yield data from the recommended list trials from 1993 to 2004 to estimate the mean yield of each recommended cultivar and then regressing that data against the year that it was first recommended revealed that genetic progress was in the order of 1% per annum (Rae *et al.*, 2005).

The impact of molecular markers

The first whole genome molecular maps of barley were published in 1991 (Graner *et al.*, 1991; Heun *et al.*, 1991) and were closely followed by QTL maps in 1992 (Heun, 1992) and 1993 (Hayes *et al.*, 1993) with well over 40 barley mapping studies now in the public domain. Despite this apparent wealth of information, barley breeders in the United Kingdom are largely relying on conventional Phenotypic Selection (PS) to maintain this progress. This is in marked contrast to the highly successful of Marker Assisted Selection (MAS) in the Australian Barley program (Langridge and

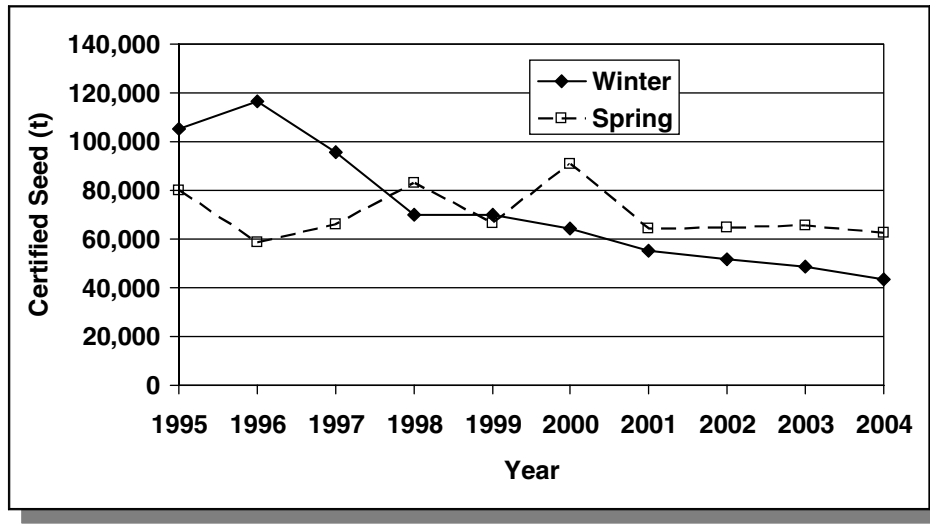

Figure B2.3 Tonnes of certified barley seed produced in the UK from 1995 to 2004. Figure courtesy of W.T.B Thomas.

Barr, 2003), which is probably a reflection of the different breeding strategies in the two countries. In the United Kingdom, improvement is being achieved in the elite gene pool, as noted above, whereas MAS has been deployed in an introgression breeding strategy in Australia. Given that most barley mapping studies have concentrated on diverse crosses to maximize polymorphism and facilitate map construction, there are very few published QTL studies that are relevant to current United Kingdom barley breeding strategies. Surveying results from eight different barley mapping populations Thomas (2003) found that there were very few instances where QTLs were co-located for three or more crosses for important traits such as yield and hot water extract.

Major gene targets

Markers have been developed for a number of known major genes and could potentially be deployed in MAS by United Kingdom breeders. Many of these major gene targets are, however, disease resistances, many of which have been defeated by matching virulence in the corresponding pathogen population. United Kingdom barley breeders have been required to select for at least some resistance to the key foliar pathogens listed in Table 2.11 since the introduction of minimum standards and have, accordingly, developed efficient phenotypic screens. There are exceptions, most notably the Barley Yellow Mosaic Virus complex, which is transmitted by infection of the roots with the soil borne fungus vector *Polymixa graminis*. A phenotypic screen therefore requires an infected site and the appropriate environment for infection and expression. Phenotypic screening can be expensive if a breeder is distant from an infected site and is subject to potential mis-classification.

Resistance due to the *rym4* allele was initially found in Ragusa and was effective against BaYMV strain 1 and a number of cultivars carrying this allele have been developed, initially by phenotypic screening. Markers to select for this resistance have also been developed, beginning with the RFLP probe MWG838 (Graner and Bauer, 1993), later converted to an STS (Bauer and Graner, 1995), and were used in some breeding programs in the United Kingdom and Europe. BaYMV strain 2, which became more frequent in the 1990s, could overcome the *rym4* resistance but another resistance, *rym5*, was identified in Mokusekko 3 as being effective against both strains. This resistance was co-located with *rym4* and the Simple Sequence Repeat (SSR) marker Bmac29 was found to be linked to it (Graner *et al.*, 1999). Bmac29 could not only distinguish between resistant and susceptible alleles but also between the *rym4* and *rym5* alleles derived from Ragusa and Mokusekko 3, respectively, but as it is 1.3 cM from the gene locus it is not effective in a wide germplasm pool, as *Hordeum spontaneum* lines predicted to be resistant by the marker were found to be susceptible (R.P. Ellis, unpublished data). Bmac29 has, however, proved to be particularly effective for United Kingdom, and European, barley breeders as they are working with a narrow genetic base and just the two sources of resistance. Other resistance loci have been identified together with suitable markers to deploy in a pyramiding strategy in an attempt to provide durable resistance (Ordon *et al.*, 2003) and a clear example of how the use of markers in MAS have evolved together with the pathogen.

Another example relates to a particular requirement of the Scotch whisky distilling industry. In grain and certain malt whisky distilleries, a breakdown product of the cyanogenic glycoside epiheterodendrin can react with copper in the still to form the carcinogen ethyl carbamate, which can be carried over into the final spirit in distilling, leading to a demand for barley cultivars that do not produce epiheterodendrin. The trait is controlled by a single gene with the non-producing allele originating in the mildew resistance donor "Arabische" used in the derivation of the cultivar Emir. The phenotypic assay for the trait involves the use of hazardous chemicals and the finding of a linked SSR marker (Bmac213) offered a simpler and safer alternative (Swanston *et al.*, 1999). The distance between the gene locus and the marker (6cM) meant that, in contrast to Bmac29, Bmac213 was not reliable in the cultivated gene pool. For instance, the cultivar Cooper and its derivatives possessed the non-producing allele yet were producers. However, the marker could still be used when the parents of a cross were polymorphic for both the phenotype and the marker. Recently, a candidate gene has been identified and markers used for reliable identification of non-producers developed (P. Hedley, personal communication).

QTL targets

Currently, United Kingdom barley breeders do not use MAS for any other malting quality targets. A QTL for fermentability was detected in a cross between elite United Kingdom genotypes (Swanston *et al.*, 1999) but the increasing allele was derived from the parent with relatively poor malting quality. When this QTL was transferred into a good malting quality cultivar, the results were inconclusive (Meyer *et al.*, 2004), probably because the effect of the gene was more marked in a poor quality background and any extra activity due to it was superfluous in a good quality background. This highlights one of the problems in developing MAS for complex traits such as yield and malting quality. Results from an inappropriate gene pool may well not translate to a target gene pool; it is therefore essential that QTL studies are carried out in the appropriate genetic background.

Future prospects

The genotyping of entries from Danish registration trials coupled with associations of markers with yield and yield stability phenotypes demonstrated that QTLs can be detected in the elite gene pool (Kraakman *et al.*, 2004) but the findings need validation before the markers can be used in MAS. At the Scottish Crop Research Institute (SCRI), extensive genotyping of UK RLT entries over the past 12 years will be undertaken in collaboration with the University of Birmingham, National Institute of Agricultural Botany, Home Grown Cereals Authority, barley breeders and representatives of the malting, brewing and distilling industries in a project funded by the Defra Sustainable Arable LINK scheme. The RLT phenotypic data set represents an extensive resource that can discriminate between the fine differences in elite cultivars and will facilitate the identification of meaningful associations within the project for validation and potential use in MAS. How MAS is then used by commercial breeders in the United Kingdom might well vary but could range from early generation selection to an enriched germplasm pool upon which phenotypic selection can be concentrated to identification of candidate submission lines carrying target traits.

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2.6 History of plant breeding technologies/techniques

Modern plant breeding is an art and a science. The two key activities in plant breeding are the creation (or assembling) of variation and discriminating (selecting) among the available variability to identify and advance individuals that meet the breeding objectives. Consequently, advances in plant breeding technologies and techniques focus on facilitating and making these two distinct activities more efficient and cost effective.

2.6.1 Technologies/techniques associated with creation of variation

Plant breeders depend on variation for plant improvement. Variation may be natural in origin or it may be artificially generated in a variety of ways. Through the years, breeders have used various technologies and techniques in the quest for desired variation.

Artificial pollination

Artificial pollination, the deliberate transfer by humans of pollen from the flower (anther) of one plant to the flower (stigma) of another plant is an ancient practice, as previously noted. Babylonians and Assyrians were known to have conducted it on date palms. These ancient cultures did this without the benefit of knowing the underlying science of pollination and fertilization. These ancient efforts were not geared toward creating variation; they were primarily for fertilization for fruit production. Science-based artificial pollination started after the discovery of sex in plants by Camerarius and the ensuing work of Koelreuter. Artificial pollination (controlled pollination) is used in a variety of ways in modern plant breeding. Naturally cross-pollinating species can be artificially self-pollinated to create variability for selection or to generate special parental breeding stock for experimentation or development of new cultivars. Experiments in heredity (e.g., Mendel's) depend on controlled pollination. These applications are discussed in detail elsewhere in this book.

Hybridization

One of the commonly used techniques in modern plant breeding to create variation is hybridization (crossing) of genetically different plants. It is commonly used to generate the initial population in which selection is practiced in a breeding program. The F_2 is the most variable generation in which selection is often initiated. Breeders working in the field often have crossing blocks where controlled hybridization is conducted. Depending on the species and breeding objective, pollination may be done manually, or with the aid of natural agents (wind, insects). Whereas hybridization for the creation of variation may entail just two parents, there are various sophisticated hybridization schemes in modern plant breeding in

which a number of parents are included (e.g., diallele crosses).

Hybridization is commonly conducted with parents that are crossable or genetically compatible. However, there are occasions in plant breeding where it is desirable or even necessary to seek to introduce genes into the breeding program from genetically distant sources. Wild germplasm is considered a rich source of genes for modern crop improvement. The term "wide cross" is used to refer to hybridization that involves plant materials from outside the pool for cultivated species. Some wide crosses involve two species (interspecific cross), or even genera (intergeneric cross). The more distant the parents used in hybridization, the higher the incidence of genetic complications pertaining to meiosis, and the lesser the chances of success. Breeders use certain techniques and technologies to boost the success of wide crosses.

Tissue culture/embryo culture

Tissue culture entails growing plants or parts of plants *in vitro* under an aseptic environment. It has various applications in modern plant breeding. Regarding the generation of variation, the specific application of tissue culture is in rescuing embryos produced from wide crosses. Due to genetic incompatibility arising from the genetic distance between parents in wide crosses, the hybrid embryo often does not develop adequately to produce a viable seed. The technique of **embryo culture** enables breeders to aseptically extract the immature embryo and culture it into a full grown plant that can bear seed.

Chromosome doubling

To circumvent a major barrier to interspecific crossing, breeders use the chromosome doubling technique to double the chromosomes in the hybrid created (which is reproductively sterile due to meiotic incompatibility) in order to provide paring partners for successful meiosis and restoration of fertility. Chromosome doubling is achieved through the application of the chemical colchicine.

Bridge cross

The bridge cross is another technique developed to facilitate wide crossing. This technique provides an indirect way of crossing two parents that differ in ploidy level (different number of chromosomes) through a transitional or intermediate cross. This intermediate cross is reproductively sterile and is subjected to chromosome doubling to restore fertility.

Protoplast fusion

Cell fusion or specifically protoplast (excluding cell wall) fusion is a technique used by breeders to effect *in vitro* hybridization in situations where normal hybridization is challenging. It can be used to overcome barriers to fertilization associated with interspecific crossing. The first successful application of this techniques occurred in 1975.

Hybrid seed technology/technique

Hybridization may be used as a means of generating variation for selection in a breeding program. It may also be done to create the end product of a breeding program. The discovery of the phenomenon of heterosis laid the foundation for hybrid seed technology. Breeders spend resources to design and develop special genotypes to be used as parents in producing hybrid seeds. Hybrid seed is expensive to produce and hence costs more than non-hybrid seed. In the 1990s, the **genetic use restriction technology** (**GURT**), colloquially, **terminator technology**, was introduced as a means of deterring the unlawful use of hybrid seed. This technology causes second generation seed from a hybrid crop to be reproductively sterile (i.e., a farmer cannot harvest a crop by saving seed from the current year's crop to plant the next season's crop). Allied techniques that drive the hybrid seed industry include male sterility and self-incompatibility, techniques used to manage pollination and fertility in the hybrid breeding industry.

Seedlessness technique

Whereas fertility is desired in a seed-bearing cultivar, sometimes seedless fruits are preferred by consumers. The observation that triploidy (or odd chromosome number set) results in hybrid sterility led to the application of this knowledge as a breeding technique. Crossing a diploid ($2n$) with a tetraploid ($4n$) yields a triploid ($3n$), which is sterile and hence produces no seed.

Mutagenesis

Evolution is driven by mutations that arise spontaneously in the population. Since the discovery in 1928 by H. Muller of the mutagenetic effects of X-rays on the fruit fly, the application of mutagens (physical and chemical) have been exploited by plant breeders to induce new variation. Mutation breeding is a recognized scheme of plant breeding that has yielded numerous successful commercial cultivars, in addition to being a source of variation.

DNA technology

The advent of the recombinant DNA technology in 1985 revolutionized the field of biology and enabled researchers to directly manipulate an organism directly at the DNA level. The most astonishing capacity of this technology is the ability of researchers to move DNA around without regard to genetic boundaries. Simply put, DNA (or gene) from an animal may be transferred into a plant. The DNA technology also allows researchers to isolate and clone genes and pieces of DNA for various purposes. This precise gene transfer is advantageous in plant improvement. Mutagenesis can now be targeted and precise instead of random, as in the use of mutagens in conventional applications.

A new category of cultivars, GM cultivars, has been developed using recombinant DNA technology. DNA technologies and techniques are exploding at a terrific rate, with new ones being regularly added while existing ones are refined and made more efficient and cost effective. One of the most useful applications of DNA technology in plant breeding is in molecular markers.

Important modern milestones associated with the creation of variation

- **Plant Variety Protection Act.** Enacted in 1970 and amended in 1994, the US Plant Variety Protection Act gave intellectual property rights to innovators who developed new crop varieties of sexually reproducing species and tuber-propagated species. The commercial seed industry is thriving because companies can reap benefits from their investments in the often expensive cultivar development ventures.
- **First commercial GM crop.** The **FlavrSavr tomato** was the first commercially approved and grown genetically modified (GM) crop for human consumption. It was developed in 1992 by the biotech company Calgene, using the antisense gene technology to down-regulate the production of the enzyme polygalacturonase that degrades pectin in fruit cell walls, resulting in fruit softening. FlavrSavr tomato hence ripens slowly and stays fresher on the shelf for a longer time. In 1995, ***Bt* corn**, engineered to resist the European corn borer was produced by the Pioneer Hibred company, while **RR (Roundup ready)** soybean, a Monsanto product, was introduced in 1996.

2.6.2 Technologies/techniques for selection

Selection or the discrimination among variability is the most fundamental of techniques used by plant breeders throughout the ages. In some cases, individual plants are the units of selection; in other cases, a large number of plants are chosen and advanced in the breeding program. With time, various strategies (breeding schemes) have been developed for selection in breeding programs.

Selection (breeding) schemes

Breeding schemes are discussed in detail in Chapters 15–18. They are distinguished by the nature and source of the population used to initiate the breeding program, as well as by the nature of the product. The most basic of these schemes is mass selection; others are recurrent selection, pedigree selection, and bulk population strategy.

Molecular marker technology

Marker technique is essentially selection by proxy. Selection is generally conducted by visually discriminating among variability, in the hope that the variation on hand is caused by differences in genotype and not by variation in the environment. Markers are phenotypes that are linked to genotypes (or precisely genes of interest). Markers are discussed in detail in Chapter 20. They are useful in facilitating the selection process and making it more efficient and cost effective. Molecular (DNA-based) markers have superseded morphological markers in scale of use in plant breeding. Marker assisted selection (MAS) is used to facilitate plant breeding (Chapter 21).

Gene mapping

Gene mapping entails a graphic representation of the arrangement of a gene or a DNA sequence on a chromosome. It can be used to locate and identify the gene (or group of genes) that conditions a trait of interest. It depends on availability of markers. The availability of molecular markers has greatly facilitated gene mapping. Furthermore, genomic DNA sequencing produces the most complete maps for species. Now, quantitative trait loci (QTLs) mapping is becoming more widespread. Modern plant breeding is greatly facilitated by genetic maps.

2.7 Genome-wide approaches to crop improvement

An organism's complete set of DNA is called its **genome**. The concept of genomics began with the successful sequencing of the genomes of a virus and a mitochondrion by Fred Sanger and his colleagues starting in the 1970s. Previously, researchers were limited to understanding plant structure and function piecemeal (gene-by-gene). With the advances in technology, whole genomes of certain species have been sequenced, thereby making all the genes they contain accessible to researchers. Because of the cost of such undertakings, whole genome sequences have so far been limited to the so-called model organisms, including *Arabidopsis*, rice, and corn. Through comparative genome analysis, researchers seek to establish correspondence between genes or other genomic features in different organisms, without the need to have whole genome maps of all organisms. In sum, the goal of plant genomics is to understand the genetic and molecular basis of all the relevant biological processes that pertain to a plant species, so that they can be exploited more effectively and efficiently for improving the species. Genomics is hence important in modern plant breeding efforts. Two of the major tools employed in genomics research are microarrays and bioinformatics.

2.8 Bioinformatics in crop improvement

Genomics programs generate large volumes of data or information that need to be organized and interpreted to increase our understanding of biological processes. Bioinformatics is the discipline that combines mathematical and computational approaches to understand biological processes. Researchers in this area engage in activities that include mapping and analyzing DNA and protein sequences, aligning different DNA and protein sequences for the purpose of comparison, gene finding, protein structure prediction, and prediction of gene expression. Bioinformatics will continue to have a major impact on how modern plant breeding is conducted.

2.9 Plant breeding in the last half century

The foregoing brief review has revealed that plant breeding as a discipline and practice has changed significantly over the years.

2.9.1 Changes in the science of breeding

It has been said several times previously that plant breeding is a science and an art. Over the last decade, it has become clear that science is what is going to drive the achievements in plant breeding. More importantly, is it clear that a successful plant breeding program has an interdisciplinary approach, for recent strides in plant breeding have come about because of recent advances in allied disciplines. High-tech cultivars need appropriate cultural environment for the desired productivity. Advances in agronomy (tillage systems, irrigation technology, and herbicide technology) have contributed to the expansion of crop production acreage. In other words, plant breeders do not focus on crop improvement in isolation but consider the importance of the ecosystem and its improvement to their success. Whereas most of the traditional plant breeding schemes and technologies previously discussed are still in use, the tools of biotechnology have been the dominant influence in the science of plant breeding.

2.9.2 Changes in laws and policies

In the United States, land grant institutions were established to promote and advance agricultural growth and productivity of the states, among other roles. Much of the effort of researchers is put in the public domain for free access. The Plant Variety Protection Act of 1970 that provided intellectual property rights to plant breeders was the major

impetus for the proliferation of for-profit private seed companies, and their domination of the more profitable aspects of the seed market where legal protection and enforcement were clearer and more enforceable (e.g., hybrid seed). Plant breeders' rights legislation was implemented in the 1960s and 1970s in most of Western Europe. Australia and Canada adopted similar legislation much later, around 1990. The US Supreme Court ruled in 1980 to allow utility patent protection to be applied to living things. This protection was extended to plants in 1985. The European Patent Office granted such protection to GM cultivars in 1999.

2.9.3 Changes in breeding objectives

Breeding objectives depend on the species and the intended use of the cultivar to be developed. Over the years, new (alternative) species have been identified to address some traditional needs in some parts of the world. By the same token, the traditional uses of some species have been modified. For example, whereas corn continues to be used for food and feed in many parts of the world, corn has an increasingly industrial role in some industrialized countries (e.g., ethanol production for biofuel). Yield or productivity, adaptation to a production environment, and resistance to biotic and abiotic stresses will always be important. However, with time, as they are resolved, breeders shift their emphasis to other quality traits (e.g., oil content or more specific consumer needs, such as low linolenic acid content). Advances in technology (high throughput, low cost, precision, repeatability) have allowed breeders to pursue some of the challenging objectives that once were impractical to do. Biotechnology, especially recombinant DNA technology, has expanded the source of genes for plant breeding in the last half decade. Also, the increasing need to protect the environment from degradation has focused breeders' attention on addressing the perennial problem of agricultural sources of pollution.

2.9.4 Changes in the creation of variability

The primary way of creating variability for breeding has been through artificial crossing (hybridization) or mutagenesis (induced mutations). Hybridization is best done between crossable parents. However, sometimes, breeders attempt to cross genetically distant parents, with genetic consequences. There are traditional schemes and techniques to address some of these consequences (e.g., wide cross, embryo rescue). The success of hybridization depends on the ability to select and use the best parents in the cross. Breeders have access to elite lines for use as parents. Furthermore, biotechnology tools are now available to assist in identifying suitable parents for a cross and also to assist in introgressing genes from exotic sources into adapted lines. Transgenesis (genetic engineering involving gene transfer across natural biological boundaries) and, more recently, cisgenesis (genetic engineering involving gene transfer among related and crossable species) can be used to assist breeders in creating useful variability for breeding. In the case of mutagenesis, advances in technology have enabled breeders to be more efficient in screening mutants (e.g., by TILLING). Products from mutation breeding, not being transgenic, are more acceptable to consumers who are unfavorably disposed to GM crops.

2.9.5 Changes in identifying and evaluating genetic variability

Identifying and measuring quantitative variability continues to be challenging, even though some progress has been made (e.g., QTLs – quantitative trait loci analysis and mapping). This has been possible because of the new kinds of molecular markers that have been developed and the accompanying throughput technologies. QTLs are more precisely mapped, in addition to the increased precision of linkage maps (marker dense). The abundance of molecular markers and availability of more accessible genomic tools has made it easier for researchers to readily characterize biodiversity.

2.9.6 Selecting and evaluating superior genotypes

Selection schemes have remained relatively the same for a long time. Here, too, the most significant change over the last half century has been driven by molecular technology. The use of molecular markers in selection (MAS – marker assisted selection) gained significant attention over the period. Most traits of interest to breeders are quantitatively

inherited. The continuing challenge with this approach is the lack of precision (the need for more high resolution QTL maps) and higher throughput marker technology, amongst others. Selected genotypes are evaluated across time and space in the same old fashioned way.

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Outcomes assessment

Part A

Please answer the following questions true or false.

1 JH Muller is associated with the discovery of the possible effect of X-rays on genetic material.
2 The term "heterosis" was coined by GH Shull.
3 Gregor Mendel is the author of the book *On the origin of species.*

Part B

Please answer the following questions.

1 The term "recurrent selection" was coined by .....
2 For what contribution to tissue culture are Murashige and Skoog known?
3 Who was Norman Borlaug?

Part C

Please discuss in the following questions in detail.

1. How is the farmer in a developing country like a plant breeder
2. Describe the contribution made by each of the following persons to modern plant breeding – Luther Burbank, Louis de Vilmorin, Joseph Koelreuter.
3. Briefly discuss the changes in the laws and policies that have impacted plant breeding over the years.
4. How has the science of plant breeding changed over the years?
5. Discuss the impact of DNA technologies on plant breeding.