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Xanthomonas Wilt

A Threat to Banana Production in East and Central Africa

Bananas and plantains (*Musa* spp.) are the world's fourth most important food crop after rice, wheat, and maize. Annual banana production in the world is estimated at 1×10^{11} kg, of which less than 10% enters the commercial market, indicating that the crop is more important for local consumption than for export (19). Approximately one-third of the bananas produced globally are grown in sub-Saharan Africa, where the crop provides more than 25% of food energy requirements for more than 100 million people. East Africa (including Burundi, Kenya, Rwanda, Tanzania, and Uganda) is the largest banana-producing and -consuming region in Africa. Uganda is the world's second largest producer after India, with a total of about 10.5×10^9 kg (18).

Banana production is threatened by various constraints such as declining soil fertility, socioeconomic problems, pests, and diseases (45). The banana *Xanthomonas* wilt (BXW) disease caused by the bacterium *Xanthomonas campestris* pv. *musacearum* endangers the livelihood of millions of farmers in East Africa (64). Low soil fertility and BXW are considered to be the two greatest threats to banana productivity in the Great Lakes region of eastern Africa including Burundi, Rwanda, northeastern Democratic Republic of Congo, Uganda, northwestern Kenya, and Tanzania (26). The disease was first reported about 40 years ago in Ethiopia on

Ensete, which is closely related to banana (70). Outside Ethiopia, BXW was first reported in Uganda in 2001 and has now spread to almost all major banana-producing districts of the country (Fig. 1). The disease has also been reported in Democratic Republic of Congo (43), Rwanda (48), Tanzania (32), Kenya (31), and Bu-

rundi (5) (Fig. 2). Pest risk analysis of BXW has been recently published for several French overseas departments (10) and countries in eastern, central, and southern Africa (50).

The disease affects almost all commonly grown banana cultivars (65), although field observation and laboratory experiments

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Fig. 1. Map showing spread of banana *Xanthomonas* wilt in Uganda (2,65).

indicate that beer banana cultivar Pisang Awak (Kayinja) is most susceptible (16,56). The banana cultivars grown in the Great Lakes region include the following: East African Highland banana subgroup (AAA-EA genome) used to make “matooke” (steamed and mashed fruit) and beer; brewing cultivar Pisang Awak (ABB genome); the dessert cultivars Sukali Ndiizi (AAB genome) and the Cavendish subgroup (AAA genome); and plantains (Gonja, AAB genome).

The impacts of BXW are both extreme and rapid, unlike those of other diseases, which cause gradually increasing losses over years. The economic impact of BXW is due to death of the mother plant that would otherwise contribute to the ratoon plant production cycles (60) (Fig. 3). Fields infested with *X. campestris* pv. *musacearum* cannot be replanted with banana for at least 6 months due to carry-over of soilborne inoculum (62). BXW has similarities to other bacterial wilts of banana, caused by *Ralstonia solanacearum*, including Moko, blood, and bugtok diseases (53). Once these pathogens have become established, disease control is very difficult and eradication impossible (16).

Economic and Social Impact

Bananas are important in the Great Lakes region, not only in Uganda, but also in adjacent countries, where they are both a food security and a cash crop (17). Food security studies reveal that in Uganda, Rwanda, and Burundi, bananas constitute more than 30% of the daily per capita caloric intake, rising to 60% in some regions (2). Bananas also provide a major source of cash income for the farmers in the Great Lakes region (44).

Between 2001 and 2007, BXW spread into more than 35 districts in Uganda, apparently from central Uganda, where banana production is less intensive and mainly subsistence-oriented, to the highly intensive production areas in western Uganda. In central Uganda, BXW incidence, measured as the proportion of affected sites within a district, reached up to 60%, but the major banana production areas in southwestern Uganda showed little or no infestation by 2006 (65). In response to the outbreak of BXW, the Ministry of Agriculture, and Animal Industry and Fisheries (MAAIF) in Uganda formed a task force in December 2001 to develop a strategy to eradicate the disease (65). The strategy emphasized cutting and burying infected banana plants, restricting movement of banana materials, decapitating male buds, sterilizing tools, and raising awareness about the disease. BXW management strategies reduced disease incidence to less than 10% in areas where they were adopted, but implementation was not sustainable due to the high costs.

As yet, there has been little analysis of the economic impact of BXW in countries

neighboring Uganda. However, if uncontrolled, BXW would spread at a rate of 8% per annum in cooking banana plantations (27), causing an estimated production loss of about 53% over a 10-year period, equivalent to a reduction from the current 4.5×10^9 kg to 2.1×10^9 kg/year (1). Overall economic losses were estimated at \$2 billion (1) to \$8 billion over a decade, arising from price increases and significant reductions in production (68). According to Abele and Pillay (1), consumers bear the major share of the losses due to reduced supply and increasing prices of bananas, whereas producers benefit from higher prices and tend to lose less than consum-

ers. Kayobyo et al. (27) predicted declines in per capita consumption of bananas by 42% and total household incomes by about 32% by the end of 2004 in the BXW-affected areas compared with the nonaffected counterparts. Similar scenarios are likely for the other countries in the region that depend on bananas as a main staple crop.

The scenario described above has significant implications for the management of BXW. Generally, management measures for crop diseases are taken based on economic threshold, when losses are greater than the costs of management (46). BXW management in this respect has three prob-

Fig. 2. Incidence of banana *Xanthomonas* wilt measured as percentage of farms infected in the Great Lakes region of Africa (13).

Fig. 3. Banana plantation damaged due to *Xanthomonas* wilt.

lems. First, producers will probably begin to manage the disease too late from an overall economic perspective, not taking into account the much higher losses to consumers that occur early. Second, there are no curative measures for BXW. Third, the disease affects banana populations quite rapidly, so that by the time the farmer begins to respond, it may be too late (12).

Disease management technologies have to be assessed for their financial viability in terms of development and dissemination costs against adoption and returns for farmers (and thus on research investment). Adoption of exotic or hybrid improved cultivars in East Africa is still low, whereas adoption of improved management techniques is significantly higher (17). The most promising technologies are those that can be delivered in a short time, require little adaptation of existing management systems, and offer high returns. For banana production, improved agronomic practices rank highest in returns on investment, followed by genetic modification for disease resistance (26). Traditional breeding methods are less profitable, as they take longer to achieve usable outputs (26). These observations favor genetic modification for resistance to BXW as a low-cost preemptive measure with minimal market distortion as old stands are gradually replaced by improved material. However, genetic modification has to take into account the potential loss of natural biodiversity that could lead to a higher risk of losses due to other diseases.

Causal Organism

The causal agent of BXW is a motile, gram-negative, rod-shaped bacterium possessing a single polar flagellum, for which the name *Xanthomonas campestris* was adopted in the 1960s and 1970s (70,71), but which was subsequently renamed *Xanthomonas campestris* pv. *musacearum* in the 1980s (72). As a typical member of *Xanthomonadaceae*, the bacterium produces yellow, circular, mucoid, slimy colonies on nutrient agar and semi-selective medium YTSA-CC (60). Recently, phylogenetic relationships were evaluated for 20 isolates of the bacterium collected within a period of about four decades, between 1968 and 2005, from Ethiopia, Uganda, Democratic Republic of Congo, Tanzania, and Rwanda. Sequence analyses of the internally transcribed spacer (ITS) locus (6) and the gyrase B (*gyrB*) gene revealed only limited (<2%) nucleotide divergence among the isolates (6). This was consistent with fatty acid methyl esters (FAME) analysis and genomic amplicon fingerprinting with repetitive sequence polymerase chain reaction (rep-PCR) profiling, both of which indicated that populations of *X. campestris* pv. *musacearum* are homogenous (6,7). Absence of any notable differences with respect to time of isolation, geographic location, or host (banana

and enset) suggests a recent introduction of *X. campestris* pv. *musacearum*, first from Ethiopia to Uganda and then across the Great Lakes region. In a laboratory-based pathogenicity test, the isolates from Uganda were observed to induce the same level of severity on all banana genotypes tested (6,56), which is additional evidence that the isolates have originated recently.

Comparison of *X. campestris* pv. *musacearum* with other *Xanthomonas* spp., based on FAME and partial nucleotide sequences of the *gyrB* gene and ITS, showed that all strains of *X. campestris* pv. *musacearum* are similar to *X. vasicola* which formerly comprised a sorghum pathogen, *X. vasicola* pv. *holcicola*, and a sugarcane and maize pathogen, *X. vasicola* pv. *vasculorum* (15,67). In addition, pathogenicity studies revealed that *X. campestris* pv. *musacearum* is able to induce a hypersensitive response in maize. Based on phylogenetic and biochemical analyses and pathogenicity studies, *X. vasicola* pv. *musacearum* has been proposed as the new identity of the bacterium causing BXW (6). However, more data on the pathogenicity characteristics of the *X. vasicola* pathovars are needed to support the new pathovar classification. The very high similarity among all banana/enset strains indicates that pathovar evolution occurred in relatively recent history (47).

Symptoms

Affected banana plants develop symptoms characterized by a progressive yellowing and wilting of leaves, and uneven and premature ripening of fruit with sections showing unique yellowish blotches in the pulp and dark brown placental scars (Fig. 4A to C) (64). Symptoms on floral parts include wilting of bracts, shriveling and rotting of the male buds, and yellow-brown flower stalks (Fig. 4D). Cross-sections of diseased pseudostems reveal yellowish bacterial ooze (55). When pseudostems and rachis are cut, pockets of pale yellow bacterial ooze appear within 5 to 15 min (Fig. 4E and F). Yellow or brown streaks occur in the vascular tissues of infected plants. Eventually, infected plants wither and the plant rots. Symptom development is rapid under favorable conditions and typically evident within 3 to 4 weeks under field conditions and 2 to 3 weeks after inoculation under screenhouse conditions (56).

Symptom expression varies depending on cultivar, growth stage, and the mode of disease transmission (35). When flowering plants are infected by insect-transmitted bacteria, the initial symptoms are wilting and withering of the male bud, with a gradual shrinking along the rachis extending toward the fingers. The shrunk part of the rachis often acquires an ashen discoloration before turning black. As the infection progresses over time, the fruits (most often those nearer to the male bud) start turning yellow prematurely, giving an

appearance of ripening. By the time these infected fingers turn yellow on the outside, infection is usually advanced and the pulp within is already rotted and discolored. As the disease progresses, the infected leaves turn yellow, wilt, and eventually die. In the terminal stages of infection, the whole bunch rots completely, all leaves dry out and die back, and stems die and collapse gradually from the top downward.

Plants can also be infected by *X. campestris* pv. *musacearum* before flowering, usually as a result of transmission through contaminated tools (4), although soilborne infection can also occur through the roots (36). When plants are infected before flowering, the initial symptom is progressive yellowing of leaves from the leaf tip toward the petioles. During the wet season, water-soaking symptoms may appear first in patches on the leaf before the leaf turns yellow. Generally, symptoms seem to progress faster during the wet season than during the dry season. The time taken to reach different stages of symptom expression may differ with cultivar and environmental conditions, but generally plants show symptoms within 3 weeks of infection.

Disease Diagnosis

BXW can be diagnosed from the typical symptoms it induces on banana, including: premature ripening of fruits, internal brown discolorations of fingers and vascular tissues, pale yellow ooze from cut surfaces, wilting of bracts and male buds, and progressive yellowing leading to complete wilting. Diseases with similar symptoms, such as Moko disease, are not known to occur in Africa. A prominent symptom of Panama disease (caused by *Fusarium oxysporum* f. sp. *cubense*) is wilting, but cut sections of the stem show vascular discoloration without any yellow bacterial ooze and fruits are not directly affected.

For more precise diagnosis, several pathogen characteristics have been examined, including a variety of biochemical tests, substrate utilization (BIOLOG), and FAME analysis (6). However, affordable, accurate, and reliable diagnostic tools are necessary and important for detecting the pathogen, studying disease epidemiology, and developing management measures. The BXW pathogen grows slowly when cultured on synthetic media and can be overgrown easily by contaminants, thus precise diagnostic techniques are needed. Recently, two semi-selective media have been developed for *X. campestris* pv. *musacearum*: CCA (39) and YTSA-CC (60). On these media, *X. campestris* pv. *musacearum* is easily identified as yellowish, mucoid, circular colonies, and the bacterium can be isolated from infected banana tissues, contaminated insect vectors, and infested soil.

Efforts are underway to develop DNA-based diagnostic methods (6,7,33). A real-

Fig. 4. Symptoms of *Xanthomonas* wilt disease on various parts of banana plant: A, yellowing and wilting of leaves; B, premature ripening of fruits and male flower damage; C, yellowish blotches and ooze in the pulp of fruits; D, wilting and shriveling of male bud; E, yellow ooze from rachis; and F, yellow ooze from cut pseudostem.

time (TaqMan) PCR assay was developed for detection of *X. campestris* pv. *musacearum* (7). Due to their close genetic relatedness, this assay also detects other *X. vasicola* pathovars, including all 36 *X. vasicola* strains currently available at National Collection of Plant Pathogenic Bacteria, Central Science Laboratory, York, UK. Negative results were obtained with 52 other *Xanthomonas* spp. Two pairs of primers were developed for detection of *X. campestris* pv. *musacearum* in a conventional PCR assay. The primers amplified products of 358 and 272 bp, respectively, from DNA extracts of the 36 *X. vasicola* isolates but not the 52 other xanthomonads. The primers were developed from a 685-bp fragment for a rep-PCR (6) that encodes methylase of chemotaxis methyl-accepting protein. Specific assays are still needed for each of the bacterial strains. The complete genomes of two isolates of *X. campestris* pv. *musacearum* and one of *X. vasicola* pv. *Vasculorum* have been sequenced (V. Aritua, personal communication) and would provide opportunities to develop additional primers.

In addition to selective media and PCR, progress has been made in developing ELISA-based diagnostic kits. Polyclonal antibodies have been generated, but initial tests showed cross-reaction with other *Xanthomonas* isolates occurring in the same niche with *X. campestris* pv. *musacearum*. Efforts are also underway to generate monoclonal antibodies (MAbs) that would be precise and specific for *X. campestris* pv. *musacearum*. The MAb approach is particularly interesting as it could be used to test plant sap in the field in a simple immunostrip format.

Disease Cycle/Epidemiology

The major sources of pathogen inoculum are infected banana plants and resi-

dues, contaminated soil, and traded banana products (seedlings, fruits, leaves, and fibers; Fig. 5). The mode of disease spread can vary significantly, depending on the production system (subsistence or commercial), agroecology, and cultivar grown. Insects, cutting tools, wind-driven rain, and infected seedlings are the major means by which the pathogen spreads within or across fields. The importance of insect vectors varies with ecological conditions, being lower in cold, higher altitude regions (41), and the importance of farm tools depends on how intensively farmers manage their crops, which to an extent is determined by the local economic importance of bananas. Male bud infection has not been observed in Ethiopia at altitudes over 1,700 meters above sea level (masl) (3). Reports from the Democratic Republic of Congo suggest that infection through the banana inflorescence is not common at an altitude of 1,700 masl (43), perhaps due to lack of adequate insect transmission. Inflorescence infections are common around Lake Victoria, which has an altitude of 1,135 masl. Several aspects of insect transmission (e.g., efficiency of transmission by various insect species, nature of transmission, acquisition of bacterial inoculum, etc.) require further investigations (10,54).

In central Uganda, the beer cultivar Pisang Awak is popularly grown in less intensive subsistence farming systems. In this region, field observations indicate that the primary means of disease spread is insects that transmit bacteria through the moist cushions that are exposed when male flowers are shed from the inflorescence (Fig. 6). The pathogen can infect both male and female parts of inflorescences through fresh scars left by fallen flower bracts (21), but the natural infection through female flowers is unlikely to be of

importance because plants are not infected when the male flower parts are removed as a BXW management practice. *X. campestris* pv. *musacearum* has been isolated from the nectar and from the ooze exuding through the cushions revealed by the fallen male flowers and the fresh openings made by the fallen bracts of flowers (54). Insects pick up the bacteria, externally on body parts or internally within organs, when they visit the banana inflorescence (20). The most abundant insects visiting banana flowers are stingless bees, *Plebeina denoiti*, fruit flies, grass flies (54), and wasps (20). The agroecology in this region, at 800 to 1,500 masl, is more suitable for insect vectors of the pathogen (41). In western Uganda, where cooking bananas are dominant and produced under more intensive commercial systems, contaminated tools are the major means of disease spread. Although the altitude, higher than 1,600 masl, is less favorable for insect vectors, the major factor here is the close attention paid to plantations by farmers, which is characterized by repeated use of cutting tools such as machetes that can spread the pathogen. In addition to insects and tools, bacteria could also penetrate into plants through roots, especially if injured by soilborne pests, e.g., nematodes and weevils (36), but clear experimental evidence is lacking.

Besides banana, the only other known natural host of *X. campestris* pv. *musacearum* is enset (70,71) (Fig. 7), although the pathogen has been reported to be able to infect *Canna indica* after artificial inoculation (51). *X. campestris* pv. *musacearum* can infect and produce symptoms on *Musa zebrina* and *M. ornata* and *Canna* lily (*Canna × generalis*), an ornamental plant, in Uganda (51). Yirgou and Bradbury (71) inoculated aubergine, barley, bean, broad

Fig. 5. A few probable sources of inoculum for long-distance spread of *Xanthomonas campestris* pv. *musacearum*: A, dessert bananas wrapped in leaf sheaths at a collection center in a local market; and B, a farmer collecting the residues from a banana collection center to take to his farm to use as mulch.

bean, castor oil, lettuce, lucerne, maize, peanut, pelargonium, potato, sorghum, sunflower, sweet pepper, tobacco, tomato, and wheat with *X. campestris* pv. *musacearum*, but no symptoms were observed. Ashagari (8) inoculated plants commonly found in enset growing regions to determine host range. *Chenopodium album*, *Colocasia antiquorum*, *Commelina* sp., *Guizotia scabra*, *Kalanchoe quartinia*, *Snowdenia polystachya*, *Solanum nigrum*, and *Tagetes minuta* were unaffected after 10 weeks, but the ornamental *Canna orchoides* had disease symptoms within 4 to 6 weeks, as did banana and enset controls. The role of alternate hosts in the disease cycle is unclear. The pathogen survives for up to 3 months in the soil in the absence of a host (42). In a separate study, banana seedlings replanted in infested fields were not reinfected after all the diseased mats

were completely uprooted from the field followed by a 6-month fallow period (62). This implies that bananas can be replanted after a relatively short period of time in fields where the crop was destroyed by *X. campestris* pv. *musacearum*.

Susceptibility of Commonly Grown Cultivars

Although BXW has been observed on both East African Highland bananas and exotic dessert and beer bananas, incidence varies by clone (63). Disease incidence was higher in brewing bananas compared with East African Highland cooking bananas in severely affected central Uganda. The exotic cultivars Pisang Awak (ABB), Bluggoe (ABB), and dessert cultivars Gros Michel (AAA) and Sukali Ndiizi (AAB), have higher sugar content in their nectar, which might make them more attractive to

insect vectors (25). In some regions of Ethiopia and central Uganda where Pisang Awak is abundant and de-budding is rarely practiced, higher rates of BXW spread have been noted at altitudes below 1,700 masl (3,25). In a study conducted in Lira district (northern Uganda), disease incidence was highest on Bluggoe (73.5%), followed by Pisang Awak (30.4%), cooking bananas (11.7%), and least in Sukali Ndiizi (2.8%) (66).

Where disease spread is predominantly through tools, relative susceptibility of cultivars is also important. For example, farmers vigorously practice de-budding in Ntungamo and Mbarara districts of Uganda where cooking East African Highland bananas are more abundant, but some of the recent outbreaks were difficult to eradicate due to use of contaminated tools on susceptible cultivars (65).

Control and Management Strategies

Management of diseases in tropical perennial crops such as banana is a challenge due to continuous association of host and inoculum over a long period of time (47). The recommended measures for BXW management involve a mixture of approaches combining exclusion, eradication, host resistance, and protection. Control of BXW and similar bacterial diseases of banana depends on prevention of disease spread (containment), reduction of disease impact in affected farms (management), and rehabilitation of previously affected areas. Awareness campaigns, advocacy and support from policy makers and the donor community are critical for managing transnational epidemics such the one experienced in the Great Lakes region. The experiences of various countries in managing BXW have been variable. In Uganda and Tanzania, regions with active political leadership have achieved >90% control of BXW, whereas the disease prevalence has almost quadrupled in eastern Democratic Republic of Congo due to civil instability (38). The United States Agency for International Development

Fig. 6. A, Parts of male flower of banana; and B and C, insects visiting flowers of banana plants infected with *Xanthomonas campestris* pv. *musacearum*.

Fig. 7. *Ensete* plant affected by *Xanthomonas* wilt.

(USAID) funded a Crop Crisis Control project (C3P) during 2005 to 2008 to help prepare for and mitigate the effects of BXW, so that sudden declines in the productivity of banana will not tip large numbers of people into food insecurity in Burundi, Kenya, Rwanda, Tanzania, and Uganda.

The specific measures taken to prevent and/or manage BXW depend on the intensity or threat of the disease in the target area (35). Areas in which less than 50% of the farms are affected, each with fewer than 50% mats infected, are included in the “epidemic expansion” phase (34). Areas with more than 75% of the farms affected, each with more than 75% mats infected, are included in the “post-epidemic” phase. A “critical transition phase” describes an

area where more than 50% of farms are affected, each with less than 50% mats infected.

In fields where disease incidence is below 50%, removing infected mats is recommended to reduce the inoculum load. In this case, mat removal is urgent because delays are likely to result in increased disease incidence. Where conditions are favorable and insect vectors abundant, the disease spreads sporadically but continuously from infected mats to new plants as soon as they flower. Where insect vectors are important, disease spread can be contained by removal of the male flowers and bunch of infected plants to reduce sources of inoculum. Eventually, entire infected mats should be removed to ensure that no infected suckers reach flowering, provid-

ing a source of inoculum for insect vectors. Where contaminated tools are the main means of pathogen dissemination, disease will most likely spread in a systematic manner starting from the infected mat and expanding outward. Unless tools are disinfested after use on each mat, the number of infected mats increases rapidly.

In areas where disease incidence exceeds 70% (post-epidemic phase), there is very little chance of harvesting anything from the few remaining mats. For farmers with small pieces of land, it becomes necessary to remove the infected mats so the land is available for alternative crops or livestock integration. Mat removal also starts the process of pathogen reduction in the soil, which is essential if banana is to be replanted in the same field. The majority of small-holder farmers in East and Central Africa would grow other crops on the farm where banana was uprooted (Fig. 8). The most appropriate replacement crops are annuals that are nonhosts of *Xanthomonas*, including beans, cassava, maize, taro, sweet potato, sorghum, tobacco, or napier grass.

Cultural practices. Timely removal of the male bud interrupts the insect transmission cycle and prevents the spread of the disease in banana types that are considered to be at greatest risk of infection. Removal of male buds (de-budding) by twisting the peduncle with a forked stick instead of cutting tools is one of the emphasized practices for preventing disease spread (Fig. 9). The disease can be contained in fields where de-budding is effectively practiced. However, adoption of de-budding has been inconsistent among farming communities (25), where farmers feel that de-budding affects the quality of the banana, especially for the juice cultivars (9).

Once BXW occurs in a field, there is no remedy other than to cut down all infected plants (Fig. 10), completely dig out the rhizomes, and place the field under fallow or a prolonged crop rotation regime. A 6-month fallow period is adequate to avoid reinfection from soilborne inoculum (62) if all infected plant material is removed. *X. campestris* pv. *musacearum* can survive more than 4 months if host debris and residues are present. Soilborne *X. campestris* pv. *musacearum* may be more important in the presence of nematodes and weevils that can create injuries on roots and thereby enhance penetration by the pathogen (36).

Bananas reproduce by forming suckers from vegetative buds on the rhizome, with several suckers arising from each rhizome. Where new plantings are to be established, suckers are dislodged from the mother plants and transferred to the new plot. Adjustments in planting practices can reduce disease incidence and support efforts to rehabilitate banana productivity on farms devastated by *X. campestris* pv. *musacearum* (36,37). Pared corms have less risk of

Fig. 8. As a result of destruction caused by *Xanthomonas* wilt, banana plantations are replaced with other crops such as A, sorghum, and B, sweet potato.

infection by *X. campestris* pv. *musacearum* if cured for 2 to 3 days before planting. Use of pest- and pathogen-free suckers produced in tissue culture can control the spread of a range of pests and diseases, including BXW (Fig. 11A). A less expensive alternative is macropagation of suckers (Fig. 11B), for which production nurseries can be located closer to farming communities, and the suckers can be made available at much lower costs than those for tissue culture.

Wilt-escaping cultivars. As yet, there are no banana cultivars known to be completely resistant to BXW; however, some cultivars escape infection through the inflorescence because they have persistent male flowers and bracts (Fig. 12), therefore the cushions on which insects could land and deposit the bacteria are not exposed. This characteristic allows the plants to escape insect-transmitted infections only, and these cultivars might not possess cell-mediated resistance. The cultivars that are known to express this trait are East African Highland cooking bananas including Nakitembe and Mbwasirume. Germplasm with similar inflorescence traits is also available in Indonesia (I. Buddenhagen, *personal communication*).

Some cultivars which shed their male flowers and expose the cushions also escape BXW infection through the inflorescence (40). These include Yangambi km5, Kikundi, Kisubi, Nakasebera, and Nakitengu. Some of these cultivars do not produce exudates on the male cushions, hence the cushions remain dry and unattractive to insects. Other cultivars have low sap pH, which could be unfavorable for growth of *Xanthomonas* within tissues (40).

Tolerant and resistant cultivars. The use of resistant cultivars is a cost-effective method of managing bacterial diseases. Development of disease-resistant bananas through conventional breeding requires resistant donor parents. High levels of cell-mediated resistance to *X. campestris* pv. *musacearum* have not been identified in banana germplasm. Screening for resistance requires a reliable and rapid method to unambiguously discriminate host reaction. Evaluating material in the field is laborious and hampered by variations in environmental conditions and nonuniform distribution of the pathogen. Early evaluation under controlled conditions with artificial inoculation is an important requirement to screen large numbers of *Musa* spp. for resistance to BXW. An *in vitro* screening method was developed for early identification of BXW resistance in small tissue-culture-grown plantlets (56). Eight cultivars of banana were screened with 16 isolates of *X. campestris* pv. *musacearum* by this method. There were significant differences in reaction among the cultivars, whereas no significant difference in virulence was observed among the pathogen

isolates. The cultivar Pisang Awak (Kayinja, ABB) was found to be highly susceptible, and *Musa balbisiana* (BB) was resistant. These reactions corresponded well with those of artificially inoculated potted plants. Therefore, the *in vitro* screening test can serve as a convenient, cheap, and rapid alternative for the evaluation of *Musa* germplasm for resistance to BXW in the field.

Even if resistant germplasm sources are identified, conventional breeding of banana is a difficult and lengthy process due to sterility of most cultivars coupled with long generation times. To circumvent these difficulties, transgenic technologies may provide a cost-effective alternative solution to the BXW pandemic. Some success in genetic engineering of banana has been achieved recently (11,22,28,30,49,57,61). An efficient method for direct gene transfer via particle bombardment of embryogenic cell suspensions has been reported in

the cooking banana Bluggoe, the plantain Three Hand Planty (49), and Cavendish banana Grand Nain (11). Hernandez et al. (23) reported that *Agrobacterium tumefaciens* is compatible with banana and transgenic plants of banana have been obtained by means of *A. tumefaciens*-mediated transformation of embryogenic cell suspensions (22,28). At present, most transformation protocols use cell suspensions, but establishing cell suspensions is lengthy and cultivar-dependent. Protocols have also been developed with meristematic tissues from various cultivars of *Musa* (30,57,61), which are applicable to a wide range of *Musa* cultivars irrespective of ploidy or genotype (57,58,61).

An attractive strategy for bacterial disease control in crops is to improve plant defense mechanisms. Recent advances in genetic engineering offer ways to transfer resistance genes found in other organisms into crop varieties without changing favor-

Fig. 9. Removal of male buds (de-budding) from banana inflorescence to control *Xanthomonas* wilt: A, farmer removing male bud; B, forked stick used for de-budding; and C, banana bunch after de-budding.

able traits. Plant defense genes from other plants and antimicrobial proteins are now potential sources of plant resistance (55). The state of genetic engineering of banana for disease resistance, including BXW resistance, has been extensively reviewed (55,59).

Of particular interest are the ferredoxin-like amphipathic protein (*pflp*, formerly called AP1) and hypersensitive response-assisting protein (*hrap*), isolated from sweet pepper (*Capsicum annuum*), which can intensify the harpinPSS-mediated hypersensitive response (14,24). These proteins have dual function: iron depletion antibiotic action and harpin-triggered hypersensitive response enhancing action. The transgenes enhanced the hypersensitive response induced by various pathogens, such as *Erwinia*, *Pseudomonas*, *Ralstonia*, and *Xanthomonas* spp., in nonhost plants through release of the proteinaceous elicitor, harpinPSS, in dicots including tobacco, potato, tomato, broccoli, and the monocots orchid and rice (24,29,52). Elicitor-induced resistance is not specific to particular pathogens, so it could be a very useful strategy (69). The International Institute of Tropical Agriculture (IITA) has negotiated a royalty-free license from the patent holder Academia Sinica, Taiwan, through the African Agricultural Technology Foundation (AATF) for access to the *pflp* gene for production of bananas resistant to BXW in sub-Saharan Africa. Genetic transformation of banana with the *pflp* gene is in progress at IITA in collaboration with the National Agriculture Research Organization (NARO) in Uganda. Several transformed lines of banana cultivars Pisang Awak (ABB), Mpologoma (AAA-EA), and Nakitembe (AAA-EA) have been generated, and are currently being evaluated for disease resistance under laboratory conditions.

Conclusion

The BXW pandemic in the Great Lakes region of East and Central Africa has threatened the livelihoods of people who depend on banana. The pathogen kills plants quickly and spreads rapidly over a large area in a short time, making the dis-

Fig. 10. Uprooted diseased banana plants in the field affected by *Xanthomonas* wilt.

Fig. 11. Clean planting material of banana for replanting of fields damaged by *Xanthomonas* wilt: A, plantlets produced through micropropagation; and B, plantlets produced through macropropagation.

Fig. 12. Wilt escaping cultivar with inflorescence having persistent male flowers and bracts.

ease one of the most dreaded in banana. The recommended measures for BXW management involve a mixture of approaches combining exclusion, eradication, host resistance, and protection. Although much of the emphasis on BXW has focused on management options based on information on other bacterial wilt diseases, more basic and strategic information on the pathogen is required. The development of disease resistant banana cultivars remains a high priority because farmers are reluctant to employ labor-intensive disease control measures. Nevertheless, some countries such as Uganda and Tanzania have achieved remarkable success in containing the impact of the disease through a mix of various management approaches.

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