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Genetic Improvement of Banana for Resistance to Xanthomonas Wilt in East Africa

Anastasi Musabyemungu^{1,2,3} | Jaindra Nath Tripathi¹  | Samwel K. Muiruri^{1,2}  | Svetlana V. Gaidashova³ | Placide Rukundo³ | Leena Tripathi¹ 

¹International Institute of Tropical Agriculture, Nairobi, Kenya | ²Department of Plant Sciences, Kenyatta University, Nairobi, Kenya | ³Rwanda Agriculture and Animal Resources Development Board, Kigali, Rwanda

Correspondence: Jaindra Nath Tripathi (j.tripathi@cgiar.org)

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ABSTRACT

Banana (*Musa* spp.) is a staple food and income generation crop, feeding millions worldwide. However, the cultivation of bananas is challenging due to biotic and abiotic production constraints. Among these factors are pests and diseases, especially banana bacterial disease. Banana *Xanthomonas* wilt (BXW), caused by *Xanthomonas campestris* pathovar *musacearum* (Xcm), has the most significant detrimental economic effect on East African banana production. The infection of BXW is rapid and severe; its impact increases over time and causes huge banana yield losses. The Xcm infects and causes disease in all types of bananas except the wild diploid type *Musa balbisiana*, which is resistant boosting plant immunity for controlling Xcm and other diseases in bananas. Resistant cultivars are the best promising management option for controlling Xcm and other diseases in bananas. All the cultivated bananas are sterile, and have a long generation cycle, which complicates their improvement through conventional breeding. Biotechnological approaches to banana improvement can complement conventional breeding by overcoming some of its challenges. Additionally, genetic engineering could speed up the process of crop improvement, especially for sterile seedless crops like bananas. It is also specific to the target gene and precise modification that avoids unwanted genes in the normal breeding process. Recent developments using genetic engineering and genome editing on bananas have been initiated to tackle these issues. This review article focuses on the challenges of traditional breeding and the progress of genetic engineering and genome editing approaches, aiming to enhance understanding of achieving an essential genetic gain of bananas against the BXW. This understanding is crucial for enhancing food security in East Africa and globally.

1 | Introduction

Banana (*Musa* spp.) is a member of the class Monocotyledons, order Zingiberales, and genus *Musa* of the family *Musaceae* (Karamura and Karamura 1995). *Musaceae* family includes *Musa* ($2x=22$) and *Ensete* ($2x=18$). *Musa* is classified into four components based on morphological traits and chromosome numbers. These are Eumusa and Rhodochlamys with $2x=22$ chromosomes and Australimusa and Calimusa with $2x=20$ chromosomes. The entire edible banana belongs to the Eumusa

(Christelová et al. 2011). Banana fertility depends on ploidy, an essential factor to consider during breeding (Karamura et al. 2016). *Musa* has two genomic groups: *Musa acuminata* (AA) and *Musa balbisiana* (BB). Moreover, bananas can be classified into three classes based on ploidy levels: diploid class, which has letters AA, AB, BB; triploid class with AAA, ABB, AAB; and tetraploid class with AAAA, ABBA, AAB, AAAB (Šimoníková et al. 2020). Most of the cultivated bananas are triploid and do not produce seeds. Therefore, plant suckers are required for clonal propagation and multiplication, which

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is often unreliable because an infected sucker used for propagation might be the leading cause of disease and pest spread (Sivirihauma et al. 2017).

Bananas are commonly grown in all tropical and subtropical regions and originated from Southeast Asia (Volkaert 2018). Three primary geographical regions of banana cultivation are Latin America and the Caribbean (36%), Africa (35%), and Asia and the Pacific (29%), with a significant fraction consumed by the local (70%–85%) population (Debnath et al. 2019). This crop is primarily grown in warm and humid climates with well-drained fertile soil of pH 6–7.5, an average temperature of 20°C, relative humidity > 60%, and an average rainfall between 1500 and 2500 mm (Reay 2019). It is well adapted from sea level to all altitudes of 1200 m (Reay 2019). Over 140 nations cultivate bananas, with an estimated 155 million tons produced annually (FAOSTAT 2022). With an estimated yearly production of 34.5 million tons, India leads the globe in banana production (26% globally), followed by China, Indonesia, and Brazil (FAOSTAT 2022).

Banana production is affected by various pests, including nematodes, weevils, diseases like bacteria and fungi, and different viral diseases (Ocimati et al. 2019). Banana Xanthomonas wilt (BXW) is the most severe and pervasive disease affecting bananas in East and Central Africa (Uwamahoro et al. 2019). BXW has been detected in most East African countries, resulting in up to 100% production losses in banana farms (Ocimati et al. 2019). BXW prevention techniques have been used, including removing the male bud to restrict stop insect transmission, using sterile agricultural tools, and uprooting diseased mats (Kikulwe et al. 2022). However, these methods were ineffective and poorly adopted by farmers, allowing for the rapid spread of BXW and the devastation of banana plantations (Nakato, Mahuku, and Coutinho 2018). Since preventive measures have proven inefficient, whereas using chemicals in bacterial disease control is problematic and harmful to the environment, BXW continues unabated. In addition, most cultivated bananas are susceptible to BXW, except the wild type of banana *Musa balbisiana*, with a fertile BB genome subgroup (Tripathi et al. 2019b). The lack of resistance in most cultivated bananas, calls for a sustainable approach to BXW management, the best being the development of resistant cultivars.

Most banana cultivars are sterile with a complex inflorescence structure where flowers produce parthenocarpic fruits (Kema 2024). In cultivated triploid bananas, limited genetic variability and difficulty of flowering pose challenges to the improvement of bananas by conventional breeding (Dzoyem et al. 2024). Moreover, the long reproduction cycle in bananas further slows down breeding using a conventional approach (Jacobsen et al. 2019). Utilizing genetic engineering to boost immunity and produce disease-resistant bananas is a complementary method to control BXW (Tripathi et al. 2010). A significant advantage of genetic engineering as gene transfer technology is acquiring the target crop genes from different intra or interspecific species, including wild species, into the target host organism (Namukwaya et al. 2012). Therefore, genetic engineering tools can circumvent inherent reproductive incompatibilities hampering traditional breeding. In addition, this modern approach can overcome some problems of undesirable traits

associated with regular breeding because it focuses on specific genes of interest (Tripathi, Lorenzen, et al. 2014). Plant improvement using genetic engineering has been widely utilized to develop varieties resistant to various diseases. Reportedly, this approach is productive, timely, and efficient in controlling plant diseases (Tripathi et al. 2017). Moreover, genetic engineering can contribute to novel applications of germplasm genes in natural breeding (Wang, Yu, and Li 2021).

Several overexpression genes conferring pests and disease resistance have been used to improve banana yield and resistance to BXW. Some proteins expressed by the defense genes in transgenic plants enhanced resistance against Xcm (Tripathi, Tripathi, and Tushemereirwe 2010; Namukwaya et al. 2012; Tripathi et al. 2013). Genetic modification methods, including *Agrobacterium*-mediated transformation, protoplast electroporation, and particle bombardment, have been demonstrated to improve banana bananas. *Agrobacterium*-mediated transformation is preferable for most plant species because it permits the integration of more prominent genes of interest in low copy. Moreover, this method is highly efficient and cost-effective (Khanna et al. 2004; Tripathi, Muwonge, and Tripathi 2012).

Most banana transformation procedures depend on generating embryogenic cell suspensions (ECS). They are the most suitable for banana genetic transformation due to their high efficiency in regenerating homogeneous plants without chimeras for various cultivars in a short period (Tripathi, Muwonge, and Tripathi 2012). ECS of most banana genotypes has been developed from immature zygotic embryos, proliferating meristems culture (scalps), corm slices, in vitro leaf bases, or immature male and female flowers (Strosse et al. 2006). Production of ECS using multiple apical meristems was reported to be the best and most feasible for many banana and plantain cultivars since scalps are always available and not season-dependent (Strosse 2003). The primary goal of this review is to discuss various strategies for controlling banana Xanthomonas wilt. The main emphasis of this review will be (1) the comprehension of the molecular characteristics of BXW, (2) highlight the progress made to control BXW agriculture practices and development of BXW-resistant cultivars using conventional breeding and genetic engineering, and (3) advances in crop improvement with the genome editing.

2 | Importance of Banana

In most regions of the world, plantains and bananas are significant staple food and cash crops (Padam et al. 2014). They are essential for generating money and food security for many people globally. Generally, small-scale rural growers mainly raise the crop for their home use or to sell nearby marketplaces (Reay 2019). It is mainly cultivated for food, raw materials for beverage processing industries, animal feed, and as a medicinal and ornamental plant (Fahrasmane, Parfait, and Aurore 2014). Banana is consumed in different forms, including cooking and roasting East African Highland bananas (EAHB) and plantains. Dessert bananas are consumed as a fruit when ripe, whereas beer bananas are used as essential components for processing alcoholic and non-alcoholic drinks (Carughi 2013). Bananas can be consumed in different forms, but many banana varieties are eaten as desserts (60%), like Cavendish. In comparison, others

(40%) are preferable as cooked or roasted bananas like EAHB and plantains (Carughi 2013). A banana is an excellent source of vitamins, especially vitamin B (Vit. B6) and vitamin C, found primarily in dessert bananas, whereas cooking bananas are rich in starch. Bananas also contain 75% water, holding minerals such as K, Mn, Mg, Cu, and phenolic compounds (Mengstu et al. 2021). Banana is consumed by over 30 million people in East Africa, with a daily consumption per person varying between 30% and 60%, particularly in East African countries like Uganda, Burundi, and Rwanda (Blomme et al. 2019). Beer bananas are raw materials for processing foods and drinks like juices, wine, and alcohol (Fahrasmane, Parfait, and Aurore 2014; Sogi 2020). Bananas constitute raw materials for natural fiber industries and supplement wood to make boards, textiles, and papers (Sarma, Govila, and Yadav 2020).

Besides nutritional values, bananas contain numerous medicinal properties (Fahrasmane, Parfait, and Aurore 2014; Apostolopoulos et al. 2017). With their antioxidant effects, bananas exhibit antidiarrheal, anti-ulcerogenic properties, and can treat constipation (Gladys and Gladys 2014). The high carotenoid levels of bananas can also protect the body against diseases such as cancer, heart problems, and diabetes (Fahrasmane, Parfait, and Aurore 2014). Bananas have been identified as relatively rich in pyridoxine, a chemical compound crucial for metabolizing unsaturated fatty acids and vitamins. Banana is a dietary potassium source, which helps manage the body's blood pressure (Ranjha et al. 2022). Likewise, bananas have various flavonoids and polysaccharides compounds essential for human health (Someya, Yoshiki, and Okubo 2002).

Bananas also boast an economic significance because they are among the most traded fruits worldwide. Bananas provide the main proportion of export revenues in the economy of many tropical countries. Regarding fruit export value, bananas appear among the top significant merchandized fruits with higher export value worldwide (Platonovskiy et al. 2024). The crop is the source of income and employment as a significant export fruit for many household farmers who depend on it (Lamessa 2021). Dessert bananas constitute 20% of global production. With an annual production of over 43 million tons, the Cavendish variety can hold the top spot among the most economically significant and internationally traded varieties (Bebber 2022).

3 | Banana Production in East Africa and Globally

Over 140 countries grow bananas and plantains worldwide in the tropics and subtropics (Heslop-Harrison and Schwarzacher 2007). An estimated annual banana production of 155 million tons is produced worldwide (FAOSTAT 2022). With an average of 34.5 million tons, India leads the globe in banana production (26%), followed by China, Indonesia, and Brazil (FAOSTAT 2022).

Bananas and plantains are essential foods for most Africans, who produce over 31 million tons annually throughout many of the continent's nations. The average yield ranges between 5 and 30 tons (FAOSTAT 2022). A large proportion (87%) of the banana produced in Africa is consumed locally, indicating that it is a staple food in the continent (Perrier et al. 2019).

Approximately one-third of the world's banana crop is produced in Sub-Saharan Africa, with the East African Great Lakes Region producing more than half of it, encompassing Burundi, Eastern Democratic Republic of Congo, Uganda, Northwestern Kenya, and Tanzania (Figure 1) (Batte et al. 2021). The region leads in global banana consumption, averaging 250 kg per person yearly, and is mainly characterized by the EAHB varieties subclass of triploid (AAA) (Perrier et al. 2019). In contrast, most of the plantain subclass's AAB clones are cultivated in West Africa (Debnath et al. 2019).

Research has shown that 70% of East African Highland bananas (Matooke) produced at the household level in the region are consumed locally, while the remaining 30% are sold globally (Akankwasa et al. 2021). This area is considered the secondary hub for banana diversification (Němečková et al. 2018; Perrier et al. 2019).

In the East African Region, Uganda is the leading producer of bananas and plantains (Figure 1) and has the highest per capita consumption rate worldwide. The banana consumption rate in Uganda is very high; one person can take 1 kg daily. In Uganda, the crop occupies up to 75% of the total cultivated area of food crops (Ochola et al. 2022). It is grown by many farmers in Uganda and consumed as a staple food. The country is considered to have the highest banana variety diversity. Among them,

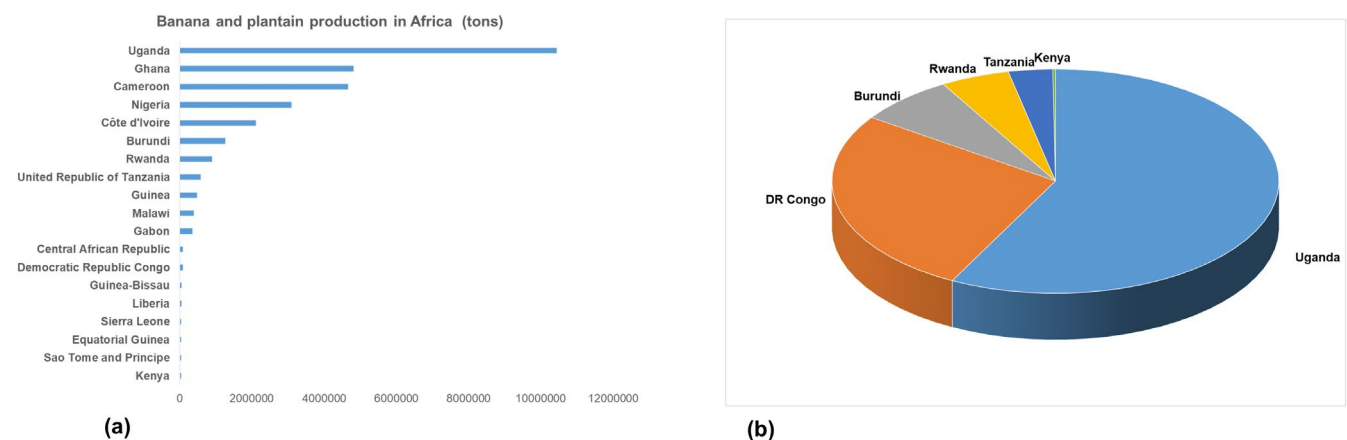


FIGURE 1 | Banana and plantains producing countries in (a) Africa and (b) East African Countries.

the Highland banana (AAA-EA) accounted for 76% of the total output (Gold et al. 2002).

Likewise, bananas and plantains constitute the second predominant crop producing calories in the Democratic Republic of Congo (DRC), with an annual consumption rate of 136.9–173.9 kg (Ekesa et al. 2013). In DRC, 67% of the population in the country depends on agriculture, where bananas and plantains are the second most significant crop for producing food and revenue (Ekesa et al. 2013). Democratic Republic of Congo is the primary producer of cooking bananas and plantains, particularly in the equatorial forests of the North and South Kivu areas (Balimwacha, Kambale, and Katembo 2021). Plantain and cooking banana parts account for 27% of the global production, estimated at 282,520 tons and 1,071,900 tons, respectively (Ekesa et al. 2013). In Burundi, bananas are grown throughout the country and constitute a valuable crop for the population of Burundian. Bananas play an important role as an essential food source and income generation crop. In Burundi, the crop is classified among the main essential crops (Kamira et al. 2013). In Tanzania, over 30% of Tanzania's population depends on bananas as their fourth principal source of nourishment and money, with an annual consumption average of 390 kg per capita (Lucas and Jomanga 2021). Similarly, in Rwanda, bananas hold great importance as basic food and revenue generation for many citizens and contribute around 32% of the household diet (Nkuba et al. 2015). Approximately 90% of households farm bananas, which occupy 23% of the land. The crop is also one of the most consumed staple diets in the country, with 197 kg as annual per capita consumption and 2.25 million metric tons as yearly production (Gaidashova, Karemera, and Karamura 2010; Gaidashova, Uwimpuhwe, and Karamura 2010). Bananas are the fundamental food for many populations in Rwanda. In Kenya, bananas are considered a critical essential food and economic crop in the country's central, western, and coastal regions, where they are mainly grown (Muthee, Gichimu, and Nthakania 2019). East African region constitutes a cradle of banana production and consumption, and the crop supports many people's livelihoods, especially smallholder farmers. Banana farming is, however, increasingly at risk from biotic and abiotic variables that lower produce quality and quantity (Blomme et al. 2020).

4 | Obstacles to Banana Cultivation in East Africa

Despite bananas' significance, several biotic, abiotic, and socio-economic factors limit their production potential (Balimwacha, Kambale, and Katembo 2021). Lack of quality and disease-free planting materials by farmers is among the most significant challenges limiting banana production (Wahome et al. 2021). Most farmers buy suckers from neighbors and thereby acquire any diseases in the planting materials. Degeneration of banana planting materials significantly affects yield (Jacobsen et al. 2019). Poor husbandry practices, inappropriate technologies, and inadequate extension services are among the causes of low banana yield (Muthee, Gichimu, and Nthakania 2019). Improper or non-use of agricultural inputs (Sharma et al. 2021) and high plant density (Ndabamenye et al. 2013) yield affect banana yield. Lack of adequate storage facilities usually leads to losses of bananas and their deterioration at the market because

they are highly perishable (Abraham, Saleh, and Zelelew 2022). Inadequate marketing systems and a lack of appropriate and effective marketing are additional challenges in banana production. Furthermore, lack of credit facilities and poor infrastructure are critical to enhancing participation in banana farming (Muigai, Gathungu, and Thogori 2021).

Besides socioeconomic factors, banana yield is threatened by abiotic stress (Ndabamenye et al. 2013). Banana yield reduction in East Africa is attributable to a decline in soil fertility and acidity (Nyamamba et al. 2020). Bananas require specific temperature ranges and optimum water during their growth. Climate change significantly impacts banana production due to unfavorable temperatures and unreliable rainfall patterns throughout the growth stages. Bananas are very sensitive to water shortage and waterlogging. Salts, oxidation stress, hypoxia, flooding, light, nutrient imbalance, and strong wind are some environmental factors limiting banana growth (Varma and Bebbber 2019).

The most significant threats to banana output are biotic factors, pests, and different diseases since they have the potential to completely devastate banana crops (Gaidashova et al. 2013). Moko disease (*Ralstonia solanacearum*), Blood disease (*Ralstonia syzygii*), and Xanthomonas wilt (*X. campestris* pv. *musacearum* (Xcm) are common bacterial diseases that harm bananas and plantains (Rukundo, Uwamahoro, and Rutikanga 2020). Numerous fungi, including Fusarium wilt (*Fusarium oxysporum* f.sp. *cubense*), Sigatoka disease (*Mycosphaerella musicola*), and black leaf streak (*Mycosphaerella fijiensis* Morelet), are the leading causes of banana output limitations (Karangwa et al. 2016). There are also reports of viruses that reduce the movement of germplasm and banana output, such as the *Banana bunchy-top virus* of the type *Nanavirus* and *Banana streak virus* of the family *Badnavirus* (Hakizamungu and Rukundo 2013a). The weevil (*Cosmopolites sordidus*) and nematodes (*Pratylenchus coffeae*, *P. goodeyi*, *Helicotylenchus multicinctus*, and *Radopholus similis*) are some pests associated with banana production losses (Hakizamungu and Rukundo 2013b).

5 | Origin and Distribution of Banana Xanthomonas Wilt in East Africa

The banana Xanthomonas wilt was initially discovered in Ethiopia in 1968 on a near relative of the *Ensete ventricosum*, then on bananas in the Ethiopian highlands in 1974 (Yirgou and Bradbury 1974). In the East Africa region, BXW was observed for the first time in central Uganda (Kagezi et al. 2007) and the Eastern Democratic Republic of Congo (DRC) in 2001 (Geberewold 2019). It moved from these areas to other nearby nations in East African Great Lakes Regions, including Tanzania, Rwanda, Burundi, and Kenya (Reeder et al. 2007). In 2006, BXW was reported in Western Kenya (Teso, Bungoma, and Busia) (Carter et al. 2010). Similarly, Tanzania reported the infection in 2006, which caused severe banana loss, especially in North Western Tanzania, Kagera, and Mwanza (Shimwela et al. 2017). In Rwanda, BXW was first observed in the Rubavu district (the northern part of Rwanda near DRC) in 2005, which later spread to Rutsiro and Rulindo districts in the northern province of Rwanda in 2007 (Uwamahoro et al. 2019). Pathogen infection progressively spread across the country, resulting in

a more than 45% incidence rate, making it a severe epidemic that decreased banana yield across the country (Rutikanga et al. 2013). The illness results in loss due to fruit rotting and plant death (Nakato et al. 2013). An assessment in 2009 and 2010 revealed that BXW was present in 12 Rwandan districts, indicating a swift spread throughout the nation. According to a 2015–2016 follow-up survey, BXW was found in all of the investigated districts in Rwanda, with occurrence rates ranging from 27% to 77%. The four central banana-growing districts, Rwamagana, Kayanza, Rusizi, and Nyamasheke, had high incidences (above 58%) (Uwamahoro et al. 2019). BXW is present in all banana regions of East Africa and has become a significant, vital banana disease. BXW is a severe disease that attacks all growing bananas, including dessert, brewing, and cooking (Tripathi et al. 2019).

6 | *Xanthomonas campestris*, Pathogenesis, and Epidemiology

Xanthomonas campestris pv. *musacearum* (Xcm) is rod-shaped, aerobic, and gram-negative; its measurement ranges from 0.7–0.9 μm to 1.8–2.0 μm . The Xcm is a motile bacterium with a flagellum used for movement (Aritua et al. 2007). It is a chemo-organotrophic bacterium with the nutrient medium of the optimal growth temperature ranges between 25°C and 30°C. According to taxonomy, Xcm is a member of the genera *Xanthomonas*, family *Xanthomonadaceae*, order *Xanthomonadales*, class *Gammaproteobacteria*, and phylum *Proteobacteria* (Night et al. 2013). *Xanthomonas* bacteria comprises 27 different species that can infect various plants and cause economic grave illnesses in approximately 400 crops, including dicots and monocots (An et al. 2020). *Xanthomonas campestris* pv. *musacearum* and *Xanthomonas oryzae* pv. *oryzae* strains were described as isogenic lines that can carry specific resistance genes to interact with specific host plants (An et al. 2020). *Xanthomonas* species is very harmful since it can be connected to other plant diseases and significantly lower the yield of host plants (Mansfield et al. 2012). In its life cycle, the *Xanthomonas* genus can go through epiphytic and endophytic stages, where it can colonize the surface of the host plant or enter through its stomata or wounds, respectively (Nakayinga et al. 2021). On entering the host through hydathodes or wounds, the bacteria attack xylem elements of the vascular system by secreting extracellular polysaccharide toxins that play the role of pathogenicity of blocking conducting vessels of the plant host, leading to significant permanent wilting and final death of the infected plant (An et al. 2020). The infection spreads systemically throughout the host plant's tissues (Ocimati et al. 2019). Pathogen infection induces the yellowing of immature fruit. It causes the secretion of yellow ooze on cutting the infected banana pseudostem (Nakato et al. 2013). Xcm can colonize plant seeds that contribute to the main chain of disease propagation (An et al. 2020). Outside the plant host, in general, the pathogen does not compete with other bacteria, which might have implications for the slow survival of the soil from the infected debris. Xcm could stay in plant residues for more than 2 years but cannot stay longer in free soil for more than 6 weeks (An et al. 2020). The longevity of BXW outside the host can vary depending on ecological factors like humidity, temperature, and availability of

conductive surfaces for bacterial survival (Nakayinga et al. 2021). In low temperatures, the infection is often latent and can persist in the vascular system without producing symptoms, while in high temperatures, the typical symptoms become evident. Once inside the host plant, bacterial infection causes molecular alterations like transcription, phosphorylation, and DNA methylation. The incubation period is short, and it only takes 3 days to produce distinctive mucoid, spherical, convex, and yellow colonies (Nakayinga et al. 2021).

The BXW infection is mainly transmitted by foraging insect vectors, which propagate the inoculum when searching for food in male bud flowers of diseased plants (Tinzaara et al. 2007). As a vegetatively propagated plant, Xcm infection is easily spread when infected planting materials are used to establish a new plantation (Nakato, Mahuku, and Coutinho 2018). Utilization of contaminated garden tools during de-leafing, desuckering, and weeding contributes to disease spreading (Blomme et al. 2017). Weevils and nematodes have been identified as vectors that transmit diseases through the banana roots (Were et al. 2015). Additionally, animals encountering infected materials, such as soil and water, can transmit the disease (Nakato, Mahuku, and Coutinho 2018). The manifestation of disease symptoms is contingent upon various aspects, including the cultivar, stage of plant growth, ambient circumstances, and transmission mechanism. Studies showed that AAA-EA cooking bananas are more susceptible to BXW than ABB cultivars (Blomme et al. 2017). Yellowing and wilting of banana leaves are the main symptoms induced by BXW (Nakato, Mahuku, and Coutinho 2018), and the fruits of infected plants exhibit premature ripening with internal discoloration and yellow ooze from the vascular tissues of cut pseudostem (Figure 2). Moreover, male buds shrivel and turn black, and the rachis dries out (Blomme et al. 2017). Infected plants can die within a month of the symptoms (Nakato, Mahuku, and Coutinho 2018). Xcm attacks every variety of bananas, including the East African Highland Banana (EAHB), leading to a complete harvest loss in susceptible plants (Tripathi et al. 2009).

Bacterial diseases have no effective chemical control (Premabati and De Mandal 2020). Eliminating the male bud to stop insects from spreading infection, heating or soaking agricultural implements in sodium hypochlorite (NaOCl) to sterilize them, burying or destroying diseased plants, and crop rotation are among cultural control techniques advised for managing BXW (Tushemereirwe et al. 2004). However, these methods are ineffective in controlling the disease spread, significantly when infected plants are cut during rainy seasons (Ocimati et al. 2019). Single diseased stem removal (SDSR) and control diseased mat by uprooting (CDMU) show enhanced efficacy in controlling the disease spread; however, adopting these methods requires much more rigorous application (Karamura et al. 2009). Moreover, CDMU and SDSR do not eliminate the disease in the soil but reduce the bacterial infection for a short period, allowing the disease to reappear (Ocimati et al. 2019). Therefore, these methods are poorly adopted, probably due to low efficacy, high labor demand, and resource requirements from small-holder growers (Nakato, Mahuku, and Coutinho 2018). The BXW outbreak has been detrimental to banana plantations in East Africa, with underestimated social and economic impacts that call for sustainable management efforts.

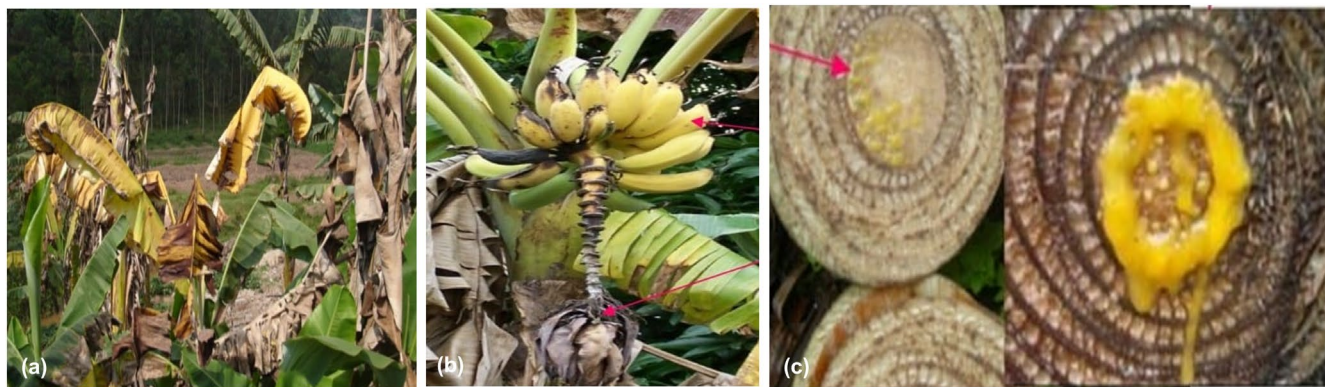


FIGURE 2 | *Xanthomonas campestris* pathovar *musacearum* infected banana plant showing disease symptoms. (a) Infected plants showing yellowing, wilting, and drying of leaves, (b) Premature ripening of banana fruit, and (c) Yellow bacterial ooze coming out from cut pseudostem.

7 | Challenges With Conventional Breeding

In 1922, banana breeding began in Trinidad, West Indies, and then in 1924, in Jamaica, to develop superior, fusarium wilt-resistant bananas for export (Persley and George 1999). IITA initiated plantain banana breeding in Africa, specifically in Nigeria, in 1980 with the primary objective of controlling a new epidemic of black leaf streak disease (Batte et al. 2019). The disease spread to the East African Region, where highland banana (EAHB) production is predominant. Therefore, with assistance from the National Agricultural Research Organization (NARO), IITA expanded its breeding operations in Uganda (Batte et al. 2019). In collaboration with scientists, the breeding program generated resilience. It started productive tetraploid hybrids for use as parents and started a project to generate high-yielding, resistant triploid hybrids (Nowakunda et al. 2023). The goal of the NARO-IITA initiative remained to improve banana cultivars with resistance to various diseases and pests, high and consistent yields, better agronomic features, and acceptable fruit quality. Although progress is being made, the banana breeding program is limited by some inherent reproductive banana challenges (Šimoníková et al. 2020), including low or infertility of most grown triploid banana cultivars and difficulties in seed production (Perrier et al. 2019). Conventional breeding method involves long generation cycles, which prolongs cultivar release (Sipen et al. 2011).

Although the compatibility of parents used in pollination and the production of viable seeds are among the factors considered in successful breeding, bananas develop fruit through the parthenocarpy system. Some cultivars can develop a few seeds with very low germination, rates because of their hard surface structure (Batte et al. 2019). It was reported that undesirable characteristics of banana hybrids produced during conventional and regular breeding (Khan et al. 2009). Unsuccessful results from the conventional breeding of bananas are sometimes associated with unfavorable linkage genes from diploid parents (de Carvalho Santos et al. 2019). Polyploidy and low genetic variability of cultivated bananas are a big challenge to conventional breeding (Sipen et al. 2011). Most of the time, banana polyploidy nature is characterized by abnormal meiosis, mainly in triploid cultivars (Šimoníková et al. 2020).

The presence of irregular chromosome pairing and unstable chromosome segregation during the meiosis phase is the main factor that induces low or no fertility in most cultivated bananas (de Carvalho Santos et al. 2019). Boosting plant immunity through genetic engineering was the best and complementary approach to overcoming challenges faced by traditional breeding in controlling banana disease against a particular pathogen (Tripathi et al. 2010). Developing host-pathogen resistance cultivars by strengthening banana defense mechanisms against pathogens is the most effective way to control bacterial infection.

8 | Enhancing Plant Defense Mechanisms

In nature, plants have evolved defense mechanisms to combat pathogens like fungi, bacteria, viruses, and pests like nematodes and insects (Fan et al. 2020). Plants respond to pathogen attacks by forming different layers of defense, including structural barriers, preformed antimicrobial compounds, and adaptive defense mechanisms (Rofida 2019). Hypersensitive response (HR) ranks among plants' best effective defense responses when in immediate contact with pathogens. HR prevents the spread of pathogen infection by causing the infected site's cells to die (Vailleau et al. 2002). Following a pathogen attack, plants produce signaling molecules like reactive oxygen intermediates (ROI), nitric oxide (NO), salicylic (SA), and jasmonic acids (JA), accumulate phenolic compounds, tissues are reinforced, vessels are blocked, phytohormone, and pathogenesis-related synthesis induced (PR) proteins (Betsuyaku et al. 2018). Similarly, plants also produce antimicrobial proteins or metabolites, such as phytoalexins (toxic secondary metabolites) (Kaur et al. 2022) and cell wall degrading enzymes (Wang et al. 2013) in response to pathogen invasion. Furthermore, plants also exhibit systemic acquired resistance (SAR) to protect uninfected sites (Vlot et al. 2008). A broad spectrum of pathogens can trigger plants' defense mechanisms and induce a long-lasting systemic response that results in resistance. Plants attacked by pathogens like fungi, bacteria, and viruses can react by expressing a broad spectrum of induced systemic resistance (ISR) against the pathogen and boosting plant defense mechanisms. HR-induced cell death prevents pathogen infection from spreading and protects uninfected plant parts by inducing the SAR (Heil and Bostock 2002). Some plant defense responses

activate transcriptional factors (TFs) of various plant genes (Vailleau et al. 2002). Plant defense mechanisms are triggered by the transcriptional control of genes, which is a crucial aspect of the plant's stress response (Campos et al. 2022). Similarly, TFs control the expression of genes in response to physiological and environmental cues (Khong et al. 2015). TFs are proteins capable of binding short DNA sequences in the gene promoter and interacting with the pre-initiation complex of transcription to activate or inhibit RNA polymerase II (Khong et al. 2015). Additionally, TFs can activate or inhibit the appearance of specific target genes in various tissues or cells in reaction to particular external conditions (Campos et al. 2022). In *Musa balbisiana*, the authors found the overexpression of several transcription factors when infected with the BXW pathogen, which triggered an immune response in the plant by activating various defense mechanisms against banana Xanthomonas wilt such as signaling molecules and phytohormones (Tripathi et al. 2019). Transgenic plants have expressed many defensive genes, including several proteins, to increase pest resistance (Fan et al. 2020). Research showed that overexpressing of Myeloblastosis (MYB) transcription factors from *Arabidopsis thaliana* enhanced the hypersensitive cell death (HCD) in reaction to virulent pathogens but induced the HR against the virulent pathogens in Tobacco plants (Fan et al. 2020). MADS-box genes (MCM1-AGAMOUS-DEFICIENS-SRF) and AGL (AGAMOUS LIKE) downloaded from *M. balbisiana* are critical regulators that play several functions in various reaction plant processes and stress reactions (Hoffmann et al. 2022). Overexpression of the above-mentioned genes was attributed to some BXW resistance in bananas (Castelán-Muñoz et al. 2019). The ferredoxin-like amphipathic protein (PFLP) and hypersensitive response assisting protein (HRAP) extracted from sweet pepper (*Capsicum annuum*) were used to enhance hypersensitivity response (HR) in bananas against Xanthomonas wilt (Tripathi, Tripathi, and Tushemereirwe 2010). Overexpression of the plant ferredoxin-like protein gene extracted from sweet pepper has increased photosynthetic carbon assimilation in rice (Chang et al. 2017). Ghag, Singh Shekhawat, and Ganapathi (2014) reported the resistance to banana fungi disease induced by defensins and ferredoxin proteins extracted from Petunia flowers. Expressing a cysteine proteinase inhibitor and/or synthetic peptide in bananas has demonstrated resistance to different species of nematodes (Tripathi et al. 2017). Rice pattern recognition receptor (PRR), XA21, has expressed resistance of banana to *Xanthomonas campestris* pv. *musacearum* (Tripathi, Tripathi, et al. 2014). The presence of the rice *NH1* gene expressed resistance to the rice bacterial blight pathogen *X. oryzae* (Yuan et al. 2007). Several antimicrobial peptides like Magainins, Cecropins, Thionins, and Attacins were reported to control a wide species of harmful bacteria (Mentag et al. 2003).

Natural resources are limited, and the world's population continuously increases. The planet's population is predicted to grow to 9.6 billion in 2050 and 12.3 billion in 2100 (Gerland et al. 2014). Therefore, crop biotechnology is required to fulfill the needs of the growing world population. Genetically modified crops aim to increase crop quality attributes like yield, nutritional value, and resilience to biotic and abiotic pressures (Kumar et al. 2022). Additionally, they have been designed to lessen the effects of climate variability by producing fewer emissions (Kovak, Blaustein-Rejto, and Qaim 2022). However, several safety concerns about genetically modified crops, like risks to human health, environmental risks, and ecology in general, have been raised (Kumar

et al. 2022). Consequently, procedures, principles, and policies were implemented to ensure these genetically modified crops were handled and used appropriately. Production of crops with genetic modification must respect the general guidelines of the Cartagena Protocol. Research on the risk assessment of transgenic banana plants established in field trials against BXW in Uganda revealed that the transgenic banana plants expressed *Pflp* and *Hrap* genes have no adverse effects on non-target living organisms such as rhizobacteria and endophytes (Nimusiima et al. 2015). No scientific report has been documented on evidence of human and environmental harm by genetically modified crops. Even though no scientific evidence has been noticed on environmental harm due to genetically modified banana, all guidelines of the Cartagena Protocol related to the safe handling, transfer, and use of genetically modified living should be strictly respected to ensure the complete protection of humans and the environment.

9 | Genetic Engineering to Improve Banana

Plant improvement using genetic engineering has been widely utilized to develop varieties resistant to various diseases, and this technique has been stated as the most efficient and least time-consuming method to control plant maladies (Ghag and Ganapathi 2017). Genetic modification has been shown as the best approach to improve plant defense against a specific pathogen. It offers the best option for developing resistant bananas by circumventing these inherent reproductive incompatibilities since it allows for the intra- or interspecific transfer of one or few genes between species (Tripathi et al. 2013). Therefore, genetic engineering tools can circumvent the challenges limiting traditional breeding. In addition, this modern approach can overcome some problems of undesirable traits associated with conventional breeding because it focuses on specific genes of interest (Tripathi et al. 2017). Genetic engineering accelerates the breeding process and can contribute to novel applications of the existing germplasm genes in natural breeding (Namukwaya et al. 2012). With gene transfer technology, it is possible to transfer the desired gene from different species, including wild species, into the target host organism (Tripathi, Lorenzen, et al. 2014). Genetic engineering was considered an ecologically acceptable and long-term strategy for managing crop bacterial infections (Premabati and De Mandal 2020). Banana resistance to BXW has recently been enhanced by utilizing various genes that resist different diseases and pests (Tripathi, Tripathi, et al. 2014; Tripathi, Tripathi, and Kubiriba 2016). Transgenic bananas that expressed the genes for *plant ferredoxin-like protein* (*Pflp*) or *hypersensitive response-assisting protein* (*Hrap*) from sweet peppers demonstrated resistance to Xcm (Tripathi et al. 2010; Namukwaya et al. 2012). The banana events that developed with *Xa21* genes from rice exhibited enhanced resistance to Xcm (Tripathi, Lorenzen, et al. 2014). *Arabidopsis thaliana* gene of elongation factor Tu receptor (*AtEFR*) exhibited resistance to Xcm in the greenhouse (Adero et al. 2023). Genetic modification methods, including protoplast electroporation (Sagi et al. 1994), particle bombardment (Daniels, Kosky, and Posada-Perez 2018), and *Agrobacterium*-mediated transformation (Namuddu et al. 2013), have been used for banana improvement. Most plant species prefer the *Agrobacterium*-mediated transformation technique among these genetic transformation

TABLE 1 | Research on transgenic and genome editing in banana and plantain.

Target gene	Origin	Banana cultivar	Explant	Trait	Genetic engineering technique	References
<i>Hrap</i>	Sweet pepper	Sukali Ndiizi, Mpologoma	ECS	Bacterial wilt resistance	Transgenic	Tripathi et al. (2010), Tripathi, Tripathi, and Tushemereirwe (2010)
Antifeedant cysteine proteinase inhibitor and synthetic peptide genes	Maize	Gonja Manjaya (AAB)	ECS	<i>Nematode resistance</i>	Transgenic	Roderick et al. (2012)
<i>Pflp gene</i>	Sweet pepper	Sukali Ndiizi (AAB)	ECS	Bacterial wilt resistance	Transgenic	Namukwaya et al. (2012)
<i>CpCYS-Mut89</i>	Papaya	Sukali Ndiizi (AAB)	ECS	Pest resistance	Transgenic	Namuddu et al. (2013)
<i>Xa21</i>	Rice	Gonja Manjaya (AAB)	ECS	Bacterial wilt resistance	Transgenic	Tripathi, Lorenzen, et al. (2014), Tripathi, Tripathi, et al. (2014)
<i>MusaBAG1</i>	Banana	Rasthali (AAB)	ECS	<i>Fungal resistance</i>	Transgenic	Ghag, Singh Shekhawat, and Ganapathi (2014)
Synthetic peptide	Synthetic	Gonja Manjaya (AAB)	ECS	<i>Nematode resistance</i>	Transgenic	Tripathi, Oduor, and Tripathi (2015)
Stacked <i>Pflp</i> and <i>Hrap</i>	Sweet pepper	Gonja Manjaya (AAB)	ECS	<i>Bacterial resistance</i>	Transgenic	Muwonge et al. (2016)
<i>RG2</i> and <i>Ced9</i>	<i>Musa acuminata</i>	Cavendish (AAA)	ECS	<i>Fungal resistance</i>	Transgenic	Dale et al. (2017)
<i>AtNPR1</i>	Arabidopsis	Sukali Ndiizi(AAB)	ECS	<i>Bacterial wilt resistance</i>	Transgenic	Tripathi (2018)
<i>AtNHI</i>	Arabidopsis	Sukali Ndiizi(AAB)	ECS	<i>Fungal resistance</i>	Transgenic	Tripathi (2018)
<i>dsRNA-ACtE</i>	Insects	Cavendish Williams, Orishele, and Gonja Manjaya	ECS	<i>Aphid resistance</i>	Transgenic	Jekayinoluwa et al. (2021)
<i>MaMADS36</i>	<i>Musa</i>	Brazilian (AAA)	ECS	Banana ripening	Transgenic	Liu et al. (2021)
<i>AtEFR</i>	Arabidopsis	Dwarf Cavendish (AAA)	ECS	<i>Bacterial wilt resistance</i>	Transgenic	Adero et al. (2023)
<i>PDS</i>	—	Rasthali (AAB)	ECS	—	G. editing	Kaur et al. (2018)
<i>PDS</i>	—	Cavendish (AAA)	ECS	—	G. editing	Naim et al. (2018)
<i>eBSV</i>	—	Sukali Ndiizi(AAB)	ECS	<i>Virus resistance</i>	G. editing	Tripathi et al. (2019)
<i>PDS</i>	—	Sukali Ndiizi(AAB);Gonja Manjaya (AAB)	ECS	—	G. editing	Ntui, Tripathi, and Tripathi (2020)

(Continues)

TABLE 1 | (Continued)

Target gene	Origin	Banana cultivar	Explant	Trait	Genetic engineering technique	References
<i>MaGA20ox2</i>	—	Gros Michel	ECS	Plant architecture	G. editing	Shao et al. (2020)
<i>LCYe</i>	—	Cavendish (AAA)	ECS	Beta carotene	G. editing	Kaur et al. (2020)
<i>DMR6</i>	—	Sukali Ndiizi (AAB)	ECS	<i>Bacterial wilt resistance</i>	G. editing	Tripathi et al. (2021)
<i>MaACO1</i>	—	Brazilian (AAA)	ECS	Extended shelf life	G. editing	Hu et al. (2021)
<i>CCDs</i>	—	Rasthali (AAB)	ECS	Beta carotene	G. editing	Awasthi et al. (2022)
Vector optimization	—	Cavendish (AAA)	ECS	Bacterial diseases	G. editing	Zhang et al. (2022)
Cas-CLOVER (<i>PDS</i> gene)	—	Sukali Ndiizi(AAB)	ECS	<i>Bacterial wilt resistance</i>	G. editing	Tripathi, Ntui, and Tripathi (2023), Tripathi et al. (2023)
<i>MusaENODL3</i>	—	Gonja Manjaya (AAB)	ECS	<i>Bacterial wilt resistance</i>	G. editing	Ntui et al. (2023)
<i>MusaPUB22/23</i>	—	Sukali Ndiizi(AAB)	ECS	<i>Bacterial wilt resistance</i>	G. editing	Tripathi et al. (2024)

options because it allows the integration of big transgenes and minimal copy numbers. Moreover, this method is highly efficient and cost-effective (Gelvin 2003; Asande et al. 2020).

Various plant tissues, including embryogenic cell suspension (Strosse 2003; Khanna et al. 2004), zygotic embryos (Nandhakumar et al. 2018), male flowers (Nandariyah, Endang, and Yunian 2021), and meristematic tissues (Villao, Flores, and Santos-Ordóñez 2021) are used as banana transformation explants. Among these, embryogenic cell suspensions (ECS) are the most suitable for banana genetic engineering (Tripathi, Muwonge, and Tripathi 2012; Tripathi, Oduor, and Tripathi 2015) because of their high efficiency in regenerating homogeneous plants for various cultivars rapidly (Strosse 2003). Genetic engineering is the best potential way to mitigate bananas' bacteria by developing resistant BXW cultivars with high efficiency and time management (Tripathi, Muwonge, and Tripathi 2012).

10 | Genome Editing in Banana

Recent advances in biotechnology have moved to genome editing as a powerful emerging tool of plant breeding for achieving sustainable crop production (Tripathi, Ntui, and Tripathi 2023). The method is the most prominent potential approach to modifying plant genomes precisely and can edit many genes simultaneously (Ntui et al. 2023). The innovative approach is used for crop improvement with desirable traits like enhancing crop disease resistance, yield, quality improvement, abiotic tolerance, plant growth, morphology, and altered plant architecture (Tripathi et al. 2023). The method is applied significantly for generating favorable crop species with a transgene-free method recognized as non-genetically modified plants with no new foreign genes introduced. Gene manipulation improves crops by modifying their endogenous genome by deleting or knocking out responsible genes of disease susceptibility or activating genes accountable to enhance defense genes (Tripathi et al. 2022). Currently, four groups of engineered nucleases are used in genome editing, including mega nuclease, Zinc finger protein (ZFNs), transcription activator-like effector (TALENs), and clustered regularly interspaced short palindromic repeat-associated protein (CRISPR/Cas) nuclease systems (Fiaz et al. 2021). CRISPR/Cas has become the most predominant technique because it is the most efficient and accurate in genome manipulation for generating the required edited plant (Tripathi, Ntui, and Tripathi 2022). CRISPR/Cas is working on silencing susceptibility genes, which have been accused of being upregulated during the pathogen infection (Ntui, Tripathi, and Tripathi 2020; Ntui et al. 2023). Many susceptibility genes linked to BXW resistance were found in resistant *Musa balbisiana* and susceptible cultivar Pisang Awark during comparative transcriptomic analysis of those two cultivars (Tripathi et al. 2019b). Suppressing the downy mildew resistance 6 (*DMR6*) ortholog in bananas has demonstrated banana resistance against bacterial diseases such as Xanthomonas wilt. Banana mutants of *MusaDMR6* were developed and showed BXW resistance in the greenhouse (Tripathi et al. 2021). Many authors have reported precise and rapid genome-edited plants regenerated from CRISPR/Cas for disease resistance, improving nutritional qualities and yield, resilient to climate change, and showing normal morphology with the desirable traits as opposed to the unmodified plants

(Tripathi et al. 2022; Ntui et al. 2023). Numerous researchers have investigated the effectiveness of genome editing and transgenic technology in eradicating pests and diseases that affect plantains and bananas (Table 1).

11 | Conclusion

In East Africa, banana *Xanthomonas* wilt is a deadly problem for farmers. It attacks all types of cultivated bananas, spreads rapidly, and can destroy the whole plantation. Controlling bacterial disease using chemical products is complex and even not environmentally friendly. Using available preventive methods is ineffective, and bacterial disease outbreaks have increased. It is hard to use traditional breeding as it presents challenges of sterility and polyploidy with long generation cycles. Improving plant immunity by activating plant defense mechanisms is the most sustainable way against pathogen disease. Plant genetic modification is the best approach for developing new cultivars with desirable traits. It is economically practical with precision and a timely management approach. Genetic engineering, especially plant genome editing, is a safe and environment-friendly approach to improving crops with the necessary qualities. Millions of people who depend on the banana harvest will have better opportunities. High-yielding disease-resistant bananas will reduce the yield gap and provide food security in the region.

Author Contributions

This review article was written by A.M. and J.N.T. and reviewed by all authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data sharing not applicable to this article as no datasets were generated or analysed during the current study.

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