Dedication:
Dirk R. Vuylsteke: *Musa* Scientist and Humanitarian

Rodomiro Ortiz*
International Crops Research Institute for the Semi-Arid Tropics, Patancheru, 502 324 Andhra Pradesh, India (present address: IITA, c/o Lambourn & Co., Carolyn House, 26 Dingwall Road, Croydon, CR9 3EE, UK)

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This volume of *Plant Breeding Reviews* is dedicated to the memory of Dirk R. Vuylsteke who died tragically in an air crash on January 30, 2000, while actively engaged in his livelihood passion, the betterment of efforts to fight hunger and poverty in tropical Africa. Dirk was a leading *Musa* scientist who contributed to and led a wide range of development projects in tropical Africa. He dedicated all his professional life to plantain and banana improvement for the small landholders of sub-Saharan Africa. Vuylsteke’s most notable contributions were in the field of *Musa*

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agronomy, taxonomy, tissue culture, breeding, and genetics. He was an accomplished, successful, and popular research manager in a diverse array of programs and projects that he led and the committees in which he participated at the International Institute of Tropical Agriculture (IITA), as well as in other national and regional committees in Africa. Dirk Vuylsteke, will continue to be a source of inspiration for the new generation of scientists joining international agricultural research for development.

I. BIOGRAPHICAL SKETCH

Dirk Robert Paul Vuylsteke, a Belgian national, was born on December 26, 1958, in Cologne, Germany, where his father was stationed while serving as officer of the Belgian Army. Dirk spent his formative years in Belgium, the Democratic Republic of Congo, and the United States of America, before obtaining his undergraduate degree from the Catholic University of Leuven (KULeuven) where he was also elected the President of the Students’ Union in the Faculty of Agricultural Sciences.

After graduating in 1982, Dirk left Belgium and moved to Nigeria, where he started his professional career as a plantain and banana researcher affiliated with the International Institute of Tropical Agriculture (IITA). Vuylsteke joined a multidisciplinary *Musa* research team at the High Rainfall Station in Onne, southeastern Nigeria, where he worked for 12 years in the improvement of plantain (*Musa* spp. AAB group). In 1994, he was transferred to Uganda to lead the newly established East and Southern African Regional Centre for the Improvement of Cassava, Banana and Plantain (ESARC), and to start breeding matooke bananas (*Musa* spp. AAA group) for the highlands of Eastern and Southern Africa (Vuylsteke 1996).

Vuylsteke’s professional career began as a research assistant (1981–1982) under the supervision of Prof. De Langhe in what was then the Laboratory of Crop Physiology and Tropical Crop Husbandry at KULeuven in Belgium. Prof. De Langhe, who had been a *Musa* researcher in the Congo until the 1960s, greatly assisted the development of plantain research at IITA through his institutional and donor contacts, especially during the years he was member of IITA’s Board of Trustees. Vuylsteke worked from 1982 to 1987 in the former Farming Systems Program of IITA as an Associate Expert through a grant from the Belgian Administration for Development Cooperation. During this time, he established and managed the *Musa* tissue culture laboratory at IITA’s High Rainfall Station as well as developed and applied plant tissue culture techniques
to enhance Musa germplasm handling and improvement. From 1987 and until 1991 he was the tissue culture scientist affiliated to the Tuber, Root and Plantain Improvement Program of IITA, through a project funded by the International Network for the Improvement of Banana and Plantain (INIBAP), and worked together with Rony L. Swennen (Musa agronomist/breeder of IITA) in plantain and banana breeding, genetic resources management, and germplasm characterization and evaluation for disease resistance, growth, and yield.

In early 1991, Ken Fischer (IITA’s director of research) convinced Vuylsteke to become a core IITA scientist in germplasm enhancement and the Officer-in-Charge of IITA High Rainfall Station. A few months later, Lukas Brader (IITA’s director general) appointed him as the leader of the newly established Plantain and Banana Improvement Program. From 1991 to 1993, Vuylsteke provided a “hands-on” leadership to the dynamic multidisciplinary research team he set up at Onne. He collaborated with advanced research institutes in Europe and the United States in the area of biotechnology, and undertook joint research activities with national scientists in sub-Saharan Africa, mainly in the area of multilocational evaluation of plantain and banana hybrids. Vuylsteke supervised graduate students and participated, sometimes as organizer, in training courses for research and technology transfer in Musa. Owing to this pro-active role in strengthening the national research capability in Sub-Saharan Africa, the Training Program of IITA awarded him in 1991 a certificate of recognition for his exemplary service to national research workers. As Officer-in-Charge, Vuylsteke had overall responsibility for management of activities at IITA High Rainfall Station. He facilitated research at, and development of, that station for six resident internationally recruited scientists, who were supported by 90 nationally recruited staff.

At the beginning of 1994, Vuylsteke accepted the proposal of F. Margaret Quin, IITA’s director of the Crop Improvement Division, to become the Team Leader of the recently inaugurated IITA-ESARC in Uganda. He also continued with his research as the Musa agronomist/breeder of ESARC, and ensured liaison and technical collaboration with relevant directors and program leaders of the National Agricultural Research Systems (NARS) and regional institutions, network coordinators, development investors, authorities of the Government of Uganda, and IITA-ESARC researchers (from 9 to 11 internationally recruited scientists) as well as training staff.

In his years at IITA-ESARC, Vuylsteke developed an interdisciplinary research project for the improvement of highland banana production systems, incorporating breeding, agronomy, postharvest physiology,
nematology and entomology, and transferred to East African highland bananas and cooking bananas the breeding methods that had been successfully applied to plantain improvement at the IITA High Rainfall Station in Nigeria. He collaborated closely with national scientists in banana-producing countries, particularly in germplasm evaluation, using a variety of mechanisms, including collaborative research, networking, graduate thesis supervision, training courses, visits, workshops, and steering committee meetings. Vuylsteke actively promoted intercenter collaboration among CGIAR institutes in Uganda in terms of logistics, communications, and research station development, and participated on behalf of IITA, in the African Highlands Initiative, an intercenter/NARS eco-regional research program on integrated natural resources management in the intensive land-use systems of the highlands of eastern and central Africa.

When in 1995 IITA changed its research structure to a project mode, Vuylsteke was elected by his fellow scientists as the coordinator of the project Improving Plantain- and Banana-based Systems, which became one of the largest of the center-research projects at IITA. With the Musa project team of 11–13 international scientist years, he developed and implemented the research strategy and agenda through a project planning (log-frame) exercise, coordinated annual planning and reporting of research work, and monitored progress to ensure achievement of project objectives and goals.

In 1998, IITA management asked Vuylsteke to be its leader for the Mid-altitude Agro-ecological Zone Working Group, and as such was also a member of the Research Program Committee (the highest research management body at IITA). As Working Group Leader of one of three agro-ecological zones in which IITA is active, he acted as the Institute’s spokesperson for the zone and ensured that the needs of the zone were well addressed in the research agenda of IITA projects. Vuylsteke also provided management and administrative support to IITA scientists working in this zone.

Vuylsteke greatly appreciated the unwavering support from his supervisors, which was given to plantain and banana outreach research and their encouragement to succeed in his professional career, both as scientist and research manager. He always acknowledged that the strong support from, and easy communications with, IITA headquarters was a critical link in the research success of outreach stations. In particular, he was indebted to the role played by Frances McDonald, assistant to the deputy-director general, and other key IITA staff. In 1993, IITA awarded him a certificate of recognition for 10 years of dedicated service. His colleagues and subordinates acknowledged that Vuylsteke, as manager,
always took a pro-active care of their well-being and represented them well while discussing research and other issues with IITA’s top management team.

His knowledge of Dutch, English, French, and German facilitated Vuylsteke’s interactions and communications with researchers worldwide. He worked well with people of widely differing backgrounds, nationalities, and gender. Vuylsteke also traveled extensively on official IITA missions throughout 37 countries in Africa, America, Asia, Europe, and the Pacific. On many occasions he was an invited keynote speaker in international conferences and presented many seminars on his Musa research around the world. Vuylsteke was the co-convener of the First International Conference on Banana and Plantain for Africa, which was held at Kampala, Uganda, in October 1996, and attended by around 150 researchers from 27 countries (Vuylsteke and Karamura 1996; Craenen et al. 2000).

Vuylsteke was a successful fund-raiser at IITA, and throughout his management career he obtained considerable additional resources (approximately US$7 million) for targeted research projects on Musa and cassava in Sub-Saharan Africa. He was always straightforward in his approach to agricultural research and maintained a high level of scientific output while also ensuring that there were tangible and practical benefits for farmers. Vuylsteke was responsible for the multiplication and dissemination to farmers and researchers of thousands of improved propagules of plantain and banana germplasm in sub-Saharan Africa. This new genetic material has been used by researchers for further local improvement and by farmers to improve their food security and raise their incomes. During his scientific career he was a prolific writer and published in excess of 100 research articles in leading peer-reviewed international scientific journals, book chapters, and newsletters. Vuylsteke was founder member of, and worked until his death in the Editorial Board of MusAfrica, the international plantain and banana newsletter published by IITA. He was also member of the Editorial Board of the African Crop Science Journal, participated actively in professional organizations, and was member of the International Society for Horticultural Science, the American Society for Horticultural Science, the American Museum of Natural History, and the African Crop Science Society. Vuylsteke showed a keen interest in all aspects of science, and discussions with him on any scientific topics were always very stimulating.

On January 30, 2000, Dirk R. Vuylsteke together with his IITA colleagues Paul R. Speijer (Dutch nematologist) and John B. Hartman (banana breeder from the United States) were in the ill-fated Kenya Airways flight KQ433 that crashed shortly after take off from Abidjan, Côte
d'Ivoire, en route to Lagos, Nigeria. They were traveling to IITA headquarters at Ibadan to attend the annual work-planning week. The loss of these three young international scientists, whose efforts were considered the most promising of all African projects carried out under the aegis of the Consultative Group on International Agricultural Research (CGIAR), was not only a great tragedy for their families, friends, and colleagues, but a significant blow to international agricultural research and to the African farmers to whom they dedicated their lives.

II. RESEARCH ACHIEVEMENT

A. Tissue Culture and Somaclonal Variation in Plantain

Vuylsteke started his professional career as an associate expert affiliated to what was then the old Farming Systems Program of IITA. Together with George F. Wilson, leader of plantain research at IITA at that time, and Rony L. Swennen, the first *Musa* scientist at IITA High Rainfall Station in Onne, they developed field multiplication techniques for rapid in vivo multiplication of plantain based on conventional planting material (suckers), (Wilson et al. 1987). In high density plantings, suckers were induced by removal of the growing point after removing the pseudostem (decapitation) or by a new technique of cutting a small hole or window in the lower pseudostem (false-decapitation).

Vuylsteke and his colleagues then investigated tissue culture techniques to address the critical issue of generating healthy planting materials. In the early 1980s, Vuylsteke had worked on tissue culture, hydroponics, and physiology of bananas and plantains with his academic mentor Prof. Edmond De Langhe, then head of the Laboratory of Tropical Crop Husbandry. During this time they quickly developed a shoot-tip culture protocol for the propagation, conservation, and distribution of plantain germplasm (Vuylsteke 1983; Vuylsteke and De Langhe 1985).

Shoot-tip culture was found to be an easy, reliable and routine technique for a wide range of *Musa* genotypes (Vuylsteke 1998a), producing multiplication rates much higher than field propagation techniques. Furthermore, there are two other major advantages of micropropagation: the production of clean planting material free from many fungal, bacterial, and pest infestations, plus the reduced amount of space needed to multiply and transport large numbers of plants. Micropropagated plants were subsequently shown to establish more quickly, grow more vigorously and taller, have a shorter and more uniform production cycle, and
produce higher yield than sucker-derived propagules (Vuylsteke and Ortiz 1996; Vuylsteke 1998 and references therein).

The availability of aseptic shoot cultures also provided a means for the international exchange of banana and plantain germplasm in combination with third country quarantine (Vuylsteke et al. 1990a,b). Based on these developments, it was possible to establish the Musa Germplasm Transit Center of INIBAP at KULeuven, which now holds the world’s largest in vitro collection of Musa accessions, representing the greatest collection of genetic diversity for plantains and bananas. More than 2,500 accessions from this collection have been exported as shoot-tip cultures by INIBAP since 1985 converting this Transit Center into the largest source of Musa genetic resources worldwide.

Although micropropagation offers many advantages for Musa, it may be adversely affected by somaclonal variation, genetic variation among plants regenerated from tissue culture. Somaclonal variation is ubiquitous in Musa, and off-types range between 0 to 70% depending on the genotype (Vuylsteke 1989, 1998b; Vuylsteke and Swennen 1990; Vuylsteke et al. 1988, 1991). Some strategies to minimize somaclonal variation are: (a) careful selection of stable source material for primary explants, (b) limited sub-culturing and multiplication (< 10 cycles, < 1 year for sub-culturing, < 1,000 plants per primary explant), and (c) nursery screening to detect and rogue off-types.

Somaclonal variation generated some interest as a potential source for genetic improvement of plantain and banana (Vuylsteke 1998b). However, the range of somaclonal variants recovered through shoot-tip culture appears to be narrow and mostly mimics naturally occurring variation or produces defective phenotypes, especially in plantains (Vuylsteke et al. 1991). Vuylsteke and his colleagues (1996b) demonstrated that somaclonal variants of plantains showing changes in leaf or inflorescence were inferior to the original clone from which they were derived, because of their low bunch mass and small fruits. Despite the lack of agronomic value represented by somaclonal variants, Vuylsteke and his colleagues at IITA realized that some types of variants might be useful in plantain breeding (Vuylsteke et al. 1995).

From 1983 to 1994, Vuylsteke was the leading scientist in Musa tissue culture at IITA. He established an efficient micropropagation laboratory at the High Rainfall Station despite the difficult and sometimes unpredictable environment of southeast Nigeria. In this effort he was strongly supported by Piers D. Austin, the Station Manager. As part of his work in the tissue culture laboratory of IITA, Vuylsteke and his colleagues (1990b) developed improved embryo culture techniques for in
vitró germination of hybrid *Musa* seed. This research was an essential precursor to developing a breeding program for plantain and banana, which started in 1987 at IITA.

Vuylsteke was heavily committed to transferring the tissue culture technology to NARS in sub-Saharan Africa through hands-on training of scientists. He also provided advice and support in setting up tissue culture laboratories in the region, particularly in Nigeria. His training manuals (Vuylsteke 1989, 1998a; Vuylsteke and Talengera 1998) are standard texts worldwide for *Musa* micropropagation and transplantation to fields.

**B. Musa Genetics and Breeding**

In response to NARS requests, IITA decided to include banana and plantain among its focus crops for breeding research, and in the 1980s initiated a strategic program for the genetic improvement of banana and plantains. The urgency was great because of the occurrence of black sigatoka, which arrived on the African continent in the 1970s and was spreading rapidly. Chemical control strategies are available but are not appropriate in the framework of the resource-poor small holdings in which the crop is grown across Africa. Vuylsteke and his colleagues at IITA decided to focus their breeding program on host plant resistance, as an ecologically sustainable component of an integrated pest management strategy.

Resistance breeding was not an easy task to undertake, because most important cultivated *Musa* clones are triploids \((2n = 3x = 33)\), causing them to be highly sterile and generally regarded as intractable to genetic improvement. Moreover, space \((6 \text{ m}^2 \text{ per plant})\) and time \((18 \text{ months from seed to seed})\) requirements also impede rapid progress towards breeding goals. Nonetheless, Vuylsteke and co-workers at IITA improved plantain and banana germplasm using a combination of conventional and modern approaches, including screening for female fertility in triploid *Musa*, interspecific hybridization with wild and cultivated bananas, ploidy manipulation \((3x\times 2x \text{ crosses and } 2n \text{ eggs})\), and in vitro culture for hybrid seed germination as well as for rapid multiplication for replicated field testing and selection (Vuylsteke et al. 1993e, 1997). On average, it took 1,000 seeds, produced from hand-pollination of 200 plants \((0.12 \text{ ha})\), to obtain one selected tetraploid hybrid per year.

As a result of this endeavor, *Musa* hybrids with stable high yield and durable host plant resistance to diseases and pests, particularly black sigatoka leaf spot, were obtained and shared with NARS breeders across sub-Saharan Africa and around the world (Table 1.1). Many NARS of the
<table>
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<th>Cross code</th>
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<tr>
<td>TMPx</td>
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<td>14 tetraploid plantains from $3x$-$2x$ crosses showing black sigatoka resistance, high bunch weight and adaptation to the humid lowlands</td>
<td>Vuylsteke et al. 1993f</td>
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<td>TMP2x</td>
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<td>14 plantain-derived diploids from $3x$-$2x$ crosses showing black sigatoka resistance and some (e.g., TMP2x 1297-3) with good combining ability in $4x$-$2x$ crosses</td>
<td>Vuylsteke et al. 1993a</td>
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<td>TMB2x</td>
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<td>Selected banana hybrids from $2x$-$2x$ crosses with black sigatoka resistance and some of them (e.g., TMB2x 9128-3) with good combining ability in $4x$-$2x$ crosses</td>
<td>Vuylsteke et al. 1993a</td>
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<td>TMBx</td>
<td>BITA-1</td>
<td>Tetraploid cooking bananas derived from $3x$-$2x$ crosses showing resistance to black sigatoka, tolerance to banana streak virus, and high bunch weight</td>
<td>Vuylsteke et al. 1993d</td>
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<td>BITA-2</td>
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<td>Ortiz and Vuylsteke 1997</td>
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<td>TMPx 1112-1</td>
<td>PITA-9</td>
<td>Tetraploid plantain, derived from the False Horn set through a somaclonal, fertile mutant included in $3x$-$2x$ crosses, showing black sigatoka resistance, acceptable bunch weight, and good fruit quality</td>
<td>Vuylsteke et al. 1995</td>
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<td>TMBx 5297-2</td>
<td>BITA-3</td>
<td>Tetraploid starchy banana with tolerance to black sigatoka and banana streak virus, heavy bunch of big fruits</td>
<td>Ortiz and Vuylsteke 1998a</td>
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<td>TMPx 7152-2</td>
<td>PITA-14</td>
<td>Tetraploid plantain with black sigatoka resistance, short cycling, acceptable bunch weight and fruit quality</td>
<td>Ortiz and Vuylsteke 1998b</td>
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<td>TM3x</td>
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<td>Secondary triploid Musa hybrids from $4x$-$2x$ crosses with black sigatoka resistance and high yield; one of them (PITA-16) exhibits virus tolerance and acceptable fruit quality in some African locations</td>
<td>Ortiz et al. 1998b</td>
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tropical world are currently testing this improved germplasm developed by Vuylsteke and co-workers at IITA for further regional release to farmers (Ortiz et al. 1997c). The success of plantain improvement at IITA has also led to the establishment or revitalization of *Musa* breeding and research teams, especially in Australia, Brazil, Cameroon, Honduras, and India.

Many of the primary tetraploid hybrids showing black sigatoka resistance were developed through crosses between a triploid plantain landrace and a diploid wild or cultivated banana (Vuylsteke et al. 1993f). Most of fertile plantains belong to the French inflorescence set, though one hybrid, PITA-9, was derived from the almost sterile False Horn inflorescence set through cross-breeding of a female-fertile somaclonal variant (Vuylsteke et al. 1995). Plantain-derived diploid hybrids were also obtained after 3x-2x crosses. Such germplasm has provided a means for both genetic research and further enhancement of the plantain genome at the diploid level (Vuylsteke and Ortiz 1995), avoiding the complex inheritance patterns of polyploid species.

From his field work Vuylsteke observed that a plantain-derived diploid produced progeny with a degenerated inflorescence typical of the False Horn plantains. He noted that somaclonal variants of False Horn plantain and their progeny carry False Horn plantain genes that regulate inflorescence morphology, which demonstrates the potential of somaclonal variation as a secondary source of variability that needs to be further explored for *Musa* germplasm enhancement, particularly to initiate breeding in otherwise inaccessible plantain gene pools.

Some of these plantain-derived diploid hybrids were crossed with other primary tetraploid hybrids to develop secondary triploid hybrids, which combine selected attributes from both parents (Ortiz et al. 1998b). Likewise, this crossing scheme was pursued mainly to re-introduce female sterility, thereby avoiding seed set as preferred for human consumption. The development of the secondary triploid hybrids suggests that heterosis for yield potential can be achieved in *Musa* either by maximizing heterozygosity through crossing unrelated parents, or by proper selection within populations of hybrids derived from full-sib parents. Indeed, genetic studies in *Musa* have shown that heterozygosity and epistasis are essential to maximize plant vigor and produce high yield (Ortiz and Vuylsteke 1996a; Vuylsteke et al. 1997).

Ploidy polymorphism in offspring derived from 3x-2x crosses, and the occurrence of segregation in tetraploid hybrids derived from crosses between heterozygous triploid plantains and a true-breeding wild, diploid banana have always been of interest to Vuylsteke. Functional
haploid gametes in the female-fertile plantains may occur because during meiosis, the distribution of chromosomes to the pole conforms with the expected triploid behavior, but with a tendency to lose lagging chromosomes. As such, poles with the haploid chromosome number give balanced and viable gametes (Vuylsteke et al. 1993a).

Further genetic research demonstrated segregation in the triploid plantain genome during the modified megasporogenesis leading to the formation of $2n (= 3x)$ eggs owing to a second division restitution (SDR) mechanism (Ortiz and Vuylsteke 1994c). Normally, SDR $2n$ eggs are the result of a normal first meiotic division (segregation occurs). However, complete omission of the second division leads to the production of aneuploid gametes in a triploid organism that has one set of bivalents and another set of univalents at metaphase I. If the univalents prematurely divide at the first meiotic division followed by complete failure of the second division, $2n$ gametes are expected. The formation of $2n$ eggs by a SDR mechanism in the triploid plantain parent provides a means for the occurrence of segregation and recombination in the triploid plantain genome during megasporogenesis, even when there is restitution of all three sets of maternal chromosomes. Hence, the production of megaspores and embryo sacs with the maternal chromosome number does not necessarily imply that these carry the intact maternal genotype.

This finding challenged the commonly accepted premise about the $3x-2x$ breeding approach, in which the triploid female genome is considered fixed, with recombination only possible from the diploid male parent. As a result, the conventional opinion that *Musa* breeding is a simple matter of breeding superior diploid pollinator lines was revised.

Genetic information is required to develop scientific breeding strategies. However, few genetic studies were undertaken in *Musa*, despite the importance of the crop, because of the high levels of sterility in the cultivated germplasm. Consequently, very few genetic markers were available in *Musa* before 1987 when the *Musa* improvement program began at IITA. The complexity of inheritance in *Musa* was baffling to plant breeders until this IITA team started unraveling the genetic systems of plantain and banana. Vuylsteke had a keen interest to incorporate this knowledge in the development of new *Musa* breeding schemes.

One of the first characteristics we investigated together in early 1992 was the occurrence and inheritance of albinism in diploid hybrid offspring obtained after in vitro germination of seeds derived from crosses between wild and cultivated bananas with plantain-derived diploids (Ortiz and Vuylsteke 1994a). Spending time and resources on this characteristic might have seemed trivial, but it provided important insights
into the *Musa* genome, e.g., that deleterious alleles (genetic load) are maintained in diploid gene pools owing to heterozygosity advantage and vegetative propagation. We learned that breeding advances through phenotypic recurrent selection in diploid banana populations were made by selecting against these deleterious alleles, although the most promising selections were highly heterozygous.

Several characteristics of the crop make genetic analysis of *Musa* difficult. The low rate of hybrid progenies recovered after interspecific-interploidy crosses, resulting in small sample sizes, is the major obstacle to genetic analysis. Nevertheless, the production of diploid testcross segregating populations, obtained from crosses of triploid heterozygous parents with a diploid homozygous recessive parent, and of diploid plantain-banana hybrids made genetic analysis in *Musa* possible. Genetic analyses in the diploids were simplified due to disomic inheritance. As a result important knowledge was gathered regarding the genetics of black sigatoka and banana weevil resistance, pseudostem waxiness, virus susceptibility, apical dominance and suckering behavior, dwarfism, bunch orientation, fruit parthenocarpy, and male fertility. The effects of genetic markers, ploidy and the environment on quantitative variation of disease and pest resistance as well as yield components were also investigated during this period. This new genetic knowledge was critical in launching IITA’s breeding strategy for plantain and banana. It was due to Vuylsteke’s encouragement and active participation in this research that these advances in *Musa* genetics were achieved.

As a direct result of the contributions of the multidisciplinary research team led by Vuylsteke, IITA received in 1994 the “King Baudouin Award,” which is the highest accolade bestowed on researchers within the CGIAR. This honor was given for developing black sigatoka-resistant plantain germplasm in just five years, and for gaining new insight into the *Musa* genome through genetic analysis, which provided the basis for new breeding strategies aimed at the achievement of new breeding objectives (Vuylsteke 1995). The success of this achievement can be measured via the outcomes of the research led by Vuylsteke on black sigatoka, a leaf spot disease that reduces plantain yield by 30 to 50%. The potential impact of black sigatoka resistant plantains was assessed by comparing use of fungicides or of resistant hybrids in the farming system (Ortiz and Vuylsteke 1994e). In southeast Nigeria, host plant resistance could have a profit advantage over fungicides of 10:1 in normal periods of plantain production or 5.5:1 in periods of scarce production.
C. Breeding East African Highland Bananas and Other Musa Genepools

At the beginning of 1994, Vuylsteke moved from Nigeria to Uganda, to take on the challenge of improving the East African highland bananas. These are known as matooke bananas, which are a highly prized staple food crop in the Great Lakes Region and form a sub-group of the Musa AAA group that are unique to the mid-altitude and highlands of East Africa. However, the genetic improvement of matooke bananas as well as their plant health status had received almost no research attention prior to this effort. Vuylsteke and his colleagues of this new IITA team in East Africa and national scientists of the National Agricultural Research Organization (NARO) began breeding highland bananas in 1994 using IITA’s successful plantain breeding program in Nigeria as a model. The unique features, culture, and end-use of highland bananas necessitated the definition of a new ideotype of matooke bananas. Investigations in recent years identified traits unique to highland bananas and a highland banana ideotype emerged (J. B. Hartman and D. R. Vuylsteke, IITA, unpublished results). The breeding strategy combined introgression of alleles from wild species and recurrent population breeding to avoid genetic erosion in the development of highland banana germplasm.

One of the first steps in the East African breeding program was to screen for seed fertility in the triploid highland bananas (Vuylsteke et al. 1996a). Most of the seed-fertile landraces belong to the Nfuuka and Nakabululu sets of matooke bananas. Seed set per hand varied with the location of the hand on the bunch, and by month of pollination. These results demonstrated that genetic improvement of the matooke breeding pool was feasible because viable seeds were obtained from several landraces and germinated in vitro (Talengera et al. 1996). Germination rates through embryo culture were on average 9% for the matooke bananas, which is significantly higher than germination in soil (1.4%). Some of these matooke hybrids developed by Vuylsteke, Hartman, and their other colleagues at IITA and NARO are undergoing testing in Uganda to assess their breeding value and further use in Musa breeding for this country and others in the Great Lakes Region of Africa.

The use of hybrid and polycross breeding may also reduce genetic erosion in Musa. A new breeding scheme was designed in the mid-1990s at IITA to exploit this phenomenon by testing banana parents for combining ability (Tenkouano et al. 1998b). The success of this scheme depends on the conservation of genetic diversity. Within the breeding program, diversity is maintained by creating separate germplasm pools
or breeding populations from different sources. Vuylsteke actively fol-
lowed the development of an evolutionary breeding scheme for *Musa*,
which ensued while producing secondary triploids (Ortiz et al. 1998b).
In this new approach, the heterozygous triploid landraces are the source
of allelic diversity, which will be released after the plantains are crossed
with a diploid accession showing resistance to a specific stress or hav-
ing another agronomically important attribute. High-yielding tetraploid
hybrids are selected according to their combining ability in the segre-
gating population. These tetraploid hybrids are then crossed with
selected diploids to obtain improved secondary triploids (Ortiz et al.
1998b). Secondary triploids result from artificial hand pollination or
through polycrosses among selected tetraploids and diploid parents.
Synthetic populations derived from polycrosses may be given to other
plant breeders, who can identify promising clones for cultivar develop-
ment with the co-operation of local farmers after both on-station and on-
farm testing and selection.

D. *Musa* Taxonomy

At the beginning of his career as *Musa* researcher at Onne, Vuylsteke
(together with Swennen) characterized the plantain genetic resources
available in the field collection at IITA High Rainfall Station. This inform-
ation was useful in organizing the plantain germplasm and in deter-
mining key morphological and quantitative descriptors for grouping
this germplasm according to their inflorescence type: French, French
Horn, False Horn, and True Horn plantains, and stature: giant, medium
and small (Swennen and Vuylsteke 1987; Swennen et al. 1995). Further
research with new statistical tools revealed that most cultivars are still
farmers’ selections from somatic mutants of this vegetatively propa-
gated triploid crop with almost no male fertility, which prevents gene
flow among landraces (Ortiz et al. 1998a). He also participated with his
Ugandan colleagues in the classification and organization of East African
banana germplasm using numerical taxonomic techniques (Karamura et
al. 2000). They determined that accessions of the East African highland
bananas formed five distinct clusters based on female and male inflo-
rescence characteristics. These distinct East African banana sets are
known as Beer, Musakala, Nakabululu, Nakitembe, and Nfuuka.

In his characteristic search for ever-improved research tools, Vuyl-
steke followed the advances in molecular taxonomy and encouraged
other *Musa* researchers to apply them for an accurate estimate of genetic
diversity in germplasm collections, and thereby improved the efficiency
of conservation and management of genetic resources (Jarret et al. 1993).
In one of his last journal articles with his former IITA colleagues (Crouch et al. 2000), it was demonstrated that classification systems in *Musa* using phenotypic indices based on agronomic characters do not always provide accurate taxonomic differentiation. Moreover, their results suggest that the traditional designations of plantain landraces based on bunch and stature morphotype do not provide a true reflection of overall genetic divergence. Other findings from this research with DNA markers also confirmed the low level of genetic divergence within the plantain landrace pool, which supports the proposed evolution of this germplasm through somatic mutation of a relatively small number of introductions.

Vuylsteke’s work in *Musa* taxonomy reflected his interest in plantain and banana evolution. From the breeding work at IITA, a challenging hypothesis emerged regarding the putative differentiation of the A and B genomes of the so-called AAB plantains. Plantains have been always reported to derive from interspecific crosses between *M. acuminata* Colla. (A genome) and *M. balbisiana* Colla. (B genome), hence the AAB genome designation. However, a trisomic pattern of inheritance was observed for genetic markers suggesting that each linkage group occurs three times instead of twice (Ortiz and Vuylsteke 1994g). Furthermore, the segregation ratios for these genetic markers indicated that there was no preferential pairing between the homologous chromosomes of the A genome. In fact, random distribution of the paired chromosomes to the cell poles is observed during anaphase I of the first meiotic division, inferring a low level of differentiation between *M. acuminata* and *M. balbisiana* genomes. Hence, the AAB genomic designation for plantain should be replaced with a more specific genetic characterization. This was further supported by segregation analysis of male and female fertility in plantain-derived diploids.

**E. Integrating Molecular Breeding into Conventional Genetic Improvement**

Vuylsteke was always interested in applying new bio-techniques in *Musa* improvement. He collaborated with his colleagues in what was then the Tropical Crop Husbandry Laboratory at KULeuven in the development of a protocol for plant regeneration by direct somatic embryogenesis of cell suspensions or protoplasts (Dhed’a et al. 1991). The aim was to obtain a new system for mass micropropagation as well as a new tool for transformation using recombinant DNA techniques. Such regeneration was achieved in cell or protoplast cultures derived from in vitro meristems.
In the late 1980s Vuylsteke started his professional interactions with Robert L. Jarret (USDA/ARS, Griffin, Georgia) to develop molecular markers for DNA marker analysis and molecular breeding (Jarret et al. 1994). This marker technology became a useful tool in Musa improvement at IITA for germplasm characterization (Crouch et al. 2000), cultivar fingerprinting (Ortiz et al. 1998b), genetic analysis (Tenkouano et al. 1999a,b), linkage mapping (Crouch et al. 1998 and references therein), and molecular breeding (Vuylsteke et al. 1998b and references therein).

Throughout his career as plant breeder, Vuylsteke strongly argued that although Musa breeders had some success in the past using essentially empirical approaches, further success would increasingly become reliant on science-based strategies, using genetic knowledge and integrating molecular marker technology. In Vuylsteke’s view, biotechnology would rarely enable significant shortcuts in the genetic improvement of Musa, but would enhance the utilization of genetic variability and overcome certain biological barriers or impediments (Vuylsteke et al. 1999). He emphasized the application of both tissue culture techniques for germplasm handling and breeding, and marker-assisted selection systems to accelerate the breeding process. Likewise, Vuylsteke always stressed the need for DNA tools for specific and sensitive diagnostics in this vegetatively propagated crop that suffers infection from several viruses.

F. Holistic Approach to Musa

Vuylsteke’s professional career was always associated with the Musa crops, although his first area of research in international agriculture was on agronomic and physiological characteristics of cassava and sweet potato for his Undergraduate (Honors) Thesis in Tropical Soil and Crop Science in 1980 at IITA. For all of us who traveled with him in Africa and other tropical locations where plantains and bananas are grown, Dirk had developed a very special feeling for these crops. Many times we stopped along the roads to visit farmer fields because he was attracted by the crop management, a specific disease or pest affecting the crop, or by the Musa germplasm variation he had observed. Similarly, in early 1993 we were distributing improved IITA germplasm for multilocalional testing in East Africa. During the trip between Bujumbura (Burundi) and Entebbe (Uganda), he became very excited upon observing the almost endless expanse of farmer fields filled with East African highland bananas.

Vuylsteke was convinced of the advantages of genetic enhancement for Musa, and it was not surprising that he ended his Ph.D. thesis in Crop
Science (Strategies for the utilization of genetic variation in plantain improvement) with the following statement:

A broad-based, improved Musa germplasm with pest and disease resistance will be a major component to achieve sustainable production of this vegetatively propagated, perennial crop. Such germplasm can be produced through conventional cross-breeding, enhanced by the utilization of innovative methods for the introduction of additional genetic variation. Also, the increased use of molecular markers will accelerate the process of recurrent selection of improved Musa germplasm and, hence, facilitate the development of new hybrids. The prospects of banana and plantain breeding are unlimited and increased efforts will at once initiate a new phase of Musa evolution.

However, the need for a holistic approach to ensure a sustainable production in plantain- and banana-farming systems was always advocated because single-component interventions do not provide adequate solutions to the complex of constraints affecting plantain production in sub-Saharan Africa (Vuylsteke et al. 1997). In this regard, he indicated that plantain breeders should aim to develop improved cultivars within improved, sustainable, and perennial production systems. To achieve this goal Vuylsteke and his colleagues at IITA defined plantain and banana ideotypes.

The two most important elements of his holistic approach were improved propagules of new cultivars adapted to a specific region, and crop husbandry techniques (including integrated pest management) for long-term productivity. They should be delivered together to the farmers as part of a technological package that has been previously tested for local adaptation with partners in target areas.

III. THE MAN

On 8th July 1983, Dirk R. Vuylsteke married Kathelyne Maria Craenen (a plant pathologist graduated from KULeuven), with whom he had two children: Sarah Maria (born June 17, 1985) and Yannick Dirk (born August 1, 1987). Dirk and his family spent most of their lives in Africa, a continent and peoples they learned to understand and love. In contrast to his high profile owing to his international research and management career, Dirk remained humble and modest, and was very much a family man.

Vuylsteke was also an avid sportsman. In his early years, his father taught him the joys of sailing, a sport that was well tuned to his free and
competitive spirit. Dirk spent much of his spare time with his family in sporting activities: sailing with Sarah, playing tennis with Yannick, and strongly supporting his wife Kathelyne’s passion for golf. In early 2000, he was elected the Commodore of the Entebbe Sailing Club where he sailed every Sunday when he was in Uganda. During his time in Africa, Vuylsteke became a competitive squash and tennis player. In one of his last weekends in Kampala, he was supporting the Ugandan National Tennis Team at the Davis Cup Tournament at the Lugogo Sports Ground.

Vuylsteke was committed to the view that responses to future projections of world food requirements will largely depend upon improved cropping efficiency and yield, which will be generated by science-based agricultural development (Vuylsteke 2000). These systems, particularly in Africa, require increased technology-based inputs, such as improved propagules and cultivars. Vuylsteke believed that locally-adapted, eco-friendly yet high yielding technology could ensure sustainable food security, protect the environment, and raise incomes, thereby alleviating poverty of the African rural poor.

After spending part of his childhood and all of his eighteen-year professional career in Africa, Vuylsteke came to view himself in many ways as a true citizen of that continent. For this reason, his family decided to deposit his ashes in Lake Victoria near Entebbe (Uganda), where he sailed frequently. It was apparent to everyone who had the privilege of working with and getting to know Dirk that he loved Africa, its people and the worthwhile life he led in that continent. He leaves behind his wife, daughter, son and parents (Hedwige and Walter). They, as the whole international community who knew Dirk, will miss him enormously, especially his broad vision, open-minded approach, unpretentious straightforward style, and irreverent sense of humor. Those who had the pleasure of knowing Dirk Robert Paul Vuylsteke will always remember him as a loving, generous and gifted man and as a great scientist who dedicated his life to improving the well-being of poor rural families across the developing world.

**SELECTED PUBLICATIONS OF DIRK R. VUYLSTEKE**


C. S. Gold and B. Gemmill (eds.), Biological and integrated control of highland banana and plantain pests and diseases. IITA, Ibadan, Nigeria.


