History and Science of Cultivated Plants

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Dedicated to farming communities around the globe who persevere to feed humanity

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Introduction

History and Science of Cultivated Plants narrates how humans transitioned from foragers to farmers and have arrived at present-day industrial agriculture-based civilization. It entails myths, historical accounts, and scientific concepts to describe how human efforts have shaped and produced easier to grow, larger, tastier, and more nutritious fruits, vegetables, and grains from wild plants. Using examples of various economically and socially important crops central to human civilization, the book describes the origin of crop plants, the evolution of agricultural practices, fundamental concepts of natural selection vs. domestication, experimental and methodical plant breeding, and plant biotechnology. A chapter on genetically engineered crops includes the fundamental concepts of recombinant DNA technology, the development of transgenic crops, and their societal impacts around the globe. The book discusses the challenges of feeding the world's growing population in the wake of the changing climate, reduced acreage, and other socio-economic constraints, and the need for a sustainable agriculture system in the 21st century and beyond.

This text treats science as a type of human activity and examines the nature, value, and limitations of scientific methods and the interaction of science with society at numerous levels. The complex interactions between the available scientific knowledge and how it influences societal decisions have been described using a few historical examples. Often, the issues related to science can be adequately resolved using a more objective and systematic approach. However, the socio-political decisions have lasting consequences, and those need to be open-ended enough to leave room for inquiry, evaluation, and innovations. The purpose of this book is to empower its readers to adopt an open-minded approach to science and technology in general and develop a fundamental understanding of the agriculture and farming communities —who contribute to the variety, quality, and quantity of foods they consume.

I am grateful to my current and former colleagues, collaborators, and friends who have generously provided many images and figures used in this book. I would especially like to acknowledge Professor Susan McCouch, Dr. Ajay Garg (Cornell University), Professor Hiro Nonogaki and Professor Pankaj Jaiswal (Oregon State University), Dr. Shekhar Pathak and Pramod Singh for numerous discussions over the years that led to meaningful insights and helped to broaden the scope of this book. I would like to thank Stefanie Buck, Mark A. Lane, Ariel Meshorer, and Daniel Thompson (Oregon State University OER Unit) for their continued support in providing help with the review, editing, illustrations, and production of this book.

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The Origins of Agriculture

1.1 Hunter-Gatherers

Before the agricultural revolution (10,000–12,000 years ago), hunting and gathering was, universally, our species' way of life. It sustained humanity in a multitude of environments for 200,000 years—95 percent of human history. Why did our ancestors abandon their traditional way of life to pursue agriculture?

For a long time, scientists, including Charles Darwin, assumed that primitive humans invented agriculture by chance, and once the secret was discovered, the transition toward agriculture was inevitable. However, this is only possible if we assume that (i) the biggest obstacle to the adoption of agriculture was a lack of knowledge about plants' life cycles and propagation and (ii) farming was easier than hunting and gathering from its beginnings. We can't verify or refute these hypotheses directly. However, studies of materials (e.g., tools made of stones and bones, fossilized seeds, rock paintings, and engravings) found in many archaeological excavations, as well as anthropological studies on present-day hunters and gatherers—who still live in various corners of the world—have contributed much to our understanding of the early history of agriculture.

Scholars' interest in the contemporary hunters and gatherers was rekindled after the 1966 Man the Hunter conference, organized by Irven DeVore and Richard Lee in Chicago. Richard Lee, a PhD student studying under DeVore, had lived in Botswana with the !Kung, one of the San (Bushman) clans of Kalahari Desert, for three years (1963–1965). He shared his experience at the conference and reported !Kung men hunt and !Kung women gather. He added, "Although hunting involves a great deal of effort and prestige, plant foods provide from 60–80 per cent of the annual diet by weight. Meat has come to be regarded as a special treat; when available, it is welcomed as a break from the routine of vegetable foods, but it is never depended upon as a staple" (1). He further added that the !Kung had a more than adequate diet achieved by a subsistence work effort of only two or three days per week, a far lower level than that required of wage workers in our own industrial society, and working adults easily take responsibility for children, old people, and the disabled. In these groups, starvation, malnutrition, and crime are nil. He argued that the social lives of the people of the Bushmen clans are more dignified than that of civilized society and concluded, "First, life in the state of nature is not necessarily nasty, brutish, and short" (1).

American anthropologist Marshall Sahlins agreed with Richard Lee, stating that Australia's indigenous people also have substantial resources when compared to the common man of industrial society and work fewer hours per day, with more time for leisure. He explained that the hunter-gatherers consume less energy per capita per year than any other group of human beings, and yet all the people's material wants were easily satisfied. Sahlins further adds, "Hunters and gatherers work less than we do, and rather than a *grind* the food quest is intermittent, leisure *is* abundant, and there is a *more* sleep in the daytime per capita than in any other condition of society" (2).

The prevailing belief till then was that in comparison to civilized societies, the hunters and gatherers were impoverished: their way of life precarious, full of hardship, and the life of people in such a state of nature, short and brutish. When the proceedings of this conference were published in 1968, such prejudices were refuted and put to rest, rousing a new interest in researchers worldwide to study contemporary hunters and gatherers.

Over the past fifty years, anthropologists, archeologists, biologists, botanists, demographers, and linguists have studied various tribes of contemporary hunter-gatherers. These studies suggest that hunter-gatherers possess tremendous knowledge about the flora and fauna present in their surroundings. They can identify edible plants from a sea of wild vegetation and know which plants' parts can be eaten raw and which need cooking or further processing. In their memories, they retain a seasonal calendar: they know when new plants sprout, bloom, and are ready for harvest or when animals and birds breed. They extract medicines, drugs, intoxicants, and poisons from various plants and make fibers for clothing, baskets, and other objects. The marks of seasonal variations and their specific geographical surroundings are visible in their diets. For example, people living in Arctic regions are entirely carnivorous; the Hadza of Tanzania are predominantly vegetarians; and the !Kung San of the Kalahari Desert in South Africa are omnivores. Regardless of their locale, hunters and gatherers consume ~500 varieties of food throughout the year and make the best possible use of the resources available to them. In comparison, today's rich urban folks hardly sample food items from fifty unique sources.

It has also been observed that most hunter-gatherers care about their environment. They do not hunt without need, waste less, and play active roles in managing their resources. For example, natives living in different parts of the world set forest fires at fixed intervals to manage the landscape. Such controlled fires help eliminate weeds and insects and promote the germination of seeds that are enclosed within hard shells (e.g., pinenuts, chestnuts, and walnuts), thus deliberately increasing the number of seed-producing plants for them to eat. Afterward, when the fire is extinguished, grass grows on the ground, and herbivores are attracted to these pastures for several months, thereby making hunting easy. Such multilevel environmental management is just one example of how these people use their knowledge of the natural world to survive outside of agricultural society.

Many foragers are also aware of how to produce food and occasionally do so in hours of need. For example, New Guinea tribes weed and prune the Sago palms that grow in the forest to increase their yield. The natives of northern Australia bury the tips of taro and eddoes into the ground to propagate new plants and channel rainwater to plains where many wild grasses grow. Subsequently, they harvest tubers and seeds for their consumption.

It is not very difficult to comprehend that compared to foraging, farming is labor-intensive and requires substantial planning to sow, weed, harvest, process, and store crops. Farming must have been a very difficult task in prehistoric times, and crop failures would have been prevalent. Thus as long as needs were fulfilled by hunting and gathering, people likely did not pursue farming despite having the knowledge required for plant propagation. For centuries, humans were sustained instead by a mixed strategy that included hunting, fishing, foraging, and some farming. When resources from the wild were plentiful, farming was abandoned. It was thousands of years before human societies began to completely rely on agriculture. The growth of agriculture was not linear but rather erratic; its adoption was not a coincidence but a slow pursuit full of trials and errors.

Archaeological evidence suggests that nomadic human tribes began farming during the Neolithic period, and so it is often referred to as the Neolithic Revolution. About 12,000 years ago, one of the first attempts at farming began in the Fertile Crescent, the Levant region of the Near East that includes the interior areas of present-day Turkey, Israel, Syria, Jordan, Lebanon, Iran, Iraq, Turkmenistan, and Asia Minor. The ancient inhabitants of the Fertile Crescent, known as Natufians, gathered wild wheat, barley, lentils, almonds, and so on and hunted cattle, gazelle, deer, horses, and wild boars (see figure 1.1).

Throughout this region, thousands of archeological excavations have been conducted and numerous objects—including grinding stones, flint, bone tools, stone sickles, dentalium, shell ornaments, and many fine tools of polished stone—have been unearthed. These show that prior to the adoption of agriculture, the inhabitants of this region had already acquired knowledge about their surrounding vegetation and used tools for cutting, uprooting, and harvesting wild plants, which could have made their transition toward farming easier. The direct descendants of the Natufians, the prepottery Neolithic people, successfully domesticated more than 150 crops, including barley, wheat, pulses, and so on. They also domesticated animals and built the first villages in human history.

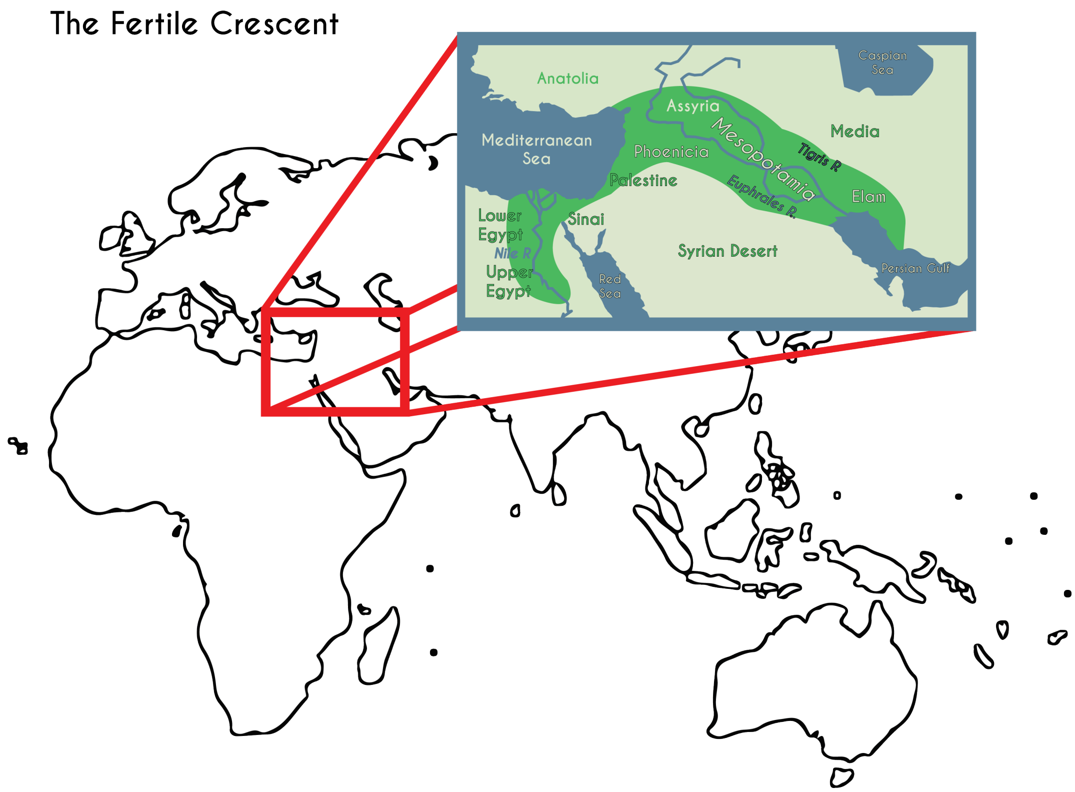

Fig 1.1 "The Fertile Crescent" by OSU OERU is licensed under CC BY 4.0.

Numerous discoveries in recent years indicate that besides the Fertile Crescent, parallel efforts of cultivation began in several other parts of the world. For example, 9,000 years ago, in China's Yellow River valley, rice cultivation began; 5,000 to 8,000 years ago, in Africa and East Asia, the cultivation of a variety of roots and tubers was underway; and 7,000 to 9,000 years ago, people in South America were growing maize, beans, and squash. Hence the history of agriculture is only 12,000 years old, and it spread around the globe relatively quickly. But how did geographically isolated human groups, unaware of one another's existence, begin farming within this short period of time, ditching the hunter-gatherer way of life?

1.2 Why Agriculture?

Australian archaeologist Vere Gordon Childe first linked the beginning of agriculture to climate change. He suggests that at the end of the last ice age (6,000–13,000 years ago), the earth's average temperature increased and glaciers moved rapidly northward. Additionally, rainfall progressively decreased in Southwest Asia and Africa; thus year after year, this region suffered spells of drought that caused the loss of vegetation and several animal species. Over a prolonged period, the rainforests turned into savannas, where herbivores dwelled only for a few months. Under the changed circumstances, humans were unable to sustain themselves throughout the year by hunting and foraging. The human groups, living on different continents and unaware of one another's existence, were forced to produce their own food, and farming began within a short span of time all around the globe.

The transition toward farming was not easy. It was not a eureka moment; agriculture was adopted under unpleasant circumstances and the obligation to produce food was indeed a farewell to the heaven for mankind. Consider the story of Eve, who, under the influence of a snake, plucks the forbidden fruit and eats it with Adam; as a consequence, they acquire wisdom and develop a sense of good and evil. The Lord God becomes angry, and as a punishment, Adam and Eve are banished from the Garden of Eden to work the ground and grow their own food to survive. To Adam, God says,

Because you listened to your wife and ate fruit from the tree about which I commanded you, "You must not eat from it,"

> Cursed is the ground because of you;
>
> through painful toil you will eat food from it
>
> all the days of your life.
>
> It will produce thorns and thistles for you,
>
> and you will eat the plants of the field.
>
> By the sweat of your brow
>
> you will eat your food
>
> until you return to the ground,
>
> since from it you were taken;
>
> for dust you are
>
> and to dust you will return.[1]

Farming was not fun. It required tremendous effort and the capacity to endure hardship.

1. From Genesis 4:23, from the *Holy Bible, New International Version*®. *NIV*®. Copyright © 1973, 1978, 1984 by International Bible Society. Used by permission of Zondervan. All rights reserved.

1.3 A Women's Enterprise

It is believed that agriculture was invented by women. The women of the preagrarian societies collected wild fruits, berries, tubers, and roots and had generational experience in identifying edible plants and knowledge about plants' life cycles and how they grow. It has been suggested that women's extraordinary vision, more developed motor skills, and ability to process finer details evolved due to the importance of their involvement in foraging activities for millions of years. For example, the average woman's eyes can distinguish about 250 shades and hues, while an average man's can only see 40–50.

When droughts became regular, the tribes of our ancestors made temporary encampments along the lakes and ponds where men ambushed animals who came to quench their thirst. Their foraging experience helped womenfolk take the initiative in growing food. They sowed the seeds of wild grasses in the surrounding marshes and planted parts of the tubers to propagate new plants.

In most traditional societies, even today, this historical association of women in agriculture is revered: often, women sow the first seeds to bestow good luck for a bountiful harvest. Invariably, across all cultures, we find a similar feminine influence in stories related to the origin of farming. For example, in ancient Egypt, Isis was deemed the goddess of agriculture: Once upon a time, a severe drought caused a widespread famine on the earth. There was nothing to eat, and cannibalism began. In such a situation, the goddess Isis offered barley and wheat from the wild to the starving people, and taught them how to produce their own food. Thus farming saved mankind from starvation.

In Greek mythology, Demeter was the goddess of fertility and the harvest. After every harvest, the first loaf of bread was offered to her as a sacrifice. She was called Ceres by the Romans, and thus grains were called "cereal." The legend of Demeter contains an interesting tale about the origin of agriculture. According to this myth,

> with the blessing of Demeter, the earth was always filled with grains, berries, and fruits. Humans took their share of this bounty and survived happily for a long time. But it came to a sudden end when Hades, the god of the underworld, abducted Demeter's lovely daughter Persephone. Persephone was Demeter's only child and the center of all her attention and devotion. Demeter desperately searched everywhere for her daughter, but it was to no avail. She fell into depression, and transformed into an ugly old woman and became unrecognizable. She encountered abuse and ill-treatment from everyone around. Only, Celeus, the king of Eleusis, warmly welcomed her. While she continued her search for Persephone, she ignored her responsibility of making the earth fertile. Her despair had an effect on the crops; famines were prevalent and people starved. Eventually, the gods intervened and plead with Demeter to bless the earth with a good harvest, and in exchange, they forced Hades to

> free Persephone. However, before releasing Persephone, Hades fed her pomegranate seeds (the food of the underworld) that bound her to the underworld forever. When the gods asked Persephone to choose where she wanted to live, she wished to remain in the underworld. As a result, Demeter was devastated. Finally, Zeus intervened and came up with a compromise that allowed Persephone to spend six months per year on the earth with Demeter and six with Hades in the underworld. When Persephone visits her mother from spring to summer, the earth is full of flowers and fruits, crops grow, and harvests are bountiful. When Persephone heads back underground, Demeter falls into a depressed state, resulting in autumn and winter. Demeter did not get her daughter fully back, so, she did not restore earth's fertility completely. However, in return for the kindness of King Celeus, she taught his son Triptolemus the art of agriculture for survival, and he later taught it to mankind.

In Mexico, Hispaniola, and Latin America (the sites of the great Mayan and Aztec civilizations), we find stories about the origin of man and corn. For example,

> Man is born from maize; maize is the mother of man.
>
> When the gods created man, the Holy Spirits chanted for his well-being and finally maize emerged from the breasts of the mother Earth to sustain humans.
>
> Mother Earth gifted her five daughters—white, red, yellow, spiked, and blue maize—to man.

Similarly, Hindu mythology has several goddesses, including Bhudevi (the earth goddess), Annapurna (the goddess of grains, who provides nutrition to everyone), and Shakti (the creator of the entire plethora of vegetation). According to the legend of Annapurna,

> Once, the Lord Shiva (who represents the male power, the Purush) and his wife Parvati (the creator of nature, a.k.a. Prakriti or Shakti) argued about who was superior between the two and the discussion quickly ended on a sour note. Shiva stressed the superiority of Purush (male) over Prakriti (Mother Nature). Enraged, Parvati deserted her husband and disappeared, which resulted in a widespread famine. Shiva's followers, who were starving, asked for his help. Shiva took a begging bowl, and his band followed him. They went from door to door, but the people themselves had nothing to eat, so they turned the beggars away. Shiva's band learned about a charity kitchen in the city of Kashi (also known as Varanasi) that was feeding everyone and decided to visit Kashi. To their surprise, Parvati owned that kitchen, and she had become the goddess Annapurna, wearing celestial purple and brown, and was serving food to the starving gods and mankind. Upon Shiva's turn, she likewise offered food to him and his followers. Shiva realized that the existence of humanity depends on nature; the brute force of male power is not enough to sustain life on Earth.

The common thread of all these myths is the appearance of the savior female deity who taught mankind to cultivate grains to survive. Although these myths have no literal value, they serve as metaphors or narratives of human experiences and survived through generational memories. They are also, in fact, consistent with the climate change theory of the origin of agriculture.

1.4 Slash and Burn: Shifting Cultivation

At the dawn of agriculture, the primitive people of the Neolithic era only had some tools made of stones and animal bones at their disposal. These tools were useless for such a monumental task as embarking on the path to farming. Fortunately, mankind's knowledge and experience of taming fire came in handy. Long before the origins of modern humans, *Homo erectus*, an ancestor of the hominid branch, had learned to light and control fire. Afterward, the members of genus *Homo* moved northwards from Africa and survived the cold weather of Europe and Asia with the help of this skill. Humans used their best weapon, fire, to create the first farms. First, they slashed the vegetation, then burned it to clear the small patches in the forests, and finally, sowed seeds in the ashes. This practice of farming, known as slash-and-burn agriculture, still survives in the Amazon rainforests and in many mountainous regions of the world. The plots created by this method are very fertile initially, but with each passing year, they are overtaken by more and more weeds, pests, and parasites, which causes a decline in their fertility. So after three to four years, the people move to another site. Thus this practice is also known as "shifting cultivation" or "swidden agriculture." In India, it is known as "jhoom" among the native Adivasi tribes (descended from an ancient forest-dwelling people). After people abandon a site, in the fallow field, grass and weeds grow, and it serves as a pasture for herbivores and hunting grounds. Slowly, the fertility of these pastures returns, shrubs and trees grow, and they become part of the forest again. In this way, the field, fallow land, and the surrounding forest are recycled. Also, weeds, insects, and other parasites are kept in balance.

Today, we are farming with highly sophisticated machines and have specialized tools for various tasks, from sowing to harvesting, and yet farming is still a tremendous task. We cannot even grasp how difficult it would have been in prehistoric times. For thousands of years, generations of mankind struggled to make farming productive. They also continued to gather and hunt to make up for the shortfall or crop failures. Since farming required much more time and effort, farming would have been abandoned from time to time if nature was bountiful. It has been suggested by various studies that agriculture did not progress smoothly; it took several thousand years before humanity could fully rely on agriculture.

So to summarize, the history of agriculture is 12,000 years old, and traces back to a time when changes in the earth's global climate led to widespread drought and a decline in natural resources, forcing our ancestors to produce their own food. For thousands of years, shifting cultivation supplemented their diets while hunting and gathering remained the main source of sustenance. The discovery of agriculture was not an accident but the product of trial and error as well as improvisation that spanned many centuries, a process that still continues today.

Animal husbandry is considered a by-product of agriculture. It has been suggested that during droughts, people survived on stored grains, and they used some grains to feed herbivores to keep them around for easy hunting. The credit to domesticating animals primarily goes to men.

1.5 The Emergence of the First Agricultural Societies

Even though agriculture started almost simultaneously in many regions of the world, its progress was not uniform. The biodiversity of various geographical regions (e.g., their flora, animals, birds, insects, and microorganisms) influenced the emergence of stable agricultural societies. In some areas of the tropics, particularly in Africa, people had great success in growing tubers like yams, potatoes, eddoe, sweet potatoes, and cassava. These plants can be propagated by burying a small part of the tuber in the ground and so did not require an understanding of the plant's life cycle. So these groups had an easy head start thanks to vegetative propagation that produced identical plants (clones), which did not differ significantly in yield. They learned to process many types of tubers and invented a very complex process of separating cyanide and starch from cassava to make starchy tapioca pearls. These undertakings helped folks sustain themselves year-round, but did not accumulate enough surplus to free a section of the population from farming, allowing them to pursue other tasks needed for the further advancement of their societies.

In South and Central America, maize was the mainstay of civilization. However, the natural structure of maize plants promotes outcrossing: on this plant, male flowers, known as tassels, hang from the tip, whereas the female flowers (silk) grow on the stem. Maize pollens are very lightweight and reach the female flowers via wind. Thus male flowers can pollinate female flowers of the same plant (self-pollination) or of another plant (cross-pollination). Although in maize, the chances of self-pollination and cross-pollination events are equal, the progeny born of selfing is inferior (gives lower yield) compared to the progeny born of outcrossing. Thus farmers need to plant different varieties of maize in the same fields to ensure maximum yield. In the absence of this knowledge, the productivity of the crop cannot be assured from one year to another. Only after such an understanding developed could people rely fully on maize farming and utilize the surplus to build the great civilizations of the Aztecs and Mayans.

In the Fertile Crescent, about thirty-two species of grass—including the wild species of wheat, barley, sorghum, millet, and oats—grow naturally. Incidentally, most grasses have complete flowers with both male and female organs, and self-pollination rules over cross-pollination. As a result, the characteristics of grasses remain stable, and crop yields do not vary from one year to another. If the plants with large grains are picked and carried forward, then crops with large seeds can be harvested for generations. Additionally, the grass seeds can be stored for a very long period of time and year-round dependence on these grains was easily established. So the early farmers of this region benefitted from growing grasses.

In the Fertile Crescent, animal husbandry began in parallel with farming. Some groups exclusively pursued this path and so developed a nomadic way of life. They moved with their herds following the availability of grazing grounds and trading the products of one farming community with another. These pastoralists thus further strengthened the stability of farming communities and broadened the region's resource base. Such advances helped the people of the Fertile Crescent settle in one place permanently and establish the first villages.

In China, along the Yellow River, people learned to cultivate rice. Rice is also a self-pollinated grass, and so these early farmers could rely on its harvest for yearlong sustenance and could store surplus seeds. Unlike their contemporaries in the Fertile Crescent, Chinese farmers could harvest two crops of rice per year and so their surplus grew even more rapidly. So they reaped similar advantages and almost simultaneously established permanent settlements.

About 5,500 years ago, an independent initiative of paddy cultivation was undertaken in the Indo-Gangetic plains that are spread across South Asia. In addition to rice, the peoples of South Asia and East Asia independently learned to grow a variety of minor grains, pulses, vegetables, fruits, tubers, roots, and oilseed crops.

As agriculture progressed, many river-valley civilizations—in the Indus Valley, Egypt, Mesopotamia, and China—came into existence. Meanwhile, the populations of hunter-gatherers remained more or less stable. As agriculture developed and productivity increased, the human population grew proportionally (see figure 1.2). The first minor jump occurred after the discovery of metals that made many more tools like plows, available to farmers. The use of a plow powered by domesticated animals resulted in a significant increase in food production. In this way, 5,000 years ago, farming began to seem like a better alternative to the hunter-gatherer's way of life. The surplus grain freed a large section of the population from farming and allowed them to invest energy in other tasks that led to the second major change—the division of labor in human society. Subsequently, the collective sharing of resources was replaced with individual ownership—private property—which gave rise to a need to ensure the succession of one's own bloodline. As a consequence, rules of strict sexual conduct for women were formulated and, like infields and domesticated animals, they became the property of men. As class divisions deepened, the unit of a family, headed by a patriarch, strengthened. Soon, tribes headed by patriarchs began to fight for control over their possessions and to expanding their domains, which gave rise to more complex and organized social and political structures, like states, nations, and religion. In societies dependent on subsistence agriculture—where property has not developed and most of the people remain engaged in agriculture—complex social structures, division of labor, crime, patriarchy, and other sociopolitical structures are also poorly developed.

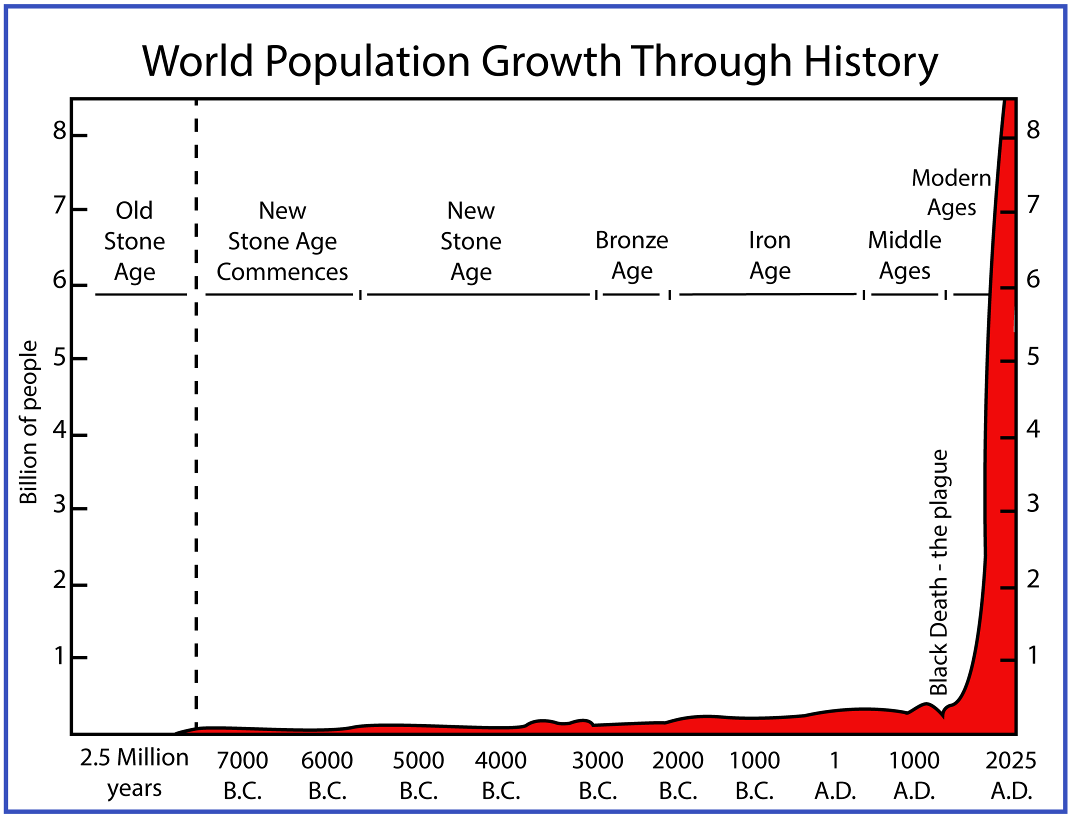

Fig 1.2 "World population growth" by [OSU OERU] is licensed under [CC BY 4.0].

Agriculture transformed human society, but this transformation also, in turn, influenced agricultural practices. While the family, private property, and various institutions were born as by-products of agriculture, these sociopolitical advancements also impacted agriculture. To this day, agriculture continues to be highly entangled with society and human history. In the following chapters, we will review the historical progress of agriculture, advancements in science and technology that influenced farming, and the impact of agriculture on humanity.

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The Origins of Crop Plants

2.1 Domestication of Plants and Animals

Tremendous natural variations exist among the individuals of any plant species. The traits that define color, shape, flavor, height, yield, and resistance to pests, pathogens, and environmental stresses are not fixed within a species. Individual plants and animals from the same species can be easily distinguished based on these characteristics.

Since the beginning of agriculture, humans have unconsciously been selecting plants and animals with desirable traits, such as large-sized grains, pods, fruits, and vegetables; sweeter and less-seeded fruits; less bitter and nonprickly vegetables; cereals with large panicles and tough rachis; non-seed-shattering plants; and so on. As a consequence of such artificial selections over many generations, unprecedented changes occurred in cultivated plants that set them apart from their ancestors and wild relatives. For example, the relentless efforts of humans led to the development of various crops, such as corn from a wild-grass teosinte; long-spiked, six-row barley from short-spiked, two-row wild barley; large tomatoes from a small berry; and a variety of less-seeded fruits and palatable vegetables from their bitter wild ancestors (see figures 2.1 and 2.2). These plants—enriched in traits that favor higher yields, productive harvest, and increased palatability—would not have come into being without the persistence of humans since the dawn of agriculture.

Artificial selection by humans counteracts the process of natural selection. In nature, small fruits are packed with seeds, thistles, thorns, and prickly leaves; have a bitter taste; ripen asynchronously; and have seeds that spontaneously shatter—all traits that favor the survival of the plants. Thus artificially selected and propagated species of cultivated plants, lacking necessary traits for survival, become more vulnerable to diseases, predators, and environmental stresses. These crops cannot survive in nature for a long time without human help.

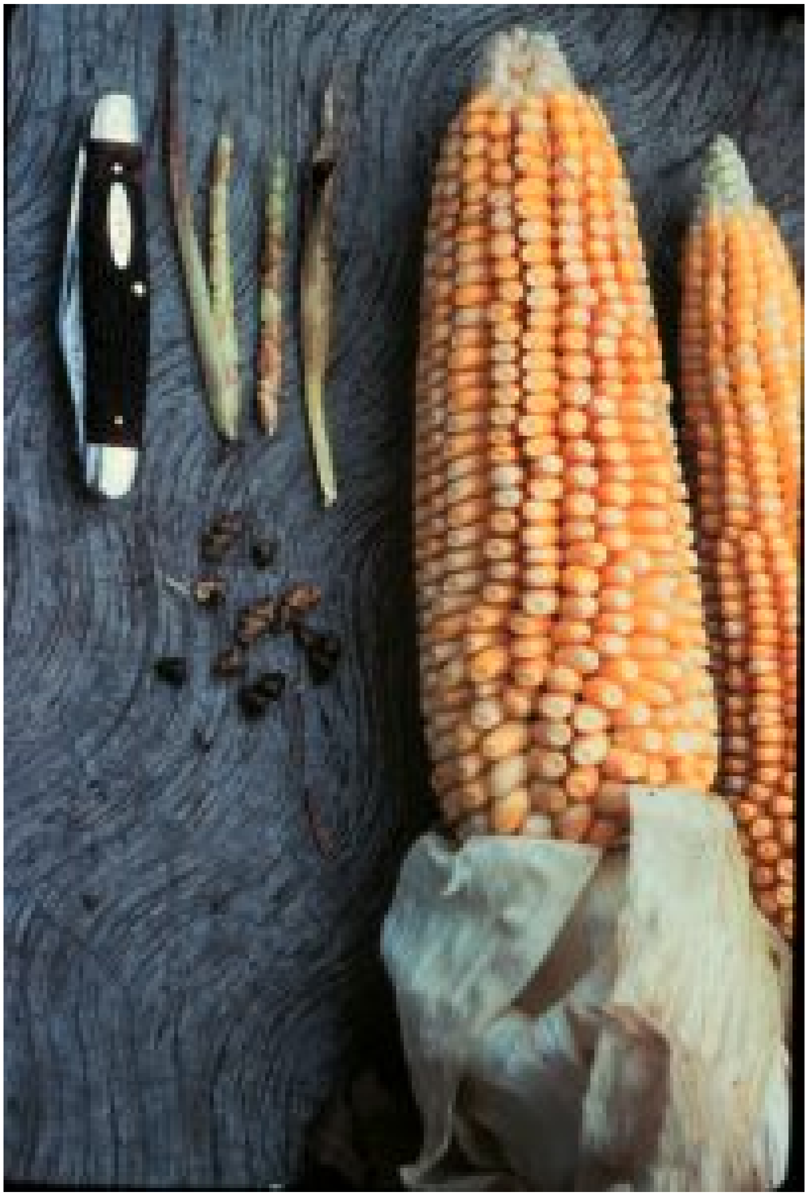

Fig 2.1 Maize is a product of artificial selection by human. A comparison of maize's ancestor teosinte (Zea mays ssp. parviglumis) and maize (Zea mays). [Photo of maize and teosinte]() by Hugh Iltis is open source.

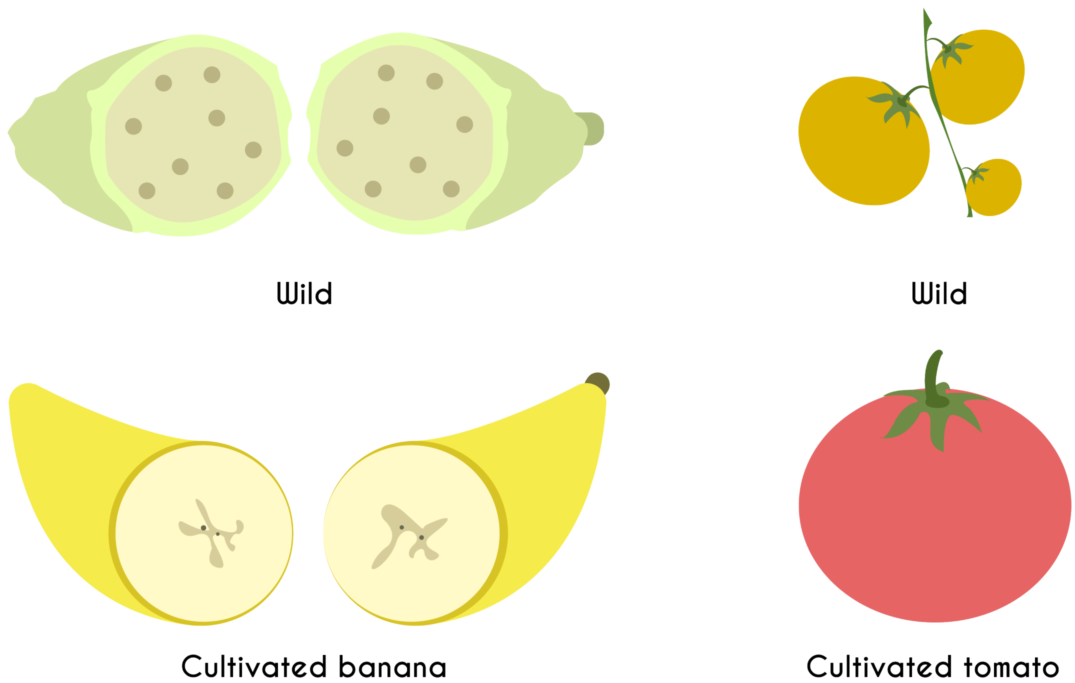

Fig 2.2 "Changes in crop plants as a result of artificial selection" by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

For several millennia, humans have put tremendous effort into providing protection and ensuring the continuous propagation of cultivated plants. We provide fertilizers, pesticides, and water and provide services such as weeding to promote the growth of crop plants. Thus domesticated plants need humans for their survival as much as human survival depends on them. These species cannot survive in nature for a long time by themselves, but with human help, they have spread globally. For some species, this dependency on humans has become total. For example, maize absolutely depends on humans for its survival. If you leave a mature cob in the field, some of its seeds may germinate on the cob, but they will soon die due to the lack of space for emerging seedlings to grow. Furthermore, maize seeds do not fall spontaneously and need human help to be detached from the cob and planted in the soil.

This mutual interdependence between crop plants and humans (and, similarly, between humans and artificially selected and bred animals) was achieved over several millennia, and this is the historical process we call "domestication." Thus to a great extent, all crop plants and domesticated animals are man-made.

2.2 Landraces of Crop Plants

n addition to artificial selection, cultivated plants were continuously subjected to the natural selection imposed by their immediate environment, geographical locality, and agricultural practices. Thus domesticated plants are products of artificial selection operating within environmentally enforced natural selection and the agricultural practices prevalent in a given region. The early domesticated plants flourished in their native environment, but when shifted to new locations, they performed poorly. Over time, the few offspring of the introduced plants acquired characteristics (i.e., via spontaneous mutations or hybridization with related species present in the new locality) that helped them stabilize in their new surroundings. This process has produced diversified varieties of crops known as *landraces*, each adapted to a specific geography, climate, or environment (seasonal variations in day length, temperature, water availability, soil quality, salinity, etc.) and its associated pests and pathogens.

The landraces differ from one another in taste, fragrance, flavor, nutrient composition, and tolerance to pathogens and environmental stresses. Before the industrialization of agriculture, traditional farmers had very small holdings but grew many varieties of the same crops for multiple uses. Typically, in a small village, one could find several cultivars of fruits and vegetables as well as many varieties of grains. Farmers have local names for each of these different varieties based on their special traits or origins. For example, more than 3,000 varieties of rice have been developed around the globe and grow in a range of climatic conditions and geographical locations, from temperate hillsides, to tropical planes, to flooded marshes in coastal regions. Each variety of rice has a name and specific usage in culinary dishes (e.g., sushi, pudding, pilaf, steamed rice, crackers, and baby food).

Similarly, more than fifty races of maize are found in Mexico—thirty races in the Oaxaca province alone. Each race includes hundreds to thousands of varieties adapted to the immediate environment and climatic conditions and each has a special use (see figure 2.3). For instance, the popcorn variety's seeds possess a hard outer cover capable of holding steam for a sufficient amount of time when heated, allowing for the full transformation of starch required for making popcorn. Conversely, the seeds from other corn varieties containing a thin seed cover do not produce good popcorn because, upon heating, they break easily, causing steam leakage. Another example is the sweet corn variety, consumed primarily after boiling or roasting, which lacks an enzyme that efficiently converts sugar to starch and thus has higher sugar content. Dent corn, the most popular corn variety grown today, has soft starch and is lightly sweeter; thus it is used for making chips and tortillas. Before 1920, flint corn was the most widespread variety because it is naturally resistant to many pests and pathogens prevalent in the tropics and is highly productive.

Fig 2.3 Examples of some of the 59 native Mexican maize landraces. Photo of maize by CIMMYT Maize Germplasm Bank is licensed under CC BY 2.0.

For centuries, farmers have been stocking seeds of different varieties separately to ensure their purity and have been careful about not mixing the seeds from multiple varieties. To avoid cross-contamination, farmers usually save seeds for the next year's sowing from the plants growing in the middle of their fields. This way, the individual varieties are maintained, but their independent evolution and development are also continued. The landraces of the various crops that have survived today are not 100 percent identical to their ancestors that existed 200 or 1,000 years ago. They are constantly changing, keeping in tune with their growing environment and adapting to the changes in it.

2.3 Centers of Crop Domestication

Nikolai Vavilov, a Russian agricultural scientist, was one of the first scientists in the world to infer that the process of domestication—the enrichment of desirable traits by human/artificial selection—also led to the loss of many useful traits (see figure 2.4). He noted that in comparison to their wild relatives, most crops easily succumb to parasites, pests, and pathogens and are less resilient under unfavorable environmental conditions. Vavilov proposed that these lost traits can be traced back to the wild progenitors and related species of crop plants, which are likely to still be present in the regions where crops were first domesticated. He further proposed that useful traits can be reintroduced in crops by employing the kind of systematic plant breeding rooted in the principles of Mendelian genetics (we describe the work of Mendel and the basic principle of genetics in chapter 5).

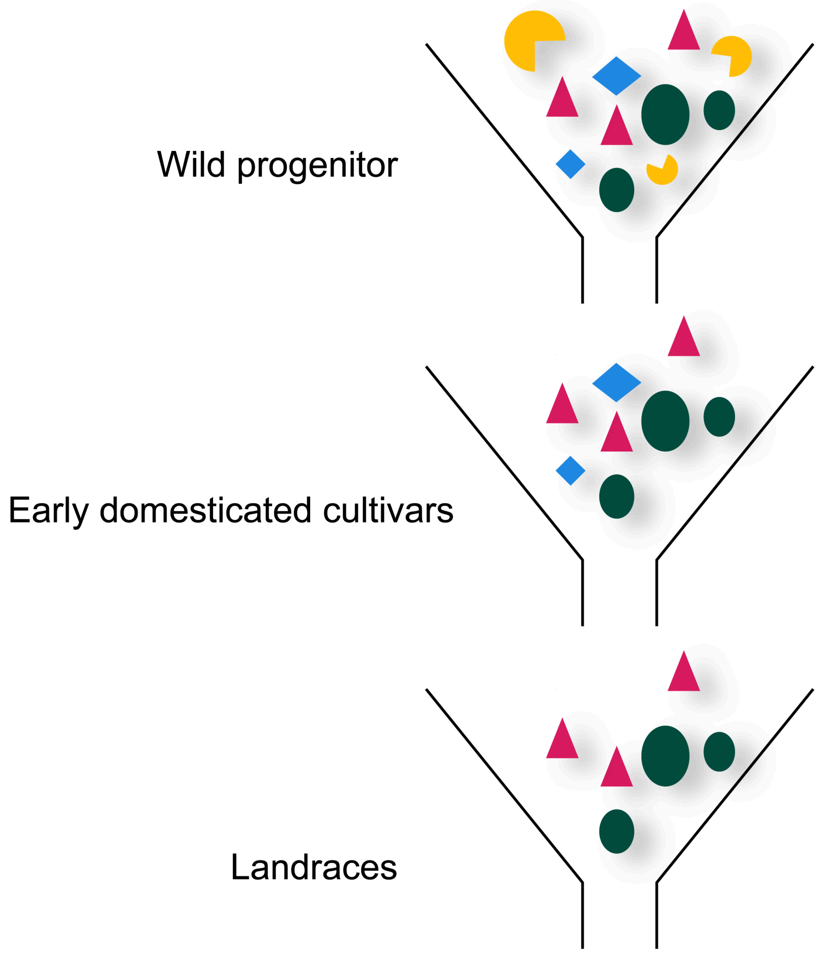

Fig 2.4 Loss of gene pool during crop domestication due to artificial selection. "Loss of gene pool" by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

In the 1920s, knowledge about the domestication centers of crop plants was lacking. So Vavilov took this herculean task upon himself and set forth on a mission to collect the germplasm (seeds, tubers, roots) of all domesticated crops and their wild relatives. He led nearly a hundred expeditions to sixty-four countries on five continents over the course of twenty years and built the world's biggest plant germplasm collection, which included 350,000 accessions of seeds, roots, and tubers representing about 2,500 plants. Based on the study of this comprehensive collection and observations about human cultures and linguistics, Vavilov proposed eight geographic centers as the birthplaces or "centers of origin" of crops—the places where the ancestors, wild relatives, and other related species of crops still live and where mankind first began their cultivation. These eight centers include China, India and the Indo-Malayan region, Central Asia (including Pakistan, Afghanistan, Turkestan, and the northwest Indian provinces of Punjab and Kashmir), the Near East, the Mediterranean, Ethiopia, southern Mexico and Central America, and South America (Ecuador, Peru, Bolivia, Chile, and Brazil-Paraguay; see figure 2.5). Overall, Vavilov associated about 640 crops with their biodiversity centers. Five-sixths of these came from the Old

World (Asia, Africa, Europe) and one-sixth from the New World (Australia, North and South America).

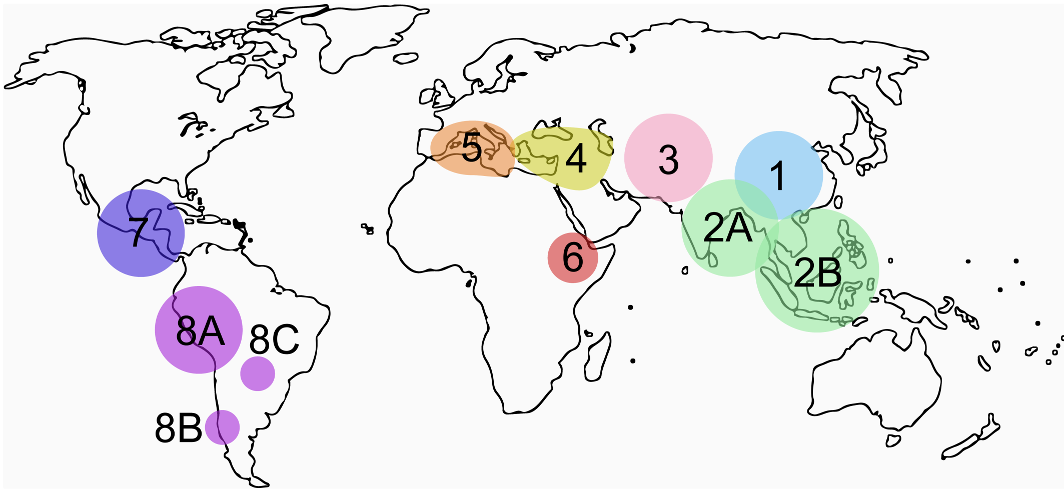

Fig 2.5 The centers of origin of cultivated plants identified by Nikolai Vavilov: 1. China; 2. India; 2a. the Indo-Malayan region; 3. Central Asia (including Pakistan, Punjab, Kashmir, Afghanistan and Turkestan); 4. the Near East (Fertile Crescent); 5. the Mediterranean; 6. Ethiopia; 7. Southern Mexico and Central America; 8. South America (small regions of Ecuador, Peru, Bolivia, Chile, and Brazil-Paraguay). "Centers of origin of cultivated plants" by OSU OERU is licensed under CC BY 4.0.

Contrary to popular belief, Vavilov's research revealed that crops did not originate in the large river valleys associated with the rise of human civilization. Rather, most crops were born in the kinds of geographically isolated regions (hills, desert-ridden areas, or cold or extremely hot regions) that comprise only 2–3 percent of the world's area. In these challenging localities, the pressure of natural selection on vegetation is robust and variable compared to other areas, and so we find high biodiversity in these areas. The list below identifies the eight centers of origin of crops and associated plant species that Vavilov identified (along with a ninth, discovered after his death).[1]

1. A clickable world map showing the center of origin of various crops is available at https://www.biodiversidad.gob.mx/v_ingles/genes/centers_origin/centers_plants1.html

It is eye-opening to see how the various kinds of produce, grains, fruits, vegetables, and spices available in supermarkets today have originated in such distant places. Since human societies have been continuously in motion, crops have moved with them, away from their centers of origin, and have been subjected to additional artificial and natural selection in their new environments. They continued to evolve and diversify as a result of spontaneous mutations, hybridization, and agricultural practices. Thus most crops also acquired genotypic and phenotypic diversity postdomestication. As a result, for many crops, their primary center of origin and the center of diversification (where many varieties of crops evolved) differ.[2] For example, the center of origin and center of diversification of maize differ significantly. However, compared to the primary centers of origin, the secondary centers occupy a large area and possess less biodiversity of plant species. The secondary centers are relatively rich in domesticated crop varieties (landraces) but lack the immediate wild progenitor and other related wild species.

After Vavilov, many archeological digs ascertained the centers of origin of additional crop species, and a new center of crop origin was identified as well (New Guinea). The fundamental research work conducted by Vavilov and his colleagues still stands; however, now scientists recommend the use of *center of diversity* instead of *center of origin* because only a crop's center of biodiversity can be identified based on data—at best, we can only guess at the center of origin. Currently, those identified by Vavilov are known as "Vavilov's Centers of Biodiversity."

Since, typically, the "centers of origin" of crops are rich in their biodiversity,[3] their exploration helps scientists comprehend the full spectrum of the gene pool available for a given crop, which can then be utilized for breeding experiments. It is important to note that the plant breeders only transfer useful traits from one variety to another by crossing and then selecting the progeny that have desirable combinations of traits. The breeders do not *create* traits. If a trait is absent in cultivated varieties of a crop species and its ancestors, progenitors, and related species, it cannot be introduced by classical breeding. Biodiversity serves as the resource bank from which scientists can borrow useful traits. It also defines the limits of classical breeding. Therefore, biodiversity centers are the insurance policies for the continuation of today's crops. Scattered across these centers are the genes/traits

2. This is also sometimes due to reasons other than human migration. One classical example is pine, which has its center of origin in northwestern China but its center of diversification in Central America (Mexico, Guatemala, and Honduras). At present, 49 out of a total of 111 species of pine are found in Mexico. The difference in the center of origin and center of diversification of pine resulted from a geological event (continental drift) long before the beginning of agriculture, which led to the isolation of various flora and fauna and thus their diversification in a new environment.
3. In simple terms, *biodiversity* refers to all cultivated varieties of crops along with their wild progenitor(s) and evolutionarily related species.

that provide resistance to pests and pathogens or the ability to tolerate environmental stresses—the raw materials for breeding advanced varieties of crops.

Table 2.1: Centers of origins (biodiversity) of crops

Center	Remarks
1. China	136 crops were domesticated in this region including rice, sorghum, soybeans, barley, radish, cabbage, mustard, onion, cucumber, pear, apple, apricot, peach, cherry, walnut, litchi, sugarcane, and poppy. Rice was one of the first crop (~ 8,000 years ago) cultivated in the Yangtze River Valley. Pigs, roosters, and dogs were also domesticated here.
2a. Indo-Malay	This region includes parts of India, parts of China and the Malay Archipelago. Here, clove, nutmeg, black pepper, coconut, hemp, banana, grapefruit, reed and velvet beans were domesticated.
2b. Indo Burma	This center includes North-East region of India and present day Myanmar (Burma). Here, ~117 crops including jute, sandalwood, indigo, bamboo, neem, rice, gram, pigeon pea, mung, cowpea, eggplant, cucumber, radish, carrot, mango, orange, lemon, tamarind, coconut, banana, hemp, pepper, cloves, nutmeg, reed, sesame, and cotton were domesticated.
3. Central Asia	This center includes North-Western India (Punjab, Haryana, and Kashmir provinces), Pakistan, Afghanistan, Tajikistan, and Uzbekistan. ~ 43 crops developed in this area, including three varieties of wheat, peas, lentils, horse lentil, gram, mung bean, mustard, linseed, sesame, cotton, hemp, onions, garlic, spinach, carrots, pistachio, almond grapes, pears and apples.
4. Near East (Fertile Crescent)	This center includes present day Turkey, Israel, Syria, Jordan, Lebanon, Iran, Iraq, Turkmenistan and the interiors of Asia Minor. ~ 150 crops including rye, barley, oats, Einkorn wheat, Durum wheat, Persian wheat, Pollard wheat, common Bread Wheat, Oriental wheat, lentils, lupine, peas, gram, pomegranate, mulberry, apple, grapes, pears, cherries, walnut, almonds, pistachios, dates, fennel, cumin, carrots, onions, and garlic were domesticated in this region. ~ 10,000 year old fossils of rye have been found at many archeological sites in this area. Evidence of earliest rye cultivation ~13,000 years ago has been found in Syria and the remains of ~ 9000 year old domesticated sheep, goats and pigs have been found in Turkey.
5. Mediterranean	This center includes regions around the Mediterranean Sea. Here, 84 crops including durum wheat, Emmer wheat, Polish wheat, oats, peas, lupine, clover, black mustard, olives, beets, cabbage, turnip, lettuce, asparagus, rhubarb, mint, hop, sage, celery, etc. were domesticated.
6. Ethiopian Center	This center includes Abyssinia, Eretria, Somaliland, and Ethiopia. 38 important crop plants including Abyssinian and emmer varieties of wheat, millet, sorghum, cowpea, flaxseed, tef, sesame, coffee, okra, indigo, castor, and gum Arabica were domesticated in this region.
7. Southern Mexico and Central America	This center includes Southern Mexico, Guatemala, Honduras and Costa Rica. Here, maize, potato, tomato, pumpkin, capsicum, chili, papaya, guava, cashew, chocolate, cotton, passion flower, tobacco, various beans, sisal, sweet potato, arrowroot etc. were domesticated. in this region, ~7000-year-old remains of maize and 10,000-8,000 years old seeds of squash have been found in the archaeological excavation.
8a. Peru, Ecuador, Bolivia Sub center (South America)	In this region, 62 species of crop plants including potatoes, maize, lima beans, tomatoes, pumpkin, capsicum, cotton, guava, passion flower, tobacco etc. were domesticated.
8b. Chile (South America)	Several varieties of potato and strawberry were domesticated in this center.
8c. Brazilian-Paraguay (South America)	Peanuts, pineapples, cashew nuts, Brazil nuts, rubber, etc. developed here.

Center	Remarks
9. New guinea* (Far East)	Recent research proves that ~ 7000 years ago, agriculture started independently in the mountainous region of New Guinea. In this area, bananas, knives, reeds etc. developed. *This center was identified after Vavilov death.

2.4 The Life and Work of Nikolai Vavilov

Nikolai Vavilov (1887–1943), a Russian scientist of the early twentieth century, was a pioneer in the field of plant biogeography and germplasm conservation. He was among the first few scientists of the early twentieth century who championed Mendelian genetics for crop improvement.

Nikolai Vavilov (see Figure 2.6) was born on November 25, 1887, in Moscow, before the Russian Revolution. He studied agriculture, and after graduating in 1911, he worked with Dmitry Pryanishnikov, a world-renowned soil scientist, for a year while also teaching at Petrovskaya Agricultural Academy. Soon, Vavilov joined a PhD program under the supervision of the Russian professor Robert Eduardovich Regel (of the Bureau of Applied Botany in Leningrad) and famous English biologist William Bateson (the director of the John Innes Horticultural Institution in Norwich, England). In the early years of the twentieth century, Bateson was the champion of Mendelian genetics; he in fact coined the term genetics to describe the study of Mendelian inheritance and the science of variation. Vavilov spent two years in Bateson's laboratory at John Innes, where he acquired necessary knowledge about Mendelian genetics.

In 1914, Vavilov returned to Russia and was appointed as a professor at Moscow University. In 1917, he became the director of the Lenin Academy of Agricultural Sciences in Saratov. He was the first scientist to start work on genetics in the Soviet Union. In this position, he set the primary agenda of the institute: to collect germplasm from all over the world in order to develop advanced crop varieties by employing the principles of Mendelian genetics. For the first decade, the newly formed Soviet government provided Vavilov with plenty of resources and grants for several germplasm collection expeditions.

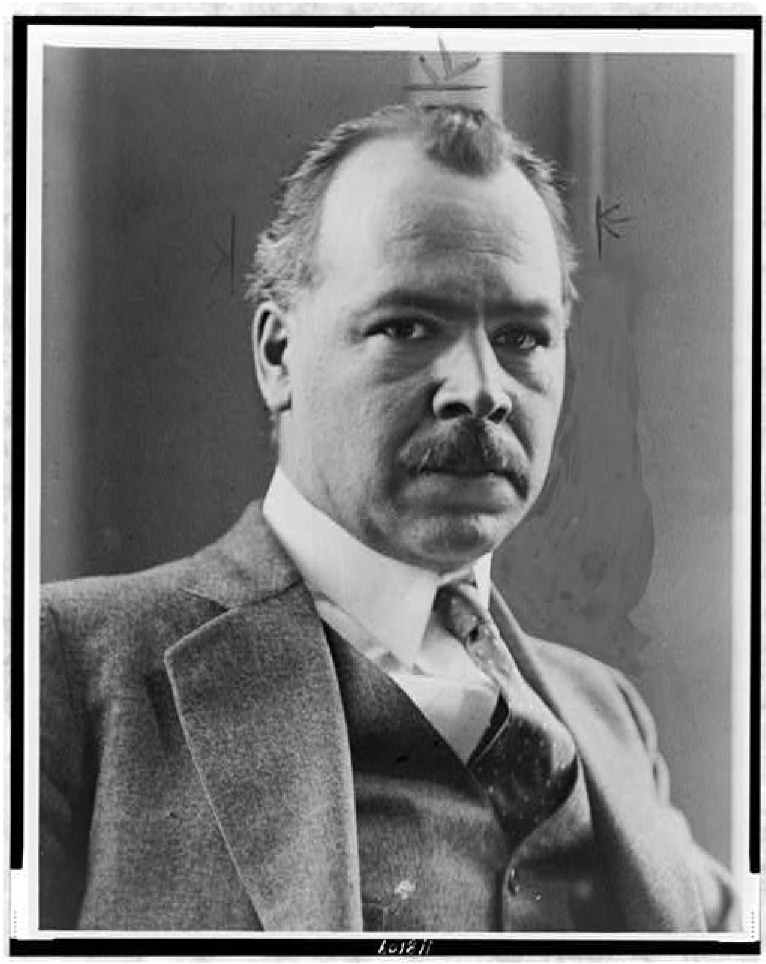

Fig 2.6 Nikolai Vavilov in 1933. "Nikolai Vavilov" by Library of Congress is licensed under no known restrictions on publication.

Vavilov, along with his team, traveled to sixty-four countries on five continents to collect seeds, tubers, and germplasm. In Kazakhstan, they found wild apples, and thus the world came to know the birthplace of this fruit. In Peru, they found countless varieties of potatoes, and in Iran, Syria, and Afghanistan, they found relatively quick-ripening varieties of wheat that possessed natural resistance to pests and parasites. Overall, Vavilov led a hundred explorations, which resulted in the collection of over 300,000 samples, accompanied by detailed descriptions. He had remarkable success in managing his extensive field trips in such diverse nations as Ethiopia, Italy, Kazakhstan, Mexico, Brazil, and the United States. In the early 1900s, traveling was rather difficult and required hopping between various modes of transportation, including extensive journeys on foot and horseback. An equally daunting task was the recruitment of local crews of porters, guides, and collaborators. However, many of Vavilov's personal qualities and his demeanor helped make these missions successful. He was physically fit, mentally sharp, and a polyglot who could converse in eight languages. He was capable of quickly developing friendships and collaborations with strangers, common folk and international scientists alike. On a personal level, Vavilov took care of everyone on his team and the people he interacted with around the world. Among his various field trips, the most historic missions included three visits to North America, Mexico, and South America in 1921, 1930, and 1932; the Mediterranean Sea and Ethiopia expedition in 1926–27; and the trip to Afghanistan in 1924, for which he received a gold medal from the Russian Geographic Society. Later, he also served as the president of that society, from 1931 to 1940. In the first decade of his career, he became the leader of Soviet agricultural policies and headed 111 institutions.

In addition to germplasm collection, Vavilov directed projects at Saratov and other research centers aimed at breeding crop varieties that could tolerate the extremely cold climate of the Soviet Union. These projects were deemed of national importance because a large area of the country suffered agricultural losses due to frost, and the damages to the wheat crop were especially devastating. However, the success of these projects required sustained work on classical breeding and the evaluation of the crossings.

Unfortunately, year after year, in the Soviet Union, grain remained in short supply and hunger was prevalent. To improve agriculture, in 1929, Stalin announced his Great Break from the Past policy, which led to the establishment of collective farms through the merging of individual family farms. The big government-run farms employed monocropping, which led to more loss of harvest. Before government-run collective farming, individual farmers sowed many varieties of seeds. If the crop was ruined in some areas due to the weather, then it would have been saved in other places, and so a good yield could be obtained elsewhere. With monocropping, the impacts of disease and frost were instead widespread. The failure of collective farms, along with rapid industrialization, caused famine. Millions of people died of hunger in the Soviet Union.

Stalin wanted to make the Soviet Union self-sufficient in terms of food production, and the responsibility for improving agricultural yields rested on Vavilov's team. Stalin gave Vavilov three years to develop advanced varieties of grains that could perform in the extremely cold and unpredictable climate of the USSR. At that time, even the best breeder could succeed only after ten to twelve years. Nikolai Vavilov knew that advanced crops could be developed by following the principles of genetics in a very methodical and systematic manner for a decade, but not in a shorter time frame. Thus he could not promise a miracle to Stalin. But he kept working hard and kept up the morale of his colleagues.

Meanwhile, scientist Trofim Lysenko claimed that soaking seeds in cold water for a day or two prior to sowing would result in higher germination rates and could possibly enhance the resilience of a crop in colder climates. Unlike Vavilov, Lysenko was from a poor proletariat background and thus more trustworthy to Soviet policy makers and Stalin, who actively sought to replace bourgeois scientists with party cadres hailing from impoverished families. They deemed Trofim Lysenko a proletarian genius who could provide an alternative to bourgeois science and thought Lysenko's experiments to be consistent with Darwin's theory of evolution.

In his desperation to bring revolutionary changes to agriculture, in 1938, Stalin appointed Lysenko as the president of Lenin Academy, the highest post for an agricultural scientist in the Soviet Union. Vavilov, as an expert geneticist, knew that Lysenko's methods would not work. He firmly opposed Lysenko's claims and, to the best of his ability, provided scientific explanations to Stalin and his cabinet, but they did not trust Vavilov. Vavilov challenged Lysenko to a scientific debate on the merit of his claims, but Lysenko campaigned against Vavilov and the science of genetics with the help of the Communist Party cadres.

Stalin and his cabinet took a highly negative stand toward genetics based on their political ideology in response to the inhumane experiments of eugenics in Germany and the US at the time. Since Vavilov was a world-renowned scientist in genetics, he was declared the leader of this unacceptable science. Thus the end of genetics in the Soviet Union meant the end of Vavilov and his colleagues. His funding was ceased, and in 1937, Vavilov's foreign travels were banned forever. More than a hundred of Vavilov's fellow scientists were sentenced to death on charges of treason. Stalin also ordered the execution of two of his (Stalin's) closest associates, Nikolai Bukharin and Nikolai Gorbunov, for supporting the science of genetics. Vavilov's position was downgraded to the head of the Institute of Applied Botany and New Crops in Leningrad, where he was to work under Lysenko. Even while working in difficult circumstances and without resources, Vavilov stood firmly by his principles. He continued to write letters to the government for the release of his associates, though his correspondence with foreign scientists was blocked. He wrote his last letter to Professor Harry Harlan in 1937. Harry's son Jack Harlan was interested in doing his PhD under Vavilov's supervision, and he had sent his application to Vavilov. In reply, Vavilov addressed Harry Harlan (not Jack) and described a variety of wheat found in China. Vavilov normally addressed Harry Harlan as "Dear Doctor Harlan." This was the first letter in which Vavilov addressed him as "My Dear Doctor Harlan" and derailed from addressing a question. The senior Harlan asked his son to abandon the idea of research with Vavilov.

On August 6, 1940, Nikolai Vavilov was arrested while on a field trip in Ukraine, though the information of his arrest was not made public for three years. However, since Vavilov was a scientist of international repute and used to correspond with scientists from all over the world, the scientific fraternity became concerned about Vavilov's well-being after his correspondence ceased. So in 1942, the Royal Society of London elected him as a member, sending a letter along with the associated certificates to Vladimir Komarov, president of the Soviet Academy. In order to accept this honor, a signature from Nikolai Vavilov was required (which would have confirmed him being alive). In reply, Komarov had the certificate signed merely "Vavilov"—by Sergei Vavilov, the younger brother of Nikolai and the physicist who headed the Soviet nuclear program. The British embassy wrote back to Komarov stating that the signature of *Nikolai* Vavilov was expected, not that of his brother. However, the Soviet government went silent, and so after this, a rumor was spread in the scientific community that Nikolai Vavilov had been murdered by Stalin.

Actually, Nikolai had been accused of misuse of government grants and treason and was sentenced to death in 1942. But from prison, Vavilov appealed to Marshal Leverentia Beria to reconsider his sentence. Beria was one of Stalin's trusted allies and the head of the Supreme Department of Legal Affairs (NKVD). In addition, Vavilov's old professor Dmitry Pryanishnikov tried his best to reduce Nikolai's punishment. He too had friendly relations with the Beria family: Beria's wife was also a student of Pryanishnikov. Despite the hopelessness, the British Royal Society also continued to press for Vavilov's safety. Whatever the reason, Beria converted Vavilov's death sentence to twenty years of rigorous imprisonment. But on January 26, 1943, Vavilov died of starvation in Saratov prison.

After Stalin's death in 1953, Russian scientists pressured Nikita Khrushchev to reinvestigate Vavilov's case. This time, all the charges against Vavilov were dismissed, and he was awarded a place in the history of the Soviet Union with posthumous honors.

Although many of Vavilov's unpublished research papers and research data were destroyed between 1940 and 1953, some material was saved by his wife, Yelena Berulina. Fatikh Bakhtev, a close associate of Vavilov who was involved in many of his field trips collecting germplasm, also survived the Stalin era. In 1957, Yelena Berulina and Fatikh Bakhtev published Vavilov's remaining material and data. This fundamental research work conducted by Vavilov's team of scientists provided insight and the direction to future research on crop domestication.

The building of the Bureau of Applied Botany is now known as the Nikolai Vavilov Institute of Plant Genetic Resources, and Vavilov is counted among the greatest scientists of the twentieth century. Vavilov's collection, his research papers, and information about his life are available on the Nikolai Vavilov Research Institute website (http://www.vir.nw.ru).

2.5 The World's First Seed Bank

In the 1920s, Nikolai Vavilov established the world's first seed bank in the building of the Bureau of Applied Botany in Leningrad, housing major collections of seeds and germplasm there that included 300,000 varieties of seeds and germplasm of 2,500 plant species. His team of scientists was also involved in conducting the detailed characterization of major crop varieties and systematic crossing experiments in experimental centers across the Soviet Union.

Hitler had a keen interest in genetics. During World War II, Germany formed a special commando squad to capture Vavilov's seed bank. On June 22, 1941, Germany invaded the Soviet Union. As the Germans advanced, they captured small seed banks in the western region, but the main seed bank in Leningrad was still out of their reach.

After the incarceration of Vavilov and many of his senior colleagues in 1942, the remaining scientists of the institute voluntarily shared the responsibility of protecting the germplasm collection during World War II. Apart from Hitler, this seed bank was also threatened by the starving people of Leningrad. In those years of war, 700,000 people died of hunger in Leningrad—including many of Vavilov's colleagues who stood protecting the seed bank. One by one, they starved to death while safeguarding the vast storehouse of seeds and tubers. Stalin was not interested in saving the seed bank, and thus the government did not provide any support. As Vavilov wasted away in prison, his associates successfully protected the germplasm collection for 900 days during the siege of Leningrad. This is a unique story of the sacrifice made by scientists to protect a seed collection for future generations.

The Leningrad seed bank also survived by pure chance. Hitler had planned to host a celebration of his victory at the Astoria Hotel on St. Isaac's Square; thus Germans did not bomb that area. The seed bank was right in front of the hotel. Similarly, when the war ended in 1944, the Germans were defeated before reaching Leningrad.

In the years since World War II, more seed banks have been established around the world, many of which also contain large amounts of seeds from Vavilov's collection. Today, this seed bank exists as part of the N. I. Vavilov Scientific Research Institute of Plant Industry in St. Petersburg (see figure 2.7). For the past century—and still today—the seeds and germplasm of various crops from this collection have been used by plant breeders worldwide to produce improved varieties of cereals, vegetables, and fruits. Much of the raw material for making advanced varieties of various crops, fruits, vegetables, and so on remains in Vavilov's seed collection for free.

Fig 2.7 Card catalogue at Vavilov Institute of Plant Industry. [Photo of card catalogue] by [Petr Kosina] is licensed under [CC BY-NC 2.0].

Even though the world population has increased more than three times over the last century, the world is now producing more food than people need. Vavilov and his fellows—many of whom themselves died of hunger—made tremendous contributions toward achieving global food security by creating a tremendous genetic resource for future crop improvement. Now that many species of plants are extinct in their centers of origin, Vavilov's seed and germplasm collection has become invaluable.

The work of Vavilov and his colleagues helped further our understanding of the importance of biodiversity and the conservation of germplasm in ensuring food security for mankind. Thanks to them, today, there are more than a hundred large and many thousands of small seed and germplasm banks in the world.

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Colonial Agriculture

3.1 Crop Exchanges before the Industrial Revolution

The migration of the human population meant that the movement of crops away from their centers of origin was inevitable. Domesticated plant species first spread to neighboring regions via nomadic pastoralists, who traded with various farming communities. As tribal wars broke out, the grains were also looted and brought to new territories. However, this spread was limited.

Credit for the initial global spread of cultivated plants (3,000 BCE to 1,000 CE) goes to the ancient Polynesian seafarers, who sailed between Southeast Asia, Africa, and South America. They helped at least eighty-four cultivated plants travel from South America to Asia and Africa (e.g., maize, amaranth, cashews, pineapples, custard apples, peanuts, pumpkins, gourds, arrowroot, guava, sunflowers, basil, and brahmi). They also brought hemp and another fifteen plants to Africa and South America from Asia. These exchanges occurred long before Europeans were aware of the existence of the Americas (1).

The second global wave of exchange ensued via the Silk Road. The first highway that connected Asia to Europe and Africa, it was built by the emperors of the Han dynasty between the second century BCE and the first century CE. It was not a single road but a network of several routes that connected various regions of China. The silk collected from many provinces in China and sent west through its primary northern route gave it its name. Later, this route was extended to Rome via Central Asia, Iran, Iraq, and Syria, while a branch from Tibet also connected India. At its peak, the Silk Road network covered 7,000 miles, much of which ran through large desert areas with sporadic human inhabitation, where water and food sources were scarce and a constant fear of robbers loomed. Thus travel on the Silk Road was not for everyone. Only Arabs, the inhabitants of Central and Middle Eastern Asia who possessed generational experience surviving in the desert and had tribal networks to rely on, were successful in traversing the Silk Road and thus dominated trade. They traveled on camels across the desert in caravans protected by armed squadrons. They stopped at meeting points where traders heading to different destinations exchanged goods, like silk, cotton, sugar, spices, china, ivory, and precious stones. Traveling alone was not an option, so individuals, small groups, missionaries, and pilgrims also joined the traders' caravans. For centuries, Arab merchants, travelers, and Sufis played a central role in the exchange of seeds and germplasm among the three continents. From India and China, they transported cotton, sugarcane, eggplants, and bananas to Central Asia and Africa; from Central Asia, they carried pomegranates, chickpeas, gram, pears, walnuts, pistachios, dates, fennel, carrots, onions, and garlic to India and China. From Africa, they procured millet, melons, coffee, and many tubers for Asia and Europe. Some sovereigns and their armies also unintentionally assisted in carrying germplasm across the Silk Road.[1]

3.2 The Columbian Exchange

The third and the most dominant wave of global plant germplasm exchange occurred between the Age of Exploration and the Industrial Revolution under European imperialists. They promoted and invested in the systematic cataloging and classification of the fauna and flora found across the seven continents, transporting germplasm in bulk and establishing plantations of cash crops worked by enslaved peoples. This massive germplasm exchange between the Old World (Asia, Europe, and Africa) and New World (the Americas and various archipelagoes) is known as the Columbian Exchange (see figure 3.1).

You might be surprised to learn that until the eighteenth century, the peoples of Asia, Europe, and Africa had not seen potatoes, tomatoes, corn, sweet potatoes, or peppers, which are now an integral part of their traditional cuisines. Acceptance of the introduced food crops in their new homes was slow, integration in the local cuisines was gradual, and acceptance in some cases was challenging. For instance, potatoes were brought from Peru to Spain in the sixteenth century, reaching Italy from Spain in 1560. However, it took more than a hundred years for Europeans to accept the potato as food. When it first arrived in Europe, there were rumors that eating potatoes cause leprosy. In the seventeenth century, Irish peasants adopted the crop due to difficult circumstances: invasion, famine, and evictions from their fertile land. They embraced the potato because it was a highly productive crop that could be grown even on the smallest amount of cultivated land.

1. As an example, Ẓahīr al-Dīn Muḥammad Bābur(1483–1530), the founder of the Mughal dynasty, invaded Hindustan (northern India) and established his capital in the city of Agra. His artisans and well-versed gardeners for the first time introduced several crops of Central Asia into India: on the banks of the Yamuna River in the city of Agra, India, they sowed watermelons, melons, musk melon, and so on and planted grapes and roses in the Agra Fort.

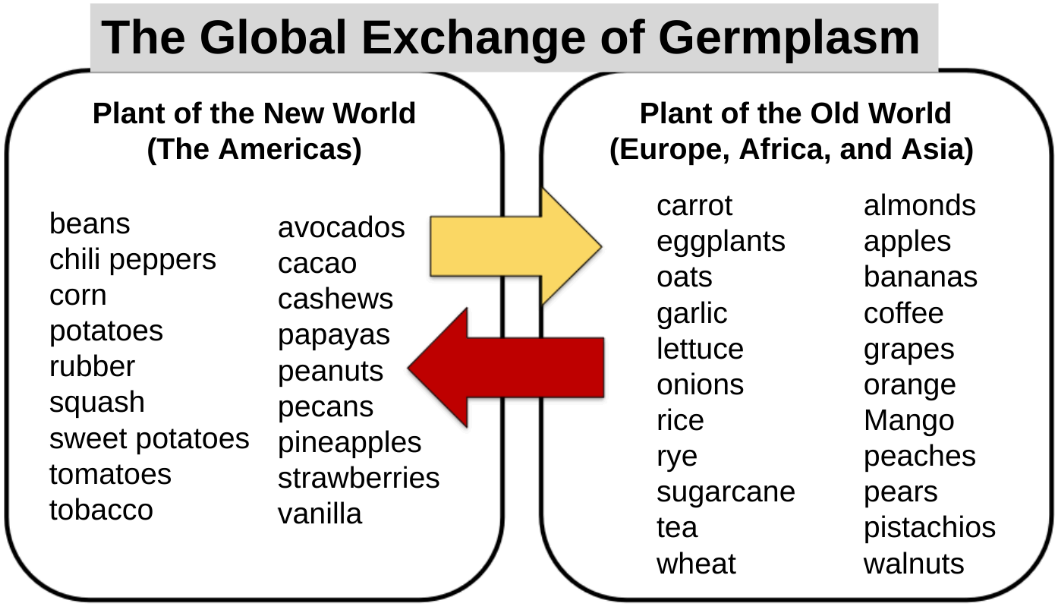

Fig 3.1 Examples of food crops exchanged between the New World and the Old World after 15th century. "The Global Exchange of Germplasm" by Sushma Naithani is licensed under [CC BY 4.0](CC BY 4.0).

During the eighteenth century, potatoes were successfully introduced in Germany due to frequent crop failures, but the French population was still apprehensive despite famine and starvation. The French eventually accepted potatoes in the late eighteenth century after much encouragement from Queen Marie Antoinette. Marie adorned her hair with potato flowers and commissioned a portrait of herself with a potato plant. She also asked gardeners to plant potatoes in the royal gardens, where guards were stationed during the day but cleverly called away at nighttime. Common folks would dig potatoes from the royal garden at night and sow them in their fields.

Later, Europeans introduced potatoes to the Ural Mountains and their colonies in Asia and Africa. For example, the British brought them to India, and in the mid-nineteenth century, officials from the Geological Survey of India sowed potatoes in the slopes of the Himalayas. Potatoes proved to be a very productive and nutritional crop in most areas and, by the middle of the nineteenth century, became an integral part of diets across Europe and Asia. Today, the potato is the most popular and affordable vegetable in the world. In Africa and Central Asia, many traditional cuisines use potatoes and chicken as their main ingredients, even though the domesticated animal's birthplace is China and the vegetable's is Peru.

Similarly, tomatoes, onions, and garlic, used in abundance in Italian cuisine, were introduced to the country only 400 years ago. Red chilies, bell peppers, pumpkins, gourds, squash, and so on spread all over the world from South America over the past three centuries. Likewise, mangoes, jackfruit, eggplants, cotton, sugarcane, and so on spread out of South Asia. This history of the introduction of cultivated plants shows us that many traditional cuisines are not as old as they are thought to be. Despite the strong sense of cultural identity we ascribe to them, they are constantly evolving and incorporating new ingredients.

We find that across cultures and religions, some food items are revered, whereas others are prohibited. During Hanukkah, Jewish people traditionally make latkes (a special pancake made of potatoes), and they eat unleavened bread, matzo, during Passover. Hindus offer basil, barley, sugarcane, sesame, and rice to their gods with their prayers. For Africans, cassava and yam are staples, but red rice is sacred and saved for special occasions. It seems that a sense of reverence for particular foods may be linked to historical memories of crop domestication because, in many cases, the revered foods are prepared from crops that are native to the areas those people lived. In contrast, apprehensions are usually associated with crops that were introduced later. For example, some vegetarian Hindu sects abstain from eating garlic and onion, as these plants were introduced from Central Asia. At the root of this prejudice is doubt and fear of the unfamiliar. Such reverence or prejudice may not seem to make logical sense but may trace back to experiences with the domestication and/or introduction of the crop in the past.

Scholars estimate one-third of all food crops grown in the world today are of American origin and were unknown to the Old World before the conquest of the Americas. Over time, these crops became integrated into European, Asian, and African cuisines. Likewise, foods previously unknown in the Americas—such as sugarcane, tea, coffee, oranges, rice, wheat, eggplants, bananas, mangoes, and so on—were brought over by European colonists. Overall, this global exchange of plant species and their cultivation at the industrial scale brought uniformity to the consumer market and actually flattened the diversity known to previous generations. In total, to date, 250,000 species of flora are known, out of which humans can identify some 30,000 plant species as edible, but only 120 are cultivated. Of these, eleven crops—wheat, maize, rice, potatoes, barley, sweet potatoes, cassava, soybeans, oats, sorghum, and millet—satisfy 75 percent of human nutritional needs, and wheat, maize, and rice alone make up more than 50 percent of the entire population's daily caloric intake.

3.3 The Rise of European Imperialism and Plantations

From the seventh century until the seventeenth century, Arabs controlled Silk Road trade. The luxurious goods they brought from China and India were first sold to the sultans of Central Asia, and the remaining items were sold in Europe. As a consequence, only a few valuable goods were auctioned in Europe, where the kings and noble classes bid on their favorite items. Arab traders made tremendous profits and controlled the market: they determined what to sell, where to sell, and at what price. In contrast, Europe had nothing of value to barter and thus had to make their payments in gold or silver. European economic thought and policies until the 1700s were based on the mercantile system, wherein economic and political stability rely on restrained imports and excessive exports. Thus unilateral trade with Arabs caused fear among the European sovereigns, who worried about the diminishment of their treasuries of gold and silver.

So in the fifteenth century, the rulers of Portugal poured their resources into developing better ships, navigational equipment, watches, maps of the world, and so on and recruited Europe's best sailors to lead armed naval squads for exploration. The Portuguese managed to reach the Canary and Azores Islands, the Caribbean, Brazil, Africa, China, India, and Southeast Asia by sea. Soon Spain, France, Britain, and Holland also managed to reach the Americas, Asia, and Africa. Thus Christopher Columbus reached the Caribbean islands in 1492, and five years later, in 1497, Vasco da Gama reached the port of Calicut in India. For the first time, Europeans saw many new crops, fruits, vegetables, ornamental plants, herbs, cattle, and other species of animals from Asia, Africa, and the Americas. From the sixteenth to nineteenth century, the various European powers competed with one another for control over the newfound lands and their wealth. Gradually, all the countries of Africa, the Americas, and Asia became European colonies.

European rulers employed new management systems in their colonies. They organized agriculture to focus on the establishment of plantations of cash crops, replacing traditional farming to maximize profits. First, sugar plantations were established in the Caribbean by exploiting slave labor, and later, this model was repeated to produce tea, coffee, cocoa, poppy, rubber, indigo, and cotton in Asia, the Americas, and Africa. The products of plantations were for the distant European markets and not for the consumption of local populations. Often, the crops and the laborers were brought to plantations from different continents. Thus colonial agriculture caused the global displacement of many people and plants.

From the sixteenth to the nineteenth century, the story of agriculture centered on these plantations' products and their availability at a cheap price in the global market. Europe's sovereign class made huge profits, and the continent prospered tremendously, but at the cost of exploiting the natural resources of the colonies and relying on slavery. Increasing trade between Europe and the colonies also affected business and trade practices during the 1500s and 1600s, which had a great impact on all spheres of society and human civilization. With this also came the Enlightenment and the birth of the ideas of democracy and universal equality. We see that massive change in agricultural practices added several new layers of complexity to human civilization, politics, and economics and eventually changed the world order forever.

In the rest of this chapter, we will explore colonial agriculture and its impact on human society through the stories of three representative plantation products: sugar, tea, and coffee.

3.4 The Story of Sugar and Slavery

3.4.1 The Discovery of Sugar

Sugarcane, a plant from the grass family, is the major source of sugar. It is a tropical crop, requiring an abundance of water and sunshine for optimum growth, and is easily damaged by frost and low temperatures. It has a very long and prominent stalk or stem (about twelve feet) that is filled with juicy fibers containing large amounts of sucrose. People enjoy chewing small pieces of the stem to consume its juice directly. This juice is also used for making sweets, puddings, and sugar (see figure 3.2).

Fig 3.2 "Sugarcane and a bowl of sugar" by Carl Davies is licensed under CC BY 3.0.

Sugarcane is a plant native to South and East Asia (covering India, Indonesia, China, and New Guinea), where its six species are found. The sweetest and the most cultivated variety of sugarcane, known as *Saccharum officinarum* (see figure 3.3), is believed to have originated in New Guinea or Indonesia and was introduced to many South Asian countries 3,000–5,000 years ago by Polynesian sailors. Where and how the cultivation of sugarcane began remains unknown. The earliest written reference to the sugarcane reed is a Vedic

Hindu text known as the Atharvaveda (which is 3,500 years old), where the use of *ikshu* (desire), the Sanskrit name for sugarcane, appears several times. It is not surprising that the sweetest plant on earth was called "desire," as sweetness is the most primitive human craving, the first taste that settles in our consciousness. We use *sweet* as an adjective to evaluate and describe the most positive, emotionally fulfilling, and abstract aesthetic experiences.

The second-oldest written reference to sugarcane is from the Greek philosopher Herodotus (484–425 BCE). Within a hundred years of Herodotus, Kauṭilya (ca. 350–283 BCE) described five types of sugar in his book *Arthaśāstra*.[2] This is the first ancient description of sugar making in the world. It is likely that in India, people learned to make sugar 2,000 years ago and developed pressing mills to extract large quantities of juice from the cane, as well as facilities for boiling the juice and extracting sugar. However, people outside of the Indian subcontinent remained largely ignorant of it until much later.

For the first time, in the seventh century, Arab traders introduced raw sugar (a.k.a. khand) to Central Asia. There, artisans invented tedious protocols for the purification and crystallization of it, thus making white granulated sugar, sugar cubes, and sugar figurines. Initially, white sugar was made in very small quantities and was so very costly that it was known as "white gold." White granulated sugar was not made available in India for a long time; the raw material continued to come from India, but for centuries, the advanced technology for making granulated sugar was not known in the country. It wasn't until the thirteenth century that the technique for making it reached India from China, and that is why it is called "Cheeni" in India today.

2. The *Arthaśāstrais* is an ancient Indian text on politics, economic policy, and military strategy written in Sanskrit by Kauṭilya, also known as Vishnugupta or Chanakya. He was a scholar at the ancient school Takshashila and the teacher and guardian of Emperor Chandragupta Maurya, who founded the Mauryan Empire in northern India.

Fig 3.3 Sugarcane (Saccharum officinarum). "Sugarcane (Saccharum officinarum)" by Franz Eugen Köhler is in the public domain.

In the eleventh century, both raw khand and white processed sugar reached the royals and lords of Europe. The word *candy* was coined for khand, and *sucre*, *sacrum*, *sucrose*, and *sugar* for the white variety. Before this, Europeans had never known such extreme sweetness, and they went crazy for it. It was so addictive that they were willing to plunder their stores of gold and silver in exchange for just a few pounds of it. But while the demand for sugar was high, so little was available that not even 1 percent of that demand could be met. It is said that once, England's King Henry IV went to considerable lengths to get just four pounds of sugar, but it could not be arranged.

The Arabs realized that there is an immense scope for expanding the highly profitable sugar trade. Islamic rulers (of Arab origin) who dominated India and Central Asia from the seventh century onward focused on increasing the production of sugar: they organized large farms for sugarcane cultivation under the leadership of landlords. These landlords set up sugar factories in the reed fields because cut sugarcane deteriorates rapidly and so must be milled within twenty-four hours. In these fields, armies of workers continuously worked, cutting and transporting sugarcane to the factory, where artisans would extract the juice and pass it along for boiling and further processing. This marked the first time in human civilization that excessive human labor was organized for cultivating a cash crop to be sold in distant markets: these were the first plantations.

Due to the efforts of the Islamic rulers, sugar production doubled, but demand quadrupled. Arab merchants could not meet the demands of sugar in Central Asia or Europe; fulfilling it was beyond their ability. There were two main obstacles: first, they had a limited amount of fuel for making sugar, and second, only a modest amount could be transported to Europe via camels and horse convoys.

3.4.2 Caribbean Sugar Colonies

Strange as it may seem, until the sixteenth century, most people in the world did not know about sugar. The sweetest thing they had known was honey, and that too was available only in small quantities. The Portuguese were the first to invest in commercial sugar plantations. They used their newly founded colonies in the Caribbean for sugarcane cultivation, where fuel for running the factories was plentiful and goods could be easily shipped worldwide. However, they were short on the workers needed to establish the plantations and run the factories. So they turned to West Africa, where they were heavily involved in the plunder of ivory. In 1505, they brought the first ship carrying enslaved Africans to the Caribbean to establish a sugar colony. Over the next twenty years, with the constant toiling of slaves, the Portuguese sugar colonies expanded from Hispaniola (present-day Haiti and the Dominican Republic) to Brazil.

Soon Spain, France, Britain, and Holland followed their example and established sugar colonies in the Caribbean islands, Guyana, Suriname, Brazil, Cameroon, and elsewhere. As the sugar industry expanded, the slave trade also grew to new peaks. In mainland Europe, many companies were formed around it (see figure 3.4 for a depiction of a regular scene at the slave market). For the next 300 years, the slave trade continued unabated. By the middle of the nineteenth century, a million Africans had been enslaved and brought to the Caribbean islands and Brazil. As a consequence, sugar production increased, and supply reached the common folks of Europe.

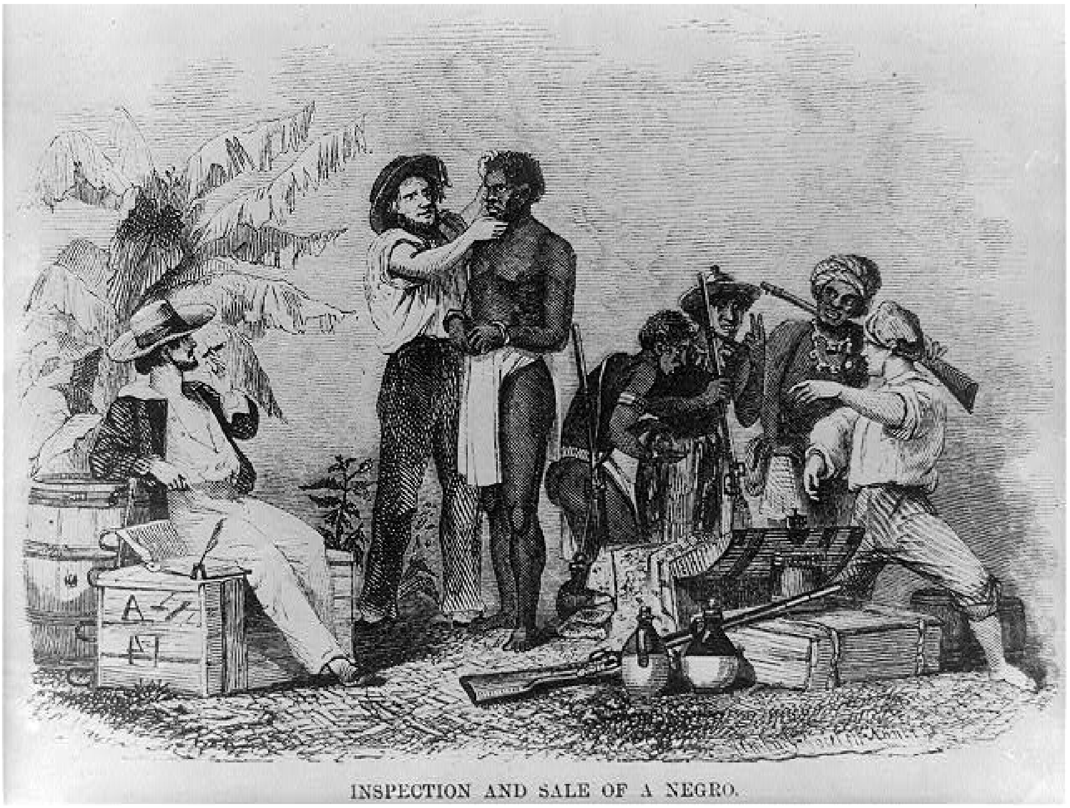

Fig 3.4 1854 reproduction of a wood engraving depicting inspection sale. [“The inspection and sale of a slave”]() by Brantz Mayer is in the public domain.

The owners of the sugar colonies, who profited from the slavery-based sugar industry, were important officials and members of influential families in Europe. While still residing in their native countries, they made tremendous amounts of money from their estates in the colonies. Although they seldom visited, each often maintained a plush bungalow on a high hill within the plantation, known as the “Great House.” The daily management of the sugar estate was left in the hands of a supervisor or slave commander (figure 3.5). The owner did not directly engage in the dirty work of interacting with the people he enslaved on a day-to-day basis. Slavery became an accepted social institution, and surprisingly, the task of its operation was shouldered by the slaves themselves. Usually, they worked for sixteen to eighteen hours a day, did not get enough food, and were not allowed to leave. They were punished and tortured routinely and could be murdered for raising a slight objection. It was common for them to die every day due to torture, hunger, and sickness. New slaves immediately replaced the dead. The eighteen- to twenty-year-old youth who were brought to sugar colonies from Africa usually died within ten years. A sense of the inhumane conditions of slave life can be drawn from the fact that from 1700 to 1810, 252,500 African slaves were brought to Barbados, a small island of 166 square miles, and 662,400 to Jamaica.

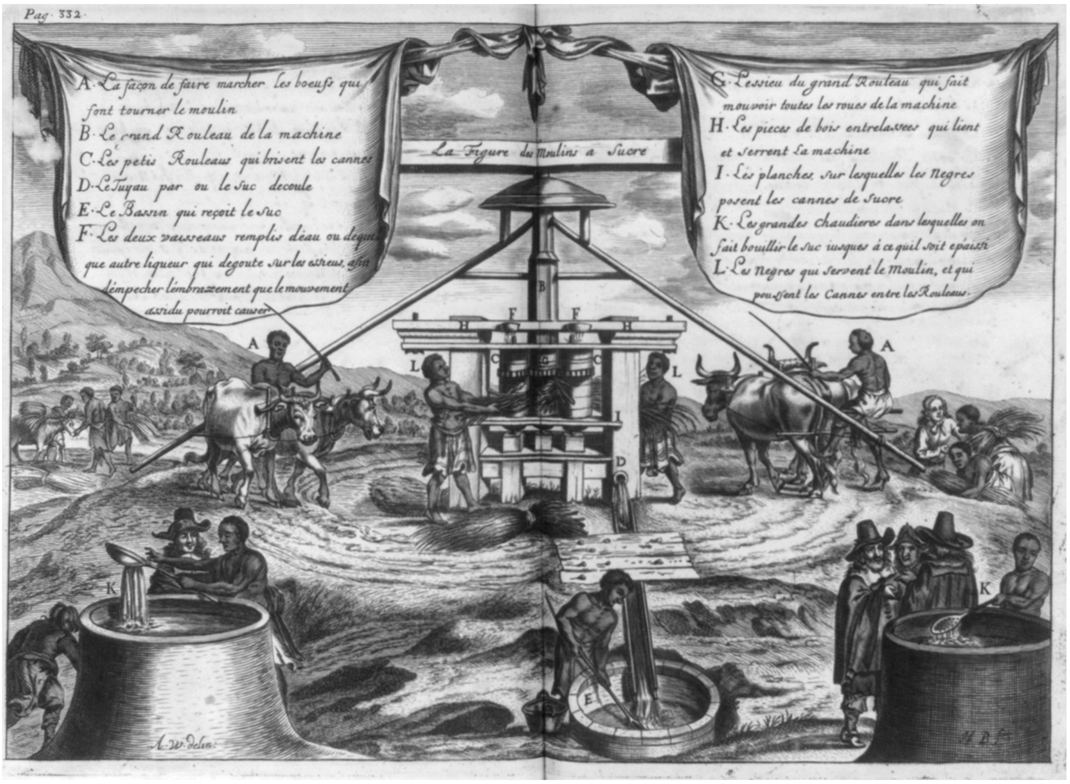

Fig 3.5 [“Sugar manufacture in the Antilles Isles”](#) by Library of Congress is licensed under no known restrictions on publication.

From 1600 to 1800, the sugar trade was the most profitable business in the world. It was a large part of “triangular trade,” wherein companies involved in the slave trade sold slaves in the Caribbean in exchange for sugars, then sugar was sold in Europe, and from Europe, armed sailors were sent to Africa for more slaves. This cycle continued for 300 years and ensured an uninterrupted supply of sugar was being sent to Europe. By the eighteenth century, sugar production in the Caribbean was so high that it became available to ordinary people at a very affordable price. However, many Europeans remained ignorant of the inhumane conditions of slaves working within the sugar colonies.

3.4.3 The End of Slavery in the Caribbean

In 1781, a public lawsuit in England that involved a Liverpool-based slave-trading company and an insurance company brought the slave trade under public scrutiny. The slave-trading company’s ship, *Jong*, lost its way, and officers onboard foresaw a shortage of drinking water in the ship due to the delayed schedule. To avoid inconvenience due to a drinking water shortage on the ship, they threw 142 slaves from the ship into the open sea. The slave-trading company had insurance on the lives of the slaves, and accordingly, they demanded compensation from the insurance company. However, the insurance company did not consider the “property damage” to be justified and refused to pay compensation. In response, the Slave Trading Company sued them. The news of this lawsuit was published in the newspapers of England, and a public conversation on slavery began.

Quakers organized and led protests against the killings, and, in 1783, 300 Quakers appealed to the British Parliament to end slavery. The appeal was dismissed. All the influential British citizens of that time, including the members of parliament and their relatives, owned sugar estates in the Caribbean; their economic interests were directly tied to the slave trade. For example, lord mayor of London William Beckford, who was also a member of parliament, had twenty-four sugar plantations in Jamaica; another parliament member, John Gladstone (father of the future British prime minister William Gladstone), owned a sugar colony in British Guiana. Therefore, it was no surprise that the Quakers’ proposal was rejected in parliament. However, the Quakers were not discouraged. They started the abolitionist movement,[3] boycotting sugar on moral grounds and urging the public to do the same. They reached out to various individuals, groups, and organizations to educate people about slavery and recruit supporters. They approached people from both the lower as well as elite classes and tirelessly campaigned against slavery.

Among the top activists of the abolitionist movement, Thomas Clarkson (figure 3.6) is particularly notable. In 1785, when he was a student at Cambridge University, he participated in the annual essay competition. The subject of that year’s essay, “The Slavery and Commerce of the Human Species,” was proposed by Peter Peckard, then the chancellor of Cambridge and a well-known abolitionist himself. Thomas Clarkson received first prize in the competition, and in writing the essay, what he learned about the cruel system of slavery made a lasting impact on him. The essay was published, and soon, he was introduced to several prominent leaders of the abolitionist movement, including James Remje and Grenville Sharp. Later, he became a full-time activist and dedicated his life to the cause.

3. See the history of the abolitionist movement and related documents at http://abolition.e2bn.org.

Fig 3.6 Thomas Clarkson addressing delegates of the Anti-Slavery Society Convention in 1840. "The Anti-Slavery Society Convention, 1840" by Benjamin Haydon is in the public domain.

Clarkson gathered testimonies from doctors who worked on slave ships and military men who had served in the Caribbean crushing the slave rebellions. He acquired the various instruments of torture (handcuffs, fetters, whips, bars, etc.) used on slaves to educate British citizens about the cruelty inflicted on the slaves within the sugar estates. He traveled 35,000 miles on horseback to collaborate with antislavery organizations and individuals. Clarkson also recruited supporters from influential political circles, such as parliament member William Wilberforce, who appealed twice to the British parliament to abolish the slave trade. His appeal was dismissed the first time, but the second time, in 1806, it passed under the heavy pressure of public opinion. Finally, in 1807, the slave trade was outlawed throughout the British Empire. The famous English film *Amazing Grace* is based on these efforts. In March 1807, on the final passing of the Bill for the Abolition of the Slave Trade, the poet William Wordsworth wrote the following sonnet in praise of Thomas Clarkson:

> Clarkson! it was an obstinate Hill to climb:
>
> How toilsome, nay how dire it was, by Thee
>
> Is known—by none, perhaps, so feelingly;
>
> But Thou, who, starting in thy fervent prime,

> Didst first lead forth this pilgrimage sublime,
>
> Hast heard the constant Voice its charge repeat,
>
> Which, out of thy young heart's oracular seat,
>
> First roused thee—O true yoke-fellow of Time
>
> With unabating effort, see, the palm
>
> Is won, and by all Nations shall be worn!
>
> The bloody Writing is forever torn,
>
> And Thou henceforth wilt have a good Man's calm,
>
> A great Man's happiness; thy zeal shall find
>
> Repose at length, firm Friend of human kind!

Although this was a significant triumph, slavery did not end. British companies stopped buying and selling slaves, but over the next thirty years, slaves continued to work as before in the plantations and mines located within the British Empire, and new slaves were supplied by other European companies as needed. Therefore, the struggle against slavery continued.

Apart from abolitionists, many others also played a crucial role in the antislavery struggle. In 1823, an idealistic clergyman, John Smith, went on a mission to British Guiana, where John Gladstone had a sugar estate. Pastor Smith narrated the story of Moses to the slaves there, describing how thousands of years ago, the Jewish slaves of Egypt gained their freedom and reached Israel. Inspired by this biblical story, 3,000 African slaves revolted. However, the rebellion was quickly suppressed, most of the rebels were killed, and Pastor Smith was sentenced to death, though Smith died on the ship carrying him back to England for execution.

British commoners were enraged by the death of Smith, which provided momentum to the antislavery movement. For the next ten years, they organized frequent antislavery protests and massive rallies while, in the sugar colonies, slave revolts continued. Finally, again under the pressure of public opinion, in 1833, the British Parliament passed the Emancipation Bill, which resulted in the legal abolition of slavery within the British Empire. The owners of the plantations were given seven years and subsidies to free their slaves. Finally, all slaves within the British Empire were legally freed on August 1, 1838.

3.4.4 Haiti: The First Free Country of Slaves

Around the time the abolitionists were campaigning to end slavery in England, the French Revolution (1789–99) began. At the time, a revolt erupted in the most valued French sugar colony, St. Dominic. Slave commanders ran the plantations in St. Dominic, where there were 25,000 whites, 22,000 freed Africans (including the slave commanders), and 700,000 slaves. The revolt was organized by slave commanders who pledged to liberate Haiti under the leadership of Toussaint, who called himself *L'Ouverture* (the opening). The slaves' destiny was tied to the sugar plantations and the factories, so they burned them. In the wake of the ongoing turmoil within France, the temporary government of France, formed after the abolition of the monarchy, saw no way to quell this uprising and liberated St. Dominic in 1793. Thus St. Dominic became Haiti, the first free country of slaves.

However, when France withdrew, Britain moved forward to take control of Haiti. British soldiers began capturing the people of Haiti and returning them to the plantations as slaves. The fight continued for another five years. Eventually, in 1798, the British gave up, and Haiti became free again. But this freedom was also short-lived. In 1799, Napoleon came to power, and he overturned the law that had freed the slaves and attacked Haiti. French troops imprisoned the rebel leader Toussaint, who died in prison in 1803. Nonetheless, the people of Haiti continued fighting Napoleon's army, resulting in the deaths of 50,000 French soldiers, and France suffered substantial economic losses. In 1804, France retreated, and Haiti finally became a free republic.

3.4.5 The American Sugar Colonies of Hawaii and Louisiana

Napoleon sold the French province of Louisiana to President Thomas Jefferson for just $15 million to make up for the enormous losses in the war with Haiti. Some of the former owners of the Caribbean sugar plantations started fresh in Louisiana.

Louisiana is suitable for sugarcane cultivation. However, it has a mild frost in the winter months, and thus sugarcane crop needs to be harvested from October to December. The additional burden of this weather also fell on the slaves, and therefore working conditions for slaves became even worse in Louisiana. Slavery continued in the United States of America until 1862. On January 1, 1863, Abraham Lincoln issued the Emancipation Proclamation and declared "that all persons held as slaves are, and henceforward shall be free." Abraham Lincoln was also the first US president who established diplomatic relations with Haiti.

Some of the former owners of the Caribbean sugar colonies chose to settle in Hawaii. The conditions were very favorable for the planters, as sugarcane farming had been underway for a long time there. It is believed that in the early twelfth century, Polynesians brought sugarcane to Hawaii from South Asia. Hawaiians used sugarcane juice in many ways, although they did not learn to make sugar. The owners of plantations in Hawaii developed a new model for recruiting workers. Instead of African slaves, they employed workers from Asian countries at meager wages. First, only men from China were recruited. When these workers demanded better wages and working conditions, they brought workers from Japan, Korea, the Philippines, Spain, and Portugal. The workers of Hawaii were divided into different linguistic, ethnic, and cultural groups, and hence they could not organize to challenge the owners. The owner successfully managed their plantations and gained tremendous profits from the sugar business for nearly a century and a half. The living and working conditions of the workers were unfair and cruel, but it was an improvement compared to slavery: they received wages for their work, had families, and the owners could not sell them and their children. It was a significant accomplishment that, thanks to abolitionists, in the nineteenth century, legal slavery ended, and plantation owners were obliged to pay wages. In 1959, Hawaii became the fiftieth state of the United States of America.

3.4.6 Indentured Labor: Girmitiya

In 1836, John Gladstone wrote a letter to the then viceroy of India, asking him to send laborers for his sugar estate. The viceroy gladly accepted Gladstone's proposal and sent 2,000 workers from India to British Guiana on a five-year work permit, along with the provisions for a paid trip back home. Like Gladstone, others made arrangements to bring indentured laborers from India when the slaves were freed (see figure 3.7). These workers carrying permits were sent to several British colonies—including Guyana, Mauritius, Suriname, the Caribbean islands, and South Africa—to work in plantations and mines.

Fig 3.7 A photograph of newly arrived Indian coolies in Trinidad, circa 1897. "Newly arrived coolies in Trinidad" is in the public domain.

The indentured workers couldn't pronounce the word *permit* and instead referred to it as "Girmit," and themselves as "Girmitiya". After a long sea voyage of two to three months, when the Girmitiya reached their destination, they were received by the overseers and were assigned the quarters of the former slaves. The Girmitiya were helpless in a foreign land and could survive only at the mercy of the owners. They worked long hours, earned less money than promised, and were treated as slaves in all practical matters.

With the arrival of indentured workers, freed slaves lost opportunities for employment, and the owners got the upper hand in setting wages. So despite the freedom they'd earned after tremendous sacrifice and struggle, former slaves remained marginalized. The European owners deliberately created a situation in which indentured workers, former slaves, and other marginalized groups all remained in competition with one another. The masters of the plantations (and also the mines) thought of Indian workers as weak, obedient children and former slaves as foolish and lazy. The owners did not pay fair wages to either: in most places, the indentured workers received even poorer wages than the former slaves. Indentured labor was cheaper than free slaves, and the indentured workers were not in a position to organize and demand fair treatment or familiarized with the historical exploitation of slaves. Thus, the planters were treating them worse than free slaves. They were the replacement of former slaves.

3.4.7 The End of the Indentured Workers System

From 1860 onward, indentured workers from India were being brought to work in plantations and mines in South Africa. After the end of a five-year contract, indentured workers were offered two options: to return to India or live as a free worker who received a small plot of land in lieu of his passage home. Returning to India was not easy; Hindu workers who had crossed the sea faced social stigma back home. Thus most people chose to stay in South Africa to start their lives afresh. They often still worked in plantations and mines, but as free workers, and on the side, they served as small-time artisans, grew some fruits and vegetables on their plots, and set up small shops. Girmitiya brought many nuts and vegetable seeds with them from India. They grew local fruits, vegetables, and corn as well as Indian crops like mangoes. In the early years, their trade remained limited to their community. While the Indian population was small in number, the chance of their having direct encounters with the whites was negligible. The relationship between whites and Indians was more like that between an owner and a slave. But gradually the number of people of Indian origin increased. Apart from laborers, a large number of Muslim and Parasi traders from Gujarat also started coming to South Africa for business. Indian shopkeepers were polite, fair, and nonintimidating to Africans. As a result, many local Africans became their customers, which infuriated the white business community of South Africa.

In 1893, Mohandas Karamchand Gandhi (figure 3.8) reached South Africa for the first time to assist a Gujarati businessman Dada Abdullah in a legal case. At that time, 50,000 Indian workers (freed after contract) and 100,000 indentured workers and their offspring were living in South Africa. He faced many insults and racial discrimination as a person of color despite being highly educated. He soon realized that Indians suffered more racist violence and social discrimination in South Africa than in Europe. Gradually he became an activist and began to lead civil rights movements in South Africa. His encounters with indentured workers were eye-opening, and he realized that the situations Indian indentured workers faced were in some ways worse than those of former slaves.

Fig 3.8
[“Mohandas K. Gandhi, 1906”] *is in the public domain.*

For the next twenty-one years, Gandhi served as an advocate for the Indian traders, small shopkeepers, and plantation and mine workers. He led a struggle against the policies of apartheid, resulting in the abolition of many discriminatory laws. While in South Africa, Gandhi established communication with the leaders of the Indian Freedom Movement and was successful in inviting a senior congressional leader, Gopalakrishna Gokhale, to South Africa. Gokhale witnessed firsthand the plight of indentured workers living outside of India. After returning home, Gokhale appealed to ban the indentured worker system. Finally, in 1917, the practice ended.

Unlike the strategies used in previous battles within the colonies, Gandhi relied on satyagraha (emphasizing the human commonality and truth) and the principle of nonviolence to fight the state of South Africa. His satyagraha experiments in Africa were instrumental to his future work. Gandhi returned to India in 1918 and led the freedom struggle there for the next thirty years, guided by the same principles, until India gained freedom in 1947.

3.4.8 Sugar from Sugar Beets

A method for making sugar from sugar beets was discovered in 1747 by German scientist Andreas Sigismund Marggraf. Marggraf's student Franz Karl Achard successfully employed selective breeding for improving sugar content in beets and then opened the world's first factory for extracting it in Silesia in the year 1801. Napoleon Bonaparte became interested in the idea of beet sugar. Sugar beets required less labor and fuel than sugarcane and could be easily grown in the cold climate of Europe. Under Napoleon's patronage, the cultivation of beet sugar was promoted, and many factories and training schools were established. In 1812, Benjamin Dalesart discovered a method of extracting it on an industrial scale, which made it so that France could rely on beet sugar. In 1813, Napoleon prohibited the import of cane sugar from the Caribbean and further promoted beet sugar production. By 1837, France had 542 sugar mills and became the largest beet sugar producer in the world, producing 35,000 tons annually. Many other European countries, including Germany, followed France's lead. In the United States, beet sugar production began in 1890 in the states of California and Nebraska.

3.4.9 Sugar Production in the Twentieth Century and Beyond

In the twentieth century, many former European colonies became independent nations. Today the largest producers of sugar are Brazil, India, China, Thailand, Pakistan, Mexico, the Philippines, and Colombia. Agriculture practices also underwent significant changes; sugar making and various other processes are now automated, with machines replacing manual labor. In most countries, independent farmers grow sugarcane and then sell it to sugar mills. Now sugar is produced everywhere in abundance—200 million tons per year—and is affordable for most people around the world. Nowadays, 70–80 percent of sugar on the market is cane sugar, and about 20–30 percent is beet sugar.

3.5 The Story of Tea

Tea is made from the leaves of *Camellia sinensis*, a small evergreen tree (ten to twelve feet tall) in the Theaceae family that is native to north Burma and southwestern China (see figure 3.9). Two varieties of the tea plant, *C. sinensis* var. *sinensis* and *C. s.* var. *assamica*, are cultivated around the world for commercial tea production. The best tea is made from a new bud and the two to three leaves adjacent to it, which are newly formed and delicate and contain the most caffeine. Therefore, *Camellia* trees are pruned into three-to-four-foot-tall bushes to promote branching and the production of new leaves, as well as to facilitate plucking them. Various processing methods are used to attain different levels of oxidation and produce certain kinds of tea, such as black, white, oolong, green, and pu'erh. Basic processing includes plucking, withering (to wilt and soften the leaves), rolling (to shape the leaves and slow drying), oxidizing, and drying. However, depending on the tea type, some steps are repeated or omitted. For example, green tea is made by withering and rolling leaves at a low heat, and oxidation is skipped; for oolong, rolling and oxidizing are performed repeatedly; and for black, extensive oxidation (fermentation) is employed.

Fig 3.9 An illustration of tea plant (Camellia sinensis) with cross-section of the flower (lower left) and seeds (lower right). [Illustration of tea plant] by Franz Eugen Köhler is in the public domain.

3.5.1 The Discovery of Tea

Tea was discovered in 2700 BCE by the ancient Chinese emperor Shen Nung, who had a keen interest in herbal medicine and introduced the practice of drinking boiled water to prevent stomach ailments. According to legend, once, when the emperor camped in a forest during one of his excursions, his servants set up a pot of boiling water under a tree. A fragrance attracted his attention, and he found that a few dry leaves from the tree had fallen accidentally into the boiling pot and changed the color of the water; this was the source of the aroma. He took a few sips of that water and noticed its stimulative effect instantly. The emperor experimented with the leaves of that tree, now called *Camellia sinensis*, and thus the drink "cha" came into existence. Initially, it was used as a tonic, but it became a popular beverage around 350 BCE. The historian Lu Yu of the Tang dynasty (618–907 CE) has written a poetry book on tea called *Cha jing* (*The Classic of Tea*) that contains a detailed description of how to cultivate, process, and brew tea.

Tea spread to Japan and Korea in the seventh century thanks to Buddhist monks, and drinking it became an essential cultural ritual. Formal tea ceremonies soon began. However, tea reached other countries only after the sixteenth century. In 1557, the Portuguese established their first trading center in Macau, and the Dutch soon followed suit. In 1610, some Dutch traders in Macau took tea back to the Dutch royal family as a gift. The royal family took an immediate liking to it. When the Dutch princess Catherine of Braganza married King Charles II of England around 1650, she introduced tea to England. Tea passed from the royal family to the nobles, but for an extended period, it remained unknown and unaffordable to common folks in Europe. The supply of tea in Europe was scant and very costly: one pound of tea was equal to nine months' wages for a British laborer.

As European trade with China increased, more tea reached Europe, and consumption of tea increased proportionally. For example, in 1680, Britain imported a hundred pounds of tea; however, in 1700, it brought in a million. The British government allowed the British East India Company to monopolize the trade, and by 1785, the company was buying 15 million pounds of tea from China annually and selling it worldwide. Eventually, in the early eighteenth century, tea reached the homes of British commoners.

3.5.2 Tea and the "Opium War"

China was self-sufficient; its people wanted nothing from Europe in exchange for tea. But in Europe, the demand for tea increased rapidly in the mid-eighteenth century. Large quantities were being purchased, and Europeans had to pay in silver and gold. The East India Company was buying so much of it that it caused a crisis for the mercantilist British economy. The company came up with a plan to buy tea in exchange for opium instead of gold and silver. Although opium was banned within China, it was in demand and sold at very high prices on the black market.

After the Battle of Plassey in 1757, several northern provinces in India came under the control of the East India Company, and the company began cultivating poppy in Bengal, Bihar, Orissa, and eastern Uttar Pradesh. Such cultivation was compulsory, and the company also banned farmers from growing grain and built opium factories in Patna and Banaras. The opium was then transported to Calcutta for auction before British ships carried it to the Chinese border. The East India Company also helped set up an extensive network of opium smugglers in China, who then transported opium domestically and sold it on the black market.

After the successful establishment of this smuggling network, British ships bought tea on credit at the port of Canton (now Guangzhou), China, and later paid for it with opium in Calcutta (now Kolkata). The company not only acquired the tea that was so in demand but also started making huge profits from selling opium. This mixed business of opium and tea began to strengthen the British economy and made it easier for the British to become front-runners among the European powers.

By the 1830s, British traders were selling 1,400 tons of opium to China every year, and as a result, a large number of Chinese became opium addicts. The Chinese government began a crackdown on smugglers and further tightened the laws related to opium, and in 1838, it imposed death sentences on opium smugglers. Furthermore, despite immense pressure from the East India Company to allow the open trading of opium, the Chinese emperor would not capitulate. However, that did not curb his subjects' addiction and the growing demand for opium.

In 1839, by order of the Chinese emperor, a British ship was detained in the port of Canton, and the opium therein was destroyed. The British government asked the Chinese emperor to apologize and demanded compensation; he refused. British retaliated by attacking a number of Chinese ports and coastal cities. China could not compete with Britain's state-of-the-art weapons, and defeated, China accepted the terms of the Treaty of Nanjing in 1842 and the Treaty of Bog in 1843, which opened the ports of Canton, Fujian, and Shanghai, among others, to British merchants and other Europeans. In 1856, another small war broke out between China and Britain, which ended with a treaty that made the sale of opium legal and allowed Christian missionaries to operate in China. But the tension between China and Europe remained. In 1859, the British and French seized Beijing and burned the royal Summer Palace. The subsequent Beijing Convention of 1860 ended China's sovereignty, and the British gained a monopoly on the tea trade.

3.5.3 The Co-option of Tea and the Establishment of Plantations in European Colonies

Unlike the British, the Dutch, Portuguese, and French had less success in the tea trade. To overcome British domination, the Portuguese planned to develop tea gardens outside China. *Camellia* is native to China, and it was not found in any other country. There was a law against taking these plants out of the country, and the method for processing tea was also a trade secret. In the mid-eighteenth century, many Europeans smuggled the seeds and plants from China, but they were unable to grow them. Then, in 1750, the Portuguese smuggled the *Camellia* plants and some trained specialists out of China and succeeded in establishing tea gardens in the mountainous regions of the Azores Islands, which have a climate favorable for tea cultivation. With the help of Chinese laborers and experts, black and green tea were successfully produced in the Portuguese tea plantations. Soon, Portugal and its colonies no longer needed to import tea at all. As the owners of the first tea plantations outside China, the Portuguese remained vigilant in protecting their monopoly. It was some time before other European powers gained the ability to grow and process tea themselves.

In the early nineteenth century, the British began exploring the idea of planting tea saplings in India. In 1824, Robert Bruce, an officer of the British East India Company, came across a variety of tea popular among the Singpho clan of Assam, India. He used this variety to develop the first tea garden in the Chauba area of Assam, and in 1840, the Assam Tea Company began production. This success was instrumental to the establishment of tea estates throughout India and in other British colonies.

In 1848, the East India Company hired Robert Fortune, a plant hunter, to smuggle tea saplings and information about tea processing from China. Fortune was the superintendent of the hothouse department of the British Horticultural Society in Cheswick, London. He had visited China three times before this assignment; the first, in 1843, had been sponsored by the horticultural society, which was interested in acquiring important botanical treasures from China by exploiting the opportunity offered by the 1842 Treaty of Nanking after the First Opium War. Fortune managed to visit the interior of China (where foreigners were forbidden) and also gathered valuable information about the cultivation of important plants, successfully smuggling over 120 plant species into Britain.

In the autumn of 1848, Fortune entered China and traveled for nearly three years while carefully collecting information related to tea cultivation and processing. He noted that black and green teas were made from the leaves of the same plant, *Camellia sinensis*, except that the former was "fermented" for a longer period. Eventually, Fortune succeeded in smuggling 20,000 saplings of *Camellia sinensis* to Calcutta, India, in Wardian cases.[4]

4. The Wardian case, a precursor to the modern terrarium, was a special type of sealed glass box made by British doctor Nathaniel Bagshaw Ward in 1829. The delicate plants within them could thrive for months. Plant hunter Joseph Hooker successfully used Wardian cases to bring some plants from the Antarctic to England. In 1933, Nathaniel Ward also succeeded in sending hundreds of small ornamental plants from England to Australia in these boxes. After two years, another voyage carried

He also brought trained artisans from China to India. These plants and artisans were transported from Calcutta to Darjeeling, Assam. At Darjeeling, a nursery was set up for the propagation of tea saplings at a large scale, supplying plantlets to all the tea gardens in India, Sri Lanka, and other British colonies.

The British forced the poor tribal population of the Assam, Bengal, Bihar, and Orissa provinces out of their land, and they were sent to work in tea estates. Tamils from the southern province of India were also sent to work in the tea plantation of Sri Lanka. Tea plantations were modeled on the sugar colonies of the Caribbean, and thus the plight of the workers was in some ways similar to that of the slaves from Caribbean plantations.

Samuel Davidson's Sirocco tea dryer, the first tea-processing machine, was introduced in Sri Lanka in 1877, followed by John Walker's tea-rolling machine in 1880. These machines were soon adopted by tea estates in India and other British colonies as well. As a result, British tea production increased greatly. By 1888, India became the number-one exporter of tea to Britain, sending the country 86 million pounds of tea.

After India, Sri Lanka became prime ground for tea plantations. In the last decades of the nineteenth century, an outbreak of the fungal pathogen *Hemilia vastatrix*, a causal agent of rust, resulted in the destruction of the coffee plantations in Sri Lanka. The British owners of those estates quickly opted to plant tea instead, and a decade later, tea plantations covered nearly 400,000 acres of land in Sri Lanka. By 1927, Sri Lanka alone produced 100,000 tons per year. All this tea was for export. Within the British Empire, fermented black tea was produced, for which Assam, Ceylon, and Darjeeling tea are still famous. Black tea produced in India and Sri Lanka was considered of lesser quality than Chinese tea, but it was very cheap and easily became popular in Asian and African countries. In addition to India and Ceylon, British planters introduced tea plantations to fifty other countries.

3.6 The Story of Coffee

Coffee is made from the roasted seeds of the coffee plant, a shrub belonging to the Rubiaceae family of flowering plants. There are over 120 species in the genus *Coffea*, and all are of tropical African origin. Only *Coffea arabica* and *Coffea canephora* are used for making coffee. *Coffea arabica* (figure 3.10) is preferred for its sweeter taste and is the source of 60–80 percent of the world's coffee. It is an allotetraploid species that resulted from hybridization between the diploids *Coffea canephora* and *Coffea eugenioides*. In the

many Australian plants back to Dr. Ward as a gift. Despite lengthy and difficult journeys, these plants survived, and so Wardian cases proved extremely useful for plant hunters, such as Robert Fortune.

wild, coffee plants grow between thirty and forty feet tall and produce berries throughout the year. A coffee berry usually contains two seeds (a.k.a. beans). Coffee berries are nonclimacteric fruits, which ripen slowly on the plant itself (and unlike apples, bananas, mangoes, etc., their ripening cannot be induced after harvest by ethylene). Thus ripe berries, known as "cherries," are picked every other week as they naturally ripen. To facilitate the manual picking of cherries, plants are pruned to a height of three to four feet. Pruning coffee plants is also essential to maximizing coffee production to maintain the correct balance of leaf to fruit, prevent overbearing, stimulate root growth, and effectively deter pests.

Fig 3.10 An illustration of coffee plant (Coffea arabica L., Arabian coffee). Illustration of coffee plant by Franz Eugen Köhler is in the public domain.

Coffee is also a stimulative, and the secret of this elixir is the caffeine present in high quantities in its fruits and seeds. In its normal state, when our bodies are exhausted, there is an increase in adenosine molecules. The adenosine molecules bind to adenosine receptors in our brains, resulting in the transduction of sleep signals. The structure of caffeine is similar to that of adenosine, so when it reaches a weary brain, caffeine can also bind to the adenosine receptor and block adenosine molecules from accessing it, thus disrupting sleep signals.

3.6.1 The History of Coffee

Coffea arabica is native to Ethiopia. The people of Ethiopia first recognized the stimulative properties of coffee in the ninth century. According to legend, one day, a shepherd named Kaldi, who hailed from a small village in the highlands of Ethiopia, saw his goats dancing energetically after eating berries from a wild bush. Out of curiosity, he ate a few berries and felt refreshed. Kaldi took some berries back to the village to share, and the people there enjoyed them too. Hence the local custom of eating raw coffee berries began. There are records that coffee berries were often found in the pockets of slaves brought to the port of Mokha from the highlands of Ethiopia. Later, the people of Ethiopia started mixing ground berries with butter and herbs to make balls.

The coffee we drink today was first brewed in Yemen in the thirteenth century. It became popular among Yemen's clerics and Sufis, who routinely held religious and philosophical discussions late into the night; coffee rescued them from sleep and exhaustion. Gradually, coffee became popular, and coffeehouses opened up all over Arabia, where travelers, artists, poets, and common folks visited and had a chance to gossip and debate on a variety of topics, including politics. Often, governments shut down coffeehouses for fear of political unrest and revolution. Between the sixteenth and seventeenth centuries, coffeehouses were banned several times in many Arab countries, including Turkey, Mecca, and Egypt. But coffeehouses always opened again, and coffee became ingrained in Arab culture.

Arabs developed many methods of processing coffee beans. Usually, these methods included drying coffee cherries to separate the beans. Dried coffee beans can be stored for many years. Larger and heavier beans are considered better. The taste and aroma develop during roasting, which determines the quality and price of the coffee. Dried coffee beans are dark green, but roasting them at a controlled temperature causes a slow transformation. First, they turn yellow, then light brown, while also popping up and doubling in size. After continued roasting, all the water inside them dries up, and the beans turn black like charcoal. The starch inside the beans first turns into sugar, and then sugar turns into caramel, at which point many aromatic compounds come out of the cells of the beans. Roasting coffee beans is an art, and a skilled roaster is a very important part of the coffee trade.

3.6.2 The Spread of Coffee out of Arabia

Coffee was introduced to Europeans in the seventeenth century, when trade between the Ottoman Empire and Europe increased. In 1669, Turkish ambassador Suleiman Agha (Müteferrika Süleyman Ağa) arrived in the court of Louis XIV with many valuable gifts, including coffee. The French subsequently became obsessed with the sophisticated etiquettes of the Ottoman Empire. In the company of Aga, the royal court and other elites of Parisian society indulged in drinking coffee. Aga held extravagant coffee ceremonies at his residence in Paris, where waiters dressed in Ottoman costumes served coffee to Parisian society women. Suleiman's visit piqued French elites' interest in Turquerie and Orientalism, which became fashionable. In the history of France, 1669 is thought of as the year of "Turkmenia."

A decade later, coffee reached Vienna, when Turkey was defeated in the Battle of 1683. After the victory, the Viennese seized the goods left behind by the Turkish soldiers, including several thousand sacks of coffee beans. The soldiers of Vienna didn't know what it was and simply discarded it, but one man, Kolshitsky, snatched it up. Kolshitsky knew how to make coffee, and he opened the first coffeehouse in Vienna with the spoils.

By the end of the seventeenth century, coffeehouses had become common in all the main cities of Europe. In London alone, by 1715, there were more than 2,000 coffeehouses. As in Arabia, the coffeehouses of Europe also became the bases of sociopolitical debates and were known as "penny universities."

3.6.3 Coffee Plantations

By the fifteenth century, demand for coffee had increased so much that the harvest of berries from the wild was not enough, and thus in Yemen, people began to plant coffee. Following Yemen's lead, other Arab countries also started coffee plantations. Until the seventeenth century, coffee was cultivated only within North African and Arab countries. Arabs were very protective of their monopoly on the coffee trade. The cultivation of coffee and the processing of seeds was a mystery to the world outside of Arabia. Foreigners were not allowed to visit coffee farms, and only roasted coffee beans (incapable of producing new plants) were exported. Around 1600, Baba Budan, a Sufi who was on the Haj pilgrimage, successfully smuggled seven coffee seeds into India and started a small coffee nursery in Mysore. The early coffee plantations of South India used propagations of plants from Budan's garden.

In 1616, a Dutch spy also succeeded in stealing coffee beans from Arabia, and these were used by the Dutch East India Company as starters for coffee plantations in Java, Sumatra, Bali, Sri Lanka, Timur, and Suriname (Dutch Guiana). In 1706, a coffee plant from Java was brought to the botanic gardens of Amsterdam, and from there, its offspring reached Jardin de plantes in Paris. A clone of the Parisian plant was sent to the French colony Martinique, and then its offspring spread to the French colonies in the Caribbean, South America, and Africa. In 1728, a Portuguese officer from Dutch Guiana brought coffee seeds to Brazil, which served as starters for the coffee plantations there. The Portuguese also introduced coffee to African countries and Indonesia, and the British established plantations in their Caribbean colonies, India, and Sri Lanka from Dutch stock.

In summary, all European coffee plants came from the same Arabian mother plant. So the biodiversity within their coffee plantations was almost zero, which had devastating consequences. In the last decades of the nineteenth century, the fungal pathogen *Haemilia vestatrix* severely infected coffee plantations in Sri Lanka, India, Java, Sumatra, and Malaysia. As a result, rust disease destroyed the coffee plantations one by one. Later, in some of the coffee plantations, *Coffea canephora* (syn. *Coffea robusta*), which has a natural resistance to rust, was planted, but others were converted into tea plantations (as in the case of Sri Lanka, discussed earlier).

European coffee plantations used the same model as tea or sugar plantations, and so their workers lived under the same conditions. European powers forcefully employed the poor native population in these plantations and used indentured laborers as needed. For example, in Sri Lanka, the Sinhalese population refused to work in the coffee farms, so British planters recruited 100,000 indentured Tamil workers from India to work the farms and tea plantations there.

3.7 The Heritage of Plantations

In the twentieth century, most former European colonies became independent countries. In these countries, private, cooperative, or semigovernmental institutions manage plantations of sugarcane, tea, coffee, or other commercial crops. Though these plantations remain a significant source of revenue and contribute significantly to the national GDP of many countries, their workers still often operate under abject conditions.

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Cataloging, Classification, and Deliberate Hybridizations

After the sixteenth century, when Europeans reached Asia, Africa, and the Americas, they saw many numerous new species of domesticated and wild plants and animals. Soon, surveying and systematic cataloging of the natural and biological resources ensued under the supervision of various experts. First, three or four experts went in small ships to survey the coastal areas of South America, Africa, and Asia. Typically, a geologist/naturalist would collect samples of rocks, soil, mineral, fossils, and plants and attach a note with each sample describing its features; an engineer's job was to draw or update the navigational maps and gather information about ports and structures of strategic importance; an artist painted landscapes and helped experts prepare sketches of valuable items. From time to time, the collections from survey ships were sent to Europe via other ships. As a result of the various surveys and expeditions, the royal gardens of Europe were overwhelmed with the vast collections from around the world, and several experts were recruited for the analysis, classification, and systematic cataloging of fauna, flora, fossils, and other types of samples.

Besides experts, both elites and common folks, especially the elites and middle-class Europeans, were taken aback by seeing thousands of varieties of fruits, vegetables, and ornamental plants from around the world. Also, many small institutions got interested in acquiring exotic plants and gardening different plant varieties. Around 1650, when the educated elites got involved in growing ferns, tulips, fruits, and so on, the publication of gardening books and nursery catalogs began, and the first nurseries and seed and landscaping companies were founded. Amateur horticulturists in Europe and around the world started the conscious selection of a variety of fruits, vegetables, flowers, and cereals. Today, many of what we consider "natural" fruits, vegetables, and flowers are the result of this conscious selection in the last 300 years. For example, in the seventeenth century, orange carrots were developed in the Netherlands for the first time by the artificial selection of yellow carrots. In the natural form, wild carrots are white and thin. Around the tenth century, the people of Afghanistan had domesticated light yellow carrots, which the Arabs had taken to Europe. In the same way, larger tomatoes, berries, and corn were developed via conscious selection. The variety selection was upheld by several organizations, and annual exhibitions of fruit and flower products began in many cities. Even today, annual agricultural fairs and exhibitions continue throughout the world, and gardeners and farmers still consciously select varieties. For example, in South Asia, farmers have developed thousands of rice varieties to thrive in different climatic and geographical conditions.

4.1 The Discovery of Sex in Plants: Self- versus Cross-Pollinated Crops

The detailed investigation of plant morphology and anatomy and how these features change in relation to the plant's habitat and/or in response to its environment led to tremendous advances in knowledge about the natural world and unveiled many mysteries. In this series, German botanist Camerarius (1665–1721) discovered sex in plants,[1] identified various parts of the flower (see figure 4.1), and classified plants into seven categories based on sex (flower structure).

1. Artificial pollination was in use since ancient times: Stone carvings from ancient Assyria (2400–612 BCE) clearly depict the artificial pollination of date palms (*Phoenix dactylifera*) and suggest that the knowledge of different sexes of date palms and the need for sexual reproduction did exist. However, this knowledge was not extended to other plants for deliberate hybridization and crop improvement. This phenomenon was also unknown to Europeans. Camareus made the first intellectual attempt to understand the structure of flowers and extended this knowledge to all plants

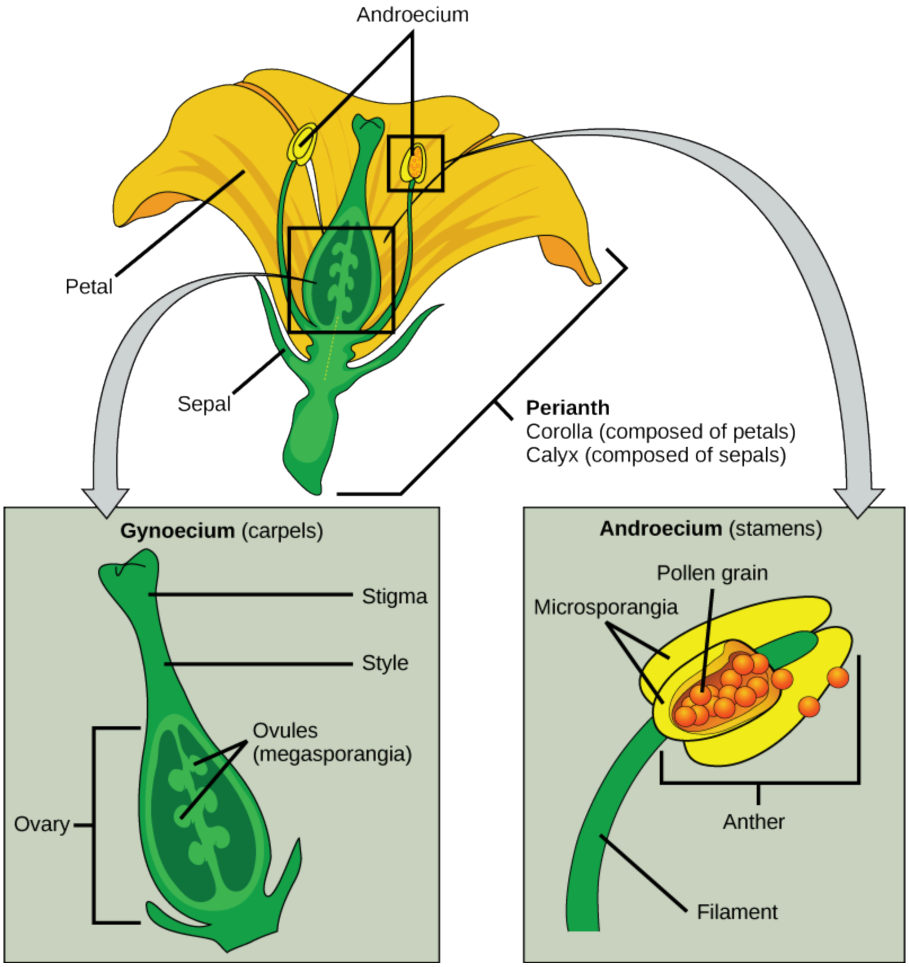

Fig 4.1 A flower is the reproductive organ of the angiosperms (flowering plants). A typical flower has four main parts—or whorls—known as the calyx, corolla, androecium, and gynoecium. The function of a flower is to produce gametes (egg cells and sperm cells), mediate the union of male and female gametes (pollination) thus forming zygotes (fertilization) with new genetic combinations and site of seed set. "Image of flower" by OpenStax CNX is licensed under CC BY 4.0.

In the seventeenth century, it became common knowledge in Europe that seeds are the product of sexual union and flowers contain sexual organs.[2] If we look around carefully, we can easily spot the difference in the structure of flowers and identify the following seven types of sexes in flowering plants:

1. *Perfect/Hermaphrodite*. These flowers contain all four floral organs (sepals, petals, stamens, and carpels). Examples are various flowers of the Brassicaceae family (i.e., mustard, radish, broccoli, etc.).

2. Many plants reproduce only asexually and do not produce seeds and flowers (e.g., money plant and duckweed). In addition, some flowering plants can reproduce asexually—including onion, potato, and gladiolus—as well as many trees that are propagated by using cuttings. The plants generated from asexual reproduction are genetically identical to their siblings and parent plant.

2. *Monoecious*. These plants bear both male and female reproductive organs. *Monoecious* means "one home." In cucumber, pumpkin, and gourd, separate male and female flowers are distributed randomly, whereas, in maize, the male flowers (tassel) hang on the top, and the female flowers are on the branch, which can be identified by their silk.
3. *Dioecious*. In some species, separate male and female plants are present (e.g., dates, papaya, and *Cannabis*).
   a. *Androecious*. These plants contain only male flowers.
   b. *Gynoecious*. These plants contain only female flowers.
4. *Andromonoecious*. These plants have male and perfect flowers (e.g., saffron).
5. *Gynomonoecious*. These plants have female and perfect flowers.
6. *Trimonoecious*. These plants have male, female, and perfect flowers (e.g., Datura).

Camerarius stated that pollen is required to reach the stigma to form fruit and seeds; this process is called pollination. Self-pollination (selfing) refers to the process when the pollen from the anther is transferred on the stigma of the same flower or another flower on the same plant. Cross-pollination (outcrossing) occurs when pollen from one plant is deposited on the flower (stigma) of a different plant of the same species. The structure of flowers determines the mode of pollination. Often, one can tell just by looking at a flower whether it self-pollinates or cross-pollinates. The self-pollinating flowers are small and monocolored; are unscented; have anthers close to stigma; and lack nectar guides. In these types of flowers, pollination and fertilization often occur in an unopened flower bud (wheat, barley, peanut), and resulting offspring are uniform. Typically, manual crossing is needed to produce hybrids.

In the wild, most flowers promote outcrossing, which supports the continuous mixing of gametes and new combinations of traits. Many species of animals (e.g., bees, butterflies, birds, and mammals) serve as pollinators; however, wind and water can also carry pollen from one plant to another. The outbreeders have many large, scented, bright-colored flowers that have nectaries present and stigmatic areas well defined and away from the anthers. We find extraordinary structural adaptations in flowers to attract a specific pollinator, and the shape and form of pollen are adapted to their mode of pollination (e.g., wind, water, insects, and mammals). For example, insect-pollinated species have sticky, barbed pollen grains, and wind-pollinated species have light, small, and smooth-surfaced pollens. The cross-pollination increases genetic variability and results in strong evolutionary potential for a species, allowing for adaptations to changing environmental and climatic conditions. However, it can be disadvantageous in certain circumstances; for example, cross-pollination can destroy well-adapted genotypes and relies on vectors for effective pollination and seed set.

Table 4.1. Examples of self- and cross-pollinated crops.

Self-pollinated crops	Cross-pollinated crops	Cross/ self-pollinated crops
Rice	Alfalfa	Cotton
Wheat	Cassava	Oilseed Rape
Barley	Corn	Tomato
Millet	Pearl Millet	Brassicas
Oats	Rye	Potato
Flax	Safflower	
Legumes (cowpea, beans, chickpea, lentil, mung bean, etc.)	Sugar Beet	
Tobacco	Sugar Cane	
Potato	Sunflower	
Tomato	Carrot	
Sesame	Cucumber family (cucumber, melons, pumpkin, squash, etc.)	
Jute		

4.2 The Classification of Plants

From the 1750s to the 1760s, the Swedish government sponsored a number of expeditions under the supervision of Carolus von Linné (Linnaeus), a professor of medicine and botany at Uppsala University (see figure 4.2). His team collected thousands of fauna and flora samples, and after a comprehensive study, Linnaeus proposed the binomial system of naming plants and animals (see figure 4.3).

Fig 4.2 Portrait of Linnaeus (1707-1778). "Carl von Linné" by Alexander Roslin is in the public domain.

The smallest unit in the Linnaeus system[3] of classification of organisms is species. He proposed that the males and females of one species can give birth to a healthy progeny, but in a different species, they may not. He then organized the species that are closest in their structure under one genus and many genera having similar characteristics into a family. Then based on further similarities, many families were grouped into an *order*, several orders were grouped into a class, and several classes were grouped into a *phylum*. Finally, all the plant phyla were grouped into the plant kingdom, and all the animal phyla were grouped into the animal kingdom (see figure 4.3). Linnaeus proposed two Latin names for the scientific nomenclature of organisms, of which the first name indicates genus and the second indicates the species. Thus the scientific name of a human is *Homo sapiens*, and the rice plant is *Oryza sativa*. In this system, the genus part of the name comes first and is

3. The original publications of Carolus von Linné (Linnaeus) are available at the Biodiversity Heritage Library website: https://www.biodiversitylibrary.org/browse/collection/37.

always capitalized; it is followed by the species name, which is not capitalized. Both names are italicized. Later, Linnaeus's binomial method was also used for naming and classifying bacteria, fungi, and other microscopic organisms.

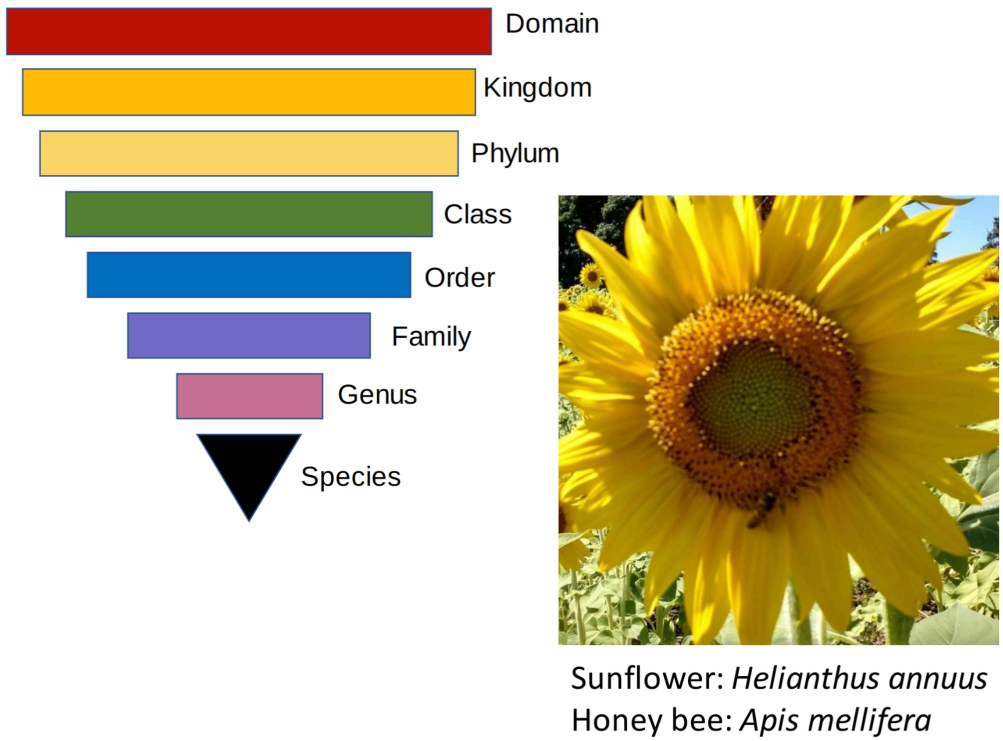

Fig 4.3 Binomial nomenclature proposed by Carl Linnaeus. "Binomial nomenclature" by Sushma Naithani is licensed under CC BY 4.0.

Linnaeus laid the foundation of taxonomy, which aims to study biological diversity and provides guidelines for classification, description, identification, and naming of living organisms. Classification is the grouping of organisms based on their shared characteristics (anatomy, structure, morphology, reproductive behavior, etc.).[4] In general, organisms that share similar features are closely related and are placed in a group. Thus the binomial system also provides an insight into the evolutionary history (phylogeny) of organisms. Just as Mendeleev's periodic table of elements helps in understanding the atomic structure of various elements, the basic understanding of the structure and relationship of organisms is derived from the classification schema proposed by Linnaeus. Historically, the binomial

4. The schema proposed by Linnaeus served as a primer for the classification of plants and animals as well as provided a framework for comparative studies for the past 300 years. However, with the advancement of gene and genome sequencing, this schema is now being modified/updated. You can find the latest information on the Tree of Life web project at http://tolweb.org/tree.

method of Linnaeus was the first major theoretical understanding in the field of biology. Linnaeus became Europe's greatest scientist in his lifetime.

4.3 Deliberate Hybridizations

Understanding the flower structure and the pollination process made artificial pollination possible and paved the path for crop improvement by deliberate hybridization. It became possible to develop new and improved varieties by crossing two varieties with desirable traits. However, in the absence of a theoretical understanding of laws that govern heredity, the selection of desirable hybrids was almost impossible and a work of trial and error. Thomas Fairchild (1667–1729), a nursery owner in England, was likely the first breeder who succeeded in creating a hybrid pink by crossing carnation and sweet William in 1717. His hybrid is also known as Fairchild's mule. Fairchild gave a lecture on the crossing in the meeting of the Royal Society that was subsequently published in its journal, *Philosophical Transactions* as "Some New Experiments Relating to the Different and Sometimes Contrary Motion of the Sap in Plants and Trees." He is also credited for writing the first book on gardening.

After forty years of Fairchild's research, Linnaeus carried out extensive crossing experiments. He described flowers as "marriage beds" of plants and considered the flower structure as one of the important criteria for developing classification schema for plants. In 1757, Linnaeus crossed two species of *Tragopogon* and identified many plants that were products of spontaneous hybridization. Because of Linnaeus, European scientists, naturalists, teachers, and amateur gardeners got interested in crossing experiments, and the information about flower structure became public knowledge. In the following sections, we describe a brief review of some of the historic crossing experiments and the success of early plant breeders.

4.3.1 The Story of the Annanasa Strawberry

In 1711, Louis XIV sent Captain Amédée-François Frézier (1682–1773) on an espionage mission to Chile and Peru, as France didn't deem it appropriate to show overt interest in Spain's colonies. Captain Frézier, an engineer by profession, traveled to South America and gathered information on fortresses, armies, supply routes, governors, and Indians (indigenous people). In Chile, he noticed a very large strawberry (see figure 4.4), almost quadruple the size compared to the alpine or woodland strawberry (*Fragaria vesca*) found in Europe or the Virginia strawberry (*Fragaria virginiana*) in North America that was brought to France by Jack Cartier (known for discovering the St. Lawrence River in the US) in the seventeenth century. Both *F. vesca* and *F. virginiana* were wild varieties and have not been domesticated. People often used to collect their fruits from the forest during the season. However, from the fourteenth century onward, wild strawberry plants were introduced as ornamental plants in European churches and in royal gardens.

Interestingly, the Chilean strawberry (*Fragaria chiloensis*) spotted by Frézier was the only species of strawberry that humans had domesticated. The indigenous people of Chile were cultivating strawberries for more than 1,000 years. In 1550–51, when Spanish general Pizarro took over Chile, his army included strawberries in the list of plunders. Later, the Spanish expanded the cultivation of strawberries in Chile, and the royalty and elites of Spain enjoyed this delicacy. However, other Europeans remained ignorant of the existence of *F. chiloensis* (see figure 4.4) for almost 150 years. In 1714, Frézier brought five stolen plants of *F. chiloensis* (also known as the beach strawberry) into France. On his return voyage, Frézier faced many challenges (the inspection and search by Spanish customs officers, a pirate attack, and a shortage of drinking water) but was successful in keeping the strawberry plants alive. In the history of the modern strawberry, this journey of the Chilean strawberry was the most important event. Surprisingly, for the next fifty years, these strawberry plants never produced a single fruit in the French royal garden despite plenty of flowering. Bernard de Jussieu, head of the king's garden, preserved and maintained several specimens of *F. chiloensis* and gifted its plantlets to other gardeners and his acquaintances. Finally, in 1766, Antoine Nicholas Duchesne explained that Frézier had selected fruit-bearing female plants in Chile, and all five plants that reached France were female. These female plants needed pollen to form fruits.

Fig 4.4 An illustration of Fragaria chiloensis (beach strawberry) by Amédée François Frézier (published in 'A voyage to the South-sea, and along the coasts of Chili and Peru, in the years 1712, 1713, and 1714'). "Planche XI" by Jean-Baptiste Scotin is in the public domain.

Duchesne was appointed the gardener of the royal gardens of France in 1760, and he worked under the supervision of Antoine de Jussieu. In the garden at Versailles, Duchesne noticed that the Chilean strawberry planted in between *F. virginiana* and the musky strawberry (*Fragaria moschata*) had produced a large fruit due to accidental cross-pollination. He then pollinated the female flowers of Chilean strawberries with pollens of the musky strawberry, which produced a huge and succulent strawberry fruit with a pineapple aroma. On July 6, 1764, Duchesne presented a bowl full of this large fruit to King Louis XVI. Madeleine Françoise Basseporte, the famous artist, painted strawberries for the royal botanic library, and Duchesne was given a grant to pursue his research on strawberries.

Bernard de Jussieu, the mentor of Nicholas Duchesne, was familiar with Linnaeus's work and had instructed Duchesne about binomial nomenclature and the role of sexes in plants. Duchesne carefully observed the various strawberry plants present in the French royal garden and learned to differentiate between their male and female flowers. After this, he started experimenting with artificial pollination. First, he pollinated Chilean strawberries with the pollen from European woodland strawberry plants, but this did not result in fruit formation, but the pollination of the Chilean strawberry with pollens from *F. moschata* or *F. virginiana* did. Today we know that these compatibilities were related to the ploidy level of different strawberry species. *F. vesca* is diploid (two sets of chromosomes), and both *F. virginiana* and *F. chiloensis* are octoploids (eight sets of chromosomes).xiii *F. virginiana* produces small, highly aromatic fruits in abundance, and *F. chiloensis* bears big fruits (the size of walnuts). Duchesne crossed *F. virginiana* with *F. chiloensis* to make the hybrid *Fragaria x ananassa* (ananassa strawberry; x indicates that the strawberry is of hybrid origin), which produces large and flavorful fruits with pineapple (ananassa) aroma (see figure 4.5). The widespread cultivation of strawberries began with *F. x ananassa*. Therefore, the evolution of the strawberry from a wild to a cultivated plant is relatively recent, and it is a by-product of transatlantic exploration that involved three continents.

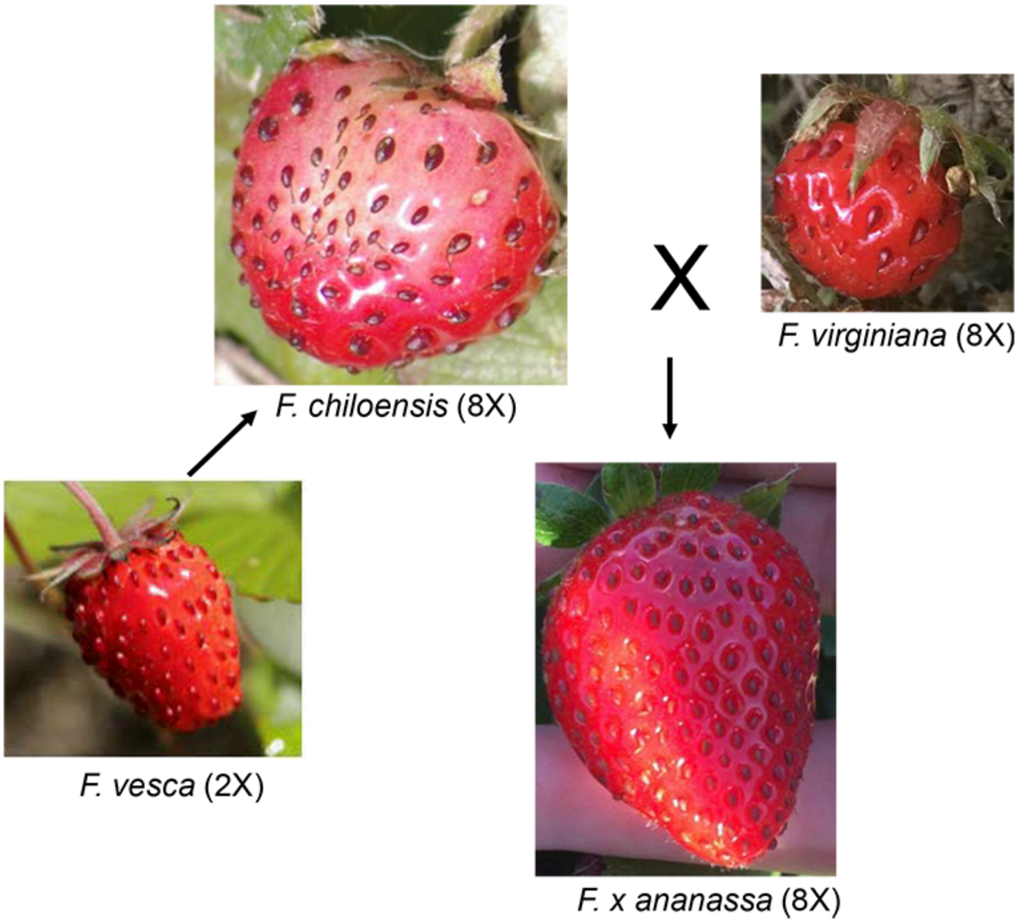

Fig 4.5 Garden strawberry, Fragaria x ananassa is an octoploid hybrid. "Garden Strawberry, Fragaria x ananassa" is a derivative of "Wild Strawberry – Fragaria vesca" by Björn S…, used under CC BY-SA 2.0, "Beach Strawberry Fragaria chiloensis" by Marisa Rafter, used under CC BY-NC 4.0, "Virginia Strawberry Fragaria virginiana" by spacecowboy, used under CC BY 4.0, and "Garden Strawberry Fragaria x ananassa" by rishnessjn, used under CC BY-NC 4.0. "Garden Strawberry, Fragaria x ananassa" is licensed under CC BY-SA 4.0 by Sushma Naithani.

Duchesne also collected strawberry plants from all over Europe, recorded the relevant information, and wrote a report on the natural history of the strawberry. He also interviewed Captain Frézier fifty years later. There are species of strawberry native to regions all around the world, and after Duchesne, many other scientists collected thousands of varieties of strawberries. These varieties of strawberries have different ploidy, fragrance, flavor, and other physical attributes and are adapted to a wide variety of climates. Today, the largest germplasm collection of strawberries is in Corvallis, Oregon.

4.3.2 The Monks of the Austro-Hungarian Empire

Interestingly, the province of Moravia of the Austro-Hungarian Empire became one of the early centers of plant breeding in Europe.[5] The educated elites of Moravia held liberal beliefs in comparison to the remaining Catholic Europe and were invested in improving both education and local agriculture. Many clergymen got inspired by Linnaeus and quickly grasped the utility of deliberate hybridization in improving the local economy. Christian Andre (1763–1831), a social reformer, was one of the pioneers who advocated for plant and animal breeding in Moravia. He founded the Moravian Sheep Breeders Association and the Pomological and Oenological Society of Brno. He collaborated with many of his contemporary horticulturists and breeders, including Jan Sedlacek and G. C. L. Hempel. Abbot F. C. Knapp (1792–1867) of the monastery of Brno was another early influence in Moravia's breeders and took a keen interest in improving fruit trees and grapevine. He had planted over a hundred varieties of grapes in the monastery's nursery and encouraged local farmers to plant fruit trees. In 1840, Knapp organized a large gathering of local farmers and forest officials and explained to them how to make hybrids.

The breeding efforts in Kuninn were also noteworthy. In 1796, Father J. Schreiber began teaching crossing as a part of the natural science curriculum in Kuninn. This school was founded by the countess Maria Walpurga Truchsess-Zeil and provided education to village children for free.

It is said that the greatest concern of the bishop of Brno around 1854 was that his subordinate clergy were paying more attention to natural science, crossing, and nursery than to religious work. It is believed that Brno's monastery narrowly escaped being closed. Some decades later, one of those priests, Gregor Johann Mendel, discovered the fundamental principles of genetics.

However, breeding in those early stages was more of an art than a standardized scientific technique. The common understanding of heredity was similar to the mixing of two colors: the mother's and father's traits mix and reach their offspring. It was with this understanding that the breeders chose the desired characteristics from the cross between two varieties. The task was as difficult as finding a needle in a haystack, and using trial and error, the breeders sometimes found the plants and animals they wanted. Only fewer than a dozen successful hybrids were made during that era, and fewer still had any significant traits. The ananassa strawberry has special significance in hybrid plants made in this era, and equally impressive is its story.

5. Until World War I, Austria, the Czech Republic, Slovakia, Croatia, and Hungry were part of the Austro-Hungarian Empire ruled by the House of Habsburg. Moravia is now in the Czech Republic.

4.3.3 The Professors and Other Professional Breeders

Apart from monks and gardeners, many professors, teachers, and other professionals pursued crossings and plant breeding experiments out of their intellectual curiosity. Particularly in Germany, Joseph Gottlieb Kölreuter, Christian Konrad Sprengel, and Karl Friedrich von Gartner have contributed significantly to the current knowledge of pollination, hybridization, and heredity. Kölreuter (1733–1806), a professor of natural history at the University of Karlsruhe, Germany, carried out more than 500 artificial hybridization experiments involving 138 species. He made important observations about the role of insects as pollinators and examined the shape, color, and size of pollen grains from ~1,000 different plant species. He noted that successful hybridization occurs only between closely related species, and in offspring, some parental traits show up more often than others. Although he did not dwell deep enough in quantifying the ratio of various inherited traits, his experimental results foreshadowed Gregor Johann Mendel's work.

Sprengel (1750–1816) followed Kölreuter's work on hybridization and made the additional observation that normal sexual reproduction in plants leads to the mixing of traits from both male and female parents and thus creates new combinations in the offspring. This was a big conceptual leap toward understanding the source of diversity among the individual of the same species and an acknowledgment that living species are constantly changing rather than being fixed.

Gartner (1772–1850) was another contemporary of Sprengel, who pursued hybridization experiments as an amateur breeder. He was the physician son of famous botanist Joseph Gartner, who was familiar with the work of both Kölreuter and Sprengel. Over twenty-five years, he carried out ~10,000 individual crossings on ~700 plants (belonging to over 80 genera) and created 350 different hybrids. He also noticed that many hybrids bore larger flowers and fruits than their parents and appeared to be from a different species from their parents. Over the years, this phenomenon was noticed by many and was later named *Hybrid vigor*.

In England, botanist Thomas Andrew Knights (1759–1838) bred fruit trees and successfully made several hybrids, including those of pears and apples. He successfully crossed apple and Siberian crab apple and produced a hybrid that is known for making good quality cider. Like Sprengel, he observed the differences between plants of the same species and the mutability of various characteristics that constantly emerge and then disappear. In addition, Knights published over a hundred research papers on various aspects of plant physiology and founded the Royal Horticulture Society. He was also a member of the Royal Society and, in 1806, received the prestigious Copley Medal. Thomas Knight also conducted extensive crossing experiments in peas and found many of the same results as Mendel.

However, he lacked the mathematical framework to analyze his results and could not decipher laws governing heredity.

Overall, by the early decades of the nineteenth century, numerous experiments of crossing drew the attention of experts and amateur gardeners on the variations among members of the same species and the potential of deliberate hybridization in improving crops and animal stock.

4.3.4 Darwin's Insights from Crossing Experiments

Charles Darwin (1809–82) conducted extensive crossings in plants to understand the implications of self-pollination and outcrossing in plants and made two important observations: (1) In nature, the floral structure of most plants favor cross-pollination, and several structural and genetic barriers prevent selfing. (2) As a result of cross-pollination, new combinations of traits continue to emerge by mixing parental characteristics, which provides the raw material for natural selection. Since plants lack mobility, the traits promoting outcrossing were enriched as a result of natural selection to ensure the continued survival of the species. Darwin also reviewed the work of his predecessors and contemporary botanists, including Kölreuter, Sprengel, Gartner, and Knights. He highlighted the differences between crops and wild plants and identified the various domestication traits in both crop plants and domesticated animals. He made it clear that the direction of artificial selection moved in the opposite direction of natural selection, which led to the development of man-made crops and domestic animals.

Darwin's most famous treatise, On the Origin of Species (published in 1859), began with a chapter entitled "*Variation under Domestication*," which encapsulated his decade-long comparative study of domesticated plants and animals with their wild ancestors, their origins, and artificial selection by humans—all of which provides a basis for his theory of the bioevolution of living organisms using natural selection. In 1868, Darwin independently published *The Variation of Animals and Plants under Domestication* to cover a detailed description of the improvement in crop plants and livestock through artificial selection, the beneficial effects of outcrossing, and the harmful effects of inbreeding.

4.4 Star Breeders of the Early Twentieth Century

4.4.1 Luther Burbank: A Plant Wizard

Overall, the concept of deliberate hybridization and selection for a desired combination of traits in offspring gained popularity during the nineteenth century and continued until the first two decades of the twentieth century. The most successful and well-known breeder of this tradition was American gardener Luther Burbank (1849–1926). Luther Burbank (see figure 4.6) was born in 1849 in the city of Lancaster, Massachusetts. He received only an elementary education before starting work on a market garden. When he was twenty-one, his father died, and with his share of the inheritance, he purchased a seventeen-acre farm in Lunenburg. On this farm, he identified a natural genetic variant of potato that was large with russet-colored skin, famously known as the russet Burbank potato. This potato variety soon became popular and is used for making french fries. Burbank sold the rights to the russet potato for $150 and bought a four-acre farm in Santa Rosa, California. A few years later, he purchased an eighteen-acre farm in the nearby town. In both these farms, he laid the necessary infrastructure for greenhouses, nursery beds, and so on so that he can carry out crossings and selection work.

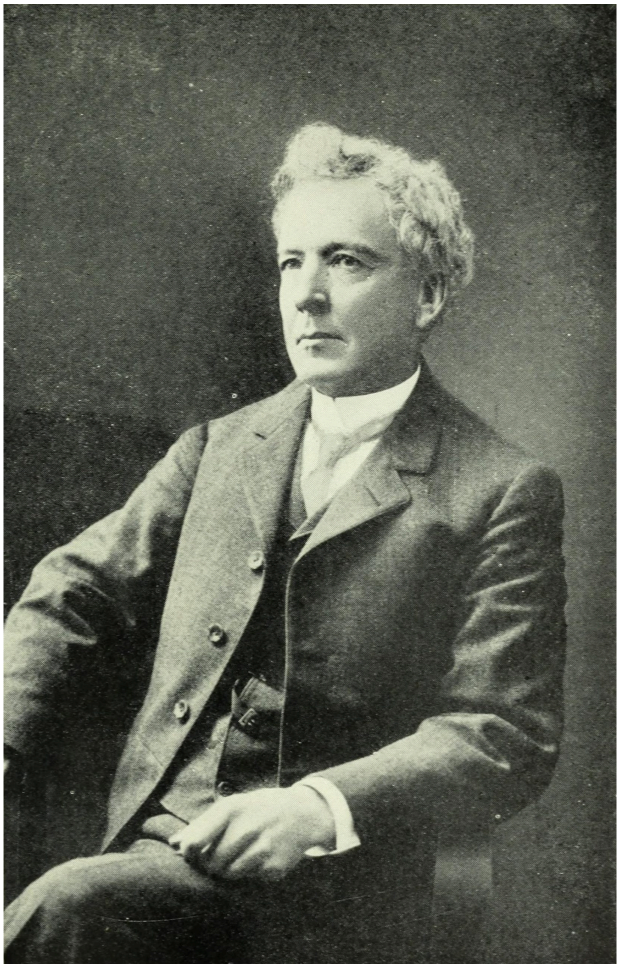

Fig 4.6 "Luther Burbank in 1915" by Gabriel Moulin is in the public domain.

Although Burbank's formal education was only up to primary school, he had learned about horticulture and farming from experience and an interest in the field. His breeding experiments were driven more by an artist's instinct rather than the scientific understanding of the laws of heredity. He read Charles Darwin's article about the changes in plants and animals as a result of artificial selection during the process of domestication. This was the article that sparked his interest in plant breeding. He understood that crossings could bring together unconnected gene pools and that finding the desired combinations of traits in the progeny is a rare event and thus requires extensive selection. From his crossing experiments, he selected the best, discarded the rest, and did not keep systematic records of crossing results and the parental strains involved. It is said that Luther simultaneously conducted more than 3,000 crossings at a given time, and millions of plants grew on his farms. Burbank perfected grafting, crossings, and hybrid selection. In his fifty-five-year career, he developed more than 800 new varieties of plants derived from 121 genera: 250 new varieties of fruit, including 113 plums and prunes, 10 strawberries, 10 apples, the russet potato; 34 spineless cacti; about 50 varieties of lilies; and the Shasta daisy.

He inevitably sold his new varieties to other growers or nurseries for further commercial production. Andrew Carnegie showed a keen interest in Burbank's work. And the Dale Carnegie Institute provided financial support to Burbank from 1905 to 1911. In 1893, Burbank published a catalog of his best plant varietals, *New Creation in Fruits and Flowers*, and also wrote other books on breeding experiments. It was the result of Burbank's efforts that, in 1930, America began to patent advanced varieties of plants.

Because Burbank worked from his own experience and did not keep accurate records, it was not possible for other scientists to review and repeat his work. Famous plant breeders and geneticists, such as George Harrison Shull, Hugo de Vries, Liberty Hyde Bailey, and Nikolai Ivanovich Vavilov, visited him to learn his methods. Shull and de Vries invested time to understand and evaluate Burbank's work and ultimately became frustrated with his random approach and lack of proper record keeping. However, Burbank became a celebrity in his lifetime and was referred to as the "high priest of horticulture" and the "plant wizard."

Burbank died on April 11, 1926, in Santa Rosa from a heart attack. Nikolai Vavilov wrote a lengthy tribute in remembrance of Burbank. In 1940, a US postage stamp was released in his honor, and in 1991, he was elected to the American Society for Horticultural Science Hall of Fame. The Luther Burbank Home and Gardens, in downtown Santa Rosa, was designated a National Historic Landmark in 2003.

4.4.2 "Crank Gardener" Ivan Vladimirovich Michurin

Ivan Vladimirovich Michurin (1855–1935), a breeder in the Soviet Union, was a contemporary of Luther Burbank, but while Burbank became a celebrity breeder in his youth, Michurin remained hidden from the world until he reached old age. Michurin (see figure 4.7) lived on a rental farm in a small town named Kozlov near Saratov. Michurin was discovered by chance by Nikolai Vavilov. In 1920, Vavilov attended a conference in Saratov. After lunch, a junior scientist from the conference took the delegates for a walk in Michurin's garden. The first meeting between young Vavilov and the sixty-five-year-old Michurin lasted several hours. Vavilov was deeply impressed by Michurin's work but was stunned by the financial condition of this breeder, who was reclusive, paid all his attention to plants, and was considered "crazy" by people in the community.

Fig 4.7 Ivan Vladimirovich Michurin, circa 1934. "Michurin in garden 1934" by Ivan Vladimirovich Michurin is in the public domain.

Like Burbank, Michurin had little formal education. His mother had died when he was a child, and his father had gone mad as Michurin reached his teens. At the age of twenty, he rented a small piece of land and started planting fruit trees in it. For fifteen years, he earned a living by working as a clerk, a watchmaker, and a telegraph operator, and when he was not working, he would continue to expand his garden. In 1899, he rented thirteen hectares (thirty-two acres) of land in Kozlov with his savings and brought along his plants. Then he spent thirty years grooming the farm. He had the passion of an artist with a keen eye of a clever gardener. He did not socialize with people and seems to be driven constantly by some sense of urgency for his nursery (that was not profitable). His economic condition did not improve, but he became famous as a "crank gardener" among the people. Throughout his life, Michurin's focus was on developing new varieties of fruit trees. He learned crossing, grafting, and plant training through trial and error. He acquired many varieties of apples, pears, peaches, apricots, and grapes from distant provinces of Russia and used grafting techniques to make them flourish in Kozlov. Typical fruit trees could not quickly grow in this wintry area, but Michurin had worked for forty-five years and developed about 350 new breeds of fruit trees that could thrive in extremely cold climates.

Vavilov sent a proposal to the Ministry of Agriculture to have experts review Michurin's breeding efforts, which was accepted. On top of that, the Soviet government rewarded him with 500 rubles, granted him the lease of the rental farm where he had set up those marvelous collections, and made that farm tax-free for his lifetime.

Vavilov's meetings with Michurin revealed new information and important details such as how to create the best hybrid variety, how to select hybrids, and so on. Vavilov succeeded in extracting and distilling the life experiences of a clever gardener and provided scientific explanations for why a particular technique worked or not. Subsequently, the Soviet government awarded Michurin the Order of Lenin and the Order of the Red Banner of Labor for his contribution to the field of agriculture. In 1928, Michurin's farm came to be known as the Genetic Station of Fruit and Berries, and in 1932, his town was renamed Michurinsk in his honor. In 1934, his farm was used for the I. V. Michurin Central Genetic Laboratory. In the last years of life, Michurin became a celebrity breeder in the Soviet Union.

4.5 Summary

Overall, in the nineteenth century, it became public knowledge that living organisms change and are not constant. One source of change in living organisms is sexual reproduction, which allows the mixing of parental traits in the offspring. It also became clear that deliberate hybridization and selection can be used for crop improvement and that many species of plants found in nature were the results of the hybridization of related plant species. Linnaeus himself saw this phenomenon and identified many naturally occurring hybrid plants. Later, many success stories of hybrids emerged, and the hit-and-miss approach of hybrid selection reached its prime in the first decades of the twentieth century with Luther Burbank and Ivan Vladimirovich Michurin. However, simultaneously efforts to understand the laws of heredity began, and a new field of genetics came into existence.

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The Early History of Genetics

> No-one can say why the same peculiarity in different individuals…is sometimes inherited and sometimes not so: why the child often reverts in certain characters to its grandfather, or other much more remote ancestor; why a peculiarity is often transmitted from one sex to both sexes, or to one sex alone, more commonly but not exclusively to the like sex.
>
> —Charles Darwin, *On the Origin of Species*

Our ancestors started agriculture with a certain sense that traits are inherited from parents to progeny. Centuries of breeding domestic animals and plants showed that useful traits could be accentuated by controlled mating, and as we have discussed in chapter 2, domestication and artificial selection gave rise to most modern crops. However, there was no rational way to predict the outcome of a cross between two parents or understanding how and why certain traits show up while others remain hidden (see figure 5.1). Until the nineteenth century, the prevailing theory was the *blending inheritance*, which was similar to the mixing of two different color paints: progeny were expected to have traits that were a blend of those of its two parents.

Fig 5.1 "Un Nouveau Nez," ("A New Nose"), a caricature by Honore Daumier, 1833. [“Un nouveau nez”]() by Honore Daumier is in the public domain.

Darwin was puzzled about the mechanism of heredity and how the substance that carries parental traits into offspring could possess two seemingly contradictory qualities: its flexibility to give rise to variations and the stability required to maintain the species. He proposed the pangenesis theory to explain the mechanism of heredity. This theory suggests that an organism continually produces a specific type of small organic particle called a gemmule that accumulates in the gonads and then is transmitted to the gametes. When gametes form embryos after fertilization, their gemmules from the parents mix like the paint of two colors. Interestingly, pangenesis was in direct contradiction with Darwin's theory of (bio)evolution. If the principles of pangenesis were correct, then the natural variations that spontaneously arise within any species would have been an exception among most individuals. Therefore, as a result of mating between an exceptional variant with "normal" individuals (and mating of its progenies with normal members for generation after generation), the variations would gradually disappear. However, Darwin's extensive research suggested that variations in different birds of the Galápagos Islands were maintained over generations. Eventually, Darwin realized that pangenesis does not explain evolution, and these two hypotheses—(bio)evolution and pangenesis—were contradictory. But he could not solve the riddle.

The greatest challenge to pangenesis came from the German zoologist August Weismann (1834–1914). Weismann experimented with mice to see if cutting off their tails generation after generation would cause any change in their offspring. However, the progeny of those mice had normal tails. He proposed the germplasm theory, which suggests that multicellular organisms consist of two types of cells: (1) germ cells, which are present in the gonads (ovaries and testes) and contain and transmit heritable information from parents to progeny, and (2) somatic cells, which carry out ordinary bodily functions. Thus the gametes (egg cells and sperm cells) produced by the germ cells serve as carriers of heredity information, and other cells of the body do not function as agents of heredity. This hypothesis discredited the ideas of inheritance of acquired characteristics as proposed by Lamarckism and pangenesis. In this way, the distinction between the hardwired inherited traits contained within the germ cells and the soft-wired traits acquired by the somatic cells was established.

However, it remained to be known how much biological contribution the mother and father make to their offspring and what rules govern heredity.

5.1 Gregor Johann Mendel: The Mathematics of Heredity

During Darwin's lifetime, a clergyman in a monastery in Moravia, Gregor Johann Mendel

(1822–84), studied the laws of genetics by crossing pea plants. Moravia, where Mendel (figure 5.2) was born and educated, was the center of plant crossing since the eighteenth century. As discussed in the previous chapter, various pastors took on crossing and hybridization experiments for improving crops and domestic animals. They included crossing and breeding experiments in natural science curricula in the classes they taught at schools. Thus Mendel's curiosity and his experiments aimed at understanding the laws of heredity come as no surprise.

Fig 5.2 Gregor Johann Mendel (1822-1884) was the first person to analyze patterns of inheritance. "Gregor Mendel" is in the public domain.

From 1856 to 1863, Mendel grew pea plants in the five-acre garden of the monastery and conducted about 29,000 crossing experiments. The pea proved to be the ideal plant for investigating heredity. The pea is a selfing plant, but it is also easy to perform artificial pollination on it. It has a short life cycle of two and a half months and can be grown in large numbers with very few resources. Thus it is possible to study several generations of this plant within a short period. Mendel selected seven contrasting characteristics of the pea plant (see figure 5.3) in his experiment: stem length (tall or dwarf), flower color (purple or white), pod shape (inflated or constricted), pod color (green or yellow), seed shape (round or wrinkled), seed color (yellow or green), and flower position (axil or terminal). For many years, Mendel developed purebreds by self-pollination. All the offspring produced by the selfing of purebreds are the same. For example, tall plants give rise to 100 percent tall progeny, and dwarf plants produce 100 percent dwarf progeny.

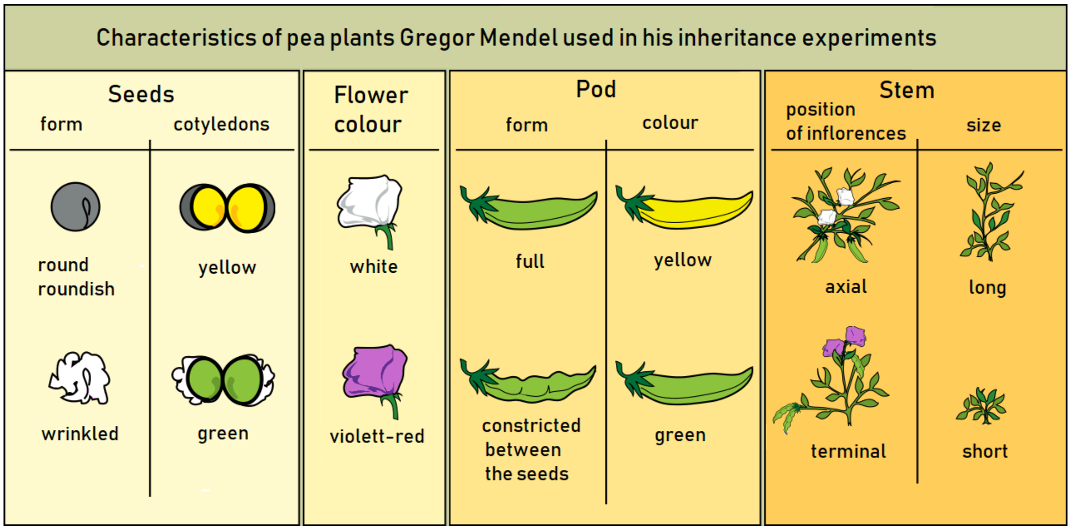

Fig 5.3 The seven characteristics of pea plants selected by Gregor Mendel. ["Gregor Mendel – characteristics of pea plants"](#) by [Mariana Ruiz Villarreal](#) and [Sciencia58](#) is licensed under [CC0 1.0](#).

Subsequently, he used purebreds of peas for generating hybrids and for studying the pattern of inheritance of various characteristics. He observed that the crossing of the purebred purple-flowered plant with the white-flowered plant produced only purple flowers in the hybrid (first hybrid generation, or F1). He repeated these experiments on the seven pairs of pea plants that exhibited contrasting traits and found every time that all the hybrids of the F1 generation showed traits from one parent, while the contrasting trait from the other parent remained hidden. He did not observe the mixing of two contrasting traits. Based on these observations, Mendel proposed the first principle of heredity, known as the law of dominance, postulating that within any (multicellular) organism, at least two factors determine a given trait, of which only the dominant factor appears in the hybrid, and the recessive factor remains hidden or masked by the dominant trait.

In the second step, Mendel crossed F1 hybrids and analyzed their progeny (second hybrid generation, or F2) and found that 75 percent of F2 plants contained purple flowers and 25 percent of F2 plants contained white flowers (see figure 5.4). Thus after skipping the F1 generation, the white flower color reappeared in the F2 generation, but the distribution of dominant (purple) versus recessive (white) traits in their flowers was 3:1 (refer back to figure 5.1). Mendel repeated these experiments on all seven traits and always got a ratio of 3:1 between dominant and recessive traits in F2 progeny.

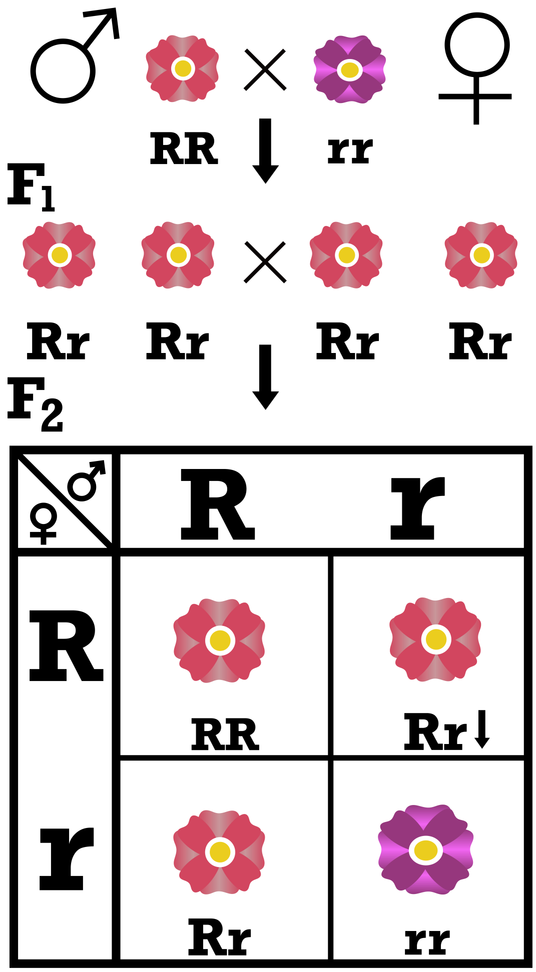

Fig 5.4 The results of monohybrid cross between purple and red flowers. "Results of monohybrid cross" by Sushma Naithani and [OSU OERU](#) is licensed under [CC BY 4.0](#).

For the first time in history, it became known that the contrasting parental traits do not mix like paints of two colors; instead, they are maintained and transmitted as independent entities. During the gamete formation, the two factors separate and are distributed equally in the gametes. The fertilization between egg and sperm cells that both contain the recessive factor gives rise to the progeny containing both recessive factors, and thus the corresponding trait reappears. Mendel suggested the second law of heredity as the following:

1. The individual has two copies of each factor. Each parent contributes one factor of each trait shown in the offspring.
2. Some traits can mask others, but the traits don't blend. The two members of each pair of factors segregate from each other during gamete formation.

Today, these factors are known as the *alleles* of a gene, which behave like alternatives to each other. Most recessive alleles cause/indicate a functional deficiency. If one allele of the pair works properly, then it hides the other's deficiency. If both alleles of a gene are effective/functional or if at least one allele of the pair is functional, then in both cases, we see a dominant trait.

Subsequently, Mendel studied the inheritance of two different traits simultaneously. For example, he crossed homozygous plants producing yellow, smooth peas with plants producing homozygous green, wrinkled peas. As expected, the F1 generation peas were yellow and smooth; only dominant traits showed up. Mendel made crosses between the F1 individuals and found that of the sixteen plants in the F2 generation, nine produced yellow, smooth peas (resembling the dominant ancestor); one produced green, wrinkled peas (resembling the recessive ancestor); three produced smooth, green peas; and three produced yellow, wrinkled peas (see figure 5.5). In the F2 generation, he found a new combination of smooth, green and yellow, wrinkled peas in equal ratio. The overall result suggested that two different traits (such as the color and shape of a pea) are transmitted independently of each other to future generations. Mendel postulated the third law of heredity (a.k.a. the law of independent assortment), suggesting that different traits—like seed shape and seed color—are inherited independently of each other.

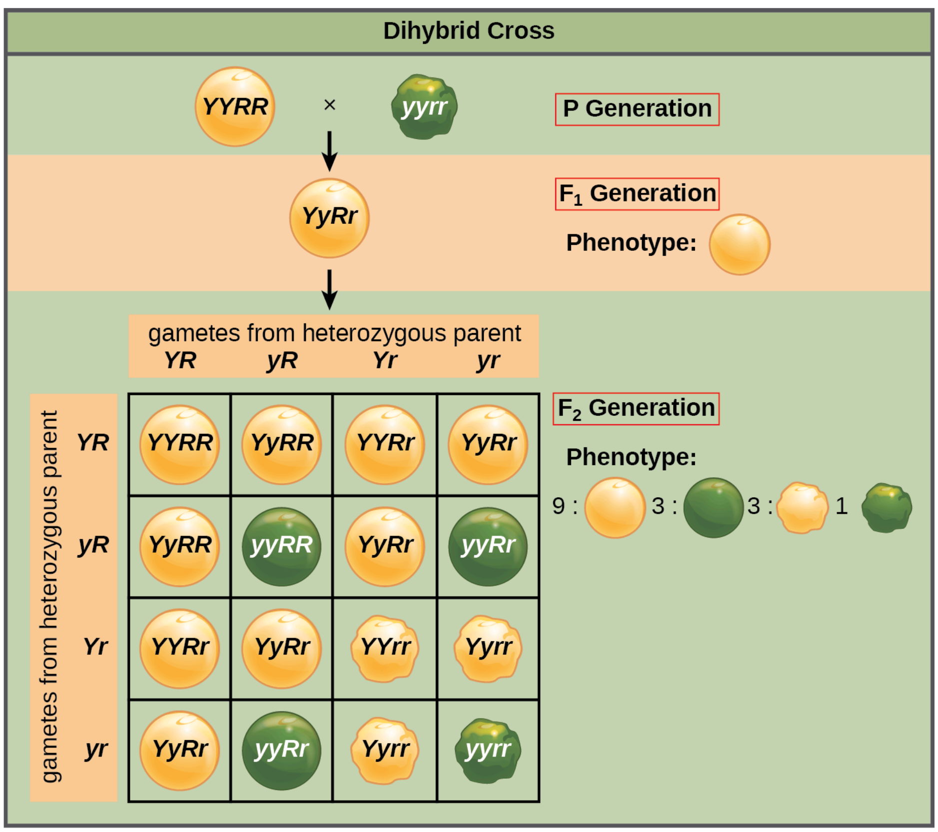

Fig 5.5 The di-hybrid cross of pea plants for seed color and seed shape. "Image of dihybrid cross" by OpenStax CNX is licensed under CC BY 4.0.

Thus Mendel's experiment revealed the role of sexual reproduction in generating variations within the same species. Today, Mendel's three laws are known as the fundamental principles of genetics. Mendel was not aware of the physical and chemical properties of the genetic material, but his discoveries led to the first concrete understanding of how the genetic material behaves.

Understanding the behavior of heredity required a mathematical approach rooted in deduction, the fragmentation of big questions into small workable hypotheses, and a good model system for studying heredity. Mendel, a trained meteorologist, had the ability to look at the data and apply math to it. In contrast, Darwin and most biologists of his time implemented the cataloging and description of the morphology of plants and animals. Today, Mendel is the father of genetics, but during his lifetime, his contributions were not valued by his peers. In later years, Mendel did the monastery's administrative work, and his three principles of genetics were forgotten for thirty-five years.

Mendel's work was no less important than Darwin's. In fact, his work explained Darwin's theory of evolution in concrete terms. Many people now wonder why Mendel's discoveries were ignored, while Darwin became one of the most popular scientists during his lifetime. Perhaps, to some extent, Darwin benefited from his family background. Both his father and grandfather were well-known doctors, and he graduated from the University of Cambridge. He developed his academic network at an early age while working with John Henslow and then got an opportunity to join the HMS *Beagle as a naturalist* (a volunteer who was not paid a salary). In contrast, Mendel was born into a peasant family. After his initial education in the village, he became a monk and pursued further education in the monastery. During his youth, he struggled to become a high school teacher and carried out experiments with pea plants in the garden. He did not get much opportunity to discuss theories with other scientists, as he was not a part of academia; none took cognizance of his work. Also, most of his contemporary scientists were naturalists involved in cataloging and describing plant and animal diversity; they lacked mathematical understanding. Therefore, most academics and scientists ignored Mendel's published papers. We have no way of knowing if Darwin ever knew about Mendel's research work.

5.2 The Rediscovery of Mendel's Laws and the Birth of Genetics

In 1900, Hugo de Vries, Carl Correns, and Erich von Tschermak independently rediscovered Mendel's work. Thus Mendel's three laws of heredity resurfaced after being buried after thirty-five years, but even then, these principles were not easily accepted. The first few who recognized the importance of Mendel's laws include Cambridge University biologist William Bateson. Bateson zealously lectured on the laws of heredity in European and American institutions to popularize Mendel's work and became known as "Mendel's bulldog." Bateson established the first genetics laboratory in Cambridge. Bateson proposed the term *genetics* for a new branch of biology rooted in the Mendelian approach and the study of inheritance and the structure function of genetic material. During this period, Vavilov had joined Bateson's laboratory and thus became the first geneticist in the USSR. Botanist Wilhelm Johannsen proposed the word *gene* for the Mendelian units of heredity (factor) and called two different versions of a gene-defining trait *alleles*, since hybrid plants show only dominant traits and appear similar to purebreds even though their genetic configuration is different. Hence in 1909, Johannsen proposed the terms *genotype* for the genetic configuration and *phenotype* for the manifested trait—that is, its outward appearance. Hugo de Vries proposed the term *mutant* for organisms with rare traits (whose numbers are less than 1 percent in a population or have a defect). In this way, gradually, terminology and vocabulary for genetics increased, and slowly it was established as a subdiscipline of biology.

5.3 Exceptions and Extension of Mendelian Genetics

In the early twentieth century, many scientists repeated Mendel's experiments and began analyzing their crossing experiments using a framework provided by Mendelian genetics. Often, the laws of heredity successfully explained their results, but less frequently, exceptions were encountered, which added new dimensions to and knowledge of heredity. Here we discuss several of such examples and how they contributed to furthering knowledge in the field.

5.3.1 Partial or Incomplete Dominance and Codominance

One exception to Mendel's first law is partial dominance. When scientists crossed the white- and red-flower varieties of the "four o'clock," they found pink flowers in the F1 hybrids. Thus in this case, the presence of a dominant allele did not completely mask the recessive allele, and the phenotype of the heterozygous F1 hybrid differs from its homozygous dominant parent. Furthermore, the selfed progeny of heterozygous F1 hybrid segregated in a ratio of 1 red: 1 white: 2 pink. However, the pink flower in the hybrid is not a result of the mixing of red and white but is due to the diminished quantity of red pigment. In fact, both allele coding for red and white are transmitted from one generation to another as discrete factors, but the red flowers are produced by plants where both factors are functional. When only one of the two works, only half the pigment is formed, and the pink color is seen.

Another exception is codominance, where both alleles (factors) determining a trait are functional. For example, in people with AB blood group, both A and B alleles are equally active and produce A and B antigens. A third allele, i, is also found in some people that do not produce any antigen due to mutations. Therefore, people with AA or Ai have blood group A; those with BB or Bi have blood group B, and others with ii have blood group O (no antigen).

Mendel proposed the basic rules of genetics based on the assumption that there are two alleles (dimorphic) of any gene. While it stands true for an individual, multiple alleles for the same trait exist within any population of a plant or animal. Many genes have several common alleles (they are polymorphic), which may show a complicated pattern of dominance and can be placed in a hierarchy. The interactions of these various alleles cannot be understood without concerted efforts of crossing and establishing a dominance series. For example, if we look carefully at the whole lentil grain, there are many patterns of small or big dots on the light-colored surface. If a lentil with a clear surface is crossed with one with a dotted surface, then the F1 hybrid shows a dotted trait. However, a crossing of the dotted lentil with spotted lentil plants produces an F1 hybrid showing a spotted pattern (here the dotted trait behaves recessively). Based on the results from such crossings, the dominance hierarchy of different alleles can be prepared, and then the results can be explained using Mendel's laws. But without understanding this hierarchy, the results cannot be explained. It is noteworthy to mention that in such cases, the dominance relations affect only the correspondence between genotype and phenotype; however, the alleles still segregate and unite randomly and follow the Mendelian pattern. The difference lies in the complex relationship between genotype and phenotype.

5.3.2 Lethal Mutations

There are many essential genes found in a living organism, known as the *housekeeping genes*, that are required for that organism's survival. Some of these genes are active in all cells of an organism, whereas others act specifically in a particular type of cell, tissue, or organ. Mutations in housekeeping genes can be lethal. Sometimes heterozygotes exhibit a phenotype or a disease, which leads to recessive homozygotes dying (and thus a progeny class is eliminated). In these cases, we do not find the segregation of F2 progeny according to Mendel's laws.

In contrast, the gametes (egg or sperm cells) contain only one allele, and thus the gametes carrying a nonfunctional allele of housekeeping genes are destroyed. As a result, only the gametes carrying the functional alleles are transmitted to the next generation. In such cases, the results of the crossing do not fit into the Mendelian hypothesis, and only the functioning allele is seen in the progeny. However, close observation can reveal decreased pollination and lower seed formation. In other instances, after successful pollination and fertilization, the embryo does not develop because both alleles of a housekeeping gene required for embryonic development are mutants. Similarly, some plants die after seed germination due to a lack of functional alleles (e.g., albino mutants that lack photosynthesis capacity). There are also instances where both alleles are necessary for the normal development of an organism. For instance, in healthy individuals, both alleles of the fibroblast growth receptor gene function, but people with a mutant allele suffer from the most common form of dwarfism (known as achondroplasia, with a normal-length body but shortened limbs).

5.3.3 Pleiotropy

Sometimes a single gene affects several unrelated phenotypic traits in the same organism, and this phenomenon is known as pleiotropy. For example, specific mutations in the hemoglobin B gene cause changes in the shape of red blood cells (from round to sickle shaped) that causes sickle cell anemia (termed this to differentiate it from dietary deficiency and other causes of anemia). Due to their shape, these cells obstruct the smooth flow of blood and have a short life compared to normal cells. As a result, people carrying the mutant gene become anemic. In addition to anemia, an enlarged spleen, muscle and heart pains, a weak immune system, resistance to malaria, and early death are associated with the mutations in the hemoglobin B gene.

5.3.4 Penetrance or Expressivity in Phenotype

Researchers also noticed that certain traits are expressed fully only under a certain environment. Thus two new terms were added:

1. *Penetrance* is whether a trait is expressed or not.
2. *Expressivity* is the degree to which a trait is expressed (fully or partially).

We see many such examples in our day-to-day lives. For instance, genetically identical hydrangeas growing in soils of different acidity (different environments) produce flowers of a different color. Many houseplants change color if their exposure to light changes or the temperature changes. We also find different pigmentation in cats, dogs, and other animals, where the colder body parts are darker while the warm body parts are lighter.

5.3.5 Epistasis

In many instances, a single phenotype is controlled by the interaction of two or more genes. This phenomenon is known as epistasis. The epistatic genes may code for proteins involved in different steps of a biosynthetic pathway or may have an additive function. In such cases, we see alterations in F2 segregation ratios. Examples of such interactions can explain the various sizes and shapes of squashes, the different skin colors of onions, or the diversity in flower colors of many plants.

Unlike animals, plants contain many duplicate genes, and some of these have redundant and/or additive functions. Thus when both alleles of a gene are mutated and are nonfunctional, we see no phenotype due to the presence of a duplicated gene that functions properly. In such cases, a phenotype is only visible if both genes (all four alleles) become nonfunctional. In contrast, the opposite is also true: sometimes, a phenotype is only visible when two or more duplicate genes are simultaneously functional in the organism. For example, for zucchini, two genes (four alleles in total) determine the fruit size. If both genes work or at least one allele of both works, then a very small disk-shaped fruit is produced. If only one gene (or one of its alleles) is functional, then a big, rounded fruit is produced. If both genes (all four alleles) become nonfunctional, then a long fruit is produced. Here crossing between the long and flat breeds of zucchini will give rise to an F1 hybrid bearing round fruits. And the selfing of F1 progeny will result in the segregation of this trait in F2 progeny as 9 disk shaped (A_B_):6 round (A_bb or aaB_):and 1 long (aabb).

5.3.6 Genetic Linkage and Chromosome Theory

Mendel was extremely fortunate with the plant model he selected for deciphering the basic laws of heredity. He chose seven traits of pea plants that gave a consistent pattern of dominance and recessiveness between two contrasting alleles. Many of Mendel's contemporaries could not find such a great experimental model or traits, and due to many deviations, their efforts were derailed. Even Bateson, the biggest supporter of Mendelian genetics, could not find an easy path and got entangled with unexpected results not explainable by Mendel's laws. In 1905, Bateson and Reginald C. Punnett made a dihybrid cross between purebreds of sweet pea plants, where the dominant parent produced purple flowers and long pollen grains (PP LL), and the recessive parent produced red flowers and round pollens (pp ll). Bateson and Punnett observed that the F1 hybrid had purple flowers and long pollen grains (Pp Ll), as expected.

However, the F2 population generated by the selfing of F1 hybrids showed a skewed ratio that did not match what was expected based on Mendel's second law of independent assortment of two independent traits. The data clearly showed that the characteristics of pollen size and flower color did not transmit independent of each other from parents to offspring. The expected ratio of the dihybrid cross was 9:3:3:1, but the results did not fit this pattern. As shown in table 5.1, the gene coding for flower color and pollen shape appears to be linked to some extent: the two phenotypic classes (purple flower + long pollen and red flower + round pollen) are larger than expected, and the number of recombinants is less than expected (1). Bateson was puzzled and could not explain these results in terms of epistasis either. However, Bateson and Punnett proposed that the F1 hybrid produced more P L and p l gametes due to some sort of physical coupling between the dominant alleles P and L and between the recessive alleles p and l (1).

Table 5.1: The results of the di-hybrid cross in sweet peas observed by Bateson and Punnett)

Phenotypes	Observed (12.3:1:1:3.4)	Expected (9:3:3:1)
Purple flower and long pollen (dominant traits; PP LL+Pp Ll)	4831	3911
Purple flower and, round pollens (recombinant; PP ll+pP ll)	390 (17.8%)	1303
Red flower and long pollen (recombinant; pp LL+pp Ll)	393 (17.7%)	1303
Red flower and round pollen (recessive traits; pp ll)	1338	435
Total plants	6952	6952

American scientist Thomas Hunt Morgan chose the fruit fly (Drosophila melanogaster) to study genetics. The fruit fly has several advantages for this study, including a short life cycle (forty to fifty days), easy propagation within milk bottles, and being amenable to the crossing. Also, with the help of a microscope, changes in the structure of the fruit fly can be easily identified. Thus it was a cheap and accessible model for the study of genetics and since then has served as an important model organism to study eukaryotic genetics. When Morgan crossed a female fly containing a purple eye (pr) and a normal wing (vg; both dominant traits: pr/pr.vg/vg) with a male fly containing a red eye (pr+) and the vestigial wing (vg+; both recessive traits: pr+/pr+.vg+/vg+), he got an F1 hybrid with the purple eye and the normal wing (pr/pr+.vg/vg+), as expected. Then he made a backcross between the F1 hybrid female (pr/pr+.vg/vg+) and the recessive male parent (pr+/pr+.vg+/vg+) (2). In these experiments, the recessive male can only produce one type of gamete, one that carries recessive red eye and vestigial wing traits. Thus the alleles contributed by the F1 female specify the F2 progeny. If both traits are sorted independently of each other, the expected ratio of these traits in the F2 progeny would be 1:1:1:1, representing both parental genotypes and two new recombinant classes.

As shown in table 5.2, he found unexpected results: a much larger number of offspring with purple eyes and normal wings or red eyes and vestigial wings was obtained in the F2 progeny. Like Bateson, he also observed a linkage between two independent traits: the linkage was not absolute, and the two types of recombinant class of progeny were in a similar proportion.

Table 5.2: The results of fruit fly backcross observed by Morgon

Genotypes and Phenotypes	Observed
pr+/pr. vg/vg+ (pruple eye+ normal wing)	1195
pr+/pr+. vg+/vr+ : (red eye+ vestigial wing)	1339
pr+/pr+. vg/vg+ (reg eye +normal wing)	151
pr+/pr. vg+/vg+ (purple eye + vestigial wing)	154
Total	2839

The progress in the field of cytology[1] helped us understand the phenomenon of linkage between genes that were observed by Bateson and Morgan independently. From the seventeenth century onward, scientists studied the structure of different organisms through microscopes and understood that organisms are made of one or more cells. The simplest forms of life, such as bacteria, are made of only one cell (unicellular), and various animals and plants are made of many cells (multicellular). Therefore, the unit of the structure and the function of life are the cell. In the late nineteenth century, high-resolution

1. The following are major discoveries in cell biology that played important role in the progress of genetics: 1839: M. J. Schleiden and T Schwann develop the cell theory. 1866: E. H. Haeckel (Häckel) hypothesizes that the nucleus of a cell transmits its hereditary information. 1869: Friedrich Miescher isolates DNA for the first time. 1879: Walter Flemming observes mitosis. 1902: W. S. Sutton and T. Boveri independently propose the chromosome theory of heredity: a full set of chromosomes are needed for normal development; individual chromosomes carry different hereditary determinants; and independent assortments of gene pairs occur during meiosis.

microscopes became available, which allowed the identification of various subcellular structures. It was natural that scientists started probing the location of genetic material within the cell. In 1879, Walter Fleming noticed a fine, threadlike structure in the center of salamander cells that shrunk and assumed a clear shape during cell division that was named chromosomes. It was clear from a series of studies that the number of chromosomes is constant for a species, and chromosome numbers vary between species. Typically, multicellular organisms have two copies of each chromosome (two sets of chromosomes) within the somatic cells, and the mother and father each contribute one set of chromosomes to their offspring. For example, human somatic cells have 46 chromosomes (23 pairs; diploid). In contrast, one set of chromosomes (23 chromosomes) is present in the gametes (eggs and sperm cells).

At the time of cell division, chromosomes first double in number and then divide equally into two daughter cells. In this way, two cells are made from one mother cell, and both daughter cells have the same number of chromosomes as their mother cell. In contrast, the cell division of a mother germ cell gives rise to gametes that only contain one set of chromosomes (haploid) and thus only one copy of each chromosome. During sexual reproduction, the fusion of male and female gametes produces a diploid embryo, and the two sets of chromosomes are restored in progeny. The behavior of chromosomes during the cell division of the germ cell grossly reminds us of Mendel's laws.

By the beginning of the twentieth century, it was recognized that chromosomes play a role in transmitting genetic traits from parents to offspring. Incidentally, the seven traits chosen by Mendel for his crossing experiments are encoded by seven genes that reside in seven different chromosomes, and thus he did not observe linkage. Therefore, Mendel did not see any contradiction in his experiments. However, besides gene linkage, Bateson and Morgan made another important observation that the linkage between two genes was not absolute and that a few recombinants are present in the F2 population. Morgan hypothesized that during germ cell division (meiosis), homozygous chromosomes interchange small regions before being divided into daughter cells, and thus the linkage between two genes located on the same chromosome occurs, resulting in the formation of recombinants (2). Thus based on the findings of cell biology and results from his laboratory, Morgan provided an explanation of the linkage between genes (2). He proposed the following:

- Genes occur in a linear order on chromosomes, and their location on chromosomes is fixed.
- Genes on the same chromosome are linked together and do not exhibit an independent assortment.
- Genes can be exchanged between chromosomes during meiosis.
- The closer genes are located on a chromosome, the less likely they will separate and

recombine in meiosis.
- Chromosomes undergo segregation and independent assortment. Therefore, genes on different chromosomes follow the law of independent assortment.

5.4 Chromosome Mapping

Several experiments in Morgan's laboratory revealed that the closer the two genes are, the stronger their association. As the distance between the two genes increases, the probability of crossing over increases, and the number of newly combined progeny (recombinant) increases in the same proportion. Thus the distance between two genes can be estimated by the number of recombinants present among the total progeny. By this method, the distance between genes can be measured in centimorgan (cM). Thus a distance of 1 cM between the two genes meant that in such cases, 1 percent of F2 progeny (of dihybrid cross) would be recombinant. Morgan's laboratory generated a vast amount of fruit fly crossing data. Eventually, one of his students, Alfred Henry Sturtevant, analyzed this data and constructed the first genetic map of fruit flies' chromosomes one by one. Subsequently, this method was applied to many other animals and plants to generate their chromosome maps.

Morgan did not directly observe the reciprocal exchange of segments between homologous chromosomes, but the assumptions he made about crossing over during meiosis proved to be correct. The crossing over (see figure 5.6) was experimentally confirmed almost two decades later by Barbara McClintock. But by then, scientists had constructed genetic maps of many organisms by following Morgan's lead. Genetic maps proved to be very useful for breeders. Genes whose phenotypes are visible served as a marker for selecting other nearby/adjacent genes that had no visible phenotype but contributed to important agronomic traits. Similarly, if one desired gene is linked to another undesirable gene, with the help of a genetic map, it became possible to estimate how many crossings will be required to break this linkage.

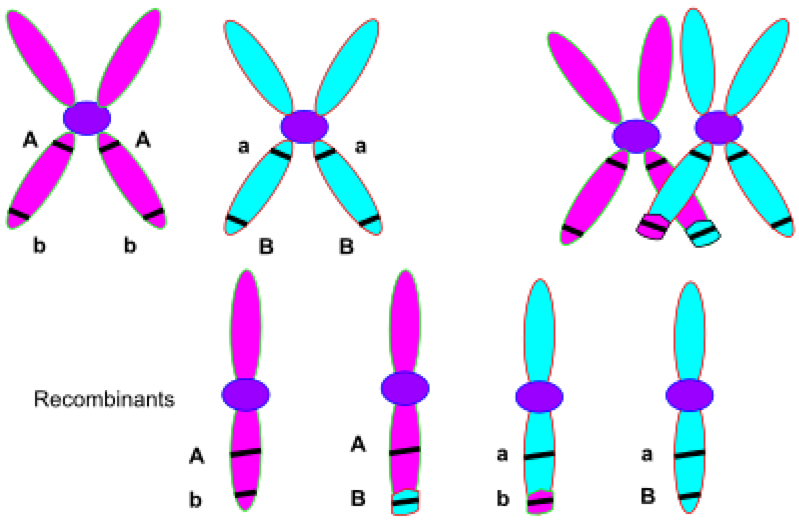

Fig 5.6 Crossing over between genes A and B results in recombinant chromosomes with new allele combinations a, b and A, B, in addition to the original parental combinations A, b and a, B. [“Chromosomal Crossover”](#) by Abbyprovenzano is licensed under [CC BY-SA 3.0](#).

5.5 Polyploidy

The study of the cells of various animals and plants revealed that the number of chromosomes within a species is fixed. Moreover, most animals are unable to tolerate a slight change in chromosome numbers. Usually, embryos that have lost or gained one or more chromosomes are unable to survive. Unlike animals, plants have a tremendous capacity to harbor multiple sets of chromosomes; this phenomenon is known as polyploidy. Many plant species have two (diploid), three (triploid), four (tetraploid), six (hexaploid), or eight (octoploid) copies of the entire set of chromosomes. Many polyploid crops have come into existence by spontaneous hybridization events between two closely related species naturally. For example, there are 28 chromosomes within emmer wheat (*Triticum dicoccoides*), 14 of which are from diploid einkorn wheat (*Triticum Urartu*; AA genome donor) and 14 from a diploid goat grass related to *Aegilops speltoides* (the BB-genome donor). Therefore, emmer wheat is a tetraploid (AABB) species. Another natural hybridization event between *T. dicoccoides* and *Aegilops tauschii* (the DD-genome donor) gave rise to hexaploid modern bread wheat (*Triticum aestivum*; AABBDD). Thus hexaploid common bread wheat has 42 chromosomes, of which 28 are from the emmer (AABB) and 14 are from *A. tauschii*.

Often the increased ploidy has a direct effect on the structure of the plant in the form of an increase in the size of the leaf, fruit, or grain—thus it adds to the agronomic value of a crop. Multiplication of chromosomes in emmer and common bread wheat had resulted in an increase in grain size and greater tolerance for adverse environmental conditions.

Similarly, as discussed in an earlier chapter, the octoploid ananassa strawberry (8 sets of chromosomes) is much larger than diploid wild strawberry varieties. Sometimes, breeders also create sterile hybrids by crossing two closely related species of different ploidy levels that disrupt the formation of seeds in hybrids. The seedless watermelon (a triploid) is one such example that was made by crossing a tetraploid with a diploid variety.

5.6 Summary

In later decades of the nineteenth century, a tremendous amount of geological and biological data suggested that both the earth and the living species inhabiting it have changed over time; in the process of adapting to new environments, new species emerge from the previously existing species, and some existing species also disappear. Mendel extended the knowledge by postulating three fundamental laws of heredity—which provided a correct theoretical explanation for Darwin's theory of evolution—to describe the origin of species in the natural world. Many new discoveries in cell biology led to the birth of genetics, a subdiscipline of biology that studies heredity and the physical and structural properties of genetic material. By 1900, cells and chromosomes were sufficiently understood to give Mendel's abstract ideas physical context. It was discovered that chromosomes contain the genes that code the various traits of an organism and that during germ cell division, the reciprocal exchange of chromosomal segments further adds to genetic diversity within a species. The observation of recombination frequencies was exploited to construct chromosomal maps and decipher the location of genes on various chromosomes and their physical relationship with one another. Chromosomal maps provided breeders with the tools for designing a rational experiment for creating improved varieties of plants and animals.

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Genetic Improvement in Cereal Crops and the Green Revolution

As the field of genetics matured, it became possible for breeders to develop improved crop varieties using Mendelian genetics, genetic maps, and markers. A breeder usually combines the desired genes from two varieties via crossing and then selects progeny containing desired traits. If four different useful genes are found in four different wheat varieties, using a step-by-step approach, a breeder could bring all four genes in the one preferred variety. However, a breeder does not create new genes; he or she only combines preexisting genes present within the genetic pool. Therefore, the biodiversity of any species determines the limits of classical breeding. This chapter summarizes the genetic improvements made in three main cereal crops—maize, wheat, and rice—using the classical breeding approach and their role in making the green revolution successful in the latter part of the twentieth century. In the process, various international agricultural research centers evolved under the Consultative Group for International Agriculture (CGIAR) umbrella, which is playing a critical role in achieving global food security.

6.1 The Story of Maize

Maize—more popularly known as corn—is the main staple crop of the Americas. Maize (*Zea mays L.*) is a member of the grass family Poaceae (Gramineae). Mexico is the center of the domestication and diversification of maize (1). Maize's ancestor is a wild grass, *Teosinte parviglumis* (2).[1] Until 1492, people outside of South, Central, and North America were unaware of maize's existence. Native Americans have been cultivating maize for ~7,000 years.

Maize is unique among the cereal crops because it is monoecious (it bears separate male and female inflorescences on the same plant). The main stem terminates in a tassel (male inflorescence), and the silk containing female flowers is on the stem. The natural structure of the maize plant favors cross-pollination. The pollen from the male flowers reaches the female flowers (of the mother plant or other nearby maize plants) via wind. Thus in maize,

1. For the story of maize's domestication and origin, see the video "Popped secret: The mysterious origin of corn—HHMI BioInteractive Video" on YouTube: https://www.youtube.com/watch?v=mBuYUb_mFXA&t=51s.

an equal possibility of self-pollination and cross-pollination exists. The pollen of different plants can reach a female flower, leading to the fertilization of the egg cell independent of one another. After successful pollination, the seeds on a cob are not uniform because each seed results from an independent pollination event. In nature, genes are exchanged continuously between maize plants, which results in new combinations.

6.1.1 Discovery of Hybrid Vigor and F1 Hybrids of Maize

In 1876, William Beal, a scientist at the Michigan Agricultural College, conducted crossings between maize varieties. To control pollination, Beal cut off the male flowers of the female parent (this process is known as detasseling) to ensure 100 percent cross-pollination from the chosen male parent and 100 percent hybrid progeny. Beal observed that the yields obtained from hybrids were higher than either of their parental varieties. In 1877, Charles Darwin also experimented with crossing maize varieties. He observed that the offspring resulting from outcrossing produced 25 percent larger cobs than from selfing and that the hybrids had a greater ability to tolerate chilling stress.

In 1908, George H. Shull and Edward East independently experimented and developed purebreds of maize. They noticed that after successive cycles of selfing, the maize plants' size and their yields decreased. This phenomenon was named *inbreeding depression* (see figure 6.1). Like Beal and Darwin, Shull also noticed that F1 hybrids are taller and healthier than their parents and produce higher yields; he named this phenomenon *hybrid vigor* or *heterosis* (see figure 6.1). Shull further made a very useful observation that after three generations of inbreeding, maize behaves almost like a purebred that can be used for producing the F1 hybrid. Such an approach could ensure 100 percent human control over pollination and good yields year after year. However, Shull did not have enough resources to continue his work on F1 hybrids of maize. In 1913, Shull migrated to Germany and became the editor of the scientific journal *Genetics*. East, a Harvard University professor, was also not able to pursue his research on maize, but he encouraged a new generation of scientists. One of his students, Donald F. Jones, crossed the two purebreds of maize to create an F1 hybrid, and afterward, by crossing two different F1 hybrids, he successfully created double-cross hybrids (see figure 6.1). Jones observed that the yield of the double hybrids was higher than single hybrids. Therefore, the most successful corn crop was the double-cross hybrid, and it laid the foundation for the widespread use of double-cross hybrids in the US. The hybrid vigor of maize was only maintained if new seeds were purchased every year, which made the seed industry commercially viable.

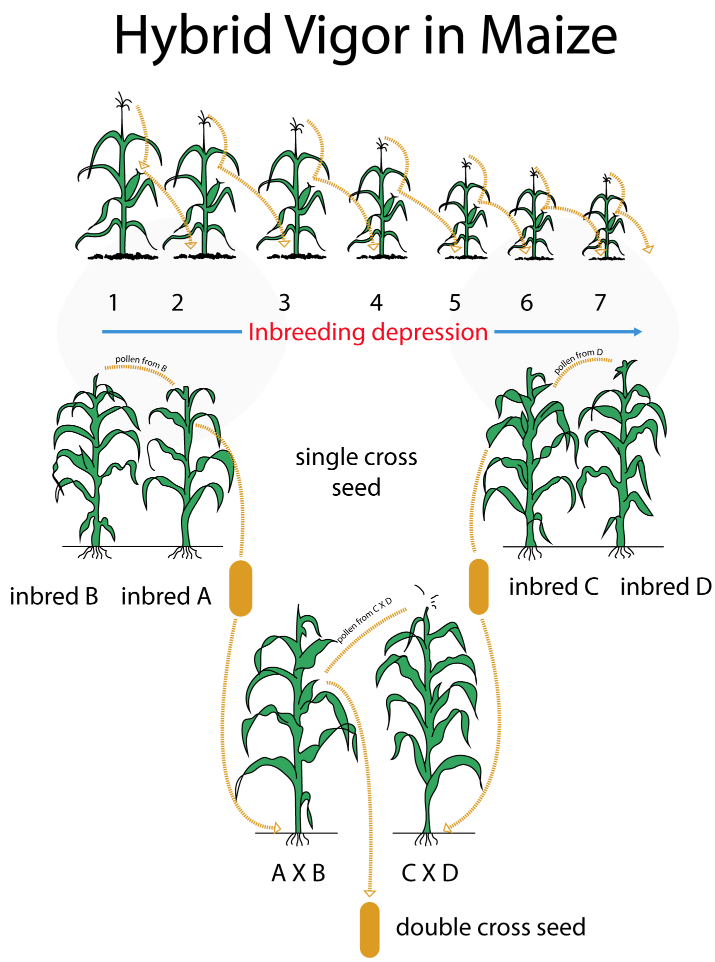

Fig 6.1 Inbreeding depression and Hybrid vigor in maize. "Hybrid vigor in maize" by Sushma Naithani and [OSU OERU]() is licensed under [CC BY 4.0]().

In the 1930s, the US Department of Agriculture helped farmers adopt F1 double-cross hybrid varieties of maize, leading to progressively higher yields. The first two hybrid varieties were grown side-by-side, and later to ensure 100 percent double hybrids, one row of pollen donor (male) was planted between every four rows of detasseled female plants. Gradually, most American farmers adopted this practice of maize cultivation. In 1933, less than 1 percent of total maize grown in the US was a double hybrid, but by 1944, it increased up to 56 percent. From 1930 to 1990, American scientists released about thirty-six improved hybrid varieties of maize, and farmers gladly adopted better varieties one after the other.

6.1.2 The US–Mexico Collaboration on Agriculture Research

In 1941, the vice president of the United States, Henry A. Wallace (1888–1965), traveled to Mexico to attend the inauguration ceremony of the newly elected president of Mexico, Manuel Ávila Camacho. Roosevelt and Wallace had also won elections in the US that same year. After attending Camacho's ceremony, Wallace spent the first two days in the Bajio region with outgoing president Lázaro Cárdenas and newly elected agriculture secretary Marte Gómez. Wallace noticed that due to maize's continuous cultivation, the Mexican soil had lost its fertility, and farming had become very unproductive. While the Iowa farmer spent ten hours to produce ten bushels of corn, it took a Mexican farmer 200 hours for the same. Wallace and his hosts discussed how the United States could help increase the productivity of Mexican farms. Wallace promised to help.

Upon his return to the US, Wallace contacted Raymond Fosdick, then the president of the Rockefeller Foundation, about providing US aid to Mexico and developing the appropriate project. Fosdick set up a three-member committee that consisted of maize geneticist Paul Mangelsdorf (Harvard University), agronomist Richard Bradfield (Cornell University), and plant pathologist Elvin Stakman (University of Minnesota) to evaluate a plan on agricultural cooperation between the US and Mexico. In 1942, these three experts recommended a pilot research program that led to the establishment of the Oficina de Estudios Especiales (OEE) program in 1943 with support from the Rockefeller Foundation and the Mexican government. The OEE's mission was to train Mexican scientists across all disciplines to support the agricultural production of four major crops: maize, beans, wheat, and potatoes. The objective of establishing the Colegio de Postgraduados at Chapingo University in Texcoco, near Mexico City, was added in later years. Mangelsdorf supervised the maize research program, and Stakman was given the responsibility of directing the wheat breeding program.

6.1.3 Maize Germplasm Collection and Breeding from the 1950s to the 1960s

In 1943, a research project on maize was started under the supervision of Professor Paul Menzaldorf with the support of the Rockefeller Foundation. Menzaldorf's team promoted F1 and double-cross hybrid varieties of maize developed by American scientists in Mexico. They also developed hybrids of local Mexican maize varieties. By 1947, ten new high-yielding double hybrids were released in Mexico under this program. In 1948, Mexico broke old records in maize production and became self-sufficient. By 1960, one-third of Mexico's farms were cultivating high-yielding hybrids, and corn production had tripled. Menzaldorf's team also began the collection of maize germplasm from Mexico and Central America. Since then, 28,000 maize varieties have been collected. This collection, representing almost all local maize varieties from eighty-eight countries, is stored at the Corn Germplasm Bank at the International Maize and Wheat Advancement Center (CIMMYT; https://www.cimmyt.org) located in Mexico City.

6.2 The Story of Wheat

Wheat is the second widely grown cereal in the world after maize. However, unlike maize, most of the wheat is consumed as food. Wheat (*genus Triticum*) has many diploid and polyploid species (see figure 6.2). The einkorn (*T. monococcum L.*), the oldest among domesticated wheat varieties, is a diploid species that contains the AA genome. A natural hybridization event between einkorn and a diploid weed goat grass with the BB genome gave rise to the emmer/durum wheat (*T. turgidum*). Therefore, emmer is tetraploid (AABB). Archaeological evidence suggests that the domestication of einkorn and emmer varieties occurred almost simultaneously (10,000–12,000 years ago) in the Fertile Crescent. Wild emmer (*T. turgidum* ssp. dicoccoides) is the progenitor of today's tetraploid durum wheat (3).

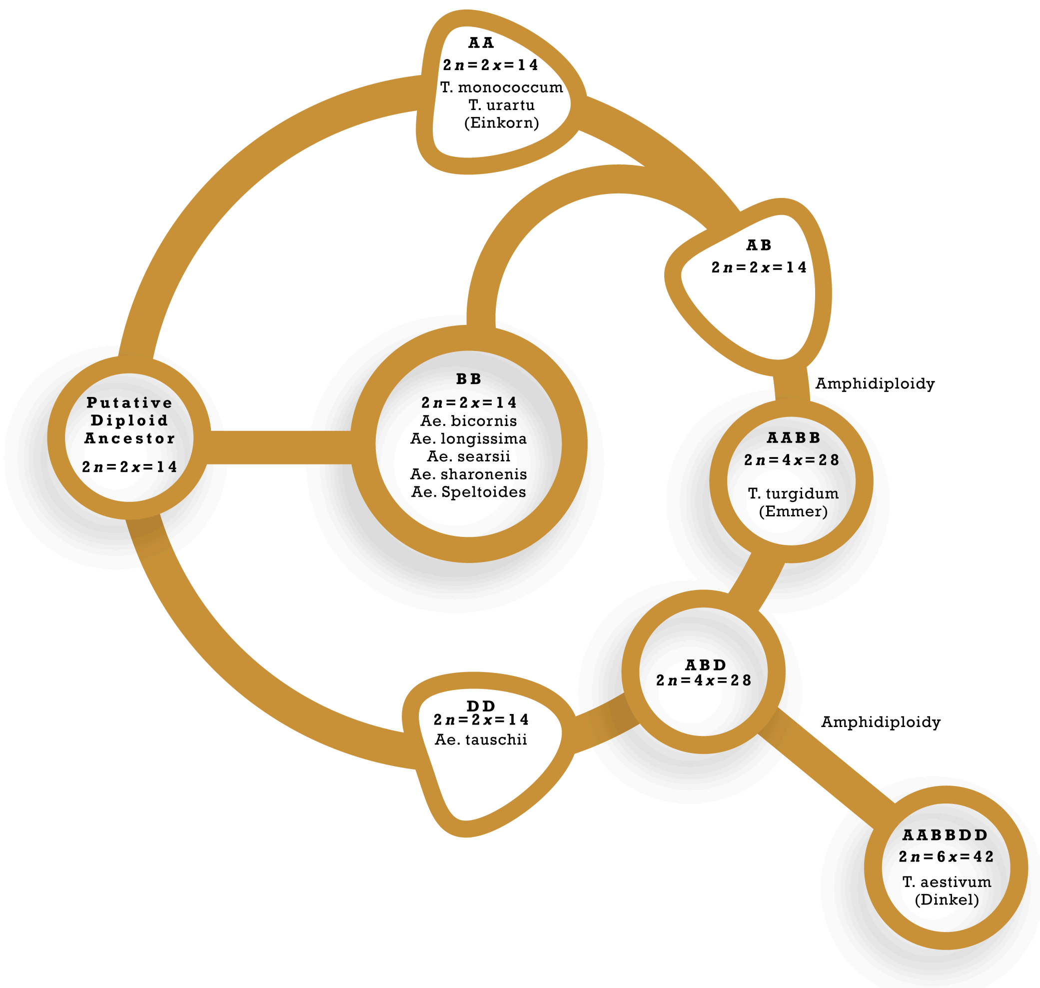

Fig 6.2 "Origins of the polyploid wheat" by Sushma Naithani and OSU OERU is licensed under CC BY 4.0.

A subsequent spontaneous natural hybridization event between emmer (AABB) and another species of wild grass, *Aegilops tauschii* (DD), gave rise to the hexaploid (AABBDD) spelt/dinkle or common bread wheat (*T. aestivum*) (3). Archaeological evidence suggests that spelt's birthplace is the southeastern mountainous region of present-day Turkey. The polyploid durum and bread wheat produce larger seeds than the diploid species and their wild ancestors and also have a greater capacity to tolerate adverse conditions. Scientists estimate that around 7,000 years ago, the emmer wheat had spread outside its center of domestication and reached India, Central Asia, Egypt, and Europe. Emmer was the main cereal crop in Egypt at the time of the Pharaohs, while spelt was one of the major cereals of the Alemannians in southern Germany, Austria, and Switzerland between the twelfth and nineteenth centuries. Over time, many local varieties of wheat emerged in different regions due to the continued artificial selection of einkorn, emmer, and spelt in a variety of climates. Although these varieties show adaptations to local climates and may differ in morphological traits, most are subspecies of *T. turgidum* and *T. aestivum*. The wild einkorn and wild emmer have brittle rachis, while their domesticated descendants have nonbrittle rachis (see figure 6.3). This domestication trait caused the loss of shattering of mature seeds, and it became possible for the farmer to harvest the crop all at the same time.

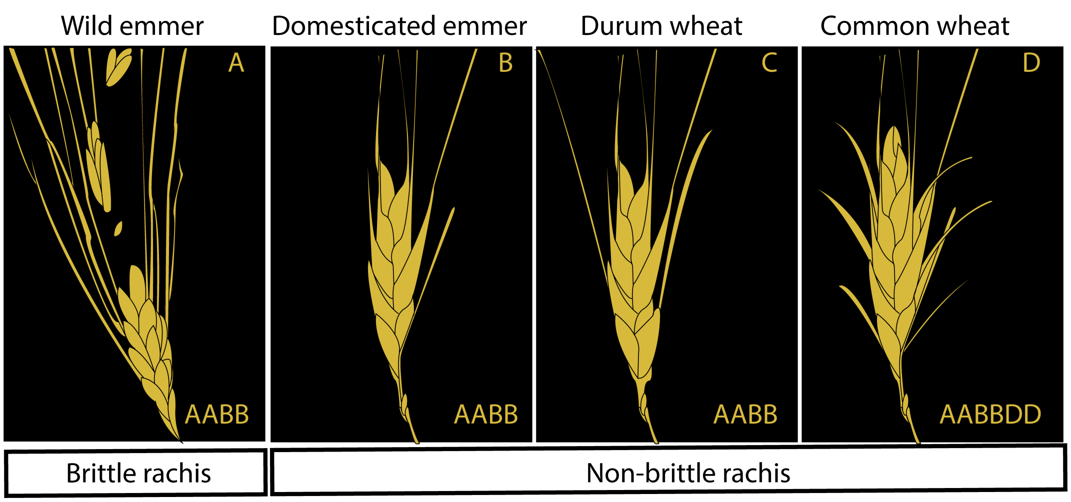

Fig 6.3 Mature seeds of the domesticated wheat species do not shatter. "Seeds of domesticated wheat" by OSU OERU is licensed under CC BY 4.0.

Spelt, emmer, and einkorn are hulled wheat species; their kernels cannot easily be extracted by threshing, and thus at harvest, the chaff remains at the kernels, and a special dehulling of the kernels is required in the mill to separate the chaff from the grain. A mutation in two genes, tenacious glume (*Tg1*) and *q* resulted in free-threshing wheat. Thus mutations in the Br1 loci on chromosomes 3A and 3B, *Tg1* on 2D, and *q* on 5A had the most profound impacts on wheat's domestication. In the last centuries, einkorn, emmer, and spelt were replaced by free-threshing durum and bread wheat. Durum (*T. durum*) is mainly used in the making of pasta and semolina. The common wheat (*T. aestivum*) is most suitable for bread, cookies, cakes, crackers, pastries, and noodles (it forms a spongier dough due to its higher gluten content and low gliadins/glutenins ratio). Ninety-five percent of wheat grown worldwide is common bread wheat, and the remaining is mostly durum.

Recently, interest in ancient wheat species has been renewed for producing high-value baking goods due to their high nutrition content, and a market for catering to food-conscious elites is slowly growing.

6.2.1 The Beginning of Wheat Breeding Program in Mexico

In 1943, Stakman directed the OEE's Cooperative Wheat Research and Production Program in Mexico. At that time, agricultural research in Mexico was almost at a standstill. There was no single agriculture scientist with a PhD and no active research program on agriculture in Mexico and South America. He recommended that Norman Ernest Borlaug (1914–2009), his former student, be brought to Mexico for a leading wheat breeding program. Borlaug had finished his PhD under the supervision of Stakman a year earlier, and he was working for DuPont as a scientist. In Mexico, George Harrar, a plant pathologist, oversaw the local unit. The three other scientists in his team (besides Norman Borlaug) were Edward Wellhausen, John Niederhauser, and William Colwell, all from the US.

Borlaug arrived in Mexico in 1944 to lead the International Wheat Improvement Program at El Batátan, Texcoco, outside of Mexico City. This was his first time traveling outside the US, and he didn't know Spanish. He camped at a research center in the Yaqui Valley in Sonora, Mexico. In the 1930s, the governor of Sonora, Rodolfo Elias Calles, had set up that research station to help farmers. The station owned land for experimental research and some animals. The first director of this station, Edmundo Teboada, worked on some varieties of Mexican wheat and built a small wheat germplasm collection. But the research station did not have any modern farm equipment or any trained scientist.

There was no maintenance for this research station. So when Borlaug reached there, it was a mess. There was no electricity, and the windows and doors were broken. But Borlaug was not discouraged and managed to set up humble arrangements for his living quarters, and in the early morning, he started working like a farmer. Borlaug established connections with farmers in the Yaqui Valley, who were relatively prosperous and had a good irrigation system compared to other wheat-growing regions of Mexico. Borlaug borrowed tractors and other machinery for research from these farmers as needed. Between 1939 and 1941, the problem farmers faced in this area was primarily rust, a plant disease that would infect their wheat. So Borlaug initiated work on the development of a wheat that can fight rust. First, he selected the wheat varieties from Teboada's collection, which showed some ability to resist rust. He then began a series of crossing and backcrossing experiments with wheat varieties to develop high-yielding, rust-resistant wheat (see figure 6.4).

Fig 6.4 “Norman Borlaug – LIFE” by Lou Gold is licensed under CC BY-NC 2.0.

6.2.2 Shuttle Breeding: Stem Rust-Resistant Wheat Varieties

Generally, it takes ten to twelve generations to combine useful desirable traits from two varieties of a crop by implementing classical breeding and selection methods. Thus at least ten years were needed for making a new breed of rust-resistant wheat. Borlaug thought that if two wheat crops could be grown per year, then a new variety of wheat could be made in five years. Fortunately for Borlaug, this opportunity was available in Mexico. In Sonora, wheat is sown in October and harvested in April. In the mountainous region of Toluca Valley in central Mexico, wheat is sown in April and May and harvested in October. Thus taking advantage of this, Borlaug began shuttle breeding. As soon as the wheat crop was harvested in Sonora (in April), Borlaug sent these seeds for sowing in Toluca. Similarly, after the crop harvest in Toluca (in October), new seeds were sent to Sonora. Borlaug’s shuttle breeding program was not well received by his seniors at the Rockefeller Foundation. Until that point, there was a general agreement that the wheat seeds need a resting period after harvest (or before sowing the following year). Stakman advised Borlaug not to waste time and resources. When Borlaug submitted his resignation in response, no one stopped him from using shuttle breeding.

Interestingly, the two locations (Yaqui and Toluca) used for shuttle breeding not only were 1,000 kilometers apart but also differed in latitude (by 10°) and elevation (by 2,000 meters; see figure 6.5). The Yaqui Valley is located at latitude 22° north and the Toluca Valley is located at latitude 12° north. Apart from this, the days of wheat cultivation in Yaqui

Valley are shorter than in Toluca. As a result, the new wheat varieties developed by shuttle breeding became neutral to day length and regional climates. Those varieties could be grown on long and short days, on highland and valley, and at any elevation. These characteristics proved to be very helpful in spreading the improved varieties of wheat worldwide. The shuttle breeding experiment also reduced the time by half required for producing a variety using traditional breeding.

Fig 6.5 Locations of Norman Borlaug's research stations in Mexico. "Borlaug Mexico locations" by CIA is in the public domain.

There was no agricultural extension program in Mexico to help Borlaug; he worked directly with the farmers. As he developed new breeds, he gave them directly to the local farmers for preliminary testing. If farmers had positive results, then the seeds of those varieties were sent to experts worldwide for detailed testing. In this way, he built collaborations with local farmers and scientists from all over the world. Between 1948 and 1950, Borlaug released eight new wheat varieties in Mexico, each of which seemed to be more resistant to rust. In addition to developing advanced varieties of wheat, Borlaug advised farmers on the right quantity of fertilizer to use and how to improve irrigation facilities. The best wheat yield in the Bajio region in Mexico without the use of fertilizers and irrigation yielded 1 ton/hectare. But after using sufficient fertilizers, irrigation, and weed management, these same wheat varieties yielded 7.5–8 tons/hectare.

In 1951–54, a rust epidemic devastated the wheat crop in North America due to the explosion of a highly pathogenic strain, 15b. By 1955, rust disease became a major challenge for American farmers. Under the pressure of this epidemic, many wheat nurseries were built around the world with the help of scientists from seventeen countries, and research on almost every kind of rust strain began. Also, the collection of wheat germplasm was undertaken afresh.

Since Borlaug already had several wheat varieties with rust resistance, he was assigned the responsibility of developing new varieties of American wheat and training other scientists. He built nurseries in Yaqui to test the wheat varieties' ability to fight rust. He selected those varieties that had larger, more seeded panicles; were rust resistant; and could produce higher yields when a sufficient amount of fertilizer and irrigation was supplied. In this way, rust-resistant, high-yielding varieties were developed.

6.2.3 High-Yielding Dwarf Wheat

By 1950, the prevalent wheat varieties were six to eight feet long, and their thin stalk was weak, which often collapsed under the weight of their own grain—a trait called lodging. Moreover, the high-yielding varieties were more damaged by thunderstorms, as they grew even taller in response to synthetic fertilizer. Therefore, the breeders wanted to create a rust-resistant dwarf variety of wheat with a strong stem that can bear more weight. Borlaug had developed the rust-resistant, high-yielding wheat varieties, but he did not have any dwarf wheat in his collection. Thus the search for dwarf wheat was ongoing. Finally, S. Sisil Samon of the US Agricultural Research Service spotted a dwarf wheat variety, Norin-10, in Japan. He sent Norin-10 seeds to Professor Orville Fogle, who sent it to Borlaug.

In 1959, Borlaug crossed Norin-10 with some of his best North American varieties to create dwarf wheat varieties with a thicker, stronger stalk (e.g., Penjamo 620, Pittic 62, Gaines, Lerma Rojo 64, Siete Cerros, Sonora 64, and Super X). These high-yielding, rust-resistant dwarf varieties can stand the high winds, are amenable to machine harvests, and respond well to the application of fertilizers and irrigation. By 1963, 95 percent of Mexico's wheat acreage was sown with these dwarf varieties. Thus a complete package was developed to increase wheat production, including improved seeds, synthetic fertilizer, pesticides and weedicides, irrigation, and machines. The implementation of this package in Mexico led to unexpected success in wheat production. In 1958, Mexico became self-sufficient, and in 1960, it started exporting wheat to other countries. The US also shared this success; from 1960 on, it became the leading exporter of wheat. These advancements in US agriculture laid the foundation for the green revolution, and millions of people worldwide were saved from starvation.

6.3 The Green Revolution

The Cold War began with the end of World War II. The world was divided into American and Soviet (USSR) camps. Apart from these two poles, there were many Asian, African, and Latin American countries that adopted a policy of remaining neutral to both camps. The nations were part of the Non-aligned Movement (NAM) in 1955, which was under the leadership of Jawaharlal Nehru (prime minister of India), Gamal Abdel Nasser (president of Egypt), and Josip Broz Tito (president of Yugoslavia). Most of the NAM countries had recently emerged from enslavement by former European empires, were economically weak, and were unable to produce enough grain for their populations. Due to continuous starvation and famine, there was a possibility of a "Red revolution" in these countries (like China and regions like Eastern Europe), which could have aligned with the USSR and alienated the US in the global politics; thus the US proposed a "green revolution" to neutralize the threat. The green revolution aimed at making developing countries self-sufficient in grain production. The hope was that if poor people could get enough food, then the need for a Red revolution would automatically disappear, and the US would not be isolated in the world.

At the heart of the green revolution were improved maize and wheat varieties developed by American scientists between 1930 and 1960 that yielded eight- to tenfold more grains when sufficient fertilizer, water, pesticides, and weedicides were applied. These modern packages of farming had been successfully implemented in Mexico and the US. The green revolution intended to repeat this experiment in Asia, Africa, and Latin America. The Rockefeller Foundation, Ford Foundation, and several other government and semigovernment organizations were given the responsibility to make the green revolution a success.

In 1960, Borlaug represented the Rockefeller Foundation in a Food and Agriculture Organization (FAO) committee. This committee reviewed the wheat-producing capacity of fifteen countries and concluded that except for India, Pakistan, Morocco, Bangladesh, Turkey, and Iran, most of the third world countries did not have agricultural scientists, and even the countries that had agriculture research programs were not capable of achieving food self-sufficiency. Thus the committee recommended training young breeders from developing countries in Mexico under Borlaug's direction. The OEE project first proposed by Wallace eventually evolved into the International Maize and Wheat Improvement Center, a training center for breeders from all around the globe with the support of the Rockefeller and Ford Foundations and the Mexican government. Borlaug was appointed its director, where he served for the next thirty years.

In addition, Menzaldorf was given the responsibility of a maize breeding program for Latin America and Africa. Under the green revolution campaign, advanced varieties of maize developed by American scientists were introduced in Latin American countries. By 1980, high-yielding maize varieties were grown in 50 percent of South America's arable land. However, the program was not as successful in introducing maize to Africa. Notably, the genetic improvement of rice was included in the green revolution's agenda, as it was the major cereal crop of Asia.

Apart from improved seeds, institutional and infrastructural changes were needed for the green revolution to succeed. Farmers of developing countries used to save the seeds for the next sowing. They did not have the money to buy seeds, synthetic fertilizer, pesticides, and farming equipment. Thus the US entered into policy agreements with developing countries, including India, Pakistan, Bangladesh, Thailand, Indonesia, Egypt, and so on. The US provided seeds, fertilizer, technology, and training. Also, the US promised continued food aid to partner countries until they achieved self-sufficiency in food production. The host governments of developing countries had to build the necessary infrastructure and banking system to provide loans to farmers.

6.3.1 The Success of the Wheat Breeding Program in Asia

In the early 1960s, under Borlaug's supervision, wheat breeding experiments began in India, Pakistan, and other Asian countries. In 1968, India harvested 16.6 million tons of wheat, for which an extra storage system was needed. Indira Gandhi, the then prime minister of India, used government schools as temporary godowns for grains during the summer months. Despite the drought in 1969 and 1970, 20 million tons of wheat were produced in India. Earlier, the average wheat production from 1963 to 1967 was 9–11 million tons. Pakistan also got about a 60 percent increase in wheat production. Between 1965 and 1970, Pakistan's wheat yield increased from 4.6 million tons to 8.4 million tons and became self-sufficient in wheat production by 1968. Thus the green revolution had tremendous success in India and Pakistan and was met with similar success in Jordan, Lebanon, Turkey, and Indonesia. In many countries, the average life expectancy and living standards improved, and mortality rates declined significantly.

6.3.2 The Story of Rice

Unlike wheat and maize, very little research and breeding experiments were done on rice when it was included in the green revolution agenda. Thus in 1960, the Ford and Rockefeller Foundations, in collaboration with many international agencies, established the International Rice Research Institute[2] (IRRI; http://irri.org) in Los Baños in the Philippines. Robert Chandler (1907–91) was appointed as the first director of this institute and was

2. Borlaug and Chandler discuss the origins of the International Rice Research Institute in a discussion filmed in 1994, now available as a multipart series on YouTube: Part 1: https://www.youtube.com/watch?v=17ySNZo3AMs Part 2: https://www.youtube.com/watch?v=TW8hpPi0rqI Part 3: https://www.youtube.com/watch?v=mEjQbo-2nZQ Part 4: https://www.youtube.com/watch?v=rQon8EfQblY Part 5: https://www.youtube.com/watch?v=jhqQwfc0-No Part 6: https://www.youtube.com/watch?v=jtuB2cTEfTU

responsible for establishing a rice germplasm collection and supervising the rice breeding program. Most of the research about rice's origin and domestication, its genetic diversity, and its genetic improvement began after the 1960s.

However, before the improved rice varieties were made available, the farmers were encouraged to use synthetic fertilizer in rice fields, and an infrastructure for irrigation was developed. From 1950 to 1970, a 25 percent increase in rice production was achieved due to the availability of synthetic fertilization and irrigation. In the 1970s, rice production increased by five to six times due to improved rice germplasm; this helped the green revolution reach a peak because more than one-third of the world's population is fed with rice. Even though there is more maize and wheat production in the world, maize only fulfills the need of 5 percent of the world's population, and wheat fulfills 20 percent. In this sense, rice was the most important and representative crop of the green revolution. Here we summarize rice's origin and genetics and the achievements of rice breeding in Asia and Africa.

6.3.2.1 The Origins of Rice

In nature, there are twenty-four species of grasses that are closely related to rice and are classified within the genus *Oryza*. These species are distributed in tropical and temperate regions in Asia, Africa, Australia, and South America. Some of these are diploid (2n = 24 chromosomes), and others are tetraploids (48 chromosomes). However, only two diploid species, *Oryza sativa* and *Oryza glaberrima*, were domesticated by humans. Interestingly, rice was independently domesticated in three different continents. *O. sativa* was domesticated in Asia and Australia. Archaeological and genetic evidence suggests that 9,000 to 11,000 years ago, the *O. sativa* subspecies japonica was first domesticated in the Yangtze River valley of China from the wild grass *O. rufipogon*. Another subspecies of rice, *O. sativa indica*, was independently domesticated 5,000 years ago in the Indo-Gangetic Plain of northern India from the wild grass *O. nivara*. In Australia, another subspecies of *O. sativa* was developed 2,000 years ago from *O. rufipogon* (4). The *O. glaberrima* was domesticated in Africa 3,500 years ago. *O. glaberrima* has evolved from the wild grass *O. barthii* in West Africa (in Mali), and then it was brought to North Africa and the Zanzibar islands (5). This rice arrived in the Americas with African slaves in the seventeenth century and has been grown in North Carolina (5). Among the two cultivated rice species, the *O. sativa* (Asian rice) is most widely grown globally and is the main staple for one-third of the human population.

6.3.2.2 The Diversity of Asian Rice

O. sativa is the most widely cultivated rice species in the world. Its japonica subspecies are grown in Southeast Asia, including China, Japan, Korea, Indonesia, Bali, Java, Sumatra, Vietnam, Cambodia, and so on. The japonica subspecies includes several thousand cultivars; some are adapted for the cold climate, while others flourish in the tropics. The varieties of japonica subspecies are broadly known as sticky/sushi rice and have a slightly sweet taste. The indica subspecies of *O. sativa* is mainly grown in the Indian subcontinent and South Asia. It also has tremendous diversity as well, including varieties adapted to rain-fed highlands and coastal regions. The cooked indica rice grains do not stick to one another and are known as basmati-type. Interestingly, the "sticky" feature is not found in the wild ancestors of rice and related wild species of the grass family. This trait, selected during domestication of the japonica subspecies, is caused by a mutation in the gene *Waxi* that blocks amylose production within the rice grain. Usually, two types of starch—amylose and amylopectin—are found in the rice grain, but only amylopectin is present in sticky rice. The glucose molecules in amylose form a simple linear structure, while in amylopectin, glucose molecules form branch chains that make amylopectin dissolve faster in hot water than amylose. Thus in sticky rice, the presence of amylopectin makes it sticky. In basmati rice, a high amount of amylose keeps the rice grain separated after cooking. In general, the ratio of amylose and amylopectin varies across cultivars, and accordingly, the different levels of stickiness and the variation in cooking time are observed (for this reason, two varieties of rice are not mixed for cooking).

Another interesting fact about rice is that rice grains are naturally red. The white color (or straw color; white is because of polishing) results from a mutation in a gene involved in the anthocyanin pigment's[3] biosynthesis. For many years, it was a mystery to scientists why humans selected white over red for grain color. This feature was selected independently in both japonica and indica subspecies. It had been speculated that it was for its aesthetics or for some cultural belief. But in both China and India (the two birthplaces of Asian rice), red is considered auspicious, and there is no indication of any cultural preference for white. Genetic studies have recently revealed that the anthocyanin biosynthesis genes are linked to seed-shattering genes, and the loss of shattering also leads to the loss of the red pigment in rice. All the wild ancestors of rice have red seeds that spontaneously shatter upon maturation. This trait is useful for the survival of the wild grasses, but humans can't harvest the crop at once. Thus a mutation that disrupted both seed shattering and anthocyanin biosynthesis gave rise to the rice plant whose straw-colored seeds did not fall upon maturation. Perhaps early humans picked a straw-colored mutant or collected seeds

3. Anthocyanin pigments are also found in many flowers, fruits, and vegetables and are beneficial for health.

from more of such plants that favored its selection and propagation. Humans probably carried these plants forward in the process of domestication. Because color and seed-shattering genes are linked, red-colored seeds became less prevalent in the cultivated rice species.

The Asian rice *O. sativa* contains more than one gene for seed shattering and the biosynthesis of anthocyanin pigments. In domestication, two mutant (shattering) genes were selected in japonica that eliminated seed shattering and the red color. In indica, only one (shattering) gene was selected, and thus many cultivars have partial seed-shattering and red-colored seeds. Therefore, farmers in India harvest the paddy before it turns yellow and then dry it in the sun. It is believed that some of the traits of japonica were later introgressed in indica cultivars, and therefore, the modern varieties of indica rice are white.

Some varieties of both indica and japonica are found to contain long-grain rice. The comparison of 174 species of *O. sativa* found in different regions and forty species of its wild ancestor *O. rufipogon* has shown that the trait of grain length has been fixed in the process of domestication in tropical japonica, indica, and basmati. Basmati rice is the longest among them. The grains of other fragrant rice are also long. In contrast, japonica and Australian rice grown in temperate regions have relatively round and small rice grains (figure 6.6). Like all cereals, humans selected rice for large seeds and panicles and for its adaptation to various climates. This is how thousands of landraces of rice came into existence.

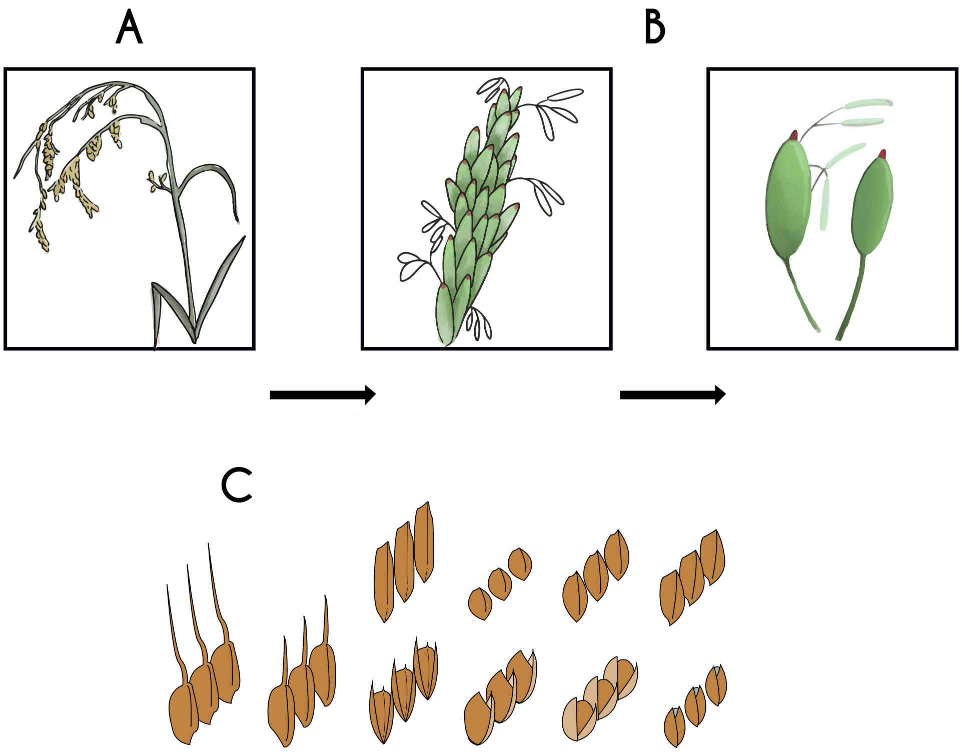

Fig 6.6 The structure of Asian rice (O. sativa) plant (A), inflorescence and flower (B), and a sample of grain diversity among various cultivars. "Rice, inflorescence, and grain diversity" by [OSU OERU](#) is licensed under [CC BY 4.0](#).

6.3.2.3 The Genetic Improvement of Rice at IRRI

After World War II, the shortage of grain and an increase in population caused widespread hunger in Asia. In 1949, the FAO established the International Rice Commission with the goal of increasing the yield of rice. The main obstacle in increasing the yield of the indica subspecies was the structure of this plant. Most indica cultivars were tall, had weak stems, and often collapsed on the ground when hit by storms or rains. Thus a strong dwarf stem was required for increasing rice productivity that can bear a heavy grain load.

In the 1950s, with FAO's help, Indian scientists at Rice Research Center, Cuttack, developed rice ADT-27 and Mahsuri rice varieties by crossing Indian rice cultivars with a dwarf Taiwanese Taichung Native 1. In the 1960s, these hybrid rice varieties were grown on a large scale in India but received only a modest increase in yields. After the IRRI opened in the Philippines in the 1960s, Robert Chandler created a team of scientists to develop high-yielding rice varieties. Two members of this team, Peter Jenning and Akiro Tanaka, formulated the strategy for creating improved rice varieties. First, they carefully studied various indica and japonica cultivars. They concluded that if indica plants can be kept standing until maturity (they used bamboo sticks to support these plants), their yields are similar to those of dwarf japonica cultivars. Second, they observed that indica cultivars respond well to the application of synthetic fertilizer. Thus the main problem in the indica subspecies was the tall and weak stem. Jenning crossed dwarf Dee-geo-woo-gen (DGWG) rice variety (Taichung Native 1's dwarf ancestor) with some indica and tropical japonica cultivars. By 1962, Jenning conducted thirty-nine crossings. He observed that first generation (F1) hybrid progeny was always tall and the F2 population segregated in the ratio of 3 tall:1 dwarf, suggesting that only one gene is responsible for stem's tallness in Asian rice. Thus dwarfism could be easily introgressed into other rice varieties. Jenning also noticed that some of the dwarf plants matured one month earlier than the traditional rice varieties. The early maturation trait was of great importance because it could save thirty days of land use, fertilizer, and water, and in some regions, three rice crops could be grown a year instead of two. Afterward, Jenning tested seeds of early maturing dwarf plants in the nursery for resistance to blast disease and observed a partial resistance in one plant labeled as IR8-288-3 (IR8). The parents of IR8 were the dwarf DGWG and the Peta rice variety of Indonesia; IR8 was 120 centimeters tall; had a strong, thick stem capable of bearing a huge panicle full of seeds; and was not affected by the change in day length and altitude (thus it could be grown anywhere). Another scientist, S. K. D. Dutta, observed that IR8 yields are 9–10 tons/hectare when synthetic fertilizer, water, and weedicide are applied in adequate amounts.

In contrast, the average yield of traditional varieties was 1.2 tons/hectare. In that scenario, the IR8 emerged as a great alternative. It is said that when the news of IR8 reached Ferdinand Marcos (then the president of the Philippines), he immediately went to IRRI and ordered a large-scale multiplication of IR8 seeds. Marcos wanted to showcase this achievement in the next election. The US was also eager to hear some good news in Asia while engaged in the Vietnam War. So amid these pressures, IR8 was released in 1966 without further testing. It is said that 3,000 farmers from the Philippines' remote islands came to IRRI to procure IR8 seeds. As expected, farmers got an increase of 5-10 times in yields by sowing IR8. With the help of IR8, starvation was temporarily avoided, and the foundation for making high-yielding rice varieties was laid.

The yield of IR8 was phenomenal, but it tasted chalky and was hard to chew. IR8 was also susceptible to various diseases, including bacterial blight and viral disease, and had only partial resistance to blast disease. Thus it required a heavy application of chemicals to keep the pests and pathogens away. In 1977, IRRI released IR36, which has a resistance to the blight and tungro viruses, and later IR64, which has an increased resistance to various diseases. Afterward, many rice varieties were developed by IRRI that showed increased resistance against many pathogens. These improved rice varieties were distributed across many rice-growing developing countries using governmental extension centers. Although the arms race between rice and its various pathogens continues, there has been no major famine due to rice shortage. The scientists at IRRI and in several other laboratories around the world are still breeding new rice varieties that can be more tolerant to abiotic stress and can withstand changing climates.

6.3.2.4 Yuan Longping's Hybrid Rice Varieties

In wild ancestors of cultivated rice (*O. rufipogon* or *O. barthii*), self- and cross-pollination occur. In contrast, domesticated rice species *O. sativa* and *O. glaberrima* favor selfing over cross-pollination. Thus unlike in corn, the phenomenon of hybrid vigor is not easily observed in rice. In 1964, a Chinese scientist, Yuan Longping, decided to change the selfing nature of cultivated rice to make high-yielding hybrids rice varieties. When Longping began his research, the predominant thinking in the field was that hybrid vigor could not be applied to naturally self-fertilizing species such as rice, but he was convinced otherwise. After nine years of hard work, he developed three varieties of rice: the first breed was a male-sterile line incapable of making pollen; the second was a maintainer line that served as a source of pollen, and the third was a restorer line that can rescue a male-sterile line from sterility. Thus a cross between male-sterile and restorer lines produces completely fertile progeny. He demonstrated that hybrid progeny obtained by crossing the male-sterile line with the maintainer line shows hybrid vigor resulting in a significant increase in the grain yield. Generally, under favorable conditions, the yield of the most popular rice varieties is 5–6 metric tons/hectare. However, under similar growing conditions, hybrid rice released by Longping in 1974 gave an average yield of 7.2 metric tons/hectare (a 20 percent increase). Since 1976, this hybrid rice has been grown in China and provides food for an additional 70 million people. Since 1994, hybrid rice varieties have been sown in India, the Philippines, Bangladesh, and Indonesia. However, Longping continued his research on increasing grain yields. In 1997, yields of hybrid rice progeny were 10 metric tons/hectare, and by 2004, it reached 12 metric tons/hectare.

Professor Yuan Longping, the father of the hybrid rice, was awarded the UNESCO Science Prize in 1987; the World Food Prize,[4] with Monty Jones (who developed NERICA rice varieties for Africa and is discussed in the following section), in 2004; and the Wolf Prize in 2004 for his contribution to agriculture. In 2007, he was elected a foreign member of the US National Science Academy.

4. "A world-brand name: Yuan Longping, the father of hybrid rice," World Food Prize, 2007, https://www.worldfoodprize.org/index.cfm/87428/40007/a_worldbrand_name_yuan_longping_the_father_of_hybrid_rice.

6.3.2.5 NERICA: The New Rice for Africa

African rice (*O. glaberrima*) was developed 3,500 years ago in West Africa from the wild *O. barthii* in the delta region of the Niger River (present-day Mali). African rice plants are more elongated and have weaker stems than Asian rice. These plants are relatively more susceptible to lodging and cannot bear the load of a heavy panicle. Also, seed shattering in African rice results in a significant loss in yields, as this trait was not selected against during domestication of African rice. However, this rice has the ability to survive in the harsh and challenging environment of Africa; it has a natural resistance against the various pests, parasites, and pathogens prevalent in its environment. Like Asian rice, African rice consists of many cultivars that represent a rich biodiversity, and many useful genes are hidden within these varieties. For example, the *O. glaberrima* CG-14 variety has a natural ability to tolerate drought, grows faster than weeds, and thrives on marginal land (e.g., deficient in phosphorus or acidic soil). Although the input costs for growing this crop are less, it has less productivity, and thus it is not widely grown.

For a long time, the Asian rice *O. sativa* has been grown in Africa on a large scale, as it is highly productive. Asian rice was introduced about 450 years ago in many countries of Africa. But Asian rice does not possess the ability to cope with Africa's environment. Its yield decreases in drought conditions, and it cannot protect itself from parasites, pests, pathogens, and insects. The input cost for growing Asian rice is very high, as farmers use large amounts of synthetic fertilizer, pesticides, weedicides, and so on. Thus the sustainable cultivation of Asian rice in Africa poses a challenge. Unfortunately, the useful traits of African and Asian rice cannot be combined using classical breeding methods, as crossings between *O. sativa* and *O. glaberrima* yield sterile hybrids. Thus the green revolution failed in improving the productivity of African rice or the resilience of Asian rice for the African environment using classical breeding methods.

However, in the 1970s, African scientist Monty Jones, working at the West Africa Rice Advancement Institute (WARDA), collected 1,500 varieties of *O. glaberrima* and developed genetically improved varieties of African rice that show high resilience in the African environment. In the 1990s, when the technology of tissue culture became easier to apply on rice, Jones's team created hybrid rice cells by fusing Asian and African rice cells to create hybrid plants from them. These plants were not sterile and can be grown from seeds. This new hybrid variety, called NERICA (New Rice for Africa), has a yield that is five times that of African rice cultivars, is resistant to various biotic and abiotic stress conditions prevalent in Africa, and has fewer input costs. NERICA also matures within three months, while its ancestral African varieties take six months. Thus Jones and his team could combine the useful characteristics of two rice species using advanced in vitro technology of plant tissue culture and surpassed the limits of traditional plant breeding. Farmers who grow NERICA also save three months of land use and labor cost and grow extra short-duration crops such as vegetables.

NERICA was Africa's first successful genetically improved crop. For this work, the United Nations awarded the 2004 World Food Prize to Jones. In the wake of this success, *Time* magazine included Jones in the list of the most influential people in the world in 2007 (6). Jones's method was subsequently applied to generate 3,000 new varieties of NERICA, which are being grown in African countries like Benin, Ivory Coast, Gambia, Nigeria, Mali, Guyana, Togo, and so on, and many of these countries have become rice exporters.

6.4 The Green Revolution's Achievements

The green revolution was successful in increasing grain production in Asia, Latin America, and Africa. It saved the lives of millions from hunger and starvation. It can be said that the green revolution played an important role in maintaining peace in the world.

It also laid the foundation of mutual cooperation among various international institutes and scientists that lasted beyond the duration and need of the green revolution. Due to the political understanding, various international institutions and government machinery, private foundations, and banks worked together to foster scientific progress and ensure the food security of the world.

The green revolution was most successful in Asia because Asian countries already had the infrastructure and roads and had already developed a capitalist market system. During this period, many Asian countries—including India, Pakistan, Turkey, China, Sri Lanka, Indonesia, Malaysia, Vietnam, and Cambodia—became not only self-sufficient in food production but exporters of grains. For example, Pakistan achieved self-sufficiency in grain production in 1969; India followed this success in 1974, which was not expected by the world at that time. Similarly, when the IR8 rice variety was first released in the Philippines, it changed the country from an importer of rice to an exporter within just three years.

Overall, due to the increase in the yield of rice and wheat, food grains became cheaper, and the conditions of starvation and famine in developing countries could be avoided. The increase in grain yield per hectare prevented the expansion of cultivated land and helped protect the forests. According to one estimate, in the absence of the green revolution, by the year 2000, the world grain production would have been reduced by 20 percent, an additional 2–2.5 million hectare of agricultural land would have been needed to satisfy the food requirement of the current world population, and the cost of grain would be 30 percent higher.

Research in international centers also benefited the US, and the country's domestic agriculture also increased. Between 1960 and 2000, in developed countries, the yield of wheat increased by 208 percent, rice by 109 percent, maize by 157 percent, potato by 78 percent, and cassava by 36 percent. Overall, the standard of living in developed countries was also improved due to the availability of cheaper food grains. Furthermore, the green revolution brought prosperity to the lives of many farmers and helped agriculture-related businesses flourish. US companies made tremendous profits by selling fertilizers, pesticides, weedicides, and agricultural equipment in the international market, and the green revolution helped recover the US from the post–World War II recession.

The green revolution failed in Africa due to various reasons, including the late inclusion of Africa on the agenda and the promotion of maize[5] instead of African crops. Furthermore, African countries lacked the agricultural infrastructure and trained professionals for disseminating adequate training to farmers about the use of fertilizers, pesticides, machines, and so on. Consequently, maize varieties that were successful in the US and Mexico were not successful in Africa. By 1998, while 82 percent of agricultural land in Asian countries, including China, India, and Pakistan, was growing genetically improved varieties of cereal crops, in Africa, only 27 percent of the area had these crops. However, many useful lessons were learned from the first phase of the green revolution (1965–85). The biggest gift of this period has been to lay the foundation for cooperation between agricultural scientists around the world. Later, scientists and policymakers succeeded in solving Africa's problems in the second phase of the green revolution (1985–2000). During this period, fourteen other CGIAR research centers were opened, each focusing on the prime regional crop (eleven major crops, including potatoes, pulses, cassava, peanuts, beans, millets, and sorghums). The goal of each of these centers, which are spread around the world, is to conserve and improve the germplasm of local crops. From time to time, these international centers release advanced varieties of one or more crops to farmers. Studies show that worldwide production of wheat, rice, and maize has increased by 1 percent, 0.8 percent, and 0.7 percent, respectively, due to germplasm improvement during the second phase of the green revolution. Similarly, yields of minor grains like sorghum and millet have increased about 0.5 percent annually since 2000. International cooperation among scientists and various governmental and private agencies was also beneficial to many African countries, and after 1980, efforts to improve the local African crops, including rice, yam, cassava, and so on, began. Even after the end of the green revolution, these efforts are continuing.

Despite a nearly threefold increase in the world's population in the last fifty years, no major famine occurred. Even today, the world's population is producing more food than is needed. The green revolution played an important role in achieving global food security.

5. Maize cultivation requires a lot of fertilizer and irrigation, but most areas of Africa lack water, and large dams could not be built for irrigation.

6.5 The Limits of the Green Revolution

The green revolution stood on the maximum exploitation of resources. Therefore, after about fifty to seventy years of intensive grain cultivation, soil fertility has decreased, groundwater levels have fallen significantly, and the overflow of agrochemicals led to the pollution of various water bodies. But by 1980, wheat production showed a slow decline by about 1.5 percent annually, and so far, it has fallen more than 20 percent than the 1970s and ’80s. On average, there has been a one-third decline in wheat production per hectare since the green revolution despite the continuous use of synthetic fertilizer, irrigation, and other mandated agrochemicals required to keep a check on pathogens and weeds. The high-yielding varieties of wheat, rice, and maize absorb large quantities of nutrients from the soil. The synthetic fertilizers replenish three major elements—nitrogen, phosphorus, and potassium (a.k.a. NPK)—but do not replace micronutrients and soil organic matter. Thus in many places, the soil has lost its normal texture, and it has turned almost sand-like. Recuperating the health of the soil is necessary, which cannot be done by continuing the green revolution’s model. The industrial method of farming needs to be reviewed and improved.

The goal of the green revolution was to achieve an increase in global food production, and during its implementation, the health of the ecosystem was not taken into consideration. The excessive use of pesticides, fertilizers, and weedicides polluted the groundwater, water bodies, and the air. Today, the entire food chain has become contaminated, and cancer and other diseases have increased in farmers and consumers. In some countries, positive efforts have been made in this direction. Today, breeders around the world are trying to develop varieties of crops that require less synthetic fertilizer, less irrigation, and fewer pesticides to grow. Recently, a super green rice variety has been released in the Philippines, which can maintain its productivity with less fertilizer and water use.

Before the green revolution, the staple diet of most Asian countries consisted of a wide variety of coarse cereals such as sorghums, millets, pulses, starchy tubers, and roots, which provided essential nutrients such as iron, calcium, vitamins, and micronutrients. There was no help for farmers growing other crops in the green revolution scheme, so these crops’ production decreased. The majority of the population’s diet has become homogenous, mainly consisting of rice, wheat, and maize. Therefore, malnutrition and devastating lifestyle diseases like diabetes increased despite getting plenty of calories.

The varieties of crops that are being grown today are few, and thousands of local varieties of crops have disappeared. Farmers no longer grow them, and thus our food sources are very limited and the diversity of crops has decreased significantly. The outbreak of several diseases has also revealed the importance of biodiversity and the limits of monocropping, which was encouraged by the green revolution. Thus despite achieving a high productivity of cereal crops, the green revolution package was not sustainable.

6.6 The Life of Norman Borlaug

Norman Borlaug, the father of the green revolution, was born on a farm near Cresco, Iowa, to Henry and Clara Borlaug.[6] He worked on the 106-acre family farm raising corn, oats, cattle, pigs, and chickens from age seven to nineteen. After completing his primary and secondary education in Cresco, Borlaug enrolled in the University of Minnesota and received a bachelor's degree in 1937, a master's degree in 1939, and a PhD in 1942. From 1942 to 1944, he was a microbiologist for DuPont, where he worked on industrial and agricultural bactericides, fungicides, and preservatives. In 1944, he accepted a position as a geneticist and plant pathologist assigned the task of wheat research and production program in Mexico, supported by the Rockefeller Foundation and the Mexican government. As described earlier, in that position, Borlaug successfully developed high-yielding, dwarf, disease-resistant wheat varieties.

He built collaborations with local farmers and scientists from all over the world. Borlaug had a deep connection with the farmers, and farming was no stranger to him. Childhood experiences had been with Barlog throughout his life. He was always trying to end hunger in the world. Equally important to his training with Stakman were his life experiences, which helped him sustain hardships for nearly two decades in Mexico's difficult conditions. When the Rockefeller and Ford Foundations cooperated with the Mexican government to establish CIMMYT, Borlaug was its first director.

He is credited with saving more than a billion people around the world from starvation. In 1970, Borlaug received the Nobel Peace Prize. For the first time, a scientist received this award. Shortly after receiving the Nobel Prize, Borlaug established the World Food Prize to honor other scientists and breeders who made outstanding contributions.

Borlaug was also awarded the US Congressional Gold Medal, US Presidential Medal of Freedom, Pakistan's Sitara-e-Imtiaz (1968), and India's second-highest civilian honor, Padma Vibhushan (2006). Overall, Borlaug was a member of the Agricultural Sciences Academies of eleven countries and received more than sixty honorary doctoral degrees and around fifty other awards. Borlaug also received extensive recognition from universities

6. For Norman Borlaug's biography, see https://achievement.org/achiever/norman-e-borlaug and http://nobelprize.org/nobel_prizes/peace/laureates/1970/borlaug-bio.html.

and organizations in six countries: Canada, India, Mexico, Norway, Pakistan, and the United States.

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Genetically Engineered Crops

The knowledge of naturally occurring intra- and interspecies gene transfer events, the advances in recombinant DNA technology, and plant tissue culture helped scientists transcend traditional breeding limits and introduce desired genes from any organism into crops. The crops containing one or more genes from other species (trans/foreign gene) are known as genetically engineered/modified (GE/GM) crops.[1] For example, many insect-resistant GE crops contain the delta-endotoxin gene from a bacterium, *Bacillus thurigiensis* (Bt).

The purpose of making transgenic crops could be to increase the crop yield, prevent damage from pests and pathogens, and increase the nutritional quality. In 1994, the Food and Drug Administration (FDA) approved the first GE crop, *Flavr Savr* tomato, for human consumption. This tomato variety has a longer shelf life due to delayed fruit ripening. Since then, the FDA has approved more than fifty GE crops.[2]

This chapter summarizes the advances made in genetics and other related technology that led to the development of genetically engineered crops and provides examples of a few success stories.

7.1 DNA Is Genetic Material

In the early 1950s, it was proven that DNA is genetic material. In 1954, Francis Crick and James Watson proposed the double-helix model of DNA based on evidence from Morris Wilkins's and Rosalind Franklin's experiments. They suggested that DNA is a double-stranded, helical structure made of four nucleotide bases: adenine (A), thiamine (T), cytosine (C), and guanine (G). The two strands of DNA are antiparallel and are connected by covalent bonds: adenine from one strand binds to thiamine in another strand, whereas cytosine of one strand binds to guanine of the second strand (see figure 7.1). Thus the nucleotide sequence of one strand is complementary to another strand. If the sequence of one strand is known, it is easy to deduce the second strand sequence. Watson and Crick explained that one strand could serve as a template for making the other strand

1. An organism containing a transgene is known as a genetically modified organism (GMO).
2. Not all GE crops are in cultivation today. Only a few are grown in the US. To see the updated information on GE crops, visit the FDA's website: https://www.fda.gov/food/consumers/agricultural-biotechnology.

due to their complementary nature. Thus DNA contains information for self-replication—a necessary qualifier for being genetic material. In 1962, Crick, Watson, and Wilkins received the Nobel Prize for the elucidation of DNA structure.

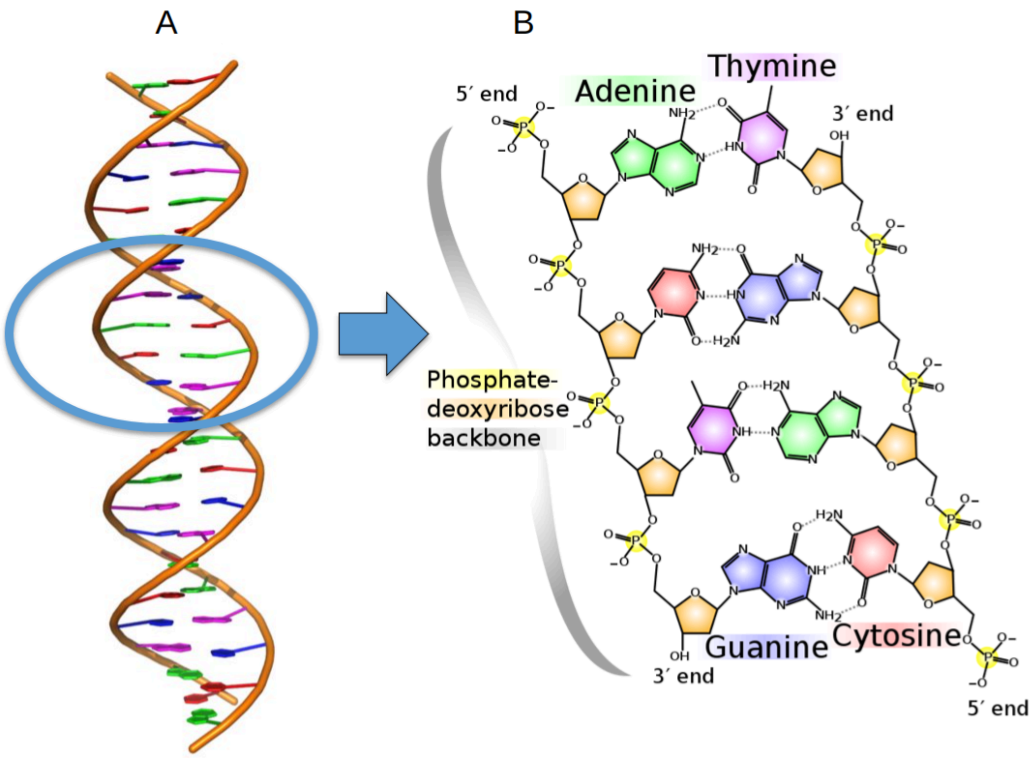

Fig 7.1 (A) Simplified representation of a double stranded DNA helix with alternating adenine residues in green, thymidine in red, cytosine in dark blue, and guanine residues in cyan. The phosphate backbone is displayed as an orange ribbon. (B) Chemical structure of DNA with colored labels identifying the four bases as well as the phosphate and deoxyribose components of the backbone. "DNA double helix" is a derivative of "DNA chemical structure" by Madeleine Price Ball, used under CC0 1.0, and "Double stranded DNA with coloured bases" by Vcpmartin, used under CC BY-SA 4.0. "DNA double helix" is licensed under CC BY-SA 4.0 by Sushma Naithani.

In 1958, Arthur Kornberg extracted a DNA polymerase enzyme from *E. coli* cells that was capable of copying DNA. He demonstrated the replication of a small DNA fragment in vitro using DNA polymerase and proved that either strand of DNA could serve as a template during DNA replication. DNA replication is a semiconservative process: four strands of DNA are made from two parental strands, and eventually, two double helixes form; each helix contains one old and one new strand. Other scientists' research showed that DNA replication is not completely foolproof, and a proofreading and repair process ensures the removal of mismatched bases and repairs DNA. Thus DNA sequences are preserved for millions of years and ensure the continuity of a biological species. However, a permanent change in the DNA sequence (mutation) can occur due to the extremely low level of proofreading errors during the DNA replication. Most single nucleotide mutations are harmless and don't affect a phenotype. However, after many generations, the accumulation of mutations could result in phenotypic changes. Thus DNA also acts as raw material for evolution.

The complete set of genetic material present in an organism is called its genome.[3] The genome of prokaryotes is made of a single circular chromosome, whereas the genome of eukaryotes consists of more than one chromosome. Individuals of the same species have the same genome size (same number of chromosomes), and chromosomes between different species vary. The structural and functional unit of the genome is a gene. The order of the four nucleotide bases determines the composition of individual genes. Several thousand genes are present within the organisms. Typically, the information from the DNA (gene) is transcribed into RNA, and a subset of RNA (messenger [m] RNA) is then translated into proteins. The proteins carry out most of the structural and functional activities within the cells. This unidirectional flow of genetic information from DNA to protein is called *central dogma* and serves as the fundamental principle for the basis of life. In addition to protein-coding mRNAs, organisms' genomes contain genes that encode various other types of structural and regulatory RNA molecules (e.g., rRNA, tRNA, and microRNA).

7.2 Recombinant DNA Technology

After the 1970s, a new branch of biology, molecular biology, came into existence. Its focus is to understand the structure and functions of genes and gene products. It was expected that the sum of the knowledge about all genes could help in understanding the whole organism. The basic principles of molecular biology were discovered by experiments

3. The animals have additional DNA inside mitochondria; plants have DNA inside chloroplast and mitochondria. These are identified separately as organellar genomes.

conducted on unicellular bacteria and fungi, and later studies on higher eukaryotes, including plants, began.

First, scientists succeeded in extracting DNA from various organisms. The next challenge was to identify the thousands of genes and then determine their function within the cell. The discovery of restriction enzymes and ligase enzymes made the identification and cloning of the individual genes possible. The restriction enzymes recognize a specific sequence of four/six/eight nucleotides within DNA and make a cut in the strand. The sites of restriction enzymes are randomly scattered within the genome, and hence they cut double-stranded DNA into small pieces. So far, more than 3,000 restriction enzymes have been discovered, of which 600 are available in the market. These enzymes were named after the bacteria where they were first identified. For example, the *EcoR1* enzyme is found in the *Escherichia coli* strain RY13, and *HindIII* was discovered in *Hemophilus influenzae*.

Bacteria make restriction enzymes to protect themselves against virus infection. When viral DNA enters the bacterial cells, these restriction enzymes slice the virus DNA and block the virus's growth. However, bacterial DNA remains protected from their own restriction enzymes by methylation of the corresponding restriction sites. In 1978, Werner Arbor, Hamilton Smith, and Daniel Nathans were jointly awarded the Nobel Prize for the discovery of restriction enzymes. In 1967, a special enzyme, ligase, capable of joining two DNA fragments, was discovered in Gellert, Lehmann, Richardson, and Hurwitz's laboratories. For scientists, the restriction enzymes served as molecular scissors, and ligase served as a molecular glue for cutting and joining DNA fragments.

The next question was how to amplify small DNA strands for their detailed analysis. Here, the knowledge about a bacteriophage lambda that infects *E. coli* bacteria explicitly came in handy. Esther Lederberg discovered the bacteriophage lambda in 1951. Esther Lederberg observed that after infecting *E. coli*, lambda could undergo either an active lytic or a latent lysogenic cycle. When the bacterial cell grows in the rich medium (rapidly dividing), then the lambda enters the lytic cycle, makes 1,000 of its copies by using resources and machinery of bacterial cells, and then destroys the host. These 1,000 lambda offspring then infect 1,000 new cells and produce 1,000,000 new progenies in the next cycle. In this way, the virus grows at the speed of a rocket. However, if bacterial cells are deprived of nutrients and are in the stationary phase (not dividing), lambda enters the lysogenic cycle resulting in the insertion of the lambda DNA into the bacterial genome without causing any trouble. However, if the situation worsens for bacteria (or it experiences heat stress), lambda enters the lytic cycle to makes use of whatever resources are available for making its copies before host cells die. For lambda, going to a lytic or lysogenic state is controlled by the repressor protein encoded in lambda DNA. When lambda DNA enters the bacterial cell, first, the repressor protein is made, which blocks the rest of lambda's genes. The rapidly dividing bacterial cells contain high levels of proteases, which can break down the repressor and allows the lambda to enter into the lytic cycle. Under nutritional deprivation, bacterial cells come to a stationary stage where the protease levels remain low, and the lambda goes into the dormant lysogenic cycle. When the host cells face stress (e.g., high temperatures), protease protein increases to mitigate the situation and recycle the nutrients. Thus in such a situation, the repressor protein is destroyed, and lambda enters the lytic cycle. Based on this knowledge of the lambda life cycle, scientists created versions of lambda in which researchers could easily turn the lytic and lysogenic cycle on or off. Furthermore, scientists found that only 75 percent of the lambda genome is indispensable; 25 percent of the lambda genome can be replaced with any DNA fragment. Thus if a gene is inserted within the lambda genome, millions of clones can be made quickly in *E. coli*. Then this DNA could be isolated, stored, and used for further experimentation. The lambda served as the first vector for cloning genes.

In the 1950s, Esther and Joshua Lederberg also observed that bacteria have many (10–1,000) small, circular DNA structures called fertility (F) plasmids in addition to a large genome. Before cell division, plasmids undergo autonomous replication and are inherited by the daughter cells. Soon, from a pathogenic bacteria, Shigella, another type of plasmid was discovered that contained antibiotic resistance genes (known as resistance [R] plasmids). It was easy to isolate plasmid DNA from bacterial cells, and also, bacterial cells have a natural capability of uptaking these small plasmids. The introduction of these plasmids into bacterial cells is called transformation. Scientists optimized protocols for increasing the efficiency of transformation and created chimeric plasmids by joining parts of F and R plasmids that contained one or two antibiotic-resistance genes, sites of restriction enzymes, and the autonomous origin of replication for *E. coli*. Thus these plasmids served as excellent vectors for cloning small DNA fragments. If a mixture of plasmid DNA and bacterial cells are plated in a medium containing a specific antibiotic, then the normal bacterial cells will die, and only transformed cells containing the desired plasmid (clone) will grow.

After the 1970s, the cloning of small DNA fragments (less than 20 kilobase pair [Kb]) in plasmid vectors and lambda-based phasmids became routine. Soon methods for DNA sequencing were invented, which made it possible to read the coded information (the order of four nucleotide bases, A, T, G, C) present within the genes. Computer analysis was used for analyzing sequencing data, and the field of bioinformatics was born. By comparing the genes present within living beings, it was found that the genetic code and genetic mechanisms are conserved among bacteria, plants, and animals. Computer algorithms are also used for assessing the similarity between the homologous genes from different organisms. The homologous genes between closely related species are more similar than distantly related species. In the late 1990s, due to advances in sequencing technology, it became possible to sequence whole genomes of bacteria, fungi, plants, and animals. Comparing the entire genome of different organisms allowed quantifying the similarities among the various organisms and deciphering the evolutionary distance between the species (see figure 7.2). In the light of modern genetics, molecular biology, and phylogenomics, we can now understand the process of biological evolution in reverse order.[4]

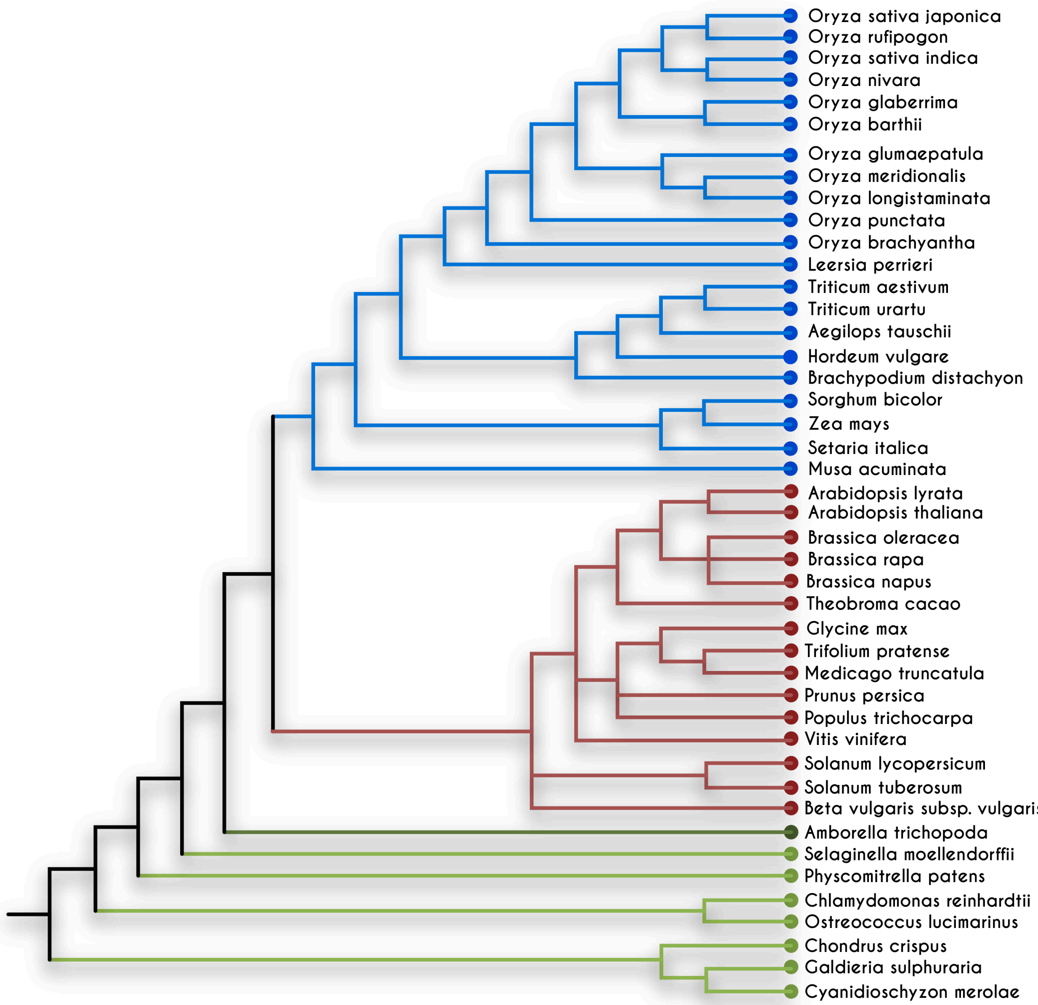

Fig 7.2 Genome sequence comparisons could reveal evolutionary histories and phylogenetic relationships between plant species. Genome sequence comparisons and phylogenetic tree were generated by Sushma Naithani using [Gramene database](). "Genome sequence comparisons" by Sushma Naithani and [OSU OERU]() is licensed under [CC BY 4.0]().

7.3 Gene Transfer in Plants

We often see swollen, round, tumor-like knots on the roots, twigs, and branches of many plants around us (see figure 7.3). These knots, called crown galls, are caused by a soil bacterium, *Agrobacterium tumefaciens*. These galls do not cause the death of the host

4. Have a look at the Tree of Life at http://tolweb.org/tree, and see the Tree of Life segment of BBC One's "Charles Darwin and the Tree of Life," narrated by David Attenborough, at https://youtu.be/H6IrUUDboZo.

plant but stunt their growth. The virulence of *Agrobacterium* strains is determined by a Ti plasmid present within the bacterium. Marc Van Montagu and his colleagues studied eleven pathogenic and eight nonpathogenic strains of *Agrobacterium* and found that all pathogenic strains had Ti plasmids and all nonpathogenic strains lacked Ti plasmids. They also noticed that the introduction of Ti plasmids into nonpathogenic strains transforms those into pathogenic strains. Thus it was concluded that *Agrobacterium* needs Ti plasmids for infecting the plants. The sequencing of the Ti plasmid revealed that it contains virulence (vir) genes and genes for the biosynthesis of auxin, cytokinins (plant growth hormones), and opines. The vir genes help bacterium infect host plants. The plant hormones promote the rapid growth of the cells at the site of infection (formation of crown galls), and opines serve as sources of energy, carbon, and nitrogen for *Agrobacterium*. Research in the 1970s and 1980s showed that *Agrobacterium*'s persistent presence within galls is not required for tumors to grow. In fact, after infecting a plant cell, *Agrobacteria* leave the Ti plasmid in the host cell, and then a large fragment of Ti plasmid, called T-DNA, gets inserted into the plant genome. The T-DNA in the plant genome continues to provide instructions for promoting the growth of the crown gall tumor and the biosynthesis of opines.

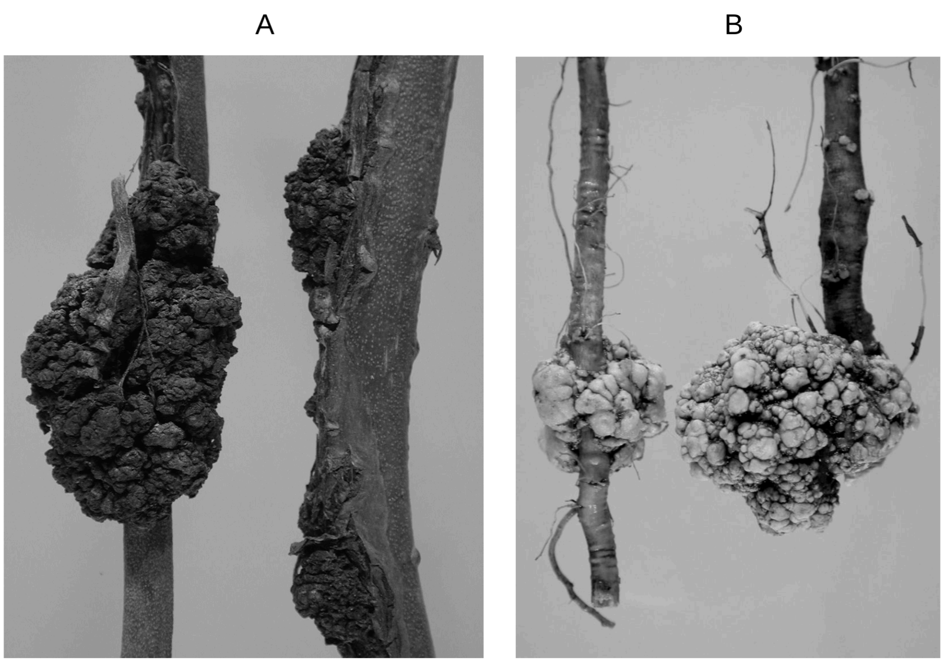

Fig 7.3 Crown galls in blueberry stem (A), and apple root (B) infected with Agrobacterium. Photos of blueberry stem and apple root by Melodie Putnam (Plant Clinic, Botany and Plant Pathology, Oregon State University) are licensed under CC BY 4.0.

If a gene is inserted within the T-DNA of the Ti plasmid using recombinant DNA technology, it can be easily transferred within a plant genome using *Agrobacterium*. Scientists modified Ti plasmid by replacing genes responsible for tumor growth with restriction enzyme sites, antibiotic resistance genes, and the E. coli plasmid replicons. Thus chimeric Ti plasmids allowed cloning of foreign genes in them and were able to replicate within both *E. coli* and *Agrobacterium*. Scientists had the flexibility of efficiently cloning genes in *E.*

coli and then use *Agrobacterium* for transferring the desired gene into the plant genome (plant transformation). Since *Agrobacterium* strains have a limited host range, they cannot transform all species of plants. The gene gun was used for transforming plant species, for which agroinfection was not an option. In this alternative method, very fine particles of gold or tungsten coated with desired DNA are bombarded on plant tissue by the gene gun. The advances in plant tissue culture made it possible to regenerate whole plants from small plant parts. Thus the combination of recombinant DNA technology and plant tissue culture allowed the bioengineering / genetic engineering of plants for important quality traits (that were not available in a given plant species' diversity pool). It became possible to introduce useful genes from bacteria, animals, and other plant species into the crop species.

Both methods of plant transformation use small plant parts to start with, and after agroinfection or gene bombardment, the selection of transgenic cells is carried out in the synthetic tissue culture media (see figure 7.4). One or more antibiotic selection makers accompany the transgene; thus only transgenic cells grow in this media while normal cells die. After several rounds of selection and multiplication of transgenic cells in the tissue culture, tests for the desired transgene are carried out. Once the insertion of the transgene is confirmed, the expression analysis and other assays are conducted, and whole plants are regenerated.

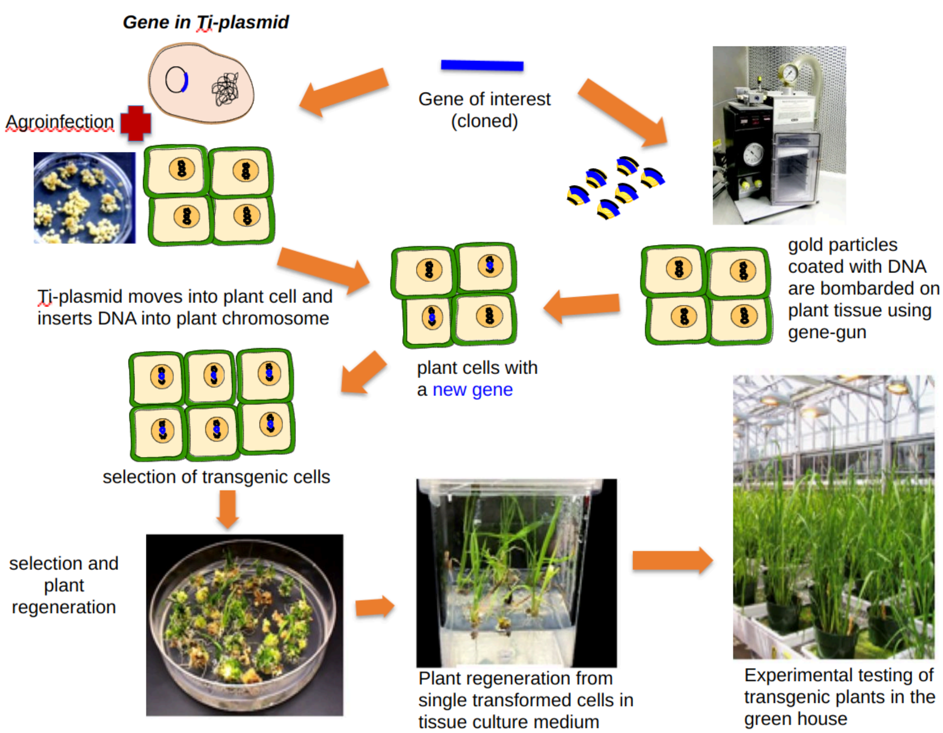

Fig 7.4 An overview of plant (rice) transformation. Sushma Naithani created the figure using photos provided by Dr. Ajay Garg (Cornell University). "An overview of plant (rice) transformation" by Sushma Naithani and Ajay Garg is licensed under [CC BY-SA 4.0](https://creativecommons.org/licenses/by-sa/4.0/).

In general, both plant transformation methods have a low efficiency, and then among the transformed plant cells, only a few show the desired level of transgene expression. Once the transgenic plants are fully developed, the second round of testing begins, and one to five of the best-performing plants are selected.

7.4 GE Crops

The GE crops made so far can be divided into three classes: (i) pest or pathogen resistant, (ii) herbicide tolerant, and (iii) biofortified with improved nutritional value (see table 7.1). At present, ~15 GE crops are being grown in 12 percent (179.7 million hectares) of the total agricultural land worldwide. In the US alone, ten GE crops are being grown on 70 million hectares. Maize, soybean, and cotton are among the most grown GE crops. Other GE crops include apple, mustard, sugar beet, papaya, potato, pumpkin, eggplant, alfalfa, poplar, rose, golden rice, golden cassava, and so on.[5]

7.4.1 The Story of Virus-Resistant Rainbow Papaya

The delicious papaya fruit is a rich source of vitamins A and C, calcium, and potassium. Papaya (*Carica papaya*) is the native plant of Central and South America. When Christopher Columbus tasted it for the first time, he was overwhelmed and named it the "fruit of the angels." After the fifteenth century, papaya spread throughout the world under the umbrella of European colonialism. Today it is grown in India, Brazil, the Philippines, Indonesia, Malaysia, Thailand, Hawaii, and the Caribbean islands. Usually, within six months after sowing the seed, the papaya grows as high as the average tree and starts bearing fruit within a year. Within three years, the papaya tree matures and produces a full yield. The cost of setting up papaya plantations is less than that of other plantations, and the farmers make decent profits from it.

The commercial cultivation of papaya first began in the Hawaiian Islands. Around 1940, papaya plantations were first established on the island of Oahu, which provided a livelihood to many local farmers. In the 1950s, an outbreak of the papaya ringspot virus (PRSV) occurred in Oahu's papaya plantations. This virus causes the stunting of trees, the deformation of leaves, the decline in their yields, and rounded spots in the infected fruit (see figure 7.5). Within a short period, the infected plant dies. Within a few years, the papaya plantations of Oahu were destroyed by the PRSV, so the industry moved to the big island of Hawaii, where the papaya industry flourished and expanded without any problems for

5. See https://www.fda.gov/food/consumers/agricultural-biotechnology.

the next four decades. In 1984, Hawaii's papaya production reached its highest point (80.5 million pounds). However, around 1990, the PRSV appeared in Hawaii. As expected, the papaya plantations of Hawaii were devastated. By 1997, the papaya production declined up to 40 percent, Hawaii's economy staggered, and many farmers' livelihoods were destroyed.

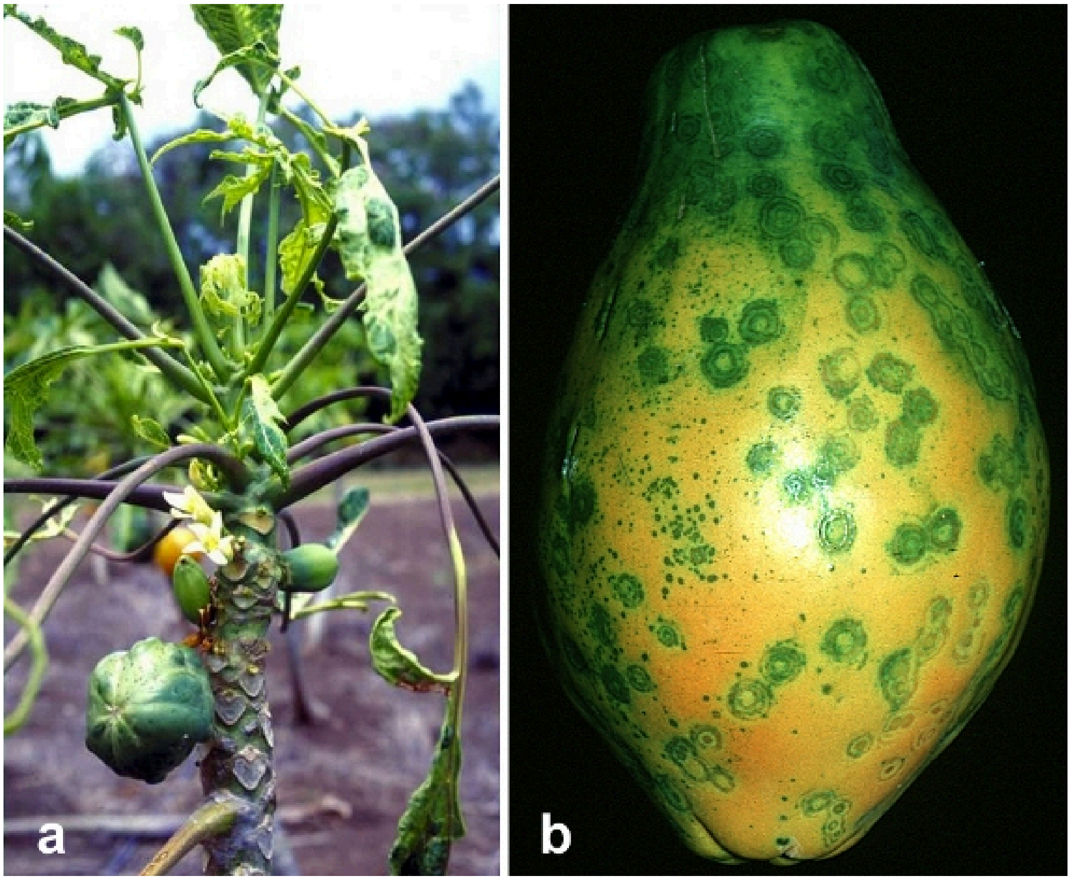

Fig 7.5 Image of Papaya Ringspot Virus symptoms on trees and fruit. [“Papaya Ringspot Virus Symptoms”] by [APS] is in the public domain.

Most of Hawaii's papaya farmers were first-generation, less-educated immigrant Filipinos. Fortunately, Dennis Gonsalves, a Cornell University professor, grew up in Hawaii and knew the importance of papaya for the local economy. He noticed the PRSV when its outbreak began in Hawaii and started a research project to save the papaya plantations from PRSV. First, he tried to find a PRSV-resistant papaya variety so that trait could be transferred to the high-yielding productive papaya varieties using traditional plant breeding methods. But he didn't succeed in finding such a variety. After this, Gonsalves identified less harmful strains of PRSV and experimented with them. He observed that if a papaya plant is first infected with a less aggressive strain, then the more harmful PRSV strain does not attack it. Until 1983, Gonsalves kept doing these experiments, but no permanent solution emerged for the disease's practical management.

Around 1983, Roger Beachy made a kind of transgenic tobacco that was resistant to the tobacco mosaic virus (TMV). After entering a living cell, TMV (like most other viruses) makes replicas of its genome using the host cells' resources, and then genome replication stops, and the synthesis of coat protein begins. The coat protein forms the virus's outer shell; thus the viral genome gets packed one by one, and the progeny of TMV busts out by destroying the host cells. Beachy cloned the coat protein gene of TMV and then transferred it into tobacco plants. Beachy's transgenic tobacco expressed high quantities of coat protein, so when TMV infected them, the coat protein present in the transgenic plant prevented replication of the viral genome, and infection was contained. Professor Gonsalves, inspired by Roger Beachy's success, decided to introduce the PRSV's coat protein gene in the papaya. In 1986, he successfully cloned this gene and transferred it within papaya plants with the help of a gene gun. As expected, the transgenic papaya showed resistance to the devastating PRSV. Field trials of these GE varieties, known as Rainbow and SunUp, began in 1992, and in late 1996, the US government approved transgenic papaya for commercial planting.

In 1998, Hawaiian farmers received Rainbow papaya seeds and the necessary advice free of cost, and Hawaii's papaya plantations got a new life. Currently, a cooperative society sells seeds of PRSV-resistant papaya varieties in Hawaii to farmers at very low prices. For the past twenty-two years, the papaya of Hawaii has been selling globally and contributes $50 million annually to Hawaii's economy. Gonsalves did not receive any grant from any government or private institution to make the GE papaya varieties. The only help he received was a small grant of $20,000 from Hawaii's senator Daniel Inouye. He created the world's first successful GE crop at a very low cost and made it available to farmers free of charge. In 2002, Gonsalves's research team was awarded the Humboldt Research Award for their contribution to agriculture.

Later, others made virus-resistant GE squash, zucchini, potatoes, and plums (see table 7.1).

7.4.2 Roundup Ready Soybeans

Weed control has always been a challenge for farmers. Weeds are wild plants (sometimes closely related to crops), are well adapted to various environments, and are more resilient than crops. Weeds compete for nutrients, sunshine, and water with crops and negatively affect crop yields (20–40 percent). In traditional societies, farmers used to burn the weeds before sowing and then afterward spent time weeding. However, this is not an option for very large agricultural fields. After 1950, chemicals were discovered that can destroy the foliage. Initially, they were sprayed in the area before sowing to eradicate weeds. But these chemicals are hazardous for human health and have chronic and acute toxicity. Furthermore, many herbicides are carcinogens, and their use poses a risk of polluting water, air, and the food chain.

In 1970, John Franz, a scientist at the Monsanto Company, discovered herbicidal activity in glyphosate.[6] Furthermore, it was found that some soil bacteria can convert glyphosate into harmless substances within a few days. Hence it posed relatively less risk of environmental pollution compared to previously used chemicals. In 1974, it was marketed as an herbicide with the trademark Roundup. In the 1970s, Monsanto also invested in plant biotechnology and began developing herbicide-resistant transgenic crops. They already had information that soil microorganisms can metabolize glyphosate into harmless products. Soon scientists discovered a gene within a bacterium that coded for an enzyme capable of degrading glyphosate. Subsequently, this gene was introduced in soybean and corn to create Roundup Ready GE varieties that survive herbicide (glyphosate) sprays while all the weeds die. In 1996, a Roundup Ready soybean was approved by the FDA for its cultivation in the US. In this way, weed management became simpler, cheaper, and more manageable. Also, farmers can plant soybeans in a closer, tighter row and get higher yields. However, the second-generation soybeans are sterile, so farmers must buy new seeds every year from the seed company. This strategy was also used for creating herbicide-tolerant corn, rice, and many other crops. More than 50 percent of GE crops currently grown in the US and worldwide are herbicide resistant (see table 7.1).

Today, more than 90 percent of soybeans, corn, cotton, and mustard growing in the US are Roundup Ready varieties. Farmers around the world are increasingly relying on herbicides for weed management. Since 1996, when genetically engineered glyphosate-tolerant Roundup Ready crops were first released, glyphosate use has risen fifteenfold globally; these quantities are beyond the natural capacity of soil bacteria to metabolize glyphosate. Therefore, glyphosate and other herbicides have generated concern among the public and policymakers due to their harmful effects on human health and the environment.

7.4.3 Insect-Resistant Bt Crops

Most of us do not like to eat any fruit or vegetable that is infested by insects. We see the clean fruit and vegetables in the market because farmers have used plenty of pesticides. If pesticides are not sprayed, one-third of the yields of most crops would be lost due to pest infestation. However, pesticides have harmful effects on human health and pollute the environment.

Scientists have been looking for an alternative to pesticides for a long time. In 1901, a Japanese scientist, Shigetane Ishiwata, was investigating the cause of silkworms' sudden deaths and found the bacterium *Bacillus* in dead larvae. He concluded that Bacillus is

6. Glyphosate (N-[phosphonomethyl] glycine) was discovered by Henri Martin in 1950.

responsible for their deaths. In 1911, Ernst Berliner also noticed that the Mediterranean floor moths' larvae were dying due to *Bacillus*'s presence. He named the bacterium *Bacillus thuringiensis* after the German city of Thuringia.

B. thuringiensis (or Bt) is a gram-positive soil bacterium that contains crystals of a delta-endotoxin protein that kills a broad category of insects. Upon ingestion, the crystal protein is cleaved into small fragments by proteases present in the alkaline environment of an insect's gut. One of the fragments generated from the crystal protein acts as a toxin. This toxin kills insects by forming pores into the cell membranes of the insect midgut. From 1920 onward, European farmers began spraying the Bt bacteria to protect their crops from pests. In 1938, commercial spore-based formulations known as Sporine made it to the market in France. Even today, organic farmers spray a similar formulation of Bt bacteria on their crops.

In the 1980s, the Monsanto Company succeeded in cloning the "cry" gene from *B. thuringiensis* that codes for the crystal protein. Subsequently, this gene was optimized for high expression in plant cells to develop insect-resistant crops (e.g., cotton, maize, eggplant, and rice). When insects feed on Bt plants, the delta endotoxin reaches their intestine, and they die. Therefore, Bt crops can protect themselves from insects. In 1995, the US government approved Bt cotton (*Bollgard cotton*) and Bt corn for cultivation. Since then, these crops are being grown in the US and many other countries. These seeds of Bt varieties sold in the market are of the heterozygous F1 hybrid. Thus, farmers cannot save seeds of Bt crops for the following year's sowing, because in the F2 generation, resistance and susceptibility traits segregate, and the insect-resistant traits get diluted in every subsequent generation. The farmers are required to buy these seeds every year, and their input costs increase.

The Bt crops do not eradicate insects completely, but their use could reduce the quantities of chemical pesticides manifold. The farm management is crucial for integrating these bioengineered crops and the chemical spray and keeping a sufficient refuge of non-GE crops to reduce the pests' selection pressure. In the US, Brazil, Argentina, and so on, practicing integrated pest management (IPM) is easy because thousands of acres of the farm are run by a single person or company. But in other developing countries, farmers have smaller agricultural land holdings and do not have enough space for "refuge." The farms are also surrounded by many neighboring farms.

Since living organisms constantly evolve, the protection offered by the Bt gene is not going to last for a long time, and eventually, it will be ineffective against insects. That is why scientists continue to make new versions of the Bt gene and search for other genes with similar properties. Thus it is expected that from time to time, scientists will release new GE varieties as the arms race between hosts and pests continues.

7.4.4 Golden Rice

The diet of poor people living in Asia, Africa, and Latin America mainly consists of rice and lacks fruits, vegetables, dairy, and meat. Consequently, millions of people have a huge deficiency of vitamin A in their bodies. According to a survey by the World Health Organization, more than 400 million people in twenty-six countries living on rice are deficient in vitamin A, due to which 500,000 children suffer from night blindness/blindness and 1 million children die annually.[7]

Vitamin A is essential for the proper development of humans and animals. It supports the healthy development of eyes, bones, and muscles and maintains adequate calcium levels and immunity. Humans cannot biosynthesize vitamin A of their own, but they get it from dairy, meat, and colorful vegetables and fruits. Red, orange, and yellow vegetables and fruits (e.g., sweet potatoes, carrots, oranges, and mangoes) contain provitamin A (β-carotene), which gets converted into vitamin A inside the human body.

For a long time, plant breeders have been searching for a rice variety in which β-carotene is found. In 1991, Ingo Potrykus, at the Institute of Plant Sciences of the Swiss Federal Institute of Technology, Zurich, started a project to bioengineer the β-carotene biosynthesis pathway in rice. In plants, the biosynthesis pathway consists of eight reactions, which are catalyzed by four enzymes. Rice contains most of the precursors for making β-carotene, but three out of four enzymes are nonfunctional. In 2000, Potrykus and his colleague Peter Beyer cloned two genes, phytoene synthase and lycopene cyclase, from the daffodil and the *phytoene*/carotene desaturase (crt1) gene from bacteria and then successfully introduced all three genes in rice plants to create the provitamin-rich variety by reconstructing the β-carotene biosynthesis pathway (see figure 7.6). One kilogram of this rice contains about eight milligrams of β-carotene, which gives them a golden hue, and thus this variety was named golden rice.[8] Once this basic strategy was successful, Potrykus signed a contract with the company Syngenta for enhancing the content of β-carotene and for large-scale experimental testing and handling. Syngenta produced an SGR2 variety of golden rice (~27mg β-carotene/kg) by replacing the phytoene desaturase in a daffodil with maize homolog. The Golden Rice Humanitarian Board has made golden rice free for farmers in developing countries with an annual income below $10,000. Later, with the help of research institutes of various countries, β-carotene biosynthesis pathways have also been enabled in many rice varieties (IR 64, Boro, PSB, RC82, etc.). After extensive testing, these GE rice varieties were found to be safe for human consumption. Unlike other GE crops, farmers who

7. For current data, visit https://ourworldindata.org/micronutrient-deficiency.
8. The story of golden rice, as told by Ingo Potrykus, is available at http://www.agbioworld.org/biotech-info/topics/goldenrice/tale.html.

grow golden rice can save the seeds of the next year's sowing. It took almost two decades before the golden rice was approved for farmers' use. In 2018, the FDA, Health Canada, and Food Standards Australia New Zealand recognized the IRRI's evaluation and approved the release of golden rice's GR2E variety. Bangladesh and China have begun the cultivation of golden rice.

A. B.

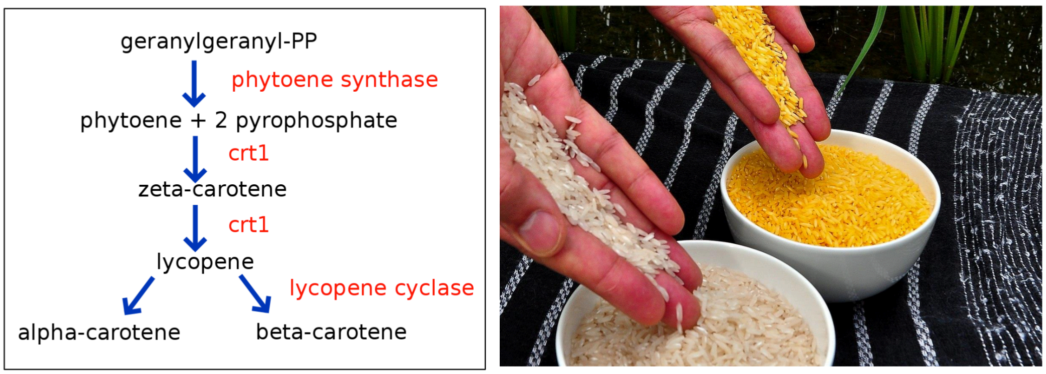

Fig 7.6 (A) Reconstruction of β-carotene biosynthesis pathway. (B) Comparison of Golden Rice with white rice. "Golden Rice, a rich source of vitamin A" is a derivative of "Golden Rice" by International Rice Research Institute (IRRI), used under CC BY 2.0. "Golden Rice, a rich source of vitamin A" is licensed under CC BY 4.0 by Sushma Naithani.

After rice, scientists started to work on biofortifying other crops using a similar strategy. For example, Maria Andrade, Robert Mwanga, and Jan Low created the golden sweet potato[9] with the support of global nonprofit agricultural research program HarvestPlus (https://www.harvestplus.org/), USAID, the Bill and Melinda Gates Foundation. Similarly, the golden cassava variety has also been developed, which has special importance for Africa.

9. Learn more about the golden sweet potato at https://www.worldfoodprize.org/en/laureates/20102019_laureates/andrade_mwanga_low_and_bouisold_template/?nodeID=88375&AudienceID=1&preview=1.

Table 7.1 Herbicide-tolerant GE crops

Crop	Herbicide	Year	Inventor
Canola	*Glufosinate*	1995	Bayer
Canola	glyphosate	1999	*Monsanto*
Cotton	*Bromoxynil*	1994	Calgene
Cotton	glyphosate	1996	*Monsanto*
Cotton	Sulphonylurea	1996	*DuPont*
Cotton	*Glufosinate*	2003	Bayer
Cotton	Dicamba	2015	*Monsanto*
Cotton	2,4-Dichlorophenoxyacetic acid (2,4-D)	2015	Dow
Maize (corn)	Glufosinate	1995	AgrEvo GmbH
Maize	glyphosate	1996	*Monsanto*
Maize	2,4-D	2014	Dow
Sweet corn	glyphosate	2011	*Monsanto*
Rice	*Glufosinate*	1999	*AgrEvo GmbH*
Soybean	glyphosate	1994	*Monsanto*
Soybean	*Glufosinate*	1996	Bayer
Soybean	Sulphonylurea	2007	*DuPont*
Soybean	Isoxaflutole	2013	Sygenta
Soybean	Mesotrione	2014	Sygenta
Soybean	Imidazolinone	2014	BASF
Soybean	2,4-D	2015	Dow
Soybean	Dicamba	2015	*Monsanto*
Sugar beets	glyphosate	2005	*Monsanto*
Sugar beets	*Glufosinate*	1998	*AgrEvo GmbH*

Table 7.2 Insect (pest)-resistant crops

Crop	Transgene	Year	Inventor
Cotton	Bt	1995	*Monsanto*
Field corn	Bt	1995	*Monsanto*
Sweet corn	Bt	1998	*Monsanto*
Potato	Bt	1995	*Monsanto*
Soybean	Bt	2016	*Monsanto*

Table 7.3 Virus-resistant crops

Crop	Coat protein gene	Year	Inventor
Papaya (Rainbow and SunUp)	Ring Spot Virus	1996	Dannis Gonsalves (Cornell University, and ARS-USDA)
Plum	Plum pox virus	2007	USDA
Potato	*Potato Virus Y*	1999	*Monsanto*
Potato	*potato leaf roll virus*	2000	*Monsanto*
Squash (not widely grown)	zucchini yellow mosaic virus	1994	Asgrow
Squash (not widely grown)	watermelon mottle virus 2	1994	Asgrow

Table 7.4 Nutritional value improved crops

Crop	Trait	Year	Inventor
Canola	*High lysine*	1994	Calgene
Maize	*High-lysine*	2006	*Monsanto*
Golden Rice	Rich in β-carotene (pro-vitamin A)	2005	Sygenta
Plenish Soybean	High oleic acid content (no trans fat)	2010	*DuPont*
Potato	Less *acrylamide, when cooked/fried at a high temperature.*	2014	J R Simplot Company
Arctic Apple	The GE Apples resist browning after being cut.	2015	Okanagan Specialty Fruits Inc.

7.5 The Impact of GE Crops

Humans have been selecting plants and animals for desired traits that suited their needs since the beginnings of agriculture 10,000 years ago. GE crops are the latest advancements made in this direction, with goals of achieving agricultural productivity and improving the available genetic stocks' quality. After 1930, these objectives were achieved using traditional breeding. In the early twenty-first century, scientists genetically engineered crops by introducing useful genes from any living forms and/or by rationally designed genes. A GE crop may contain one or more transgenes from bacteria, viruses, animals, or plants. However, more than 99 percent of it is similar to its mother plant (see figure 7.7). In general, crop plant species contain 30,000–50,000 genes, and less than five genes are introduced in any given GE crop. In this sense, GE crops are closer to the domesticated varieties.

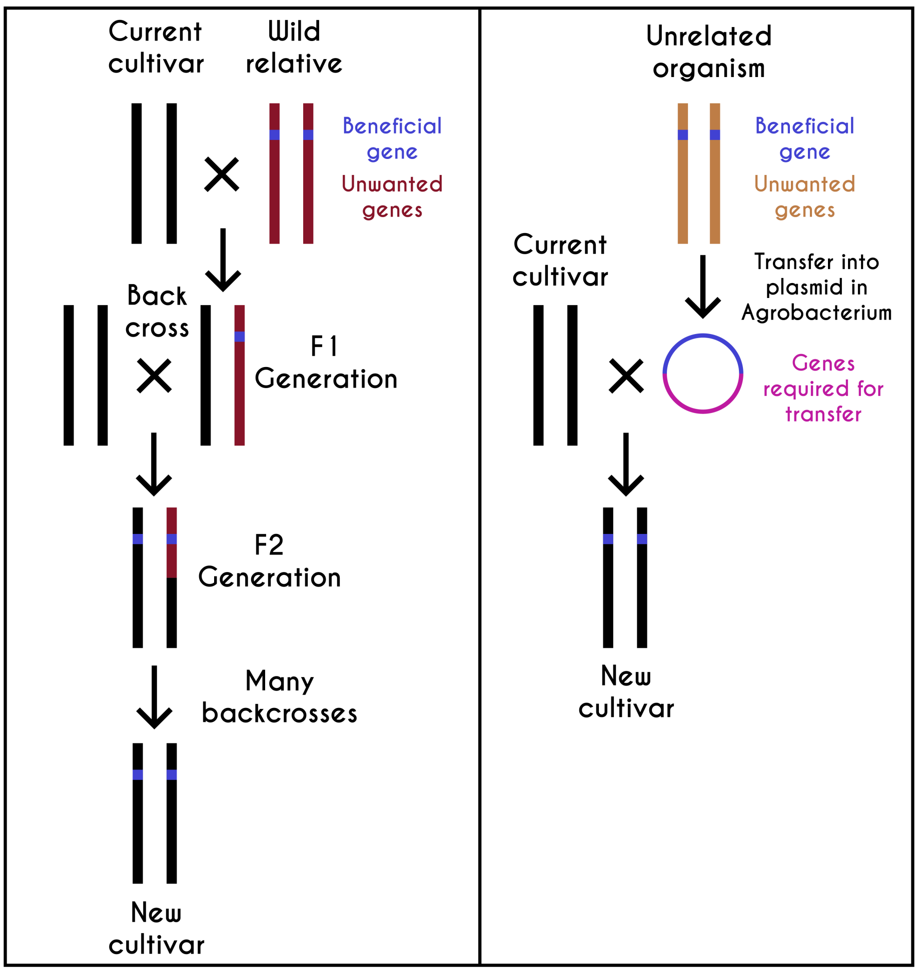

Fig 7.7 A comparison between conventional plant breeding and genetic engineering. "Breeding transgenesis cisgenesis" by Smartse is licensed under CC BY-SA 3.0 / image cropped.

Interestingly, people have adopted more than 1,000 high-yielding varieties (generated by traditional breeding), but GE crops have aroused significant anxiety around the world and have faced consistent opposition globally. There has been a constant debate about the technology and impacts of GE crops. The first and foremost concern is if GMO food is safe. GE crops undergo extensive safety trials before they are released for cultivation and are approved by the FDA. The data from various GE crops' safety trials in the last twenty-five years show that GMO food is safe. In 2016, the US National Academy of Sciences published a review of GE crops prepared by an independent committee of eighteen experts. This 600-page report (1) concluded that there is no evidence that anyone has had a problem digesting GMO foods so far. However, people have raised issues related to allergies and the presence of toxins in GMO food. Overall, GMO food is deemed safe by the experts. Today most experts, scientific institutions, and governments agree that GMO food does harm human health. According to an estimate, millions of people in twenty-eight countries have been consuming GMO food products daily for the past twenty-five years, and so far, none died due to eating such foods (1).

Contrary to what the experts have revealed, there is increasing anxiety among consumers about GMO products. This issue has not been settled for the people yet. Many nongovernmental organizations, consumer groups, and ordinary people worldwide are worried about the safety of consuming GMO food. No one has currently investigated GMO products' long-term effects on humans; therefore, both opponents and supporters of GMOs can't say anything definitively on the matter. For a long time, consumer groups had been advocating to clearly label products that are GMO, since in the US, this had not been required by law. Under consumers' pressure, the labeling of GMO (and more of non-GMO) products appeared increasingly, and in 2016, US Congress passed a law requiring the labeling of GE food (the bioengineered). Hence, the data on the long-term effects of GMO food on human and animal health may become available in the future.

Another issue is how much more productive GE crops are than the high-yielding breeds developed during the green revolution. In the last twenty-five years, the claims made about GE crops' increased productivity have not been fully met. The 2016 National Science Academy report (1) stated that the productivity of GE crops grown from 1990 to 2015 is not significantly higher than the high-yielding varieties of the green revolution era. Overall, the GE crops made the farmers less prosperous than the green revolution because agriculture's input cost (for buying seeds, fertilizer, irrigation, pesticides, fungicides, herbicides, etc.) is very high and leaves a small margin for profit. Compared to the green revolution era, today's farmers have smaller and less fertile farms in developing countries, and government assistance and subsidies have declined.

Did GMO technology improve the quality of food? Without a doubt, this technology has created many nutrient-rich crops—like golden rice, cassava, and sweet potato; high oleic acid–containing canola; Plenish soybeans; and so on—and offers an opportunity for further improvements. There is tremendous scope for solving malnutrition by using GMO technology. In addition, the genetic engineering of model and crop plants has provided a conceptual understanding of gene functions and many fundamental biological processes.

Besides genetics and genomics, immense progress has been made in vitro tissue culture technology. Together, the new knowledge and advancement in tools served as a foundation for next-generation CRISPR/Cas9 gene-editing technology that has a high potential for developing new biofortified and stress-tolerant varieties of crops.

At the beginning of the twenty-first century, GE crops were presented as a promising alternative to a non–environmentally friendly industrial farming system. But looking at the last twenty-five years, it is clear that GE crops have become an integral part of it. The folks who oppose GMOs argue that most GE crops ensure profit to corporations by encouraging increased use of pesticides, weedicides, fungicides, and fertilizers. To date, more than 50 percent of GE crops are herbicide resistant. The use of glyphosate and other herbicides has exceeded the safety threshold and poses threats to human health and the environment. The continuous spray of herbicides has led to the rise of superweeds that are increasingly adapting to various herbicides and require more potent mixtures (including two or more chemicals) or higher doses for effective control. Thus GM crop-based weed management is not sustainable. Additionally, the reliance on both high-yielding and GM crops on heavy inputs of energy and fertilizers also needs careful reevaluation.

7.6 Toward a Sustainable Future

The FAO projects the global population to grow to 9.7 billion by 2050. The biggest challenge of the twenty-first century is to keep the productivity of crops sustainable without causing further destruction to the environment and depletion of natural resources. Despite its overall efficiency, the current industrial agricultural system relies heavily on natural resources and energy. For example, half of the world's habitable land and more than 70 percent of global freshwater withdrawals are used for agriculture. Also, agriculture is a significant source of global pollution: 26 percent of global greenhouse gas emissions[10] and 78 percent of the global ocean and freshwater eutrophication is caused by agriculture.[11]

10. Agriculture is the prime source of greenhouse gases, including carbon dioxide (CO2), nitrous oxide (N2O), and methane, which cause the depletion of the stratospheric ozone layer and global warming. N2O has 300 times the warming potential of CO2. Usually, N2O is destroyed in the upper atmosphere by solar radiation. But current human activities (e.g., agriculture and livestock) have significantly increased N2O emissions and caused the perturbation in its natural cycle, resulting in its accumulation in the atmosphere. A comprehensive study by the Global Carbon Project and the International Nitrogen Initiative suggests that agriculture has contributed to a 70 percent rise in the global N2O levels. See the Global Carbon Project website for more details: https://www.globalcarbonproject.org/nitrousoxidebudget.
11. See https://ourworldindata.org/environmental-impacts-of-food.

Agriculture is the prime source of greenhouse gases, including carbon dioxide (CO2) and nitrous oxide (N2O), which cause the depletion of the stratospheric ozone layer and global warming. Therefore, the agricultural production systems have a big impact on global climate change, natural resources, and all living beings' health.

It is important to note that a continuous increase in agriculture productivity alone cannot solve hunger in the world. Natural resources are finite, and their overexploitation will have disastrous consequences. Therefore, we must explore other avenues for bringing efficiency to ensure food security. Today, enough grain is being produced worldwide to meet the need of 10 million people. Theoretically, if food is distributed equally among all the people of the world, then 75 percent of it is enough to feed the entire population of the world, and one-fourth can be saved, although achieving such equity at the global level is difficult to achieve due to various sociopolitical reasons. Nonetheless, it suggests that there are additional avenues where progress can be made beyond agriculture production.

It is noteworthy that more than 40 percent of all food produced worldwide is wasted in processing, transportation, supermarkets, and kitchens. Many fruits and vegetables are discarded because of their lack of aesthetic appeal or uniformity. Moreover, readymade, cheap, and readily available food requires extra production to compensate for its regular trashing as it expires on the supermarkets' shelves. When food is wasted, all the resources to grow, process, package, and transport are wasted along with it. Besides, the waste is a source of significant greenhouse gases. Overall, the current agricultural production systems and consumers' lifestyles put a burden on natural resources, the environment, and energy. If consumers do not change their habits, then the agricultural production system will remain in its current form. Both farmers and consumers will have to strive together to build a new sustainable agricultural production system.

In past decades, the gradual progress in plant genetics, genomics and breeding, precision agriculture, organic agriculture methods, and growing consumer awareness has been paving the way for the agricultural production system's future. Better management of agriculture, natural resources, the environment, and human resources is required in the agriculture sector. The formula for successful and sustainable agriculture will have elements from industrial farming, GM technology, precision agriculture, and organic farming. Equally important is to foster a culture of conscious consumption and change in consumers' behavior to create new, sustainable, just, diverse, and healthy agricultural production systems. The issue of agriculture has never been limited to production. It has given rise to human civilization and its polytheistic cultures. Change in agriculture is intricately associated with a change in human society. Only a better society can build a better agricultural system.

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