P.M. Priyadarshan
S. Mohan Jain *Editors*

Cash Crops

Genetic Diversity, Erosion, Conservation
and Utilization

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Editors
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Preface

Breeding crop plants in the current century is a daunting challenge. Plant breeders have already made much effort in developing new high yielding plant varieties. These efforts are further augmented with the advent of new stresses related to climate change. Any successful breeding programme solely depends on the availability of genetic diversity. Genetic diversity and genetic variation are to be separately dealt with. While genetic diversity is the range of genetic characteristics in a crop, the genetic variation refers to the genetic differences among individuals in a specific trait, which are based on DNA sequence.

Staple or food crops like cereals, wheat, rice, and maize are absolutely essential for sustenance. However, there are other crops like coffee, tea, cocoa, cotton, oilseeds, sugar cane, oil palm, date palm, and rubber that are grown only for raising income to the farmers. A differentiation of food with cash crops suggests that most food crops are considered not to be traded much through markets. But this definition does not hold good for developing countries where most of the crops are grown for revenue. However, the debate on the differentiation between food crops and cash crops still continues.

A looming threat to the world in the current century is population explosion where food and nutrition security, climate change, and ever-growing human population growth have become major global issues. Estimates suggest that the world population will reach close to 10 billion by 2050, with a food gap of 70% between the crop calories available in 2006 and projected calorie demand in 2050. A sustained average annual growth in agricultural production of 44 million metric tons per year, for 30 years, is essential to meet this demand. Breeding activities have achieved a linear increase at an average rate of 32 million metric tons per year. Creating and utilizing new genetic diversity is the only option before the plant breeders to make the production of new varieties more sustainable. Breeding new cash crop varieties will ensure increased food and nutrition security. This challenge is further made intriguing since most cash crops are long term in nature.

Crop diversity around the world is declining, posing a challenge to both environment and food security. With the advent of Green Revolution, staple crops like wheat, rice, soybean, and corn have become dominant in arable lands worldwide.

The lack of genetic diversity and increasing uniformity of any crop may render the same unsustainable. Hence, the FAO in 2018 had set out a new set of conservation guidelines titled, "Voluntary Guidelines for the Conservation and Sustainable Use of Farmers' Varieties." This publication highlights how crop genetic diversity enables resistance to environmental and climatic shocks (https://reliefweb.int/sites/reliefweb.int/files/resources/ca5601en.pdf) and functions as a tool for researchers and policymakers. The FAO notes that almost all countries report the "genetic erosion" of crops, with maize, wheat, and rice accounting for 51% of all plant-based food.

The loss of crop genetic diversity poses a "particularly severe" threat to global food security and nutrition—one that risks the achievement of sustainable development goals (SDG 2 by FAO = zero hunger) on eradicating hunger and malnutrition by 2030. It entails the necessity to provide the farmers and local communities with the information and support in relation to crop conservation and sustainable utilization. Yet, almost 690 million people remain chronically undernourished, amid signs of diminishing momentum towards reaching Zero Hunger.

There are several upcoming innovative technologies that are being implemented in breeding new plants. The use of "CRISPR single base editors" is one such tool that brings much promise in deriving new genetic diversity. Single base editing can produce genotypes with broad-spectrum disease resistance that ensures higher yield under climatic stressful conditions. Speed breeding by creating artificial climatic conditions to breed plants through raising more generations per year is another innovative option. The applications of most promising futuristic technologies are breeding for C4 photosynthesis, high-throughput phenotyping, RNA-seq (whole transcriptome shotgun *sequencing*), metabolomic profiling, phenomics, genomic selection, and climate resilient breeding with artificial intelligence. However, these technologies must go a long way before successfully being implemented in commercial breeding programmes.

Beginning with a chapter on introduction to cash crops, this book contains 14 other chapters on cardamom, cocoa, coconut, cashew nut, coffee, date palm, ground nut, jute, lentil, mustard, oil palm, rubber, sugar cane, and tomato authored by well-known scientists on their respective crops. This book is expected to assist students, researchers, scientists, and faculties as a guide to genetic diversity of cash crops.

We gratefully acknowledge the guidance and assistance rendered by all the reviewers who have done a meticulous job with respective chapters. Finally, we profusely thank Springer Nature for publishing this book.

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About the Editors

P. M. Priyadarshan is a prominent *Hevea* rubber breeder. He began his research career by breeding triticale and wheat while doing MPhil and PhD degrees at Chaudhary Charan Singh University, Meerut, under the guidance of Prof. P.K. Gupta. During the 1980s he focused on the in vitro culture of spices. He joined the Rubber Research Institute of India (Rubber Board, Ministry of Commerce, Govt. of India) as a Plant Breeder in 1990 and specialized in breeding *Hevea* rubber for sub-optimal environments. He was a visiting scientist at the Hardwood Tree Improvement and Regeneration Centre, Purdue University, USA. In 2009, he became the Institute's Deputy Director and managed its Central Experiment Station until 2016. He has been involved in breeding cereals, spices, and *Hevea* rubber for 32 years. He is a reviewer of several international journals like *Industrial Crops and Products* and *Tree Genetics and Genomes*. He has published several research papers and chapters in journals and books of international repute like *Advances in Agronomy*, *Advances in Genetics*, and *Plant Breeding Reviews*. He has edited books on *Breeding Plantation Tree Crops* (Springer), *Breeding Major Food Staples* (Blackwell-Wiley), and the *Genomics of Tree Crops* (Springer). He also authored books on the *Biology of Hevea Rubber* (Springer) and on *Plant Breeding: Classical to Modern* (Springer).

S. Mohan Jain received his MPhil, 1973, and PhD, 1978, from Jawaharlal Nehru University, New Delhi, India. He was a postdoctoral fellow in Israel and USA and visiting scientist/professor in Japan, Malaysia, Germany, and Italy. He worked in both academia and industry and served as a Technical Officer, Plant Breeding and Genetics, International Atomic Energy Agency (IAEA), Vienna, Austria, 1999–2005. Dr. Jain is on the editorial board of *Euphytica, In Vitro, Propagation of Ornamental Plants* and reviewer of *Plant Cell and Organ Culture*, *Plant Cell Reports*, and few others. His has more than 165 publications in peer-reviewed journals, book chapters, and conference proceedings and has edited 65 books. He was an invited speaker and acted as a Chairperson in several international conferences worldwide. He was awarded Nobel Peace Prize certificate, in commemoration of the awarding to IAEA of the Nobel Peace Prize for 2005. He was also former consultant to IAEA, the European Union, the Government of Grenada, Iranian Date Palm Company, and the Egyptian Government. Currently, he is Adjunct Professor, Department of Agricultural Sciences, University of Helsinki, Helsinki, Finland.

Cash Crops: An Introduction

P. M. Priyadarshan and S. Mohan Jain

Abstract Cash crops are grown for cash generation rather than for sustenance. The commodities are produced and consumed as fruits, flowers, foliage, stems, roots, latex, or any plant parts that are consumed directly or processed products as fiber, rubber, sugar, beverages, and biofuel. An array of crops like wheat, corn, oats, potatoes, cherries, apples, strawberries, soybean, bananas, cotton, jute, oranges, jojoba, jatropha, groundnut, and brassicas come under the umbrella of cash crops. Breeding activities have achieved a linear increase at an average rate of 32 million metric tons per year against an expected turnover of 44 million metric tons per year. The ensuing climate change, low agricultural diversity, and high intensity of agricultural inputs can exacerbate food insecurity and instability. Conserving crop biodiversity is an urgent undertaking. The Inter-governmental Panel on Climate Change (IPCC) predicts that 25–30% of plant species will be extinct or endangered in the next century. As such, cash crops are utilized by humans to earn money, and such crops are prone to climate changes. Hence, safe guarding the existing diversity and producing new diversity in cash crops are of utmost importance.

Molecular marker techniques like SSRs, DArTseq, and SNP genotyping assays in cash crops are on the progress. In many crops, data obtained through PCR analysis of DNA fragments from ancient DNA samples have shown evolutionary changes within the gene pool over a long time. During the last three decades, under the auspices of FAO, the international community has strived to developing and maintaining a global system on plant genetic resources for food and agriculture. CGIAR centers make significant contributions to both the global system and SDG Target 2.5 through international PGRFA collections. Case situations on cacao, coffee, sugarcane, and *Hevea* rubber are explained.

Keywords Cash crops · Genetic diversity · Molecular tools · Genomics · Climate change · Biotechnology

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1 Introduction

Cash crops are grown for cash generation rather than for sustenance. The commodities are produced and consumed as fruits, flowers, foliage, stems, roots, latex, or any plant parts that are consumed directly or processed products as fiber, rubber, sugar, beverages, and biofuel. An array of crops like wheat, corn, oats, potatoes, cherries, apples, strawberries, soybean, bananas, cotton, jute, oranges, jojoba, jatropha, groundnut, and brassicas come under the umbrella of cash crops. However, some of the major crops are cocoa, coffee, oil palm, sugar cane, and rubber.

Current estimates are that nearly 690 million people are hungry (8.9% the world population) (FAO 2020). The world is not on track to achieve Zero Hunger by 2030. If recent trends continue, the number of people affected by hunger would surpass 840 million by 2030. Hence, the world requires a dramatic increment in food production in the next 30 years. The current human population of 7.7 billion is expected to reach 8.6 billion in 2030 and 10 billion by 2050 (Pourkheirandish et al. 2020). Concurrently, the effects of climate change pose a looming threat to agriculture via drought and salinity that limit agricultural land and water use (Godfray et al. 2010).

The history of agriculture shows that wild grains were collected and consumed starting from 20,000 BC onwards. The eight Neolithic founder crops viz. emmer wheat, einkorn wheat, hulled barley, peas, lentils, chickpeas, bitter vetch, and flax were cultivated from 9500 BC in the eastern Mediterranean area. Rice was domesticated in China some 10,000 years ago (Gross and Zhao 2014). The Anthropocene epoch is believed to have made the man-made changes in Earth's biodiversity and biogeography (Martin et al. 2019). Anthropocene epoch is an unofficial unit of geologic time, used to describe the most recent period in Earth's history when human activity started to have a significant impact on the planet's climate and ecosystems. Such changes in the human-mediated spread of crops beyond their regions of domestication into other parts of the world are central to these arguments (Khoury et al. 2016). Analyses made after 1950s indicate that there have been major influxes (and subsequent domination) of crops into the food supplies, diets, agricultural economies, and farmlands in many parts of the world (Nelson et al. 2016).

Agricultural trade liberalization in the 1980s encouraged the production and export of a few select crops or genotypes at the regional- or country-level (Li 2015). Such programs only ensured that patterns of crop diversification over the past 50 years have differed drastically among regions. At the same time, climatic limitations to growing certain crops in higher latitudes also have likely led to less drastic or immediate shifts in agricultural diversity in these regions, as compared to lower latitudes (Ramankutty et al. 2002). Furthermore, existing global evaluations of crop diversity have primarily focused on taxonomic diversity measured as crop species richness across global scales (Khoury et al. 2016; Martin et al. 2019).

By the year 2050, the world population may reach nine billion and the demand for food may grow by 70% (Dhankher and Foyer 2018). Breeding activities have achieved a linear increase at an average rate of 32 million metric tons per year (Alston et al. 2009) against an expected turnover of 44 million metric tons per year

(Tester and Langridge 2010). The ensuing climate change, low agricultural diversity, and high intensity of agricultural inputs can exacerbate food insecurity and instability (Dhankher and Foyer 2018). For instance, current estimates indicate that an increase of 1 °C might cause a 10–20% reduction in the world's production of maize (Tito et al. 2018). In fact, meta-analyses of climate change and its impact suggest that by 2030 crop yields may be decreased by 50% (Campbell et al. 2018).

The livelihood of millions of smallholder farmers and the survival of several national economies in Africa, Latin America, and Asia depend on crops usually considered commodities, or minor or orphan crops like coffee (*Coffea arabica* L.) and cacao (*Theobroma cacao* L.) (Davis et al. 2019; Farrell et al. 2018; Schroth, et al. 2016). For coffee, rapid deforestation and climate change may lead to the extinction of many wild African species (Davis et al. 2019). Such crops are at risk due to climate change (Davis et al. 2019; Schroth et al. 2016). For cacao, mostly grown in West Africa, the maximum temperature tolerated (38 °C) could be exceeded during hot and dry *El Niño* years (Schroth et al. 2016). The rising temperatures, longer droughts, and excessive rainfall have reduced coffee yields by 30% in Colombia since 2008 (Van der Vossen et al. 2015).

2   Genetic Diversity Utilization and Exchange of Germplasm

Conserving crop biodiversity is an urgent undertaking. The Inter-governmental Panel on Climate Change (IPCC) predicts that 25–30% of plant species will be extinct or endangered in the next century (Foden et al. 2018; Sintayehu 2018). As such, cash crops are utilized by humans to earn money, and such crops are prone to climate changes. Hence, safe guarding the existing diversity and producing new diversity in cash crops are of utmost importance. Crop diversity around the world is declining posing a challenge to both environment and food security. With the advent of Green Revolution, staple crops like wheat, rice, soybean, and corn have become dominant in arable lands of the world. The option to keep the environment intact is to conserve and to produce newer genetic diversity of crops. Under these circumstances, cash crops ensure food, nutrition, and income to the farmers in addition to conserving genetic diversity.

Genetic diversity can be defined as any quantitative measure of the variability of a population, which reflects the equilibrium between mutation and the loss of genetic variation (Carvalho 2019). Molecular markers for plants were initially isoenzymes (Tanksley 1983). In due course, DNA markers could be used to detect allelic variation in the genes underlying the target characteristics (Collard and Mackill 2007). The popularization and modernization of genetic markers led to primers developed to detect variability in accessions (Camacho et al. 2017).

New technologies, like next-generation sequencing (NGS), have permitted the accumulation of large quantities of molecular data through the analysis of marker regions (Goodwin et al. 2016). Such studies make estimates of genetic diversity extremely robust.

Molecular Tools and Genome Editing

Molecular marker techniques are employed in the evaluation of genetic diversity and construction of genetic and physical maps. Physical mapping of linked markers helps in relating genetic distances to physical distances (see Nadeem et al. 2017 for a review). Large amounts of sequence data and genomic and cDNA libraries shall be made available over time. They could be used to draw genes coding for potentially useful traits. SSR, DArTseq, and SNP genotyping assays in cash crops are on the progress (De Wever 2019; Spinoso-Castillo et al. 2020; Ali et al. 2019; Pootakham et al. 2020). In many crops, data obtained through PCR analysis of DNA fragments from ancient DNA samples have shown evolutionary changes within the gene pool over long time (Utge et al. 2020). However, it is very unlikely that such data can replace the germplasm conservation of whole organisms but can give definite leads to genetic diversity (Rasmussen 2020).

Genome editing is another new area that stems promise towards creating genetic variability at will (Xu et al. 2019). The clustered regularly interspaced short palindromic repeats (CRISPR) is one such technique that is largely being used to manipulate genomes as desired (Zhu et al. 2020).CRISPR-Cas genome editing technology has altered plant molecular biology beyond all expectations that allows precise genetic manipulation and provides the opportunity to create germplasm with beneficial traits. CRISPR-Cas can be combined with double-haploid (DH) production (Dwivedi et al. 2015) and speed breeding (Watson et al. 2018) to create more desirable genetic variation. DH lines are derived by crossing a genotype with an inducer line whose haploid chromosome set is lost in the zygote. This is followed by doubling the remaining haploid chromosome compliment to achieve a completely homozygous line. This is raised in a single generation (Wolter et al. 2019). The genotype subjected to multiplex genome editing can be used for DH production for immediate homozygous fixation of the edited alleles. In this way, multiple generations of selfing can be avoided to fix homozygosity (Jacquier et al. 2020).

The base editing system enables precise C»T or A»G editing in a specified sequence range by fusion of Cas9 nickase with cytidine or adenine deaminase (Gaudelli et al. 2017). Zong et al. (2018) demonstrated the usefulness of base editing for generating new transcriptional alleles in wheat. Using enhanced base editor, three regulatory elements in the *TaVRN1-A1* promoter in wheat protoplasts were targeted that are involved in the regulation of vernalization. A variety of mutations in all three targeted regulatory elements were identified through deep-sequencing. The EvolvR system is yet another elegant way by which site-specific genetic diversity can be generated (Halperin et al. 2018). It relies on the fusion between an engineered error-prone polymerase domain to a Cas9 nickase. It enables the diversification of all nucleotides at a specific site and within a tuneable window length of up to 350 bp. In this window, the mutation rate can be elevated to more than seven million times (Wolter et al. 2019). If a large collection of random mutations is required at a specific locus, EvolvR has an advantage over base editing in terms of a larger diversity of mutations.CRISPR enables exploitation of wild relatives of crops as a

valuable source of allele mining and expansion of crop germplasm. This should address issues related to genetic impoverishment of many crops and the resistance of wild plants against a broad range of stresses (Østerberg et al. 2017). Unfortunately, the development of new crop varieties by genome editing is hampered by strict GMO (genetically modified organism) regulation, like the European Union, where the authorization of new varieties developed by genome editing techniques is subjected to time and cost-intensive admission procedures. But most other countries are not facing such an impediment. However, on a global scale, CRISPR-Cas will continue to revolutionize plant breeding through creation of new germplasm.

The continuous deforestation and excessive utilization of fossil fuels has resulted in escalation of concentration of CO_2 from 280 to 400μmol^{-1}. CO_2 concentration may further elevate to twofold, i.e., up to 800μmol^{-1} by the end this century. Emission of dangerous gases, especially CO_2, is the main factor for the greenhouse effect and warmer average global temperatures (Vaughan et al. 2018). From 1990 to 2016, the climatic events that occurred are manifold (Fig. 1). Derivation of new climate-smart crop varieties is the answer for guaranteed food security (Wheeler and Von Braun 2013; FAO 2015). Molecular markers are also used to assess plant response to climate change. The microgeographical genetic differences, and various molecular markers, indicated that although phenotypic plasticity buffers against environmental changes when the climate events become more extreme, such resistance weakens (Jump and Peñuelas 2005). The use of molecular markers is crucial as it indicates adaptability to climate changes. There are a range of strategies available like high-throughput single-nucleotide polymorphism (SNP) genotyping, genomic selection, and trait mapping to enhance sustainable crop production and resilience to climate change (Pourkheirandish et al. 2020). Various genomic approaches for the development of climate change resilient crops are given in Table 1. The "pyramid" approach to introducing favorable alleles and gene combinations is also prime (Nutan et al. 2020).
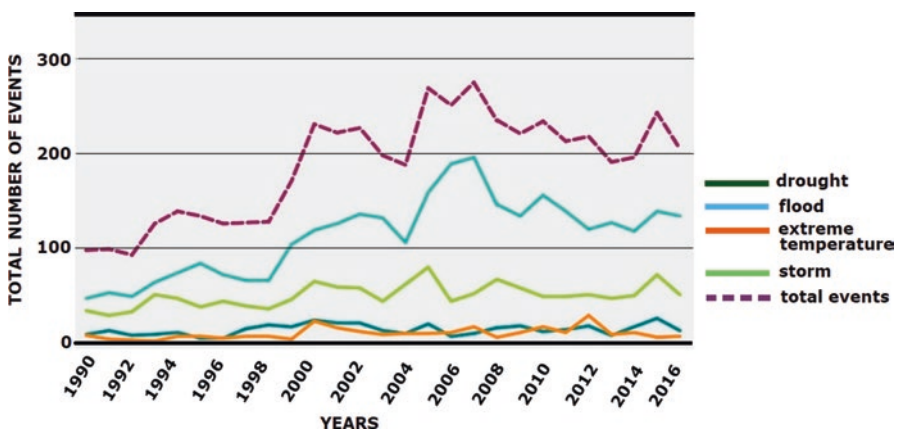

Fig. 1 An increasing number of extreme climate-related events occurred during 1990–2016. (Source: Food and Agriculture Organization (FAO) based on data from the Emergency Events Database (EMDAT) (https://www.emdat.be/)

Table 1 Summary of different approaches, which can be used to improve crop diversity and resilience

Approach	Desired outcome
Using genomics to improve crop plant diversity and resilience	
Accessing genetic diversity of crop wild relatives (CWRs)	Diversification of the existing breeding resources
	Domestication of completely new crops using wild species
De novo crop domestication	Controlled genome duplication or bridging the genomes of two related species
Engineering polyploidy	
Harnessing plant-microbe interactions	Optimal choice of suitable crops for the specific soil type and geographic location
The challenge of climate change and plant diseases	Prediction of pathogen evolution and prevalence and deployment of suitable protective measures ahead of time
Genome editing for nutritionally enhanced crops	Editing of target genes to improve crop nutritional value
Accessing new breeding targets using genomic technologies	
Third-generation sequencing	Use of long sequencing reads for higher quality reference genome construction
Accurate gene prediction and functional annotation	Precise candidate gene identification
Analysis of the non-coding part of genome	Identification of new functional genomic sequences and breeding targets
Pangenome as a reference sequence	Inclusion of species-wide genomic variation in the analysis
Pairing genomics with other emerging technologies	
Machine learning and crop plant genomics	Use of artificial intelligence for crop genotype and phenotype prediction
Speed breeding	Shortening the breeding cycle
High-throughput phenotyping	Increased resolution, accuracy and speed of plant phenotyping

Adopted from: Pourkheirandish M. et al. 2020; courtesy: Frontiers in Plant Science

CGIAR Gene Banks

During the last three decades, under the auspices of FAO, the international community has strived to developing and maintaining a global system on plant genetic resources for food and agriculture. This system owes international bodies that monitor the status of the conservation and use of plant genetic resources for food and agriculture (PGRFA), develop, support, and implement instruments that are responsible for conservation and utilization of germplasm. During 2015, the Sustainable Development Goals were adopted, including Target 2.5 concerning the sustainable management of genetic diversity (Halewood 2020).

CGIAR centers make significant contributions to both the global system and SDG Target 2.5 through international PGRFA collections. Their contributions are:

- Assembling and conserving PGRFA,
- Adding value to those materials through extensive characterization, evaluation, and documentation,
- Health testing, and,

- Supplying samples that are free of pests and diseases to researchers, plant breeders, farmers, national and community gene banks, and seed companies around the world.

CGIAR collections include over 760,000 accessions of crops, forages, and trees, originally from 207 countries, as well as pre-bred materials. Over the last 10 years, the CGIAR Centers' gene banks have distributed more than 1.1 million PGRFA samples to recipients in 163 countries (Halewood 2020). Such transfers amount to nearly 23% of all PGRFA following the norms of multilateral system of access and benefit sharing created by the International Treaty on Plant Genetic Resources for Food and Agriculture. Even though CGIAR never addresses the diversity of cash crops directly, many genetic resources are scattered in several of its institutions and other academic universities and bodies like USDA. A common platform to coordinate the conservation and use of genetic resources of cash crops is an urgent need. As case examples, cocoa, coffee, sugar cane, and rubber are explained in a little detail here.

Cacao

Cacao (*Theobroma cacao* L.), "the food of Gods" is next to tea and coffee as a beverage. Native to Amazon basin, cocoa was domesticated and distributed to different regions by the natives Mayas, Aztecs, and Pipil-Nicaraos (Bartley 2005; Malhotra and Apshara 2017). There has been a phenomenal increase in the geographical expansion of cocoa genetic resources over the last 30 years (Bartley 2005). Currently, 40–50 million people depend on cocoa for their livelihood, and the production is 3.97 mt contributed by Africa (71%), Latin America (14%), and Asia and Oceania (14%) (Anga 2013). Cóte d'Ivoire is the major cocoa producer followed by Ghana, Cameroon, Nigeria, and Brazil (Pipitone 2016; Malhotra and Apshara 2017).

The first introduction of cacao was by Alonso Pinzón in 1510 in southern Yucatan (Bartley 2005). In the sixteenth century, the Europeans started to cultivate cacao in Asia and Africa where the Criollo, Amelonado, and the Trinitario hybrids started their route of dispersal from the Americas to the old world. Cacao was domesticated to southeast Asia (to Indonesia) in 1560 by the Dutch (Van Hall 1932). Around 1770, the Dutch introduced cacao to Peninsular Malaysia (Thong et al. 1992). In 1798, the British took cacao to Madras, India, from the island of Amboina, and it was introduced into Ceylon (now Sri Lanka) from Trinidad at about the same time (Ratnam 1961; Wood 1991). Remnants of the ancient Criollo, Amelonado, and Trinitario populations can still be found in Asia and Pacific regions, such as Indonesia and South Pacific (Fiji and Samoa) (Susilo et al. 2011).

The "Upper Amazon" stretching from Marañón River in Peru to the frontier of Brazil is the location of cacao's primary gene pool. Here, a series of major river systems in Peru, Ecuador, Colombia, and Brazil flow into the Marañón and Amazon rivers. Wild cacao populations are found in these river basins in both spontaneous

(without human interference) and subspontaneous forms (wild cacao trees exploited by man) prior to European occupation (Almeida 2001; Bartley 2005). It is hypothesized that gene flow in cacao is limited, and mating is likely confined within patches (Chapman and Soria 1983).

During late 1920s, there was an outbreak of "witches' broom" disease (WBD) in Trinidad. This necessitated a search for genetic resistance in the Upper Amazonian. During the 1930s and 1940s, wild germplasm was collected from the Upper Amazon basin of Ecuador and Peru (Pound 1945; Wood and Lass 2008). The Pound collection (named after the collector F. J. Pound) is the foundation to the modern cacao breeding programs. The tributaries of Rio Ucayali, Rio Morona, and Rio Marañón contributed to the pound collection (Pound 1945; Bartley 2005; Zhang et al. 2009). Thus "Pound collection" was established in Iquitos, Peru. Approximately 80% of the world's chocolate production comes from the Forastero type of cacao. This is a variety favored over the Criollo for its disease resistance and high yield (Rusconi and Conti 2010). The third genetic group, Trinitario, is a hybrid of Criollo and Forastero derived in Trinidad. Trinitario is cultivated in many parts of South and Central America, Africa, South-East Asia, and Oceania for its aroma, productivity, and disease-resistance property (Wickramasuriya and Dunwell 2018).

A considerable portion of the global cacao diversity is in situ. This includes two international collections maintained at the Cocoa Research Centre of the University of the West Indies (CRC/UWI), Trinidad and Tobago, and at the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE), Costa Rica (Laliberté et al. 2018). Laliberté et al. (2018) further enumerated the following strategies for cacao genetic conservation:

- Cacao gene pool is conserved in situ and ex situ for the long term by a global network of partners.
- Global system for the safe exchange of cacao germplasm is strengthened.
- Use of cacao genetic diversity is optimized.
- Effectiveness of global efforts to conserve and use cacao.
- genetic resources is assured.

CATIE (Centro Agronómico Tropical de Investigación y Enseñanza, Cost Rica) has international collection of cocoa, coffee, and other cash crops. The collections were initiated in the decade 1940 and were put in 2004 under the article 15 of the International Treaty for Plant Genetic Resources for Food and Agriculture (ITPGRFA) and thus in the public domain, which means that every accession is available for everyone for investigation, experimentation, or training.

The International Cacao Collection at CATIE (IC3) is one of the two most diverse and important gene banks worldwide, in particular, the ten currently defined genetic groups are represented by accessions. IC3 was founded in Turrialba, Costa Rica, in 1944 and declared as an international gene bank by IPGRI (now The Alliance Biodiversity International) in 1978. Currently, the collection preserves 1235 wild and cultivated genotypes from countries of origin of cacao, but also from producing countries in America, Africa, and Asia. Genetic resources are conserved in the field in the form of six trees per accession, over 10 ha at two replications located in La

Montaña Farm in Turrialba 602 m.a.s.l. and in La Lola Farm in Matina, the Atlantic Coast at 40 m.a.s.l. The conservation in two places assures the accurate and safety preservation in case of lose any accessions and the better evaluation of the accessions for production, resistance against pests and diseases, and quality (see: https://www.catie.ac.cr/en/products-and-services/collections-and-germplasm-banks/international-cocoa-collection) (Dominique Dessauw and William Solano, CATIE, personal communication).

Global Network for Cacao Genetic Resources (CacaoNet) could finalize the Global Strategy in 2012 (Laliberté 2012). The Global Strategy provides a clear framework to secure funding to ensure conservation of cacao diversity to directly benefit millions of small-scale cacao farmers. The International Cocoa Organization, Côte d'Ivoire and International Cocoa Germplasm Database (ICGD), University of Reading, are the two other active genetic resources.

Coffee

Coffee is an important agricultural export commodity in many Asian, African, and Latin American countries, providing a livelihood to more than 125 million people worldwide. The genus *Coffea* comprises more than 124 species of which only two species (*Coffea arabica*—arabica coffee and *C. canephora*—robusta coffee) are commercially cultivated for beverage production (Misra 2019). These 124 species are distributed in Africa, Madagascar, the Comoros Islands, the Mascarene Islands (La Réunion and Mauritius), tropical Asia, and Australia (Krishnan et al. 2015). Climate change poses unprecedented challenges to sustainable coffee cultivation. World coffee production is estimated at 169.34 million bags (one bag with 60 kg) in 2019/2020 (International Coffee Organization).

Possibly around the sixth century, from its center of origin in Ethiopia, coffee made its way to Yemen, with the first record of consumption as a beverage by practitioners of Sufism around 1450 (Weinberg and Bealer 2001). From there, coffee spread to Cairo, Damascus, and Istanbul, leading to the birth of the coffeehouse. Following this, coffeehouses opened in Europe, the first one in Venice in 1645 and in Oxford in 1650. Dutch East India Company commenced coffee cultivation in Java using seeds obtained from Mocha in Yemen in the 1690s (Vega et al. 2008).

In the 1960s, FAO took the initiative to prevent loss of genetic resources and enlarge the genetic base through collecting mainly *C. arabica* germplasm along with noncultivated species (Engelmann et al. 2007; Krishnan 2013; Vega et al. 2008). In addition to these international collecting missions, local researchers within origin countries have performed their own collecting missions, such as in Ethiopia, Madagascar, and Cote d'Ivoire (Labouisse et al. 2008). The FAO report, *State of the World's Plant Genetic Resources*, released in 1998, documented 21,087 coffee accessions conserved worldwide (Anthony et al. 2007). The FAO World Information and Early Warning System (WIEWS) Coffea *Germplasm Report* (2009–2011) is the most comprehensive inventory of coffee germplasm held in living collections. In

2016, the Global Crop Diversity Trust, in partnership with World Coffee Research, led the development of the Global Conservation Strategy for Coffee Genetic Resources, which was scheduled for completion in early 2017 (Engelmann et al. 2017; Bramel et al. 2017: https://cdn.croptrust.org/wp/wp-content/uploads/2017/07/Coffee-Strategy_Mid_Res.pdf).

CATIE has one of the most important coffee collections in the world, with nearly 2000 introductions. The collection began in 1949 with materials introduced from Brazil, Guatemala, and El Salvador, and later, in the 1960s, it was strengthened with wild *Coffea arabica* materials from Ethiopia and Yemen, including the original materials collected by FAO, ORSTOM (now IRD), and IPGRI. This is considered the fourth largest collection of Coffea spp. in the world and the most important collection of *C. arabica* in the American continent, due to the number of introductions and the genetic diversity conserved. It is considered one of the four Origin collections in the world, the only one outside the African continent, according to the Global Strategy for the Conservation of Coffee Genetic Resources developed by the Global Crop Diversity Trust and World Coffee Research (WCR). The agreement signed with the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO) defines it as the most important "International Collection" of *C. arabica* under public domain.

The collection has different types of genetic material such as:

- Wild Arabica coffee genotypes collected by FAO and ORSTOM in Ethiopia, IPGRI in Yemen, as well as diploid species;
- Varieties, mutants, and selections with resistance to coffee rust;
- Inter- and intraspecific hybrids; and,
- Research material.

These genetic resources are considered as the genetic heritage of the region, in relation to their potential to be able to respond quickly to current and future problems of Latin American coffee growing. For more than 60 years, this collection has contributed to genetic improvement programs around the world. The accessions with resistance to rust allowed the generation of some F1 hybrids. CATIE plays a leading role in asexual reproduction via somatic embryogenesis and by micro-cuttings (William Solano, CATIE, personal communication; Mata-Quirós et al. 2017).

Sugar Cane

As a perennial C_4 grass crop, sugarcane is cultivated worldwide in tropical and subtropical regions as a major source of sucrose (Park et al. 2015), with a global crop value of $61 billion a year (FAOSTAT 2016). Sugarcane accounts for 75% of global sucrose production (Kandel et al. 2018). In addition to its importance as a food crop, it has one of the highest solar energy conversion efficiency and highest biomass yield among the known crops (Lam et al. 2009; Henry 2010; Byrt et al. 2011).

Modern sugarcane cultivars are derived from interspecific hybridizations between the domestic and wild species *Saccharum officinarum* ($2n = 80$) and *Saccharum spontaneum* ($2n = 40$–128). Both species are highly polyploid (Aitken et al. 2005), with a basic chromosome number of $x = 10$ for *S. officinarum* and $x = 8$ for *S. spontaneum* (D'Hont et al. 1998). The genome of current sugarcane cultivars is composed of approximately 70–80% *S. officinarum* and 10–20% *S. spontaneum*, with only 10% from the recombination of these two species (D'Hont et al. 1996).

Modern cultivars have limited genetic variation (Fickett et al. 2020). Almost 20 *S. officinarum* clones are involved in the genealogy of sugarcane cultivars with only a few being used extensively (Raboin et al. 2008). Basic crosses are made with clones of *S. spontaneum, S. robustum,* and species of other genera within the *Saccharum* complex to broaden the genetic base (Moore et al. 2013; Ming et al. 2010).

A "World Collection of Sugarcane and Related Grasses" (WCSRG) is maintained at the National Germplasm Repository of the USDA-ARS Subtropical Horticulture Research Station, Miami, FL, USA. A total of 342 *S. spontaneum* clones were assessed using stratified random sampling over geographical origins and principal component cluster groups to select a 75-clone core collection (Tai and Miller 2001). By and large, this is one of the largest sugarcane germplasm collections in the world. There is yet another base broadening (basic breeding) program at the USDA-ARS Sugarcane Research Unit in Houma, Louisiana (Fickett et al. 2020).

Rubber

Rubber is an industrial raw material indispensable to humans with more than 55,000 vivid products made from it. The *para* rubber tree, the *Hevea brasiliensis* (Willd. *ex* A. Juss.) Müll. Arg., (Euphorbiaceae), is the chief contributor to natural rubber production worldwide. *Hevea* rubber is native of Amazon basin (Priyadarshan and Clément-Demange 2004). *Hevea* has eleven species, all native to Amazon that are inter-crossable (Priyadarshan and Goncalves 2003). All *Hevea* species have $2n = 36$ chromosomes, with the exception of one triploid clone of *H. guianensis* ($2n = 54$) and the existence of one genotype of *H. pauciflora* with $2n = 18$ (Baldwin 1947; Majumder 1964). Although *Hevea* behaves as a diploid, it is believed to be an amphidiploid ($2n = 36$; $x = 9$) that stabilized during the course of evolution (Clément-Demange et al. 2000).

It is difficult to evaluate how narrow the genetic base initially was for what has now become the "Wickham" domesticated population (Dean 1987; Baulkwill 1989). Much importance was conferred to a small number of 22 seedlings disseminated from Singapore to Malaysia after 1876. A significant part of the Wickham seedlings which germinated in Kew Gardens was then sent to Ceylon (now Sri Lanka), raised, and disseminated to different countries, especially India. However, it is significant that the original Wickham stock was collected in only one Brazilian site, Boïm, on the Western banks of the Tapajoz river, not far from Santarém. All

these contentions are debatable (Thomas 2001). Directional selection applied to such populations for more than a century, and the low fruit-set in *Hevea* probably further contributed to the narrow genetic base (Priyadarshan 2016). Genetic diversity can now be compared to that of the available wild Amazonian populations by use of molecular genetic markers (Priyadarshan 2017a, b).

Since the introduction of rubber to southeast Asian countries by Wickham and Cross in 1877 through Kew Botanic Gardens, there have been attempts to enrich the germplasm with new genetic diversity (Simmonds 1989). *Hevea* rubber was evolved because of evolution spanning over thousands of years. Today, the cultivation of *Hevea* rubber spans to several continents and new environments that are both optimal and suboptimal (Priyadarshan 2003). With the initiatives taken up by the IRRDB (International Rubber Research and Development Board), 64,734 seeds, 1413 m of budwood from 194 high yielding trees and 1160 seedlings were collected during 1981 from Acre, Rondonia, and Mato-Grosso states of Brazil, from 60 different locations spread to 16 districts (Nouy 1982; Tan 1987; Simmonds 1989). Of this, 37.5% of the seeds went to Malaysia and 12.5% to Côte d'Ivoire while half of the collections were retained in Brazil. The clonal selections were brought to Malaysia and Côte d'Ivoire after quarantine measures (of 1 year in Guadalupe Island) for South American Leaf Blight (SALB—*Microcyclus ulei*). After the establishment of two IRRDB Germplasm Centers in Malaysia and Côte d'Ivoire, other IRRDB member countries were supplied with budwood from this material according to their request. Malaysia alone established 8900 seedlings and 109 clones from this exploration (Pushparajah 2001). Crosses between Wickham and Amazonian accessions could introduce more variation. Breeding at IRCA (Institut de Recherches sur le Caoutchouc en Afrique), Côte d'Ivoire, under the auspices of CIRAD (Centre de coopération internationale en recherche agronomique pour le développement), involve utilization of Amazonian accessions (Clement-Demange et al. 1998).

Identification of all Wickham clones could be done with 13 probes associated with restriction enzyme *EcoRI* (Besse et al. 1993). The cultivated clones are genetically close to the Mato-Grosso genotypes. A comprehensive map of genomic variation across rubber tree plastomes (plastid genomes) exhibited higher genomic variants in wild rubber than that of cultivated ones (Feng et al. 2020). mtDNA of Wickham clones has lesser variation because their female progenitors are all primary clones (Supriya and Priyadarshan, 2019). The cytoplasmic donors of most of the improved clones are either PB 56 or Tjir 1. While the cytoplasm of PB 56 was transferred through PB 5/51, the cytoplasm of Tjir 1 was through RRII 105, RRIM 600, and RRIM 605 (Priyadarshan 2017a, b).

The original 22 seedlings of Wickham collection from which the day-to-day *Hevea* clones were evolved had been genetically narrowed to enrich the *Hevea* gene pool. Also, these populations were subjected to several rounds of controlled crossing that further narrowed the diversity. Moreover, the strategy followed by the breeders to select only the desirable genotypes and to reject the unwanted ones (without precisely assessing yield and other secondary attributes) is the main reason that reduced diversity. Concerted efforts to infuse the Amazonian germplasm through controlled crossings never met with enriching the diversity as desired and

as expected. This is because selection was and is always been in favor of higher yield. Of late, it is noteworthy that effrots are being incurred to breed *Hevea* at molecular level.

3 Future Perspectives

The conservation of crop genetic resources, including their wild relatives, is of utmost importance for the future of mankind. Most crops be stored in seed gene banks. But for crops that produce recalcitrant (non-storable) seeds such as cacao, coffee, and coconut, in vitro and cryopreserved collections provide an alternative (Panis et al. 2020). International gene banks have a collection of over 760,000 conserved accessions of various plants, most of these accessions are within the multilateral system governed by the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA) (Lee et al. 2020). However, in spite of the success in collection and conservation, only a small portion of the genetic diversity has been used in crop breeding programs. Genetically diverse plant germplasms stored in ex situ gene banks are excellent resources for breeding new high yielding and sustainable crop varieties. Some gene banks do follow cost-effective genotyping technologies. However, the adoption of modern phenotyping is lagging. These phenotyping tools and high-throughput genotyping must accelerate the derivation of more resilient food crops for the future (Nguyen and Norton 2020).

Li et al. (2018) pointed out two major limitations preventing the exploitation of gene bank genetic resources for breeding programs:

- Time and available resources for thorough characterization of accessions at a large scale.
- Identifying and introducing the allelic variance into elite breeding materials.

This missing characterization data makes searching of an accession with specific desirable agronomic trait a daunting task (Wambugu et al. 2018). The gene banks are increasingly required *to move beyond providing basic passport data* that defines only the identity and origin to thoroughly catalogue agronomic, physiological, and genetic traits (Anglin et al. 2018). A three-step strategy that combines genomics and phenomics to effectively mine gene bank genetic resources has been proposed (McCouch et al. 2013):

- Obtain a sample of sequence information from the genomes of all non-duplicate plant samples in the world's gene banks that are available under the terms and conditions of the ITPGRFA. This may perhaps come up to two million. This "fingerprint" for each plant will serve as the basis for assessing genetic relationships which can be used to systematically select subsets of material for in-depth investigations.
- Analyze the phenotypes of gene bank accessions to evaluate their traits and overall performance. This is rather costly, intellectually challenging, complex, and

time-consuming process. All gene bank accessions cannot be evaluated under all relevant environments, even with high-throughput phenotyping technologies. The genetics of high-performing offspring can be traced back to DNA inherited from wild or landrace donors. Such donors must be quite often less productive.

- Create an internationally accessible informatics infrastructure to catalogue the world's seed/genetic diversity. Details of passport, genomic, and phenotypic information can be directly linked to seeds and genetic stocks. This can augment plant improvement programs. This is a task that requires unprecedented effort. Currently, seed data are recorded and managed by different people like gene bank curators, agronomists, and breeders following database systems. This calls for a coordinated system of data management and benefit sharing.

When we consider coffee as an example, *C. arabica* is an allotetraploid ($2n = 4x = 44$) originating from a hybridization event of the two diploid species *C. canephora* and *C. eugenioides* ($2n = 2x = 22$). Interestingly, these progenitor species harbor a greater level of genetic variability and are an important source of genes to broaden the narrow Arabica genetic base. Merot-L'anthoene et al. (2019) selected 8580 unique and informative SNPs from *C. canephora* and *C. arabica* sequencing data, with 40% of the SNP located in annotated genes. A panel of *C. canephora* accessions was successfully discriminated, and over 70% of the SNP markers were transferable across the three species. Furthermore, the canephora-derived subgenome of *C. arabica* was shown to be more closely related to *C. canephora* accessions from northern Uganda. This study is a clear indication of the wide range of variability available in cash crops.Gene bank phenomics still lag in evaluating available plant genetic resources despite the development of DNA technology (Philipp et al. 2018). High-throughput phenotyping (HTP) using sensors and imagers is a promising, efficient, and cost-effective approach to collect phenotypic data for multiple traits across large-scale trials that can then be used together with genomic data for accurate selection in breeding (Araus and Kefauver 2018). With a comprehensive phenomics approach combining pedigree, genomic, and phenotyping data (McCouch et al. 2013), the true value of gene bank genetic resources is evident. Such strategic efforts are prime to double our current rate of genetic gain to feed the growing world population under the anticipated dynamic climate changes.

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Part I
Beverages