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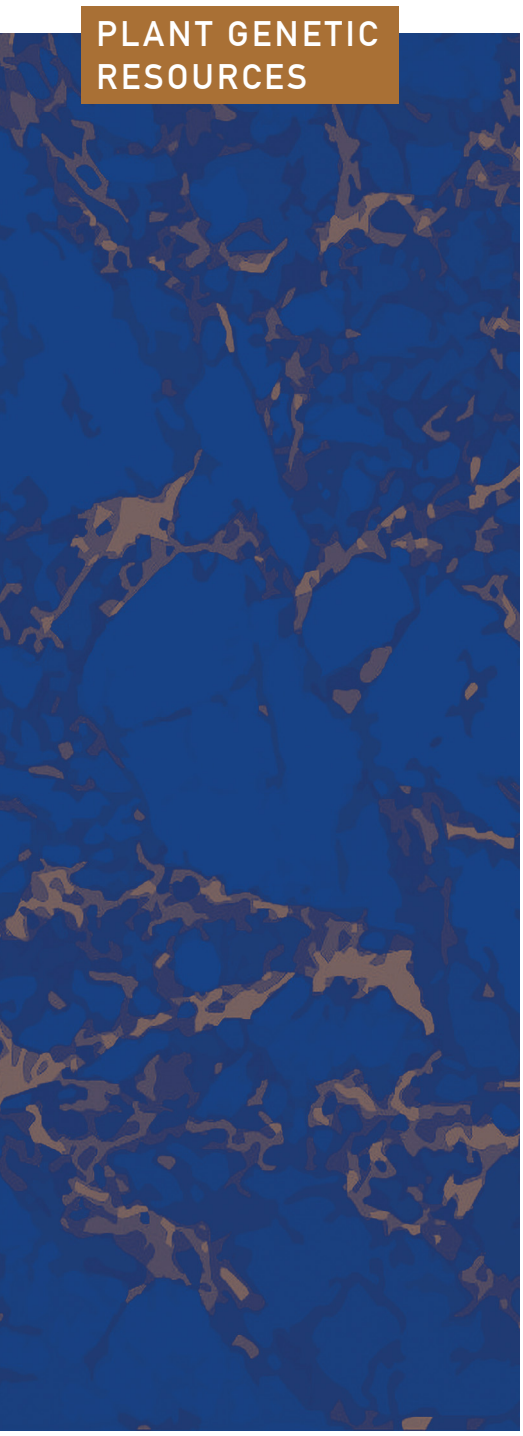
Xu Liu (Editor-in-Chief) and
Yunbi Xu (English Editor-in-Chief)

Crop Germplasmics

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Xu Liu (Editor-in-Chief) and
Yunbi Xu (English Editor-in-Chief)

Crop germplasmics is a scientific field dedicated to the study of diversity of crops and their wild relatives, as well as its utilization. It encompasses theories, technologies, and management systems involved in the formation, conservation, research, and utilization of crop diversity. This book introduces the theoretical and technical frameworks of crop germplasmics, providing a comprehensive overview of the discipline. The book begins with an Introduction that outlines the main themes, followed by a detailed exploration of fundamental theories. Subsequent chapters delve into specific theories, technical methods, and significant advancements within the workflow of germplasm. Topics covered include investigation and collection, safe conservation, phenotypic evaluation, genotyping and gene mining, germplasm enhancement, multi-omics research, big data construction, sharing and utilization, value assessment, property rights protection, and efficient management.

The book emphasizes a seamless integration of academic rigor and accessibility, reflecting the cutting-edge and forward-looking nature of the discipline's development. It serves as a valuable reference for professionals working with germplasm, as well as for postgraduate teaching, crop genetics and breeding, and basic research.

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Preface

Crop germplasm are strategic assets that are essential for ensuring food security, promoting green development, and safeguarding the seed industry, making them vital for the nation and the world. The government places great importance on the development of these resources. Chinese President Xi Jinping has emphasized the need to enhance the collection, conservation, and development of the germplasm. Despite a century of cultivation and research in the field of crop germplasm, the theoretical and technological framework remains incomplete, significantly hindering sustainable management practices. Crop Germplasmics is a newly established discipline that has evolved concurrently with the study of crop germplasm. It is a scientific field dedicated to exploring the diversity, conservation and utilization of the crops and their wild relatives. The discipline encompasses theories, technologies, and management systems related to the formation, conservation, research, and utilization of genetic diversity.

In 2022, we commemorated the 100th anniversary of Soviet scientist N.I. Vavilov, a pioneer in crop germplasm, first proposed the Law of Homologous Series in Variation. In the history of science and technology over the past century, the development of crop germplasm has undergone a journey from nothing to something, and from weakness to prosperity. Looking back at the progress of science, the pioneers such as C.R. Darwin, A. de Candolle, N.I. Vavilov, H.V. Harlan, and J.R. Harlan, as well as Yuchen Dong have made groundbreaking, foundational, and innovative contributions to this discipline over the past century. In China, renowned scientists like Shanbao Jin, Ying Ding, Dingan Liu, Yuchen Dong, Qiaosheng Zhuang, and Kansheng Cheng have dedicated their lives to this field, achieving remarkable accomplishments. As history has progressed into the 21st century, the discipline has been further developed by the introduction of the theory of Synergis Evolution of Crop Germplasm with the Cultural Environments and the advancement of multi-omics technologies, leading to a more mature stage of development in this field. We write this book in an attempt to enhance and perfect the discipline. The book identifies three foundational theories: the theory of the centre of origin of cultivated plants, the law of homologous series in variation, and the theory of synergistic evolution of crop germplasm and cultural environment. Additionally, the book defines four fundamental characteristics of crop germplasm: genetic diversity, genetic integrity, genetic specificity, and genetic accumulativeness. Simultaneously, a disciplinary technical framework was proposed for the first time, encompassing six major technical systems: extensive investigation, complementary conservation, precise evaluation, in-depth research, active enhancement, and shared utilization. The book elaborates on the theoretical foundations, technical methods, significant advancements, and developmental trends related to investigation and collection, conservation, phenotypic evaluation, genotyping and gene mining, germplasm enhancement, multi-omics research, extensive data construction, shared utilization, value assessment, property rights protection, and efficient management. It provides comprehensive descriptions of the theories, techniques, and notable progress in the investigation, conservation, evaluation, research, enhancement, utilization, and management of crop germplasm.

Crop Germplasmics is at the forefront of international development, exploring the theoretical foundations that underpin each technological direction while offering a detailed and concise overview of technological achievements. This book not only reviews the century-long history of the discipline but also outlines the development trends and key directions for theories and technologies based on a comprehensive assessment of the current state of the field. In particular, it highlights the significance of modern omics technology, biotechnology, and information technology in relation to crop germplasm, fully reflecting the progressive and forward-looking nature of the discipline. Crop Germplasmics is the first academic monograph in the field of crop germplasm. Its publication addresses a significant gap in the discipline, promotes leapfrog advancements, and enhances the training of professionals in germplasm. The book plays a crucial guiding role in the sustainable development of germplasm and provides essential support for related fields such as crop genetics and breeding. Crop Germplasmics is characterized

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by its theoretical depth, scientific strength, professional scope, systematic approach, and timely relevance. It serves as a valuable reference for germplasm workers, graduate-students, and researchers in crop genetics and breeding, as well as related basic research areas.

The authors of Crop Germplasmics are all experts in the field of germplasm. While actively promoting research initiatives, they have dedicated considerable time and energy to compiling this book. We would like to express our sincere gratitude to all the advisors, editors, authors, and reviewers who have contributed significantly to the writing, reviewing, and editing of this book. We extend special thanks to the translators for their excellent work, which has made the English version of this book accessible to the international audience.

Xu Liu

October 2024

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Chapter 1

Introduction: Crop Germplasmics

It is estimated that there are at least 750 000 species of plants on Earth, of which 300 000 to 500 000 species are higher plants, about 30 000 species are edible and 7000 have been collected or cultivated by humans (Wilson, 1992). There are 9631 plant species for food and agriculture in China, including 3269 cultivated species and their wild relatives, 4144 species for food gathering and grazing and 2218 species of weeds and poisonous plants. For diversity of crop species, there is a total of 870 different crops, covering 1281 cultivated species and 3308 wild relative species, including 38 food crops (64 species and 372 wild relative species); 62 cash crops (99 species and 541 wild relative species); 176 vegetables (156 species and 209 wild relative species); 86 fruit crops (142 species and 501 wild relative species); 80 forage and manure crops (180 species and 196 wild relative species); 128 ornamental crops (203 species and 595 wild relative species) (Liu *et al.*, 2008). Globally, there are about 120 crops of importance, of which 30 provide 95% of calories and protein consumed by humans, and 17 (including wheat, rice, maize, potato, barley, sweet potato, cassava, soybean, oat, sorghum, pearl millet, rye, peanut, broad bean, peas, banana and coconut) occupy 75% of the arable land and contribute 90% of food supply in the world. Wheat, rice and maize provide more than 50% of the global food energy intake. It should be noted that the importance of crops varies greatly from region to region. For example, in Central Africa, cassava contributes more than half of the plant-derived energy.

The emergence and development of crops is a typical dynamic process from domestication to improvement. During this process, various germplasm were created through natural and artificial selection. In the initial stage, wild plants were domesticated for human survival and gradually became primary varieties, which then were spread from the original places to many other places and evolved into various landraces adapted to different natural or humanistic environments. In the past one or two hundred years, with the emergence and development of modern genetics, genetic improvement was implemented to develop modern cultivars from landraces with greatly improved yield, quality, resistance and other agronomically important traits.

Crop germplasm are strategic resources for global food security and green development, as well as the material basis for the innovation of agricultural science and technology and the development of the modern seed industry. The discipline of crop germplasm, which can be defined as "crop germplasmics", is based on the theory of the centre of origin of cultivated plants, the law of homologous series in variation and the theory of synergistic evolution of crop germplasm with human cultural environments, depending on the technologic system composed of several genetic characteristics, including diversity, integrity, specificity and accumulativeness. It is the science relevant to the genetic diversity, and the utilization of crops and their wild relatives. It is also the basis for the development of other agricultural and biological sciences.

1.1 Purposes, Importance and Development of Crop Germplasmics

1.1.1 Purposes and Importance of Crop Germplasmics

Crop germplasmics is a science that studies the diversity and utilization of crops and their wild relatives, covering the theories, technologies and distribution of crop germplasm.

Crops are cultivated plants. According to the main purposes of use, crops can be divided into categories of food, cash, horticulture, forage and green manure. Food crops are those harvested mainly for human consumption as staple food, including cereals (such as rice, wheat, barley, oats, rye, maize, sorghum, foxtail millet and broomcorn millet), legumes (such as soybean, mung bean and broad bean) and roots and tubers (such as potato, sweet potato and cassava). Cash crops, also known as industrial raw materials, can be divided into fibre crops (such as cotton, hemp and bamboos), oil

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crops (such as soybean, peanut, rapeseed, sesame, castor and sunflower), sugar and hobby crops (such as tobacco, tea), medicinal crops, aromatic crops, seasoning crops (such as pepper, star anise) and rubber crops (such as rubber and koksaphyz). Horticultural crops include fruits, vegetables and ornamental plants (such as peony, tulip, dogwood, rhododendron, rose and carnation). Forage crops generally refer to plants cultivated for the purpose of raising animals, including forages that are harvested for stems and leaves (such as alfalfa, red clover, birdsfoot trefoil and *Stylosanthes* in Leguminosae, and perennial ryegrass, cattail grass, *Leymus chinensis* in Gramineae) and feed crops that are harvested for grains, roots, tubers and green leaves. Broadly speaking, cultivated trees and medicinal plants also belong to the category of crops. Crops are the foundation of agriculture and are closely related to human survival and development.

Diversity is a universal feature of all things in the world, which is true in the biological world, as there are variations in all living organisms. Diversity is the basic feature of biological system as the life has different types of changes in genes, cells, organs, individuals, populations, species, communities, and ecosystems. Biodiversity is the collection of all variations of organisms and their systems. Biodiversity usually includes three levels, namely, ecosystem, species and genetics. Biodiversity is the result of the evolution of life on the earth for billions of years and the fundamental basis for human survival and sustainable development. It is therefore self-evident for the significance of biodiversity conservation for the continuation and future development of civilization.

Crop germplasmics mainly focuses on the genetic diversity of crops and their wild relatives. As crops are related to the sustainable development of agriculture, forestry, fishery, animal husbandry and even industry, the conservation and utilization of crop diversity is related to human food, clothing, housing, and transportation, as well as people's expectation for a better life, which is not only associated with the current socio-economic development, but also with the survival and development of future generations. Therefore, the development of crop germplasm has extremely important practical and strategic significance for mankind.

1.1.2 Development of Crop Germplasmics

In 1831, the British explorer, Charles R. Darwin (1809–1882) started his "Beagle" tour around the world. Through studying the geology, flora and fauna along the way, he found that there were both similar and different species in each region. Later, he carried out many studies on paleontology, biogeography, morphology, embryology and taxonomy and published his famous work *On the Origin of Species* (Darwin, 1859), which demonstrated the origin of species and the diversity of life in nature from artificial selection, survival competition and adaptation, and proposed the theories of natural selection on the origin of species, making him the founder of theory of evolution. Darwin (1868) published his monograph *The Variation of Animals and Plants under Domestication,* which described in detail the extensive variations in cultivated plants such as wheat, maize, peas and fruit trees, and explored the sources and patterns of these variations, as well as the great role played by heredity and selection. Darwin's theory on evolution and genetic variation opened the door to exploring the origin of cultivated crops.

At the end of the 19th Century, Swiss botanist P. A. de Candolle (1806–1893), for the first time, systematically studied the origin of cultivated plants from the perspectives of history, language, archaeology, and botany as well as biological evolution combined with historical geographical distribution. He published his monograph *The Origin of Cultivated Plants*, which indicated that China, Southwest Asia, Egypt and tropical America were the regions where plants were first domesticated in the world (de Candolle, 1883).

In 1894, the Bureau of Applied Botany was established in Russia and was renamed the Department of Applied Botany and Breeding in 1916, specialized in the collecting and research of cultivated plants, particularly collecting germplasm of European barley, wheat, alfalfa, and other crops. After the establishment of the Soviet Union in 1922, it was renamed the All-Soviet Research Institute of Applied Botany and New Crops and reorganized into the All-Soviet Research Institute of Plant Industry in 1930. The geneticist N. I. Vavilov became the leader of the institute and carried out global plant explorations for collecting germplasm. From 1916 to 1940, the team led by Vavilov carried out more than 180 missions on scientific plant investigations, 40 of which were abroad by visiting more than 50 countries and regions, covering Asia, Europe, Africa, North America and South America. In 1929, Vavilov organized plant explorations for collecting germplasm in China, Japan, and the Korean Peninsula. Through global exploration and seed exchanges, Vavilov collected more than 250 000 accessions of germplasm, including over 36 000 accessions of

wheat, 23 000 of legumes and grasses, nearly 18 000 of vegetables, over 12 000 of fruits and 10 000 of maize. These germplasm materials were evaluated at various experimental stations in the Soviet Union and became valuable materials for Vavilov and other Soviet scientists to study cytology, genetics, and breeding. Based on global plant investigations, Vavilov first proposed The Law of Homologous Series in Variation (Vavilov, 1922), and the theory on the centres of origin of crops (Vavilov, 1926). He was the first scientist to propose the *ex situ* conservation of germplasm and became the founder of the discipline of crop germplasm. To commemorate the achievements of Vavilov, the All-Soviet Research Institute of Botany was renamed as the Vavilov All-Russian Institute of Plant Genetic Resources (VIR).

In 1898, the Department of Agriculture of the United States established the Bureau of Seed and Plant Introduction, which funded more than 10 global plant surveys every year. Through the global germplasm collecting activities by a group of plant explorers, the number of collected germplasm increased sharply. At present, more than 80% of the germplasm in the genebank of the United States come from abroad. Among these plant explorers, a barley breeder Harry V. Harlan (1882–1944) met and became a friend with Vavilov when he was the head of the American barley project in 1921 and later participated in the global plant surveys on numerous occasions. Harlan became the first scientist in the world to put forward the opinion that plant germplasm were threatened by extinction, which deeply influenced his son Jack R Harlan (1917–1998). After 35 years of plant investigation in 45 countries around the world (including China in 1974), Jack Haran collected many germplasm and made him deeply understand crop domestication. He believed that the centre of crop origin proposed by Vavilov was the centre of diversity, not necessarily the centre of crop evolution or domestication. Based on a proposed concept on "pan region" (referring to the area of 5000–10 000 km spread by crops during domestication), Harlan (1971) improved Vavilov's theory on the origin of crops and the centre of diversity. He believed that the *ex situ* conservation is necessary for crop germplasm that had evolved for thousands of years. In view of the great value of wild relatives for crop breeding, he advocated that wild relatives should also be conserved *in situ* and put forward the concept of "three-level gene pools" (Harlan, 1975), which lays a theoretical foundation for collecting, conservation and enhancement of crop germplasm. Jack Haran was the first person to clearly propose the concept of the threat of the disappearance of crop germplasm. He was also one of the advocates of the International Board for Plant Genetic Resources, which was later renamed the International Plant Genetic Resources Institute under the Consultative Group for International Agricultural Research (CGIAR).

Frank Meyer (1875–1918), a plant explorer, was another important person in the history of crop germplasm in America. Frank came to China in 1905 and later went to Mongolia, Russia, Afghanistan, Korea and Japan to carry out plant investigation. He first discovered wild ginkgo (*Ginkgo biloba*) in China. With the establishment of crop resources survey methods in arid areas, preservation techniques for long-distance transportation of living plant materials and collecting and drying specimen, Frank introduced more than 2500 plants from all over the world to the United States, including Chinese pecan (*Carya cathayensis*), Chinese wild peach (*Prunus davidiana*), elm (*Ulmus parvifolia*), *Pistacia chinensis*, etc., and also introduced elite local varieties of peach, pear, hawthorn, jujube, persimmon, lemon and chestnut. He has made important contributions to the cultivation of fruit trees, ornamental trees and 'greening' tree species in the United States. Also, the germplasm introduced by him for many crops such as wheat, barley, sorghum, alfalfa, wheatgrass (*Agropyron cristatum*) and spinach are still preserved in the national genebank of the United States. In particular, thousands of soybean landraces were introduced from China, which laid the material foundation for the genetic improvement and industrial development of soybean in the United States (Tan *et al.*, 2021).

In 1947, the United States Department of Agriculture and the National Agricultural Research Services jointly planned and developed a regional plant introduction system. Four plant introduction stations were established in four research management regions in the United States, namely, the Northeastern Regional Plant Introduction Station in New York; the Southern Regional Plant Introduction Station in Georgia, the North Central Regional Plant Introduction Station in Iowa, and Western Regional Plant Introduction Station in Washington. In 1958, the United States established the first national genebank in the world. The United States is also one of the countries in the world to initiate research on crop germplasm.

China is one of the important centres of origin and diversity of crops in the world. Under the long-term natural and artificial selection, abundant

and diverse landraces were developed. In the long history of farming, consistent planting by farmers became the original way to use and conserve the landraces. In 1840s, China became a semi-colonial and semi-feudal country. It was unable to collect and preserve crop germplasm, as its people also lack the awareness of active conservation. Until the first half of the 20th Century, several scientists, represented by Jin Shanbao and Ding Ying, collected some germplasm of wheat and wild rice during their research work, carried out screening, evaluation, and utilization, and became the pioneer of research on crop germplasm in China. At the call of the older generation of scientists such as Jin Shanbao and Dai Songen, the Ministry of Agriculture continuously supported to collecting missions nationwide from 1955 to 1956 and more than 210 000 samples of germplasm of different crops were collected and conserved by the Chinese Academy of Agricultural Sciences and relevant agricultural research institutes in different provinces (Liu *et al.*, 2018).

In 1959, Ms Dong Yuchen, a germplasm scientist and visiting scholar returned from the All-Russian Vavilov Institute of Plant Genetic Resources, analysed the situation of crop germplasm in China and put forward the concept of crop variety resources, marking the beginning of the discipline of crop germplasm in China. Subsequently, Ms Dong conducted an extensive and systematic investigation of wild relatives of wheat in China and identified the distribution and habitats of 110 species of 10 genera of *Triticeae* in northern China. She was successful in making crosses between wheat and *Agropyron, Psathyrostachys* and *Psathyrostachys* for the first time in the world and obtained several strains with more flowers and more grains, outstanding resistance and high quality. At the same time, she found two accessions of tetraploid wheat, whose F_1 chromosomes of intergenic hybrids with *Aegilops* and rye can be naturally doubled for generating grains and she clarified the cytological mechanism of such natural chromosome doubling and created more than 20 amphiploids. Ms. Dong is considered the founder of the discipline of crop germplasm in China.

1.2 Concepts, Connotation and Roles of Crop Germplasmics

1.2.1 Basic Concepts and Connotation

Crops are the plants domesticated from wild plants and cultivated to meet human needs. From the perspective of botany, agronomy and genetics, crops and their wild ancestors are very different in morphology and fertility habits, but they can still be mutually hybridized. In modern plant taxonomy, it is suggested that they belong to the same species.

The germplasm named by Weismann (1893) first refers to the genetic material passed from the parent generation to the offspring and now it is extended to include the carrier of genetic material. Germplasm refer to the carriers with genetic information and value for actual or potential utilization, also known as genetic resources, commonly known as variety resources. In practice, germplasm and germplasm are in common use. When gene-related information is obtained, germplasm can also be called gene resources.

Crop germplasm are the carriers of genetic information of crops and their wild relatives and have values of practical or potential utilization. They are represented by plants, seeds, roots, stems, leaves, buds and other asexual reproductive organs and vegetative organs, as well as callus, meristem, pollen, zygotes, cells, chromosomes, chromosome fragments, genomic segments, genes, and nucleic acids (DNA, RNA).

The term accession is the basic unit of crop germplasm in conservation and utilization. An accession generally has characteristics of a relatively stable genetic structure, obvious characters, and self-reproduction or replication. In practice, a crop variety, a population or subpopulation, or a new type of a wild relative is considered as an accession. The number of accessions preserved in a gene bank (or a nursery) refers to the number of germplasm with official accession numbers preserved in conservation facilities. Accession has a unique accession number associated with the physical material.

1.2.2 Categories of Crop Germplasm

The major categories of crop germplasm include wild relatives, landraces, enhanced germplasm, breeding lines, cultivars, and genetic stocks.

Wild relatives: refer to the wild plants relevant to the ancestors of cultivated crops, or plants with common primitive ancestors with cultivated crops but not domesticated as cultivated form, which are homologous or partially homologous in genome composition. In addition, there are also "weedy" relatives, which are closely related to cultivated crops. They are companion plants established during the domestication of wild plants into crops, or related plants that degenerate into weed types.

Landraces: also known as local, farmer's or traditional varieties, refer to the crop varieties developed by farmers using traditional methods to select

for many generations. It is the result of long-term natural and artificial selection. Landraces are often only cultivated in local areas, with specific environmental adaptability and stress resistance, suitable for local special diets, culture, and habits. Thousands of years after crop domestication and before modern hybridization breeding, landraces were planted all over the world. Even after the beginning of modern breeding, land races still existed for a long time. But with the improvement of productivity, landraces inherited many obvious shortcomings. However, landraces often have some special economic values that may not be important at present but could be important in the future or are not important here but may become important in other places. Landraces are germplasm with important breeding potential. In fact, a small number of good landraces are still planted in agricultural production systems; some primary cultivars were developed with landraces as parents, and most modern cultivars also have a genetic relationship with landraces.

Enhanced germplasm: refers to the genetic recombination or mutation induced by conventional hybridization, distant hybridization, chromosome engineering, gene manipulation and other technical means, and then through artificial selection to improve the target traits and obtain genetically stable new germplasm with improved target traits, but general traits may not be necessarily prominent. Compared with the original germplasm, the enhanced germplasm is more easily used by breeders.

Breeding lines: refer to the strains or breeding materials obtained by modern genetic improvement technology, which are genetically stable but cannot be directly applied in crop production. It also includes the direct parents (such as inbred lines) of advanced new varieties and hybrids that have not yet gone through the variety approval or registration procedure.

Cultivars: refer to the breeding-true populations obtained by using modern genetic improvement techniques and can be directly applied in crop production. In China, it is necessary to pass the approval or registration procedure to see a crop plant become a cultivar. The cultivars include three groups. The first group was bred and used in production in the past but not used any more. The second group is still used in production. The third group was approved or registered but not used in production. Generally, the genetic diversity of modern cultivars is lower than landraces, but they adapt to current new production methods and consumption habits, with better yield, better quality, stronger resistance and wider adaptability. Modern cultivars are not only the basic materials for breeding but also important germplasm.

Genetic stocks/genomic stocks: refer to the plant materials used for genetic or genomic research, including mutants, artificial mutagenized polyploids, somatic fusion materials, materials derived from hybridization (such as addition lines, substitution lines, translocation lines, etc.), introgression lines and mapping populations.

According to the degree of difficulty in breeding and utilization, Harlan and de Wet (1971) proposed the concept of gene pools, which divided germplasm into three gene pools:

Primary gene pool (GP-1): equivalent to a biological species, including the crops and their wild relatives that are easily crossed-fertilized with each other to produce fertile hybrids (chromosome pairing and gene separation are normal), and have no reproductive isolation.

Secondary gene pool (GP-2): including the species with certain reproductive isolation between each other, which can undergo gene transfer but present certain difficulties. Serious sterility (poor chromosome pairing) of the hybrid usually happens. The F_1 generation is too weak to grow up to maturity. It is difficult to obtain new germplasm of the desired type in the offspring. GP-2 generally covers the relatives of the same genus of cultivated crops, but not all species of the genus belong to GP-2. For example, in Genus *Hordeum*, only *Hordeum bulbosum* belongs to the secondary gene pool. Some species which are not from the same genus may belong to the same secondary gene pool. For example, the species of *Aegilops* are included in the secondary gene pool of common wheat (*Triticum aestivum*).

Tertiary gene pool (GP-3): including the species that cannot hybridize with cultivated form, or that produce abnormal, lethal, or completely sterile hybrids, and mainly covering relatives from other genera of cultivated crops. Gene transfer between crops and species of GP-3 is very difficult, requiring embryo rescue, chromosome doubling or bridge species (first crossing with cultivated crops to produce hybrids, which then crossed with the species of GP-3) to obtain hybrids.

1.2.3 Formation of Crop Germplasm

1.2.3.1 Domestication of Wild Plants and Origin of Crops

Crops originated from the domestication of wild plants, which is the basis of agricultural origin.

However, the origin of crops is not the same as the origin of agriculture. The cultivation of many crops was much earlier than the human settlement, which is the direct characteristic of the origin of agriculture.

Studies showed that world agriculture originated independently in 6–8 regions after the late Ice Age (12 000 years ago). Over the years, archaeologists have believed that the origin of agriculture first occurred in a narrow area called the Fertile Crescent in the Near East, where people soon learned to grow grain plants, raise children, and spread their lifestyle to other places. However, archaeological evidence in recent years showed that the domestication from wild plants to crops and from wild animals to livestock can be greatly ahead of time and the origin of agriculture is a long and complex gradual process rather than a radical revolution. On this basis, scientists established the protracted domestication model (Lev-Yadun *et al.*, 2000). For example, the original collectors in the Near East began to grow rye as early as 13 000 years ago, but they were still highly engaged in gathering foods from the wild in the next 1000–2000 years. They completely settled down about 10 500 years ago and began to domesticate wheat and barley at that time. It was previously believed that plant domestication first occurred in the Jordan Valley and the southern Levant (now Israel and Jordan), but later botanical, genetic and archaeological evidence pointed to a small area in the Crescent Valley, which is in the upper reaches of the Tigris and Euphrates rivers in southeastern Turkey and northern Syria. Neolithic agriculture in the Near East mainly involved cereal crops such as wheat and barley and legumes such as lentils, peas, chickpeas, and other beans. The wild species and cultivation types of these crops were found in many Neolithic sites in the core area of the Crescent. Since then, these crops have spread to the central and southern regions of the Levant.

Although crop cultivation first occurred in the Near East, other regions also had their own plants domesticated independently. For example, rice was domesticated along the marshes of the Yangtze River Basin in China 11 000 years ago and became the staple food about 7000 years ago. During a period of more than 4000 years, food gathering activities were still popular, however, people continuously domesticated the wild and semi-wild plants for cultivation.

Mexico is one of the centres of origin of agriculture and the birthplace of maize, which was domesticated in the middle reaches of the Balsas River in southwestern Mexico (a tropical forest area with seasonal drought). Maize spread at least 6000 years ago and was continuously domesticated during its spreading time. Evidence includes the discovery of 7100-year-old maize pollen remains in the tropical Gulf Coast region of San Andrés, 6000-year-old maize cob remains in the arid highlands of Tehuacén and Oaxaca valleys, and 6000–7700-year-old maize pollen, phytoliths and starch granules in southern Central America and northern part of South America. In addition, cucurbits were domesticated in the tropical coastal region of Ecuador in 10 000–11 000 years ago, much earlier than the emergence of farming villages.

Due to the different geographical distributions of plant species on the earth, the places for initial domestication of crops (the origin of crops) are also different. Not only the wild relatives of crops are an important part of crop germplasm, but also the original landraces and even semi-domesticated varieties developed in the early stage of domestication are important sources of germplasm.

1.2.3.2 Spread of Crops and Formation of Landraces

After a crop was domesticated, humans would take it to new areas for planting. However, due to the different environmental conditions (such as temperature, rainfall, sunshine, soil, pests, and diseases) in the new areas, crops might produce new adaptability, where they faced two fates: they were not able to survive in the new environments and disappeared; or they adapted to form new landraces. In addition, residents in those regions might have different living, cultural or religious habits, where farmers might develop more landraces for special uses through conscious or unconscious selections. Even farmers in different regions had their own specific cultivation practices (such as sowing, harvesting) and post-harvest treatments (such as processing, storage, transportation), which also resulted in different types of landraces.

Overall, most crops in the Eastern Hemisphere were domesticated during the Neolithic period. The first stage of crop spread was due to the early expansion of agriculture. Trade routes between the Arabian Peninsula, East Africa, Europe, and Asia played a crucial role in the inter-regional spread of crops. The second stage of crop dispersal originated from marine exploration, especially the discovery of the American continent in 1492, which highly facilitated the global exchange of germplasm. One of important results of crop dispersal was the emergence of the secondary centres of diversity, that is, the crop diversity was greatly improved after

it was introduced to a new area. For example, the introduction of kidney beans, maize, and cassava from Latin America to Africa and Asia resulted in the formation of many landraces; the diversity of finger millet increased significantly after its spread from East Africa to South Asia thousands of years ago. However, it should also be noted that with a widespread, some cultivated crops were marginalized in specific regions, which is quite common in the Americas.

1.2.3.3 Crop Improvement and Formation of Modern Germplasm

After Mendel discovered the three laws of genetics, breeding by professional breeders has become the main means of crop improvement, which greatly accelerated the breeding process. Under the guidance of genetic breeding theory, breeders have continuously innovated breeding techniques and methods using wild relatives and landraces and developing new germplasm and varieties to meet various needs and adapt to different environments. In particular, the new farming system also has an important impact on the formation of germplasm. For example, modern agricultural production requires breeders to develop lodging resistance, disease and insect resistance, stress resistance, high quality, high yield, and suitability for mechanized operations. The newly developed varieties were later used by breeders as basic germplasm in the following breeding practice, resulting in breeding lines and subsequent varieties, which are also an important part of crop germplasm.

In addition, genetic researchers have created many genetic materials; in the past two or three decades, genomics researchers have created many genomic materials, which are also an important part of germplasm.

1.2.4 Roles of Crop Germplasm

1.2.4.1 Historic Roles of Crop Germplasm

Crop germplasm are the material basis for the rise of agricultural civilization. It was the gathering, domestication and utilization of plant resources that led to agricultural activities and human development. Under the influence of natural and social environments, the increasing types of domesticated crops and the continuous emergence of various local varieties had promoted the development of agricultural civilization and led to establishment of states, religions, culture and education adopted to the needs of agricultural production and human life.

A. Crop diversity hastened agricultural civilization in the world

Ancient people all over the world began to domesticate plants almost at the same time, so diverse crops were developed around the world, such as rice, wheat, barley, maize and soybeans, which marked the beginning of the era of agriculture. Along with primitive agriculture and the settlement life of ancient humans who changed from hunters and gatherers to producers by improving crop productivity, the multiple birthplaces of farming civilization were emerging around the world.

Chinese agricultural civilization. During the period covering 8000–10 000 years ago, China's early agriculture established two major systems, *i.e.*, southern paddy agriculture represented by rice and northern dry farming represented by foxtail millet, combined with livestock breeding and handicraft industry. The paddy agriculture in the south was initiated in the humid south of the middle and lower reaches of the Yangtze River, so the water-loving rice was selected as the main crop to domesticate. The dryland farming in the north was closely related to the natural conditions of the Yellow River Basin, which was dry and cold in spring, autumn and winter and hot and rainy in summer, therefore, foxtail millet, which adapted to low soil fertility and low water supply in the seedling stage, was selected as a main crop. In the long process of the development of agricultural civilization, in addition to rice and foxtail millet, Chinese ancestors also domesticated many other crops, including soybean, broomcorn millet, buckwheat, cabbage, peaches, apricots, plums, pears, oranges and litchis.

Ancient Babylon agricultural civilization. About 9000 BCE–8000 BCE, Sumerians living in the Tigris River and Euphrates River Basin began with agricultural production. In this fertile soil, humans domesticated wheat, barley, oats, figs, rye, peas, lentils, dates and so on. About 7000 BCE, the ancestors in the two river basins also domesticated sheep, goats, pigs and other livestock. Around 5000 BCE, the Sumerians pioneered farmland irrigation technology, which promoted the development of mathematics, astronomy, architecture and other relevant technologies. In the subsequent millennium, the climate gradually became dry. Sumerians created excessive irrigation, which resulted in soil desertification and salinization. The planting area of the main crops such as wheat continued to decrease until the ancient Babylon Dynasty in 1800 BCE. The decline of agriculture led to the depletion of resources the destruction of the Sumerian Empire, and the disappearance of the earliest farming civilization.

Ancient Egyptian agricultural civilization. About 5000 BCE, the ancient Egyptians began to reclaim land for planting barley and wheat. In addition, people in the basin of the Nile River also planted broad beans, onions, lettuce, cucumbers, flax, olives and grapes. Around 3200 BCE, the Egyptians began the construction of a farmland irrigation system and gradually domesticated the Nile geese, donkeys and cats. About 2000 BCE, Egypt invented the ox-drawn wooden plough, soil-loosen rake and metal sickle. About 3500 BCE, small states began to appear in the Nile River Basin, and in 3100 BCE, Menis united Egypt. After thousands of years of Egyptian civilization, it was conquered by the Assyria in 671 BCE, by the Persians in 525 BCE and by Alexander in 323 BCE, when the ancient Egyptian civilization declined.

Ancient Indian agricultural civilization. From 6000 to 4000 BCE, people in the basin of the Indus River began primitive agriculture by planting barley and wheat and domesticating jujube and cotton. By 2500 BCE, rice, wheat and barley were widely cultivated in India, while cattle, sheep, pigs, chickens and other livestock were domesticated, thereby raising one of the world's earliest farming civilizations. It reached its peak in 2600 BCE, however, disappeared around 1800 BCE.

Agricultural civilization in the Andes. The main birthplaces of American agriculture are Central America and the Central Andes. The Indians in Peru began to plant beans and quinoa in 6000 BCE and began to plant maize, potatoes, pumpkins, and peppers between 5000 BCE and 4000 BCE. The crops domesticated by local Indians also include tomatoes, peanuts, zucchini, and strawberries in addition to sweet potatoes, avocados, cocoa, and sunflower. The development of agricultural civilization in Central and South America promoted the emergence and development of Indian civilization, including Mayan, Aztec and Inca civilizations.

B. Variety diversity of crops enriched human farming and economic life

The cultivated plants by ancient people were very different in many ways from what we grow today. When we eat big, sweet pears or apples, you would not believe that their ancestors were just sour and astringent with hard and small fruits; the cereal crops, which germinate and ripe uniformly, are convenient to cultivate and harvest, however, their ancestors were only some 'weeds' with fragile ears, and inconsistent mature grains, which was easy to shatter after maturing. Tomato which is one of the most popular vegetables nowadays, was native to the north of the Andes in South America. With the discovery of the New World, it was brought to Europe by Spanish colonists. At that time, the fruit of tomatoes was small and angular and the branches and leaves had an unpleasant smell. However, after long-term cultivation, the tomato fruit changed from small to large, the shape changed from polygonal to round, the pulp became thick, and the unpleasant smell disappeared. Crop varieties with various shapes, colours and tastes were developed to adapt to specific agricultural environments and improve the quality of people's lives.

With the continuous improvement of production tools, water irrigation systems and the miniaturization of farming organizations, a highly developed agricultural civilization appeared on the Chinese land-mass. In ancient China, it was recognized that under certain soil and climatic conditions, specific crops and varieties were cultivated and planted and each crop or variety had its own suitable environment or met the specific human needs. Under local natural or cultivated conditions, many distinctive varieties for each crop were developed through the selection of farmers, which greatly promoted the prosperity and development of agricultural civilization. The early agricultural civilization, which was limited to the plains which were warm and humid, rapidly extended to a wider area with the emergence of varieties adapted to diverse ecological and environmental conditions. It extended the area of cultivated land, contributed to the farming economy and fed more people.

With the rise of agricultural civilization, human beings can consciously cultivate different varieties to meet their living habits or needs and this has led to great changes in human society and economy. The cultivation of varieties with early-maturing trait can enable humans to migrate to cold and short-growing season areas. For example, buckwheat became an early maturing crop suitable for cold and high-altitude environments, provided an important food source for the survival and development of the Yi people in Liangshan mountainous area, Sichuan Province and created a distinctive Yi buckwheat culture. Developing early mature varieties of crops enable humans to produce food in a relatively short period of time to meet urgent food needs or respond to natural disasters. Cultivating drought-resistant crops enabled human beings to settle down in arid areas with harsh environments. For example, planting drought-resistant foxtail millet and broomcorn millet allowed people to migrate to the dry areas in northern China and create the dryland agricultural production system in the Loess

Plateau. Planting multiple varieties can effectively prevent serious damage from pests and diseases, ensuring a certain harvest yield in each growing season. More importantly, in the long-term production practice, human beings have developed many high-quality varieties, including varieties with good taste and rich nutrients, playing an important role in raising human living standards. The elite local varieties were also selected as 'tributes' to emperors in China. For example, 'Jingxidao', a famous tribute variety of rice was planted at the foot of Yuquan Mountain in Beijing.

C. Landscape diversity of crops casted agricultural cultural heritage

China's long and enviable history of farming culture, coupled with the huge differences in nature and humanities across regions, has created important agricultural cultural heritages with a wide range of types, obvious characteristics and high unity of economic and ecological values. They are the agricultural cultural models created by the Chinese under unique and diverse natural conditions with their diligence and wisdom and contain the philosophical thought of the unity of man and nature offering high historical and cultural value. They were developed and improved in the long-term coordinated development with various environments and agricultural biodiversity, traditional knowledge and technology systems, and unique ecological and cultural landscapes.

Production system based on landraces. In the existing agricultural cultural heritage, landraces with abundant diversity are usually the core component. For example, Aohan of Inner Mongolia, which was recognized as a global important agricultural heritage system in 2012, is the birthplace of dryland farming system in the world. At present, 218 landraces in the dryland farming in Aohan, Inner Mongolia have been identified for crops of foxtail millet, maize, sorghum, broomcorn millet, sesame and vegetables. In 2014, the dryland terrace system in Shexian, Hebei Province, which was likewise identified as an important agricultural cultural heritage in China, retained 171 traditional varieties in Wangjinzhuang village alone, the core area of the heritage, including 15 varieties of grain crops, 31 of vegetables, 5 of oil crops, 14 of dry and fresh fruits, plus 12 medicinal plants, fibre and tobacco. Hani terrace in Yuanyang, Yunnan province, which was listed as a globally important agricultural heritage system in 2010 and as a world cultural heritage in 2013, remains with nearly 200 rice landraces.

Farming knowledge and techniques based on native species. Agricultural cultural heritages have created a lot of farming knowledge and techniques on the conservation and utilization of native species. An example of the integrated system is the rice-fish symbiotic system in Qingtian, Zhejiang Province, which has a history of 1200 years of farming rice and fish in the same field. As recorded in Qingtian County Annals, the rice-fish symbiotic system is to raise fish together with rice in paddy fields. Rice provides shelter and organic food for fish, while fish play the functions of weeding in rice fields, loosening soil and increasing fertility, providing oxygen, and killing pests. This ecological cycle greatly reduces the dependence of the system on external chemical substances such as fertilizers and pesticides, improves soil aeration and environment, and ensures the ecological balance of farmland. Another example is the dryland farming technology based on foxtail millet and broomcorn millet, which have been cultivated for more than 8000 years in China. Archaeological and genetic studies showed that foxtail millet originated from the hilly area from the eastern foot of the Taihang Mountains to the Yanshan Mountains, and broomcorn millet originated from the Loess Plateau in the middle reaches of the Yellow River. With these outstanding drought-resistant crops and their diversity, the dryland farming technology and dryland agriculture in ancient northern China, which have become important agricultural cultural heritage sites today, were developed.

Unique ecological landscape based on landraces of native species. In many agricultural cultural heritages, we can observe the perfect integration of the utilization of landraces of native crops, traditional knowledge and technology with farmland, village and the environment to establish a unique agricultural ecological landscape and support the sustainable development of local society and economy. A typical example is Yuanyang Hani Terrace which is in the south of Ailao Mountain in Yuanyang County, Yunnan Province. It is a masterpiece left by Hani people from generation to generation. It consists of rice, terraces, water systems, villages, forests and mountains. The Hani people are accustomed to transplanting rice in June every year, so Yuanyang in summer is full of green waves of rice. By October, as the rice ripens, fields in the mountains have become golden yellow and in winter it is the most beautiful season to see terraces filled with water flashing the graceful and tortuous outline of the landscape. This beauty of the landscape has lasted for hundreds of years and has become an important agricultural cultural heritage.

1.2.4.2 Strategic Positions of Crop Germplasm

Since human survival and life must rely on food, fibre, fuel, shelter, medicine, and industrial products directly from plants as well as animals that use plants as fodder, and plants are often domesticated and cultivated by humans as crops, the importance of crop germplasm is self-evident.

Crop germplasm are strategic resources for achieving sustainable agricultural development, and ensuring food security, green development, nutrition, health, and security of seed industry. They are indispensable for the survival and sustainable development of human society, the original innovation of life science and the material basis for obtaining intellectual property rights and biological products. Throughout the history of crop genetics and breeding, various breakthrough achievements largely depend on the discovery and utilization of key germplasm.

A. Strategic resources for safeguarding food security

According to statistics, from 1961 to 2020, the world average yield of rice, wheat and maize increased by 146.6%, 219.1% and 196.3%, respectively and reached 4608.9 kg/ha, 3474.4 kg/ha and 5754.7 kg/ha, respectively. Genetic improvement plays an important role in yield increase, and germplasm play an important role in genetic improvement. For example, the dwarf genes *Rht1* and *Rht2* in wheat landraces used by the International Maize and Wheat Improvement Center (CIMMYT) and the Chinese rice landrace 'Dijiaowujian' (carrying the semi-dwarf gene *sd1*) used by the International Rice Research Institute (IRRI) to improve lodging resistance and density tolerance by reducing plant height resulted in the first 'Green Revolution' and a significant reduction in the world's hungry population during the 1950s and 1960s. The sterile wild rice germplasm (containing cytoplasmic male sterile gene *WA532*) was discovered in China and its scientific utilization contributed to the three-line hybrid rice with a greatly improved yield since the 1970s. Elite germplasm such as 'Aimengniu' and 'Fanliu' for wheat and 'Huangzaosi' for maize have been effectively utilized in breeding, which has made great breakthroughs in wheat and maize productivity, importantly contributing to food security in China.

B. Strategic resources for supporting agricultural green development

Green development is an efficient, harmonious, and sustainable way of economic growth and social development. It is important to support green development by exploring germplasm for developing new crop varieties with high use efficiencies for light, temperature and nutrients in soil to reduce the usages of pesticides, water and fertilizers. For example, the resistance to rice dwarf disease found in wild rice (*Oryza nivara*) material has solved the major disease hazards that had been prevalent in Southeast Asian countries since 1970s. China had identified and evaluated tens of thousands accessions of rice germplasm, and identified accessions with resistance to black-streaked dwarf virus and developed new varieties with good resistance that overcome the problem of 'rice cancer'. In the early 1990s, wheat scab caused up to $2 billion in economic losses to wheat production in the United States every year. Later, by using the Chinese cultivar 'Sumai 3' (containing the scab resistance gene *Fhb1*), the issue caused by the scab was largely solved. Soybean cyst nematodes cause more than 1 billion USD in economic losses in the United States each year in the 1950s. Scientists used soybean landraces 'Beijing Xiaoheidou' (containing resistance genes *Rhg1* and *Rhg4*) and bred a series of disease-resistant varieties, which saved the American soybean production.

C. Strategic resources for safeguarding security of nutrition and health

Mining special and elite germplasm with high quality is the basis for breeding new varieties with nutritional function for improving people's health. For example, after the discovery of the high lysine content gene of *Opaque-2* in maize, a number of hybrids with lysine content two times higher than ordinary maize hybrids were developed, and the tryptophan content was also increased, which significantly improved the edible and feeding value of maize. CIMMYT identified a tropical maize germplasm with a zinc content up to 96 ppm, and bred 11 high-zinc maize varieties, which partially solved the 'hidden hunger' problem caused by zinc deficiency in Latin America. China identified and selected special varieties rich in linoleic acid and β-glucan functional component from thousands of oat germplasm, which were proven to have obvious effects on lipid reduction and blood glucose regulation.

D. Strategic resources for advancing the competitiveness of seed industry

Developing varieties is the core of seed industry development. Germplasm can be regarded as the chip of variety development. The old saying goes well: "The cleverest housewife can't cook

without rice." Without germplasm, it would be impossible to breed the advanced varieties; the variety development will not be successful, the original innovation of seed industry will be difficult to sustain and improvement of the competitiveness of seed industry will become a castle in the air. The main reason why maize hybrids from multinational companies such as Corteva occupy an important position in the international seed markets is that they have access to most of the world's maize germplasm for in-depth data and utilization.

In addition, due to the continuous discovery of new uses of plants as medicine, energy, shelter, fuel, entertainment and cultural purposes, the development of new varieties of special crops has become a requirement for upgrading diversified consumption, so crop germplasm also play an important role in expansion of plant industries.

1.2.5 Improvement of the World's Agricultural Development by Crop Germplasm

1.2.5.1 Genetic Vulnerability

When it comes to the strategic position of crop germplasm, the concept of genetic vulnerability is often mentioned. It refers to the potential risk of biotic or abiotic stress changes when a few genetically uniform crop varieties are widely planted. The assessment of genetic vulnerability mainly considers two factors: on one hand, the relative planting area of each variety and, on the other, the degree of similarity between varieties, *i.e.*, their genetic correlations.

Growing multiple varieties with a narrow genetic base, or growing the same variety on a large scale, can lead to serious genetic uniformity. Examples of such are numerous, especially in smaller countries. A more extreme example happened in Netherlands, where the top three varieties of each of the nine crops accounted for 81%–99% of their total area and one variety accounted 94% of the total area of barley. The variety 'Sonalika' occupied 67% of the cultivated area of wheat in Bangladesh in 1983 and the same variety occupied 30% of the cultivated area of wheat in India in 1984. The rice variety 'IR36' was planted in 11 million ha in Asia in 1982. By 1990, all rice hybrids in China carried the same male sterile gene and even all modern rice varieties carried the same dwarf gene, which is also a typical phenomenon of genetic similarity.

Genetic uniformity does not necessarily bring immediate huge losses, but its risk cannot be underestimated. The most known example of huge loss caused by the uniform varieties was the great famine in Ireland between 1845 and 1848, which led to death of more than 1.5 million people. The main reason was that only 2–4 varieties of potato with uniform genetic composition were planted and resulted in serious outbreak of potato late blight. The threat of such genetic vulnerability was not obviated. In the 1980s, a new race A2 of potato late blight attacked Europe, Asia and Latin America. In 1992, a new race with resistance to all resistance genes appeared in Mexico. Since then, this rapidly mutated race has been detected in many parts of North America.

Another negative example happened in 1970 due to the large-scale planting of maize hybrid (of which 85% contained cytoplasmic male sterile gene *cms-T*) in the United States. The hybrid maize carrying *cms-T* was seriously susceptible to the southern leaf blight that was epidemic during the year and caused a loss of 25% of maize production in the country and for a value in excess of 1 billion dollars, for even more loss in the southern states, where it was a total failure in seriously infected fields.

Other famous examples include the outbreak of rice brown spot (*Helminthosporium oryzae*) in 1943, caused by a single variety coupled with typhoon attacks, which led to the Great Famine in Bangladesh and India as more than 2 million people lost their lives. In 1972, the winter wheat variety 'Bezostaya' was planted in 15 million ha in the Soviet Union, but it was destroyed due to a colder winter than usual. In the 1970s and 1980s, barley variety 'Zaoshu 3' was widely planted in the Yangtze River Basin of China, resulted in a large outbreak of yellow mosaic disease and a significant reduction in production. In 1979, 40% of Cuba's sugarcane cultivation area was planted for the same variety, which was attacked by sugarcane rust and led to the loss of more than 1 million tons of sugar worth some 500 million USD. In Central America, all five banana varieties were derived from the variety 'Cavendish' sensitive to a fungal disease (black Sigatoka), resulted in an annual yield loss of about 47% in Honduras and other Central American countries.

1.2.5.2 Genetic Erosion

The genetic erosion concept was first put forward by the Food and Agriculture Organization of the United Nations (FAO) at the technical meeting of collecting, utilization and conservation of plant genetic resources in Rome in 1967. It refers to the loss of genetic diversity, including the loss of a

single gene and a group of genes (such as special allelic variation combinations in local varieties). In a broad sense, genetic erosion also refers to the loss of varieties or species, *i.e.,* modern varieties or new species replace local varieties or native species, so that the number of local varieties or species planted is greatly reduced or even disappears. For example, in China, nearly 10 000 wheat landraces were planted in 1949, which accounted for 81% of the total number of wheat varieties planted in the 1950s, however, the number of landraces of wheat decreased to about 1000 in the 1970s. In the United States, 86% of apple, 95% of cabbage, 91% of maize, 94% of peas and 81% of tomato landraces were lost during 1804–1904. It should be noted that this loss of variety may lead to a decrease in genetic diversity, but not necessarily, because the genes in a lost variety may exist in other modern varieties.

In addition, the establishment of new agricultural systems often leads to habitat destruction, such as irrigation systems and extensive use of agrochemicals, which have a significant impact on wild relatives of crops. Overgrazing, overexploitation, deforestation, new pests and diseases, urbanization and wars may cause genetic erosion of crop germplasm.

1.2.5.3 Dependency of the World's Agricultural Development on Crop Germplasm

There is a phenomenon of aggregated origin of crops from different geographical regions in the world. The importance of these crops varies greatly across countries after they were spread to other regions of the world. In other words, the agricultural development in different countries was largely dependent on crop germplasm originated elsewhere. For example, there are 17 most important cultivated crops as food sources in the world, for which North America and Australia, in terms of production, are dependent on 100% crops from other regions, China on about 62%, and western Central Asia on 31%.

If more food crops are included, the above conclusion is also fully established. Generally, America and Europe are highly dependent on germplasm from other regions, while Asia is relatively independent, but still needs the support of germplasm from other regions.

Taking China as an example, among the top 30 crops ranked by yield, many of these originated from other countries. For example, the top one is maize originated in Mexico, and the third top is wheat originated in Western Asia. In addition, sweet potato, potato, cucumber, tomato, eggplant, watermelon, sugarcane and cotton were also introduced from other countries. Generally, the dependency of China on exotic germplasm was 46%–55% (Flores-Palacios, 1998). The development of grain, cotton, oil, sugar, tobacco, fruit, vegetable and other crops are inseparable from using the germplasm from other parts of the world.

In contradistinction, the exchange and utilization of crop germplasm between different regions plays an extremely important role in the development of world agriculture. For example, Japanese wheat germplasm and Chinese Taiwan rice germplasm were used to achieve a leap in food production in Latin America and Southeast Asia and led to the 'First Green Revolution'. Chinese wheat germplasm 'Sumai 3' and soybean germplasm 'Beijing Xiaoheidou' were used by the United States to solve the key problems in wheat and soybean production, while American maize germplasm 'Mo17' and European wheat germplasm 1B/1R translocation lines were used by China to achieve a significant improvement in disease resistance and yield of maize and wheat.

1.3 Theories, Tasks and Research Directions of Crop Germplasmics

1.3.1 Basic Theories of Crop Germplasmics

1.3.1.1 Theory of the Centres of Origin of Cultivated Plants

Swiss botanist Condell first proposed that cultivated plants should have original centres and believed that most cultivated plants originated from the Old World. The theory of the centres of origin of cultivated plants proposed by the Soviet geneticist Vavilov in 1926 has a great influence. He put forward eight centres of origin of crops in the world (including China, India, Central Asia, Near East, Mediterranean region, Ethiopia, southern Mexico-Central America and South America), plus three sub-centres (India-Malaysia, Chile, and Brazil-Paraguay). These centres can be called "primary centres of origin" as this is where the wild relatives of crops exist. Vavilov also found that there were variations and rich diversity in the places that were far away from the primary centres of origin, which were called "secondary centres of origin" (Vavilov, 1926). After 1940, the theory of the centres of origin of crops has been constantly revised, for example, by P. M. Zhukovsky, a student of Vavilov, and A. C. Zeven, a Dutch breeder by adding four centres to make 12 major centres of

origin of crops in the world (Zeven and Zhukovsky, 1975). American geneticist J. R. Harlan believed that the centres of origin of crops proposed by Vavilov were actually the earliest regions of agriculture but the centres of genetic diversity are not necessarily the centres of origin. Some species may originate from several different regions. Therefore, the theory of centres and Non-centres of Agricultural Origin was proposed including three centres in the Near East, China and Central America and three pan-regions in Africa, Southeast Asia and South America (Harlan, 1971). Later, the 'diffuse origins', which means that the origin of crops could diffuse in time and space, was also put forward (Harlan, 1986). The centre of crop origin should be distinguished from the origin of agriculture, and a new central theory of crop origin was put forward, in which the origin of agriculture is called the nuclear centre, and the region with rich diversity formed after the crops were spread from the core centre was called the region of diversity (Hawkes, 1983).

1.3.1.2 The Law of Homologous Series in Variation

The Law of Homologous Series in Variation was first proposed by Vavilov in 1922. It was believed that similar variations could be found in different crops in the same geographical area, *i.e.,* if a certain trait or phenotype was found in one crop, the same trait or phenotype could be found in other crops in the same area (Vavilov, 1922). The results of modern comparative genomics and molecular biology also support this law. It is believed that under the same or similar environments, due to the combined action of natural and artificial selection, the genes controlling specific traits in different crops would have the same or similar mutations to result in the same phenotype.

The Law of Homologous Series in Variation has been expanded. Different species in the same ecological area show convergent evolution, while the same species in different ecological areas show divergent evolution. Convergent evolution refers to the morphological, physiological and molecular similarity of different species in the process of evolution due to adaptation to the same or similar environments. For example, chickpeas and broad beans in the Himalayas region have the characteristics of small grains and small pods, while flax, wheat and barley in the Mediterranean countries have the characteristics of large grains. Divergent evolution refers to different groups of the same species, due to long-term living in different environments, presenting multiple directions of variation and characteristics or different ecotypes, and even differentiating into multiple species with different morphological and physiological features. Convergent evolution and divergent evolution are the general characteristics of biological evolution in nature and the basis for creating a diversity of crop germplasm.

1.3.1.3 The Theory of Synergistic Evolution of Crop Germplasm and Cultural Environments

The Theory of Synergistic Evolution of Crop Germplasm and Cultural Environments is about the interaction, interrelation and mutual development between crops and their germplasm and the human environment (Liu *et al.*, 2022). On one hand, planting different crops or different types of crops in a specific environment will lead to the formation of corresponding dietary habits and cultural environment; on the other, eating habits and cultural environment will have a profound impact on crops and their germplasm, and even lead in their evolution. In the traditional Chinese food culture system, the "waxy"[1] trait was considered as the core by steaming and cooking for the special taste and multi-purpose, which perfectly reflects the relationship between crops germplasm and cultural environment for the coordinated evolution.

The Synergistic Evolution Theory of Crop Germplasm and Cultural Environments has a guiding role in the work of modern crop germplasm and crop breeding, such as emphasizing the efficient use of landraces and paying attention to farmers' rights in conservation and use of crop germplasm and associated traditional knowledge and cultural environments.

1.3.2 Basic Features of Crop Germplasm

A fundamental task of crop germplasmics is to investigate four basic features of germplasm, including genetic diversity, genetic specificity, genetic integrity and genetic accumulativeness, among which genetic diversity is the core and foundation. Genetic diversity and genetic specificity describe the overall situation and special situation of genetic variation from the population and individual perspectives respectively. The genetic specificity of individuals constitutes the genetic diversity of the whole, which is the main objective of investigation and evaluation. Genetic integrity is the foundation

[1] **Waxy** rice, sorghum, maize and millets etc. with many excellent characteristics in terms of starch type and content and economic value, have been grown in China for a long history.

of collection and conservation of germplasm to protect from the loss of genetic diversity. Genetic accumulativeness is the foundation of germplasm enhancement, which requires the optimal combination of original genetic specificity to broaden the genetic basis.

1.3.2.1 Genetic Diversity

Genetic diversity in the broad sense refers to the sum of various genetic information carried by organisms on Earth, while genetic diversity in the narrow sense mainly refers to the genetic variation within species. Genetic diversity can be measured by the degree of genetic variation. Genetic variation is a kind of variation in an organism that can be inherited to future generations. Therefore, genetic diversity can be evaluated at different levels such as genome-wide, genome segments and genes. In recent years, it has been found that there is also an epigenetic variation including variation in methylation and acetylation of DNA and histone, in which gene expression changes but DNA sequences remain unchanged. It is important to note that groups or populations composed of individuals are the basic units of evolution, therefore, genetic diversity includes not only its levels but also its distribution patterns, *i.e.,* the genetic structure of a population.

Studies showed that genetic diversity was decreasing from wild relatives to landraces and modern cultivars. In general, the diversity in wild relatives and landraces is high, especially for landraces of cross-pollinated crops such as maize and pearl millet. The variation between individual varieties of self-pollinated crops such as rice, wheat and barley, and vegetatively propagated crops such as potatoes and bananas were relatively low, but the number of their varieties is extremely large. However, it should be noted that the genetic diversity in wild relatives may also be reduced due to habitat changes; the landraces in many areas gradually disappeared due to the extensive cultivation of modern cultivars, whereas the genetic diversity of the varieties used in production had greatly decreased. The genetic uniformity of modern cultivars tends to increase, especially if developing too many derived varieties from a few major varieties will greatly reduce genetic diversity.

Studying genetic diversity has important theoretical and practical significance. First, it can be used to reveal the evolutionary history of species or populations (including the time, place and ways of crop origin, the degree of selection and target selection during crop improvement), provide important information for further analysis of the potential in their evolution and improvement, and especially help to reveal the reasons and processes of rare or endangered species. Secondly, it can be used to clarify the size, spatial and temporal distribution of genetic variation within species and their relationship with environmental conditions, which helps take scientific and effective measures to collect and conserve germplasm. Therefore, genetic diversity is one of the core objects of research on conservation biology. In the process of collecting and conservation of germplasm, the most important consideration is genetic diversity at a large scope. Whether a series of samples with the highest genetic diversity are collected and effectively conserved can be used to measure the success of collecting and conservation of germplasm. This is also the theoretical basis for the extensive collecting of domestic germplasm and the introduction of foreign germplasm. Thirdly, studying genetic diversity helps understand the origin and evolution of biodiversity, especially deeply understanding micro-evolution. Fourthly, the evaluation of genetic diversity, especially the in-depth identification and evaluation at the phenotypic and genomic levels, is helpful to identify useful resources with outstanding target traits, develop elite germplasm that breeders are more willing to use and provide support for the efficient utilization of germplasm.

Genetic diversity is the cornerstone of the formation, conservation, and utilization of crop germplasm. The study of genetic diversity runs through the whole chain of collecting, conservation, identification and enhancement of germplasm. It should focus on germplasm of specified geographic region, conserved in the genebanks and nurseries, and core collections that can represent germplasm conserved in genebanks, and specific types of germplasm.

1.3.2.2 Genetic Specificity

There may be differences in genetic composition or genome composition among germplasm, even among individuals of the same germplasm (such as landraces). Genetic specificity refers to the unique allelic variations or allelic variation combinations of different target genes, which in turn affect phenotypes or traits. However, all phenotypes are the results of the interaction between genes and genes, and between genes and environments. When evaluating genetic specificity, it is necessary to clarify the interactive characteristics between genes and

genes and genes and environments, to understand in depth the intrinsic relationships from genotypes to phenotypes. Genetic specificity and genetic diversity are both related and differentiated. There are significant differences in meaning between them. The former focuses on individuals, while the latter emphasizes the whole.

Therefore, the essence of collecting and conservation is to effectively conserve different germplasm with genetic specificity. The essence of identification and evaluation is to identify the genetic specificity of germplasm and to identify elite ones with single or multiple target traits in a specific environment. The essence of germplasm enhancement is to transfer the outstanding traits of specific materials to the target varieties for further improvement and utilization.

1.3.2.3 Genetic Integrity

Genetic integrity refers to all genetic information carried by germplasm collected or conserved. The wild relatives and landraces of crops have the characteristics of genetic heterogeneity, *i.e.,* there are more genetic variations among wild relatives and within populations, or among individuals of landraces, which are genetically heterozygous. Therefore, appropriate sampling is very important in collecting germplasm. It is necessary to ensure that the genetic diversity of obtained samples can represent the genetic diversity of the protected objects, that is, to maintain their genetic integrity.

In the *ex situ* conservation of germplasm, no matter how long the preservation time is and how the regeneration is implemented, the conserved germplasm should display no genetic change, or no genomic mutation within a reasonable period, and no significant genetic drift. For the *in situ* conservation of germplasm, the co-evolution of wild relatives or landraces with the environments is inevitable, and there will be a certain degree of genomic mutation, but the genetic integrity cannot be significantly reduced by human factors or natural disasters.

To ensure the genetic integrity, it is necessary to carry out an extensive investigation of germplasm and to understand the sampling techniques before collecting germplasm. In the conservation of germplasm, it is necessary to study effective conservation technologies, to establish efficient monitoring and early warning technologies, and develop scientific technologies for regeneration and multiplication to achieve effective and safe conservation of germplasm.

1.3.2.4 Genetic Accumulativeness

A plant genome generally comprises between 50 000 to 60 000 genes. In genetic improvement (including germplasm enhancement and breeding, the former is also called pre-breeding), the different allelic variations of these genes are extensively recombined and aggregated, *i.e.,* genetic accumulativeness. For most genes controlling important traits, we can find so-called 'favourable' allelic variations that meet the different needs of human beings. The essence of germplasm enhancement is to aggregate these favourable allelic variations to a certain degree. While maintaining good traits, we can overcome bad traits by eliminating genetic encumbrance. If we want to transfer exogenous genes from wild relatives, we must first overcome two major problems, hybrid incompatibility and offspring sterility. For the same trait, the aggregation of different favourable alleles can produce a cumulative effect, and for different traits, the aggregation of different alleles can produce a systematic effect.

Therefore, it is necessary to strengthen the in-depth study of germplasm by applying theories and methods of omics to carry out the exploration of gene resources of important traits, obtain key genes and their elite alleles or haplotypes and finally realize the intelligent design of the optimal combination of allelic variations to create new gene resources and elite germplasm.

1.3.3 Extended Features of Crop Germplasm

Tasks of crop germplasmics also include research on five extended features of germplasm, *i.e.* co-evolvability, regeneratability, value-adding ability, marketability and legislability. Co-evolvability relates to the theoretical guidelines for *in situ* conservation and periodic surveys; regeneratability is the basis for sharing and utilization of germplasm; value-adding ability is the basis for strengthening the share and use of information of germplasm; marketability is the way to realizing the economic values of germplasm; and legibility is the basis of management of germplasm according to laws.

1.3.3.1 Co-Evolvability

The *in situ* conservation of germplasm refers to the conservation of wild relatives of crops in their original habitats without external human interference. Broadly speaking, the *in situ* conservation of germplasm also includes on-farm conservation, which means that crop landraces are conserved by farmers through selecting and cultivation in their

original farmland. Under these two methods, crop germplasm are subject to natural selection, while also being subject to artificial selection under on-farm conservation. The natural mutations generated by selection will continue to accumulate, leading to a co-evolutionary phenomenon between germplasm and the environment. The co-evolution of germplasm emphasizes "change", which means that when genetic diversity increases or decreases during the *in situ* conservation process, it will create new phenotypes that adapt to the natural or human environments. This is the theoretical basis for *in situ* conservation, periodic surveys and collecting activities.

1.3.3.2 Regeneratability

The *ex situ* conservation of germplasm is mainly through the preservation of seeds, plants, tube seedlings, tissues or organs (such as roots, tubers, bulbs, stem tips, dormant buds, pollens, and embryos). These germplasm can produce new individuals of offspring through sexual reproduction, vegetative reproduction or tissue culture, to expand the number of individuals to meet the needs of germplasm distribution. It must be emphasized by the renewability of germplasm that it cannot improve or decrease the genetic diversity during the renewal process.

1.3.3.3 Value-Adding Ability

In the process of collecting, conserving, identifying, researching and enhancement of germplasm, massive amounts of information will be generated to form big data of germplasm. Big data is a powerful value-addable function on germplasm However, big data of germplasm itself cannot produce value. Only by carrying out scientific and effective professional analysis and in-depth mining of big data, revealing the possible correlations between variables, interpreting the results of analysis, and formulating solutions to problems, can the value of big data be demonstrated.

1.3.3.4 Marketability

Economic methods can be used to assess the value of crop germplasm. By constructing the value models, the use value and non-use value of crop germplasm can be systematically assessed to highlight their important roles in the development of social economy and culture and science and technology. Establishing and completing the property rights system over crop germplasm to safeguard the national interests and the security of crop germplasm through the commercialization for the rational allocation of various elite germplasm, can maximize the effectiveness and improve the utilization efficiency of germplasm, promote innovative development of seed industry and ensure global food security.

1.3.3.5 Legislability

The Convention on Biological Diversity, the International Treaty on Plant Genetic Resources for Food and Agriculture, and the Seed Law of the People's Republic of China all stipulate that the country has sovereignty over germplasm. Genes/alleles or other markers identified in germplasm, and from which the new gene resources developed can be legalized for intellectual property rights under relevant national laws. The legalization of germplasm management is of great significance to promote the effective conservation and rational utilization of germplasm.

1.3.4 Research Directions of Crop Germplasmics

"Extensive investigation, complementary conservation, comprehensive evaluation, in-depth research, innovative enhancement, sharing and utilization" refers to the principles and key tasks for crop germplasmics in China. The tasks of crop germplasmics can be divided into three parts: basic work, applied basic research and basic research. The basic work mainly includes investigation and collecting, trait characterization, cataloguing and registration, conservation, monitoring and early warning, multiplication, distribution, information management, and germplasm management. The applied basic research includes technical standards development, evaluation, gene resource identification and germplasm enhancement. Basic research mainly solves major scientific problems in the conservation and utilization of crop germplasm, involving the origin, evolution and conservation biology of germplasm.

The theories and practices of crop germplasmics run through the whole research chain. Solving major scientific issues in conservation and utilization, overcoming key technical problems and promoting the operation of the research system are among the core tasks.

1.3.4.1 Extensive Investigation

Extensive investigation refers to the comprehensive and in-depth surveys of crop germplasm and the

collecting of samples. The investigation consists of finding out the species, distribution area and diversity of crop germplasm, revealing their temporal and spatial dynamic changes, and proposing the overall conservation plan. Germplasm investigation focuses on collecting samples for the study of genetic diversity, collecting extensive samples for their conservation and utilization and collecting samples for rare and endangered germplasm. It involves the collecting of germplasm in specific regions and the introduction of germplasm from other countries, which can also be carried out through international exchange. During investigation, germplasm can be collected from farmers or resource owners or sampled from the field (especially from the natural environment).

1.3.4.2 Complementary Conservation

Complementary conservation means that on the basis of extensive investigation, the overall conservation strategy is put forward by top-level design and scientific planning. Various conservation methods and techniques are used to conserve all types of germplasm, such as wild relatives, landraces, enhanced germplasm, breeding lines, released varieties and genetic materials, to ensure the genetic integrity of crop germplasm.

Germplasm conservation can be generally divided into *ex situ* conservation and *in situ* conservation. The former mainly includes genebanks and germplasm repositories or field genebanks. A genebank mainly conserves seeds, tissues, organs, DNA, etc., while a germplasm repository mainly preserves living plants. According to conservation purposes, the genebank can be divided into long-term (base collection), medium-term (active collection) and short-term (working collection). Because the seeds of wild relatives of crops are often recalcitrant, dormant and difficult to germinate, there are technical difficulties in their *ex situ* conservation Therefore, *in situ* conservation, which also co-evolves with the environment, becomes one of the important ways to conserve wild relatives of crops. In addition, the conservation of landraces in their original farmland by farmers is essentially a way of *in situ* conservation.

To achieve the secure conservation of germplasm, it is very important to improve the conservation facilities and minimize human interference. However, studies have shown that samples conserved in genebanks (nurseries) or *in situ* conservation sites (areas) often have the possibility of losing genetic integrity, therefore they must be monitored. If a certain threshold is reached, *i.e.*, when the viability drops to the critical point, an early warning signal must be issued; the genebank (nursery) must take action to multiply and regenerate the samples.

Before entering the conservation process, germplasm should be documented. Documentation refers to characterizing the basic traits of the collected samples before they are sent to the genebank for conservation, and then the samples are assigned with accession numbers, plus the passport data, which refers to basic information. The given accession number, like the resident identity card number, is unique in the world. For the conservation of living plants, it is required to be sent to the germplasm nursery, while the basic traits should be characterized and catalogued. For the *in situ* conservation, it is necessary to inventory based on the populations identified.

The registration of germplasm is different from their documentation. It mainly carries out orderly information registration against confusion in management by assigning a unified identity number. The scope of registration, which is wider than that of documentation, includes public germplasm preserved in genebanks, elite germplasm obtained through identification and evaluation, improved germplasm or genetic materials obtained by conventional means, enhanced germplasm or genetic materials by biotechnological research and breeding materials and new varieties with new plant variety rights. Under certain conditions, the registered germplasm can be catalogued and then sent to the genebanks and repositories for conservation.

1.3.4.3 Comprehensive Evaluation

Comprehensive evaluation refers to the evaluation of germplasm to identify the phenotypes and genotypes of important traits, analyse the genetic diversity and genetic specificity and data mine elite germplasm with outstanding target traits.

There are some differences between characterization and evaluation. Characterization refers to the identification of a single trait or genomic segment/gene, while evaluation refers to the comprehensive analysis of multiple germplasm on a particular trait or genomic segment/gene or the integration analysis of multiple traits or multiple genomic segments/genes. Characterization and evaluation involve two categories of research. The first category is to identify and evaluate phenotypes (called phenotyping), and the second category is to identify and evaluate

genotypes (called genotyping). Integrative identification of germplasm embodies three meanings: identifying target traits in multiple environments, identifying genotypes at the whole genome level or gene level, performing integrative analysis and obtaining elite germplasm with outstanding target traits and clear genetic background.

1.3.4.4 In-Depth Research

In-depth research refers to the application of theories and methods of modern genetics, physiology and biochemistry, omics and molecular biology to tackle and overcome the scientific and technical problems involved in the process of collecting, conserving, evaluating and enhancement of germplasm. The transformation of germplasm into gene resources is the core task for in-depth research.

There are some important scientific problems in the conservation and utilization of crop germplasm, including the origin and evolution of germplasm, ethnobotanical, biological, physiological, biochemical and omics basis of germplasm for secure conservation, the biological basis of genetic composition and utilization effect of elite germplasm, the biological basis of large-scale germplasm enhancement and effective utilization, as well as the valuation of germplasm. Basic research on these major issues is the cornerstone to support the development of theories for crop germplasmics. The application of system biology theories and methods to integrate the panomics research with analyses of big data from multi-omics (genomics, epigenetics, transcriptomics, proteomics, metabolomics and phenomics, etc.) is critical for solving the major scientific issues in the conservation and utilization of germplasm, which also represents an important international frontier in the present and future of crop germplasmics.

Germplasm have national sovereignty, but no intellectual property rights. However, genes can have intellectual property rights. Therefore, strengthening the exploration of genetic resources, clarifying the intrinsic relationship from genotype to phenotype (G to P) such as genotype by environment interaction, and transforming germplasm into gene resources are the core of crop germplasmics in the future. Gene resource exploration includes two major objectives. One is gene discovery, which refers to the discovery of new genes and their function by mapping and cloning genes and verifying the gene function of genomic regions that control target traits. The second is allele mining, which serves to clarify the size, expression, and genetic effect of allele variations of genes on target traits, mine favourable alleles or haplotypes and propose efficient utilization schemes. With the rapid development of genomics, it has been found that the phenotype of many traits is related to the DNA sequence around the gene, such as the regulatory sequence, so the discovery of gene resources has extended beyond the gene itself. In particular, the key objective in gene resource mining is allelic variation mining, but the latter is based on gene discovery.

1.3.4.5 Innovative Enhancement

Innovative enhancement refers to the integrative application of conventional methods, biotechnology, information technology and other technical means to improve the use efficiency of germplasm by reconstructing existing genetic variation combinations and creating new variation types that do not exist in existing germplasm, providing elite materials for genetic improvement and basic research.

Germplasm enhancement, also known as pre-breeding, refers to the scientific research activities of creating new crops, crop types and genetic materials using various natural or artificial variations. Natural variations generally come from germplasm preserved in genebanks. Artificial variations refer to genetic variations that do not exist in nature but are created by transposon insertion, physical and chemical mutagenesis, transgenic, gene editing and other relevant methods. The purpose of germplasm enhancement is to transform those germplasm that prove difficult to use in breeding into materials that are easily used for breeding and to transform exotic germplasm that are not suitable for local environments into breeding materials that can be used locally, thereby broadening the genetic diversity of modern cultivars. Germplasm that are not suitable for breeding mainly include wild relatives, landraces and artificial variation materials, while exotic germplasm mainly refers to landraces, open-pollinated varieties, populations, hybrids and inbred lines that prove difficult to be used directly in breeding due to poor adaptability to the local environments. Therefore, germplasm enhancement is a bridge between germplasm and genetic breeding. The enhanced germplasm can also be called bridging germplasm. Crop germplasm enhancement faces a great challenge due to its long cycle and slow impact. Once proven successful and implemented, however, it will bring a breakthrough leap in crop genetics and improvement.

1.3.4.6 Sharing and Utilization

Germplasm are the national strategic resources and the global wealth with effective conservation and efficient utilization as important tasks of crop germplasmics to realize "utilization in conservation and conservation in utilization". The construction of big data is the basis for promoting the effective conservation, efficient utilization and orderly management of germplasm. Distribution and sharing of information are the main technical ways of utilization of germplasm.

The direct utilization of germplasm in production, indirect utilization in breeding, scientific research and scientific publicity needs to be achieved through distribution. The big data or information system of germplasm, consisting of a genebank management system, data and information on collecting, catalogue and registration, characterization and evaluation, and data on distribution from genebank (nursery), is critical in these regards.

1.3.5 Features of Research on Crop Germplasm

1.3.5.1 Basic Features

The foundational feature of crop germplasmics is mainly reflected in the fact that germplasm are the basis for crop breeding. They are the 'chip' of variety breeding and the basic provenance of seed industry development. Without good germplasm, breeding will encounter great difficulties. For example, so far, insect-resistant resources with breeding value are rarely found in crop germplasm; it is time-consuming and labour-intensive to find new resistance sources across species and adopt transgenic strategies to solve problems. The consolidated foundation of germplasm represents the possibility for breakthroughs in breeding. There are numerous examples, such as the discovery and utilization of dwarf germplasm which led to the first green revolution. In addition, the investigation, collecting, conservation, evaluation and sharing of germplasm are basically routine work, which has the nature of basic features.

1.3.5.2 Public Features

Crop germplasm are strategic resources to ensure food security, green development, nutrition and health, and seed industry development. The purpose of germplasm research is to provide public goods for scientific and technological progress and social development, which has significant public features. According to Article 11 of the Seed Law of the People's Republic of China (revised as of March 1, 2022), the State has sovereignty over germplasm. Therefore, germplasm research is usually supported by public projects, aimed at seeking social impacts. They have the feature of large scale, large investment, broad benefits long service cycle and far-reaching impacts. The public feature of germplasm is not equal to the "valuelessness" of germplasm. Not only can germplasm create huge social benefits, but also generate important ecological and economic benefits.

1.3.5.3 Long-Term Features

The nature of crop germplasm determines their long-term management feature. On the one hand, the change of climate, environment, economy and human social activities has led a serious loss of germplasm, particularly landraces and wild relatives; on the other, with the deepening of genomics and other omics research, new technologies such as cytology, genetics, and molecular biology have extended the concept of conservation from conserving individual or population to DNA and genes, so that the investigation, collecting, conservation, enhancement, and utilization of crop germplasm must be sustained persistently.

1.3.5.4 Multidisciplinary Features

As discussed previously, the main tasks of crop germplasmics cover basic work, basic research and applied basic research. The research objects include all cultivated crops and their wild relatives; it is not only closely related to the natural science, covering the field of biology such as plant taxonomy, genetics, genomics, cytology, botany, zoology, microbiology, ecology, plant physiology, biochemistry and molecular biology, the field of agronomy such as crop breeding, pathology, entomology, cultivation, and the field of information such as information systems and processing, big data, Internet and Internet of Things, but also closely related to the social science such as politics, economy and culture. Therefore, crop germplasmics is a multidisciplinary subject with a wide coverage and strong intersection, which involves the integration and comprehensive application of multidisciplinary theories and technologies.

Because of the basic, public, long-term, and multidisciplinary features of research, the development of germplasm needs the participation of Government departments, technical departments,

and the whole society. Crop germplasm management has become a highly complex system of engineering.

1.4 History, Status and Trend of Research in Crop Germplasmics

1.4.1 History of Crop Germplasmics

1.4.1.1 The First Period: Subject Formation with Focus on Germplasm Collecting and Preliminary Study

A. The formation of crop germplasmics in the world

The advent of Darwin's theory of evolution and the theory of genetic variation in the mid-nineteenth century opened the prelude to the exploration of the origin of cultivated crops. In 1882, Swiss botanist Alphonse de Candolle (1806–1893) published the famous book "The Origin of Cultivated Plants," which played an important role in promoting the emergence of crop germplasmics. However, the study of crop germplasmics started with the global collecting of germplasm in the early 20th Century. Especially in the 1920s, the famous Soviet scientist N. I. Vavilov travelled to more than 60 countries on four continents of Asia, Europe, America and Africa, and collected more than 150 000 samples of various crop germplasm. Through studies on phenotypic diversity and geographical distribution, he proposed theories of the Centres of Origin of Crops and the Law of Homologous Series in Variation. Since then, the study of crop germplasm has gradually developed into an independent discipline, crop germplasmics.

In 1898, the US Department of Agriculture established the Plant Introduction Office. Since then, a total of 200 professional expeditions have been taken to collect germplasm around the world. At present, it conserves more than 600 000 accessions, more than 80% of which are collected from abroad, becoming the world's largest collection of plant germplasm. In 1946, the United States adopted the Agricultural Market Act, and then established a series of regional plant introduction stations to strengthen the collecting of global germplasm and led the research of germplasm onto the right track.

B. Formation of crop germplasmics in China

In the first half of the 20th Century, only a few agricultural scientists carried out some scattered comparisons, classification, and documentation of landraces of major crops in China. In 1925, Jin Shanbao, a Chinese pioneer of crop germplasm, collected more than 900 wheat varieties from 790 counties of 26 provinces and made a precise observation on morphology for many years. In May 1928, he published the Preliminary Classification of Wheat in China. This is the first Chinese scientific paper on wheat classification.

In 1926, Ding Ying, a Chinese pioneer of crop germplasm, discovered wild rice in the Xiniuwei swamp near Guangzhou and obtained the stems and natural hybrids of wild rice with locally cultivated rice. After the selection and identification of the lines of individual plants from 1927 to 1930, the stable line W2-2 was obtained. In the yield comparison test, it was ranked first for three consecutive years and named Zhongshan 1 in 1933. This was the first rice variety bred with wild rice in China.

With the establishment of the Central Agricultural Experimental Institute in 1931, some wheat varieties were introduced from abroad (207 varieties from the United States and 205 from the Soviet Union), and 3959 wheat ears were collected in the basins of the Yellow River and the Yangtze River. In 1932, the organization purchased more than 1700 varieties of world wheat collection, which was established by British wheat expert John Percival; the initiative of Luo Fu (then the chief technician of the Institute), Shen Zonghan presided over the comparison test of wheat adaptability in 39 sites of 8 provinces for several years and expanded his tests to 11 provinces later.

In 1937, Jin Shanbao collected wheat varieties from Yunnan and found a special type of wheat variety. In 1942, he went to Yunnan for an on-the-spot investigation and collected 15 varieties of wheat, which was called Tiekemai by local people. After years of research, Jin Shanbao named this new type of wheat *Triticum aestivum* ssp. *yunnanense* King in 1959.

In the high level of agricultural cooperatives in the 1950s, the Ministry of Agriculture of China organized national surveys on landraces and collected more than 210 000 samples of various crop varieties (types), which were called 'original materials' at that time. Dong Yuchen, the founder of crop germplasmics in China, put forward the concept of "crop variety resources" after she returned from the Soviet Union in 1959. The Institute of Crop Breeding and Cultivation of CAAS established a crop variety resource research unit to be engaged in research on germplasm of wheat, rice, maize, sorghum, millet and introduction. In addition to its research work, the research unit was also responsible for the organization and coordination of relevant work throughout the country. This marked the formation of crop germplasmics in China. On April

18, 1978, the Institute of Crop Germplasm of CAAS was established with the approval of the Ministry of Agriculture and Forestry.

1.4.1.2 *The Second Phase: The Scientific Development with Focus on Collecting and Preliminary Evaluation of Germplasm*

A. Development of crop germplasmics in the world

Since the 1960s, crop germplasmics have developed rapidly. Many countries in the world, such as the Soviet Union, the United States, Japan and Australia, have strengthened their existing crop germplasm institutions, and some other countries established germplasm research institutions. Many national and international research institutions have constructed modern crop genebanks. For example, the United States established the National Seed Storage Laboratory (NSSL) in Fort Collins, Colorado in 1958 and established the world's first modern low-temperature genebank for long-term seed storage, which currently conserves 560 000 accessions, ranking the first in the world. In recent years, developing countries such as India and Brazil have paid great attention to the collecting of germplasm and conserved more than 390 000 and 290 000 accessions, respectively. By 2008, more than 1750 genebanks were established in the world, and more than 7.4 million accessions, of which 70%–75% are duplicated materials, were conserved in these genebanks.

The CGIAR-affiliated research centres hold 11 genebanks conserving nearly 700 000 accessions. In particular, the Svalbard Global Seed Vault (SGSV) was built in Norway in 2008. More than 1.12 million accessions are stored as a secure backup, involving 5481 species, including rice and wheat (150 000 accessions), barley (80 000), sorghum (50 000), kidney beans (40 000), maize (35 000), cowpeas (30 000), soybeans (25 000) and chickpeas (20 000), which came from 89 genebanks across countries and international organizations, especially the CGIAR centres.

In 1974, CGIAR established the International Board for Plant Genetic Resources (IBPGR), which evolved into the International Plant Genetic Resources Institute (IPGRI) in 1994 and the Bioversity International in 2006. At the same time, FAO established a global network for plant genetic resources.

B. Development of crop germplasmics in China

On October 15, 1986, the National Crop Genebank of CAAS was inaugurated, which was an important landmark event in the development of germplasm in China. At present, The Chinese national conservation system, which is composed of one national crop genebank, one duplicate genebank, 10 medium-term genebanks, 43 germplasm nurseries, 224 *in situ* conservation sites and a germplasm information system, has been established. More than 540 000 accessions of more than 350 crops have been conserved, ranking the second largest collection in the world. The China National Crop Germplasm Information System contains more than 700 databases (datasets) such as databases of crop germplasm catalogues, germplasm surveys, germplasm introduction, germplasm conservation, monitoring, characterization and evaluation, molecules, images, and distribution and utilization, with a total of more than 2.1 million data records. In 1997, the China Crop Germplasm Information Network was established and opened to provide online query, analysis and sharing of germplasm information, as well as online access to physical materials. At present, the website has more than 400 000 visits per year.[2]

At the same time, through extensive evaluation and in-depth analysis, Liu Xu and his research team put forward the concepts and theories of the hierarchical structure of plant germplasm for food and agriculture. It was the first time to clarify the 9631 plant species for food and agriculture in China, including 3269 species of cultivated and wild relatives, belonging to 528 crops. The cultivation history, utilization status and development prospects of these crops were described and the species diversity of native crop germplasm was described. The relationship between the distribution of crop germplasm and the origin, planting history, temperature and water resources and geographical environments were indicated. The distribution and richness of germplasm of 110 crops in China were specified. Given the lack of standards, quality controls and technical manuals for operation and technical indicators in scientific research, cross-sectoral, cross-regional, multi-crop and multi-disciplinary comprehensive studies were carried out to develop technical indicators, specifications, and systems for managing crop germplasm. A total of 366 descriptors, data standards and data quality control specifications for 120 crops were systematically developed, and a technical specification system for classification, cataloguing and description of crop germplasm was established. Research in crop germplasm has achieved standardization, normalization and the whole process, end-to-end quality control, which is of great

[2] Chinese Crop Germplasm Information Network (CGRIS).

significance to in-depth research, scientific management and sharing of crop germplasm in China and the world.

1.4.1.3 *The Third Phase: Subject Booming with Focus on Germplasm Enhancement and In-Depth Research of Crop Germplasmics*

A. Rapid development of research in crop germplasmics in the world

Although there are many of passport information and characterization data, the huge number of accessions makes the management of germplasm and accurate identification an aporia. Therefore, Australian scientists O. H. Frankel and A. H. D. Brown proposed the idea of constructing a 'core collection', that is, using about 10% of the samples (or 2000–3000 accessions) to represent the diversity of the original collection (Frankel and Brown, 1984). Because the scope of genetic diversity and the distribution of germplasm are different among crops, scientists conducted in-depth discussions in both theory and practice to develop core collections. To date, core collections have been constructed for at least 60 crops worldwide.

Germplasm enhancement and in-depth research are the basis for strengthening the utilization of germplasm and have received extensive international attention over the past 20 years. For example, the Generation Challenge Program (GCP) initiated by the CGIAR has cooperated with more than 200 institutions in 54 countries to evaluate the genetic diversity of germplasm, conduct in-depth identification of important traits and associated genes, and create new germplasm. In 2010, CGIAR launched the Agricultural Biodiversity Program, which involved several international research organizations and many national organizations. In addition, special programs have been established for some specific targets, such as the Borlaug Global Rust Initiative (BGRI) on wheat stripe rust and the Global Late Blight Initiative (GILB) on potato late blight.

The Latin American Maize Project (LAMP) was implemented in the 20th Century. A total of 813 accessions from 11 countries were preliminarily identified from 12 113 landraces of South America. Through the evaluation of agronomic traits at 21 test sites, 270 accessions were selected for combining ability analysis (using local elite inbred lines, single hybrids and synthetic varieties as testers), and several tropical and subtropical germplasm that can be used for temperate maize breeding were identified. Based on this, the United States launched the Germplasm Enhancement of Maize (GEM) in 1994. The basic idea was to use the germplasm of non-maize-belt tropical and subtropical maize to cross-fertilise temperate elite inbred lines for broadening the genetic basis of breeding in the USA. GEM materials generally carry 25% or 50% of tropical and subtropical germplasm and can be used in breeding not only for temperate maize but also for tropical maize. At present, the GEM program is not only attended by 48 U.S. organizations (including 26 companies, 21 public research units, and 1 non-governmental organization) but also 16 organizations outside the United States (including 12 international companies, and 4 international public research organizations). The U.S. Department of Agriculture funded $1.3 million annually, which, however, cannot be allocated to those companies and organizations based outside the United States. Recently, an allele diversity project (AD) was established in the US GEM program to accelerate the development of pure lines of maize landraces using doubled haploid (DH) technology.

In 2012, the Mexican government and CIMMYT jointly launched a seven-year Germplasm Evaluation Program called 'Seeds of Discovery' (SeeD), with an annual budget of 10 million US$. The purpose was to identify and utilize the genetic diversity of maize and wheat landraces. The technical approach is to use high-density molecular markers to identify and evaluate more than 28 000 maize and 150 000 wheat accessions from the CIMMYT genebank. After identifying elite resources with outstanding target traits such as nutrients and resistance to heat, drought, disease and poor soil stresses, bridge germplasm containing 75% or more of the elite inbred line genome and 25% or less of the landrace genome were created and provided to breeders around the world.

B. Rapid development of research in crop germplasmics in China

Since the beginning of the 21st Century, with the support of National Crop Germplasm Conservation Project, the Scientific and Technological Support Program, 973 Program and 863 Program, and the Key Research and Development Program, Chinese researchers in crop germplasm have developed technical specifications for collecting, multiplication and regeneration, conservation in genebanks and nurseries in-depth evaluation. A new viewpoint of "conservation in utilization and utilization in conservation" has been proposed by specifying the theoretical basis of creating genetic balance by genome rearrangement for being easy to use new

enhanced germplasm in breeding, and how to conduct targeted research to meet the need of crop breeding for comprehensive trait coordination and basic research on specific resources, which have promoted the further development of crop germplasm and supported China to be placed in the international forefront of research on crop germplasm.

The accurate identification of various crop germplasm has been carried out, and remarkable results have been achieved in the exploration of gene resources. To cope with the change of climate and environment and meet the needs for the improvement of green conservation and people's living standards, the requirements for varieties in production are becoming more and more strict. To this end, based on the identification of basic agronomic traits, more than 30% of germplasm preserved in genebanks, nurseries and *in vitro* banks in China were evaluated in multi-year and multi-locations for disease and insect resistance, stress resistance and quality traits, and more than 17 000 accessions of rice, wheat, maize, soybean, cotton, rapeseed, vegetables and other crop germplasm were screened, from which a number of elite germplasm urgently needed for crop breeding were identified. In recent years, Chinese scientists have led the draft and fine-mapping of the whole genome of rice, wheat, cotton, rapeseed, and cucumber, which provides opportunities for genome-wide genotyping. So far, more than 70 000 accessions of rice, wheat, maize, soybean, cotton, millet, cucumber and watermelon have been evaluated by high-throughput sequencing, resequencing, and SNP[3] technologies. In addition, the origin, domestication and spread of rice, cotton, *Brassica* crops, citrus, apple and loquat were analysed to achieve new understanding and knowledge at the genome-wide level. Using the association analysis, a number of genes controlling important agronomic traits were obtained in a variety of crops and the type of allelic variation, distribution and genetic effects of genes were explored in depth to provide solutions for further utilization of germplasm. China is also the first country in the world to carry out large-scale research on core collections. With the support of the national programs, core collections have been constructed for rice, wheat, soybean and many other crops, and the core collections with specific traits have also been established for some key crops.

[3]A single nucleotide polymorphism (**SNP**) is a one-base variation in a single DNA nucleotide that occurs at a specific position in the genome.

High-efficient technology for crop germplasm enhancement and utilization has been continuously improved and has played an important role in crop breeding. In fact, germplasm enhancement made major progress in the 20th Century and developed rapidly in the 21st Century. For example, scientists represented by Professor Yuan Longping in China, the winner of the highest National Science and Technology Awards, became an international leader of hybrid rice breeding by creating and using new germplasm such as wild abortive type, Gang D type, Yinshui type, Honglian type and temperature-sensitive sterile line. In 1969, Professor Yan Ji at Sichuan Agricultural University created new germplasm of wheat 'Fanliu', which was widely used as a parent to breed a series of wheat varieties with a large planting area. Professor Li Qingqi at Shandong Agricultural University created a new germplasm of wheat 'Aimengniu', which was used as a parent to breed 13 wheat varieties with a cumulative planting area of 2.06 million hm^2 during the period of 1983–1996; Li Zhensheng, the winner of the highest National Science and Technology Awards, systematically studied the distant hybridization between wheat and *Elytrigia repens*, transferred a number of elite genes from *Elytrigia repens* to wheat, and developed a series of new wheat varieties such as 'Xiaoyan 4', 'Xiaoyan 5' and 'Xiaoyan 6'. 'Xiaoyan 6' for a total planting area of 3.6 million hm^2 in 1988, which not only made outstanding contributions to wheat breeding in China but also laid a foundation for chromosome engineering breeding in wheat. Professor Chen Peidu at Nanjing Agricultural University introduced the powdery mildew resistance gene *Pm21* from *Dasypyrum villosum* into wheat and bred a number of new varieties with high resistance or immunity to various races of powdery mildew. Since then, researchers in the Institute of Crop Sciences of CAAS have achieved large-scale transfer and effective utilization of exogenous genes by creating new technologies such as overcoming distant hybridization barriers based on physiological development indicators and backcross of single receptor parent, increasing the frequency of heterologous translocation induction by irradiation at different developmental stages of living floral organs, and developing high-density specific markers to track small-fragment translocations or genes. The hybrids between wheat and *Psathyrostachys*, *Agropyron* and *Eremopyrum* and their derivatives were obtained, and seven new wheat varieties carrying elite genes from the P genome of *Agropyron* were developed. It has solved the issues associated with using the P genome of *Agropyron* to improve wheat

and implemented the whole process of innovation from technology, material to product, which laid a solid material and technical foundation for leading the new direction for wheat breeding.

The concept of backbone parents was proposed, and their inheritance was revealed. Based on Chinese Wheat Varieties and Their Pedigrees published in 1983, Professor Zhuang Qiaosheng edited the monograph for Chinese Wheat Variety Improvement and Pedigree Analysis in 2003, which systematically summarized the achievements and experiences of China's breeding practices in the past 50 years from the perspective of selecting parents and making cross-fertilisations. It is particularly noteworthy that Professor Zhuang Qiaosheng proposed the concept of backbone parents. Subsequently, the team conducted phenotypic and gene chip analysis on 37 backbone parents and their derived varieties in different periods and ecological regions. It was found that the backbone parents were significantly superior in key breeding target traits such as yield, disease resistance and stress resistance. They have genomic segments of many elite genes/QTL clusters closely related to yield, disease resistance and stress resistance, and the allelic variation in the segment shows stronger breeding impacts. Similar conclusions were obtained in the study of the backbone parents of rice and maize. The formation and use effect of the backbone parents as well as the genetic mechanism to develop similar or breakthrough varieties was revealed theoretically. The theory of backbone parents has important guidance for the comprehensive improvement of staple food crops in the future.

The theoretical and technological foundation of crop germplasmics has become consolidated. Liu *et al.* (2023) developed a theoretical framework for crop germplasmics by defining basic concepts and features and considering it as the science of studying and utilizing the diversity of crops and their wild relatives. Crop germplasmics is based on the theory of the centres of origin of cultivated plants, the law of homologous series in variation and the theory of synergistic evolution between crop germplasm, human environment and social development. This speciality relies on the technical system of genetic diversity, integrity, specificity and accumulativeness and is supported by the theories, technologies, and management systems of investigation and collecting, conservation, evaluation, enhancement and sharing services of crop germplasm. It further clarified the key principles of research on crop germplasm, that is "extensive investigation, complementary conservation, comprehensive evaluation, in-depth research, innovative enhancement, and share and utilization".

Box 1. History of development of crop germplasmics in the world

(**Modified from Frison *et al.*, 2011**)

Before 10 000 years ago: Domestication and geographic spread of crops

- Humans started to transition from nomad hunters to sedentary farmers.
- In the last 1000 years: Development of agriculture and agricultural biodiversity.
- Cultural contacts and interactions result in crop diffusion and global transfer of PGRFA (Plant Genetic Resources for Food and Agriculture).
- Sumerians and Egyptians actively collect PGRFA.
- The discovery of America boosts intercontinental exchange

Since the 19th Century: Science realised the value and potential of genetic diversity

- The European famine of the 1840s demonstrated the important role of genetic diversity in agriculture (potato varieties in countries such as Ireland lost resistance to late blight, leading to the complete destruction of potato production).
- Charles Darwin's and Gregor Mendel's discoveries prove the importance of genetic diversity for biological evolution and adaptation.
- Between the 1920s and 1930s, N. I. Vavilov identified the main areas of crop origins and their genetic diversity.

By the mid-20th Century: Scientific and institutional developments; concerns regarding genetic erosion and vulnerability

- In 1958, the United States built the world's first national genebank in Fort Collins, Colorado.
- In the 1960s and 1970s, the Green Revolution boosted productivity but contributed to the loss of genetic diversity.
- In 1972, the UN Stockholm Conference on Human Environment called for strengthening of PGRFA conservation activities.
- In 1971, the US National Academy of Sciences raised concern over crops' genetic vulnerability after a major maize epidemic.

- In 1972, the American Academy of Sciences proposed to pay close attention to the genetic vulnerability caused by genetic uniformity and a 25% yield loss order of words due to epidemic of maize leaf blight in southern states of the United States.
- In 1980, the United States established the world's first national germplasm nursery in Corvallis, Oregon.
- In 1984, Australian scientists Frankel and Brown proposed the concept of core collection.

In the 21st Century, the management policy of germplasm has been adopted, the legal framework of global germplasm has been established and the international agricultural research centres have been more involved in the conservation and utilization of germplasm

- In 1961, the International Union for the Protection of New Varieties of Plants was established. National legislation, including intellectual property rights, was strengthened.
- In 1974, the International Board for Plant Genetic Resources (IBPGR) was established, which evolved into the International Plant Genetic Resources Institute (IPGRI) supported by the Consultative Group on International Agricultural Research (CGIAR) in 1991 and renamed Bioversity International in 2006, mainly responsible for promoting the global activities on plant germplasm.
- After 1979, the member states of the Food and Agriculture Organization of the United Nations (FAO) and non-governmental organizations began consultations on germplasm policy and legislation.
- In 1992, the Convention on Biological Diversity (CBD) under the Environmental Programme of the United Nations came into force, which was the first global binding agreement on biological diversity.
- In 1996, FAO developed the Global Plan of Action for the Conservation and Sustainable Use of Plant Genetic Resources for Food and Agriculture.
- In 2001, the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) was signed and entered into force on 29 June 2004.
- In 2004, CGIAR launched the Global Generation Challenges Program (GCP) dominated by the international agricultural research centres and implemented for 10 years.
- In 2004, the Global Crop Diversity Trust was established by FAO and Bioversity International.
- In 2008, with the support of the FAO and countries around the world, especially the Norwegian government, the Global Seed Vault in Svalbard was operated.
- In 2011, FAO developed the Second Global Plan of Action for the Conservation and Sustainable Use of Plant Genetic Resources for Food and Agriculture.
- In 2011, Genesys was online, which is managed by the Global Crop Diversity Trust and integrated the data of 4.3 million accessions in 450 genebanks in the world by 2020.
- In 2014, with the support of the Mexican government, the International Maize and Wheat Improvement Center (CIMMYT) jointly launched the 'Seeds of Discovery' Program (SeeD) with relevant global research organizations.

Box 2. Brief history of development of crop germplasmics in China

Crop domestication and dissemination

- Around 10 000 years ago, broomcorn millet and foxtail millet were domesticated, and then dryland agriculture began.
- Around 10 000 years ago, rice was domesticated in China and rice farming began to take shape.
- Before 5000 years ago, wheat was introduced into China.
- In the 16th Century, maize, sweet potato, tobacco and many other crops were introduced from America to Europe, and then to China.

Formation and development of crop germplasmics

- From 1955 to 1958, the Ministry of Agriculture organized the first national survey and collecting of crop germplasm.
- In 1959, Dong Yuchen proposed the concept of 'crop variety resources'.
- In 1964, Jin Shanbao and Liu Dingan edited and published the first crop variety records in China: Chinese Wheat Variety Records.
- In 1978, the Institute of Crop Germplasm of Chinese Academy of Agricultural Sciences was established.

- During the 30 years after the late 1970s, supplementary national collecting of crop germplasm and special investigation for collecting of key crop germplasm in key areas was carried out.
- In 1981, Crop Variety Resources, edited by Xu Yuntian and Dong Yuchen, was published by the Agricultural Press in Beijing.
- In 1982, the Journal of Crop Variety Resources was launched.
- In 1984, the first National Crop Genebank was constructed and put into use at CAAS.
- In 1986, the second National Crop Genebank was established at CAAS.
- In 1986, the Genetic Resources Branch of Agronomy Society of China was established.
- In 1994, the Chinese Crop Germplasm was published by China Agricultural Press in Beijing.
- In 1998, the project of Developing Crop Core Collections, Important New Gene Discovery and Utilization launched as the first batch of the 973 Program.
- In 1999, Dong Yuchen was elected as an academician of Chinese Academy of Engineering.
- In 2000, Journal of Plant Genetic Resources was launched.
- In 2001, the Crop Germplasm Conservation and Utilization Project was initiated.
- On October 1, 2003, the Regulations of Crop Germplasm were put into force.
- In 2003, Conservation, Evaluation and Utilization of Crop Germplasm Collection in China won the first prize in the National Science and Technology Progress Award.
- In 2004, the National Key Scientific Facilities for Crop Genetic Resources and Genetic Improvement was constructed.
- In 2005, China initiated and held the first International Symposium on Genomics-based Plant Germplasm Research.
- In 2006, the project of Basic Research on Genetic Composition and Utilization Effect of Backbone Parents of Major Crops was funded.
- In 2006, the book series Chinese Crops and Their Wild Relatives edited by Dong Yuchen and Liu Xu was published by China Agriculture Press.
- In 2009, the Diversity, Indicator System and Their Application of Chinese Crop Germplasm won the second prize in National Scientific and Technological Progress Award.
- In 2009, Liu Xu was elected as an academician of the Chinese Academy of Engineering
- In 2015, the Ministry of Agriculture, the National Development and Reform Commission, and the Ministry of Science and Technology jointly issued the National Medium- and Long-Term Development Plan for Conservation and Utilization of Crop Germplasm (2015–2030).
- In 2015, the Ministry of Agriculture initiated the third national survey and collecting of crop germplasm.
- In 2019, the General Office of the State Council issued Suggestions on the Conservation and Utilization of Agricultural Germplasm (No. 56 [2019]).
- In 2021, a new national crop genebank was constructed and put into operation.
- In 2021, the project of Mining and Utilization of Crop Germplasm was funded by the National Key Program.
- In 2021, the special project of Accurate Identification of Crop Germplasm was launched by the Ministry of Agriculture and Rural Affairs.
- In 2022, the National Key Laboratory on Crop Gene Resources and Breeding was approved for construction.
- In 2022, The first list of national crop genebanks and nurseries was designated by the Ministry of Agriculture and Rural Affairs.

1.4.2 Developmental Status and Trend of Crop Germplasmics

With the rapid development of modern science and technology and the change in international political and economic trade patterns, the development of crop germplasmics shows new trends, such as globalizing the collecting scope, integrating conservation systems, standardizing research and utilization, and protecting property rights.

1.4.2.1 Transformation from Extensive Collecting to the Targeted Collecting of Crop Germplasm

Through the efforts of decades, collecting crop germplasm around the world achieved remarkable results. About 7.5 million accessions were collected and stored in genebanks (nurseries). In the future, collecting will mainly focus on germplasm with

diversity and specificity. Through international exchange, new germplasm from other countries will be obtained to fill the gaps in collections. At the same time, the centres of crop origin or centres of diversity are still the focus of future investigation and collecting. The main research areas include sampling strategy, discovery of new species and new types, distribution, origin and evolution of species and populations, centres < of diversity enrichment and evolutionary trend of crop germplasm.

1.4.2.2 *Transformation from Only Emphasizing Quantity to Simultaneous Increase of Quantity and Quality of Crop Germplasm*

In recent years, with the continuous progress of various technologies, most countries have established a standardized, large-scale, and intelligent conservation system for *in-situ* and *ex-situ* conservation. *Ex situ* conservation includes long-term genebanks, duplicate genebanks, medium-term genebanks, field genebanks, and *in vitro* genebanks low-temperature seed banks to the modern conservation system, including a low-temperature bank, an *in vitro* bank, cryopreservation bank and DNA bank to ensure the genetic integrity of conserved germplasm. At present, China having established 224 *in situ* conservation sites, stands at the forefront of the world. On the whole, the conservation of germplasm presents a development trend from general conservation to legal protection, from single approach to multi-approach conservation, and from sovereign protection to property rights protection. According to the characteristics of catalogued germplasm, the conservation of the specific and diverse germplasm should be emphasized with appropriate methods that are adopted to achieve safe conservation on the premise of fully guaranteeing their genetic diversity, genetic integrity and viability. The main research areas include the law of co-evolution of farmers, crops and germplasm and effective mechanism for conservation, the physiological, biochemical and genetic basis of safe conservation, synchronous improvement of the quantity and quality of germplasm, preservation technologies of prolonging the life of germplasm, genetic drift in the conservation process and early warning technology for safe conservation.

1.4.2.3 *Transformation from General Evaluation to Accurate Identification of Crop Germplasm*

In recent years, with the development of phenomics and the improvement of facilities of phenotypic evaluation, carrying throughput and measuring throughput have been significantly improved, which provides the possibility for large-scale evaluation of germplasm. Australia, the United Kingdom, France and Germany have established national platforms for phenotypic evaluation. Some multinational seed companies such as Corteva and Syngenta also consider the phenomics evaluation platform as the core technology for accurate identification of germplasm. At the same time, SNP markers, gene chips and resequencing are widely used in genotypic characterization. High-throughput phenotypic and genotypic evaluation and wide use of omics technologies have greatly improved the efficiency of the discovery of gene resources. The awareness of intellectual property protection has been further strengthened. The accurate identification of germplasm should be orientated to meet the major needs in food security, green development, health and safety, industrial development, people's expectation for a better life, beautiful rural construction and scientific development. The main research areas include the key technologies for intelligent evaluation, large-scale accurate identification and in-depth exploration of elite germplasm and genes, coordinated expression of important target traits and their genetic basis and the genetic composition and use of special types of germplasm such as landraces and backbone parents.

1.4.2.4 *Transformation from Traditional Methods to New Technologies for Germplasm Enhancement*

In the future, the large-scale creation of new germplasm with outstanding traits, clear genetic basis, breeders' desire to use and easy-to-use breeding should be emphasized. On the one hand, the means of germplasm enhancement will be diversified. In addition to the traditional means such as distant hybridization, chromosome engineering, cell engineering, mutagenesis and population improvement, the newly developed technologies including gene editing, exogenous gene introduction and whole genome selection are being used in germplasm enhancement. Even the derived ways for initial domestication, re-domestication and de-domestication will be used in germplasm enhancement. On the other hand, in addition to important target traits such as high yield, better quality, disease and insect resistance and stress tolerance, germplasm enhancement also pays attention to the needs for green environments, efficient use of natural resources, and mechanization.

The coordinated expression of general traits has become a hot spot. The main research areas include the development of new technologies for large-scale germplasm enhancement, gene polymerization design and their genetic effects, efficient detection and tracking of genes of target traits and their genetic effects, and coordinated expression of target traits.

1.4.2.5 Transformation from General Distribution to Special Target Services for Sharing and Utilization of Crop Germplasm

In 2004, the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) was implemented, and a multilateral system of access and benefit share was established; in 2007, the distribution of germplasm started to follow the Standard Material Transfer Agreement (SMTA) harmonized with the Treaty. The utilization of crop germplasm in the future will focus on various needs such as food security, green development, health and safety, industrial development, people's expectation for a better life, beautiful rural construction and scientific development. Through the germplasm registration system and special target service of germplasm, it aims to promote the effective use of germplasm and share the benefits.

(Authors: Xu Liu, Yu Li, Zongwen Zhang, Jing Wu; Translators: Zongwen Zhang, Yu Li)

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Chapter 2

Basic Theories of Germplasmics

The discipline of germplasmics was developed in the 20th Century. Researchers initially used morphological, archaeological, historical and other methods to understand the origins, domestication, varieties and evolution of crops; with the development of genetics and genomics, a range of modern biotechnological methods have also been widely used to study the origins and evolution of crops, breakthroughs being made in some areas. The theory of the centres of origin of cultivated plants (crops), the law of homologous series in variation and the theory of synergistic evolution of crop germplasm and cultural environments have been established, laying a theoretical foundation for the development of crop germplasm.

2.1 Introduction to the Theory of the Centres of Origin of Crops

Understanding where crops originated and how wild plants evolved is of great importance for collecting germplasm and developing germplasm enhancement strategies. Over the past 100 years, crop geneticists and botanists around the world have done a lot of research exploring and validating the origins of crops in many ways, with various hypotheses being proposed. Among them, Vavilov's theory on the centres of origin of crops has been widely recognized.

2.1.1 The Centres of Origin of Crops

2.1.1.1 Candolle's Theory of Crop Origins

The origins of crops have long been assessed and documented by botanists, breeders and agronomists. Although the predecessors have done a lot of research, it was the Swiss botanist Alphonse Pyrame De Candolle who started to explore in modern times the origins of crops using scientific methods. He studied a variety of crops using the methods of natural taxonomy, plant geography, archaeology, history and linguistics and proposed that the region where the wild ancestors of crops grew was the place where they were first domesticated, that is, their region of origin. The crops may have been domesticated first in China, South-West Asia (with Egypt) and tropical Africa. He published the book *Origine des plantes cultivées* (Origin of Cultivated Plants) in 1882, which is famous in the field. Due to the limited conditions at that time, the information collected in this book was not sufficient and lacked evidence from cytogenetics, and molecular biology and some of the data has already been proved wrong but it still has immense value as a reference for studying the origins of crops.

2.1.1.2 Vavilov's Theory of Centres of Origin of Crops

Nikolai Vavilov, a geneticist in the former Soviet Union, was not only a famous scientist studying the origins of crops but also the founder of the discipline of plant germplasm. During the 1920s and 1930s, he organized plant expeditions to more than 60 countries, across four continents and collected more than 300 000 specimens and seed samples of crops and their wild relatives. With the help of morphological classification, hybridization tests, cytology and immunology, as well as plant geography, archaeology, history and linguistics, a set of theories was established to determine the geographical centres of origin of cultivated plants.

After analysing the geographical distribution of genetic diversity of more than 600 plant phenotypes, Vavilov proposed his famous theory of the centres of origin for major cultivated plants, which include eight centres and three sub-centres. These centres (sub-centres) were: 1. The Chinese Centre including mountains in central and Western China and their adjacent lowlands; 2. The Indian Centre including Myanmar and Assam (Eastern Indian province) and 2a. The Indo-Malaya (Malaysia) Sub-centre; 3. The Central Asiatic Centre including the Northwestern India (Punjab, provinces along the border in the North West, Kashmir), Afghanistan, Tajikistan and Uzbekistan and the West of Tianshan Mountains; 4. The Near-Eastern Centre including the interior of

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Asia Minor, the whole of Transcaucasia, Iran and mountainous Turkmenistan; 5. The Mediterranean Centre including coastal borders of the Mediterranean Sea; 6. The Ethiopian Centre including the mountains of Ethiopia and Eritrea; 7. The South Mexican and Central American Centre including the Antilles; 8. The South American Centre including Peru, Ecuador and Bolivia and 8a. Chile Island and 8b Brazilian-Paraguayan Sub-centres (figure 2.1). The eight Centres are separated by deserts, mountains or oceans, with a lot of diverse variation materials and plants still to be excavated, all of which are treasure houses of crop resources (Vavilov, 1951).

Vavilov also proposed the concepts of "primary crops" and "secondary crops". The terms "Primary crops" refer to ancient crops that have been cultivated for a long time, such as wheat and barley; the terms "Secondary crops" refer to those that were initially considered as weeds in the field and are now cultivated with weeds mixed with primary crops, such as rye (*Secale cereale*) and oats (*Avena sativa*). Vavilov issued some important statements on the significance of local varieties, exotic and foreign materials, introduction theories, etc. His theory of the Centres of crop origins and related theories have been playing a particularly important guiding role in crop breeding.

2.1.1.3 *Zhukovsky's Theory of the Centres of Crop Origin*

After Vavilov's Eight Centres of Origins of Crops was proposed, his student P.M. Zhukovsky and the Dutch breeder A.C. Zeven revised his theory. In 1975, they published the *Dictionary of Cultivated Plants and Their Centres of Diversity*, which expanded the geographical scope of the eight original centres of Vavilov and added four new centres of origin, referred to as the *Mega-centre theory of cultivated plants*.

According to this theory, there are 12 mega-centres for the origin of crops, which almost cover the whole world: (1) Chinese-Japanese Region; (2) Indochinese-Indonesian Region; (3) Australian Region; (4) Hindustani Region; (5) Central Asian (6) Near Eastern Region; (7) Mediterranean Region; (8) African Region; (9) European- Siberian Region; (10) South American Region; (11) Central American and Mexican Region; (12) North American Region (Zeven and Zhukovsky, 1975).

Zhukovsky also believed that the distribution of wild species was very narrow and proposed the concept of Primary gene microcentres to describe the narrow region where wild species distributed and the cultivated species first domesticated, while cultivated species were widely distributed and

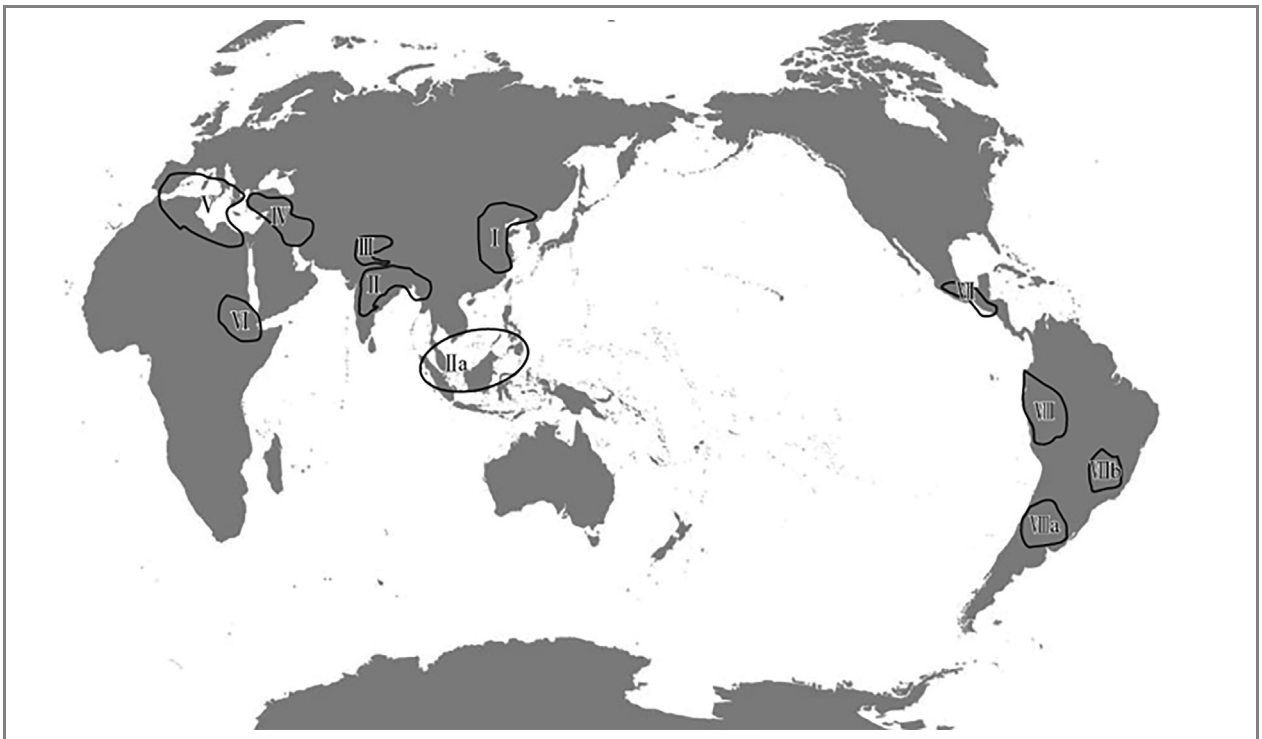


Figure 2.1 Schematic diagram of eight centres of origins (Vavilov, 1951). I. The Chinese Centre; II. The Indian Centre; IIa. The Indo-Malaya (present-day Malaysia) Sub-centre; III. The Central Asiatic Centre; IV. The Near-Eastern Centre; V. The Mediterranean Centre; VI. The Ethiopian Centre; VII. The South Mexican and Central American Centre; VIII. The South American Centre; VIII a. Chiloe Sub-centre; VIII b. Brazilian-Paraguayan Sub-centre.

varied, so he also proposed the concept of Secondary gene megacentres to describe the region where cultivated species were spread.

2.1.1.4 Harlan's Theory of the Centres of Crop Origin

American geneticist Jack Rodney Harlan believed that the original centre of crops proposed by Vavilov was the earliest area where agriculture originated, but there is no centre of variation for some crops and their wild ancestors and the genetic diversity centre is not necessarily the centre of origin, while the centre of origin is not necessarily the centre of genetic diversity. Some species may originate from several different regions. For example, the coverage of the Near East is limited, but there are mainly wild wheat species and their varied populations, which can be called the centre of origin of wheat. However, there are wild species and different variation types of sorghum in the Southern Sahara and North of the equator. The domestication of sorghum may be highly dispersed. Harlan called this area a noncentre. The Centres and Noncentres system was proposed (A1 Near East, B1 China, C1 Central America and A2 Africa, B2 Southeast Asia, C2 South America) (Harlan, 1971) (figure 2.2). Later, Smith (1989) added the North America Centre to this system.

The study found that selection pressures varied across regions leading to great differentiation in crop morphology and wild species in specific regions and the origin of crops showed diffusion across time and space. Therefore, Harlan also put forward the Diffusion Origins of Crops. According to the temporal and spatial factors of crop evolution, crops are divided into the following categories: 1. Endemic crops domesticated in a given region and rarely spread; 2. Semi-endemic crops originating from a region but spread moderately; 3. Monocentric crops originating from a given region but widely spread without the secondary centre of diversity; 4. Oligocentric crops that originate from a given region but are widely spread with one or more secondary centres of diversity; 5. Noncentric crops are domesticated in a wide area (Harlan, 1976).

2.1.1.5 Hawkes' Theory of the Centres of Crop Origin

John Gregory Hawkes, a British plant breeder, believed that the original centre of crops should be separated from the original region of agriculture, so he put forward a new theory for the original centre of crops. In this theory, the place where agriculture originated was called the core centre and the area where crops spread from the core centre and formed rich population types was called the region of diversity. At the same time, Hawkes used "Minor centres" to describe places where only a few crops originated (Hawkes, 1983) (table 2.1).

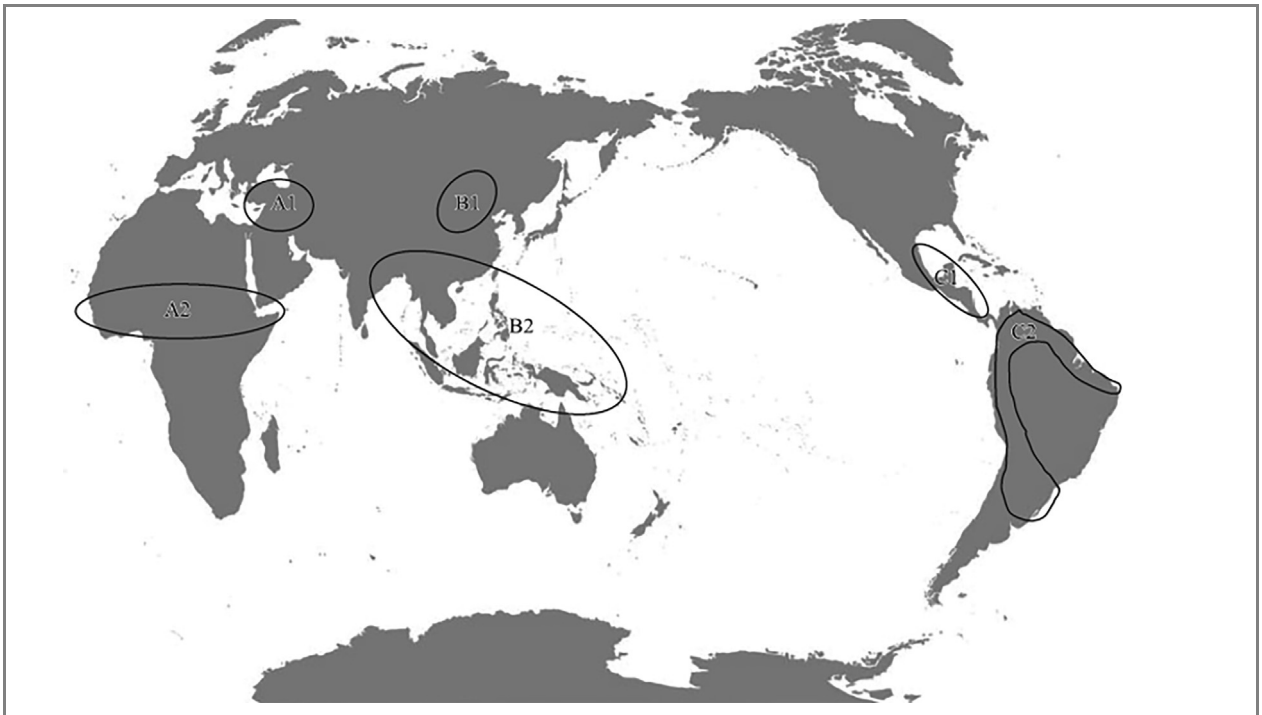


Figure 2.2 Schematic diagram of centres and noncentres system (Harlan, 1971). A1. Near East Centre; B1. China Centre; C1. Central American Centre; A2. African Noncentre; B2. Southeast Asia Noncentre; C2. South America Noncentre.

2.1.1.6 *Summary of the Theories of the Centres of Crop Origin*

The scientific research on the theory of crop origins was pioneered by Candolle and Vavilov, revised by Zhukovsky and others and different theories were put forward by Harlan and other scientists. According to the imbalance in the distribution of crop species on the Earth, the scientists represented by Vavilov named several regions with extremely rich species and a large number of variations as crop origin centres and determined eight original centres. On the other hand, scientists represented by Harlan found that the original centre for some crops was not the region where dominant genes are concentrated and the original centre for some crops was not consistent with the centre of diversity, and the origin centre proposed by Vavilov may be the region where agriculture originated earliest in the world, the domestication of crops exists in the centre and noncentre systems and some crops are of dispersed origins, so it is not even necessary to discuss the original centres (table 2.2).

Although these theories differ, a common thread is that plant domestication occurred in different parts of the world and crops can have a large number of populations with genetic diversity in different regions of origin or domestication. Modern crop breeding shows that the theory of the centre of crop origin proposed by Vavilov and related theories developed by its successors have played an important role in crop breeding and effectively guided the collection of germplasm. Due to the existence of various genes in the original centres, which tend to balance under certain conditions and establish a balanced ecosystem with complex ecological environments, various genes coexist and evolve, to prevent species from becoming extinct. Therefore, more desirable germplasm can be found in the original centre. For example, sterility genes and restoration genes coexist in the original centre

Table 2.1 Hawkes's theory of centre of crop origins.

Nuclear centres	Regions of diversity	Outlying minor centres
A. Northern China	I. China	1. Japan
	II. India	2. New Guinea
	III. Southeast Asia	3. Solomon Islands, Fiji and South Pacific
B. Near East	IV. Central Asia	4. Northwestern Europe
	V. The Near East	
	VI. The Mediterranean region	
	VII. Ethiopia	
	VIII. West Africa	
C. Southern Mexico	IX. Meso-America	5. United States, Canada
		6. The Caribbean
D. Central to Southern Peru	X. Northern Andes (Venezuela to Bolivia)	7. Southern Chile
		8. Brazil

Table 2.2 Theories of the centre of crop origins.

Representative scientists	Candolle	Vavilov	Zhukovsky	Harlan	Hawkes
Major theories	1. The wild ancestor of a crop designates the place where it was first domesticated, that is, the place of origin 2. There are three places where humans first domesticated crops	1. The law of homologous series in variations 2. Eight centres of origin of crops 3. Primary centres of origin and secondary centres of origin 4. Primary crops and secondary crops	1. 12 Megacentres of crops 3. Primary gene microcentre and Secondary gene megacentre	1. Centres and Non-centre system 2. Diffusion origins of crops	1. Unclear centres 2. Regions of diversity 3. Minor centres

and resistance germplasm materials can also be obtained in the original centre. At the same time, with the growth of population and economic development, deterioration of the ecological environment and changes in farming practices, some important crop germplasm have sharply reduced or even become extinct. The theories of the original centre can effectively guide what crop germplasm can be introduced and conserved to prevent endangered species from extinction. In recent decades, germplasm collection in different countries has focused on these original centres, where there is the richest genetic diversity. For example, the former Soviet Union had been sending expeditions to Mexico, Peru and Bolivia since 1925 and had collected more than 9000 accessions of potato germplasm by 1991. The information about the original centres for some crops is shown in table S1 and the information about the major crops originating in China is shown in table S2.

2.1.2 Methods for Determining the Centres of Origin of Crops

How one determines the origin of a particular cultivated species has become the central subject of research on crop origin. The major research methods include determining the classification of crops by morphological and cytological approaches, clarifying the distribution of wild species and their relatives and studying the origins and spread of crops by integrating archaeological and historical evidence. With the development of modern biotechnologies, the use of genetics and molecular biology techniques such as cytology, molecular markers and genomics has become increasingly important.

2.1.2.1 Morphology

During the early times, inadequate transportation and less intercommunication contributed to the limited range of human activities and it was difficult to introduce and domesticate plants coming from other places, thus crops have been grown by humans using only those available locally. Therefore, morphological investigation to identify the wide variation distribution of the wild species and relatives is critical for understanding the origins of crops.

Researchers have already obtained diverse results by identifying large populations of ancestral or wild species of crops. For example, it is recognized that soybean originated in China and wild soybean is the ancestor of cultivated soybean. China has found and collected more than 90% of the world's wild soybean resources. There are not only typical wild soybeans and cultivated soybeans, but also a series of transitional types between them. Wild cabbage is widely distributed in the Mediterranean Sea cliffs, Northern Spain, Western France and South and South-West England and thus it has been deduced that Sicily may be the centre of the origin of cabbage. Common wheat is derived from a natural cross-fertilisation between cultivated emmer wheat *Triticum dicoccon* Schrank and Tausch's goatgrass *Aegilops tauschii* that are distributed from the Transcaucasia to Central Asia, where it originated, this hypothesis has also been supported by molecular biology studies (Pont *et al.*, 2019). In addition, all known wild species of buckwheat are distributed in South-West China and recent genomics studies also support that this region is the original centre of cultivated buckwheat (Zhang *et al.*, 2021b).

As wild tea trees were discovered in India, some scholars believed that tea trees originated there. Later, Chinese scientists found a large number of wild tea trees in the Southwest mountainous area and shrub-type tea trees in the Shennongjia area of China. After comparative studies, the wild tea trees found in India and the tea trees introduced from China to India belong to the same variety of Chinese tea trees, suggesting that China is the origin of tea trees. In recent years, developing high-quality reference genomes at the chromosome level of the tea tree (*Camellia sinensis* var. *sinensis*) has revealed the adaptive evolutionary mechanism of cultivated tea tree and further supports that the tea tree originated from South-West China (Xia *et al.*, 2020).

The diversity of wild species distribution also suggests that some crops may have multicentric origins. The origin of modern barley was thought to be the Fertile Crescent (around Mesopotamia). But Vavilov reported that barley from Tibet in China had a naked grain, awnless or with semi-awned traits and Tibet may be one of the other original centres of barley (Vavilov, 1951). In recent years, Chinese scholars have found a wide range distribution of wild barley in several places on the Qinghai-Tibet Plateau and the genetic diversity of wild barley in Tibet is also richer than that in the Middle East. Therefore, they concluded that the Qinghai-Tibet Plateau and its surrounding areas are also a centre of the origins and evolution of cultivated barley. Subsequent genome sequencing and other work further support this view (Mascher *et al.*, 2017; Dai *et al.*, 2012). Waldson and Vavilov first proposed that corn originated in Mexico, Guatemala and Honduras in Central America. Until now, there are still many places in those areas where the wild ancestor of corn – teosinte, can be found.

2.1.2.2 Phytoarchaeology

Phytoarchaeology provides the most important method for studying the origins of crops. Especially with the emergence of flotation technology, archaeologists can scientifically collect plant remains *in situ* to address the origins of crops and other important academic issues.

Archaeological research on the origin of staple crops

The origin of rice, especially Asian cultivated rice (*Oryza sativa*), has been disputed. Chinese scientists have unearthed Neolithic cultural sites containing carbonized grains of rice and primitive tools made of bone, stone and ceramics dating back to 7000 BCE. The oldest rice was found in the Yangtze River Valley (6500 BCE) and Northern Jiahu in Henan Province (6000–7000 BCE). The best and most complete evidence of the existence of early rice came from the two sites of the Pengtoushan Culture, the Pengtoushan and the Bashidang (7500–6100 BCE). Therefore, rice may have originated in the Yangtze River basin more than 7000 years ago. Silva *et al.* (2015) established a database for the evidence collected from rice archaeological remains with 400 rice sites from East Asia, South East Asia and South Asia to facilitate the studies on the original centres of rice and believed that China was the correct place for the origin of rice and the middle and lower reaches of the Yangtze River were two dual original centres.

Wheat originated from the Fertile Crescent of West Asia and the earliest wheat remains unearthed from archaeological sites in the Early Pre-Pottery Neolithic B (EPPNB) period of 10 500–9500 years ago. However, the most accurate archaeological evidence of wheat planting in China is at the Donghuishan site in Minle, Gansu Province. A joint team of Chinese and American archaeologists concluded that the cultural accumulation and wheat remains in the Donghuishan site could be traced back to the Siba Culture period. The absolute date was 3600 years ago.

Archaeological exploration of the origins of other crops

Buckwheat is one of the crops originating from the Qinghai-Tibet Plateau and surrounding areas of China and plays an important role in the history of agricultural development and food culture. Chinese researchers obtained a batch of carbonized plant samples at the Donghuishan Site in Minle County, Gansu Province using the flotation method and the soil samples from the cultural layer in the *in-situ* profile. In these plant samples, three complete carbonized buckwheat grains were identified for the first time. According to carbon isotope dating, the grain is 3610–3458 years old. This discovery shows that buckwheat was cultivated as a crop in the Hexi area as early as the Neolithic Age. It also provides new evidence for the origin of buckwheat in the Qinghai-Tibet Plateau of China.

The "First granary in the world" was discovered at the Cishan Cultural Site in Wuan City, Hebei Province, which dates back to about 10 300 years ago. The 88 cellars contained grains of more than 50 000 kg. Researchers conducted a systematic analysis of phytoliths and carbon-14 dating of some ash samples and confirmed that the early crop broomcorn is about 10 000–8700 years old while foxtail millet is about 8700–7500 years old, the earliest evidence of the age of broomcorn and foxtail millet, indicating that broomcorn may have originated in the middle and lower reaches of the Yellow River (Lv, 2018).

2.1.2.3 Historical Linguistics

When a crop was first cultivated and used, the local people must have given it a name and since it was closely related to the people's life at that time, it left related characters/pictograms, name records and even myths and legends. If there is no record of the crop in local history, it is difficult to prove that the crop was domesticated locally, or even if it was the origin of the crop. Therefore, the origins of crops can be presumed through literature records, historical legends and related information.

Wheat is believed to have been introduced into China during the Yin and Shang Dynasties at the latest about 3000 years ago. When the Shang people created oracle bone inscriptions, they made a pictograph for wheat, "來", with the upper part like a ripe ear of wheat and the lower part like a root of wheat. In the *Zuo Zhuan-18th years of Chenggong*, it was recorded that "Zhou Zi had elder brothers with no wisdom. He could not identify bean from wheat, so he could not establish himself as heir." As can be seen from this story, wheat was widely cultivated in Northern China as early as the Spring and Autumn Period. Before the mid-19th Century, it was believed that peaches originated in Persia, but Darwin refuted this because there was no ancient Hebrew name for peach in Persia and he concluded that peaches originated in the Northwest of China based on his research on peach kernel specimens collected from different countries. The *Classic of Mountains and Rivers* first appears in the story of Kuafu pursuing the sun and his body becomes the peach forest. The ancient literature *The Book of Songs*, *Shang Shu* and *Zuo Zhuan* also have the