Chapter 11
Biotechnology Approaches in Breeding for Biotic Stress Resistance in Yam (*Dioscorea* spp.)

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Abstract Yam (*Dioscorea* spp.) is a major staple and cash crop in tropical and subtropical regions. However, biotic (fungus, viruses, tuber rots, nematodes, insects, etc.) and abiotic stresses (drought, low soil fertility, etc.) substantially impact the productivity and quality of yam crop in regions where it is majorly cultivated.

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Developing and deploying resilient cultivars is a cost-effective and environmentally sound approach to enhance productivity in stressful environments. Breeding initiatives in yam to develop improved cultivars have long relied on conventional or classical methods, which are time-consuming and labor-intensive. However, in recent years, biotechnological approaches are being successfully introduced into yam genetic improvement to shorten the breeding cycle, optimize parent selection, predict cross and progeny performances, identify seedling sex, and break interspecific hybridization barriers among yam species. The approaches include next-generation sequencing-based genotyping, transcriptomics, metabolomics, genetic transformation, gene editing, genome-wide association studies, genomic prediction, marker-assisted selection, in vitro culture, ploidy analysis, and somatic hybridization. Although several advances have been attained in yam research to identify regions controlling key traits for biotic stresses, there is low translation to widespread applications in yam cultivar development. This chapter reviews the status and prospects of resistance breeding for yam and discusses biotechnology approaches in breeding multiple-stress-resistant cultivars. In addition, it provides insights in to the broader implementation of biotechnological tools in yam breeding and research.

Keywords Marker technology · Anthracnose · Yam mosaic virus · Nematode · Variety development

11.1 Introduction

Yam is a generic name for ~600 species of the *Dioscorea* genus (Wilkin et al. 2005; Darkwa et al. 2020a). Of these species, 11 are widely cultivated. These include *D. alata* L., *D. rotundata* Poir., *D. esculenta* (Lour.) Burkill, *D. cayenensis* Lam., *D. bulbifera* L., *D. dumetorum* (Kunth) Pax, *D. trifida* L., *D. opposite* Thunb., *D. japonica* Thunb., *D. nummularia* Lam., and *D. pentaphylla* L. (Darkwa et al. 2020a). In addition to these cultivated species, there are semi-domesticated and wild species such as *D. burkilliana* J. Miège, *D. minutiflora* Engl., *D. praehensilis* Benth., *D. schimperiana* Hochst. Ex Kunth., *D. semperflorens* Uline, *D. mangenotiana* J. Miège, *D. smilacifolia* De Wild. & T. Durand, etc., grown on a subsistence basis or collected from the wild to fill the hunger gap during drought and lean periods (Adewumi et al. 2021). Based on its economic importance, yam ranks fourth among root and tuber crops following cassava, potato and sweet potato worldwide and the second to cassava in West Africa (Alabi et al. 2019). It is cultivated for starchy underground and aerial tubers rich in vitamin C, dietary fiber, vitamin B6, protein, potassium,

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and manganese and low in saturated fat and sodium (Arnau et al. 2010). The crop provides 200 cal a day to ~300 million people in tropical and subtropical countries (Price et al. 2017, 2020). Some yam species are sources of secondary metabolites used for industrial and pharmaceutical purposes (Price et al. 2018).

West Africa is the major producer and consumer of yam. Six countries, namely Nigeria, Ghana, Côte d'Ivoire, Benin, Cameroon, and Togo, accounted for 92% (~67 million tons) of the global yam production in 2018 (FAO 2020). In these countries, referred to as "the African yam belt", the per capita consumption is high, ~40 kg per person per year with significant disparities (9–73 kg) among ethnic groups (Bricas and Attaie 1998). In this region, yam represents an opportunity for poverty alleviation as ~5 million people directly depend on its value chain for income (Mignouna et al. 2020). The yam production is also part of religious and socio-cultural events (Sartie and Asiedu 2011; Darkwa et al. 2020a; Obidiegwuet al. 2020).

Biotic (fungus, viruses, nematodes, insect pests) and abiotic (drought, low soil fertility, etc.) stresses are among the major yield-limiting factors in low input yam farming systems (Arnau et al. 2010; Frossard et al. 2017; Darkwa et al. 2020a; Matsumoto et al. 2021; Morse 2021). These factors keep the average yam yield at ~10 t ha^{-1}, far below its potential (40 and 50 t ha^{-1} for *D. rotundata* and *D. alata*, respectively) (Frossard et al. 2017; FAO 2020). In the last two decades (1998–2018), yam production in West Africa doubled from ~34 to 67 million tons, as a result of rapid expansion of cultivated lands (from ~3.6 to 8.1 million hectares). During the same period, the productivity oscillated between 8 and 12 t ha^{-1} with a decreasing trend (FAO 2020). The current extensive yam farming and the search for new fertile lands will soon reach the limit due to rapid population growth. Besides, expanding cultivated lands is often associated with deforestation, which could exacerbate climate change in the region. Table 11.1 provides an estimate of yield losses associated with major yam biotic and abiotic stresses. Fast population growth and climate change will most probably worsen these stresses in sub-Saharan Africa (Srivastava et al.

Table 11.1 Yield losses associated with major biotic and abiotic factors in yam production

Factors	Species	Yield loss (%)	Distribution	Reference
YMV	*D. rotundata*	40–50	West Africa	Adeniji et al. (2012)
YAD	*D. alata*	80–90	Worldwide	Penet et al. (2016)
Tuber rots	*D. rotundata*	25–40	West Africa	Bonire (1985), Acholo et al. (1997)
Nematode	*D. rotundata*	~40	West Africa	Atu et al. (1983), Kolombia et al. (2017)
Drought + heat	*D. alata*	18–33	West Africa	Srivastava et al. (2012)
Low soil fertility	*D. rotundata*	33–70	West Africa	Matsumoto et al. (2021)
Waterlogging	*D. alata & rotundata*	~57	West Africa	Igwilo and Udeh (1987)

YMV Yam mosaic virus, *YAD* Yam anthracnose disease

2012; Thiele et al. 2017; Friedmann et al. 2018). An extensive use of external inputs (fertilizers, pesticides, irrigation, etc.) to control these constraints is unpractical for the predominantly resource-poor farmers and harmful to the environment. There is, therefore, a need for developing high-yielding varieties with resistance to biotic and abiotic stresses and deliver them to farmers through a functional seed system (Friedmann et al. 2018; Mondo et al. 2021a). Breeding for resistance has several advantages over using chemicals or any other external input: it is cost-effective, practical, usually long-lasting, efficient, and safer for the environment and humans (Hua et al. 2020).

Yam breeding still largely relies on conventional or classical methods for variety development. These are, however, time-consuming and labor-intensive (Darkwa et al. 2020a). It takes more than ten years to get a variety released using conventional approaches. Therefore, a range of biotechnological approaches are being successfully introduced into yam research. These approaches include next-generation sequencing (NGS)-based genotyping procedures, transcriptomics, metabolomics, genetic transformation (or transgenics), gene editing, marker-assisted selection, ploidy analysis, etc. (Darkwa et al. 2020a). The approaches aimed at shortening the breeding cycle, optimizing the breeding program as well as fast developing yam varieties to meet end-user' preferences (Tamiru et al. 2017; Friedmann et al. 2018; Darkwa et al. 2020a).

Among the advanced approaches adopted by the International Institute for Tropical Agriculture (IITA) and research partners under Africa Yam and NSF-BREAD projects, Genome-wide association studies (GWAS) are currently underway. GWAS efforts are to determine quantitative trait loci (QTLs) linked to various traits such as yam mosaic virus (YMV), yam anthracnose disease (YAD) resistance, dry matter content, tuber browning index, plant sex, etc. in *D. rotundata* and *D. alata* and thus facilitate marker-assisted breeding in yam (Gatarira et al. 2020; Darkwa et al. 2020a; Sugihara et al. 2020; Mondo et al. 2021b). In vitro culture is routinely used for germplasm conservation; multiplication (meristem culture) of disease-free plants; embryo rescue for interspecific crosses and chromosome doubling of diploids (Aighewi et al. 2015; Babil et al. 2016). In addition, somatic hybridization and transgenesis activities have been reported (Arnau et al. 2010; Nyaboga et al. 2014; Manoharan et al. 2016; Syombua et al. 2021). Semi-autotrophic hydroponic (SAH) technology has been implemented in yam breeding at IITA and holds potential for reduced breeding cycle and rapid quality seed delivery in West Africa (Pelemo et al. 2019).

Although several advances have been made in yam research to identify genomic regions associated with key economic traits (www.africayam.org), their applications in yam breeding programs are limited. This chapter reviews current and prospective biotechnology approaches for breeding varieties that are resistant to biotic stresses.

11.2 Genetic Resources and Diversity Analysis for Yam Resistance Breeding

To put the biotechnological approaches in context, it is essential to appreciate the extent of diversity and understand the taxonomic and cytological complexity of yams. The world checklist in Royal Botanic Gardens, Kew includes 644 accepted species for the family Dioscoreaceae from five genera: *Dioscorea, Rajania, Tacca, Stenomeris,* and *Trichopus* (Govaerts et al. 2007). Yams belong to the genus *Dioscorea* L., which is the largest genus in the family Dioscoreaceae, in the order Dioscoreales. This genus is made of ~600 species and thus constitutes ~95% of the family species (Govaerts et al. 2007, 2017).

The genus *Dioscorea* is subdivided into five sections based on gross morphological characters. The section Enantiophyllum is the largest in terms of the number of species and includes the most important yam species such as *D. alata*, *D. rotundata,* and *D.cayenensis*. Other members of this section are *D. opposita*, *D. japonica,* and *D. transversa* (Bai and Ekanayake 1998). Members of this section are characterized by vines that twine to the right, i.e., in the clockwise direction when viewed from the ground upwards (Bai and Ekanayake 1998). The other sections containing cultivated yam species are Lasiophyton (*D. dumetorum* and *D. hispida*), Macrogynodium (*D. trifida*), Combilium (*D. esculenta*), and Opsophyton (*D. bulbifera*), which are characterized by vines twining to the left (Onwueme and Charles 1994; Bai and Ekanayake 1998).

Gene flow among these yam species is often constrained by pre-and post-zygotic barriers resulting from the evolutionary divergence among them (Mondo et al. 2020, 2021a). However, spontaneous and controlled interspecific hybrids of *D. rotundata* with its wild relatives (*D. abyssinica, D. burkilliana*, and *D. praehensilis*) and between *D. alata* and *D. nummularia* were reported (Akoroda 1985; Scarcelli et al. 2006; Arnau et al. 2010; Loko et al. 2013; Lebot et al. 2019a; Mondo et al. 2020, 2021a).These interspecific crosses allow broadening the genetic base of cultivated yam species and introgress resistance and adaptation trait genes. Reports showed that most failures in interspecific hybridizations were linked to differences in ploidy levels among *Dioscorea* species (Arnau et al. 2010; Mondo et al. 2020, 2021a). CIRAD-Guadeloupe had established embryo rescue techniques that hold the potential to facilitate interploidy crosses in yam breeding (Abraham et al. 2013).

In addition to the large genetic diversity in terms of species, there are several cultivars within each yam species and whose names vary greatly with local and national languages and their sources. This makes the assessment of the diversity of local landraces challenging, as more often, several names are used for the same clone or a single name may be allocated to several cultivars (Azeteh et al. 2019a; Kouakou et al. 2019; Adewumi et al. 2021; Bakayoko et al. 2021). Therefore, more elaborate and robust studies are necessary for West Africa to effectively determine the genetic diversity of yam within the region to facilitate the conservation efforts and use of existing variability in the crop improvement programs. In response to this, several genetic diversity studies have been conducted on yam worldwide and in West Africa in

particular. These included inventories and characterizations of local landraces using phenotypic traits, isozymes, and molecular markers (Darkwa et al. 2020a). Due to limitations of phenotypic markers (limited number, highly influenced by environment and plant developmental stages); molecular markers were introduced as stable and abundant across the genome. Molecular markers used in previous genetic diversity studies for yam include random amplified polymorphic DNA (RAPD) (Asemota et al. 1995), amplified fragment length polymorphism (AFLP) (Mignouna et al. 1998; Terauchi and Kahl 1999; Mignouna et al. 2002a, b), simple sequence repeat (SSR) (Arnau et al. 2009; Loko et al. 2017; Mulualem et al. 2018), inter simple sequence repeat (ISSR) (Ousmael et al. 2019), and single nucleotide polymorphism (SNP) markers (Agre et al. 2019, 2021a, b, c; Darkwa et al. 2020b; Bhattacharjee et al. 2020; Bakayoko et al. 2021). There is an increasing interest in combining phenotypic and genotypic information while dissecting functional genetic diversity in plants. The trend is explained by the fact that a large part of the variability discovered by DNA markers is non-adaptive while variations detected by phenotypic markers/characters are often under environmental influence (Arnau et al. 2017; Agre et al. 2019). The effectiveness of combined analysis vis-à-vis separate use of molecular or phenotypic markers in dissecting genetic diversity and defining genetic group has been reported (Sartie et al. 2012; Agre et al. 2019, 2021a, b, c; Darkwa et al. 2020b) and has been adopted. Despite the large number of yam diversity analysis studies, little research has been conducted in determining the sources of resistance to major biotic and abiotic stresses among breeding lines and landraces in West Africa. Most studies had a general focus and did not target specific traits in characterizing the germplasm.

Yam genetic diversity is seriously threatened by genetic erosion due to absent/poor germplasm conservation facilities and the lack of financial support for germplasm maintenance in most West African countries (https://www.iita.org/research/genetic-resources/). Even though accessions of *D. rotundata, D. alata, D. cayenensis, D. bulbifera,* and *D. dumetorum* are available in large quantity across the West and Central Africa, Azeteh et al. (2019a) warned that *D. esculenta, D. liebrechtsiana, D. schimperiana,* and *D. trifida*, are at high risk and are increasingly rare. Research and maintenance of existing diversity are still weak in most of the West African countries. Farmers only maintain the species and genotypes suitable to their needs, an attititude which accelerates genetic erosion in most countries (Adewumi et al. 2021). Semi-domesticated species, such as *D. praehensilis,* are threatened by bushfires and deforestation in countries like Ghana (Adewumi et al. 2021). Furthermore, only on-farm conservation is done in most countries without any backup in the form of in-vitro culture or cryopreservation, despite the exposure of conserved materials to environmental stresses exacerbated by climate changes (Adewumi et al. 2021). The few existing conservation initiatives often focus on cultivated species and neglect wild relatives, which are crucial in crop improvement programs as they possess genes for resistance to pests and diseases and are the source of genes for adaptation traits (Mondo et al. 2021a).

It is noteworthy to recognize the conservation efforts by IITA and its partners in West Africa. The IITA maintains the largest collection of yams in the world (Darkwa et al. 2020a). Its yam germplasm collections steadily increased from 3319 in 2010

to 5788 in 2018 and from 8 to 10 species during the same period (IITA 2018). These accessions were mainly collected from West and Central Africa, and *D. rotundata* constitutes ~68% of the collection. Other species in the IITA collection include *D. alata* (21.8%), *D. burkiliana* (6.2%), *D. abyssinica* (1.6%), *D. cayenensis* (1.5%), *D. dumetorum* (1.3%), *D. prehensilis* (1.2%), *D. bulbifera* (1.2%), *D. esculenta* (0.4%), *D. preusii* (0.17%) and *D. mangenotiana* (0.14%). All these accessions are grown annually in the field, but 1544 of these are also maintained as in vitro plantlets for conservation and research purposes. The entire IITA core collection is undergoing genotyping by sequencing (GBS) and detailed phenotyping for identifying sources of resistance genes to broaden the genetic base of currently used breeding populations as well as for cryo-conservation.

11.3 Highlights of Classical Genetics and Breeding

11.3.1 Cytogenetics and Yam Genome Size

Dioscorea is a problematic genus for cytogenetic investigations. Counting chromosomesis challenging due to their small size and their tendency to stick together. Besides, satellites of chromosomes are often as large as the chromosomes themselves (Bousalem et al. 2006). The basic number of chromosomes of *D. rotundata, D. alata,* and *D. trifida* (the three main cultivated yam species) is $x = 20$ (Arnau et al. 2010). *Dioscorea rotundata* is predominantly diploid ($2n = 2x = 40$); *D. cayenensis* is dominated by triploid males ($2n = 3x = 60$); while *D. alata*is polyploid with diploid, triploid, and tetraploid individuals ($2n = 4x = 80$). The ploidy status trends, as above-described, have recently been confirmed by Gatarira (2021) in the IITA core collection of eight species using three methods (chromosome counts, SNP marker, and impedance flow cytometry).

Previous reports showed that triploid and tetraploid yam cultivars are often more vigorous and productive compared with diploid counterparts (Lebot 2009; Arnau et al. 2010). Besides, there are reports demonstrating an association between a cultivar/species' ploidy level and its ability to flower (or sex of the flower it produces) or produce viable seeds in yam. For instance, triploids are either male or non-flowering (sterile) compared to diploid individuals which are highly fertile and form viable seeds (Abraham and Nair 1991; Girma et al. 2014, 2019). Besides, cross-pollination success is highly influenced by parents' ploidy statuses; such that inter-ploidy hybridization is seldom successful and when successful seedling survival rate is low (Lebot et al. 2019a). Studies manipulating/doubling the chromosome number using in vitro polyploidy induction have been successful (Babil et al. 2016).

11.3.2 Breeding Objectives and Farmers' Trait Preference Criteria

Although varying with regional priorities and the species involved, the main yam breeding objectives are:

- High and stable tuber yield
- Good tuber quality including low flesh oxidation rate (browning of the cut tuber), taste, texture, dry matter content, aroma, etc.
- Tuber characteristics that facilitate harvesting and meet consumers' needs (size, shape, culinary quality, tuber texture/smoothness)
- Plant architecture (e.g. dwarf types) that suppresses staking
- Resistance to abiotic (drought and low soil nutrients) and biotic stresses (virus, fungi, rots and nematodes).

These breeding objectives change over time and are influenced by farmers' and other end-user's local/regional preferences. These local trait preferences include short growth cycle, resistance to in-soil deformation, long storability of harvested tubers, and acceptable culinary qualities for both consumers and processors. Unfortunately, many of these traits are still missing in released varieties, and thus, explain their low market penetration (Darkwa et al. 2020a). Therefore, to boost the adoption of new varieties, the focus of yam breeding programs in West Africa should be led by farmers' and other end-user's expectations.

In West Africa, expectations from a variety vary significantly with the local preferences of each ethnic group. In general, farmers' preferences for yam varieties are driven by the culinary quality of tubers, productivity, market demand, seed propagation rate, quality of chips, maturity period (double/early harvested), post-harvest storage aptitude, resistance to biotic and abiotic factors, multiple roles as food and for ceremonies (Akoroda 1993; Adewumi et al. 2021). White color and elongated or round tubers are ideal traits for commercialization (Silva et al. 2017). Also, with the above traits, giant ceremonial tubers are used for socio-cultural events (Akoroda 1993). Consumers and processors mostly target yam varieties with superior eating quality such as mealiness, taste, and softness (Addy 2012). Besides, processors look for varieties with shorter processing time, gel strength and elasticity, low viscosity, and paste stability at low temperatures, pasting properties of flours that increase the range of options for consumers on the local and export markets (Addy 2012). Low moisture content is critical in yam export as this enhance storability and the yam shelf-life. Varieties with high dry matter and starch content are increasingly preferred to making flour used in many dishes such as the "Amala" in West Africa.

Efforts at modernizing yam processing in West Africa were hindered by the failure to design a single product meeting different ethnic groups' expectations. Besides, consumers are not paying for the extra cost incurred in new yam products; they perceive them as expensive compared to their advantages (Bricas and Attaie 1998).

11.3.3 Yam Breeding Challenges and Mitigation Methods

The complexity of yam reproductive biology and the expected low research investment returns have limited the attention given to yam breeding. The complexity lies mainly in its unpredictable and low flowering behavior. These sexual reproduction abnormalities result from continuous vegetative propagation following domestication (Mondo et al. 2020). Some genotypes do not flower at all or flower in some years and under particular conditions (Girma et al. 2019; Darkwa et al. 2020a). Besides, there are differences in flowering intensity among male and female plants, poor synchronization of flowering periods, low pollen viability, low stigma receptivity, low fruit and seed set, and low seed viability (Lebot et al. 2019a; Agre et al. 2020; Mondo et al. 2020, 2021c). Before understanding its cytology, some cultivated yam species, such as *D. alata*, were thought to be completely sterile, and thus, unable to undergo hybridization (Arnau et al. 2010).

Several breeding methods and techniques are used in yam improvement, including the domestication of wild species, introduction and selection, hybridization (intra- and inter-specific crosses), cytogenetic and mutation techniques, in vitro culture, transformation, and molecular breeding (Arnau et al. 2010; Darkwa et al. 2020a).

Despite its limitations (labor-intensive and time-consuming), conventional, also referred to as traditional breeding, is the major contributor of improved yam cultivars released in West Africa. Collaborative research between IITA, National Root Crops Research Institute (NRCRI, Umudike, Nigeria), and the Crops Research Institute of Ghana (CRIG) developed and released 15 *D. rotundata* clones in Nigeria and two in Ghana for the period of 2001–2016. With the advent of the AfricaYam project, several other *D. alata* and *D. rotundata* varieties have been released in Nigeria, Ghana, Benin, and Côte d'Ivoire (Table 11.2).

Up to date, no improved variety from molecular breeding has been reported (Darkwa et al. 2020a). Advances achieved in incorporating molecular markers in yam breeding programs in West Africa are discussed in Sect. 11.4 on the current status of yamomics resources.

11.3.4 Yam Breeding Scheme

The yam breeding scheme is a cyclic and incremental process (Fig. 11.1). It starts with goal setting followed by creating and identifying variability, evaluation, and selection of superior variants in a target set of environments and final release into the production system. As the yam cycle is very lengthy from the parental selection to the release process, SAH techniques are optimized at the IITA for rapid multiplication of seed yam using explants such as nodal leaves (Pelemo et al. 2019). Correct product profiling and choice of desirable parents for crossing are stepping stones in the process. Parent choice is based on trait profiling and genetic merits' studies in breeders' working collections, gene bank accessions, landrace cultivars, and related

Table 11.2 List of released yam varieties across WestAfrica

SN	Clones	Species	Country of release	Year of release	Attribute traits	Disease reaction
1	TDr8902677	*D. rotundata*	Nigeria	2001	Stable yield, very good cooking and pounding qualities, cream non-oxidizing tuber flesh, 25% tuber dry matter	Tolerant to YMV
2	TDr8902565	*D. rotundata*	Nigeria	2001	Stable yield, very good cooking and pounding qualities, cream non-oxidizing tuber flesh, 35% tuber dry matter	Tolerant to YMV
3	TDr8902461	*D. rotundata*	Nigeria	2001	Stable yield, very good cooking and pounding qualities, cream non-oxidizing tuber flesh, 26.7% tuber dry matter	Tolerant to YMV
4	TDr8902665	*D. rotundata*	Nigeria	2003	Stable yield, very good cooking and pounding qualities, cream non-oxidizing tuber flesh, 35.3% tuber dry matter	Tolerant to YMV
5	TDr8901213	*D. rotundata*	Nigeria	2003	Stable yield, very good cooking and pounding qualities, white non-oxidizing tuber flesh, 29.8% tuber dry matter	Tolerant to YMV
6	TDr8901438	*D. rotundata*	Nigeria	2003	Stable yield, very good cooking and pounding qualities, white non-oxidizing tuber flesh, 29.3% tuber dry matter	Tolerant to YMV

(continued)

Table 11.2 (continued)

SN	Clones	Species	Country of release	Year of release	Attribute traits	Disease reaction
7	TDr9501924	*D. rotundata*	Nigeria	2003	Stable yield, very good cooking and pounding qualities, white non-oxidizing tuber flesh, 35% tuber dry matter	Tolerant to YMV
8	Drn20042	*D. rotundata*	Nigeria	2008	High yielding (35 t ha^{-1}), pests and diseases tolerant, very good for fufu, frying and boiling	Tolerant to YMV
9	TDa9801176	*D.alata*	Nigeria	2008	High yielding (26–30 t ha^{-1}), pests and diseases tolerant, very good for fufu, frying and boiling, suitable for rainy and dry yam production seasons	Tolerant to YAD
10	TDa9801168	*D. alata*	Nigeria	2008	High yielding (24–28 t ha^{-1}), pests and diseases tolerant, good for pounding and boiling	Tolerant to YAD
11	TDa9801166	*D. alata*	Nigeria	2008	High yielding (26–30 t ha^{-1}), pests and diseases tolerant, very good for fufu, frying and boiling, suitable for rainy and dry yam production seasons	Tolerant to YAD
12	TDr9519158	*D. rotundata*	Nigeria	2009	High yielding (29.4 t ha^{-1}), pests and diseases tolerant, good for pounding and boiling	Tolerant to YMV

(continued)

Table 11.2 (continued)

SN	Clones	Species	Country of release	Year of release	Attribute traits	Disease reaction
13	TDr8902602	*D. rotundata*	Nigeria	2009	High yielding (31.5 t ha^{-1}), pests and diseases tolerant, good for pounding and boiling	Tolerant to YMV
14	TDr8902660	*D. rotundata*	Nigeria	2009	High yielding (31 t ha^{-1}), pests and diseases tolerant, good for pounding and boiling	–
15	TDa0000194	*D. alata*	Nigeria	2009	High yielding (37.5 t ha^{-1}), pests and diseases tolerant, good for pounding and boiling	Tolerant to YAD
16	TDa0000104	*D. alata*	Nigeria	2009	High yielding (30 t ha^{-1}), pests and diseases tolerant, very good for fufu, frying, boiling and pounded yam	Tolerant to YAD
17	TDa0000364	*D. alata*	Nigeria	2010	High yielding (33.3 t ha^{-1}), good for "*Amala*", frying and boiling	Tolerant to YAD
18	TDr95/19177	*D. rotundata*	Nigeria	2010	High yielding (30 t ha^{-1}) under dry season planting	Tolerant to YAD
19	TDr8902475	*D. rotundata*	Nigeria	2010	High yielding (31 t ha^{-1}), very good for yam fufu, frying and boiling	Tolerant to YMV
20	TDr9800933	*D. rotundata*	Nigeria	2016	High yielding (39.8 t ha^{-1})	Tolerant to YMV
21	TDr98Amo064	*D. rotundata*	Nigeria	2016	High yielding (43.9 t ha^{-1})	Tolerant to YMV

(continued)

Table 11.2 (continued)

SN	Clones	Species	Country of release	Year of release	Attribute traits	Disease reaction
22	TDa1100316	*D. alata*	Nigeria	2019	High tuber yield (33 t ha^{-1}) and stability, high dry matter (30.5%), tuber flesh non-oxidation or browning after cut	Tolerant to YAD
23	TDa1100201	*D. alata*	Nigeria	2019	High tuber yield (34 t ha^{-1}) and stability, high dry matter (33.5%), tuber flesh non-oxidation or browning after cut	Tolerant to YAD
24	TDa1100432	*D. alata*	Nigeria	2020	High dry matter content, high yield (43 t ha^{-1}), excellent boiling and pounding quality	Tolerant to YAD
25	TDr0900067	*D. rotundata*	Nigeria	2020	Potential yield of 22 t ha^{-1} and high dry matter content (30.85%)	Tolerant to YMV
26	TDr10/00048	*D. rotundata*	Nigeria	2020	Potential yield of 24 t ha^{-1} and high dry matter content (30.9%)	Tolerant to YMV
27	MankrongPona	*D. rotundata*	Ghana	2005	Potential yield of 45–70 t ha^{-1} and 34.63% dry matter	Tolerant to YMV
28	CRI Pona	*D. rotundata*	Ghana	2005	Potential yield of 26–42 t ha^{-1} and 33.4% dry matter	Tolerance to YMV
29	CRI Kukrupa	*D. rotundata*	Ghana	2005	Potential yield of 42–50 t ha^{-1} and 33.42% dry matter	Tolerance for YMV
30	TDa0000003	*D. alata*	Ghana	2017	–	Tolerant to YAD
31	TDa0100029	*D. alata*	Ghana	2017	–	Tolerant to YAD
32	TDa0100004	*D. alata*	Ghana	2017	–	Tolerant to YAD

(continued)

Table 11.2 (continued)

SN	Clones	Species	Country of release	Year of release	Attribute traits	Disease reaction
33	TDa0000046	*D. alata*	Ghana	2017	–	Tolerant to YAD
34	TDa0100113	*D. alata*	Côte d'Ivoire	2021	Potential yield of 40 t ha^{-1} and good culinary qualities	Tolerant to YAD
35	TDr0102562	*D. rotundata*	Côte d'Ivoire	2021	Potential yield of 30 t ha^{-1} and good culinary qualities, multiple tubering	Tolerant to YMV
36	TDa0100018	*D. alata*	Côte d'Ivoire	2021	Potential yield of 25 t ha^{-1} and good culinary qualities	Tolerant to YAD

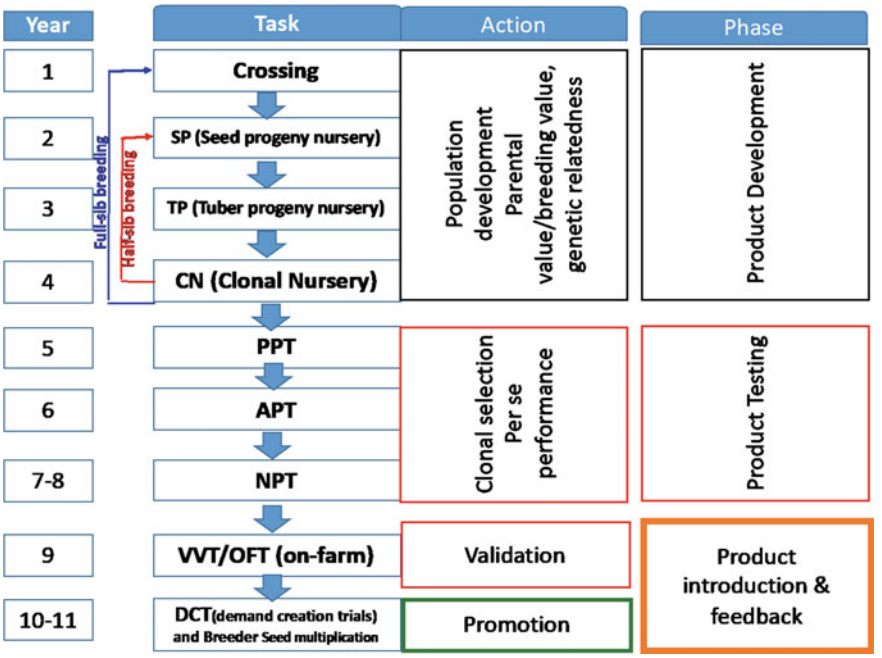

Fig. 11.1 Yam breeding scheme (*PPT* Preliminary performance trial; *APT* Advanced performance trial; *NPT* National performance trial; *VVT* Variety validation trial; *OFT* On-farm trial)

wild relatives. Parental selection for crosses considers diverse aspects: agronomic traits, tuber quality, ploidy status, flowering ability, cultivar sex, cross-combination ability, etc. (Arnau et al. 2010; Lebot et al. 2019a; Mondo et al. 2020).

Yam is mainly a dioecious plant with male and female flowers developed on different individuals (Tamiru et al. 2017; Agre et al. 2020; Mondo et al. 2020, 2021c). Thus, separate crossing blocks of males and females are required. When natural pollination is desired, male and female individual plants are grown close (1 × 1 m) to each other, and their vines are trained onto the same stakes. Polycross design (Fig. 11.2) is cheap and easy to conduct, especially when using fertile parents, although the male parent of the progenies is usually unknown (Arnau et al. 2010; Norman et al. 2018). Pedigree reconstruction of open-pollinated progenies is possible using molecular markers (Norman et al. 2020). The purity of crosses is ensured by hand pollination of parents grown in isolated plots/blocks. Although not systematically specified, the separation distance between male and female blocks usually ranges from 500 to 1000 m (Mondo et al. 2020). The same isolation distance is maintained between crossing blocks and wild environments to prevent unwanted pollen sources. Multiple planting dates are advised to increase the chances of synchronization of the flowering of male and female parents. It is noteworthy that male genotypes flower earlier than female counterparts, and thus, planting females 2–4 weeks before males will promote a synchronized flowering of parents (Mondo et al. 2020).

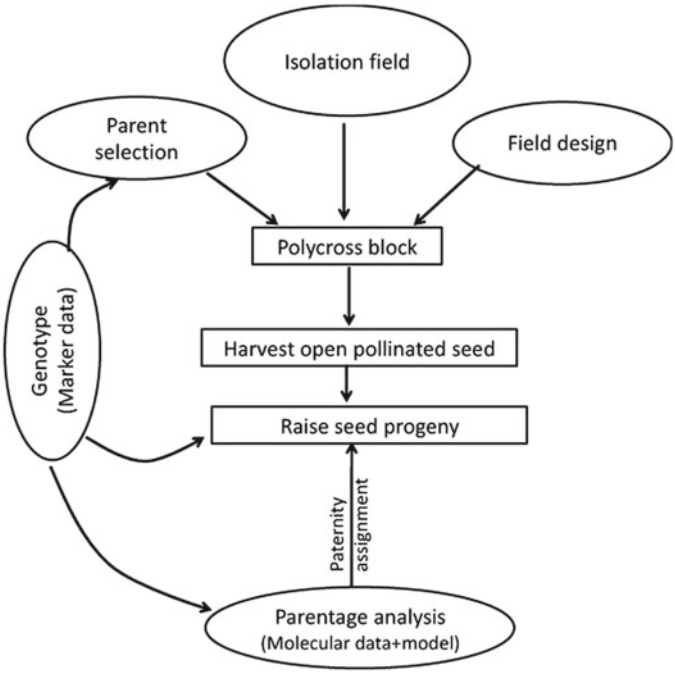

Fig. 11.2 The scheme used for yam polycross and parentage reconstruction

For controlled (hand) pollination, female inflorescences are bagged with thrip-proof cloth-bags 2–7 days before the flowers open, varying with the spike length (Darkwa et al. 2020a; Mondo et al. 2020, 2021c). Supervised hybridization through hand-pollination is recommended to ensure biparental crossing (Arnau et al. 2010). The male flower usually opens at noon, and the period of good pollen viability is rather short (2–4 h) (Mondo et al. 2020). Therefore, the indicated time for hand-pollination is 12 noon to 3 pm, after which the pollen viability decreases significantly, depending on the prevailing weather conditions (Arnau et al. 2010). It is noteworthy that female flowers are fully receptive for 6–10 days, although better results are achieved at least one day after anthesis. After pollination, flowers are kept covered for two weeks to ensure the purity of offspring from crosses (Arnau et al. 2010).

At physiological maturity when fruits start drying, botanical seeds are collected before they disperse from the capsules. These are then processed by releasing seeds, testing viability (using seed weight) and stored at appropriate temperature for about 3–4 months until the dormancy is broken (Abraham 1992). The following season, those seeds are grown in seedling trays or nursery beds (Fig. 11.3) which are filled with appropriate growing media such as carbonized rice husk and coco peat. Seed germination starts 10 days after sowing and continues for one month (Darkwa et al. 2020a). The seedlings are then transplanted to pots in a screenhouse or nursery bed in the field for single plant selections. Next steps include early clonal generation evaluation nursery, preliminary performance trial, advanced multi-location and multi-season performance trial, and on-farm variety validation trial for an official release and commercial deployment (Arnau et al. 2010; Darkwa et al. 2020a).

Only a limited number of traits are evaluated at the seedling (F_1) and the first clonal generations (C_1): flesh color, tuber oxidation, and disease symptoms (Darkwa et al. 2020a). Tuber yield is much stable from the second clonal generation (C_2),

Fig. 11.3 Yam seedlings established on seedling trays

with positive relationships with following generations. Therefore, selection for traits such as shoot vigor, disease severity, tuber shape, tuber yield, and other tuber yield components is best conducted from C_2 stage (Abraham 2002; Arnau et al. 2010).

11.4 Current Status of Yam Omics Resources

As mentioned in the introduction, various biotechnology tools are being introduced in yam breeding programs. Although there has been no report on the successful release of a yam variety using biotechnological tools (Darkwa et al. 2020a), several achievements in the path to its incorporation into yam breeding have been realized. These include the recent development of the reference genome sequences for *D. alata* (Cormier et al. 2019; Bredeson et al. 2021), *D. rotundata* (Tamiru et al. 2017; Sugihara et al. 2020), and *D. dumetorum* (Siadjeu et al. 2020), discovery of several molecular markers and genes through yam metabolomics and transcriptomics. Therefore, this section provides an overview of the use of biotechnology tools in yam breeding programs.

11.4.1 Reference Genome Sequences

Advances and decreased cost in genome sequencing through NGS technologies enabled the generation of millions of novel markers and high-density genetic maps in major food crops, including yam (Tamiru et al. 2017; Bhattacharjee et al. 2018; Cormier et al. 2019; Siadjeu et al. 2020; Bredeson et al. 2021).

Tamiru et al. (2017) developed and released the reference genome sequence of *D. rotundata* accession TDr96_F1. Its genome size is 594 Mb, out of which 76.4% is distributed among 21 linkage groups (http://genome-e.ibrc.or.jp/home/bioinformatics-team/yam). The results of gene prediction using the genome sequence showed a total of 26,198 genes in *D. rotundata.* Recently, an improved version of the *D. rotundata* sequence has been released, covering a total of 636.8 Mb and distributed on 20 linkage groups of the genome with an N_{50} of 137,007 bp (Sugihara et al. 2020) (https://www.pnas.org/content/pnas/suppl/2020/12/02/2015830117.DCSupplemental/pnas.2015830117.sapp.pdf).

Cormier et al. (2019) established the first high-density genetic map of *D. alata* using GBS. In that *D. alata* high-density map, 20 linkage groups were identified, and 1579 polymorphic markers were ordered. The consensus map length was 2613.5 cM with an average SNP interval of 1.68 cM. This corresponded with estimated genome coverage of 94% and thus, promoted further investigations on the inheritance of key traits and the development of molecular breeding tools. Recently, a reference genome for *D. dumetorum* has been developed, and the assembly represents 485 Mbp of the genome with an N_{50} of over 3.2 Mbp (Siadjeu et al. 2020). A total of 35,269 protein-encoding gene models and 9941 non-coding RNA genes were

predicted, and functional annotations were assigned. The establishment of these reference genome sequences in yam has opened a new avenue for exploitation and thorough understanding of yam genetics, genomics, and domestication, essential for successful yam breeding (Scarcelli et al. 2019; Darkwa et al. 2020a; Sugihara et al. 2020).

11.4.2 Molecular Marker Uses in Yam Improvement Programs

Cytogenetic techniques and different types of markers (isozymes, RFLP, RAPD, AFLP, SSR, and SNP) are relevant in yam breeding. These markers have been used, with different levels of reliability, in genetic diversity studies, phylogenetic relationships, estimation of population structures, cultivar fingerprinting, mapping of major effect genes and QTLs, identification of elite genotypes in crop breeding programs, and for validation of progenies originating from genetic hybridizations (Tamiru et al. 2015; Darkwa et al. 2020a). Molecular markers and genotyping systems in yam breeding have recently been reviewed by Darkwa et al. (2020a). Early use of markers in yam was mainly for diversity studies, parentage analysis, origin and phylogenetic studies, and identification of genes controlling major diseases such as YAD and YMV (Arnau et al. 2010).

From 2015, there was a shift from the predominance of genetic diversity studies to QTL analysis with the start of the AfricaYam project. IITA and its partners are making substantial efforts to develop diverse molecular markers both for Guinea and water yams (Tamiru et al. 2015, 2017; Cormier et al. 2019, 2021; Darkwa et al. 2020a). For instance, Tamiru et al. (2015) developed 90 SSR markers from an enriched genomic library of yellow Guinea yam (*D. cayenensis* Lam.) with assumption that these SSRs could be successfully transferred to the two major cultivated species (*D. rotundata* and *D. alata*). A higher level of transferability to *D. rotundata* (94%) was reported due to its proven relatedness with *D. cayenensis* (Dansi et al. 2013), while it was low with *D. alata* (57%).

The AfricaYam Project has made significant efforts to develop genomic resources to transform yam breeding in West Africa (https://africayam.org). It developed markers for major traits such as plant vigorand sex, flowering intensity, number of tubers per plant, tuber yield, flesh tuber oxidation, disease resistance (mostly anthracnose and viruses), tuber appearance, and spines on tuber surface. Different regions controlling numerous traits were identified through different gene model actions and need validation to implement marker-assisted selection in yam breeding (https://africayam.org) fully. The application of these novel methods will enhance yam breeding efforts and ensure quick delivery of high-yielding, nutrient-dense, and climate-resilient varieties to farmers in West Africa.

Effective integration of marker-assisted selection in yam breeding will allow this crop to be efficiently and quickly improved by drawing on genomic advances reported

in other crops such as maize, cassava, rice, potato, beans, etc., for which the molecular research is more advanced. Among the advantages is shortening the breeding cycle by speeding up the identification and transfer of desirable genes. In fact, markers will make possible the selection at early growth stages for traits that could only be assayed at late stages such as flower sex, tuber yield, and quality, etc. (Mignouna et al. 2008; Desta and Ortiz 2014; Hickey et al. 2017; Friedmann et al. 2018; Agre et al. 2020). Besides, the use of markers will significantly reduce the cost that could otherwise be spent in phenotyping large numbers of plant materials as done in conventional breeding. Furthermore, reliability in selection will be improved by controlling inconsistent year-to-year symptom phenotypic data that hinder conventional yam breeding (Arnau et al. 2010; Saski et al. 2015; Tamiru et al. 2015; Cormier et al. 2019). In contrast to phenotypic descriptors, molecular markers are insensitive to environmental effects. Moreover, using molecular markers will provide a deeper understanding of genes controlling the expression of traits of interest in opposition to conventional breeding. Another key advantage of molecular markers in yam breeding is to facilitate the pyramiding of genes from different sources of resistance for more durable resistance to major diseases (Arnau et al. 2010).

11.4.3 Other Genomic Tools in Yam Improvement

Many other novel genomic tools are being introduced in yam breeding including next-generation-based genotyping procedures, transcriptome sequencing, and metabolomics (Darkwa et al. 2020a).

Genotyping by sequencing (GBS) is a next-generation genotyping procedure which helps to unravel the magnitude of genetic similarity and diversity within and between cultivated species and their wild relatives (Spindel et al. 2013). The GBS procedure is based on minimizing genome complexity with restriction enzymes, coupled with multiplex NGS for high-density SNP discovery (Elshire et al. 2011). A successful application of GBS in Guinea yam breeding is the case study by Girma et al. (2014). Using 2215 SNP markers, this study elucidated the nature of genetic diversity within and between *D. rotundata* and *D. cayenensis* and five wild relatives (*D. mangenotiana, D. praehensilis*, *D. togoensis*, *D. burkilliana*, and *D. abyssinica*). Furthermore, Siadjeu et al. (2018) and Bhattacharjee et al. (2020) showed the potential of the GBS to unlock genetic diversity and population structure in *D. dumetorum* and *D. rotundata* accessions, respectively.

Transcriptome sequencing uses genome-wide differential RNA expression to better understand biological pathways and molecular mechanisms that control important but complex traits in plants. Narina et al. (2011) successfully used transcriptome sequencing in water yam (*D. alata*) to investigate gene expression by the large-scale generation of ESTs from a susceptible (TDa950310) and two resistant (TDa8701091 and TDa950328) yam genotypes infected with the anthracnose (*C. gloeosporioides*).

Gene expression of flavonoid content (purple flesh color) to characterize the transcriptomes of tubers from a purple-flesh and a white flesh variety of *D. alata* tubers is another application of the transcriptome sequencing procedure (Wu et al. 2015). Besides, SuperSAGE transcriptome profiling identified flowering and sex-related genes in *D. rotundata* (Girma et al. 2019). A total of 88 tags were expressed in male, female, and monoecious plants. Among these tags, 18 matched with genes for flower development and sex determination previously identified in many plant species. Siadjeu et al. (2021) used transcriptome sequence to reveal candidate genes involved in the post-harvest hardening of *D. dumetorum* and thus opened an avenue for improving the storability of this yam species.

Metabolomic techniques produce extensive biochemical phenotypes that can be indicative of quality traits. In fact, desirable quality traits are often directly linked with metabolite composition, thus providing a path to metabolite-marker-based breeding (Bino et al. 2004; Fernie and Schauer 2009). This explains the increasing interest in metabolomics in complement to genomics in yam studies. Price et al. (2016, 2017, 2018, 2020) and Lebot et al. (2019b) are the most relevant reports on the potential for application of metabolomic technology in yam breeding. Metabolite profiles provided enormous insight into biochemically related species and revealed *Dioscorea* species as potential sources of essential compounds such as shikimic acid (Price et al. 2016). Besides, a large number of unknown metabolites highlighted the understudied nature of the genus *Dioscorea.* Price et al. (2017) identified a subgroup of metabolites useful for accurate species classification and emphasized the possibility of predicting tuber composition from leaf profiles. Metabolic differences were accession-specific and usually confined to compound classes and, therefore, support trait-targeting for metabolite markers. Price et al. (2018) investigated the cross-species carotenoid profiling of 46 yam accessions belonging to five species (*D. alata, D. bulbifera, D. cayenensis, D. dumetorum,* and *D. rotundata*). They found non-significant differences between the *D. rotundata* and *D. alata* accessions on β-carotene content and provitamin A activity. Besides, they elucidated the absence of a link between yellow tuber flesh color and provitamin A content in yam, as opposed to reports on cassava and sweet potato. Linking biochemical signatures with several agronomic and sensory characters offers potential to expedite the selection and consequently the breeding cycle. Lebot et al. (2019b) developed and optimized a high-performance thin-layer chromatography (HPTLC) protocol for rapid quantification of individual sugars, allantoin, phenolic acids, catechins, and saponins in yam tuber flours. This technique was successfully used for the rapid quantification of compounds related to tuber flour quality of 522 accessions from eight *Dioscorea* species.

Genome-wide association studies (GWAS) were used to identify and understand the genetic architecture of genes responsible for complex traits by exploiting linkage disequilibrium. As opposed to QTL analysis which assays only allelic diversity that segregates between the parents, GWAS uses natural populations (collection of individual varieties or inbred lines) and thus increases the power to dissect historical recombinations. This technology is currently implemented at IITA (under AfricaYam

and NSFBREAD projects), to determine QTLs linked to various traits in *D. rotundata* and *D. alata*, to facilitate marker-assisted breeding in yam (Darkwa et al. 2020a; Gatarira et al. 2020; Mondo et al. 2021b; Agre et al. 2021b).

11.4.4 Genetic Transformation and Tissue Culture

Efforts in establishing an efficient genetic transformation system of *D. rotundata* were reported by Nyaboga et al. (2014) and were intended to open up many avenues to produce disease-resistant yams through pathogen-derived resistance strategies that would not be possible using conventional breeding approaches. Zhu et al. (2009) used the *Agrobacterium tumefaciens*-mediated transformation of *D. zingiberensis,* with leaves and calli as explants, in developing a method to produce transgenic *D. zingiberensis* plants. The application of the CRISPR/Cas9-based genome-editing system in *D. zingiberensis* (Feng et al. 2018) and *D. rotundata* (Syombua et al. 2021) has been successful. Zhao-wei (2012) tested the callus-cultivating effects of different *D. opposita* explants to establishan efficient plant regeneration system for further use in the genetic transformation of that yam species.

11.5 Biotechnology Approaches in Breeding for Biotic Stress Resistance in Yam

Yam is subject to pests and pathogens throughout the growing season, from the seedling stage to post-harvest storage (Morse 2021). These diseases and pests result in reduced yield and low tuber quality, decreasing the tuber's market value substantially. The most important diseases affecting yam production and storage are anthracnose, viruses, tuber rots, and nematodes. The most important pests are weevils, termites, beetles, mealy bugs, and aphids (Korada et al. 2010; Kolombia et al. 2020; Adewumi et al. 2021). In this book chapter, we are only focusing on efforts done in breeding for resistance to YMV and YAD, as they arethe most economically damaging diseases of major yam species (*D. alata* and *D. rotundata*) worldwide. Due to significant losses during yam storage, a brief discussion is included on yam nematodes.

11.5.1 Genetic Engineering for YMV Resistance

YMV is the most economically important and widespread *D. rotundata* disease (Azeteh et al. 2019b; Kumar et al. 2021).YMV is caused by an aphid-transmitted poty virus that infects several *Dioscorea* species (Azeteh et al. 2019b). It is also transmitted mechanically and perpetuated across generations through planting materials (Ita et al.

2020; Nkere et al. 2020). Infected plants usually show inter-veinal mosaic, curling, molting, and stunted growth (Thouvenel and Dumont 1990; Adeniji et al. 2012; Azeteh et al. 2019b). These symptoms result in decreased photosynthetic ability and significant yield losses (40–50%) (Adeniji et al. 2012; Bömer et al. 2016; Mignouna et al. 2019). Infected plants are thus less vigorous and may produce few small tubers with less starch content. The most common YMV symptoms are shown in Fig. 11.4.

Effective control measures rely on healthy planting materials (Amusa et al. 2003). Sources of resistance and tolerance to yam viruses have been identified. This allowed the development and release of several tolerant *D. rotundata* varieties by IITA and partner national yam breeding programs (Arnau et al. 2010; Darkwa et al. 2020a). However, these efforts in developing resistant cultivars are hindered by the high variability in African YMV isolates and the rapid pathogen evolution, generating genetic variants that can overcome the host plant's resistance. Cases of resistance

Fig. 11.4 Yam plant showing symptoms of severe YMV

breakdown have been reported (Bousalem et al. 2000; Ayisah and Gumedzoe 2012). Pyramiding of genes from different sources could provide more durable resistance. However, pyramiding genes through conventional breeding is a challenging and time-consuming target. Biotechnology and molecular tools were then introduced to speed up the variety development process as well as add precision in the identification, transfer, and pyramiding of resistance genes.

Mignouna et al. (2002b) developed the first *D. rotundata* mapping population to determine chromosomal regions with genes or QTLs for YMV resistance. Furthermore, a genetic linkage map of *D. rotundata* was developed based on 341 co-dominantly scored AFLP markers, segregating in an intraspecific F_1 cross. One QTL for YMV resistance was associated with the marker P16/M16-126 on linkage group 1 and explained up to 24% of the total phenotypic variance (Mignouna et al. 2002a, b, c). Two other QTLs were linked to P14/M22-418 and P17/M22-238 on linkage group 8 and explained 22 and 35% of the phenotypic variance on the maternal linkage group, respectively. Two QTLs for YMV were also detected on the paternal linkage group 4 and were associated with the markers P12/M19-241 and P16/M15-81 that explained 13 and 16% of the phenotypic variation, respectively (Mignouna et al. 2002a, b, c). With the ongoing AfricaYam project, several genomic regions linked with YMV have been identified alongside some putative genes involved in plant defense mechanisms (Agre et al. 2021b). The effort is ongoing for the conversion of SNP markers into KASP for MAS application.

11.5.2 Molecular Breeding Tools for Yam Anthracnose Disease (YAD) Tolerance

YAD is caused by a fungus, *Colletotrichum gleosporoides* Penz., and is recognized as one of the most devastating diseases of yam. Although more important on *D. alata* (Abang et al. 2003; Penet et al. 2016; Lebot et al. 2019a), YAD is also a threat to *D. rotundata* farmers in West Africa (Kwodaga et al. 2020). Yam anthracnose is characterized by discrete leaf necrosis before expanding to dieback of emerging stems, shoots, and extensive defoliation (Penet et al. 2016). These symptoms affect the crop's photosynthetic activity, which translates into a reduction in yield (Abang et al. 2003). Depending on the growth stage when the crop is infected and prevailing weather conditions, yield losses can be as high as 80–90% in West Africa (Nwankiti and Ene 1984; Mignucci et al. 1988; Green 1994). Furthermore, yam anthracnose leads to genetic erosion in large-scale field collections of susceptible yam varieties (Orkwor and Asiedu 1995). Characteristic symptoms of YAD are illustrated in Fig. 11.5.

The use of genetically resistant planting materials is a cost-effective and environmentally sound control measure. Several sources of resistance to anthracnose were identified in Ilesde Caraïbesand Guadeloupe germplasm collections and provided opportunity for resistance breeding (Arnau et al. 2010). In IITA and in WestAfrica, the effort has been concentrated on identifying stable sources of resistance to YAD

Fig. 11.5 Yam plants with symptoms of yam anthracnose disease

as no immune varieties were reported (Darkwa et al. 2020a). However, conventional breeding for YAD resistance is negatively affected by the pathogen's genetic diversity (heterogeneous population) due to its ability to undergo sexual recombination (Abang 1997; Abang et al. 2003). A more durable resistance would be achieved by pyramiding resistance genes from different sources into a single genotype (Arnau et al. 2010; Saski et al. 2015; Tamiru et al. 2015; Cormier et al. 2019). This is a time-consuming and uncertain target with conventional breeding approaches.

First efforts in integrating molecular tools in YAD resistance breeding identified a major dominant gene "*Dcg-1*" as the gene controlling resistance to the most predominant Nigerian virulent strain (Mignouna et al. 2002a). Petro et al. (2011) constructed an intraspecific genetic linkage map of *D. alata*using 523 polymorphic AFLP markers and nine putative QTLs. These QTLs were identified for YAD resistance on five different linkage groups. The phenotypic variance explained by each QTL ranged from 7.0 to 32.9%, while all significant QTLs accounted for 26.4–73.7% of total phenotypic variance depending on the isolate (Petro et al. 2011). In the search for more markers, Saski et al. (2015) utilized the NGS techniques such as expressed sequence tags (EST) sequencing, de novo sequencing, and GBS profiles on two *D. alata* genotypes, viz. TDa9500328 (resistant to anthracnose) and TDa9500310 (susceptible to anthracnose). They developed a comprehensive set of EST-SSRs, genomic SSRs, whole-genome SNPs and reduced representation SNPs for resistance to YAD. Further, a genetic linkage map of *D. alata* was developed from 380 EST-SSRs on 20 linkage groups to identify QTLs controlling YAD resistance (Bhattacharjee et al. 2018). Linkage analysis found that a robust QTL on linkage group 14, at a position interval of 71.1–84.8 cM, explained 68.5% of the total phenotypic variation. The high-density genetic map of *D. alata* developed by Cormier et al. (2019) using GBS had opened new avenues for further investigations on the inheritance of key traits such as disease resistance and the development of molecular breeding tools.

Narina et al. (2011) successfully used transcriptome sequencing in *D. alata* to investigate gene expression by the large-scale generation of ESTs from a susceptible

(TDa 95/0310) and two resistant (TDa 87/01091 and TDa 95/0328) yam genotypes infected with YAD. Transcriptome analysis was also used by Hua et al. (2020) to understand the defense mechanisms and the function of ethylene against *Botrytis cinerea* and *Colletotrichum alatae* in *D. alata*. This study showed a high accumulation of endogenous ethylene levels in the resistant cultivar.

Agre et al. (2021c) used SNP-based GBS sequencing platform to genotype 204 *D. alata* full-sib offsprings in developing a high-density genetic linkage map with 3182 SNP markers. The total length of the genetic map was 1460.93 cM with an average of 163 markers per chromosome, and thus, represented the most saturated *D. alata*genetic map todate. Four QTLs were detected for YAD resistance on three chromosomes. The proportion of the phenotypic variance explained by these QTLs ranged from 29.54 to 39.40%. In addition, plant defense response genes including GDSL-like Lipase/Acylhydrolase, Protein kinase domain, and Fbox protein were also detected within the QTL regions.

11.5.3 Development, Validation, and Deployment of Trait-Linked Markers for YMV and YAD

Marker discovery for YMV and YAD resistance is ongoing at IITA and other research institutions in collaboration with several international partners and national agricultural research programs across sub-Saharan Africa and beyond. The next step is the conversion of already identified QTLs to diagnostic SNP markers. These markers will then go through verification and subsequent deployment in breeding programs. The application of these novel methods will enhance yam breeding efforts and ensure quick delivery to farmers of varieties combining high yield potential, disease and pest resistance, and climate resilience in West Africa.

11.5.4 Yam Nematode Resistance Breeding

Yam nematode is caused by a range of species, including *Meloidogyne* spp., *Scutellonema* spp., and *Pratylenchus* spp. Nematode symptoms include galling and "crazy root" syndrome on tubers, distorting tubers, dry rot, and cracking, which reduce the tuber quality (Kolombia et al. 2020). Depending on the level of infection, nematodes can cause high levels of loss during storage, reduce harvestable yield and seed tuber viability, and predispose tubers to secondary rots and rapid deterioration (Coyne et al. 2006; Nyaboga et al. 2014). The severity of nematode damage is generally proportional to the nematode population. Nematode populations build up in the soil if yams are grown in the same place in successive seasons (O'Sullivan 2010). This might be accentuated by short fallows, as currently observed in West Africa. During a fallow,

nematode populations decline through both the lack of appropriate host plants and by direct antagonism from other soil organisms (O'Sullivan 2010).

The use of resistant varieties can be an effective strategy in controlling yam nematodes, although no varieties are known to be tolerant to nematodes (Nyaboga et al. 2014). These authors argued that transgenic plants would be an alternative approach to improve the nematode resistance in yam. In fact, several transgenes have been used to confer plant resistance to both tropical and temperate plant-parasitic nematodes (Nyaboga et al. 2014). However, no conventional or biotechnological approach is reported in breeding yam for nematode resistance in West Africa or

Table 11.3 Biotechnological applications in yam breeding for biotic and abiotic stresses

Species	Technology	Stress	Objectives	References
D. alata	Transcriptome analysis	*Botrytis cinerea, Colletotrichum alatae*	Understanding the defense mechanism and the function of ethylene	Hua et al. (2020)
D. alata	Hormonal regulations of dioscorin genes	High-temperature, low-temperature, and drought	Elucidate the regulatory mechanisms of dioscorin gene *Da-dio5* expressions	Liu et al. (2017)
Dioscorea spp.	Metabolomics	Diseases and abiotic stresses	Inventory of metabolites with biomarker potential in abiotic and disease resistance	Friedmann et al. (2019), Price et al. (2020)
D. alata	Tissue culture	Salinity	Development of protocol for in vitro salt tolerance screening	Wheatley et al. (2003)
D. alata	EST-sequencing	Anthracnose	Identification of QTLs for resistance	Bhattacharjee et al. (2018)
D. alata, D. rotundata	–	YAD, YMV	QTL identification	Mignouna et al. (2003)
D. alata	Transcriptome sequencing	Anthracnose	Germplasm characterization	Narina et al. (2011)
D. rotundata	*Agrobacterium*-mediated transformation	Field and storage pests and diseases	Developing transformation and regeneration system	Nyaboga et al. (2014)
D. alata, D. rotundata	Genome-wide association studies	YAD, YMV	Identification of genome regions controlling resistance	IITA (Unpublished), Agre et al. (2021b)
D. alata	Whole-genome sequencing	Anthracnose	QTL mapping	Saski et al. (2015)
D. rotundata	Genome-editing using CRISPR/Cas9	–	–	Syombua et al. (2021)

elsewhere. Table 11.3 provides some of the biotechnological tools used for biotic and abiotic resistance breeding in yam.

11.6 Conclusions

Molecular and biotechnology approaches provide a deeper understanding of genes controlling biotic expressions at a genotype or population level. Efforts in their integration as routine tools in yam breeding programs are ongoing to implement modern yam breeding programs following a recent initiative to modernize crop breeding led by the Excellence in Breeding (EiB) platform of the CGIAR. Genetic information derived from heterotic group mapping has been employed to classify progenitors for elite population development. Three product profiles for early, intermediate, and late maturity white and water yams have been developed as a useful guide for current and future genetic improvement efforts for yam. The adoption of the electronic phenotypic data capturing process using the field book in addition to the development and application of digital disease phenotyping app and the management and storage of generated data on the Yambase have also yielded significant improvements in yam breeding. Rapid cycle genomic selection and prediction along with complementary molecular and biotechnological approaches and accurate phenotyping for biotic stress in yam breeding will result in more efficient and accelerated improvement of this vital crop which is imperative in light of the exponential human population growth, food demand, and climate change challenges. These technologies will particularly be useful in breeding for biotic resistance as they will facilitate the pyramiding of resistance genes from different sources for a more durable resistance effectively. Besides, these tools will facilitate broadening the genetic base of existing breeding populations by breaking interspecific incompatibility barriers among yam species and wild relatives.

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