

The performance of East African highland bananas released in farmers' fields and the need for their further improvement

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Abstract

East African highland bananas (AAA, EAHB) form over 80% of the banana cultivars in the Great Lakes region and are a source of food and income for over 40 million in the region. The production of these bananas has been constrained by pests, diseases, soil fertility decline and most recently climate change stresses. Farmers have been managing these problems using cultural practices. These are sometimes effective, such as for *Xanthomonas* wilt control, but can also be very demanding. For others, no cultural control practices exist, such as for instance for nematodes in established plantations. The banana research program of the National Agricultural Research Organisation (NARO) in Uganda therefore focuses on the improvement of bananas for pest/disease resistance and fruit quality through conventional and molecular breeding to sustain banana production. In collaboration with the International Institute for Tropical Agriculture (IITA), the NARO breeding program has developed and officially released a number of banana hybrids to the farming communities, including 'Kabana 6H' (syn. 'M9') and 'Kabana 7H' (syn. 'M2'). The released and promising hybrids have resistance to black leaf streak and tolerance to nematodes and weevils. Their overall consumer acceptability is not significantly different from that of the landrace local check. The recipient communities value the hybrids since they are being widely distributed through sales and giveaways in addition to recipient farmers expanding their plots. However, these hybrids are susceptible to *Xanthomonas* wilt, and are very tall and prone to wind damage. There is an opportunity to improve the hybrids for above-mentioned and other traits exploiting *Musa's* over 36,000 genes in the sequenced genome.

Keywords: breeding, consumer acceptability, hybrids, pest and disease resistance

INTRODUCTION

East African highland bananas (AAA, EAHB) form over 80% of the banana cultivars in the Great Lakes region and are a source of food and income for over 40 million people in the region. In Uganda, banana is the main staple food with an annual per capita consumption of 400 kg, the highest in the world (FAOSTAT, 2013). Without bananas, Uganda would be a net importer of food. Annual banana production in Uganda is estimated to be 10 million tons of cooking bananas locally known as 'Matooke' and 1 million ton of juice/beer bananas, predominantly 'Pisang Awak' (ABB genome), locally known as 'Kayinja', valued at USD 534 and 16.7 million, respectively (Kalyebara et al., 2006). Many rural communities earn income from sale of bananas to the urban centres. The crop is perennial, with a broad root and leaf network which maintains soil structure and provides soil cover throughout the year. The banana cropping system, therefore, is also an important component of sustainable environmental management. Banana is generally tolerant to long dry spells, can grow in a wide range of environments and farming systems, and saves on labor for opening land seasonally. Because of the importance of this crop, many of the regional countries have allotted banana a high research and development priority.



Banana production faces many constraints including banana weevil, nematodes, black leaf streak, Fusarium wilt, banana bacterial wilt and more recently drought stress (Tushemereirwe et al., 2001). Farmers manage some constraints with cultural control techniques, many of which are effective in keeping the pest and disease pressures below threshold levels. However, cultural control involves manipulating the environment of the plant host and the parasite. It is a continuous and tedious process for the farmers and can only work in the short run. Furthermore, diseases such as Fusarium wilt are not controllable by cultural practices. Use of resistant cultivars is a more effective and durable option for the management of banana problems (Smale et al., 2007).

The improvement of bananas in Uganda was started by the National Agricultural Research Organization (NARO) in partnership with the International Institute for Tropical Agriculture (IITA) in the early 1990s with medium and long-term approaches. In the medium-term approaches, banana hybrids were accessed from international breeding programmes such as the Fundación Hondureña de Investigación Agrícola (FHIA), through the International Transit Centre (ITC) of Bioversity International, and evaluated for agronomic performance, pest and disease resistance and consumer acceptability (Table 1). Following these evaluations, successful genotypes were released as 'Kabana 1', 'Kabana 2', 'Kabana 3', 'Kabana 4' and 'Kabana 5'. Although these genotypes are high yielding, have good pest and disease resistance (especially for black leaf streak and Fusarium wilt) and meet preferred traits as a dessert type, they do not meet consumer demands for cooking traits.

Table 1. Banana genotypes introduced in Uganda from other breeding programs.

Genotype	Attributes/utilization options
FHIA-01	Cooked as food Ripened for dessert Juice extraction Resistant to Fusarium wilt (race 1), black leaf streak
FHIA-02	Cooked as food Ripened for dessert Juice extraction
FHIA-17	Ripened for dessert Juice extraction Resistant to Fusarium wilt (race 1), black leaf streak
FHIA-23	Ripened for dessert Juice extraction Resistant to Fusarium wilt (race 1), black leaf streak
Yangambi Km5	Juice extraction Resistant to Fusarium wilt (race 1), black leaf streak, banana weevil and nematodes
FHIA-25	Juice extraction Resistant to Fusarium wilt (race 1), black leaf streak

In the meantime, NARO and IITA embarked on improving East African highland bananas (EAHBs) for yield, disease and pest resistance. The landraces were evaluated for pollen fertility and the female fertile clones identified (Ssebuliba et al., 2006). These were crossed with a wild diploid to generate synthetic tetraploids with EAHBs in their background. The synthetic tetraploids acted as breeding materials that were crossed with improved diploids to generate secondary triploids that were evaluated for agronomic, disease and pest resistance. This paper presents the progressive improvement of EAHBs at various levels of development in order to identify opportunities, challenges and future prospects for banana improvement.

Strategy for improving East African highland bananas

Conventional breeding of EAHBs involves controlled crossing of triploid (3x) landraces

with diploids (2x), and crossing of the resulting tetraploid hybrids (4x) with diploids (2x). The resultant progenies go through several rounds of selection. They are evaluated for agronomic performance in early evaluation trials (EET). In the EET, selection is based on the performance of single clones. The genotypes that are selected from the EET are further evaluated for black leaf streak response, yield and consumer acceptability in a preliminary yield trial (PYT). The promising genotypes from the PYT, that are combining high yields, resistance to black leaf streak and consumer acceptability, are evaluated further for reaction to nematodes and banana weevil, and then taken for participatory on-farm evaluation with farmers.

MATERIALS AND METHODS

Newly developed EAHB hybrids were evaluated for agronomic performance in early evaluation trials (EET). Single clones of each genotype were planted in a completely randomized design (CRD) along with the landrace 'Mbwazirume' (AAA genome, EAHB subgroup). Data collected included: flowering dates, used to compute days to flowering; number of standing leaves at flowering; harvest date used to compute days from flowering to harvest; number of leaves at harvest; bunch weight; youngest leaf spotted at flowering; number of suckers at flowering; plant height at flowering, and girth at 100 cm (Craenen, 1998). The crop cycling index ($CCI=HTS/PHT$) was computed from the height of the tallest sucker and the height of the mother plant at flowering. The harvested bunches were used for sensory evaluation by panels composed of farmers of at least 25 members to establish the acceptability of the hybrids using a structured 6 point hedonic scale of overall acceptability, appearance, taste, flavor and texture, ranging from 1 for extreme disapproval to 6 for extreme approval (Nowakunda et al., 2000). Selection of promising EAHB hybrids was based on black leaf streak response, culinary acceptability and bunch weight.

The selected EAHB hybrids were further evaluated for yield in a randomized complete block design (RCBD) in the preliminary yield trial (PYT). The harvested bunches were also used for sensory evaluation as described for EET. Pot assays are conducted to assess the response of these promising EAHBs to nematode and weevil response (Kiggundu et al., 2003; Sadik et al., 2010; Dochez et al., 2009).

RESULTS AND DISCUSSION

Twelve EETs have been completed by NARO since 2000, constituting over 4000 'Matooke' hybrids (Table 2). A total of 126 (2.9% of the hybrids evaluated) were selected to be used either as parents (tetraploids and diploids) for further improvement or as candidate cultivars to be evaluated for release to farming communities. The selections at EET, based on performance of a single clone for at least two seasons, include 24 (19%) tetraploids, 32 (25.4%) diploids and 70 (55.6%) triploids. The number of hybrids selected per EET ranged from 2 hybrids (0.9%) to 21 hybrids (4.2%).

The selected triploid hybrids were evaluated in PYT. Four PYTs have been completed since 2005 (Table 3). Thirteen (13) hybrids have been selected and advanced for on-farm evaluation at three sites in central Uganda (Nakaseke, Mpigi and Kimemyedde). Two 'Matooke' hybrids 'M9' and 'M2' combining high yields and resistance to black leaf streak with high consumer acceptability, have been released as 'Kabana 6H' (2010) and 'Kabana 7H' (2013). Two more hybrids 'M19' and 'M20' are candidates for release.

Table 2. Selection rate of EAHB hybrids for early evaluation trial.

Trial	YOP	No. clones	4x	2x	3x	Total	% selection
EET1	2000	420	16	2	0	18	4.3
EET2	2002	500	0	3	18	21	4.2
EET3	2003	200	0	2	13	15	7.5
EET4	2004	350	0	2	9	11	3.1
EET5	2005	231	0	2	0	2	0.9
EET6	2006	130	0	1	3	4	3.1
EET7	2007	420	2	3	4	9	2.1
EET8	2008	340	0	4	4	8	2.4
EET9	2009	361	0	2	3	5	1.4
EET10	2010	340	0	4	2	6	1.8
EET11	2011	560	4	4	5	13	2.3
EET12	2012	570	2	3	9	14	2.5

YOP = year of planting.

Table 3. Selection of EAHB hybrids from the preliminary yield trials.

Trial	YOP	No. hybrids	No. selections
PYT1	2005	18	4
PYT2	2006	13	4
PYT3	2007	9	0
PYT4	2009	11	5

YOP = year of planting.

Pest and disease-resistant 'Matooke' hybrids

Black leaf streak has been the primary target constraint of banana breeding. Using the youngest leaf spotted (YLS) and the number of standing leaves (NSL) at flowering as indicators of resistance (Craenen, 1998), 'Matooke' hybrids have been selected for black leaf streak resistance (Table 3). Orjeda (1998) suggested that bananas require more than 70% of active leaf foliage at flowering for proper development of the banana fruits. In most resistant banana genotypes, black leaf streak symptoms are observed on older leaves at flowering. This indicates that either symptoms are developing at a slower rate or disease development is arrested early. The several rounds of selection have ensured that the black leaf streak resistance is successfully introgressed from the wild and improved diploid bananas we are using as male parents.

Currently, banana weevil resistance is one of the secondary target breeding traits. Promising EAHB hybrids are assessed for corm damage due to weevils at harvest (Kiggundu et al., 2003). EAHB hybrids with significantly less cross-sectional corm damage than the susceptible local check are considered tolerant to the banana weevil (Table 4). Growing traditional banana cultivars has become difficult due to these pests and developing genotypes resistant/tolerant to banana weevil will solve the long-standing problem of short plantation life. Tolerance to banana weevil has previously been attributed to biophysical factors like corm diameter, resin/sap production, corm dry matter content and corm hardness (Kiggundu, 2000). Selecting male fertile diploid bananas for these biophysical characters will be plausible.

Tolerance/resistance to nematodes has also been a secondary breeding target at NARO and some of the promising hybrids have exhibited levels tolerance to *R. similis* under screenhouse conditions (Table 5). These hybrids, when inoculated with *R. similis* show percentage root necrosis that is significantly less than the susceptible local check, 'Mbwazirume'.

The hybridization of 'Matooke' with wild and improved diploid banana modifies the unique taste of 'Matooke' as perceived traditionally. During the several rounds of selection

promising materials have been assessed for culinary attributes using consumer methods of sensory evaluation techniques (Nowakunda et al., 2000). The acceptability scores for the three EAHB were above 3.5 and were considered acceptable to the consumers (Table 6). Consumer acceptability tests are also used to document feedback from end-users.

Table 4. Means ($\pm$ standard error) of total cross-section corm damage scores of banana hybrids tested evaluated at NaRL 2006 to 2011.

Genotype	% cross section weevil damage
12571s-15 (M20)	6.8 $\pm$ 2.44*
12603s-1 (M19)	8.8 $\pm$ 1.66*
Butobe	15.0 $\pm$ 6.00
Yangambi Km 5	0.0 $\pm$ 0.00
Mbwazirume	10.0 $\pm$ 6.00

* indicates significantly difference ($P>0.05$) from the susceptible control cultivar 'Mbwazirume' by Dunnett's test.

Table 5. Percentage root necrosis on promising East Africa highland banana hybrids, 8 weeks after inoculation with 400 nematodes (*Radopholus similis*) plant⁻¹.

Genotype	Root necrosis (%)
12571s-15 (M20)	2.3a
12603s-1 (M19)	3.3a
Yangambi Km 5	4.3a
Mbwazirume	9.3b
LSD(0.05)	1.32

Values are means of 10-12 replicates compared by Duncan's multiple range test. Values with the same letter are not statistically different ($P>0.05$).

Table 6. Means for consumer preference scores for cooked 'Matooke' hybrids compared with the local cultivar 'Mbwazirume'. Farmers in Mukono in central Uganda (2013).

Cultivar	Taste	Aroma	Mouth feel	Color	Acceptability
M9	3.7 $\pm$ 0.0	3.6 $\pm$ 1.4	4.1 $\pm$ 1.4	3.1 $\pm$ 1.4	3.5 $\pm$ 1.5
M19	3.9 $\pm$ 1.3	3.7 $\pm$ 1.4	3.6 $\pm$ 1.6	2.9 $\pm$ 1.2	3.5 $\pm$ 1.3
M20	5.1 $\pm$ 1.2	4.7 $\pm$ 1.3	4.8 $\pm$ 1.2	4.3 $\pm$ 1.2	4.5 $\pm$ 1.3
Mbwazirume	5.5 $\pm$ 0.8	5.3 $\pm$ 0.9	5.4 $\pm$ 1.0	5.4 $\pm$ 1.0	5.4 $\pm$ 0.8

Score on 1-6 hedonic scale: 1 = extreme disapproval; 6 = extreme approval.

Promotion and access of released 'Matooke' hybrids

The likelihood of farmers adopting the released (improved) 'Matooke' hybrids 'Kabana 6H' and 'Kabana 7H' depends on both varietal attributes (performance) and availability of planting materials to the farming community. 'Kabana 6H' and 'Kabana 7H' are maintained by NARO, and farmers can access tissue-culture plants from private tissue-culture laboratories. NARO has also undertaken efforts to promote and distribute these hybrids in all the four regions of Uganda (northern, eastern, central and western). Whether 'Matooke' hybrids are meeting the aspirations of the participating farmers may be assessed through parameters such as number of suckers distributed by the farmer (sales and gifts), number of plants used to expand, number of bunches sold, price sucker⁻¹ and price bunch⁻¹ (Table 7). The farmers have also been mobilized to participate in a 'revolving sucker' scheme where for every planting material a farmer receives he/she donates two suckers for every sucker received for a secondary beneficiary.

Table 7. Status of the progress in the distribution and expansion of 'Kabana6H' and 'Kabana 7H' plots in northern Uganda (2014).

Activity	Mean	Min	Max
Plants received	58.2	30	90
Plants used for expansion	113.6	28	400
Plants given to other farmers	65	3	330
Plants sold	257.4	15	2000
Price sucker ⁻¹	1529.4	2000	3000
Bunches sold	43.2	20	180
Average price/bunch	5073.5	3750	12500

Future prospects

The efficiency of current banana breeding efforts is very low due to the modest scale of breeding operations and several limiting factors such as the high cost and space requirements, long generation of the crop, low female/male fertility, polyploidy, complex banana genetics and absence of sources of resistance (Lorenzen et al., 2010). Improving 'Matooke' with black leaf streak as the primary target constraint has successfully generated hybrids combining high yields with resistance to black leaf streak and consumer acceptability. However, our breeding goals need to shift to address weevils and nematodes as primary constraints. This calls for obtaining, screening and deploying a wide diversity of diploids for nematode and weevil resistance. Diploid improvement as a pre-breeding activity has long been recognized as best route of introgressing these traits into hybrids (Tézenas du Montcel et al., 1996).

East African highland banana (EAHB) breeding also has to integrate innovations in biology and genetics to enhance improvement. For instance, molecular markers that are co-inherited with a trait can be used to introgress that trait more efficiently in Marker Assisted Selection (MAS) or Marker Aided Recurrent Selection (MARS). However, limitations in generating appropriate segregating populations due to either male or female sterility and the high ploidy levels of bananas constrain the task of tagging molecular markers to traits of economic importance. Nevertheless efforts to generate, phenotype and genotype diploid populations segregating for resistance to banana weevil and Fusarium wilt are underway (Ssali et al., 2013). Furthermore, the application of molecular markers has been limited to simple monogenic traits.

The application of genomic selection (GS) proposed by Meuwissen et al. (2001) to breeding populations using high marker densities is emerging as a solution to the limitations of MAS. Genomic selection predicts the breeding values of lines in a population by analyzing their phenotypes and high-density marker scores. Estimates of the contribution of all marker effects can be used simultaneously to predict the performance of banana hybrids (Ortiz and Swennen, 2014).

The participatory on-farm evaluation of the promising EAHB hybrids has been limited to a few sites in Uganda. Yet 'Matooke' are equally important in terms of utilization, taste and the cultural attachment to the people in the East Africa region. There is need for a wider multi-location, gender-sensitive participatory varietal selection (PVS) process in other countries in the region to evaluate promising 'Matooke' hybrids. This calls for stronger collaboration of key stakeholders operating at regional and national levels. Already the collaboration between NARO and IITA has selected 27 'Matooke' hybrids called NARITAs (NARO/IITA hybrids) that could be evaluated for their agronomic performance and consumer acceptance in a range of target end-user environments. Collaboration with male and female farmers will allow quantitative assessment of the suitability of each NARITA hybrid to local farming conditions, while sensory evaluations by consumers will provide qualitative feedback on taste and other organoleptic features, as well as processing potential.

Currently, there are two EAHB hybrids already released to the farming communities in Uganda, and another five promising hybrids are being evaluated on farm with high black leaf

streak resistance, and tolerance to weevils and nematodes. The molecular breeding program is using the products of the classical breeding efforts to introgress the traits difficult to address. For instance, 'Kabana 6H' is being transformed using *Xanthomonas* wilt resistance genes and provitamin A enhancement genes. This hybrid has an EAHB background with resistance to *Fusarium* wilt race 1 and black leaf streak, and tolerance to weevil and nematodes. With the addition of *Xanthomonas* wilt resistance, these hybrids make uniquely resilient banana cultivars for most of the key banana constraints on low-input supported small holdings. A mix of all these cultivars on a small-holder farmers' field will greatly improve sustainability and productivity of the current EAHB banana cropping systems.

CONCLUSION

In conclusion, the NARO/IITA breeding program has been advancing about four hybrids to on-farm evaluation every five years. The released and promising hybrids have resistance to black leaf streak and tolerance to nematodes and weevils. Their yield performance is more than 1.5 times higher than the local landraces and overall consumer acceptability is not significantly different for that of the local landrace check. The recipient communities value the hybrids since they are being widely distributed through sales and giveaways in addition to recipient farmers expanding their plots. However, these hybrids are susceptible to *Xanthomonas* wilt, and are very tall and prone to wind damage.

Future activities will focus on improving the EAHB breeding pipeline exploiting *Musa*'s over 36,000 genes in the sequenced genome. The breeding program will introgress weevil and nematode resistance building on the leaf streak resistance. Additional traits such as resistance to *Xanthomonas* wilt will be introduced using molecular breeding. Consequently, a mixture of hybrids deployed will hopefully improve sustainability and productivity of small EAHB holdings.

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