Review

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Review

Adding Value to Cassava Genetic Resources Conserved at CIAT. Part I: A Review of Fifty Years of Collection, Conservation, Characterization and Distribution

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Abstract

The Alliance of Bioversity International and CIAT curates the world's largest cassava (*Manihot esculenta* Crantz) germplasm collection, held at its Future Seeds genebank in Cali, Colombia. Since first collection expeditions in 1969, a primary focus was to assemble and conserve the diversity from the crop's center of origin in the American tropics. Later additions expanded representation from Asia and Africa as secondary centers of diversity. The collection consists mainly of landraces (about 5000 accessions), bred lines from CIAT (375) and from partner institutions (253), and related wild *Manihot* (377 accessions from 23 species or subspecies). Secure conservation, first as a field collection and then in a slow-growth *in vitro* system, gave priority to pathogen testing and methods to assure successful clonal propagation over many generations. Cryopreservation research is ongoing to achieve additional security and efficiency. CIAT extensively characterized accessions through morphological, biochemical and molecular criteria. As a core goal, the collection has been a foundation for genetic improvement of the crop globally. The paper provides perspectives on the future management and use of the collection in the context of the recently established Future Seeds genebank facilities at CIAT, and new tools and technologies that support more effective conservation, evaluation and use.

Keywords: *ex situ* conservation; cassava collection; cassava genebank; cassava conservation; cassava landraces; genetic resources distribution; wild *Manihot*

1. Introduction[1]

CIAT's[2] activities in collection, conservation, characterization, evaluation and use of crop genetic resources, particularly for tropical forages, beans and cassava, date from the earliest years of the center's founding in 1967. In 2017, CIAT published a detailed 50-year, center-wide history [1], including some detail on the crop and forage species collections. Schultze-Kraft et al. [2] and Debouck

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[1] Elements of this paper are extracted from a comprehensive internal CIAT consultancy report by C. Hershey that covers the 50-year history of the cassava germplasm collection and the use of landrace varieties in breeding.

[2] The institution formerly known as the International Center for Tropical Agriculture (CIAT) merged with Bioversity International in 2019 to form the Alliance of Bioversity International and CIAT (the Alliance). Since most of the history reported here refers to the pre-2019 era, the name *CIAT* is most frequently used here as the institutional name.

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et al. [3] published histories of the forages and beans collections, respectively. The current work covers a similar history for the cassava collection at CIAT.

While CIAT gives highest priority to the cultivated species *M. esculenta*, it also maintains a small collection of wild relatives, among the approximately 100 species of the genus *Manihot*. The roles of the germplasm collection have continually evolved from the early years – from initially being a direct source of recommended varieties, to parents in breeding populations where the focus is on more targeted and specialized traits to address arising problems and opportunities. These traits may include, for example, resistance to new pests and diseases, specialty quality traits, or physiological traits associated with productivity under new climate conditions and new production or processing systems. The 50 years of the cassava collection's history are just the beginning of CIAT's commitment to its conservation *in perpetuity*, for continued human and environmental benefit. The body of the paper is organized *topically* to cover collection, conservation, evaluation and use, across more than half a century of the life of the genebank. Table S1 provides a broad-sweep *chronological* overview of activities and outputs over this history.

2. Cassava as a Global Crop

Since its domestication 7-10,000 BCE in the neotropics, this resilient species – *Manihot esculenta* – has sustained livelihoods with its reliable production of starchy roots. After the arrival of Europeans in the Americas in the late 15th century, cassava's importance expanded from its evolutionary homeland into both Africa and Asia. But only in roughly the past 50 years has the crop evolved from being mainly a subsistence, poor farmers' crop – often grown on lands marginal for soil fertility and/or acidity, and drought challenges – to a multi-purpose crop that supports a wide range of agricultural, consumer and industrial needs. It now ranks 3rd in food crops production in the tropics and 7th globally. It is especially notable as a critical source of food calories in Africa, where Nigeria, DR Congo and Ghana account for over half of the continent's production. In the Americas, Brazil alone produces nearly 70% of the region's total. Thailand, Indonesia and Vietnam dominate as producers of starch for industry, with very fast growth in Cambodia and Lao PDR.

Production shifted dramatically in the last half century – most notably an astounding five-fold increase in Africa from 1972 to 2023 (Figure 1). This is primarily due to the increased area planted, but also with modest yield improvements. Just four countries (Nigeria, DR Congo, Thailand and Ghana) account for over half of current global production. Much of the research effort in Africa over the past five decades has focused on minimizing yield losses from the widespread cassava mosaic disease, and more recently the cassava brown streak disease, currently limited to eastern Africa. In Asia, production over the same period has more than tripled, resulting from both increased yields and area planted. Conversely, in the center of the crop's origin, the Americas, production has fallen by 22%, with yield increases somewhat offsetting reduced area planted.

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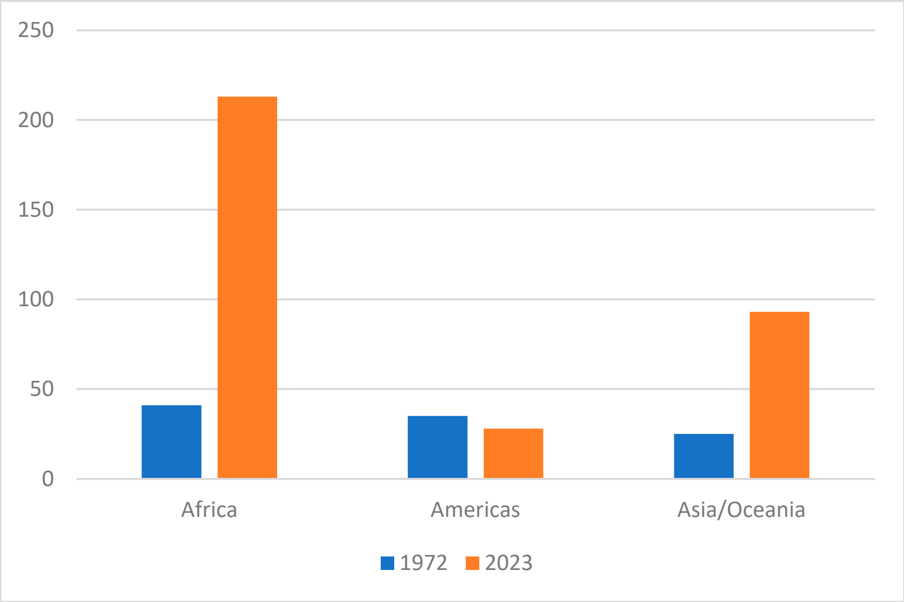

Source: FAOSTAT, 2025

Figure 1. Change in global cassava production (MT fresh roots) 1972-2023, by region.

Cassava stands out among crops that are well-positioned to adapt to climate change and to provide high yields under modest inputs. The fact that it is most important in areas of the world where people are least able to absorb instability in income or food supply, places a special burden and responsibility to invest in more resilient, more productive, more consumer-oriented varieties. The opportunities to exploit these and other features will center around the integration of improved production practices and genetic resources. The latter includes collection, conservation, evaluation and use of genetic resources to develop varieties for changing needs.

3. The Foundations of Current Genetic Diversity

3.1. Impact of Natural Selection and Human Influences

Nature and farmers together have applied a wide range of selection forces toward the slow and continual genetic changes in landrace varieties during cassava's long history of domestication and traditional cultivation. There are several ways that we can get insights into these selection forces:

- Characterization of the physical and biological environments where cassava was historically grown. This provides some understanding of the adaptations and resistances that were required for the crop to succeed.
- Characterization of the end-uses and trait preferences, including through archeological findings, historical records, and current uses in traditional systems.
- Surveys, participatory research and other forms of interaction with farmers, processors and consumers to understand current-day and future varietal preferences.
- Measurement of cassava genetic diversity through field and laboratory evaluations across a range of environments and uses.
- Molecular characterization (especially direct measures of DNA polymorphisms) and studies of associated genotypic and phenotypic variation, as well as evidence for patterns of crop evolution and distribution.

3.1.1. Climate and Agroecosystems

Although cassava appears to have been domesticated in a rainforest environment, the crop, like many of its wild relatives in the genus *Manihot*, has adapted especially well to seasonally dry areas, broadly defined by distinct rainy and dry seasons across the year. Brief periods of drought stress

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during the normal rainy season can create severe constraints for many crops, especially during sensitive developmental events such as pollination. However, cassava is well-known for its ability to tolerate and recover from brief or even extended drought periods, providing a primary driver for its popularity in the seasonally dry areas across the tropics.

Historically, cassava spread from the humid Amazonian and Orinoco rainforest habitats – west and north to the inter-Andean valleys of Bolivia, Peru, Ecuador, and Colombia; to meso-American and the Caribbean; and east to drier coastal Brazil, where the crop can be found in areas with as low as 500mm/yr rainfall.

Although the species as a whole retained its intolerance to low temperatures (especially sub-freezing), over millennia some landraces gradually adapted to the mid-altitude tropics, and even up to a limit of around 2,000 masl. Cassava also spread to the extremes of its latitudinal temperature adaptation, to the northern and southern hemisphere subtropics. Production became especially significant in the subtropics in southern Brazil, Paraguay and Argentina. This distribution was probably relatively recent compared to the time frame for domestication in the warm tropics. The specific physiological adaptations for response to daylength or to low winter temperatures have not been well-studied. In general, adaptation to low winter temperatures seems to have been more a function of crop management rather than genetic adaptation, e.g. cutting back stems at the onset of cold weather, to avoid freezing and to allow a second season of growth.

3.1.2. Biotic Environments

As a vegetatively propagated crop, cassava is especially vulnerable to many pests and pathogens that can be transmitted from one crop cycle to the next via stem planting pieces. Further, because of a long growing season of up to a year or longer, there is an extended opportunity for attack by pests or pathogens with varying seasonal adaptations. Nonetheless, historically – and mainly prior to the intensive research on cassava begun by the International Agricultural Research Centers – cassava was often referred to as a *rustic crop*. It was thought to be highly tolerant to biotic-induced stresses in the environment, and to require little care to reliably produce reasonable yields. This perception changed dramatically as data accumulated from systematic research. One of the revelations was the response when cassava landraces were moved from their native area of production in traditional systems to completely different environments. This mass movement across diverse environments was first carried out by CIAT soon after establishment of the cassava collection in Colombia. The process of introducing traditional cassava landrace varieties into new environments provided some of the first broad evidence that cassava could be highly vulnerable to damage from many pests and diseases.

The Americas – the crop's evolutionary homeland – are also the center of diversity of pests and diseases. The literature reports over 200 species of arthropods attacking cassava [4]. Among them, various species of mites and whiteflies are the most devastating. Hillocks and Wydra [5] list some 40 bacterial, fungal and nematode pathogens. Nearly any cassava plantation anywhere in the world will probably demonstrate some level of infestation or infection with pathogens, but most are not serious. However, some diseases such as cassava bacterial blight, cassava mosaic disease, witches broom disease, or various root rot pathogens can be devastating if inoculum load and weather conditions are suitable, if vectors are present (for some pathogens), and the host plants lack resistance. The viruses tend to be more continent-specific but there is continuing risk of introductions to new areas. Most notably, the cassava mosaic virus, a Begomovirus, is widespread in Asia and Africa but so far has not been reported in the Americas.

Within the Americas, it can be assumed that many of these pests and pathogens have been associated with cassava for centuries, or even millennia, and have certainly impacted the evolution of resistance mechanisms in landraces selected by growers.

3.1.3. Production Systems and Soils

Key crop management practices important to the evolution of cassava's genetic diversity are likely to include:

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- *Scaled harvesting over extended periods of time*. With the normal rapid physiological deterioration of cassava roots after harvest, a common practice was to harvest small numbers of plants as needed for household use. In this sense, cassava does not have a well-defined *maturity* period. This practice would have favored the accumulation of alleles that contributed to achieving and maintaining good pre-harvest root quality for extended periods of time.
- *Intercropping of multiple species along with cassava* was probably the norm in most traditional areas of production. This practice would have driven selection for traits such as canopy suitability (e.g. competition for light and weed control), and systems adaptation to competition for water and nutrients.
- *Low use of added nutrients*. In traditional systems soil nutrients would be optimized mainly with crop rotations, use of fallow periods, and intercropping of compatible species. In general, under these conditions, cassava would have been selected for the capacity to extract/use nutrients efficiently. Cassava is adapted better than many crops to the low fertility and highly aluminum-saturated, weathered soils of the Amazon rainforest and tropical savannas.

3.1.4. Cassava Processing and Use

Each pathway and step in the food chain evolved with specific grower and consumer preferences, which in turn generated an important segment of cassava landrace diversity.

Starch content and quality play defining roles in a variety's acceptability for specific uses. However, ranges for preference and acceptability vary for different products, among consumer groups, and by region. Consequently, landrace varieties show a wide range of starch content and functional properties. Additionally, there can be a large environmental influence. Long periods of drought and of high temperatures tend to reduce root starch content. Levels can also drop dramatically if root starch reserves are mobilized as sugars and translocated for foliage regrowth, such as may occur with the arrival of rains after a drought period, or after defoliation from pest or disease attack followed by recovery regrowth. Use of roots for fresh consumption versus processed products strongly influenced genetic diversity of physical and biochemical features.

One of the main differentiating traits for post-harvest management is root cyanogenesis. All known cassava varieties produce cyanogenic glucosides, mainly linamarin, in both root and leaf tissues. Varieties with low cyanogenic potential (CNP) (generally pegged at about 100 ppm CN^- or less, on a DM basis) are considered safe to eat after simple boiling. Those with higher levels must be processed in more complex ways (e.g. grating, fermenting, mashing, roasting) to reduce cyanogens to safe levels for human consumption. There is still debate about the underlying reasons for apparent farmer selection of high CNP types in some systems. Traditionally it was thought that pest and disease resistance was a likely factor, but there has been little research evidence to support this theory. Repelling wild foraging mammals seems more credible, and sometimes even preventing theft from humans. Farmers sometimes speculate that high CNP types produce higher quality flour (e.g. *farinha* or *garri*), but this has not been experimentally verified. In any case, a wide range for CNP exists in landrace varieties.

Cassava storage roots have a notoriously short post-harvest storage period under ambient temperature and humidity conditions. Typically, within a matter of a few days, a physiological deterioration begins, causing black streaks throughout the root parenchyma. As this process advances, the roots become unacceptable for most uses, initially for human consumption and eventually for animal feed or industrial processing. For reasons still not well understood despite many years of study, genetic variation for reduced post-harvest physiological deterioration, while present, seems to be rather narrow among all landraces.

Since there are many different processes and many different final products from cassava, there should be a wide range of variation in quality-related traits in the collection. The significant growth in starch, animal feed, energy and other industrial uses is more recent. Specific demands for these newer traits from industrial markets have impacted breeding program goals, but not the genetic diversity of traditional landrace varieties that make up germplasm collections.

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The use of cassava varieties in religious or cultural situations has been noted in the literature (e.g., [6,7]). These uses perhaps made a fascinating but probably quite minor contribution to the overall diversity of the species.

3.2. Effects of Reproduction Systems

Cassava has a dual reproduction system, both sexual and clonal, which had an immense impact on the evolution of the crop's diversity. In general terms (with some exceptions) a cassava variety is a clone, i.e. all the plants of a variety are genetically identical. For those varieties that *are* monoclonal, any individual can fully represent the variety for purposes of developing an *ex situ* collection. This contrasts with an outcrossing crop like maize, where every plant in an open-pollinated variety is genetically distinct, and multiple plants must be sampled to achieve good representation of the population of different alleles.

At the same time, the individual plants of all known cassava varieties are highly heterozygous. Therefore, every seed[3] produced from sexual recombination (*botanical seed*), whether from self-pollination or from crossing with a different variety, will be genetically distinct by relatively random inheritance of alleles from male and female parents. Seed production is the principal process that allows farmers to develop new varieties with their own resources and within their own set of varieties. Farmers are not likely to control or be aware of genetic recombination leading to this new variation arising in their fields, but they may be aware that seedlings are potential new varieties. In some cases, they may consciously propagate and even provide special care for seedlings resulting from natural crosses.

If seeds are produced in a farmer's field, they fall to the ground and can be consumed by foraging animals or be carried off by insects or birds, deteriorate from microbial activity, or possibly germinate after some period of time, such as after burning in a *slash and burn* system. Seedlings will normally have low vigor relative to stake-derived neighbors due to the much higher carbohydrate energy reserves in stem pieces. Seedlings will often have low yield due to competition from nearby neighbors. Furthermore, plants from seeds will tend to have a tap root (a generally undesirable trait) that produces the main part of the plant's yield, while a plant from a stem piece will have thickened roots in a circumference around the planted stem piece.

These differences require keen observation from the farmer, who would need to understand that such plants will only express their full potential in future generations of clonal propagation. However, farmers certainly also *unknowingly* harvested stem cuttings from seed-derived plants and incorporated them into the set of propagative material for the next planting season.

New recombinants may be given new names, but sometimes they are given the same name as, and are mixed with, the variety to which they are most similar. In the latter case, a variety would be multi-clonal, and the collector would be best advised to sample several plants of each variety to have a good chance of sampling intra-varietal diversity. This possibility illustrates the importance of understanding varietal management practices at the collection site.

Based on modern breeding experience, the chances of genetically superior clones arising from randomly produced true seed in farmers' fields would be quite low. This is especially true in situations where farmers are cultivating single clones contiguously over at least a few hundred square meters, thus increasing the chances of effective self-pollination (where pollen is transferred between different plants of the same clone). This farmer-breeder process would be successful mainly if multiple varieties are planted in near proximity to one another, with the possibility of pollination among unrelated genotypes.

In one of the most intensive studies of farmer selection from cassava seedlings, Duputíe et al. [8] showed how Amerindian cultivators in the Guianas purposely increase their variety options through

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[3] Throughout the text, the term *seed* indicates botanical seed resulting from a pollination event, while the stem pieces used for clonal propagation are labeled as *stakes* or *stem pieces* (in contrast to the common use of the term *seed* in the literature or by growers to also refer to stem pieces).

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seeds. Apparently, in this region seedling-derived plants are often incorporated into the variety group (and variety name) to which they are most similar. The researchers concluded that farmers were aware that agronomic quality may be lower in first generation seed-derived plants. They also noted that landrace identity may be progressively lost through the incorporation of genetically different, but morphologically similar, seedling-derived clones. Understanding of these varietal development and management systems is important for designing both *ex situ* and *in situ* conservation systems.

At the time of the collection of the great majority of CIAT's cassava germplasm accessions in the 1960s and 1970s, this farmer practice of generating and exploiting diversity from seedlings was barely known from research observations. The recent, more precise documentation of how farmers have consciously and unconsciously exploited seedlings in their production systems to maintain diversity adds significantly to our understanding of the meaning of the term *variety* for farmers, and consequently for genebanks. On the other hand, the extent of this process of seedling selection should not be exaggerated. For the majority of production systems throughout the Americas, it appears that seedlings probably had a rather slow and minor role in the creation of diversity for most farmers even though in the longer evolutionary timeline it was the major contributor to the development of new varieties.

3.3. Distribution of Landraces from Centers of Origin

In general, throughout cassava's early history, individual varieties arose and were maintained in relatively limited geographic areas – shared among farmers within villages and among neighboring villages. Less commonly, exchange occurred across broader regions, such as during migration and development of new settlements. These dynamics meant that many thousands of distinct varieties were developed throughout the cassava production zones of the Americas. Many of them had relatively narrow adaptation to the specific conditions and end-uses in the area where first selected. Because of vegetative propagation, any given variety could not further genetically adapt to a new environment or a new use, such as happens readily with seed-propagated and cross-pollinated crops like maize. Ongoing studies based on genotyping of CIAT's collection (discussed further in a later section) indicate a limited number of currently existing accessions that were widely spread geographically within the Americas prior to formal research activities, and some possibly even to Asia [9–11].

Kistler et al. [12] shed light on cassava variety development and distribution through a wide-ranging study designed to understand how the specific landscape of cassava interfaces with clonal reproduction and selection. One of the major findings – impacting how we think about ancestral and current genetic diversity of landraces – was that all cultivated cassava worldwide, ancient and modern, share large, identical haplotype blocks. They found that 82% of all landraces from the Americas have a second-degree or closer relative collected elsewhere. Varieties near the center of cassava's origins (SW Amazon basin) tend to have spread more widely, and with small genetic variations over time due to new varieties arising from seed. Distant varieties, such as those in meso-America or the Caribbean, were more genetically stable and spread less widely. The research also found that 59% of tested cassava genomes included non-*esculenta* ancestry, certainly a significant contributor to the trait diversity available for farmer selection.

3.4. Impact of Landrace Replacement by Bred Varieties for on-Farm Diversity

Farmers appear to have cultivated, processed and consumed cassava in much the same ways over many centuries, and in some systems, up to current times. For these traditional purposes and systems, demand for substantially different new varieties was limited. The introduction and application of science-based crop breeding technologies came into play only toward the middle of the 20th century – a relatively short time span to impact overall genetic diversity across most cassava-growing areas. Until the 1970s, nearly all farmers grew traditional landraces. However, in that era, global efforts were underway, especially with the *Green Revolution* crops like wheat and rice, to breed

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high yielding varieties that would replace traditional ones. It was an opportune time to prepare for the eventuality of new cassava hybrids significantly replacing traditional landraces. This foresight drove the establishment of a comprehensive collection of landraces from cassava's center of origin, along with the knowledge about the crop that had been passed down over centuries from the caretakers of that diversity.

4. Collection and Acquisition

4.1. Planning for First Collections

CIAT's first Annual Report (1969) stated among the goals of its newly established Roots and Tubers Program: *to explore and collect cultivars and related wild species of* Manihot *in the countries where variability is present, with emphasis in the primary centers of origin (Northern South America and Middle America), in order to establish a germplasm bank representative of the world's variability*.

A focus on assembling landrace varieties was especially important for cassava, as there had been only modest research on the crop up to that time. There were a few important collections located in Brazil, the Malagasy Republic, Uganda, Congo, Colombia and India. However, these were local or regional collections, and most had not been well-evaluated or extensively used. Further, most collections were established outside the area of cassava's origins in the Americas and therefore were probably of rather limited genetic diversity.

CIAT solicited the support of one of the region's preeminent botanists, Victor Manuel Patiño, director of the Botanical Garden of Valle as team leader. Dr Patiño commenced work in May of 1969 and followed up for two years with a landmark contribution to global efforts in cassava genetic resources collection.

Early collection planning included broad targeting of cassava growing regions throughout the Americas and the Caribbean. However, at that time there were major constraints to bringing materials from Brazil because of potential threats of coffee rust for Colombia's coffee industry. The gap for introduction of Brazil's landraces lasted for almost 20 years until the development of *in vitro* techniques and accompanying changes to quarantine regulations.

The initial phase of collecting in 1969 focused on Colombia, to establish methods and protocols and because of ease of access in the host country. Patiño's team collected a total of 611 accessions from 20 Colombian departments. These landraces were processed through Colombian quarantine and established on the CIAT farm near Palmira, Valle. In 1970 the collection was extended to other countries, and by the end of that year, the genebank held the following accessions (total from 1969 plus 1970 collections) (CIAT Annual Report 1970):

- Colombia - 1,884
- Ecuador - 123
- Puerto Rico - 60
- Panamá – 118
- Peru - 8
- Venezuela – 330 (Still in quarantine in Bogota)
- Mexico – 70 (Still in Mexico, awaiting shipment to Colombia)

4.2. Collection Procedures

4.2.1. Type of Plant Material Collected

Collection procedures were largely consistent across several years and countries. For cultivated cassava, by far most of the collection and acquisition was of clonal material. There do not appear to be reports of the collection of botanical seeds from farmers' fields, and in vitro collection was attempted only at the experimental level. What is currently identified in the genebank as a *landrace variety* should largely be genetically identical to what farmers grew in the collection sites. There were, however, a few seed introductions from Brazil (mainly derived from institutional collections rather

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than farmers' fields) in the earlier years before development of *in vitro* exchange. These accessions would not have a genetic equivalent anywhere else.

Sampling of stem pieces means that the collectors are managing a bulky and perishable planting material. Typically, collectors cut five to six stem pieces, of about 50-60 cm long, usually from a few different plants (Figure 2). The bundle would weigh a few kilograms. The logistics of managing collected material on a lengthy trip in remote places can be challenging, but collectors appear to have generally planned for and managed these tasks without undue difficulty.

Photo by C. Hershey

Figure 2. Alvaro Amaya (l) and Pablo Daza (r) from CIAT receive stem pieces from a Tikuna farmer (also Magüta: *people of the painted fish*) in Amazonas Dept., Colombia during a collection expedition in 1979.

4.2.2. Passport Information and Accession Coding

From the earliest times of crop genebank establishment, collectors understood the importance of accurate documentation. However, in the first decade of cassava collection by CIAT (late1960s to late 1970s), some of the information that would later be of value to curators and users (especially breeders) was not keenly evident. Consequently, most cassava accessions have only rudimentary passport information: location (normally given as approximate km from a village within a State or Department); name of the farmer (usually a male head of household, even if women were the principal caretakers of the crop); and local variety name. Geographic coordinates were added later based on best estimates from the collectors' description of collection site. It would be impossible today to identify most of the specific farms from which genebank accessions originated.

For about half of the landrace accessions, altitude (masl) of the collection site was recorded. There is no precise definition of what constitutes *lowlands* or *highlands* in terms of cassava adaptation, but from broad experience in accession evaluations, material collected from areas in the tropics below and above an altitude of about 1,200-1,400 masl could be differentially adapted to ambient temperature. Only 11 accessions were collected above 2000 masl, all from Colombia (Table 1).

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Table 1. Collections according to altitude ranges (m above sea level).

Altitude range (masl)	No. of accessions in range	Countries/regions of origin
>=2000	11	Colombia: Antioquia, Narino, Cundinamarca, Magdalena
1600-1999	151	Colombia: 135; Ecuador: 4; Peru: 12
1200-1599	270	Colombia: 255; Ecuador: 6; Guatemala: 3; Mexico: 3; Venezuela: 3
800-1199	275	Brazil: 28; Colombia: 204; Ecuador: 14; Guatemala: 6; Mexico: 1; Peru: 16; Venezuela: 6
0-799	1784	(Most regions)
Altitude not registered	2614	

Figure 3 shows the collection sites, where known, of accessions added to the genebank in the first three decades. Details are found in databases of the CIAT Genetic Resources Program, especially https://www.genesys-pgr.org/c/cassava.

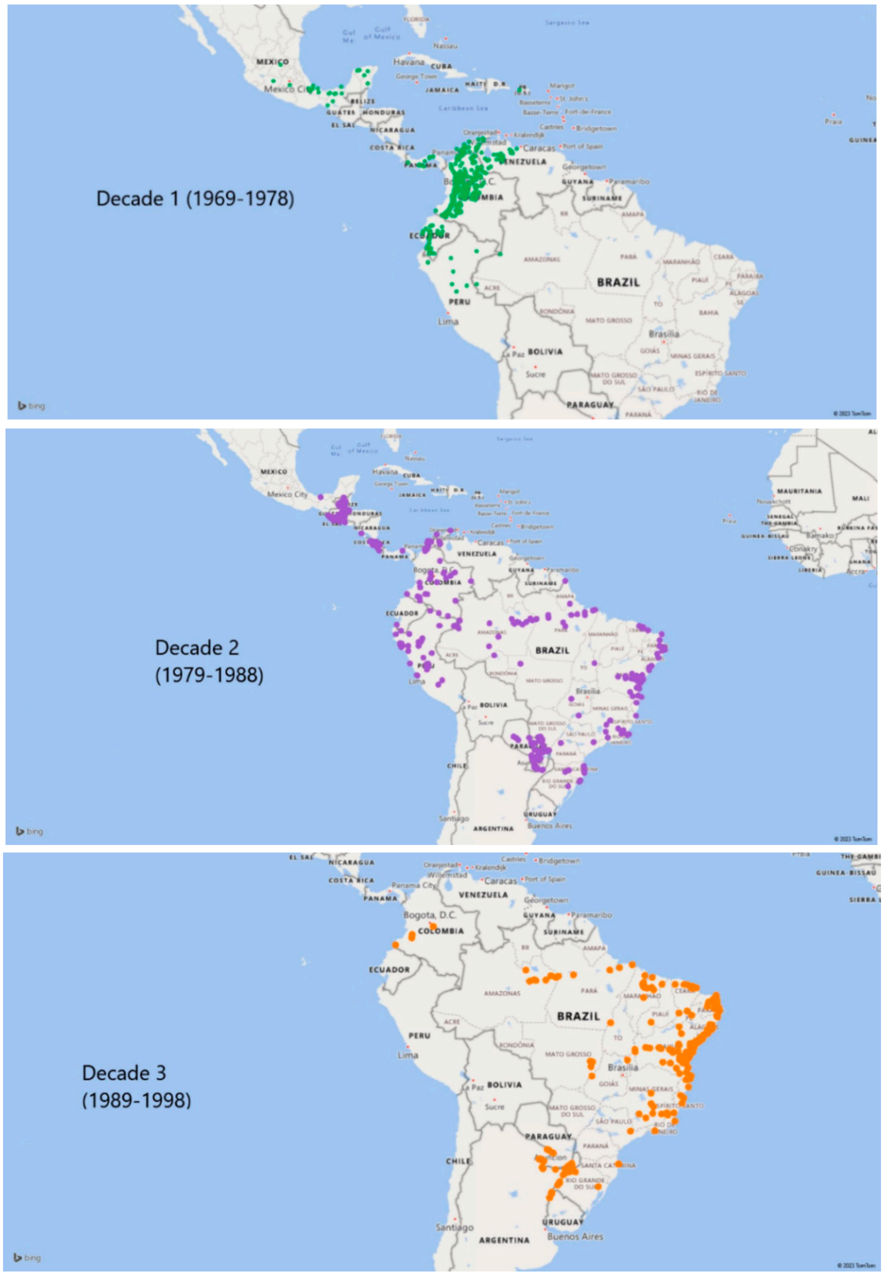

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Figure 3. Collection sites for landrace varieties added to the CIAT cassava collection over three decades, beginning with initial genebank establishment in 1969. Some accessions acquired from institutional genebanks do not have geo-referenced collection sites and therefore are not included here.

When a newly collected sample was introduced into the Colombian quarantine process, CIAT assigned a standard genebank code. All materials had the prefix *M* (indicating the genus *Manihot*), followed by a two- or three-letter country code, followed by sequential numbering within each country, beginning with the number 1 (e.g. MCOL 1, MECU 1, MVEN 1, etc.)[4].

In 1982 a working group sponsored by the International Board for Plant Genetic Resources proposed a format that greatly expanded the information recommended to record during a collection expedition [13]. This new format (Figure S1) gave considerable emphasis to the farmers' knowledge and experience, as well as general production conditions and collectors' professional observations. For each collected variety, farmers were asked to provide the main positive and negative traits for production and use, such as yield, earliness, ability for extended harvest, resistance to pests and diseases, and root quality for specific end uses.

These more complete formats were used in two later, significant collections in Colombia – those involving the accessions COL 2068 to COL 2214 in the Amazonas region in 1979, and again in 1986/87, for accessions COL 2266 to COL 2419, and Col 2520 to COL 2624, mainly from the *Llanos Orientales* (eastern plains) of Colombia [14].

While expanded passport information would be noteworthy and useful, its value would not generally justify extensive re-collection in areas already sampled over the past decades. The complexity and cost of new collections with better on-site characterization, relative to likely benefits, would be very high.

What was not yet well-recognized by many collectors in those early years was the *importance of input from women farmers and users* of the cassava varieties. In many traditional production systems, women may be the main caretakers of genetic diversity and are often more knowledgeable than men about variety traits. Usually, however, male farmers would take responsibility for interacting with male collectors. Collections led by Jan Salick in Peru [7] were significant exceptions.

Thorough crop collecting is a labor-intensive process. Time and funds are usually in short supply. Possibilities to sit and have a coffee or a *mate* and a conversation with a farmer (where valuable anecdotal or historical data might have been collected) were often difficult to fit into the schedule. Collections were often focused on sampling as extensive a genetic diversity in as short a time as possible. We are poorer for that, with much of the farmer knowledge not captured. Importantly however, in this compromise between maximizing the numbers of accessions collected, versus the information about them, there remains the possibility of continuing to gain insights about accessions through effective, targeted evaluation now that they are securely conserved in the genebank.

4.3. Continuing Collection and Acquisition Beyond the Early Genebank Establishment

The Patiño-led early collection expeditions in 1969 and 1970 were certainly the largest individual contributions to the CIAT genebank. Accessions from these two years represent approximately one third of the landrace varieties in the current collection. In other words, the first two years of collection contributed about half as many landrace accessions to the genebank as did the following 50 years (Figure 4). In the ensuing years after the Patiño collections, additions came mainly from three general sources:

- Small to medium-sized collections (up to a few hundred accessions), from expeditions funded and organized to fill gaps.

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[4] In the literature and in databases, the two- or three-letter country codes may be in upper or lower case. Current standard use is for all upper case. More recently (the date is not well-documented) the letter M was dropped, since it does not add any information about the accession.

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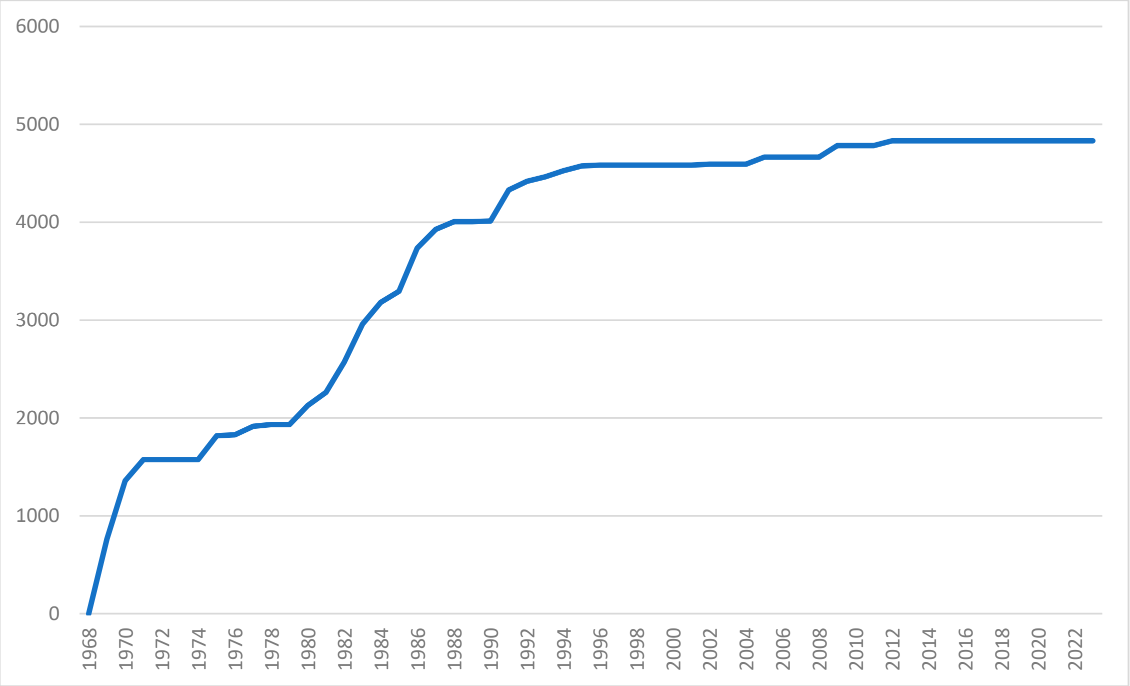
- Many small *opportunistic* collections where scientists travelling to a region for other purposes saw an opportunity to collect varieties that they believed might not already be in the germplasm collection.
- Acquisition of copies of accessions, sometimes including partner program hybrids, from existing collections held by national or regional programs. In the Genesys database, landraces and hybrids are identified separately, but sometimes the lack of solid historical information makes it difficult to be completely accurate.

Figure 4. Cumulative growth across years of the CIAT cassava collection, with number of successful[a] introductions of landrace varieties.



[a] *Successful* refers to accessions that have survived and have been retained to present time.

Based on early Annual Reports, CIAT intended to progressively and rationally add to the collection, after the initial push in 1969-1970. According to this early vision, the genebank would host an *ex situ* collection representing a high proportion of the global genetic diversity of cassava. Among the challenges to meet this goal is that scientists had few methods at the outset to measure or understand in much detail either the range of diversity collected or what remained uncollected (*gap analysis*). As a result, collection priorities revolved mainly around getting representative samples from the most important production areas, rather than on more precise descriptions of genetic diversity.

A secondary goal evolved in recognition of the important diversification that would likely take place on the margins of the main production areas, i.e. where less common or even rare selection pressures would act on the species' evolution. Some examples are exploration of diversity in:

- Areas of very low rainfall (seasonally dry and semi-arid).
- At higher altitudes (up to or somewhat beyond about 2000 masl).
- At higher latitudes (both north and south of the equator, but especially south, where most subtropical cassava is grown), where photoperiod and low winter temperatures were unique drivers of selection.
- In high pH soils (while cassava is broadly adapted to neutral and low pH soils).

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- In areas of known moderate to high pest or disease pressure in search of new sources of resistance.

Collecting additional landraces from areas previously not sampled, or inadequately sampled, is a critical part of a comprehensive conservation strategy. Globally, Hershey [15] estimated that collection of an additional 5000 or more landrace varieties was needed in order to fully represent the species genetic diversity. Priorities should be based primarily on information about: (1) genetic diversity available, especially in the crop's centers of origin and diversity; (2) gaps in current genebanks; and (3) areas in danger of genetic erosion. Priority countries in the Americas are: Bolivia, Brazil, Colombia, the Guianas, Haiti, Nicaragua, Peru, and Venezuela. In hindsight, perhaps one of the more unfortunate consequences of early collection strategies was to give insufficient priority to the Guianas – Guyana, Suriname and French Guiana. The Guianas served as a crossroads for cultural exchange between the Caribbean, the Amazon, and the Orinoco regions. While the specific participation of cassava in these exchanges is not known, it seems very likely that cassava trade would have been an important element, since all those regions cultivated cassava for several thousands of years.

Apart from organizing collection expeditions, CIAT also had multiple opportunities to collaborate with national, regional and international programs to introduce existing accessions from other genebanks. After the initial concentrated two years of collection in 1969-71, this was the main way that new accessions were added to the CIAT collection.

Table 2 shows the addition of accessions by decade, and according to type of germplasm. Table S2 provides more detail on regional and institutional origins of most of the collection's landrace varieties.

Table 2. Number of accessions in CIAT collection by biological status, according to decade of introduction.

Decade of introduction	Landraces	Bred Lines	Wild Species	Total
1969-1978	1722	3	0	1725
1979-1988	2242	100	0	2342
1989-1998	576	123	504	1203
1999-2008	83	34	0	117
2009-2018	165	3	0	168
2019-2023	0	0	0	0
Unclassified	306	402	365	1073
Total	5094	665	869	6628

Source: Genesys consultation, 2023.

4.4. Asia and Africa as Additional Sources of Diversity

Asia and Africa are important secondary centers of diversity for cassava, but it seems unlikely from an evolutionary perspective that a notable level of mutation has occurred since introduction to Africa some five centuries ago, or even less likely, after introduction to Asia a few centuries later. Nonetheless, environmental conditions and farmer selection will have shifted allele frequencies to match local needs and preferences in these continents. One of the most revealing stories about distribution of cassava throughout its American homeland, and then to Asia and Africa, will be our growing capacity to genotype landraces and identify clonal equivalents throughout the world.

Historically, introduction of cassava diversity from most of Asia (India excepted) to CIAT in Colombia was relatively straightforward from a quarantine standpoint. However, the situation changed with the discovery of the Sri Lanka strain of cassava mosaic disease (CMD) in 2015 [16] and its subsequent spread across several countries. Introduction from Africa to Colombia was more complex because of the widespread presence of CMD on that continent already at the time of the founding of CIAT and IITA. Many of the materials introduced to CIAT from Asia and Africa were hybrids with traits of specific interest to breeding programs, rather than attempts to introduce representative diversity from either continent.

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Early introductions from Africa to the CIAT germplasm collection in the late 1980s were aimed at accessing sources of resistance to CMD – mainly developed in hybrids at IITA. CIAT and IITA developed an arrangement with the Scottish Crop Research Institute (SCRI) in Dundee to act as an intermediate recipient, to further verify the freedom from any pathogens, and especially the CMD virus, before onward shipping to Colombian quarantine authorities. CIAT then did additional pathogen testing before any materials moved to the field (see [17] and CIAT Annual Reports).

4.5. Cassava Landrace Density as an Indicator of Local and Regional Diversity

The literature provides widely varying suggestions about number of varieties that individual farmers typically grow (*on-farm landrace density*) – from just a few up to dozens (e.g., [6,7,18]). The concept of *density* can also be applied regionally, i.e. number of varieties across a defined region. We calculated number of varieties collected at each registered site, based on the following assumptions (with the recognition that these assumptions likely do not hold up in every case):

- Each recorded, distinctively named *collection site* consisted of a single farm or closely associated set of farms in a small community.
- All varieties recognized by farmers and/or collectors as being distinctive were collected. (Though rarely noted, collectors sometimes considered whether to collect a variety based on if it may already have been collected on a nearby farm.)
- Varieties obtained through acquisition from official organizations such as experiment stations or schools did not influence the possible repeat collection of those same varieties from farmers in the region.

Importantly, the analysis could not include Brazil, since most of the accessions from Brazil in the CIAT genebank do not have geo-location information. The same is true of some small collections such as those from Cuba and Costa Rica. Despite these limitations, we can draw some tentative conclusions.

Table 3 compares relative landrace varietal density among nine countries. This summary includes 2,318 accessions (or about half the number of landraces in the collection) from 1017 sites whose coordinates could reasonably be expected to be the location of actual collection. Despite several reports in the literature about high numbers of varieties managed by individual farmers, Table 3 appears to show that on a country-wide basis, individual farmers typically grow from one to three varieties. Continent-wide, the average is 2.3 varieties collected per site. In only two countries – Colombia and Paraguay – does the maximum reported varietal density per collection site exceed ten.

Table 3. Comparison of landrace varietal density across countries, represented in the CIAT cassava collection.

Country[a]	Collec-tion sites per country	Total varieties in study[b]	Mean variety density per collection site[c]	Max. variety density per collection site[c]	Area of produc-tion 1980 (1000 ha)[d]	Hectares per landrace variety	Landraces per 1000 ha
Argentina	43	61	1.4	4	18	287	3.4
Colombia	639	1606	2.5	34	165	103	9.7
Ecuador	60	109	1.8	8	20	183	15.2
Guatemala	64	88	1.4	5	4	40	2.2
Mexico	29	37	1.3	2	1	26	37.0
Panama	9	10	1.1	2	1	104	10.0
Paraguay	89	169	1.9	12	171	1010	1.0
Peru	60	167	2.8	9	103	619	1.6
Venezuela	24	71	3.1	8	39	544	1.8
Total or mean	1017	2318	2.3		521	225	4.4

[a] Largest producer in the region, Brazil, is not included because collection site coordinates are not available for many of the landrace accessions.

[b] Includes only landrace varieties with registered collection site coordinates.

[c] A *collection site* is typically a field or a few fields from an individual farm managed by a household, but maybe a few adjoining farms in a village. Individual collectors varied somewhat in their collection procedures.

[d] Source: FAOSTAT. 1980 was chosen as a relative midpoint in the collection and acquisition of accessions of landrace varieties.

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From collection information for Colombia, it is possible to further analyze varietal density in a few Departments where mostly indigenous communities were sampled (Table 4). One collection site in the Department of Guainía, in the remote central eastern region, had 36 putative varieties, which is the maximum from any site (potential duplicates might be confirmed at a future date). Guainía also had the highest department-wide diversity of 15.8 varieties per site, from a total of nine collection sites.

Table 4. Examples of high on-farm cassava diversity based on number of collected landrace varieties in three Departments of Colombia.

Department	Site/farm name	Range of CIAT codes	No. collected
Amazonas	El Encanto (km 1)	Col 2166 - 2191	25
	El Ventura km 6	Col 2152 -2164 + Col 2202 + Col 2211	16
	Vereda El km 6	Col 2068 - 2077 + Col 2203	11
Guainía	Bellavista	Col 2356 - 2371	16
	El Sejal	Col 2266 - 2281	16
	La Ceiba	Col 2356 -2355	22
	Sarrapio	Col 2384 - 2419	36
	Yuri Caño Boron	Col 2302 - 2333	32
Putumayo	Buena Vista 100	Col 2579 - 2593	15
	La Samaritana Kms:10	Col 2594 -2607	14
	San Marcelino Kms:10	Col 2567 - 2578	12

[a]These data must be interpreted with some caution. It is not always clear from the collectors' notes whether a collection site is a single farm or multiple farms combined. As well, land tenure arrangements vary considerably, from sole to community ownership, such that it may be difficult to distinguish between farm and community or village, especially in indigenous communities. The accessions analyzed for the table do not include institutional acquisitions.

One of the notable, and perhaps expected, trends is the higher density of landrace varieties in regions closer to the Amazon basin. This corresponds to areas that tend to be more traditional farming systems, often with shifting cultivation (*slash and burn*, or *swidden*). In these systems, varietal diversity appears to be valued more highly than in more modern ones. Overall, these analyses support the hypothesis that breeders do not necessarily need to provide many, or even several, viable varietal options to farmers in order to achieve significant impact. In general, but certainly with some exceptions, farmers are accustomed to growing only a few varieties.

4.6. Collector Perspectives and Practices Enrich the Genebank

Most collectors for the CIAT cassava collection were not extensive note-takers. Dr Mario Mejia Gutierrez was an exception. He led five collection expeditions in Colombia in the late 1980s with support from the International Board for Plant Genetic Resources (IPBGR) and CIAT [14]. The goal of those collections was to cover important areas of diversity not included in the Patiño expeditions of 1969-1970. Dr Mejia provided extensive detail about the climate, agricultural practices and socioeconomic conditions of the regions in which he was collecting. He described historical migration and trade routes that likely contributed to cassava diversity and its distribution, especially along river routes. In several ways, he presents a model for how collection missions should be planned and executed.

4.7. Molecular Tools as a Support for Planning and Analyzing Collections

Much reporting from collection expeditions and from household and farmer interviews has assumed that cassava growers have a very high capacity to accurately distinguish varieties from each other. However, molecular tools showed that farmer ability to identify unique genotypes is quite variable among growers and among regions. CIAT's Cassava Genetics section developed an

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economical fingerprinting protocol with a panel of 96 SNPs (*SNPY-CHIP*), which was effective in differentiating thousands of genotypes at a high level of confidence. This array was applied, for practical use, for the first time to characterize and differentiate 173 cassava landraces among indigenous communities from the Amazonas Department in southeast Colombia, in collaboration with the Amazonian Institute of Scientific Research (SINCHI) [19]. In a later study, in a survey of 37 households in the Cauca Department, almost 75% of farmers believed they were using improved bred varieties [20]. In fact, based on molecular confirmation, only 10 of those households were doing so. Conversely, 10 households who thought they were *not* using improved varieties were doing so. This discrepancy confirms the difficulty, in some regions, for farmers to correctly identify or recall the specific varieties of cassava they are growing.

In Vietnam, Ocampo et al. [21] studied on-farm varietal composition using both farmer interviews and the SNPY-CHIP panel. The results are somewhat unusual compared to most reported collections, in that farmer-reported variety identification through vernacular names is relatively consistent. Of the 1570 samples collected across six agroecological zones throughout the country, there were 97 different variety names based on farmer identification. The SNPY-CHIP panel showed 85 distinct genotypes, indicating just a 12.4% overestimation of diversity that would have been made based on names alone.

These studies reinforce the importance of fingerprinting tools for the identification of unique genotypes in the process of collecting and acquiring new accessions, as well as for the analysis of patterns of use, adoption, or assessment of genetic diversity.

4.8. Wild Manihot Species Acquisition

As with the related species of many crops, the foremost risks of genetic erosion for wild *Manihot* are the consequence of the expansion of human activity into native habitats, mainly in the form of agriculture, forestry and urbanization. Climate change will increasingly create additional risks for these species, throughout their range of distribution. They often have very specific habitat requirements and typically are somewhat sparsely distributed in already-difficult environments. The largest center of diversity is in central Brazil, in the Cerrado (savanna) region, where agriculture has expanded rapidly since the 1970s. For example, of 41 habitats identified and surveyed in the late 1970s, only one locality remained for wild *Manihot* twenty-five years later [22].

CIAT's goals regarding collection of wild *Manihot* species have been less systematic and less consistent than for cultivated cassava. From the earliest years, CIAT envisioned the possibility of collecting and conserving these wild relatives (CIAT Annual Report, 1969) as a hedge against genetic erosion and as a resource for breeding. However, that a modern taxonomic monograph on *Manihot* was not developed until 1973 [23] meant that the earliest planning for wild species collection could only be based on scattered and somewhat outdated taxonomic literature.

Given the number of wild species (about 100), their sporadic distribution, often in remote areas, and the sparse funding that has been allocated, proper wild species collections have rarely been possible. CIAT's Biotechnology Research Unit (BRU) and Genetic Resources Program (GRP) began preliminary work on wild *Manihot* in the early 1980s, but official introduction of several of them into the genebank did not begin until 1992, resulting from the renewed interest arising from various studies (e.g., [24]). Interest was further piqued by the somewhat revolutionary hypothesis of Antonio Allem of Brazil's CENARGEN that cassava originated in the southwest Amazon basin from the *M. esculenta* subsp. *flabellifolia* and subsp. *peruviana* [25]. The CIAT Cassava Program collaborated by establishing a modest field collection, hybridization efforts, and characterization through genotyping (Table 5). Most of these accessions were introduced as true seed from expeditions led by Allem, supported by IPBGR from 1992 to 1995. The subsequent origin of propagules, and different forms of propagation in the field over various cycles of regeneration are somewhat unclear from the records. Some of the seeds were difficult to germinate, and these were propagated through excising embryos and culturing them on sterile media. If some of the accessions were generated through seeds, these seeds would have resulted in plants with different allelic patterns compared to the original

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accessions, but would not be expected to have any unique alleles relative to their parents. Currently, as with cultivated cassava, CIAT no longer holds a field collection of wild species.

Table 5. ***Manihot*** **wild species and subspecies held** ***in vitro*** **at CIAT.**

Species	Principal country of origin	Accessions *in vitro*
AES (aescolifolia)	Mexico	4
ALT (alutacea)	Brazil	4
ANM (anomala)	Brazil	0
BLO (brachyloba)	Colombia	0
CAE (caerulescens)	Brazil	17
CEC (cecrophila)	Unknown	6
CHL (cholorsticta)	Mexico	2
CTH (carthaginensis)	Colombia	26
DCH (dichotoma)	Brazil	0
EPR (epruinosa)	Brazil	2
FMT (filamentosa)	Brazil	3
FLA (esculenta subsp.*flabellifolia)*	Brazil	170
FRU (fruticulosa)	Unknown	1
GLA (glaziovii)	Brazil	1
GUT (guaranitica)	Paraguay	0
HAS (hastatiloba)	Unknow	0
IRW (irwinii)	Unknown	1
JAC (jacobinensis)	Brazil	6
JNP (janiphoides)	Brazil	2
LON (longepetiolata)	Unknown	6
ORB (orbicularis)	Unknown	8
PEL (peltata)	Unknown	0
PIL (pilosa)	Unknown	1
PNT (pentaphylla)	Brazil	1
PER (esculenta subs. *peruviana)*	Brazil	87
PSE (pseudoglaziovii)	Brazil	1
PUR (purpureo-costata)	Unknown	0
QPT (quinquepartita	Brazil	0
RUB (rubricaulis)	Unknown	0
SPR (sparsifolia)	Brazil	2
TPH (triphylla)	Unknown	9
TST (tristis)	Brazil	16
VIO (violacea)	Brazil	1
	Total:	**377**

4.9. Breeding Lines and Genetic Stocks as Part of the Genebank

Elite breeding lines may or may not become successful varieties. These breeding lines – the equivalent of *breeder's seed* in a seed-propagated crop – may be lost unless specific steps are taken to preserve them. CGIAR genebanks operate under a shared policy framework that allows for the incorporation of experimental breeding lines into crop genebanks, but the criteria and procedures are nuanced and center specific. For cassava, that preservation is often best carried out through *in vitro* conservation, and the facilities and expertise for this reside mainly in the CIAT Genetic Resources Program.

Beginning in the mid-1980s, CIAT's breeders, jointly with the GRP, decided to include bred lines that had reached *elite* status into the collection. In general, the basis for qualifying as an elite breeding line was the following:

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- Selected through the full breeding pipeline, from seedling trial to replicated yield trials, with testing across at least three sites and over two years in advanced yield trials.
- Selected for superiority in a range of target traits, especially plant architecture, yield, dry matter and pest/disease tolerance for target environments.

These *in vitro* stocks can have multiple purposes, including as a(n):

- Pathogen-free, genetically verified basis of a multiplication program for stem planting pieces.
- Identification touchstone for any possible future need to confirm true *type* of a bred variety in breeding nurseries or farmers' fields.
- Pathogen-free source for distribution to other genebanks or breeding programs.
- Source of time-based milestones for study of genetic gains across years.

One of the challenges is that number of breeding lines grows steadily over years. These lines could thereby slowly and steadily encompass an ever-greater proportion of the resources allocated for germplasm management. As a result, in the mid-1990s CIAT discontinued the practice of routinely adding new elite lines from its breeding program into the genebank. Periodically there also have been introductions of varieties or breeding lines from partner breeding programs, and this practice continues. To date the main contributors were programs in Brazil, Colombia (mainly hybrids developed prior to CIAT's foundation), Indonesia, Nigeria, and Thailand.

As with advanced breeding lines, genetic stocks can also be temporary or permanent parts of a genebank, depending on objectives and guiding operational principles of the bank. For example, in the mid-1990s CIAT incorporated a mapping population into the germplasm collection to ensure that it would be widely available to participants in the Cassava Biotechnology Network.

4.10. Current Status of the CIAT Cassava Collection

In 2008 the Global Crop Diversity Trust (*Crop Trust*) brought together cassava genebank experts from around the world to discuss and develop *Manihot* conservation strategies [15]. The strategy report estimated that CIAT captures about 55% of total global diversity for cassava. With further analyses of recent genotyping data from CIAT, IITA and others, these numbers will likely be modified.

By mid-2025, the CIAT cassava collection (*Manihot esculenta*) consisted of the components listed in Table 6, for a total of 5574 accessions. (*Losses* are discussed further in a later section).

Table 6. Sources of the CIAT cassava collection, with estimated original numbers collected or acquired, current accessions *in vitro*, and causes of major losses, where reported.

Origin	**Prefix of accession code**	**Original total**[a]	**Current *in vitro* total**[b]	**Est. no. of landraces in current total**[c]	**Historical causes of quarantine and field losses**[d]
Argentina	ARG	129	115	108	
Bolivia	BOL	7	7	7	
Brazil	BRA	1453	1294	1167	
China	CHN	2	2	2	
Colombia	COL	2826	1932	1902	CBB[e], salt spots in field
Costa Rica	CR	189	182	182	
Cuba	CUB	77	75	73	
Dominican Rep.	DOM	5	4	4	
Ecuador	ECU	205	112	112	Undefined quarantine issues
Fiji	FJI	6	6	6	
Guatemala	GUA	92	81	81	
Indonesia	IND	254	247	225	
Malaysia	MAL	80	71	62	
Mexico	MEX	111	100	96	

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Nigeria (IITA)	NGA	19	18	0	
Panama	PAN	141	42	42	CBB, salt spots in field
Paraguay	PAR	220	203	201	
Peru	PER	616	397	397	CCMD[f] & CBB in quarantine
Philippines	PHI	6	6	4	
Puerto Rico	PTR	102	15	15	CBB, salt spots in field
Salvador	SLV	8	8	8	
Thailand	TAI	31	30	4	
USA	USA	9	8	8	
Venezuela	VEN	350	231	231	
Vietnam	VNM	9	9	9	
CIAT hybrids	AM, CG, CM, CT, SG, SM	408	379	0	
Total		**7355**	**5574**	**4946**	

[a] Estimated based on highest accession number within a country of origin, including both landraces and partner hybrids.
[b] Based on Genesys consultation August 2025.
[c] Other accessions are mostly CIAT or partner hybrids.
[d] Discarded in quarantine or lost from the field collection since origin of collection in 1969. Postulated as most likely scenarios from CIAT Cassava Program Reports over multiple years. Later losses *in vitro* are typically less associated with country of origin.
[e] Cassava bacterial blight.
[f] Cassava common mosaic disease.

5. Pest and Pathogen Management As a Fundamental Conservation Concern

Many cassava pathogens, including viruses, bacteria and fungi, are readily transmitted from one generation to the next via clonal propagation. Conversely, mites and insects are controlled relatively easily with the protocols of *in vitro* systems. For any genebank, optimum phytosanitary status of accessions is fundamental for good management. Not only do pests and diseases present a threat to the goal of conservation *in perpetuity*, but they also critically impact the possibility of sharing accessions with interested parties, especially internationally – a core function of the CIAT genebank. From the relatively basic tools of 50 years ago to the molecular diagnostics of today, there is now a high assurance that any accessions currently conserved and offered for exchange are free of pathogens of quarantine significance.

5.1. Plant Health Considerations for Early Establishment of the Collection

All early cassava collections (through the 1970s) were in the form of mature stem cuttings. Aware of the importance and dangers represented by introduction of pests and pathogens, CIAT cooperated closely with the plant pathologists of the Instituto Colombiano Agropecuario [Colombian Agricultural Institute] (ICA) to develop phytosanitary protocols. ICA stipulated that introductions from countries outside of Colombia would be quarantined in an insect-free and specially adapted greenhouse at the ICA-Tibaitatá station near Bogotá, a region where no commercial cassava is cultivated due to the high altitude.

To inactivate potential viruses, cuttings were treated at 52°C for 20 min, or at 50°C for 60 min, with hot water. Although some viruses, mycoplasma-like organisms and bacteria could apparently be inactivated by thermotherapy, repeating the treatment was deemed necessary to attempt, as much as possible, a completely virus-free stock. After the treatment the cuttings were protected with a fungicide to avoid root-rots and stem-rots during sprouting (CIAT Annual Reports 1969 and 1970).

Despite these early measures, in 1970 the newly established collection in the CIAT station began showing signs of cassava bacterial blight (CBB). This was a potentially devastating development. CBB was known to be highly damaging in susceptible clones, and most accessions appeared to be

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susceptible. In addition to causing defoliation and lower yields, the bacteria became systemic and were passed from one clonal generation to the next via infected stem pieces. Difficulty in conservation and propagation, along with quarantine implications for distribution of germplasm, could negate many of the potential benefits of the collection. Fortunately, CIAT pathologists developed effective protocols to eradicate CBB through careful selection of symptom-free planting material and an indexing system based on rooted sprouts. CIAT was able to keep the collection at headquarters CBB-free during the remaining span of over 30 years of the continuation of a field collection.

The CIAT station also has several other endemic pests and diseases, most of which cause low or moderate damage levels in locally adapted varieties. However, given the broad genetic diversity of the germplasm collection, pests and diseases showed highly variable effects across the range of introduced accessions. The Cassava Program (especially Breeding, Pathology, and Entomology sections) frequently took advantage of ongoing low to moderate pest and disease pressure, and sometimes more severe outbreaks, to evaluate accessions for genetic resistance whenever possible. Chemical control, even in the field collection was used expeditiously, since it could reduce or destroy biological control agents, thereby exacerbating infestation and damage by pests in the longer term.

One of the most important sanitary practices was to prohibit the entry of stem pieces into the headquarters station from outside sources, such as from breeding trials in other regions of Colombia, except in special cases with appropriate phytosanitary inspection and monitoring. The main pathogen targets were the causal agents of CBB, superelongation disease (SED) and the potential for various unknown pathogens, especially viruses.

5.2. Managing the on-Going Phytosanitary Status of the Accessions

From the time of genebank establishment up to current times, there has never been a *breathing space*, where the plant protection specialists were not busy with one or another of the phytosanitary threats to the dual functions of cassava germplasm conservation and exchange. Table S3 highlights the chronology of phytosanitary practices, based on the expanding knowledge base and tools associated with diagnostics and cleaning of clonal materials [26].

The continuing challenges tend to be from viruses and a handful of diseases with unknown causal agents. A principal challenge for accession *cleaning* has been for cassava frogskin disease, first reported in 1971, and eventually becoming a major threat to cassava production in several areas of Colombia, Ecuador and Central America. This disease would become a key reason for eliminating the field collection at the CIAT-Palmira station in the early 2000s. By 1985, a highly sensitive graft indexing test was developed using the indicator variety *Secundina* (COL 2063), implemented for the collection and for sensitive experiments elsewhere. However, up to the current time, the causal agent(s) have not been confirmed. A possible complex of pathogens was implicated [27], but more recent research demonstrated that single torrado-virus infections can cause the classical symptoms of the disease [28]. Fully resolving the causal agent(s) is critical to the collection's future phytosanitary integrity.

The cassava witches broom disease (CWBD) is another devastating disease whose causal agent eluded scientists for many years. In 2009, a phytoplasma was reported to be associated with disease symptoms [29]. A more recent report identified a fungal pathogen as a more likely causal agent. Using a metagenomic approach, Leiva et al. [30] identified a member of the *Ceratobasidium* genus as strongly associated with CWBD symptoms. The fungus is present in diseased samples collected since the first recorded CWBD outbreaks in Southeast Asia and is transmissible by grafting. The fungus' full role as causal agent is yet to be confirmed. CWBD and CFSD illustrate some of the continuing difficult challenges for accession management through better testing and cleaning protocols for key pathogens.

Toward this end, in 2009 CGIAR took the significant step of forming a system-wide working group on genebank plant health. The group is a network of germplasm health units that provide phytosanitary services to genebanks and breeding programs. Members work to improve the efficiency, quality, and safety of germplasm movement within and outside CGIAR, and to strengthen

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the capacity of national partners to comply with international phytosanitary standards. Genebanks holding major clonal collections – e.g. CIAT, IITA, Bioversity and CIP – form a subgroup that focuses on plant health issues and solutions for collections held as *in vitro* cultures.

6. Evolving Conservation Methods for Long-Term Security and Genetic Integrity

Initially, when the collection was first established in the late 1960s, there was little thought given to options for clonal conservation other than as a field collection. By the mid- to late 1970s, the promise of *in vitro* slow growth conservation started to become a reality. At this point, there was the concept that an *in vitro base collection* should be the most secure system available for long-term conservation, and the field collection would be a *working collection*. By the late 1980s, cryopreservation evolved as a realistic option for cassava, and became the goal as a possible base collection, while both slow growth *in vitro* and field accessions would form active or working collections (for characterization, evaluation, distribution and use in breeding). Although there has been great progress toward cryopreservation technologies, it is not yet fully operational at CIAT. Additionally, there are options for other forms of conservation that have emerged and are discussed here – including potted plants in the greenhouse with limited growth (*bonsai* method) and true seeds (Table S4).

6.1. The Field Collection

Space, labor, phytosanitary and multiple other challenges impact viability and security of a field-based cassava collection. Guidelines for conservation and regeneration evolved into a system that balanced the overwhelming priority for safe conservation with the need to provide planting material for trials inside and outside the CIAT headquarters station.

Jaramillo [31] detailed the agronomic and phytosanitary practices that are fundamental to managing a field collection. Apart from the general management recommendations for cassava production (e.g. land preparation, soil fertility management, weed control), the field collection required some additional attention. Based on a perennial plant, a field collection might theoretically be maintained for several years without renewal. However, practical experience showed that long-term plantings of highly diverse accessions are fraught with potential problems. There is wide variation in their behavior beyond one or two years in the field; both physical and phytosanitary issues can come into play. On the physical side, large differences in growth habits can mean that very vigorous, highly branched clones out-compete small, low-vigor neighbors to the point of threatening existence of the latter. Large plants tend to lodge, and to become unwieldy to access for observation or management.

Appropriate timing of planting and harvest cycles for clonal renewal helped manage both the physical and biological risks of field conservation. The standard protocol implemented by the late 1970s was that the genebank accessions were planted in overlapping cycles to avoid having vulnerable young plants as the *only* representative of any given accession. In general, this system involved replanting the collection every year, while leaving each previous planting in the field until it was about 18 months old, thereby giving a 6-month overlap. Based on years of experience, 18 months appeared to be about the maximum time that the accessions could practically be managed at the headquarters station without undue risks of losses.

By the late 1990s, an increasing whitefly infestation at the CIAT station resulted in troubling increases in cassava frogskin disease (CFSD). While risk to all trials was a concern, the germplasm collection was of special priority because of the critical need to minimize losses of any accessions. Despite many years of not knowing the causal agent, relatively effective means of control had been developed, especially the selection of propagative stem pieces from symptomless plants (observation of roots post-harvest, before stakes were cut). Confirmation of pathogen-free planting material could be accomplished by grafting onto highly susceptible indicator plants, usually the variety *Secundina.* However, by 2003, whitefly populations continued to increase, along with CFSD-infected accessions. Conservation as a field collection was becoming untenable. The Cassava Program made the difficult

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decision, in consultation with the Genetic Resources Program, to discontinue the field-grown collection.

Although the field genebank was discontinued, there was continuing need by various research teams to have access to field-grown plants for various types of trials. As many as 2000 accessions, generated from CFSD-free stock, continued to be multiplied and evaluated for additional years within the Cassava program, but no longer technically considered a formal part of conservation of genebank accessions. Projects tended to focus on the core collection (see later section) or a *mini-core* subset.

6.2. Slow-Growth In Vitro Methods

Two publications from the University of Saskatchewan, a few years after first establishment of CIAT's genebank, demonstrated successful *in vitro* cultivation of cassava as rooted plantlets derived from meristems, cultured in sterile media [32,33]. After a brief developmental period to adapt the technology to local conditions, CIAT initiated an *in vitro* genebank in 1978. As might be expected, there were considerable genotypic effects in response to culture media and growth room conditions. By the early 1980s, the technology and facilities were sufficiently developed to move the entire cassava collection to *in vitro* culture. While there has been continual fine-tuning of protocols and upgrading of facilities, the key steps developed in the mid- and late 1970s proved to be robust, at least for the cultivated species.

Modifications to slow *in vitro* growth rates included incorporating growth retardants and managing light and temperature to extend the time required for regeneration. Cassava cultures under slow growth can be stored for an average of a year (varying between 4 and 19 months, depending on the genotype).

In vitro slow growth conservation of the cassava collection was a landmark success and paved the way for several other technologies and protocols as well, e.g. for pathogen cleaning, rapid multiplication, related work in anther culture for doubled haploid production, mutation, and more recently for transformation and gene editing.

CIAT produced a comprehensive manual on cassava *in vitro* conservation management in 2010, representing learning and experiences over almost 30 years [34]. Some fundamental activities are illustrated by a current flow chart (Figure 5). These include acquisition, pathogen indexing and cleaning, in vitro conservation, and generation of material for safety back up, characterization, experimental use, and distribution. With the inauguration of the Future Seeds genebank complex at CIAT in 2022, the *in vitro* growth rooms and preparation facilities have been substantially upgraded, now also providing sufficient space for mainstreaming cryopreservation. In September 2023, a partial duplicate of the cassava collection (over 3,000 accessions) was transferred to the *Future Seeds* facility to evaluate plant growth and conservation performance under the new temperature and lighting conditions.

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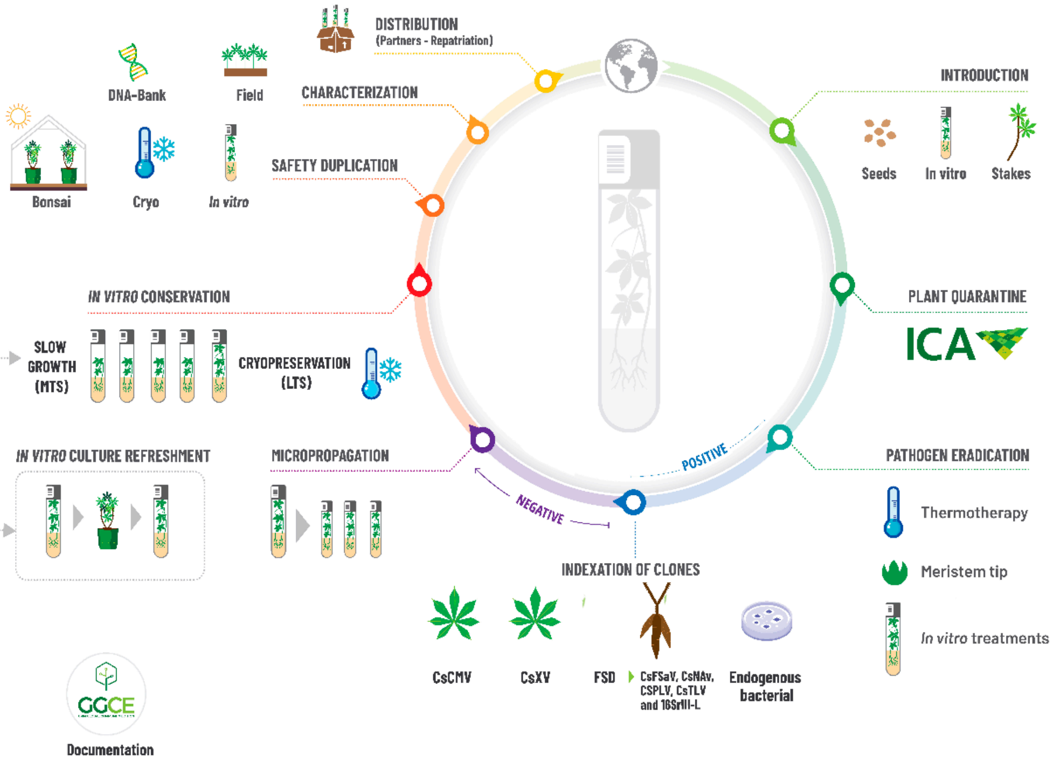

Figure 5. CIAT *in vitro* conservation laboratory operational scheme for *Manihot* germplasm management.

During the first half of 2024, the most critical accessions — those affected by bacterial contamination, low vigor, and/or with limited plantlet availability — were identified and prioritized for further transfer to the new facility. The final relocation of the entire *in vitro* cassava collection was completed during the second half of 2024. The new facilities for conservation extend over 427m^2 versus 175m^2 in the old genebank. Additions to space and facilities include a second subculture room and a dedicated sterilization room. Area in the active growth room was increased from 12 to 47 m^2. Additionally, in 2024, a dedicated cryobank laboratory was constructed to house cryogenic storage tanks for cryopreserved samples. Extra space offers capacity for training and research projects aligned with the innovation and community engagement aims of *Future Seeds*.

Despite the broad success of *in vitro* conservation, a major drawback of the system is the delayed access to the accessions for research involving mature plants. Regenerating plants from *in vitro* to provide planting material for field trials, is painfully slow. While in theory this should be possible in 8-9 months, the reality is that often around 18-24 months are required to obtain the required stakes for field trials. This can take even longer for a second level of multiplication for larger trials. After the field genebank was eliminated in 2003, the field testing of accessions became considerably more challenging.

6.3. Security Backup Duplicates

A security backup copy for *in vitro* cultures is also referred to as safety duplication or a *black box* security system to indicate the protected legal status of the materials. Even if conserved in the facilities of a different organization, the cultures legally remain under the control of CIAT. They can only be returned to CIAT for the purpose of replacing lost materials, or, alternatively, destroyed. The system began as a collaboration between CIAT and the International Potato Center (CIP) in Lima, Peru, based on an agreement signed in 2005. The centers collaborated to duplicate each other's collections of cassava and sweetpotatoes, i.e. CIAT held an inactive copy of CIP's sweetpotato collection and CIP held an inactive copy of CIAT's cassava collection. Refreshed material was sent approximately every 12-18 months from the base curating center to the security backup center. According to Genesys records, the most recent batch of 600 cassava accessions was sent to CIP in

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2023. Since the establishment of the backup agreement with CIP, CIAT has sent 35,692 samples representing 5,744 accessions. Wild species accessions were initially considered to be part of the backup agreement; however, restrictions imposed by Peru's plant health authority (SENASA) limited the import permit exclusively to *M. esculenta*.

In 2018 CIAT and AGROSAVIA of Colombia established an alternative security backup at the La Selva research center in Rionegro, Antioquia. Apart from the convenience of dealing only with internal Colombian quarantine measures (rather than international regulations between Colombia and Peru), this backup system allowed for duplication of some of the wild species. After conducting visits and technical adjustments to install and operate growth chambers in AGROSAVIA, the first batch of cultures was shipped to the La Selva facilities in October 2023.

The Covid-19 pandemic during 2021 and 2022 created substantial challenges and disruptions to cassava *in vitro* conservation at CIAT, and led to a die-off of most safety duplicated accessions at CIP. However, rather than re-initiating the safety duplicate at CIP, the genebank focused on strengthening the AGROSAVIA-based system.

6.4. Critical Challenges and Successes in the Search for High-Efficacy Cryopreservation

Cryopreservation is the storage of germplasm at ultra-low temperatures (-196^{o}C) using cryogenic media, typically liquid nitrogen. This temperature effectively stops the biological activity of the plant cells and nearly eliminates the need to regularly subculture the plants *in vitro*. Panis et al. [35] list some of the advantages and disadvantages for cryopreservation:

Advantages:

- Minimum space requirements
- Low long-term maintenance costs
- High genetic stability
- Long-term storage (>100 years)
- Largely independent of stability of electrical supply[5]

Disadvantages:

- Restricted availability
- Restricted accessibility
- Access to liquid nitrogen in some situations
- Need for specific protocol development
- High initial workload and costs to cryopreserve clonal plants

CIAT pioneered research on cassava cryo in 1985 and has given varying degrees of research emphasis to improving the techniques since that time.[6] Several procedures have been developed that involve the extraction of freezable water from the tissue cells before rapid cooling. If the cell interior is sufficiently dehydrated, it undergoes a process called *vitrification*, which is direct transition from the liquid phase into an amorphous phase (or *glassy state*), while avoiding the formation of lethal crystalline ice. A modification of this technique, called *droplet vitrification*, further reduces the chance for ice crystal formation. It achieves this through the application of ultra-fast cooling and rewarming rates, using aluminum foil and small amounts of cryoprotectant solutions. The technique has now been developed for different crops, including cassava. The droplet vitrification methodology appears to be technically mature [36], to be implemented as a long-term conservation and safety backup method. The new Future Seeds facility at CIAT has laboratory and cryobank area in place and is in the process of implementing the technique. Initially, in a pilot phase, cryo could be considered a backup system, but eventually would likely become the base collection. Some poorly understood

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[5] Added by the authors of the current report.

[6] Cryopreservation research has been managed for many years under the leadership of CIAT's Biotechnology Research Unit (BRU). In the future, cryopreservation of the cassava collection will be mainstreamed as part of the genebank operations in CIAT's Future Seeds facilities.

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risks remain. These include long-term mutation from background ionizing radiation, which could suggest the need for some periodic recovery, testing and renovation as part of best practices for cryopreservation.

At CIP, CIAT and IITA, 30% minimum plant regrowth (the successful development and regeneration of the whole plant) is used as a threshold for potato, yam and cassava, and 20% for sweetpotato. After more than 30 years, and with only sporadic and low-level funding for the most part, CIAT has refined the technology to a high level of success for nearly all tested genotypes. In tests of 1466 clones, including the most representative collections from Brazil, Colombia, Peru, Venezuela, and other countries, as well as some improved hybrids, only 2-3% showed a response of under 30% recovery with the droplet vitrification protocol (R. Escobar, pers. comm.)

Escobar [37] suggested that a cryopreservation *unit* should consist of 100 meristems of each target accession, distributed in cryovials of 10 meristems each. In addition, each vial should include a *sentinel clone* with known high post-freezing response (such as BRA 856) as a monitor for the system.

Protocols have also been adjusted for wild *Manihot* species, some of which behave very poorly *in vitro* or even in the field, making their successful conservation very challenging. Plants have been recovered from cryopreservation for *M. esculenta* subsp. *flabellifolia, M. esculenta* subsp. *peruviana* and *M. carthaginensis*.

An international feasibility study of independent experts proposed a global *cryovault* for conserving vegetatively propagated species, along the line of Svalbard for seed conservation [38]. Nearly a decade later, development of regional *cryohubs* for clonal and recalcitrant crops is now in progress – one in the Americas led by CIP, one in Africa led by IITA and a third in Europe led by the Alliance of Bioversity and CIAT. The CIP cryovault was officially inaugurated in Lima, Peru in November 2025, and is anticipated to include the CIAT cassava collection (https://cipotato.org/cipatplanttreaty/regional-cryohubs-recalcitrant-crops/).

6.5. The Bonsai Conservation System

After elimination of the field genebank, just a single *in vitro* collection in one site would have implied an unacceptable level of risk. The 2002 CIAT Genetic Resources Annual Report notes: As *a result of the cleaning and indexing effort launched in 1996, 73% of the cassava collection is now indexed against viruses of quarantine importance and available for distribution. As a by-product of this work 2,169 clones have been established as a bonsai collection that may result in a low-cost alternative to the field genebank, before the work on the cryo-collection is completed.*

The colloquially named *bonsai* conservation system embodies the concept of producing cassava plants with moderately restricted growth by limiting container size, plant nutrients and water, along with strategic pruning. It is designed to offer space efficiency, resource conservation, phytosanitary control, and accessibility, relative to a field collection.

To serve as a valid conservation system, these plants should ideally be grown under highly controlled, insect-free and limited-access conditions in a greenhouse. Initially, there was considerable experimentation on the growth conditions that would achieve the best balance between slow growth (minimize space used and extended regeneration times) and multiplication rates (number and quality of propagules that could be obtained to produce material for field trials). From this perspective, priority for the bonsai collection would be for materials most used/requested by CIAT research programs. There was informal discussion about the possibility of ICA certification of phytosanitary status of the bonsai plants, especially to qualify for international shipments. However, this was in fact not pursued vigorously and did not materialize due to FAO recommendations for the safe international movement of cassava only as *in vitro* cultures [17]. Nevertheless, the bonsai collection has served as a valuable local backup, enabling the recovery of accessions that had lost viability or vigor due to contamination or poor response under *in vitro* conditions.

Niño-Jimenez et al. [39] describe research to refine the bonsai system, working with conservation system variables to minimize loss of material. Modification of the substrate, use of a biological inoculant, moist chamber conditions, fertilization and controlled pruning allowed the establishment

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of accessions in plastic containers with a loss rate of less than 4%. Maintaining plants for more than three years (and even cases of more than 5 years) is possible and comparable to or better than that achieved with *in vitro* techniques. This system is not yet reported from other cassava germplasm collections.

6.6. True Seeds to Conserve Allele Diversity

Although cassava *ex situ* collections appear to have been conserved around the world exclusively as clonal repositories (field, greenhouse or *in vitro*), hypothetically conservation of the full genetic diversity of the species as true seed is also possible. For the development of new varieties, breeders are interested in sources of specific alleles and those sources do not need to be specific genotypes (or varieties). However, there are no standardized recommendations for genebanks consisting of true cassava seeds. There would be several advantages to this approach, but also some challenges. Although fully controlled experiments for long-term storage have not been done, IITA reports storing seeds (of approximately 6-8 per cent moisture content at 5^{o}C and 60% RH) with no difference in seed viability between the ages of 0 and 7 years (IITA Annual Report, 1979). Seeds can also be stored in liquid nitrogen, presumably for a much longer period, and therefore potentially with less complexity in managing a regeneration system [40,41].

Because cassava landraces are all highly heterozygous, their progeny – whether from self- or cross-pollination – will segregate widely. Reproducing the parent genotype through seed is not possible. However, seeds can be used to conserve the full array of the alleles in a given accession, if the appropriate pollination and sampling methods are used. A working group on cassava conservation strategies [15] suggested that the best way to develop seed populations for genetic resources conservation purposes would be by selfing plants within each landrace accession. This technique has the advantage that only the alleles from that specific accession are passed on to progeny through the seed, as opposed to *mixing* or *dilution* that would be caused by crossing with other accessions (or if open-pollinated seeds were collected). A disadvantage of selfing is that cassava often suffers moderate to severe inbreeding depression. The plants that result from self-pollination will generally be less vigorous than the parent. This loss of vigor can compromise their ability to continue to produce seeds, or even to reproduce vegetatively.

As gene tagging becomes more precise, faster, and more economical, best parents can be identified regardless of whether they are derived from seed or are original landrace varieties. Apart from being an effective long-term conservation system, especially in a cryopreserved state, seeds are an easier way to exchange genetic resources internationally.

One major challenge is that obtaining seeds from cassava, especially from controlled pollinations, is a somewhat tedious and costly process. Significantly, there is currently not a field collection at CIAT. Further, the ability to produce seeds varies widely among accessions – from profuse seed producers to those clones that produce no seeds under most conditions. However, research and continuing practical experience shows that extended daylength through supplementary red lighting can improve flowering in cassava [42,43].

6.7. Conservation Challenges and Solutions for the Wild Manihot Species

The wild *Manihot* species are notoriously difficult to maintain *ex situ*. In nature, they are mostly perennial, and all appear to be cross pollinating and to reproduce primarily by seed. The main efforts in conservation have been by Embrapa-CNPMF in Cruz das Almas, Bahia; CENARGEN in Brasilia; the Federal University of Brasilia (Dr Nagib Nassar); IITA in Ibadan, Nigeria; and CIAT in Colombia.

Much of the reporting on early work with wild species conservation at CIAT was in relatively obscure internal documents, such as annual reports, conference proceedings or newsletters. Fortunately, many of these documents have become more available and more easily accessed in recent years, especially through the CGIAR centralized repository of documents (https://cgspace.cgiar.org/home).

Some of the topics reported concern:

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- Methods to break seed dormancy.
- Developing techniques for embryo rescue and *in vitro* culture techniques for difficult-to-germinate seeds.
- *In vitro* slow growth methods for longer-term conservation, tailored to different species.
- Cross-compatibility between various wild species and cultivated cassava.
- Modest efforts to evaluate for traits of importance to cassava breeding.

In the first years after their introduction, CIAT grew some of the wild species in the field on approximately a 2-year renovation cycle. Given the broad ecological range of adaptation of the *Manihot* species, it is difficult to mimic their necessary edaphoclimatic conditions for propagation. The CIAT station is perhaps especially poorly suited to many of the species, which generally originate in lowland high-temperature conditions, in poor soils on forest margins, and often dry environments. Many are adapted to somewhat acid soil conditions, in contrast to CIAT's more pH-neutral or alkaline-tending soils. A different pest and disease complex is present at CIAT compared to most of their native habitats. Plants often grow poorly, do not produce seeds, and stem cuttings do not sprout well.

Suggestions for mitigation of the challenges include seeking out sites with more suitable edapho-climatic conditions specific to the wild species needs. In the end this was not possible with available funding. For at least the past 30 years, only a very few wild species have been used in field experiments. However, the Breeding and Genetics sections of the Cassava Program carried out modest evaluations and crossing experiments.

Chavez et al. [44] reported on priorities for development of techniques for conservation and utilization of wild *Manihot* spp.:

- Develop methods for breaking dormancy and overcoming seed sterility.
- Develop techniques for embryo rescue, for seeds that germinated poorly with conventional germination procedures, and for their subsequent *in vitro* culture.
- Develop methods for *in vitro* conservation from vegetative tissue of wild *Manihot*.
- Study the cross-compatibility relationships (interspecific crosses between wild species and cultivated cassava.

Given what we know now about the challenges in each one of these objectives, this was a very ambitious set of ideas for a modest project. Nonetheless, this important early progress set the stage for subsequent successes in maintaining up to 33 wild species in the genebank (including the two *M. esculenta* wild sub-species *flabellifolia* and *peruviana)*.

Accessions are currently held as *in vitro* cultures (Table S4), and many of these are being established as part of the security backup system with AGROSAVIA in Colombia. Many are also duplicated as *bonsai* plants in a greenhouse at CIAT. Seed conservation for long term storage, with a pool of seeds that represents the alleles of a population, and based on on-going reliable seed production, remains a goal yet to accomplished.

6.8. Genetic Stability In Vitro

In addition to the capacity for continual secure regeneration over many subculturing generations (*in perpetuity* conservation), long term genetic integrity is also fundamental to an effective *in vitro* system. This parameter has been a concern addressed from the very early days of establishment of the *in vitro* genebank, with increasingly sophisticated tools over time. Early trials compared accessions kept continually in the field with those that progressed through multiple cycles of *in vitro* culture, with no evident morphological differences (CIAT Annual Reports). Angel et al. [45] were first to test whether longer-term *in vitro* storage of cassava germplasm (10 years) caused genetic changes detectable at the DNA level, based on RFLPs and RAPDs. No DNA rearrangements or polymorphisms were detected in plants retrieved from *in vitro* storage. They concluded that cassava germplasm can be safely conserved *in vitro* for long periods without compromising genetic integrity. Mafla et al. [46] also evaluated genetic stability of six accessions after 20 months of slow growth

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storage in medium supplemented with silver nitrate. The evaluations – morphological (20 descriptors), biochemical (profiles of 15 isozyme systems involving 20 genes) and molecular (AFLP fingerprints) – confirmed genetic stability of in vitro plants over this relatively short time frame. Nonetheless, molecular tools have advanced logarithmically since the mid-1990s, and a renewed look at *in vitro* genetic stability is warranted.

6.9. Genetic Diversity Lost Over Time

Safekeeping of a collection implies an obligation to monitor and document losses, assess the reasons for those losses, and recommend steps for improvement. Losses of accessions, at some level, are a normal part of what nearly every genebank experiences. In general, clonal collections represent greater levels of risk for loss – brought about by factors such as: 1) greater exposure to variables in the external environment (field); 2) the need for more frequent renewal as compared to seeds in cold storage (field and *in vitro*); 3) greater risks of pathogen infection and transfer via cloning (field and *in vitro*); 4) an artificial growth environment (*in vitro*) that is not uniformly suitable for all accessions; or 5) sensitivity to disruptions in laboratory security and stability.

Table 6 shows estimated cassava accession losses since year of original collection, from each country of origin. Not much detail is available for causes of losses for specific groups of materials. Where rather large losses are noted – especially Colombia, Ecuador, Panama, Peru and Puerto Rico – disease issues during the quarantine phase of introduction seem to be most notable. These were usually situations where disease symptoms were detected in the collected material after introduction into the quarantine process. The normal and appropriate response by quarantine officials was to destroy infected material. Introductions into quarantine were often formally registered into the genebank and assigned accession codes prior to actual pest or pathogen assessment, but in fact some of them never arrived at the CIAT facilities in Palmira.

Other significant losses occurred from variable and unsuitable soil conditions, especially highly saline areas. The CIAT headquarters station suffered initially from sectors of soils with high salinity. Within a few years after establishment of the germplasm collection (by the mid-1970s) managing this problem became better understood, by simply planting only in areas without identified salinity problems.

After the post-quarantine field establishment, complete accession losses from pests and diseases seem to have been low. The field collection was consistently monitored on a regular basis specifically to identify potential pest and disease issues. If risk levels for any problem rose to a threshold level, control measures were taken to prevent losses.

In vitro losses have been due to the convergence of several likely factors. These included bacterial or fungal contamination, loss of vigor due to environmental stress caused by infrastructure adjustments in 2011, low response of some accessions to *in vitro* treatments, and poor rooting especially for wild species. Recent annual reports of the Genetic Resources Program also highlight management challenges that contributed to *in vitro* losses. Notably, there was a subculturing backlog and some loss of accessions during the lockdowns of the COVID-19 pandemic in 2021 and amid the subsequent civil unrest in Colombia. There was limited access to the *in vitro* collection, which exacerbated contamination with both endophytic and other bacteria, besides the loss of plant vigor due to aging, causing some continuing losses.

Losses among the wild *Manihot* relatives have been strongly associated with the highly divergent adaptation of the different species to all forms of conservation (field, potted plants, *in vitro*). For example, there is an acute challenge of lack of continued root production under *in vitro* conditions. Consequently, level of losses is closely associated with species identity. Perhaps not surprisingly, the most successful have been accessions of the two *M. esculenta* subspecies, *flabellifolia* and *peruviana*.

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In 2011 CIAT reported 883 accessions of 33 wild species or subspecies *in vitro*.[7] However, following genebank renovations, and the collection's temporary relocation in 2011 there was a progressive decline in root production of wild species *in vitro* and increasing bacterial contamination. Since the field collection had already been eliminated, there was no copy available as a backup to replace accessions lost *in vitro*. The current 377 accessions (Table 5) from 22 species and 2 subspecies represent a loss of almost 52% compared to 2011 pre-relocation numbers.

Since 2021, CIAT began to categorize accessions for risk of loss and causes of loss *in vitro*. The primary indicators include the progressive decline in explant viability and physiological vigor, microbial contamination, and recalcitrance to *in vitro* conditions, especially in wild species. Transfer of the *in vitro* genebank to the new Future Seeds facility in 2024-25 was also demanding of resources and placed stress on the conservation integrity.

Given this history of losses – with about 25% of cassava accessions lost since their original introduction – what measures were taken or should be taken to recover any lost genetic diversity? The principal attempts at recovering lost material are reported for Peru, both through collection expeditions [7][8] and re-introduction from the Peruvian national cassava genebank. Collection expeditions are complex and costly, so funding is challenging for re-collection, except in the more extreme conditions of loss, or where there is strong evidence that alleles of high value could be retrieved. In comparison with the need to collect in areas not previously explored, re-collection in areas where only low or moderate loss occurred will probably continue to have a low priority. Comparison of genetic diversity between CIAT and national genebanks, especially from Brazil, can further help identify gaps in the collection.

Providing greater future security includes managing contamination, staying current on subculturing, and further research on the diverse culture demands of the wild species. The addition of a fully functional safety backup strategy, and future implementation of a cryo-collection, will help reduce losses to very low and acceptable levels. The genebank is now setting the stage for a future of greater stability in the Future Seeds facilities. The parallel bonsai conservation scheme (potted) plants, including the wild species, and the security backup arrangement with AGROSAVIA in La Selva facilities in Colombia further contribute to reduced threats of losses.

6.10. Managing the Error Rate in Accession Identification

An error in accession identification is generally not as serious as complete loss of an accession, i.e. the genetic value of the material remains the same for possible future use. However, such errors do decrease the value of an accession by potentially introducing confusion and follow-up errors of many types. In general, identification errors generated prior to complete bank genotyping [9] cannot readily be corrected, given the lack of a field collection as a reference for true-to-type confirmations. Typically, these errors are only identified if a well-known accession does not *look like it is supposed to look*, in the eyes of the professionals (often the plant breeders) after a period of regeneration either from the field or the *in vitro* collection. Since the environment can cause many phenotypic variations in cassava, generally only very distinctive variations of the more stable traits, such as those used for *characterization* (see Table S5), will support an error diagnosis. That said, there have been multiple examples, based on the authors' personal experiences, of errors identified in this way. Sometimes alternative sources to recover the original genotype are available, and sometimes they are not.

Germplasm conservation, especially of an annual, clonally propagated crop, has many steps in every renovation and conservation phase, each with the potential for introduction of human error in accession identification. Hypothetically, the error rate for an annually renewed clonal collection

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[7] While *flabellifolia* and *peruviana* are subspecies of *M. esculenta*, they are found only in the wild, and therefore listed here with the wild species rather than cultivated cassava, *M. esculenta*.

[8] Unfortunately, the materials re-collected by Salick et al. did not successfully pass through ICA quarantine in Bogota, and were ultimately not included in the CIAT collection.

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might be on the order of ten or more times that of a seed-based collection of orthodox seeds, where regeneration takes place only very infrequently.

With the field collection, for about the first decade after establishment, these multiple steps usually meant hand-writing a field or greenhouse label, hand-entering IDs in field or lab notebooks, and then typing of those notes by a secretary or specialized data transcriber for archiving and reporting.

Each of the following steps (among others) during the years of extensive manual information management allowed introduction of potential human errors:

Collection and introduction:

- Mistakenly collecting more than one clone as part of a variety designation and assigning them to a single accession number.
- Potential for misinterpretation or misunderstanding between collector and farmer/donor of a variety name or its characteristics. This may be especially acute in the case of indigenous languages.
- At the time of collection, labelling of stem bundles.
- Labelling of plants during quarantine.
- Developing laboratory notes during quarantine.
- Re-labelling of stem bundles for shipment to CIAT experiment station.
- Updating accession inventories by handwriting, typing or other manual entry form.
- Developing the fieldbook to include new introductions to the field collection.

Field conservation:

- Labelling of stem bundles from each plot at harvest.
- Chance of lost labels during transportation, treatment, replanting.
- Developing the field book for annual regeneration.
- Typing inventory for annual reporting and archiving purposes.

In vitro conservation:

- During initial culturing from the field collection:
    - Labelling of stem pieces in the field.
    - Labelling of pots in the greenhouse to produce shoots for meristem culture and registry in lab notebook.
    - Labelling of containers during processing of shoot tips, and meristem extraction and registry in lab notebook.
    - Labelling of test tubes for slow growth culture and registry in lab notebook.
    - Typing or digitizing any of the above information.
- During periodic regeneration (1 to 2 years):
    - Labelling of containers during subculturing processing and registry in lab notebook.
    - Labelling of new test tubes to begin new grown cycle and registry in lab notebooks.
    - Typing or digitizing any of the above information.

Estimation of past or current error rates is difficult, but at both field and laboratory level, there was continual attention to improving systems to reduce error rates. Most of these issues have been managed by moving toward barcode-enabled tracking and may further be improved in the future by RFID tags to ensure sample integrity *in vitro.* An effective documentation system is fundamental for ensuring data integrity, traceability, secure storage, and controlled access to information associated with each accession.

For several years, the field and *in vitro* cassava collections at CIAT were managed using an Oracle database (latest was V.7.0). The system recorded basic passport information, distribution records and micropropagation events. The system included barcode-based identification and mobile data capture tools. In 2016, a customized version of the GRIN-Global database was implemented, expanding the tracking of historical information and operational activities. The collection is currently transitioning

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to the GRIN-Global Community Edition (GGCE). This upgraded platform provides enhanced inventory control functionalities, enabling real-time tracking of germplasm movements across conservation workflows and precise identification of the physical location and status of each conservation unit.

Currently, accession passport data and associated characterization and evaluation information are publicly accessible through Genesys (https://www.genesys-pgr.org/), a global portal for plant genetic resources.

7. Characterization and Duplicate Identification

The classical terminology for describing genebank accessions has been *characterization* and *evaluation*. Although molecular data are not easily observable traits in the traditional sense, FAO and CGIAR genebank practice now treat genetic marker profiles as an integral extension of characterization. *Grower and consumer knowledge* (or *cultural information*) is generally considered a part of passport data, but was usually de-prioritized in early collections. Now, there is greater appreciation of that knowledge.

Long before genebanks were established, cassava farmers certainly recognized a broad array of color, shape, size and behavior traits that allowed them to distinguish among their varieties. Following from this knowledge, there also often evolved a perceived association between these easily observed traits and traits of importance in productivity, resistance, quality and others. For example, farmers might associate *purple petiole color* with good cooking quality if their best tasting varieties consistently had purple petioles. Farmers and processors sometimes associate high cyanogenic potential with good starch quality. Such associations may be strongly held but should be examined based on systematic research evidence.

While *characterization* and *evaluation* historically constitute two distinct ways of describing the genetic diversity within collections, in fact there is a continuum between the two categories – from highly heritable to low heritability, and from traits that appear to have no economic value for users, to those that are of fundamental importance.

7.1. Characterization Based on Morphological Traits

Cassava breeders and genebank managers have generally come to rely on basically the same key traits as farmers for distinguishing plants in the field. Although CIAT developed a basic set of characterization criteria soon after establishment of the field collection in the early 1970s, the descriptor list for cassava evolved modestly over time. IBPGR convened a group of experts in 1983 to formalize a recommended list. In 1995 cassava specialists from seven countries met in Cruz das Almas, Bahia, Brazil and updated the list, resulting in the publication by Fukuda and Guevara [47]. Fukuda et al. [48] compiled information that had evolved over time, jointly and in parallel between Embrapa/CNPMF in Brazil, CIAT and for the first time integrating input from Africa (Table S5).

Some of these descriptors do not fully meet the criteria for being *stable*, i.e. with little environmental influence on their expression. In fact, several of the traits suggested for scoring at harvest are clearly quantitative in nature, and in fact very influenced by environmental conditions. These include yield and yield components, root quality traits like starch or dry matter content, cyanogenic potential, and post-harvest deterioration. It is not quite clear why these traits are on the descriptor list; in standard practice, they should be viewed more as criteria for *evaluation*. The CIAT collection has been fully characterized, and these data are available in Genesys.

Cassava has never had the benefit of extensive morphological marker gene studies. Hershey and Ocampo [49] described eleven new, tentatively simply inherited traits, some of which became part of the descriptor package (Table S6). However, there is currently little interest in further exploring the classical genetics of crop descriptors since there is now the easy possibility of many thousands of DNA-based markers.

While morphological descriptors remain useful for a quick field comparison of materials, or to describe new varieties being released to farmers, they have never provided the level of confidence

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required to confirm duplicate accessions. Even where the characterization criteria for two clones fully match, this has not been considered sufficient evidence of clonality. Nonetheless, even with the use of molecular-based description, there is still the broad expectation that the verification of variety identity should include field-based morphological descriptors.

7.2. Revelations from Local Variety Names

Farmers almost always assign names to their landrace varieties. The integrity of these names within a household and community is critical for purposes of associating varieties with their uses in the production and food systems. Names often indicate:

- An identifying plant trait – especially shapes or colors of plant parts such as leaves, stems or roots.
- Origin (e.g. *Caucana*, *Llanera*, *Venezolana*, or *Palmireña*), especially if introduced from outside the farm or village.
- An honor to a respected person or the donor of the variety.
- Special features related to use or taste, such as exceptional *sweetness* or *bitterness*.
- A growth trait such as earliness, branching habit or height.

Of the 4406 landrace accessions that were registered with common names in 2023, 72% of those names are unique. However, names that were perhaps identical at the farmer level, may have minor spelling variations in the genebank registry. This is probably true for many names, but especially for those in a local language not familiar to the collectors. An extreme example seems to be from a collection expedition in Pasco province of Peru by Jan Salick and colleagues in 1986 [7]. Seven accessions were given the following names by the collectors: *Yapam, Ya'Pam, Yapamam, Ya'Pamam, Yapaman, Yapamon*, and *Yapamuen*. It is reasonable to hypothesize that some of these different spellings could be the result of slightly different ways that individual collectors heard the pronunciation of a given name.

Some of the most common local names across regions (English translations and number of repetitions in parentheses) are:

- *Algodona* (cottony) (27)
- *Amarilla, La Amarilla, Yuca Amarilla* (yellow) or *Yema de Huevo* (egg yolk) (68)
- *Blanca, La Blanca* or *Yuca Blanca* (white) (150)
- *Brava* or *Yuca Brava* (bitter) (26)

Interestingly, names rarely appear to derive from traits related to pest or disease resistance, or adaptation to soil, climate or cultivation practices. This lends some support to the hypothesis that *all* successful varieties will necessarily have basic adaptation to these biotic and abiotic conditions within the production environment where they were grown. Names would therefore not be determinative in distinguishing among varieties.

Some of the descriptive names assigned by farmers can certainly provide breeders with a clue about possible traits of interest for breeding. Names related to early maturity (*Seismesina* (six months); *Sietemesina* (seven months); or *Temprana*, *Tempranura*, *Tempranita* (early)) should be good candidates to prioritize for evaluation of root bulking patterns. *Yema de Huevo* and *Yuca Amarilla* will have yellow root flesh and should be candidates for high carotenoid content for biofortification breeding.

Apart from giving due regard to the donor-provided name, the genebank curator and breeder should rely on other criteria, especially thorough phenotyping, to confirm traits. Additionally, names have little value in the identification of duplicates – either to suggest that same names indicate duplicates or that different names necessarily indicate genetically distinct clones.

7.3. Characterization Based on Gene Products

Molecular tools evolved quickly, beginning about a decade after the establishment of the genebank, and have moved to the forefront for diversity analysis and duplicate identification. These tools are broadly grouped into those that measure differences in biochemical markers (*gene products*),

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and those that measure DNA sequence variations (Table S7). Some recent comprehensive reviews provide a more complete background, with hundreds of references for possible follow-up, for example [50–54].

7.3.1. Isozymes

Isozymes are enzymes that have the same basic biological function but differ slightly in their amino-acid sequences. Isozyme analysis was used already in the 1950s as one of the earliest molecular tools for assessing genetic differences. CIAT initiated cassava isozyme research in the 1980s based on the αβ-esterase system. At the time, it was perceived as a powerful advance toward precision variety identification and diversity analysis, and phylogeny and evolution studies. To function in these roles as markers, isozymes should be:

- **Polymorphic** – show variation among different cassava accessions.
- **Heritable** –passed on from parent to offspring without being affected by environmental factors.
- **Stable** – detected reliably and consistently in different tissues and stages of development.
- **Independent** – do not influence each other or other traits of interest.

After exploratory work, CIAT identified 12 isozyme systems with a good fit to these criteria [55]. These isozyme patterns are published as part of the cassava database available in Genesys.

Chavarriaga et al. [56] reported on a study of the core collection, where a total of 57 alleles were detected among the 12 isozyme systems, with an average of 4.75 alleles per system and a range of 2 to 9. The most polymorphic systems were EST, PGM, and PRX, which together accounted for 47% of the total variation. The least polymorphic systems were ACP, AAT, G6PDH, and TPI, which accounted for only 7% of the total variation.

7.3.2. Metabolomics

In the mid-2010s, CIAT began to tap into the promising results of metabolomics being used by the Paul Frazer laboratory at the Royal Holloway University of London [57]. These analyses were based on the generation of pan-metabolomes for root and leaf tissues to enable the identification of metabolic sectors underlying traits of interest. For example, tolerance to whiteflies was linked to cell-wall related phenylpropanoids or apocarotenoids in the leaves. In general, for the leaf metabolome there was a clear correlation with genotypic data, as would be hoped for in a diversity analysis. However, the analysis of the root metabolome did not reveal an association with adaptive or agronomic traits. The authors suggest that a greater in-depth study of the root metabolome could be important for linking selection criteria with consumer-preferred quality traits. In terms of genebank management, metabolomes appear to be somewhat less definitive for characterization, compared to DNA markers.

7.4. Characterization Based on DNA Markers

Genebanks are increasingly exploiting the rapidly evolving capacity to look more precisely at variations in DNA sequences among accessions. All environmental influences are eliminated, and the number of variants is potentially in the hundreds of thousands. DNA -based markers are useful, *inter alia*, for the following:

- Identifying duplicates
- Determining genetic distances between individuals or populations
- Taxonomy
- Developing hypotheses about evolution, domestication and early distribution
- Measuring genetic integrity under long term storage conditions (slow growth *in vitro* or cryopreservation)
- Correlating traits of interest with DNA variations to facilitate selection (genome-wide association analysis)
- Identifying heterotic groups to maximize genetic gain

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A detailed history of cassava genomic characterization is provided at https://phytozome-next.jgi.doe.gov/info/Mesculenta_v8_1.

7.5. Marker-Based Duplicate Identification and Implications for Accession Management

From the first days of establishment of the cassava germplasm collection, genebank managers understood that there would be duplicates among collected materials. The appearance of duplicates has straightforward explanations in most cases. Collectors working across many farms could not possibly be discriminating enough to recognize or to make judgements about collected varieties that may look very similar but could either be actual clonal duplicates or simply be very similar in morphological traits. Even within a given field, two plants of the same clone can look rather different, and farmers themselves might not distinguish varieties with accuracy. *Nominal duplication* could occur from labelling/tracking errors at field and/or *in vitro* conservation systems during decades of conservation efforts based on handwritten labels (as noted in the previous section). In these cases, the same code could be assigned even to very distinct accessions. The extent of either type of error is not currently quantified.

Based on review of passport and characterization data, and field observations, Hershey [15] estimated that 10-20% of CIAT’s collection could be duplicated accessions. Duplicates matter on several levels: they add costs to conservation and evaluation, introduce errors into estimates of genetic diversity, and increase the risks of introducing unwanted inbreeding into breeding systems.

At the farm level, *complete* or *true* duplicates (all base pairs on all chromosomes identical) come about in only one way: they derive from a single seed at some historical point in time, followed by generations of clonal propagation. But the inverse is not always true: not every plant derived from a single seed will be complete duplicates of each other. There may be introduction of somatic mutations over multiple clonal propagation cycles to create sub-clones. This is well-documented in clonally propagated crops like potato, especially in older varieties [58,59].

The technology for confirming clonal duplicates has developed slowly. Methods that rely on passport data or characterization simply do not, by themselves, confidently identify duplicates. None of the analyses applied up to 2024 had come close to providing the required level of confidence for elimination of duplicates broadly across the genebank accessions.

Carvajal et al. [9] analyzed 5302 accessions in CIAT’s cassava collection with SNP and SilicoDArT markers. Based on these marker patterns, about 52% of accessions demonstrated possible redundancy (or duplication), with a range from 2 to 87 accessions within clusters, while a total of 1567 (29.6% of total) accessions had no redundant accessions identified. Based on these analyses, the likely *minimum* number of unique accessions in the collection (from both redundant and non-redundant clusters) would be 2518. However, exact redundancy remains to be confirmed with higher density markers, ideally combined with field and laboratory comparisons of the most stable descriptors. This basic information will support a fully rational system for conservation, evaluation and use.

Table 7 shows data from 12 of the larger SNP/SilicoDArT redundant groups (from 20 to 86 landrace accessions per group). Some redundant varieties have broad geographical dispersal while others have remained more local. Groups with large numbers of tentative duplicates may be especially informative. Identical accessions (or differing only in a limited array of somaclonal variations) that have been collected across broad geographical areas were probably passed down over many generations because of their exceptional qualities for growers and consumers and traded across regions.

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Table 7. Redundancy groups identified by two molecular marker systems and categorized by region and country of origin. Larger groups per country are highlighted.

	SNP and SilicoDArT group codes, and the number of distinctly named landrace accessions that appear simultaneously in both groups[a]												
SNP:	**127**	**703**	**739**	**752**	**1182**	**2313**	**2443**	**2713**	**2729**	**2889**	**3094**	**4535**	
SilicoDArT:	**3139**	**517**	**1273**	**3217**	**4747**	**2459**	**4531**	**3924**	**3639**	**4480**	**3461**	**4313**	**Country Total**
South America													
Argentina			15			1							**16**
Brazil	8	2	9		1	10		1		1	1	3	**36**
Colombia	2		2	2	32	10	39	2	19	1	35	81	**225**
Ecuador	1							1		18	1	1	**22**
Paraguay			2			1							**3**
Peru	6			1								1	**8**
Venezuela	1	1		7		4		3		3	19		**38**
Subtotal:	**18**	**3**	**28**	**10**	**33**	**26**	**39**	**7**	**19**	**23**	**56**	**86**	**348**
Meso-America/Carib.													
Costa Rica	3	10	1	9		2		9	1				**35**
Cuba	2			1									**3**
Guatemala	1	24		2									**27**
Mexico				14							1		**15**
Panama				3				3		3	2		**11**
Puerto Rico				2									**2**
Salvador	3	3											**6**
Subtotal:	**9**	**37**	**1**	**31**	**0**	**2**	**0**	**12**	**1**	**3**	**3**	**0**	**99**
Asia/South Pacific													
Fiji	1												**1**
Indonesia	14										1		**15**
Malaysia		1											**1**
Thailand	1												**1**
Subtotal:	**16**	**1**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**1**	**0**	**18**
Total accessions:	**43**	**41**	**29**	**41**	**33**	**28**	**39**	**19**	**20**	**26**	**60**	**86**	**465**
Total countries:	**12**	**6**	**6**	**9**	**2**	**7**	**1**	**6**	**3**	**5**	**7**	**4**	**18**

[a] While the two marker systems strongly coincided in their grouping of accessions, small differences existed. Numbers indicated here include only accessions appearing together across both marker systems.

Source: Adapted from [9].

SNP/SilicoDArT group 127/3139 is especially notable for the fact that its varietal components were collected across 12 countries – broadly throughout the Americas as well as in Thailand, Indonesia and Fiji. Widespread distribution of specific varieties (or closely related varieties) offers both opportunity and caution to breeders. First, their value within the genebank seems obvious, in terms of a genotype having broad grower and consumer appeal (although phenotypic performance is not necessarily an indicator of breeding value). On the other hand, breeders need to be very aware of the possibility of the deleterious effects of inbreeding if crossing different accessions that are in fact genetic duplicates or near-duplicates.

In contrast to 127/3139, three groups – 4535/4313, 3094/3461 and 2443/4531 are large groups of almost exclusively Colombian origin. While these landraces are highly appreciated locally, either they were not extensively introduced to other countries, or they may have been introduced but failed to gain farmer adoption.

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There appear to be some regional differences in levels of redundancy (or uniqueness). Across eastern and western South America, the rates of potential duplication are rather similar: nearly 30% of accessions are unique in both areas. On the other hand, only 16% of accessions collected from Meso-America and the Caribbean are unique. This may be due to cassava's likely origin in South America, and the tradition of developing new varieties from seedlings which is reported to be more prevalent near the center of origin [12]. Ongoing comparative studies between CIAT and IITA genebank data will provide insights into possible examples of historical movement of varieties from the Americas to Africa as well.

8. The Core Collection as a Tool for More Effective Conservation, Evaluation and Use

8.1. Purposes and Procedures

By the second half of the 20th century, many genetic resources programs established or expanded *ex situ* collections, but breeders often gave low priority to broad-scale evaluations of less-*adapted* germplasm. The *core collection* concept addressed the interest in streamlining and prioritizing conservation and evaluation, especially in large collections. Originally conceived by Frankel [60], a core collection would represent: *with a minimum of repetitiveness, the genetic diversity of a crop species and its wild relatives*. These collections are normally 5-10% of the total.

The CIAT cassava core collection of 630 accessions was developed at a time (mid-1990s) when a reasonable level of agronomic evaluation existed for the collection, but only rudimentary molecular data were available [61]. Criteria for inclusion in the core were based on four major types of information. Within these types, accessions were randomly chosen for inclusion in the core, except where otherwise indicated:[9]

- **Base number of landrace accessions**. As a starting point, the accessions from each country that were known to be landraces were flagged as candidates for the core; accessions from most countries are highly represented by landraces. Based on somewhat subjective criteria, the number of landraces was adjusted by an estimated proportion of duplicates for each country.
- **Adjustments based on diversity of origins**. There are a few source countries that constitute most of the collection (Colombia, Brazil, Venezuela, Peru, Paraguay). But many countries with smaller representation in the bank should also be important sources of diversity. To give them appropriate representation, they were weighted more heavily in the core, i.e. inversely related to the country's collection size. This part of the core collection consists of 440 accessions (70% of total core).
- **Diversity of morphological characteristics**. A total of 100 accessions (16% of total) were chosen based on their inclusion in the *in vitro* pilot genebank, which had been selected during the early experimental phase of the *in vitro* bank development, based on multiple diversity criteria.
- **Diversity of alpha-beta-esterase banding patterns**. At the time of the core definition, the only available molecular classification was with the alpha-beta esterase system. Fifty-one accessions (8% of core) were selected based on diversity within this group.
- ***A priori* (non-random) selection based on predetermined criteria**. Based on multiple criteria of agronomic diversity and geographic origin (e.g. studies from the Cassava Biotechnology Network; landrace varieties of widespread use; and selection as elite clones (landraces or hybrids) by CIAT or IITA). This group includes 121 accessions (19% of core).

Table 8 shows representation of each country in the core, and on which criteria. More details are available in Hershey et al. [61].

Table 8. Basis for accessions selected for the CIAT cassava core collection. (Some accessions meet multiple criteria).

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[9] Because some accessions were included in multiple criteria, the sum of percentages is greater than 100.

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Geographic origin or group	Base no. of accessions at time of core formation	Number of accessions selected based on various criteria				
		Origins	Morphological diversity	Diversity of esterase isozymes	*A priori* selection	Final number in core from each group[a]
Argentina	16	2	4	0	3	8
Bolivia	3	1	2	0	3	3
Brazil	1637	110	13	15	20	101
China	2	1	0	0	2	2
Colombia	1907	111	15	13	14	142
Costa Rica	147	9	7	5	4	23
Cuba	74	10	5	1	2	18
Dominican Rep.	5	2	2	0	4	9
Ecuador	117	25	6	0	4	32
Fiji	6	1	0	0	2	2
Guatemala	91	8	6	0	2	15
Indonesia	51	1	0	2	5	7
Malaysia	68	8	0	1	6	15
Mexico	100	14	6	0	2	20
Panama	42	6	2	0	2	9
Paraguay	192	25	8	3	7	40
Peru	405	63	10	3	2	76
Philippines	6	1	0	0	2	2
Puerto Rico	15	1	2	0	4	7
Thailand	8	0	0	0	4	4
USA	9	0	0	0	4	4
Venezuela	240	41	9	3	3	55
CIAT hybrids	317	0	3	5	27	33
IITA hybrids	19	0	0	0	3	3
Total	**5477**	**440**	**100**	**51**	**121**	**630**

[a] Since original development of the core collection one accession has been lost from the *in vitro* collection.

8.2. Genebank Management Implications

Establishment of the core had a series of implications for genebank management at CIAT. Defining the core helped highlight some of the gaps in the collection. For several countries with likely moderate to high genetic diversity, there are few accessions, which created somewhat of a challenge for how these countries should be represented and balanced against others in the core. Examples are Bolivia, Dominican Republic and Puerto Rico. Some countries with probable high cassava diversity currently have no representation in the core, such as the Guianas.

The main conservation implication of the core collection to date has been the prioritization for cryopreservation. After development of cryo-techniques with good recovery results, CIAT proceeded to first apply those protocols to the core.

From the time of core establishment, several projects have prioritized it to gain insights into genetic diversity of the whole collection. Among the first of these was the evaluation of several root and leaf quality traits [62]. These traits are based on time-consuming lab analyses, so evaluation of the core was a logical starting point. Over subsequent years, the core has also been prioritized as an effective means to estimate total diversity for several pest and disease resistance evaluations.

Rare or geographically restricted alleles may not be represented in the core collection. We cannot necessarily assume that a trait does not exist in the whole collection if it does not appear in the core. As molecular tools become more precise and more cost-effective, there will be greater possibility to

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extend searches beyond the core to the entire collection for rare alleles, without the initial high costs of field evaluation.

Elias et al. [63], based on molecular markers, concluded that the CIAT core collection poorly represents the Amazon and Orinoco basins and the diversity of indigenous communities. This premise could certainly be a concern, and merits further study. However, only 59 accessions from a total of about 907 accessions from indigenous communities in Amazon and Orinoco basins of Colombia and Peru were included and analyzed for this study by Elias et al. That representation is perhaps too small to conclude broadly that the core does not adequately represent the diversity of these regions.

8.3. Sharing the CIAT Core Collection Internationally

A report of the *Manihot* Genetic Resources Network [64], suggested sending the CIAT core collection to Brazil. However, Brazil was more focused on creating a core collection from their own substantial collection and therefore chose not to receive the one from CIAT. Longer-term plans call for Africa to also receive this sub-collection, when introduction of vegetative material is more readily accepted.

In 2001, CIAT and the Thailand Department of Agriculture (DOA) jointly agreed to introduce the core collection to the Rayong Research Center of the DOA. As an indication of the complexity of international shipments of clonal cassava material, even for an advanced technology country like Thailand, this introduction of 628 accessions took five years to complete – from 2002 to 2007 – and was done in 14 *in vitro* batches. Nearly all the clones were successfully passed through quarantine, established in the field and evaluated for multiple traits. The DOA then characterized these accessions and evaluated them for an array of quality traits. The characterization data are available on Cassavabase.

Part of the core collection was also introduced to Vietnam and to Laos, with a main goal of evaluating these materials for possible resistance to cassava mosaic disease (after the reported presence of the causal virus in SE Asia in 2015) and to cassava witches broom disease. Three shipments from CIAT, totaling 232 accessions from the core, were sent in 2020 and 2021. Mortality in the first two shipments was high, and final overall survival was only 131 accessions, or 21% of the core. In this sense, the group of materials being evaluated in Vietnam could be considered a *mini-core*, but not one based on specific criteria. At this writing, the evaluation in Vietnam is underway, especially for CMD resistance. The Introduction to Laos was less successful and next steps are being planned (J. Newby and Thuy C., personal communication).

In 2024, 185 accessions from the core collection were distributed to the Chinese Academy of Tropical Agricultural Sciences (CATAS) for the purpose of evaluation and possible use in breeding (along with 256 landrace accessions and hybrids not in the core).

8.4. The Future of Cassava Core Collections

CIAT understood from the outset that the criteria for defining the original core collection in 1994 were far from ideal, in that they were based on somewhat subjective and low-precision assessments of genetic diversity. Nonetheless, there is a certain *historical momentum* that has occurred with this set of clones. More than 30 years after definition of a core collection that was based on rather rudimentary criteria, the varietal components remain now just as they originally were selected. As more discriminating data become available, there are increasing arguments to redefine the core. For example, Santos et al. [65], based on the Brazilian cassava collection, provide suggestions on how to integrate morphological and agronomic traits, along with molecular markers to best define a core.

The ideal core collection would be a global one, including material from multiple collections around the world, duplicated and accessible in several institutions. Currently, the exchange of vegetative material between Africa and the Americas significantly limits this option, but it can be an eventual goal.

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9. Adding Value to Cassava Genetic Resources Through Their Use in Variety Development[10]

9.1. General Principles

Over its 50-year history, use of the CIAT cassava collection has largely focused on the original purpose described by CIAT's founders in 1969: *as a source of genes to improve cassava traits of grower and consumer interest, through selection and breeding*. This has involved a continual learning and innovation process for genebank managers, breeders and others who aim to understand and apply appropriate criteria for variety acceptance and adoption. Hershey [66] provides a broad overview of the process and progress in cassava breeding, including a review of the use of genetic resources.

The value of a crop germplasm collection is generally measured through its *use* as a global public good – past, present and future – not as a static museum display. From this perspective, the CIAT cassava collection has convincingly proven its value, and promises a high likelihood of continuing to do so. Understanding the appropriate balance of emphasis to be allocated to germplasm, for different purposes, is an ongoing evolutionary process for research planners.

Cassava germplasm collection by CIAT, beginning in the late 1960s, coincided generally with the establishment of several national breeding programs around the world, and renewal of some existing ones. For most of them, there were no bred varieties available. Breeders had no option but to build from a base of landraces. Fifty years later, this situation and this decision process about use of landraces from genebanks provide many alternative options. There are six main steps in the pathway of extracting value from existing genebanks to create impact through new varieties:

1) Gaining knowledge about traits of value, especially from end-users, that contribute to breeding program goals.
2) Distributing accessions with desired traits, or their progeny, to partners.
3) Incorporating target traits from the collection into candidate varieties, usually over generations of recurrent selection, but more recently through gene editing options.
4) Full testing over years and locations representative of client farmers, and with consumers.
5) Varietal release, multiplication, distribution – according to country norms and protocols.
6) Farmer adoption at scale, driven ultimately by consumer demand.

9.2. Local and International Access and Use System for the Genebank Accessions

Access to genebank accessions for users outside of Colombia involves a complex system of infrastructure, technical capacity, institutional support, and an appropriate set of goals for their use. Most of the cassava genebank accessions fall under the Multilateral System of the International Treaty on Plant Genetic Resources for Food and Agriculture (ITPGRFA). Access to the germplasm is regulated by the Standard Material Transfer Agreement (SMTA) for the purpose of research, breeding and training for food and agriculture. Legally, accessions that are part of the Multilateral System are fully available for sharing and free use for all signatories of the Treaty. In practical terms, not all accessions are always available, due to conservation considerations such as ongoing pathogen cleaning, renovation or other temporary operational issues. The Genesys database is continuously updated to reflect availability of accessions for shipment.

9.3. Distribution of Landraces and Their Hybrid Derivatives to Partners

Sharing alleles of value in the germplasm collection with partners and other interested entities is one of the genebank's core activities. This happens in several ways, sometimes as *in vitro* cultures of genebank accessions, but most commonly in indirect form, as hybrid seed that includes landrace varieties in the pedigrees. The genetic components of the collection have been shared through thousands of *in vitro* cultures and hundreds of thousands of seeds over the past 50 years.

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[10] Greater details about exploiting value of the cassava germplasm collection are covered in Part II of this series and are presented here as an introduction only.

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Figure S2 summarizes the history of *in vitro* shipments from 1979 to 2025 – a total of 30,626 *in vitro* samples to CIAT users and 26,516 to non-CIAT users. Outside of CIAT, main users were partners in National Agricultural Research Systems, at 7,831 samples. Around the year 2000, distribution accelerated when the collection was certified against diseases of quarantine importance.

The main purposes of external germplasm requests were direct evaluation of accessions for their value *per se* or for breeding, basic research (e.g. cryopreservation, embryogenesis, genomics and gene editing), and training. Some of the largest shipments were for the purpose of introducing the core collection to Thailand and Lao PDR.

Two accessions were distributed more than 200 times: the landrace variety COL 1505 and the CIAT hybrid, CM 523-7. Another 17 accessions were distributed more than 100 times. CIAT projects received just over half of the distributed accessions, while external institutions and partners received 46%. Four shipments, to Peru, Paraguay, Cuba and Ecuador, were carried out to restore lost germplasm to countries of origin.

10. Summary: Adding Future Value Through More Complete Landrace Diversity, Conservation Security, and Knowledge

10.1. Broad Strategies for Future Accession Management and Use

The concept of *added value* ties together the multiple threads of history covered in this paper. The collection brings value to society especially by contributing toward improved traits in new varieties, with subsequent benefits for producers, processors and consumers. CIAT's multiple R&D partnerships around the world, and their connections to cassava users, are the main drivers for continuing benefits from the collection.

10.1.1. Collection and Consolidation of Genebank Accessions

Further collection seems fully warranted, and the means of establishing logical priorities are now at hand. Some of the gaps are already known based upon important areas of cassava diversity that have not been adequately covered (or not covered at all) by past collections, e.g. Guyana, French Guiana, Suriname and Bolivia[11]. The already-completed genotyping of the collection will allow a more sophisticated gap analysis as a reasonable second step to determine priorities. CIAT and IITA will together define patterns of diversity according to geographic origins, and from that, extrapolate areas needing further collection. Coordinated collection in Asia and Africa, especially of older landraces, will make important contributions to global knowledge and to sources of traits for breeding. This will be a long and complex process (perhaps in 15-20 years?), but with potentially high-value end products.

10.1.2. Conservation

Consolidating all landraces on a global basis into a unified collection, with security backup, can act both in support of conservation in perpetuity of cassava genetic resources, and their effective use toward improved varieties.

The principal bases for current cassava conservation are via slow growth *in vitro*, including security backups, and a parallel *bonsai* duplicate. Nonetheless, as a system looking toward conservation in perpetuity, additional security and cost savings are warranted. The fine-tuning of cryopreservation seems at hand, with the likelihood of being able to move the entire collection into a more secure, lower cost conservation system.

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[11] In September 2011, 24 accessions from Guyana were received in Colombia, but had to be discarded as they did not meet the sanitary standards required for release by ICA. As a result of this situation, an updated protocol was developed for the shipment of *in vitro* samples intended for introduction into the collection, aiming to improve handling conditions and ensure compliance with phytosanitary requirements.

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Towill and Walters [67] discussed the possibility of a *doomsday* cryo vault along the lines of the one for orthodox seeds at Svalbard, and in 2017 an international feasibility study of independent experts proposed such a vault for clonal crops [38]. In 2025, CGIAR introduced the Genebanks Accelerator as part of its new research portfolio, to modernize and expand the role of its global genebanks. It builds on decades of conservation work and positions genebanks not just as repositories of crop diversity, but as engines of innovation, resilience, and equitable access to genetic resources. In the case of clonal crops, inter-Center and partner collaboration in cryopreservation is a key initiative. CIP has recently inaugurated a CryoVault aimed at consolidating cryopreserved backups for several vegetatively propagated crops, including cassava.

The Crop Trust has made commitments to several crops, including beans at CIAT, for funding of conservation in perpetuity. A similar funding commitment for cassava will be a strategic investment in one of the world's most important crops.

A backup seedbank (botanical seeds), both at CIAT and in Svalbard could be contemplated. However, without a field-based collection currently at CIAT, generating those seeds (ideally, from self-pollination of each accession) would involve considerable cost and complexity. If seed production is to be accomplished, it would most likely be as an adjunct activity to some other initiative involving a field planting of the cassava collection.

Conservation of the wild *Manihot* species – *in vitro* (slow growth or cryo), as a *bonsai* planting, in the field and as seeds – is complex and difficult. Without their inclusion in Annex 1 of the International Treaty, their conservation remains at risk and new collection missions are more difficult. *In situ* conservation, while not generally a priority within the CGIAR system, will also be extremely important to protect the wild species in their broadly at-risk native environments.

10.1.3. Characterization and Evaluation

For characterization, focus now shifts to full analysis of genotyping results. An early application is projected to be for duplicate identification [9]. To the extent that this involves confirmation with side-by-side comparisons in the field, the full process is likely to involve several years. It is still too early to precisely determine a duplication level in the collection, but this will become progressively clearer.

The genotyping data can be used to verify the validity of the selection of accessions for the core collection. There will need to be some balance of weight given to any newly arising information about diversity that is over- or under-represented in the current core collection, versus the fact that the current core already has a long history of associated evaluations.

Data recovery and updating from some early evaluations (early 1970a) is an ongoing, slow process. Within a year or two, and after all reasonable efforts at recovery, CIAT should be able to close the books on this process, and assume that archival data not already discovered is unlikely to become available in the future.

Conventional field evaluation for standard agronomic and quality traits of the current genebank accessions will have limited continuing utility for breeding programs. If the IITA and CIAT collections are eventually merged, then field evaluation could involve a major investment of resources for cross-continental trait discovery.

10.1.4. Exchange and Use

Exchange and use of genebank accessions rely fundamentally on the assurance of pathogen-free samples. Viruses remain the key challenge. Diagnostics and cleaning are becoming progressively more precise, allowing quarantine agencies to open avenues for further exchange. On the other hand, greater precision in viral identification, or even viral RNA incorporated into plant genomes, has been a *double-edged sword*. On the one hand it supports quarantine agencies in their goal of reducing pathogen threats. On the other hand, the increasing ability to detect viruses or segments of viral RNA that does not present a quarantine threat can very much slow down and complicate the legitimate exchange of germplasm.

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Since about 40 years ago, the germplasm collection has been used mainly as a *second-tier* resource, after evaluation of breeding lines reveals lack of sufficient genetic diversity for target traits. If the breeder can access traits within improved lines, that is generally a more efficient pathway than the process of pre-breeding to bring those traits from landrace varieties. This is even more so the case for the wild species: recovery of traits from wild species into advanced breeding lines is slow and difficult, even with advanced breeding tools. However, there are some areas where full evaluation of the collection will continue to be justified, especially targeting newly arising pest or disease issues, fine-tuned quality traits, and biochemical traits such as for pharmaceuticals or biologicals.

Some breeders envision a day when casava varieties will be developed through an inbred-hybrid breeding system. This would allow taking full advantage of heterosis (maximized by crossing two fully homozygous lines). Additionally, it will allow much greater control by the breeder for trait integration into varieties that are already high performing in most traits. Development of an inbred-hybrid breeding system will need support from collection diversity analysis, and identification of heterotic groups.

10.2. Investment in the Future

The CIAT cassava collection has historically provided a very high return on investment in breeding. When the collection was established, very little breeding had been done on the crop. There were few bred varieties and an insignificant area planted to them – relative to total production area. The genetic gap between bred varieties and landraces was very small.

However, recommendation of landraces directly as new varieties was a short-lived process. Their use mainly as parents in breeding was already extensive within just a few years of the genebank establishment. Even in breeding, genetic gains attributable to continuing direct use of accessions as parents greatly declined from the 1990s forward. There were, however, key traits such as amylose-free (*waxy*) starch, and resistance to cassava mosaic disease and cassava brown streak disease that emerged from new evaluations in the 2000s. The collection has not been planted in the field for the past 20 years, and it has not undergone comprehensive evaluation for any traits since that time. There have only been ongoing evaluations from small subsets of the collection, especially focusing on the core collection.

The collection has held relatively steady numbers over about 25 years – in the 5,000 accession range for landrace varieties. The large burst in growth of Latin American materials during the initiation of collection in 1969/70 is not going to be repeated with new collections. However, it is reasonable to expect that some valuable new diversity can be identified and incorporated into the bank from the Americas. Much more significant gene bank growth would occur if the addition of African and Asian landraces was to become a reality. The process of introduction for both Africa and Asia would involve a multitude of science- and policy-based decisions and resources allocated, especially including quarantine protocols. This exchange among continents, preferably in both directions between CIAT and IITA, would open significant avenues of opportunity for collaboration in the secure conservation and effective use of a truly global collection of cassava genetic diversity.

10.3. Future Seeds–Pathways Forward for the Cassava Collection

CIAT's *Future Seeds* genebank facility is giving new life to the conservation, evaluation and use of beans, forages, cassava, possibly along with other species. The new complex, inaugurated in 2022, and fully functional since 2024, integrates leading edge conservation facilities with center-wide upstream and downstream research, along with partner training and collaboration, that ultimately provide sustainable benefits to farmers and consumers.

For cassava, Future Seeds offers greater security of conservation, emerging better knowledge of the landrace varieties that gave rise to the modern versions of this critical staple crop, and more possibilities to expand acquisition for a truly global collection. The genebank is aiming toward a fully cryopreserved cassava collection as a landmark step toward high-level long-term security. Integrating genomics information with field and lab experience will provide a further boost to fully

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exploiting the genebank for meeting demands from climate change, challenges to natural resources conservation, urbanization, mechanization and evolving consumer needs.

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References

1. Lynam J. and Byerlee D. (2017) Forever pioneers – CIAT: 50 years contributing to a sustainable food future… and counting. CIAT Publication No. 444. International Center for Tropical Agriculture (CIAT). Cali, Colombia. 140 p. (https://hdl.handle.net/10568/89043)
2. Schultze-Kraft, R. Peters, M., Wenzl, P. (2020) A historical appraisal of the tropical forages collection conserved at CIAT. Genetic Resources. 1. 51-68. 10.46265/genresj. (https://www.researchgate.net/publication/348088069_A_historical_appraisal_of_the_tropical_forages_collection_conserved_at_CIAT)
3. Debouck, D., Santaella, M. and Santos, L. G. (2021) History and impact of a bean (Phaseolus spp., Leguminosae, Phaseoleae) collection. Genetic Resources, 2(4), pp. 21–43. doi: 10.46265/genresj.WJEU8358.
4. Bellotti, A.C. (2001) Arthropod pests. In Hillocks, R.J. and A.C. Bellotti (eds.) Cassava: biology, production, and utilization. CABI Publishing, pp. 209-236.
5. Hillocks, R.J. and K. Wydra. 2002. In Hillocks, R.J. and A.C. Bellotti (eds.) Cassava: biology, production, and utilization. CABI Publishing, pp. 261-280.
6. Boster, J.S. (1984) Classification, cultivation, and selection in Aguaruna cultivars of *Manihot* esculenta (Euphorbiaceae). In: G. Prance and J. Kallunki, ed, Ethnobotany in the Neotropics. Advances Econ. Bot. 1: 34–47.
7. Salick, J., Cellinese, N., Knapp, S. (1997) Indigenous diversity of cassava: Generation, maintenance, use and loss among the Amuesha, Peruvian Upper Amazon. Economic Botany 51, 1: 6–19. (http://www.jstor.org/stable/4255913).
8. Duputie, A., Salick, J., Mckey, D. (2011) Evolutionary biogeography of *Manihot* (Euphorbiaceae), a rapidly radiating Neotropical genus restricted to dry environments. Journal of Biogeography 38(6), 1033-1043. https://doi.org/10.1111/j.1365-2699.2011.02474.x
9. Carvajal-Yepes, M., Ospina, J.A., Aranzales, E., Velez-Tobon, M., Correa Abondano, M., Manrique-Carpintero, N.C., Wenzl, P. (2024) Identifying genetically redundant accessions in the world's largest cassava collection. Front Plant Sci. 14:1338377. doi: 10.3389/fpls.2023.1338377.

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10. Thuy, C.T.L., Lopez-Lavalle, L.A.B., Vu, N.A., Hy, N.H., Nhan, P.T., Ceballos, H., Newby, J., Tung, N.B., Hien, N.T., Tuan, L.N., et al. (2021) Identifying new resistance to cassava mosaic disease and validating markers for the CMD2 locus. Agriculture 11, 829. (https://doi.org/10.3390/agriculture11090829)
11. Zhao, K., Long, E., Sanchez, F., Chavarriaga, P., and Monroe, J. G. (2026) Unlocking genetic diversity in Colombian cassava landraces for accelerated breeding. New Phytologist doi:10.1111/nph.70918
12. Kistler, L., de Oliveira Freitas, F., Gutaker, R. M., Maezumi, S. Y., Ramos-Madrigal, J., Simon, M. F., Mendoza F., J. M., Drovetski, S. V., Loiselle, H., de Oliveira, E. J., Vieira, E. A., Carvalho, L. J. C. B., Ellis Perez, M., Lin, A. T., Liu, H.-L., Miller, R., Przelomska, N. A. S., Ratan, A., Wales, N., … Allaby, R. G. (2025). Historic manioc genomes illuminate maintenance of diversity under long-lived clonal cultivation. Science, 387(6738), eadq0018. https://doi.org/10.1126/science.adq0018
13. Gulick, P., Hershey, C., Esquinas-Alcazar, J.T. (1983) Genetic Resources of Cassava and Wild Relatives. Rome: International Board for Plant Genetic Resources (IBPGR). 56 pp.
14. Mejia G., M. (1991) Diversidad de la yuca *Manihot esculenta* Crantz en Colombia. Vision Geographica-Cultural. Corporacion Colombiana para la Amazonia-Araucara. 165 pp. (https://repository.agrosavia.co/bitstream/handle/20.500.12324/32432/39430_23185.pdf?sequence=1&isAllowed=y)
15. Hershey, C.H. (2010) A Global Conservation Strategy for Cassava (*Manihot esculenta*) and Wild *Manihot* Species. The Crop Trust, Crop Strategy, Cassava. (https://www.croptrust.org/fileadmin/uploads/croptrust/Documents/Ex_Situ_Crop_Conservation_Strategies/Crop_Conservation_Strategy_Cassava.pdf)
16. Wang, H. L., Cui, X. Y., Wang, X. W., Liu, S. S., Zhang, Z. H., & Zhou, X. P. (2016) First Report of Sri Lankan cassava mosaic virus Infecting Cassava in Cambodia. Plant Disease, 100(5). DOI: 10.1094/PDIS-10-15-1228-PDN A
17. Frison, E.A. and Feliu, E. (eds.). (1991) FAO/IBPGR Technical Guidelines for the Safe Movement of Cassava Germplasm. Food and Agriculture Organization of the United Nations, Rome/International Board for Plant Genetic Resources, Rome. https://cgspace.cgiar.org/server/api/core/bitstreams/dac36560-4c12-4351-829b-c60b6641994a/content
18. Elias, M., Panaud, O., Robert, T. (2000) Assessment of genetic variability in a traditional cassava (*Manihot esculenta* Crantz) farming system, using AFLP markers. Heredity 85:219-30.
19. Peña-Venegas, C., Stomph, T., Verschoor, G., Lopez-Lavalle, L.A., Struik, P. (2014) Differences in manioc diversity among five ethnic groups of the Colombian Amazon. Diversity 6:792-826.
20. Floro, V.O., Labarta, R.A., Becerra López-Lavalle, L.A., Martinez, J.M., Ovalle, T.M. (2018) Household determinants of the adoption of improved cassava varieties using DNA fingerprinting to identify varieties in farmer fields: A case study in Colombia. Journal of Agricultural Economics 69:518-36. DOI: 10.1111/1477-9552.12247.
21. Ocampo, J., Ovalle, T., Labarta, R., Le, D.P., de Haan, S., Vu, N.A., Kha, L.Q., Becerra Lopez-Lavalle, L.A. (2022) DNA fingerprinting reveals varietal composition of Vietnamese cassava germplasm (*Manihot esculenta* Crantz) from farmers' field and genebank collections. Plant Mol Biol. 109(3):215-232. doi: 10.1007/s11103-021-01124-0.
22. Nassar, N.M.A. (2006) Cassava genetic resources: Wild species and indigenous cultivars and their utilization for breeding of the crop. In: First International Meeting on Cassava Breeding, Biotechnology and Ecology; Ortiz, R., Nassar, N.M.A. (Eds.) Universidade de Brasilia: Brasilia, Brazil, pp. 5–31.
23. Rogers, D., Appan, S. (1973) *Manihot* and *Manihotoides* (Euphorbiaceae). A computer assisted study. Flora Neotropica Monograph 13: 1–272.
24. Bertram, R. (1993) Application of molecular techniques to genetic resources of Cassava (*Manihot esculenta* Crantz - Euphorbiaceae): interspecific evolutionary relationships and intraspecific characterization. Thesis Dissertation, University of Maryland at College Park, USA.
25. Allem, A.C. (1994) The origin of *Manihot esculenta* Crantz (Euphorbiaceae). Genet. Resour. Crop Evol. 41, 133–150.
26. Cuervo-Ibañez, M.; Niño Jimenez, D.P.; Aranzales, E.; Velez, M.; Martinez Vivas, A.M.; Wenzl, P. (2023) Phytosanitary evaluation of the *in vitro* cassava collection (*Manihot esculenta* Crantz): Collection history and

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phytosanitary evaluation. Poster presented at the 12th International Congress of Plant Pathology. 20-25 August 2023, Lyon, France. [Poster ID: P3.7-012] 1 p. https://hdl.handle.net/10568/132762

27. Carvajal-Yepes, M., Olaya, C., Lozano, I., Cuervo, M., Castaño, M., Cuellar, W.J. (2014) Unraveling complex viral infections in cassava (*Manihot esculenta* Crantz) from Colombia. Virus Res. 186:76-86. doi: 10.1016/j.virusres.2013.12.011.
28. Jimenez, J., Caicedo, S., Pardo, J.M., Gil-Ordóñez, A., Alvarez-Quinto, R., Mollov, D. and Cuellar, W.J. (2024) Single torradovirus infections explain the mysterious cassava frogskin disease in the Americas. Scientific Reports, 14(1): 29648. https://doi.org/10.1038/s41598-024-81142-2
29. Alvarez, E., Mejía, J.F., Llano, G.A., Loke, J.B., Calari, A., Duduk, B. and Bertaccini, A. (2009) Characterization of a phytoplasma associated with frogskin disease in cassava. Plant Dis. 93, 1139–1145.
30. Leiva, A.M., Pardo, J.M., Arinaitwe, W. et al. (2023) Ceratobasidium sp. is associated with cassava witches' broom disease, a re-emerging threat to cassava cultivation in Southeast Asia. Sci Rep 13, 22500. (https://doi.org/10.1038/s41598-023-49735-5)
31. Jaramillo, G. (2012) *Manihot* genetic resources at CIAT (Centro Internacional de Agricultura Tropical). In: Ospina, B. and Ceballos. Cassava in the Third Millennium: Modern production, processing, use and marketing systems, CIAT, Cali, Colombia. Pp. 321-341.
32. Kartha, K.K., Gamborg, O.L. (1975) Elimination of cassava mosaic disease by meristem culture. J. Phytopathol. 65:826-828.
33. Kartha, K.K., Gamborg, O.L., Constabel, F., Shyluk, J.P. (1974) Regeneration of cassava plants from apical meristems. Plant Science Letters 2(2):107-113. (https://doi.org/10.1016/0304-4211(74)90066-2).
34. Mafla B., G., Aranzales R., E., Cuervo I., Maritza and Debouck, D. (2010) Access and benefit-sharing from an international cassava collection kept in trust with the treaty [poster]. Centro Internacional de Agricultura Tropical (CIAT), Cali, CO. 1 p. https://www.slideshare.net/slideshow/accessbenefitsharingcassava-3903214/3903214
35. Panis, B., M., Van den Houwe (2020) I. Challenges and Prospects for the Conservation of Crop Genetic Resources in Field Genebanks in *In vitro* Collections and/or in Liquid Nitrogen. Plants 9, 1634. doi:10.3390/plants9121634
36. Escobar, R.H., Muñoz, L., Rios, A., Núñez, A., Tohme, J. (2014) Using a droplet-vitrification method to partially overcome the recalcitrance of cassava to cryo storage. ISHS Acta Horticulturae 1039: II International Symposium on Plant Cryopreservation. DOI:10.17660/ActaHortic.2014.1039.29
37. Escobar, R.H. (2005) Aspectos logísticos de manejo y determinación de la estabilidad genética de materiales crioconservados de yuca (*Manihot esculenta* Crantz). Tesis de maestría. Palmira, CO, Universidad Nacional de Colombia, sede Palmira. 99 p.
38. Acker, J.P., Adkins, S., Alves, A., Horna, D. and Toll, J. (2017) Feasibility study for a safety back-up cryopreservation facility. Independent expert report: July 2017. Rome (Italy): Bioversity International. 100p.
39. Niño-Jimenez, D.P., Aranzales, E., Erazo, J. C., López, J., Vélez, M. (2016) The Bonsai as an alternative safety duplication system of the world cassava collection preserved at CIAT. Centro Internacional de Agricultura Tropical (CIAT), Cali. CO. 1 p. (Poster presentado en el II Simposio de Recursos Fitogenéticos Neotropicales, 3 al 5 de Noviembre del 2.016. Universidad Nacional de Colombia sede Palmira. Valle del Cauca. Colombia). https://hdl.handle.net/10568/78102
40. Marin, M.L., Mafla, G., Roca, W.M., Withers, L.A. (1990) Cryopreservation of cassava zygotic embryos and whole seeds in liquid nitrogen. Cryo-letters 11:257-264. (https://hdl.handle.net/10568/83253)
41. Mumford, P. M., and Grout, B. W. W. (1978) Germination and Liquid Nitrogen Storage of Cassava Seed. Annals of Botany, 42(1), 255–257. https://doi.org/10.1093/oxfordjournals.aob.a085447
42. Baguma, J.K., Mukasa, S.B., Nuwamanya, E., Alicai, T., Omongo, C., Hyde, P.T., Setter, T.L., Ochwo-Ssemakula, M., Esuma, W., Kanaabi, M., Iragaba, P., Baguma, Y., Kawuki, R.S. (2023) Flowering and fruit-set in cassava under extended red-light photoperiod supplemented with plant-growth regulators and pruning. BMC Plant Biol. 23(1):335. doi: 10.1186/s12870-023-04349-x.
43. Pineda, M., Yu, B., Tian, Y., Morante, N., Salazar, S., Hyde, P., Setter, T., Ceballos, H. (2020) Effect of Pruning Young Branches on Fruit and Seed Set in Cassava. Front. Plant Sci., Sec. Plant Breeding 11, 1107. (https://doi.org/10.3389/fpls.2020.01107)

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44. Chávez, R., Roca, W. M., Arias Garzón, D., Withers, L. A., Williams, T. (1988) Establishment and operation of a pilot *in vitro* active genebank of cassava. Centro Internacional de Agricultura Tropical (CIAT), Cali, CO. 7 p. https://hdl.handle.net/10568/71310
45. Angel, F., Barney, V.E., Tohme, J., and Roca, W.M. (1996) Stability of cassava plants at the DNA level after retrieval from 10 years of *in vitro* storage. Euphytica 90:307-13. DOI: 10.1007/ BF00027481.
46. Mafla, G., Roa, J.C., Ocampo, C.H., Gallego, G., Jaramillo, G., Debouck, D.G. (2004) Efficacy of silver nitrate for slow growth conservation of cassava (*Manihot esculenta* Crantz). Determination of viability and genetic stability. Sixth International Scientific Meeting of the Cassava Biotechnology Network. CIAT, Cali, Colombia, 8-14 March 2004. http://ciat-library.ciat.cgiar.org/Articulos_CIAT/CBN-VI%20(Version%20Final).pdf
47. Fukuda, W.M.G.; Guevara, C.L. (1998) Descritores morfológicos e agronômicos para a caracterização de mandioca (*Manihot esculenta* Crantz). Embrapa, Cruz das Almas, BA, Brasil. 38p.
48. Fukuda, W.M.G., Guevara, C., Kawuki, R., Ferguson, M.E. (2010) Selected Morphological and Agronomic Descriptors for the Characterization of Cassava. Ibadan, Nigeria: IITA.
49. Hershey, C.H. Ocampo N., C.H. (1989) New marker genes found in cassava. Cassava Newsletter (CIAT). 13(1):1-5. (https://hdl.handle.net/10568/88664)
50. Amelework, A.B., Bairu, M.W. (2022) Advances in Genetic Analysis and Breeding of Cassava (*Manihot esculenta* Crantz): A Review. Plants 11, 1617. (https://doi.org/ 10.3390/plants11121617)
51. Becerra Lopez-Lavalle, L.A. (2017) Molecular approaches in cassava breeding. In: Hershey C, editor. Achieving Sustainable Cultivation of Cassava Volume 2 Cultivation techniques. Cambridge, UK: Burleigh Dodds Science Publishing Limited.
52. Becerra Lopez-Lavalle, L.A., Bohorquez-Chaux, A. and Zhang, X. (2021) Identification of Cassava Varieties in Ex-Situ Collections and Global Farmer's Fields: An Update from 1990 to 2020. In: Frediansyah, A., editor. Cassava – Biology, Production and Use.
53. Ferguson, M., Rabbi, I., Kim, DJ. et al. (2012) Molecular markers and their application to cassava breeding: Past, present and future. Tropical Plant Biol. 5, 95–109. (https://doi.org/10.1007/s12042-011-9087-0)
54. Ferguson, M.E., Shah, T., Kulakow, P., Ceballos, H. (2019) A global overview of cassava genetic diversity. PLOS ONE14:e0224763. DOI: 10.1371/journal.pone.0224763.
55. Ocampo, C., Hershey, C.H., Iglesias, C., Iwanaga, M. (1992) Esterase isozyme fingerprinting of the cassava germplasm collection held at CIAT. In: Roca, W., Thro, A.M., editors. First International Scientific Meeting Cassava Biotechnology Network. Cartagena de Indias. Colombia: CIAT, p. 81-89.
56. Chavarriaga-Aguirre, P., Maya, M.M., Tohme, J. et al. (1999) Using microsatellites, isozymes and AFLPs to evaluate genetic diversity and redundancy in the cassava core collection and to assess the usefulness of DNA-based markers to maintain germplasm collections. Molecular Breeding 5, 263–273. (https://doi.org/10.1023/A:1009627231450)
57. Perez-Fons, L., Ovalle, T.M., Drapal, M., Ospina, M.A., Gkanogiannis, A., Bohorquez-Chaux, A, Becerra Lopez-Lavalle, L.A, David Fraser, P.D. (2023) Integrated genetic and metabolic characterization of Latin American cassava (*Manihot esculenta*) germplasm. Plant Physiology 192: 2672–2686. (https://doi.org/10.1093/plphys/kiad269)
58. Amundson, K. R. (2021). Haploid Induction and Somatic Mutations of Potato. Doctoral dissertation, University of California, Davis. https://escholarship.org/uc/item/8nk358tm
59. Clot, C. R., van der Hulst, R. G. M., and van Eck, H. J. (2025). Resolving a century-old enigma: potato 'Bolters' originate from instability of the StCDF1.3 allele. Theoretical and Applied Genetics, 138, Article 245. https://doi.org/10.1007/s00122-025-05030-7
60. Frankel, O.H. (1984) Genetic Perspectives of Germplasm Conservation. In: Arber, W.K., Llimensee, K., Peacock, W.J. and Stralinger, P., Eds., Genetic Manipulation: Impact on Man and Society, Cambridge University Press, Cambridge, 161-170.
61. Hershey, C.H.; Iglesias, C., Iwanaga, M., Tohme, J. (1994) Definition of a core collection for cassava. In: Meeting of the International Network for Cassava Genetic Resources (1, 1992, Cali, Colombia). International network for cassava genetic resources: Report. International Plant Genetic Resources Institute (IPGRI), Rome, IT. p. 145-156. (International crop network series 10). (https://hdl.handle.net/10568/55840)

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62. Wheatley, C.C. (1993) In: CIAT Cassava Program Report, 1987–1989: Cassava Utilization, 1989 (CIAT Working Document No 91). Centro Internacional de Agricultura Tropical, Cali, Colombia, 1993, pp. 567–568.
63. Elias, M., Mühlen, G., McKey, D., Roa, C., Tohme, J. (2004) Genetic diversity of traditional South American landraces of cassava (*Manihot esculenta* Crantz): an analysis using microsatellites. Economic Botany 58(2):242-256. DOI:10.1663/0013-0001
64. IPGRI (1994) International Network for Cassava Genetic Resources: report of the first meeting of the International Network for Cassava Genetic Resources / organized by CIAT, IITA and IBPGR and held at CIAT, Cali, Colombia, 18-23 August, 1992.
65. Santos, C.C. dos, Andrade, L.R.B. de, Carmo, C.D. dos, Oliveira E.J. de (2023) Development of cassava core collections based on morphological and agronomic traits and SNPS markers. Front. Plant Sci. 14:1250205. doi: 10.3389/fpls.2023.1250205
66. Hershey, C.H. (2020) Cassava genetic improvement: Theory and practice. Cali (Colombia): International Center for Tropical Agriculture. 443 p. (https://hdl.handle.net/10568/110397).
67. Towill, L.E., & Walters, C. (2000) Cryopreservation of germplasm for conservation of genetic resources. In: Engelmann, F., & Takagi, H. (Eds.), Cryopreservation of Tropical Plant Germplasm: Current Research Progress and Application. IPGRI, Rome, Italy, pp. 39–52.

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