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Review

Cassava breeding: past, present and future

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ABSTRACT

Cassava is a remarkable crop with immense significance. Its role extends from being a key staple ensuring food security in Africa to serving as a competitive source for industrial starch production in Southeast Asia. The broad range of uses for cassava roots and leaves has led to a diverse set of breeding objectives. Varieties of cassava intended for starch and animal feed production require a few clearly defined traits. On the other hand, ethnic products for human consumption involve various root quality characteristics that remain poorly understood. Over the past three decades, investments in cassava breeding have increased significantly. Despite the rapid and successful integration of new technologies into breeding programs, significant knowledge gaps persist. The lack of critical protocols has limited the full potential of these technologies. Research progress in cassava, therefore, has been uneven: while genetic transformation and the development of the first molecular map occurred in the 1990s, the implementation of proper flowering control—a key breeding protocol—was only widely adopted by 2020. Cassava is one of the few major crops whose breeding relies on heterozygous progenitors, which has considerably hindered the impact of marker-assisted and genomic selections. This review outlines past achievements in cassava research, identifies critical research gaps, underscores the need for integrating conventional and advanced technologies, and emphasizes the importance of prioritizing impact-driven investments over technology-driven ones.

1. Introduction

Cassava (*Manihot esculenta* Crantz) is a perennial shrub typically cultivated as an annual crop. Alongside rice, maize, sugarcane, and bananas, it stands as one of the principal sources of energy in the diets for millions of people in tropical regions across the globe (FAO, 2024). Beyond its role as a staple food crop ensuring food security, cassava has emerged as an increasingly important raw material for industries involved in starch production, animal feed, and bioethanol. Remarkably, it ranks as the second most significant source of starch globally, following maize (Stapleton, 2012; Vilpoux and Junior, 2023).

Table 1 displays global cassava production metrics (FAOSTAT) for the latest five-year span (2019–2023), with Oceania's data omitted. The distribution of the cassava harvested area is predominantly in Africa at 80 %, Asia at 13 %, and the Americas at 7 %. Contrasting this, yield distributions vary significantly. Africa's average yield is considerably lower than the global mean and roughly one-third of Asia's. The Americas' yield is marginally above the global average, whereas Asia's yield is notably superior when compared with other regions.

Cassava is a remarkably resilient crop that thrives in marginal conditions where few other crops could survive (Burns et al., 2010; El-Sharkawy, 2012). Despite some misconceptions, cassava demonstrates a strong response to adequate agronomic practices (Howeler et al., 2013; Masunga et al., 2024), particularly to K fertilization (Chua et al., 2020). A significant proportion of cassava varieties exhibit drought tolerance (Alves and Setter, 2004; El-Sharkawy, 2004), can thrive in degraded soils (Howeler, 1992, 2001; Howeler et al., 1982), and display resistance to many prevalent diseases and pests (Bellotti, 2002; Hillocks and Wydra, 2002).

Moreover, the crop is naturally tolerant to acidic soils and offers the convenient flexibility of being harvestable at the farmers' discretion (Cock, 1982), depending on market conditions or household needs.

When cassava roots are predominantly sold to processing facilities for the production of dried chips, starch, or ethanol, the adoption of improved varieties and available cultural practices is remarkably high, resulting in high yields. Conversely, when cassava is grown for direct consumption at the household level or in local markets after artisanal processing, the adoption of new varieties is limited, leading to lower

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Table 1
World statistics of cassava roots production during the 2019–2023 period. Within parenthesis is the ratio between different regional parameters and the respective global data. Source: official or estimated data from FAOSTAT.

Region	Area harvested (million of ha)	Production (million of t)	Yield (t/ha)
Africa	**24.99 (0.80)**	**200.45 (0.63)**	**8.02 (0.78)**
Nigeria	9.88 (0.32)	56.92 (0.18)	5.76 (0.56)
Uganda	1.13 (0.04)	2.33 (0.01)	2,06 (0.20)
Americas	**2.03 (0.07)**	**26.64 (0.08)**	**13.13 (1.29)**
Brazil	1.20 (0.04)	18.07 (0.06)	15.03 (1.47)
Paraguay	0.18 (0.01)	3.12 (0.01)	17.25 (1.69)
Asia	**4.18 (0.13)**	**91.79 (0.29)**	**21.96 (2.15)**
Thailand	1.51 (0.05)	31.97 (0.10)	21.18 (2.07)
Cambodia	0.60 (0.02)	13.66 (0.04)	22.83 (2.23)
Global[a]	**31.20 (1.00)**	**318.88 (1.00)**	**10.22 (1.00)**

[a] Production of cassava in Oceania is negligible and has been omitted and in Europe non-existent.

yields (Ceballos et al., 2021).

The small-scale processing facilities commonly found in rural areas, especially for ethnic products, offer a distinct contrast to the large industrial plants (Johnson et al., 2003; Scott, 2021). While breeding objectives for dry chips, starch, and ethanol production are well-defined—centered on achieving high and consistent fresh root yield (FRY), high dry matter content (DMC), and upright plant architecture—defining objectives for cassava's ethnic uses, such as direct root consumption, presents a more nuanced challenge. These objectives vary significantly by region, often reflecting cultural and gender influences, and lack efficient tools for assessing preference-related traits. Moreover, there is still much to learn about the biochemical and genetic foundations of these quality attributes (Dufour et al., 2021; Thiele et al., 2021; Valle, 2021).

In conclusion, the cultivation of cassava is influenced by various factors, including processing methods and breeding objectives. While industrial facilities prioritize specific goals for commercial yields, artisanal methods in ethnic communities highlight the complexity of objectives for direct consumption. Despite challenges, cassava demonstrates resilience and adaptability to diverse conditions. Moving forward, an exploration of cassava's botanical origin, domestication, and cytological characteristics will provide valuable insights into its genetic diversity and evolutionary history, informing future approaches to breeding and cultivation.

2. Botanical origin, domestication and cytology

Cassava belongs to the Euphorbiaceae family. The 98 identified Manihot species (Rogers and Appan, 1973) evolved in the Americas, spanning from southern USA (*M. davisiae* Croizat, *M. walkerae* Croizat, *M. angustiloba* (Torr.) Müll.Arg.) to central Argentina (*M. anisophylla* (Griseb.) Müll.Arg and *M. grahamii* Hook). While many species are endemic to Brazil or surrounding countries in South America, a second center of diversity exists in Mexico and Central America.

The evolution of *M. anisophylla* and *M. grahamii* offers a glimpse into sympatric speciation. Both species are native to the central Córdoba province in Argentina, with overlapping geographic distributions. However, they occupy distinct ecological niches: *M. anisophylla* thrives in rock crevices along riverbanks, whereas *M. grahamii* prefers richer and deeper soils (see Fig. 1). Although the taxonomic analysis of Manihot species conducted by Rogers and Appan in 1973 provides valuable insights, an updated revision of the genus is now imperative.

The prevailing hypothesis suggests that cultivated cassava (*Manihot esculenta* Crantz) originated in South America (Allem, 2002; Isendahl, 2011; Olsen and Schaal, 1999, 2001; Nassar and Ortiz, 2008; Watling et al., 2018). However, the botanical origin of cassava remains unclear, and its ancestry is still uncertain. Several alternative theories have been proposed (Allem, 2002; Allem et al., 2001; Bertram, 1993; Bertram and Schaal, 1993; Nassar, 1978, 2000).

The domestication of cassava is estimated to have occurred at least 3000 years ago (Brown et al., 2013), although evidence suggests it likely

Fig. 1. Illustration of sympatric speciation. The geographic distribution of *M. anisophylla* (**A-B**) and *M. grahanii* (**C-D**) overlaps in Central Córdoba Province (Argentina). **E.** *M. esculenta*. *Source: H. Ceballos*.

happened even earlier (Watling et al., 2018). Archaeological findings related to vegetatively propagated crops are generally scarce, and cassava is no exception. However, remarkable ceramic artifacts from the Mochica Culture in Peru (dating back 2200 to 1200 years ago) already depict cassava roots (Fig. 2). It is important to note that the Mochica Culture emerged in an area distant from where cassava likely underwent domestication.

Analyses conducted during diakinesis and metaphase I consistently reveal the presence of 18 small and similar bivalents (Hahn et al., 1990; Wang et al., 2011). Consequently, cassava is considered a functional diploid. Indeed, during the introgression of the recessive amylose-free (waxy) mutation, the expected 3:1 segregation ratio could be confirmed (Aiemnaka et al., 2012). Some programs aim at the release of triploid clones (Hahn et al., 1990; Sreekumari et al., 1999), but this practice is not common.

All cytologically analyzed Manihot species exhibit 2n = 36 chromosomes (de Carvalho and Guerra, 2002; Jennings, 1963). Through comparisons of chromosome numbers across several species, it has been proposed that the genus Manihot could be an allotetraploid derived from the family's basic number, x = 9 (Jennings, 1963; Magoon et al., 1969). There is a remarkable cytological consistency within the genus, not only in terms of chromosome number but also in their small size and metacentric to submetacentric morphology (de Carvalho and Guerra, 2002; Magoon et al., 1969; Umanah and Hartmann, 1973). This uniformity accounts for the reported weak reproductive isolation barriers among Manihot species, and the high fertility observed across interspecific hybrids (Colombo et al., 2000; de Carvalho and Guerra, 2002; Jennings, 1963; Nassar and Freitas, 1997). The expected size of cassava genome is around 750–772 Mb (Kuon et al., 2019; Lyons et al., 2022).

Cassava cultivation was widespread during pre-Columbian times. In the 1500s, the Portuguese introduced the crop to West Africa, where it rapidly became popular because of its resilience, ease of cultivation, and versatility. Subsequently, cassava spread eastward and eventually reached Asia, where it was further disseminated by the Spanish, notably in the Philippines.

Moving from its cytogenetic traits and historical spread, the next section will delve into cassava's varied roles in food and industry, examining its impact on economies and its growing presence in global markets. We will look at cassava's enduring presence in traditional diets, its critical contribution to food security, and its innovative uses in commercial sectors, underlining cassava's evolution from a local staple to a globally significant crop.

3. Utilization of cassava and markets

The storage roots of cassava typically contain around 35 % DMC, with approximately 75–85 % of this dry matter comprising starch (Rickard et al., 1991; Sánchez et al., 2009). Given the low concentrations of proteins and oil/fat in cassava roots, the starch is readily extractable and of excellent quality (Ceballos et al., 2007). Consequently, starch represents the primary product of the crop. This starch serves as an important energy source in the diets of millions of people, especially in Sub-Saharan Africa (Caccamisi, 2010). Moreover, it can be extracted and commercialized across a spectrum of facilities, from small and rudimentary to large and sophisticated. Additionally, roots can be dried for animal feed or ethanol production. The diverse uses of cassava roots lead to a wide range of root quality traits. It is useful to distinguish two distinctive uses of cassava as they define the breeding objectives that released varieties should have for farmers to adopt them (Ceballos et al., 2021; Johnson et al., 2003; Scott, 2021): **1)** Artisanal processing or direct household processing for human consumption; and **2)** Industrial production of starch, dried root chips for animal feeding and, more recently, ethanol.

The starchy root of cassava, while commercially valuable, is notoriously susceptible to rapid post-harvest physiological deterioration (PPD), leading to spoilage within days if not processed or consumed promptly. This deterioration stems from an oxidative process involving reactive oxygen species, with the extent of PPD positively linked to the root's dry matter content (DMC). Attempts to phenotype PPD are traditionally laborious and complex (An et al., 2024; Djabou et al., 2017; Reilly et al., 2003, 2007; Sánchez et al., 2013). Although high carotenoid levels seem to reduce PPD (Morante et al., 2010), these aspects provide limited insight into PPD's full expression. Emerging deep learning image-based analysis technologies present a promising solution, potentially streamlining the phenotyping of PPD with greater efficiency and accuracy.

3.1. Artisanal processing or direct household processing for human consumption

Cassava leaves and roots contain cyanogenic glucosides (Du et al., 1995; Mkumbira et al., 2003; Ospina et al., 2024; Wheatley and Chuzel, 1995), which can often reach toxic levels for human consumption. These glucosides are broken down by the enzyme linamarase, releasing the volatile poison hydrogen cyanide (HCN).

There are various products by which humans consume cassava roots. While all processing methods effectively release HCN, they may impart a bitter flavor that is often disliked by consumers. The simplest and most common method is boiling. Although boiling the roots is crucial for the food security of millions, little attention has been given to identifying and understanding the quality traits preferred by consumers, aside from the necessity of low HCN levels (Dufour et al., 2021, 2023).

Fig. 2. Illustration of ceramic artifacts from the Mochica Culture (Perú). **A**. Bottle depicting cassava roots. **B**. Vessel depicting a man with a cassava plant in his left arm (*Source: Museo Larco, Lima-Perú* (www.museolarco.org)*:A: ML 006643 and B:ML 009705*).

Hyperspectral imaging (HSI) and near-infrared spectroscopy (NIRs) are innovative techniques poised to improve our ability to quantify post-harvest quality traits, offering nuanced insights and precision in assessment. Recent efforts have highlighted DMC, mealiness, cooking time, and texture as key traits for boiled cassava (Meghar et al., 2024). However, high-throughput phenotyping for these traits is not yet available, except for the use of water absorption as an indirect method to predict cooking time (Tran et al., 2021).

There are various ethnic-related alternative methods of consuming cassava roots beyond boiling. Fermentation of the roots is frequently employed to soften them, a crucial practice in many regions across Africa and the Amazon basin where grinding the roots proves challenging due to limited access to machinery and electricity. There is a notable diversity in the ability of roots from different genotypes to soften through fermentation (Chijioke et al., 2024). Nonetheless, as of today, there are no biochemical or genetic tools available to elucidate the response to fermentation of cassava roots across different genotypes.

Garri, fufu, attiéké, and batons are examples of the diversity of popular products based on cassava, especially in West Africa. In the Americas, farinha and cassabe are prevalent in certain regions. Fermented cassava starch is utilized for baked products like pão de queijo, chipá, and pandebono, which are highly popular in South America. Cassava in Indonesia can be consumed in various forms such as krupuk, gaplek, tiwul, gathot, etc.

Breeding objectives for cassava aimed at human consumption present a complex tapestry of challenges, contrasting the more straightforward goals of industrial varieties. In response, multidisciplinary teams—encompassing breeders, social and food scientists, nutritionists, and gender experts—have recently made strides in crafting detailed target food product profiles (TFPPs) that resonate with diverse market demands and culinary traditions (Dufour et al., 2023). While consumer tastes are notably specific, varying widely across regions and genders, the scientific community is embracing this diversity, working to develop advanced high-throughput phenotyping tools that promise to capture this range of preferences more effectively. Although understanding the biochemical and genetic underpinnings of these preferences is still emerging, there is an optimistic push towards translating these complex preferences into clear, actionable indicators that will drive the next generation of cassava breeding.

The limited availability of reliable and affordable phenotyping tools partially explains why cassava varieties for human consumption often fail to satisfy consumer preferences, leading to limited adoption. This situation is particularly regrettable as it is precisely in such circumstances that technology aimed at enhancing people's livelihoods is most essential.

3.2. *Industrial production of starch, dried root chips for animal feeding and ethanol*

The requirements for industrial processing of cassava roots into starch, dried chips, or ethanol present a stark contrast to those for human consumption. These requirements remain consistent across regions and product profiles, with a relatively concise list: high and stable DMC, high and stable FRY, optimal harvest index and an erect plant architecture (Kawano, 2003; Kawano and Cock, 2005). Ensuring stable productivity implies resistance or tolerance to prevalent biotic and abiotic stresses. Root quality attributes such as cyanogenic potential hold minimal relevance for these markets. A reliable and rapid sprouting of stem cuttings upon planting is important but has not received adequate attention in research.

The adoption of improved varieties for the industrial processing of cassava also presents a notable contrast with those intended for human consumption, often surpassing 95 % of the planted area. In such scenarios, cassava has emerged as an important alternative for improving the livelihoods of resource-limited farmers (Ceballos et al., 2021).

Finally, cassava foliage has an excellent nutritional quality for animal and human consumption and offers great potential (Folorunso et al., 2006; Lancaster and Brooks, 1983; Yeoh and Chew, 1976). However, the concentration of HCN in the leaves is typically high, and it is crucial to employ proper processing methods to release it effectively. In spite of this potential, the use of foliage remains limited to certain regions of the world (Achidi et al., 2005; Aloys and Ming, 2006).

In conclusion, the diverse uses of cassava necessitate tailored breeding objectives to meet varied market demands. Challenges in artisanal processing include managing cyanogenic potential and addressing consumer preferences, hindered by time consuming phenotyping methods and dissection of genetic control of traits. Conversely, industrial applications prioritize stable dry matter content, erect plant architecture, and stress resistance, with less emphasis on root quality. The widespread adoption of improved varieties for industrial processing underscores cassava's role in improving farmers' livelihoods. Additionally, the potential of cassava foliage remains largely untapped due to processing challenges and limited utilization. These distinctions in breeding objectives and market demands segue into exploring implications for cassava breeding strategies.

4. Plant reproduction, architecture and their implication for breeding

Cassava can be propagated either from stems or botanical seeds (Alves, 2002). Stem propagation is the conventional method for commercial production, while seed propagation is essential for breeding purposes. It is important to note that the root itself is not a reproductive organ. During harvest, farmers typically remove and discard the young branches. Before harvesting the roots, the main stems are cut and bundled together in groups of approximately 50 stems each. The length of these stems can vary from 1 to 2 m depending on the cultivar and growing conditions.

Stems are stored under conditions that vary based on the region and environmental factors. When stored vertically, it is important to position the stems in an upward orientation to account for apical dominance. Typically, the storage period can last for up to two months. A fundamental requirement and, therefore, a significant breeding objective is for the planting material to have the ability to sprout quickly and vigorously after planting. Immediately before planting, farmers usually cut the stems into planting stakes or cuttings. Optimal stakes should ideally possess 5 to 7 nodes and be approximately 20 cm in length (Ceballos and Calle, 2010).

Cuttings from green stems (slightly lignified) have the potential to sprout, but they are more prone to attack by pathogens and insects and tend to dehydrate quickly. Cuttings from stems older than 18 months are overly lignified, contain minimal food reserves, and exhibit reduced viability, resulting in delayed and slow sprouting with poor vigor. Typically, in a segregating breeding population, each stem yields, on average, 7–8 stakes. Released varieties should generally produce at least 10 good-quality cuttings, making this a key breeding objective as well.

Vegetative multiplication of cassava presents numerous limitations. The planting material is both bulky and perishable, while the low multiplication rate hampers breeding efficiency and the dissemination of newly released varieties. Additionally, stems collected from diseased plants serve as the primary source of inoculum for various diseases induced by viruses like cassava mosaic (CMD) and cassava brown streak (CBSD), bacteria such as bacterial blight (*Xanthomonas axonopodis* pv. *Manihotis*), fungi including witches' broom (Ceratobasidium sp) or super-elongation disease (*Sphaceloma manihoticola*), and even pathologies of unknown etiology like frogskin disease. Moreover, infested stems play a crucial role in the dispersal of insects such as the green mite (*Mononychellus tanajoa*) and red mite (Tetranychus spp.), scale insects like *Aonidomytilus albus* and *Saissetia miranda*, and mealybugs such as *Phenacoccus herreni* and *P. manihoti* (Bellotti, 2002; Hillocks and Wydra, 2002; Legg et al., 2014; Leiva et al., 2023). To address these challenges, various alternatives have been developed, including tissue culture,

semi-autotrophic hydroponics (SAH), and rapid multiplication approaches based on one or two-node cuttings (Sheat et al., 2024).

Sexual reproduction, a fundamental component of conventional breeding, is widespread and relatively straightforward to achieve (Alves, 2002; Kawano, 1980). Reported incompatibilities are minimal, with only recent suggestions of partial self-incompatibility (Bandeira e Sousa et al., 2021). Self-pollination is feasible, although limited by protogyny (Contreras-Rojas et al., 2009; de Freitas et al., 2016; Kaweesi et al., 2016; Kawuki et al., 2011; Sheela et al., 2008). Male and female flowers suitable for pollination are typically found on separate branches of plants from the same genotype. Notably, the first sequenced cassava genome originates from an S_3 partially inbred line (Lyons et al., 2022).

Propagation from true seed occurs sporadically in farmers' fields and serves as the starting point for generating valuable genetic diversity (Eke-Okoro et al., 2001; Elias et al., 2001; Pujol et al., 2005). Shamans and forward-thinking farmers have historically played, and continue to play, crucial roles in an informal genetic improvement process (Salik et al., 1997; Sambatti et al., 2001).

Cassava is a diclinous and monoecious species, meaning that either female (pistillate) or male (staminate) flowers are produced in inflorescences (racemes or panicles) within the same plant (Alves, 2002; Ramos Abril et al., 2019). Euphorbiaceous flowers (technically they are false flowers), have undergone a unique evolutionary process, leading to the use of the term "cyathia" (singular: cyathium) to identify them. However, they will be referred to as male and female flowers in this article. Female flowers are single and reduced to a pistil, which is protected by petal-like bracts. Male flowers are similarly reduced to a single stamen but form inflorescences consisting of ten single-stamen flowers (Fig. 3). They are also covered by bracts. Pistillate flowers are positioned in the lower section of the raceme or panicle inflorescence and typically open 10–14 days before the male flowers, which are located towards the apex of the same inflorescence and are more abundant.

Inflorescences always develop at the apex of the stem. Buds below the inflorescence begin to sprout as soon as flowering is induced, enabling further plant growth (Alves, 2002; Jennings and Iglesias, 2002). Consequently, each flowering event leads to branching (Fig. 3).

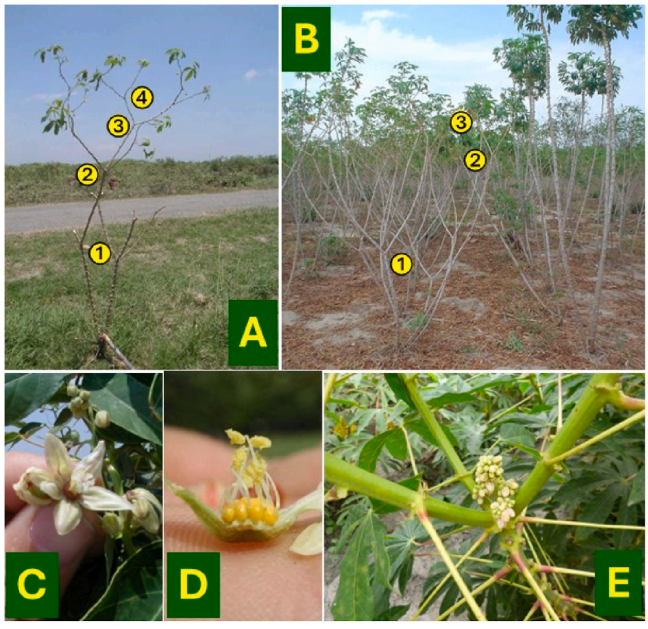

Fig. 3. Flowering and plant architecture in cassava. **A**. Illustration of a plant that has undergone four flowering (or branching) events. B. Contrast between an undesirable plant architecture (left plant) with early and frequent branching and an erect phenotype (right plant). **C**. Female flower. **D**. Male flower, **E**. Illustration of branching below the inflorescence assuming apical dominance inhibiting the development of the inflorescence.

While some genotypes flower early and often (3–5 times during a growth cycle), others flower infrequently, late, or not at all. Flowering and branching patterns in cassava are highly heritable traits. Typically, during the initial flowering event, branches asume apical dominance (Fig. 3), resulting in underdeveloped inflorescences that often abort (Bandeira e Sousa et al., 2021). Consequently, breeders initiate the crosses usually at the second or third flowering event.

Farmers often favor erect, non-branching types due to their facilitation of cultural practices and increased production of vegetative planting material, which is easy to transport and store. However, this preference poses a significant challenge for breeders, as genotypes with erect plant architecture tend to flower late and infrequently. Consequently, producing botanical seed from these genotypes may require up to 16 months after planting. In extreme cases, making crosses and obtaining segregating progenies may be practically impossible.

Cassava breeding primarily involves generating half- or full-sib families through open or controlled pollinations, respectively. In open pollinations, a field planting design devised by Wright (1965) is implemented to maximize the occurrence of crosses among all progenitors, while minimizing the occurrence of self-pollinations, which still happen relatively frequently. Various publications detail the protocols for controlled pollinations in cassava (Gonçalves Fukuda et al., 2002; Jennings and Iglesias, 2002; Kawano, 1980). Achieving synchronization of flowering for planned crosses often presents a significant challenge. In summary, there are significant challenges related to both vegetative and sexual reproduction of cassava:

- The low vegetative multiplication rate (typically 1:8 in segregating populations) means that considerable time is necessary to produce sufficient planting material for multi-location evaluation trials.
- Genotypes with erect plant architecture, which are most desirable for breeding purposes, often exhibit late and sparse flowering. Consequently, crossing nurseries must remain in the field for up to two years, with botanical seed collection typically occurring 12 months after planting (MAP) the nurseries or later in non- or late-flowering genotypes.
- Implementing inbreeding is particularly challenging due to protogyny in cassava. Self-pollinating erect genotypes would require cloning, significantly lengthening the breeding process to unacceptable durations. Attempting to self-pollinate seedling plants unavoidably relies on early flowering genotypes, leading to plants with unacceptable plant architecture.
- Achieving proper recombination of desirable genotypes to approximate panmixia in cassava is inherently difficult.

In conclusion, cassava's propagation methods, whether through stems or botanical seeds, serve different purposes, with stem propagation common for commercial production and seed propagation essential for breeding. However, both methods present challenges, such as perishability and the need for rapid sprouting after planting. The intricate flowering biology of cassava has been a limiting bottleneck for breeders, including difficulties in achieving synchronization of flowering and proper recombination of desirable genotypes. These complexities underlined the need for innovative approaches in cassava breeding.

Recent advancements in inducing early and prolific flowering in cassava have significantly facilitated its breeding. Extended photoperiod has been shown to trigger earlier flowering in late-flowering germplasm. Additionally, pruning techniques and the application of plant growth regulators have been demonstrated to promote abundant flowering (Oluwasanya et al., 2021a; Pineda et al., 2020a, 2020b; Santos et al., 2023). It is now possible to obtain seeds from direct crosses, open- or self-pollinations from non-flowering genotypes within six months. The possibility of self-pollinations without the undesirable consequence of favoring early branching types (Ceballos et al., 2015) facilitates the possibility of inbreeding elite cassava germplasm.

Transitioning into the section on Plant Breeding, we further explore

strategies and technologies aimed at enhancing cassava breeding efficiency and effectiveness.

5. Cassava breeding

Several reviews on cassava breeding have been conducted over the years (Amelework and Bairu, 2022; Ceballos and Hershey, 2017; Covarrubias-Pazaran et al., 2022; Jennings and Hershey, 1985; Jennings and Iglesias, 2002; Kawano and Cock, 2005; Kongsil et al., 2024; Xiao et al., 2025), providing insights into the evolution of cassava breeding.

Plant breeding boasts one of the highest rates of return among investments in agricultural research. The significant increase in crop productivity during the twentieth century was attributed to genetic gains achieved through breeding efforts (Evenson and Gollin, 2007; Renkow and Byerlee, 2010; Pingali, 2012; Pingali and Kelley, 2007). Cassava has also benefited from technological advancements in breeding (Eriksson et al., 2018; Johnson et al., 2003; Kawano, 2003; Malik et al., 2020), with new varieties developed in Africa, Asia, and the Americas meeting the needs of farmers, processors, and consumers, resulting in millions of dollars in additional income for small farmers. Furthermore, advancements in tissue culture, genetic transformation, and molecular biology have made significant positive contributions to cassava breeding (DeVries and Toenniessen, 2001).

5.1. Institutional development

The earliest documented report on cassava variety assessment and selection likely dates back to Bahia state, Brazil, in 1899 (Zehntner, 1919; as reported by Gonçalvez Fukuda et al., 2002). Modern breeding programs were initiated during the first half of the last century in various countries, including Brazil (Graner, 1935), Ghana (Hahn et al., 1979), India (Abraham, 1957), Indonesia (Bolhuis, 1953), Madagascar (Cours, 1951), and Tanzania (Jennings, 1957; Nichols, 1947). However, apart from Brazil, most of these early efforts were discontinued due to the dismantling of the colonial system.

Conditions changed significantly in the 1960s with the establishment of the International Center of Tropical Agriculture (CIAT) in Colombia and the International Institute of Tropical Agriculture (IITA) in Nigeria, both incorporating cassava into their research agenda. This period also witnessed a rapid expansion of cassava research programs on a national level (Gonçalves Fukuda et al., 2002; Westwood, 1990). The creation and consolidation of the international and national research centers marked a new era for cassava, characterized by successful breeding projects, establishment of germplasm collections, modernization of cultural practices, and the development of new processing methods (Jennings and Iglesias, 2002). Numerous countries, including Brazil, Colombia, China, Cuba, India, Indonesia, Nigeria, Thailand, Uganda, Vietnam, and others, have made significant strides in cassava research through their national research centers.

5.2. Evolution of breeding objectives

There is ample evidence to suggest that breeding objectives have evolved over time alongside the development of cassava breeding programs, the emergence of new information and tools, and the evolution of markets, which have introduced new requirements but also offered new opportunities. Early efforts primarily concentrated on enhancing yield and ensuring stable production, often with particular emphasis on developing tolerance or resistance to biotic and abiotic stresses (Dufour et al., 2023; Jennings, 1957; Nichols, 1947).

The release of improved varieties to meet these fundamental requirements eventually revealed certain unforeseen weaknesses that traditional landraces, by default, would not have possessed, as they had been selected by farmers through decades of informal trial and error. Quick and reliable sprouting of stem cuttings, for example, is a key requirement for varieties to be adopted. However, this trait is generally not evaluated during the selection process in breeding programs, as they often avoid prolonged storage of planting materials. Consequently, selected germplasm may later reveal a lack of storability when handled under typical farmers' conditions.

Another learning experience occurred with the release of the variety Rayong 60 in Thailand. While this variety boasted high and consistent dry root yield, it relied heavily on high FRY, but at the expense of desirable levels of DMC. Although farmers were initially satisfied with its performance, processors soon began to reject roots from this variety due to their low DMC, resulting in diminished yields of the final products, such as dried root chips or starch. As a consequence, in Southeast Asia, subsequently released varieties are required to meet a minimum threshold of DMC.

At CIAT, there are four clearly defined cassava breeding pipelines defined by their distinctive traits:

a) High and stable DMC (combined with high FRY) for industrial use and animal feed.
b) Good cooking quality cassava (fresh or processed) for human consumption.
c) Biofortified cassava with high pro-vitamin A for nutrition enhancement.
d) Novel starch properties such as low (or high) amylose and the small granule mutations for the food, starch, and ethanol industries (Ceballos et al., 2021).

Table 2 provides a simplified assessment of trait importance across key cassava value chains. Reliable sprouting is crucial for 'industrial' uses like dried chips, starch, and ethanol production, where large monocrop plantations are common. In contrast, cassava for human consumption is often grown in smaller plots, especially in regions with ample rainfall.

Erect plant architecture holds particular importance in commercial plantations for the *industrial* value chains, as they often rely on semi-mechanized planting and harvesting methods. High DMC is a critical trait for industrial end uses, as the price paid to farmers is directly correlated with it. While DMC also carries significance for other end uses such as gari or farinha, the price paid to farmers is not yet dependent on DMC in those cases.

The stability of DMC is a relatively new concept that is likely to become even more significant in the future. Cassava is typically harvested at the end of the dry season, just before the onset of the rainy season. Under these conditions, DMC generally reaches its maximum, and the planting material may need to be stored for a short period. However, if rain arrives before harvesting, the plants will resume growth after their semi-dormant state during the dry season. Energy from the roots would be utilized to promote this growth, leading to a sharp reduction in DMC around two weeks after the start of the rainy season. It may take up to two months for the roots to regain their DMC, and for some clones, DMC may not recover at all.

The extent of DMC decline and the rate of recovery if cassava is in the field when the rainy season begins are genetically controlled. Erratic rainfall patterns, exacerbated by climate change, pose a growing challenge. Therefore, it is highly desirable for the roots of new cassava varieties to not only have high DMC but also for this trait to remain as stable as possible.

High and stable FRY has frequently been the foremost trait in various breeding programs. Achieving this requires released varieties to exhibit tolerance or resistance to the primary biotic and abiotic stresses, as well as demonstrate low genotype × environment interactions. This trait holds particular significance for *industrial* cassava. Conversely, for human consumption, quality rather than productivity emerges as the predominant feature that cassava varieties must possess to guarantee adoption by farmers and acceptance by consumers. As depicted in Table 2, quality traits such as hydrogen cyanide (HCN) content, cooking time, poundability, texture, taste, and fermentability of roots are

Table 2
Summary of the most important value chains for cassava worldwide. For each value chain a subjective assessment of the relative importance of different traits is provided.[a]

Value chain	Adequate sprouting	Erect plant architecture	High & stable DMC	High & stable FRY	Low HCN	Cooking time	Taste and texture	Fermentability of roots	Mealiness/ poundability	Starch properties	High carotenoids
Industrial end uses											
Dried chips (SE Asia & LAC)	***	**	***	***							*
Ethanol (SE Asia & LAC)	***	**	***	***						**	
Starch (SE Asia & LAC)	***	**	***	***						**	
Human consumption											
Boiled roots (LAC & Africa)	*	**	**	**	***	***	***		***		**
Garri/Eba (Africa)	*	*	**	**			***	**			*
Fufu (Africa)	*	*	**	**				***	***		
Farinha (South America)	*	*	**	**					**		*
Cassabe (LAC)	*	*	**	**				***	**		*

[a] (*) Somewhat important; (**) Important; (***) Fundamental.

fundamental factors for the human consumption of cassava roots at the expense of productivity traits. Regrettably, there is a substantial lack of information regarding the genetic and biochemical bases for these traits, resulting in the unavailability of high-throughput selection protocols at present (Dufour et al., 2023).

Early bulking is an important, yet poorly defined, trait. Cassava is generally harvested 10–12 MAP, so any variety that allows for commercial harvest the roots at 6–8 MAP would be considered an early bulking clone (Amelework and Bairu, 2022). It is not clear if early bulking occurs because of an earlier initiation or a faster accumulation of starch in the roots or both alternatives (El-Sharkawy, 2004; Wholey and Cock, 1974). Early harvesting, unavoidably, has a negative impact on yields and can only be justified for specific circumstances for the farmer or the region (e.g., short growing season due to high latitudes, growing cassava between two rice crops, etc.). There is no clear understanding of the genetic or physiological basis for early bulking.

The identification of the amylose-free (Ceballos et al., 2007) and small-granule (Ceballos et al., 2008) starch mutations marked a

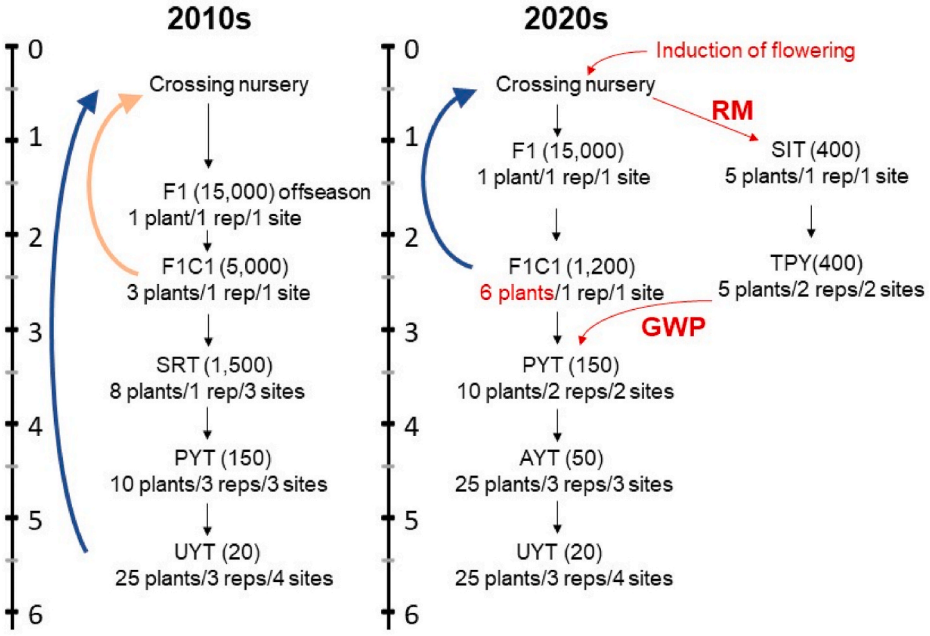

Fig. 4. Illustration of the latest evolution of breeding schemes at CIAT. On the vertical axis is time (in years). F1: seedling nursery; F1C1: cloned seedling nursery; SRT: single row trial; PYT, AYT and UYT: preliminary, advanced and uniform yield trials, respectively; GWP: genome-wide prediction; SIT: seed increase trial; TPY: training population yield trials; RM: rapid multiplication. Upward arrows indicate the duration of each breeding cycle (the orange arrow is for the rapid-cycling for high-carotenoids or waxy starch breeding).

significant breakthrough in cassava research, paving the way for enhancing the already significant market of the starch industry. However, it has also revealed a significant bottleneck for the introgression of important traits with simple inheritance, such as those controlled by a single gene.

5.3. Breeding scheme

Numerous articles outline the typical evaluation scheme employed by various cassava breeding projects (Gonçalves Fukuda et al., 2002; Jennings and Iglesias, 2002; Kawano and Cock, 2005). Besides the recent ongoing efforts to implement genomic selection, cassava breeding has traditionally relied on phenotypic recurrent selection, a process that typically spans several years to complete a cycle. Fig. 4 replicates the latest breeding protocol initially published by Ceballos et al., in 2021.

The breeding scheme has undergone continuous evolution, particularly since the 2010s. The seedling nursery (**F1**) is now planted in the off-season and grown for only 5–6 months. During this short stage, there is a possibility to select for pubescence in the apex (1–2 months after germinating the seed) and for late or (hopefully) absence of branching, both of which are pertinent to all product profiles. At harvest, roots could be visually and rapidly inspected for pigmentation of the parenchyma (e.g., PSY) or waxy starch, depending on the breeding targets. Since the F1 is grown for a shorter period than usual, only three stem cuttings can be collected from each seedling plant.

Subsequently, the **F1C1** stage involved planting at least three plants per genotype during the regular planting time, with a growth period of one year. At harvest, the breeder might opt for a light selection for FRY and/or DMC. However, this selection is conducted with minimal pressure due to the small unreplicated sample and considering that the F1C1 may have been planted at CIAT headquarters (potentially not accurately representing the target environmental conditions).

Each of these three plants provides planting material for three single row trial (**SRT**), which are planted in three different locations. This is a very important innovation over previous schemes. The multi-location planting of SRT allows an early attention to the always troublesome issue of GxE interactions.

The subsequent stages include the preliminary (**PYT**), advanced (**AYT**), and uniform (**UYT**) yield trials, each with an increasing number of plants per plot and the inclusion of more than one repetition per location. These trials are also planted in, at least, three locations. However, the AYT stage was no longer conducted in the late 2010s. Selected genotypes from these trials were integrated into the crossing nurseries (indicated by blue upward arrows). Rapid cycling, as described by Ceballos et al. (2013), was adopted for traits with high heritability, such as carotenoid content (depicted by orange upward arrows) or waxy starch.

The development and implementation of the flower inducing technology shortened the duration of crossing nurseries in the 2020s (Oluwasanya et al., 2021a; Pineda et al., 2020a, 2020b; Santos et al., 2023). The F1 is grown for seven months, which allows F1C1s to have six plants per genotype and then PYT to grow in two locations (Fig. 4 right scheme). Selections for PYT are made based on the total genetic value predicted using genome-wide prediction (GWP). The F1C1 clones with the best predicted breeding value are cycled back to crossing nurseries as progenitors for the next cycle of improvement (black upward arrows). The GWP training population is selected from the breeding population based on the pedigree.

Rapid multiplication (RM) is performed in green house to obtain five plantlets from each seedling. The plantlets are transplanted into the seed increase trial (SIT). The following growing cycle, the training population yield trials (TPY) are established at two locations for phenotyping. The SIT and F1C1 clones are genotyped for genome-wide prediction.

6. Inheritance of relevant traits

The inheritance of traits plays a significant role in determining the most effective methods for enhancing them. Three primary inheritance categories can be identified, with examples from cassava, along with the most suitable breeding methods (Fig. 5). Unfortunately, there is a notable lack of information regarding the inheritance of many relevant traits in cassava. Table 3 summarizes the type of inheritance for different traits and provides useful references.

6.1. Agronomic traits

FRY, a fundamental trait in most product profiles (Table 2), exhibits a heritability ranging from low to intermediate and is heavily influenced by genotype-by-environment interactions. Extensive evidence underscores the importance of non-additive genetic effects for FRY, as observed in both conventional quantitative genetics (Ceballos et al., 2015, 2016; Yuanjit et al., 2023) and molecular studies (Bandeira e Sousa et al., 2021; de Andrade et al., 2022; Wolfe et al., 2016a). Empirical findings from a decade of genomic selection research in Africa and Brazil, as predicted by Ly and colleagues (2013), confirm its potential to enhance resistance to CMD and CBSD, and augment DMC and carotenoid content. However, notable advancements in FRY remain elusive (Mbanjo et al., 2021; Yonis et al., 2020). In essence, the genetic regulation of FRY is characterized by dispersion across numerous loci, featuring significant interactions within (dominance) and among (epistasis) them, as well as between genotypes and the environment.

Increasing DMC represents another crucial objective for most product profiles (Table 2). Unlike FRY, the inheritance of this trait primarily follows an additive pattern (Ceballos et al., 2015; de Andrade et al., 2022; Kawano, 2003; Kawano et al., 1987; Rabbi et al., 2017). Both conventional and molecular methodologies converge in highlighting the significance of additive and non-additive effects in the inheritance of both FRY and DMC. Genetic enhancements for elevated DMC have been realized through conventional breeding (Kawano, 2003; Kawano et al., 1987), further reinforcing the prevalence of additive genetic effects and relatively high narrow sense heritability.

Molecular approaches are shedding new light on the inheritance of DMC. GWAS studies have pinpointed two major loci on chromosome 1, alongside individual loci on chromosomes 6, 12, and 16. Although not attaining statistical significance, regions spanning much of the genome were found to exert influence on the trait (Rabbi et al., 2022).

Selecting clones to maximize dry root yield (DRY), a combination of high FRY and DMC, presents challenges. Empirical findings from selection indices, integrating both parameters, reveal that maximizing DRY often involves compromises, yielding clones with high FRY but lacking desirable DMC, or vice versa, along with clones exhibiting acceptable levels of both FRY and DMC (Joaqui et al., 2016).

The significance of harvest index in breeding various crops, including cassava, has long been acknowledged (Kawano, 1990). Harvest index demonstrates high heritability at each evaluation stage in the breeding process. Compared to FRY, the interaction between genotype and evaluation stage is notably lower for harvest index. Consequently, indirect selection for yield through harvest index proves to be more effective than direct selection by yield itself, particularly in the early evaluation stages of the breeding process (Kawano et al., 1998). Rabbi et al. (2022) identified two genomic regions significantly linked with harvest index on chromosomes 2 and 12. However, as expected, several other regions scattered across chromosomes 3, 4, 6, 8, 9, 14, 15, 16, and 18 were also found to be associated.

6.2. Quality traits

The inheritance of amylose-free (e.g., waxy) starch, controlled by a single recessive gene at the GBSS locus in cassava (Aiemnaka et al., 2012; do Carmo et al., 2020) and other crops (Hannah, 2000), is

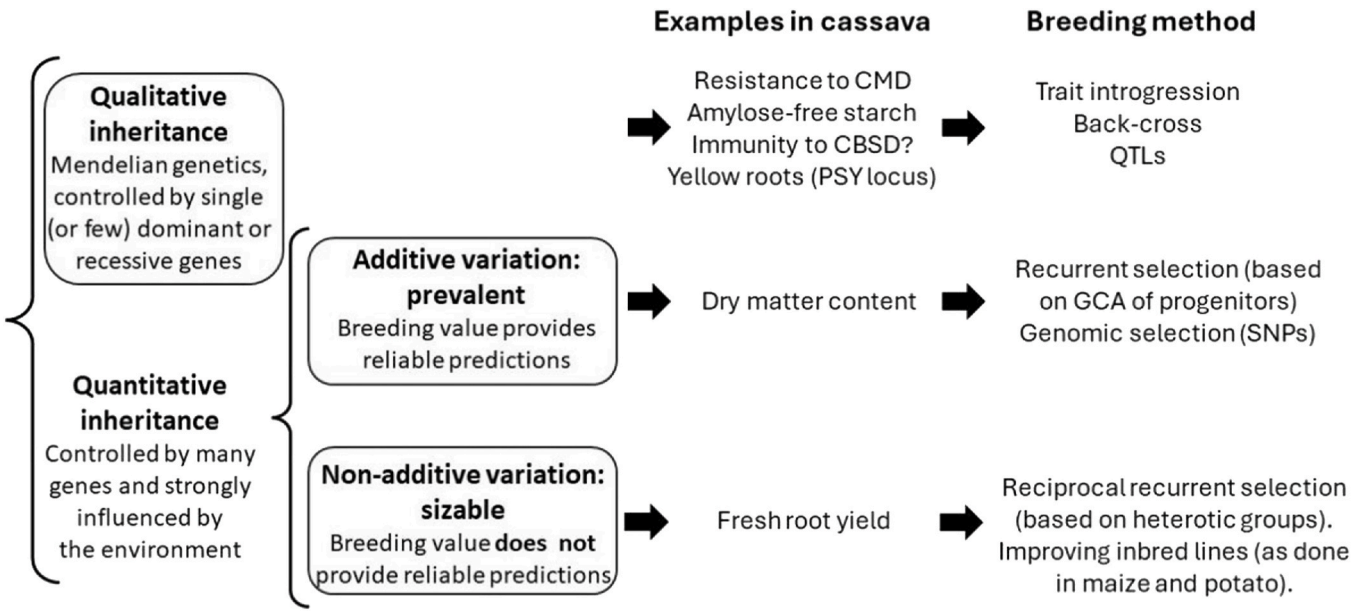

Fig. 5. Primary inheritance categories in plant breeding, with examples from cassava, along with the most suitable breeding method(s).

Table 3
Type of inheritance controlling the expression of relevant traits in cassava, along with useful references (simplified citations).

Trait	Inheritance	References
Fresh root yield	Complex, non-additive	de Andrade et al., 2022; Ceballos et al., 2015; Wolfe et al., 2016a
Dry matter content	Complex, additive	de Andrade et al., 2022; Ceballos et al., 2015; Kawano et al., 1987; 2003; Rabbi et al., 2017
Amylose-free starch	Simple recessive	Aiemnaka et al., 2012; Ceballos et al., (2007); do Carmo et al., 2020
Pulp color (PSY)	Simple dominant	Esuma et al., 2016; Ikeogu et al., 2019; Rabbi et al., 2014; 2017; Welsch et al., 2010
Carotenoids content	Complex additive	Morillo-C. et al., 2012;
Branching/ flowering	Complex [a]	Baguma et al., 2024
HCN content	Complex [a]	Balyejusa Kizito et al., 2007; Ogbonna et al., 2021; Whankaew et al., 2011;
Harvest index	Complex [a]	Kawano et al., 1998; Rabbi et al., 2022
CMD resistance	Simple dominant	Akano et al., 2002; Rabbi et al., 2014; Wolfe et al., 2016b;
CBSD resistance	Simple dominant	Kawuki et al., 2016; Kayondo et al., 2018; Nandudu et al., 2023; Sheat et al., 2019; 2022, Sheat and Winter, 2023;
CBB	Complex [a]	Jorge et al., 2000; Li et al., 2017; Ntui et al., 2024; Umemura and Kawano, 1983; Zhang et al., 2022,
Whiteflies resistance	Simple/ dominant	Bohorquez-Chaux et al., 2025; Jaramillo et al., 2005; Nye et al., 2023; Pérez et al., 2005a;
Mites resistance	Simple	Bellotti (2002); Ezenwaka et al., 2018; Onzo et al., 2009; Rabbi et al., 2022
Thrips resistance	Simple	Bellotti (2002)
Tolerance to PPD	Complex [a]	Luna et al., 2021; Mbinda and Mukami, 2022; Morante et al., 2010; Rahmawati et al., 2021
Cooking time	Complex additive [a]	Dufour et al., 2023; Iragaba et al., 2019; Tran et al., 2021
Cooking quality	Complex [a]	Dufour et al., 2023; Iragaba et al., 2023; Uchendu et al., 2021

[a] There is no convincing evidence on the relative importance of additivity and dominance.

well-documented.

Carotenoid content inheritance in cassava roots (Welsch et al., 2010) and other crops' seeds, tuberous roots, and tubers is closely linked to the phytoene synthase (PSY) locus, exemplified by golden rice (Schaub et al., 2005). In cassava, PSY dictates variation in total carotenoids content, correlating with parenchyma pigmentation intensity. Visual examination of root cross-sections enables effective high-throughput genotype selection at the PSY locus.

Despite proper genotype at the PSY locus, significant variation in carotenoid content persists in yellow roots (Fig. 6). This variability, substantial among genotypes, necessitated a high-throughput protocol based on NIRS (Ceballos et al., 2013; Sánchez et al., 2014), likely influenced by additional carotenoid biosynthesis loci like beta-carotene hydroxylase (Diretto et al., 2007). Rabbi et al. (2022) identified another putative gene, betacarotene dioxygenase, influencing carotenoids content.

The biosynthetic pathway for cyanogenic glucosides involves cytochrome P450 (CYP) enzymes of the CYP79 family. Down regulation of paralogous genes CYP79D1 and CYP79D2 by RNA interference (Jørgensen et al., 2005) or CRISPR-Cas9 mediation (Gomez et al., 2023) results in a significant reduction in cyanogenic glucosides in cassava tissues. These genes encode the first committed enzymes in linamarin and lotaustralin synthesis. There is a large variation for cyanogenic potential (HCN) in cassava (Sánchez et al., 2009). There is plenty of evidence regarding the influence of genotype by environment interaction (Bokanga et al., 1994; Mtunguja et al., 2016) as well as age of the plant and timing of planting (Ospina et al., 2024) on HCN.

Postharvest physiological deterioration presents a significant challenge for the cassava value chain. It has been estimated that introducing varieties with extended shelf life could yield benefits of approximately US $35 million for Thai cassava farmers and factory owners (Vlaar et al., 2007) or millions of tons (An et al., 2024). PPD has large impacts for the economy and food security. Unfortunately, PPD is positively correlated with DMC, meaning that varieties prized for their high DMC tend to deteriorate more rapidly. Conversely, high carotenoid content tends to reduce PPD (Morante et al., 2010).

Assessing PPD is challenging, and there is currently no reliable high-throughput protocol for phenotyping it (Posom et al., 2023; Rahmawati et al., 2021; van Oirschot et al., 2000; Venturini et al., 2016). Environmental factors and genotype-by-environment interactions further complicate matters (Luna et al., 2021). Consequently, the inheritance of the reaction to PPD is low and complex. No reliable source of tolerance to PPD has been found through alternative sources such as *M. walkerae* (Bertram, 1993) or polyploidy (Moyib et al., 2015). Not surprisingly,

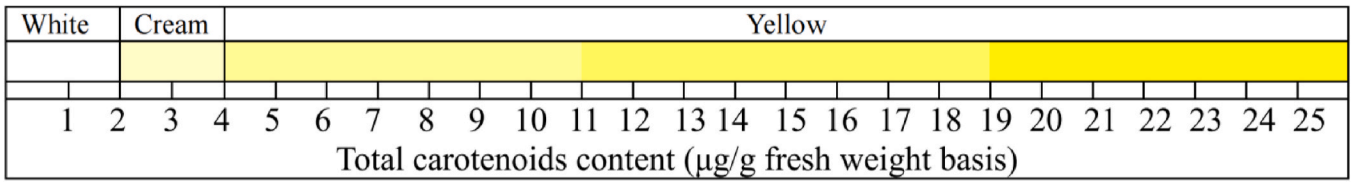

Fig. 6. Diagram illustrating the range of variation for carotenoids content in fresh cassava roots (µg/g fresh weight basis). The PSY locus explains the change in concentration from white (<2 µg/g) to yellow (>4 µg/g) roots. There is, however, a large variation (4–25 µg/g) in carotenoids content that is not explained by PSY.

therefore, no QTL associated with PPD has been mapped thus far (Mbinda and Mukami, 2022). Despite significant investments in genetic transformation and/or gene editing, no promising products have yet been developed (Liu et al., 2017; Vanderschuren et al., 2014; Xu et al., 2013; Zidenga et al., 2012).

Cooking time and cooking quality are fundamental traits for the direct consumption of cassava through boiling the roots. Although some advancements have been achieved in developing high-throughput phenotyping protocols (Tran et al., 2021), further improvements are needed. Unfortunately, there remains a gap in our understanding of the biochemical and genetic foundations underlying cooking time and quality (Dufour et al., 2023; Iragaba et al., 2021, 2023; Uchendu et al., 2021). Preliminary findings suggest that cell wall polysaccharides play a primary role in determining cooking time in boiled cassava roots.

6.3. Horticultural traits

Non-branching plant architecture, often late or non-flowering, garners increasing interest. Genetic control over branching and flowering, influenced by environmental factors like photoperiod duration and temperatures, manifests as a relatively stable trait. Long days and low temperatures promote earlier flowering in genotypes otherwise late or non-flowering (Oluwasanya et al., 2021b; Pineda et al., 2020a; Santos et al., 2024).

However, a notable asymmetry in progenies produced by early and late flowering genotypes has hindered thorough studies of the inheritance of branching and flowering in cassava. While it has been demonstrated that some variation is controlled by the Flowering Locus T (Adeyemo et al., 2017), field observations across numerous full- and half-sib families have failed to reveal clear segregation patterns for this important trait. This suggests that multiple genes are likely involved, rendering the inheritance of branching and flowering in cassava tentatively complex (Table 3). Regarding plant type, several regions across many chromosomes exert influence, yet no locus attains statistical significance according to Rabbi et al. (2022).

Branching/flowering and cyanogenic potential exhibit several common features. Both traits are governed by one or two major genes (FT locus and CYP79 loci, respectively), implying simple Mendelian inheritance. However, the observed phenotypic variation for these traits suggests polygenic or quantitative inheritance: there exists a continuous spectrum of phenotypic expression strongly influenced by environmental factors. It can be hypothesized that the genetic regulation of these traits relies on a limited number of loci. The substantial phenotypic diversity may be explained by a hypothetical allelic dosage effect at these few loci and a pronounced evolutionary sensitivity to environmental conditions (e.g., drought-induced elevation in HCN levels, Srihawong et al., 2015), which could also account for the strong genotype-by-environment effects.

6.4. Diseases

A stable and dependable source of resistance to CMD was identified in cassava in the 1990s. This resistance is conferred by a single major gene located on chromosome 12, commonly referred to as the CMD2 locus (Akano et al., 2002). Additionally, two other loci on chromosome 14 have been identified (Rabbi et al., 2022). Molecular markers for CMD2 are readily available and have been extensively utilized for selection purposes in Africa and Southeast Asia (Houngue et al., 2019; Thuy et al., 2021).

Breeding for resistance to CBSD poses challenges due to the minimal correlation between symptoms in the leaves and roots, as well as difficulties in accurately assessing resistance levels in the field (Kawuki et al., 2016). Although grafting techniques have been employed to ensure disease inoculation and reliable assessment of resistance levels, field evaluations remain challenging and require several years. Despite these obstacles, significant progress has been made over the years in developing sources of resistance to the disease. Concurrently, research efforts have been dedicated to developing genomic tools to aid in breeding (Kayondo et al., 2018). However, genomic predictions are hindered by significant environmental effects and genotype-by-environment interactions (Nandudu et al., 2023; Somo et al., 2020).

A significant breakthrough regarding CBSD has recently been reported (Sheat et al., 2019, 2022, Sheat and Winter, 2023). Several sources of immunity to the disease have been discovered in accessions from the germplasm collection at CIAT. These findings are highly promising for two main reasons: firstly, the level of resistance exhibited by these materials surpasses previous reports, and secondly, the inheritance of immunity appears to be relatively simple and dominant, indicating high heritability.

There is currently no known source of immunity in cassava to the bacterial blight (CBB) induced by *Xanthomonas campestris* pv. *manihotis* (Berthet and Boudar). However, there is considerable variation in the response to the disease, including reliable and stable sources of resistance. Studies, such as that by Umemura and Kawano (1983), have reported that resistance is a quantitatively inherited trait ($h^2 = 0.63$), predominantly controlled by additive genetic factors. Furthermore, the identification of several quantitative trait loci (QTLs) associated with resistance, as reported by Jorge et al. (2000), further supports the notion of quantitative inheritance. Recent research has linked two leucine zipper transcription factors to resistance to CBB (Li et al., 2017; Zhang et al., 2022). Consequently, the development of cultivars with reasonable levels of resistance to CBB does not present significant challenges for cassava breeders.

6.5. Pests

Cassava stands out among crops for having reported sources of resistance to whiteflies (Bellotti, 2002). While several whitefly species can infest cassava, *Bemisia tabaci* (Gennadius) poses a particular threat due to its role as a vector of CMD and CBSD in Africa. MECU72, a male sterile landrace from Ecuador, offers stable and effective resistance to various whitefly species. Additionally, there are a few other landraces from Ecuador and Peru that exhibit similar resistance. The transfer of this resistance to progenies is relatively straightforward, and a cultivar derived from MECU72 (Nataima-31) has already been released in Colombia. Diallel studies, with MECU72 as one of the progenitors, have revealed significant general combining ability effects for the reaction to whiteflies (Jaramillo et al., 2005; Pérez et al., 2005a).

Crosses between MECU72 and susceptible progenitors resulted in

progenies with limited phenotypic variation (all progenies showed a resistant phenotype similar to MECU72), preventing the detection of QTLs. Research efforts, therefore, focused on elucidating the biochemical mechanisms underlying this resistance (Irigoyen et al., 2020; Nye et al., 2023). Genetic studies faced challenges due to the male sterility of MECU72. Eventually, however, one progeny from MECU72 was male fertile and could be self-pollinated. The resulting S1 family (AM1588) with 183 individuals segregated widely for the reaction to whiteflies (Bohorquez-Chaux et al., 2025).

This breakthrough development allowed the identification of several QTLs. One of them, on chromosome 8, explained 35.44 % of the phenotypic variation.

There are various mite species that can impact cassava, but the green mite (CGM) *Mononychellus tanajoa* (Bondar) is especially devastating, particularly in Africa. While there is limited reported variation in cassava's reaction to mite infestation, biological control methods involving different phytoseiid mite species have proven effective in South America, where CGM has historically been less of a concern (Bellotti et al., 1987).

As part of collaborative efforts between CIAT and IITA, several phytoseiid species were introduced from South America into Africa. However, only *Typhlodromalus aripo* succeeded in establishing and surviving under the conditions on the continent. *T. aripo* significantly reduces CGM populations, resulting in increased FRY by at least 30 % (Bellotti, 2002). The survival of the predator mite depends on the pubescence of the plant's apex, while the efficiency of biological control hinges on the volatiles emitted by the host plant. Both characteristics are determined by the cassava genotype. Therefore, the control of CGM presents a unique example of the interaction between genetic effects and biological control (Onzo et al., 2009; Zundel et al., 2007).

Resistance to thrips is likewise associated with the pubescence of leaves in the apical section of the plant (Bellotti, 2002; van Schoonhoven, 1974). Selection for this trait is straightforward and can be conducted at the seedling stage, typically within the first 1–2 months after germination. Pubescence in the leaves is stable and highly heritable. Consequently, selecting materials that exhibit the optimal response to both mites and thrips can be effectively achieved early in the breeding process through a simple visual inspection using a magnifying glass.

6.6. Abiotic stresses

Cassava's resilience to water deficit stress conditions is well-documented (El-Sharkawy, 1993). Numerous studies highlight significant variations in cassava productivity during drought periods (Alves and Setter, 2000, 2004; Adjebeng-Danquah et al., 2016; de Oliveira et al., 2017; dos Santos Silva et al., 2021). The plant's high stomatal sensitivity, which regulates evapotranspiration under water stress, stands out as a key physiological trait enabling cassava to maintain acceptable root yields in such conditions (El-Sharkawy and de Tafur, 2007).

Phenotypic evaluation of drought tolerance in cassava, however, remains a challenging task. To begin with, it is not clear what 'drought tolerance' in cassava means. Physiologists tend to prioritize a high productivity ratio under stress compared to optimal conditions. Conversely, farmers and breeders may emphasize harvested root yield during drought periods. However, quantifying productivity under drought conditions is often hindered by low heritability.

Several traits have been linked to 'drought tolerance' in cassava: stomatal conductance, leaf formation and other growth parameters, water-use efficiency, leaf scars and leaf life, leaf photosynthesis, storage root and shoot harvest, fibrous root measurements, water stress responses, osmotic regulation under extended water stress, abscisic acid accumulation (Alves and Setter, 2000, 2004; El-Sharkawy, 2004; El-Sharkawy and Cock, 1987; El-Sharkawy et al., 1992; Lenis et al., 2006; Okogbenin et al., 2013).

Proxy traits have proven effective in evaluating drought tolerance across various crops. For instance, the anthesis-silk interval in maize (Bolaños and Edmeades, 1996) and carbon isotope discrimination in different crops (Monneveux et al., 2007) and have been successfully employed as proxy traits for indirectly selecting for drought tolerance. In 2007, El-Sharkawy and M. de Tafur linked carbon isotope discrimination to cassava's response to water stress. Similarly, Alves and Setter (2000; 2004) associated abscisic acid (ABA) accumulation with drought tolerance/susceptibility in cassava. Certain genotypes prioritize using photosynthates for extending storage root length rather than expanding root girth to survive drought conditions, albeit potentially compromising root yield (Adjebeng-Danquah et al., 2016). These authors suggested that the storage root length-to-girth ratio could elucidate the pattern of photosynthate accumulation in cassava roots under stress. However, these traits have not yet been utilized for selecting drought-tolerant cassava cultivars. In Brazil, indices like the drought tolerance index and drought tolerance stability index have been employed (de Oliveira et al., 2017; dos Santos Silva et al., 2021), but they rely on root harvests at the season's end.

Despite challenges in defining drought tolerance in cassava and assessing it phenotypically, several genomic studies have been undertaken (dos Santos Silva et al., 2021; Orek et al., 2020; Shan et al., 2018; Turyagyenda et al., 2013).

7. Promising innovations

7.1. The role of inbred progenitors

Shifting towards inbred-parent-based breeding in cassava improvement programs represents a strategic response to challenges associated with using heterozygous parents, which traditionally complicate trait integration to align with dynamic market and environmental demands (Collard and Mackill, 2007; Peng et al., 2014; Zhang et al., 2024). This approach enhances breeders' ability to select traits and cross parents more accurately, streamlining the development of targeted cultivars and improving productivity.

Prioritizing inbred lines for trait introgression boosts the efficiency and adaptability of breeding programs, addressing previous inefficiencies by reducing the time and cost associated with developing new varieties with specific traits of interest (Zhang et al., 2021). Utilizing inbred parents allows for consolidating breeding pipelines, resulting in cost savings and a more focused development of varieties tailored to specific market needs, thereby optimizing resources (Zhang et al., 2024). Moreover, this breeding strategy facilitates the rapid integration of superior traits into popular varieties, ensuring that cassava production can swiftly adapt to changing demands and challenges (Zhang et al., 2024). Lastly, inbreeding can play a fundamental role in genetic studies. For two decades, efforts to identify markers associated with whitefly resistance from MECU72 were unsuccessful. However, the development of a self-pollinated progeny ultimately enabled the detection of several QTLs (Bohorquez-Chaux et al., 2025).

7.2. Consequences of inbreeding: inbreeding depression and deleterious alleles

Cassava's historical clonal propagation has led to inbreeding depression and the persistence of deleterious mutations, hindering efforts to enhance its performance (de Freitas et al., 2016; McKey et al., 2010; Wang et al., 2014). Challenges persist due to the accumulation of genetic load (Contreras-Rojas et al., 2009; de Freitas et al., 2016). Plant breeders have explored strategies such as polyploidy to mitigate these issues, yet challenges remain, particularly in managing trait introgression during backcrossing (Ceballos et al., 2016; Labroo et al., 2021; van de Peer et al., 2021).

Advancements in genomic technologies, like the Cassava HapMap, offer opportunities for targeted breeding efforts by identifying and characterizing deleterious mutations (Long et al., 2023; Ramu et al.,

2017). Whole genome sequencing holds promise in predicting and purging these mutations to potentially improve crop performance (Wang et al., 2014; Wu et al., 2023). While the severity of inbreeding depression varies among cassava families, some demonstrate resilience, offering avenues for overcoming challenges (de Freitas et al., 2016; Contreras-Rojas et al., 2009).

In summary, addressing the genetic load in cassava presents both challenges and opportunities for plant breeders. Leveraging genomic technologies offers potential pathways to improve cassava breeding efforts and ensure the resilience and productivity of this vital food crop. Alternatively, genetic load can not only be predicted but also reduced through simple conventional recurrent selection approaches. This was demonstrated in temperate maize (since the 1930s), tropical maize (since the 1990s), and potato (since the 2010s). In every one of those examples, initially, inbreeding could barely go beyond S_3 or S_4 levels of inbreeding. However, after one or two cycles of partial inbreeding, homozygous lines (e.g., S_6) could be readily obtained. This strategy can now be implemented in cassava, facilitated by the availability of early and profuse flowering protocols that have been recently developed.

7.3. Evaluating within-family variation

The use of (partially) inbred progenitors or employing nonadditive models can significantly enhance the efficiency and productivity of variety selection processes, aiding in the identification of superior cassava clones (Heslot and Jannink, 2015). Variation among offspring from heterozygous parents is substantial, while differences between families are relatively minor across diverse cassava populations and environments (Cach et al., 2005; Calle et al., 2005; Ceballos et al., 2016; Jaramillo et al., 2005; Pérez et al., 2005a, 2005b).

For complex traits like FRY, the within-family variation is 6–13 times higher relative to the differences between families and non-additive variances are considerably larger than additive variances (Ceballos et al., 2015). Incorporating nonadditive components into prediction models could lead to less biased and more accurate parent selection for crossing, particularly in cassava breeding where nonadditive variation is prevalent, especially for traits with low heritability (Munoz et al., 2014).

7.4. Genetic diversity as a driver for market differentiation and wild relatives as a source of traits

While breeding goals for the industrial processing of cassava are well-defined and validated through widespread acceptance of released varieties, enhancing cassava varieties for ethnic culinary purposes remains a challenging task. Only recently have focused efforts begun to unravel the essential physicochemical and sensory traits relevant for these culinary applications. It is imperative for breeders to identify the primary factors driving varietal acceptance and to establish efficient high-throughput selection protocols. This knowledge is also pivotal for the future development of molecular markers to streamline the selection process.

Recent advancements in sequencing technology have enabled researchers to explore the intricate cassava genome, focusing on tapping into the genetic diversity of wild relatives for potential trait enhancement (Lyons et al., 2022). While there is recognition of the potential benefits of utilizing the genetic diversity of wild cassava relatives, it is essential to acknowledge the ongoing necessity for precise genome assembly tools, particularly with the expanding scope of genomic variation. Tools like Purge Haplotigs have played a role in refining cassava genome assemblies and facilitating in-depth analyses of gene families, setting the stage for further progress (Kuon et al., 2019).

Maximizing the use of these genetic resources in breeding programs remains paramount. Continuous developments are anticipated to propel cassava research and breeding forward, ensuring the crop's adaptability and relevance amidst evolving market demands and environmental challenges.

7.5. The prudent use of molecular tools

The practical implementation of molecular tools in cassava breeding faces numerous challenges, primarily due to difficulties in translating genetic discoveries into validated markers directly applicable in selection processes. These hurdles are multifaceted, encompassing issues such as linkage drag, polygenic traits, and prolonged breeding cycles (Ferguson et al., 2012; Stam and Zeven, 1981; Tanksley et al., 1989).

Molecular markers offer a clear and direct method for identifying cultivars in the field (Alzate et al., 2010; Fu et al., 2014; Rabbi et al., 2015) and for duplicating accessions in germplasm collections (Carvajal-Yepes et al., 2024). These are obvious and straightforward applications of molecular markers.

Despite efforts, Marker-Assisted Selection (MAS) reliability in cassava breeding remains a significant obstacle (Collard and Mackill, 2007; Ige et al., 2021, 2022; Ikeogu et al., 2019). Ongoing research aims to enhance MAS effectiveness by expediting the selection process through marker identification for traits challenging to measure or time-consuming (Baguma et al., 2024; Mbe et al., 2024). Reported traits include dry matter content, total carotenoid content/PSY (Ikeogu et al., 2019; Rabbi et al., 2017), resistance to Cassava Mosaic Disease (CMD2), root number, shoot weight, harvest index (Okeke et al., 2017; Rabbi et al., 2017; Somo et al., 2020; Wolfe et al., 2016b; Yonis et al., 2020; Zhang et al., 2018), resistance to cassava green mite (Ezenwaka et al., 2018), resistance to cassava brown streak disease (Kayondo et al., 2018) and cyanide content (Ogbonna et al., 2021). However, as stated earlier, phenotypic selection for resistance to green mite and carotenoids content related to PSY is a reliable and simple alternative.

The transition from marker discovery to routine application in breeding programs requires rigorous validation studies (Akano et al., 2002; Balyejusa Kizito et al., 2007; Fregene et al., 2001; Okogbenin et al., 2012; Rabbi et al., 2014, 2022). However, validating assays across diverse genetic backgrounds poses a significant challenge in translating research findings into practical applications. This hurdle may be addressed by incorporating novel trait-linked markers into the process (Ige et al., 2021; Platten et al., 2019). For instance, studies on resistance to cassava mosaic disease have identified crucial loci such as CMD2 on chromosome 12, along with markers SSRY106, NS158, and others, pivotal in parent selection (Akano et al., 2002; Ferguson et al., 2012; Lokko et al., 2006; Okogbenin et al., 2012; Olasanmi et al., 2021). Recent advancements include SNP markers capable of distinguishing between resistant and susceptible genotypes with an accuracy exceeding 80 % (Thuy et al., 2021).

Molecular markers have been crucial in confirming genes related to various traits, including starch biosynthesis (Chavarriaga-Aguirre et al., 1998; Mba et al., 2001). Marker-based studies, including genome-wide association studies (GWAS), have identified significant SNPs for different starch traits (Hu et al., 2021; Phumichai et al., 2022; Rabbi et al., 2022; Sunvittayakul et al., 2022).

Markers like S1_24155522 and S5_3387558 have been pivotal in identifying genomic regions enhancing provitamin A content in cassava (Ige et al., 2022), aiding breeding for low hydrogen cyanide content with markers like S16_640082 (Chaicharoen et al., 2023).

SNP marker integration shows promise in expanding breeding efforts for low cyanide cassava varieties (Collard and Mackill, 2007). Significant genomic regions have been identified for traits like root mealiness and fiber content (Uchendu et al., 2021). However, the lack of applicable assays poses challenges to MAS programs. Future efforts should focus on developing frameworks to convert genetic mapping outputs into reproducible and cost-effective genotyping assays, with KASP SNP technology emerging as a promising solution due to its efficiency and effectiveness in high-throughput screening (Chaicharoen et al., 2023; Ige et al., 2022).

Markers linked to dry matter content exhibit poor predictive accuracy (Ige et al., 2022). Robust estimation of allele substitution effects, particularly for markers like S1_24155522 in carotenoid accumulation,

is crucial (Ige et al., 2022). Exploring co-associations with other traits, such as cassava green mite and cassava brown streak disease, could enhance their utility (Ntui et al., 2024). Haplotype-based association analysis, leveraging linkage disequilibrium (LD), offers robustness due to haplotypes' multi-allelic nature and stronger LD with Quantitative Trait Loci (QTLs) compared to individual SNPs with low minor allele frequency (MAF) (Hess et al., 2017; Meuwissen et al., 2014). The substantial progress achieved through conventional recurrent selection to enhance DMC levels (Kawano, 2003; Kawano and Cock, 2005; Kawano et al., 1987) must be considered when evaluating the actual promise of MAS for this trait.

7.6. Genomic selection

Genomic selection (GS) leverages background genome data to harness the cumulative effect of markers, particularly beneficial for traits controlled by many small-effect loci. This enhances breeding efficiency by predicting performance using molecular markers, accelerating the identification of superior genotypes through integration of genotypic and phenotypic data to estimate genomic breeding values (GEBV), expediting the development of superior cassava varieties (Ceballos et al., 2021). Consequently, GS technology holds substantial promises for fast-tracking progress in cassava breeding, especially in clonally propagated crops, where it has demonstrated significantly higher genetic gain compared to phenotypic selection, particularly when halving the generation cycle (de Oliveira et al., 2012).

Long-term genetic gain from GS depends on trait relationships, breeding scope, and program cost-effectiveness (Hickey et al., 2017). Implementation of GS targets maximum gain across multiple traits, prioritizing yield-related traits feasible for high-throughput phenotyping to enhance breeding efficiency (Araus et al., 2018; Crain et al., 2018). Constraints include genotyping cost, crop generation time, and existing genetic diversity in cassava. Despite model variations, little difference exists in predictive ability (de Andrade et al., 2019). Phumichai et al. (2022) found consistent cross-validation results, with random forest (RF) and regularized kernel Hilbert space (RKHS) methods demonstrating higher accuracy for yield-related traits, attributed to their ability to capture nonadditive genetic variation (Phumichai et al., 2022; Wolfe et al., 2016a), mirroring findings in wheat (Phumichai et al., 2022).

Population structure affects genomic prediction efficiency, with within-cluster cross-validation less efficient than random cross-validation. Under GS, genetic variance declines faster than under phenotypic selection, necessitating timely adjustments in breeding or training populations (Gaynor et al., 2017; Tessema et al., 2020). To ensure long-term success in cassava breeding programs with GS, it is crucial to adapt population structures that preserve genetic diversity while maximizing genetic gain in GS operations.

LD decay and effective population size (Ne) are critical factors in gGS. LD decay informs marker density optimization for accurate prediction models, with rapid LD decay requiring higher marker density. LD persistence over longer distances enhances prediction accuracy. Ne influences genetic diversity, recombination, and population structure, affecting model accuracy. Understanding these factors is crucial for maximizing genetic gain in breeding programs through efficient marker use and accurate predictions. The study by Phumichai et al. (2022) investigates the relationship between genetic diversity and population structure in cassava (*Manihot esculenta* Crantz). Using genomic data, the study analyzes patterns of genetic variation across different cassava populations. Phumichai et al. highlight the impact of cross-pollination on LD decay, noting that LD decays more rapidly in cross-pollinated species compared to self-pollinated ones due to increased recombination (Flint-Garcia et al., 2003; Phumichai et al., 2022). Despite the allogamous nature of cassava, LD patterns may impact prediction accuracy in GS breeding (Jannink et al., 2010; Yabe et al., 2018). Nevertheless, the observed LD in this study suggests potential for enhanced accuracies in GS breeding using this population (Phumichai et al., 2022).

In summary, the GS approach can enhance selection accuracy, improving agronomic traits and adaptability beyond traditional methods. Integrating GS into cassava breeding promises genetic gains, particularly when combined with multi-trait strategies and advanced breeding tools. Continuous breeding and strategy optimization are vital for maintaining GS effectiveness. After a decade of GS applied to cassava and substantial investments made, it is imperative to evaluate not just its future potential but its proven efficacy, especially concerning challenging traits like FRY.

7.7. Genetic transformation and genome editing

Cassava genetic transformation initiatives trace back to the 1990s, marked by substantial investments aimed at generating valuable germplasm. Efforts spanned various areas, including herbicide tolerance (Sarría et al., 2000), cyanogenic potential reduction (Jørgensen et al., 2005), root starch content enhancement (Ihemere et al., 2006), improvements in starch quality traits (Luo et al., 2022; Raemakers et al., 2005; Zhao et al., 2011), leaf retention (Zhang et al., 2010), resistance to CMD and CBSD (Beyene et al., 2016; Fofana et al., 2004; Vanderschuren et al., 2007), cold tolerance (An et al., 2016), and nutritional quality enhancement (Gaitán-Solís et al., 2015; Stupak et al., 2006; Welsch et al., 2010). Regrettably, some transformation protocols yielded unintended outcomes, such as the loss of the CMD2 resistance source to the virus (Beyene et al., 2016). No genetically modified cassava varieties have been released to date.

Concerted efforts are directed towards leveraging biotechnological interventions to amplify cassava yield by optimizing source-sink interactions (Rodrigues et al., 2019; Yan et al., 2019; Yu et al., 2015). These interventions target the augmentation of photosynthetic carbon assimilation and the rerouting of chloroplastic glycolate away from photorespiration (de Souza et al., 2020). Moreover, endeavors encompass the attenuation of post-harvest physiological deterioration, reinforcement of disease resistance, biofortification, and bolstering stress tolerance in cassava cultivation (Hu et al., 2018; Narayanan et al., 2019; Veley et al., 2023). Despite the considerable promise of genome editing for addressing pivotal traits in cassava, governmental regulations heavily oversee food products derived from biotechnology, with only a select few countries permitting their usage (Turnbull et al., 2021).

7.8. Phenomics

Conventional breeding methods address challenges but hinder long-term research due to laborious and destructive nature. Developing non-destructive, real-time monitoring tools for cassava traits is crucial. Integration of phenotyping tools from high-through with machine learning models should further enhance elite genotype selection while optimizing resources for enhanced genetic gain. Unmanned aerial vehicles (UAVs) bring to precision the tasks of breeding by utilizing aerial image phenotyping and machine learning (Selvaraj et al., 2020), still with hurdles in data processing.

Phenomics provides spectral imaging and sensor technologies, which may be of important use to plant nutrient phenotyping in cassava breeding. These could be very promising techniques with high predictive ability for the total carotenoid content (de Carvalho et al., 2022) and could be applied to forage and crop evaluation in quality.

Mobile Near-Infrared Spectroscopy (NIRS) indicates a promising technique for in-field phenotyping of the pasting properties of the roots of cassava with machine learning models (Nkouaya Mbanjo et al., 2022). However, affordability and portability in tools such as SCiO support NIR use (Nkouaya Mbanjo et al., 2022). It is due to the high potential that NIRS technology has been considered as a tool for rapid, simultaneous, and accurate analysis of cassava quality traits (Alamu et al., 2020; Belalcazar et al., 2016; Kanaabi et al., 2023; Namakula et al., 2023;

Nkouaya Mbanjo et al., 2022), which could exert an important impact on the transformation. Despite its proven utility and diverse applications, NIRS has its limitations. For instance, the current protocol for evaluating cyanogenic glucosides only enables differentiation between bitter and non-bitter genotypes (Kanaabi et al., 2023) as the standard errors of predictions remain high (Chaiareekitwat et al., 2024; Sánchez et al., 2014).

Various omics datasets, such as proteomics, metabolomics, and transcriptomics, provide valuable insights into cassava traits (Ding et al., 2023; Perez-Fons et al., 2019; Nye et al., 2023; Ramulifho and Rey, 2021; Shan et al., 2018; Vanderschuren et al., 2014). Proteomics studies elucidate essential proteins involved in starch biosynthesis and stress tolerance, facilitating high-grade product production and understanding of abiotic stress responses (Ramulifho and Rey, 2021; Vanderschuren et al., 2014; Shan et al., 2018). Metabolomics analyses establish connections between low lignification and whitefly susceptibility, while identifying pathways related to viral interactions (Perez-Fons et al., 2019; Nye et al., 2023). Despite their potential, scalability remains a challenge, particularly for early-stage selection.

8. Evaluating technological impact

In the realm of basic gain from selection, direct selection involves the identification of individuals based on their phenotypic performance for a specific trait. This process is quantified using a fundamental equation: ($G = S{\cdot}h^2$), where G represents the gain from selection, S is the selection differential, and h^2 denotes the heritability of the trait. Breeders improve gains by refining selection criteria, increasing selection differentials, and using new breeding technologies. They directly optimize indirect selection through technological advancements.

Indirect selection relies on choosing individuals based on traits genetically correlated with the target trait of interest. This method exploits genetic correlations between traits, enabling genetic gain even when directly measuring the target trait is difficult. The gain from indirect selection (G_{indirect}) is influenced by the genetic correlation (rg) between the target and correlated traits, as well as the heritability (h_x) and selection differential (S_x) of the correlated trait. By leveraging these relationships, breeders can indirectly enhance the trait of interest, thus achieving genetic gain through indirect means.

Furthermore, relative efficiency RE calculated as genetic gain calculated by the first trait or strategy (G_1) divided by genetic gain achieved by the second trait or strategy (G_2) and serves as an important metric for comparing the effectiveness of different breeding strategies or improvement of traits in achieving genetic gains. RE can be evaluated on a per cycle, per dollar invested, and per time basis. By calculating RE on these bases, breeders can effectively assess the efficiency and effectiveness of different strategies, aiding in decision-making and resource allocation in breeding programs.

MAS can enhance gain per year, cycle, and dollar by streamlining tasks and optimizing resource utilization, especially in early generation selection. It achieves this through factors like the relative efficiency of selection in early generations, dependent on traits' heritability, genetic correlation between markers and traits, and marker assay accuracy. MAS reduces breeding cycle time via background genome selection and ensures quality control within breeding programs.

Conversely, GS can accelerate breeding, capturing both small and large effect QTLs and replicating elite and exotic alleles, thus enhancing gain per year and dollar spent. Breeders should integrate GS with other approaches for optimal breeding outcomes.

9. Concluding remarks

The future of cassava breeding depends on the sensible integration of emerging technologies, particularly when they demonstrate clear advantages over conventional phenotypic approaches. Transitioning toward inbred-parent-based systems can help overcome challenges posed by heterozygous progenitors, thereby improving breeding efficiency and adaptability. Although inbreeding depression remains a concern, inbreeding remains the most straightforward strategy for systematically eliminating deleterious alleles. Exploiting within-family variation and the genetic diversity present in wild relatives will further strengthen breeding programs.

Hybrid breeding, molecular tools, genomic selection, genome editing, and phenomics offer promising avenues for accelerating genetic improvement, despite regulatory and scalability challenges. Continuous refinement and integration of these diverse strategies will enable cassava breeding to meet evolving demands, ensuring greater resilience and productivity under changing environmental and market conditions.

Recent advancements in CRISPR-based technologies, molecular markers, and omics disciplines—including proteomics, metabolomics, and phenomics—together with predictive models for trait selection powered by artificial intelligence and machine learning, provide valuable insights that may be incorporated into cassava breeding pipelines. Nevertheless, developing innovative and efficient methods for the introgression of useful traits remains one of the major challenges for the future of cassava improvement.

CRediT authorship contribution statement

Hernán Ceballos: Writing – review & editing, Writing – original draft, Data curation, Conceptualization. **Sean Fenstemaker:** Writing – review & editing, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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