Diploid Banana Hybrids
TMB2x5105-1 and TMB2x9128-3 with Good Combining Ability, Resistance to Black Sigatoka and Nematodes

A. Tenkouano, D. Vuylsteke1, J. Okoro, D. Makumbi, R. Swennen2, and R. Ortiz
Crop Improvement Division, International Institute of Tropical Agriculture, PMB 5320, Oyo Road, Ibadan, Nigeria (International mailing address: c/o Crop Improvement Division, International Institute of Tropical Agriculture, PMB 5320, Oyo Road, Ibadan, Nigeria (International mailing address: c/o Crop Improvement Division, International Institute of Tropical Agriculture, Katholieke Universiteit Leuven, Kasteel- Lagada, Belgium (International mailing address: c/o Crop Improvement Division, International Institute of Tropical Agriculture, PMB 5320, Oyo Road, Ibadan, Nigeria (International mailing address: c/o Crop Improvement Division, International Institute of Tropical Agriculture, PMB 5320, Oyo Road, Ibadan, Nigeria (International mailing address: c/o Crop Improvement Division, International Institute of Tropical Agriculture, Katholieke Universiteit Leuven, Kasteelpark Avenberg 13, B-3001 Leuven, Belgium)

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The International Institute of Tropical Agriculture (IITA) aims to develop genetically improved plantain and bananas (Musa spp.) by utilizing genetic resources of various ploidy and geographic origins. Most of the cultivars currently used worldwide are triploid (2n = 3x = 33) natural interspecific hybrids derived from the two wild diploid banana species M. acuminata Colla, and M. balbisiana Colla, which contributed the A and B genomes, respectively (Simmonds, 1962; Simmonds and Shepherd, 1955). Hybridization among various subspecies of M. acuminata produced a range of diploid (AA) accessions from which triploid AA types originated by chromosome restitution. Hybridization between AA diploids and M. balbisiana (BB) resulted in many AAB and ABB types. Dessert bananas are predomi-
nantly AAA types that can be eaten raw when ripe while the AAB (plantain), ABB (cooking banana), and AAB East African highland types require some form of heat processing before they can be eaten. These cultivars are invari-
antly susceptible to the black Sigatoka leaf spot (caused by Mycosphaerella fijiensis Morelet), which causes yield losses of at least 33% in Africa (Mobambo et al., 1993).

Worldwide, nematodes are among the most important biotic constraints to the productivity of banana and plantain. The burrowing nematode Radopholus similis (Cobb) Thorne, the root-
lesion nematodes Pratylenchus coffeae (Cobb) Sher & Allen and Pratylenchus goodeyi Sher & Allen, the spiral nematode Helicotylenchus multicinctus (Cobb) Golden and root-knot nematodes (Meloidogyne sp.) are the most
common plant-parasitic nematodes associated with banana and plantain in Africa (Speijer and Fogain, 1999). The root-knot nematodes are sedentary and only cause localized lesions, but the other species feed, migrate and multiply in the roots and corm, causing extensive root necrosis which reduces the size of the root system and hinders the uptake of water and nutrients. Plant growth and yield are affected by reduction in the mechanical (anchorage) and physiological (uptake and transportation of water and nutrients) functions of the root system (Speijer and De Waele, 1997). Furthermore, affected plants become vulnerable to uprooting and toppling, especially during bunch filling or when strong winds prevail as frequently occurs in the tropics (Stover and Simmonds, 1987). Yield losses ranging from 30% to over 80% per crop cycle have been attributed to nema-
todes in Africa (Speijer and Fogain, 1999).

R. similis is considered the most important of the plant-parasitic nematodes known to cause damage to bananas and plantains (Gowen and Quénéhervé, 1990).

The control of M. fijiensis and R. similis in large-scale banana plantations relies mainly on the use of fungicides and nematicides, re-
spectively. However, these chemical products are not recommended in rehabilitation farming systems, due to their high cost and their hazard-
ous effect on the environment. Breeding for host plant resistance is the most economical and environment-friendly approach for control-
ling black Sigatoka and other pests. Diploid accessions have been traditionally regarded as the best sources of resistance genes and have been used predominantly as pollinators in crosses with triploid landraces to produce primary diploid and tetraploid hybrids (Rowe and Rosales, 1996). Subsequent improvement of the primary diploid or tetraploid hybrids involves backcrossing to the parental acces-
sions or intercrossing to produce secondary triploid hybrids (Ortiz, 1997a).

Inheritance studies in 3x-2x or 4x-2x cross-breeding suggested that most traits of economic importance are more predictably inherited from the diploid parents than from parents with a higher ploidy status (Tenkouano et al., 1998, 1999). Furthermore, genetic analysis is easier in a diploid background due to disomic in-
heritance to facilitate and accelerate breeding. This provided a justification for investment in the development of diploid breeding stocks as pursued by major programs worldwide (Ortiz and Vuylsteke, 1996).

Following the successful development of plantain-derived diploids [TMB2x (Tropical Musa plantain-derived diploid) series] and their registration in the public domain (Vuyl-
steke and Ortiz, 1995), IITA focused on the production of banana diploids [TMB2x (Tropical Musa banana-derived diploid) series]. One breeding approach used to produce banana diploids was to intermate diploid accessions belonging to different M. acuminata subspe-
cies to diversify and broaden the resistance base. After several crosses were made and the resulting progenies evaluated, the most promising diploid banana hybrids, TMB2x 5105-1 and TMB2x 9128-3, were selected. These diploid breeding stocks were developed IITA from 1988 to 1990 and their breeding values in 2x-2x and 4x-2x crosses were as-
sessed in subsequent years. These potential parental clones are ready for distribution to breeders and geneticists for use in germplasm enhancement and genetic analysis of the Musa genomes.

Origin
TMB2x5105-1 (Fig. 1) and TMB2x9128-3 (Fig. 2) are F1 progenies obtained from crosses between subspecies of M. acuminata. The female parent of TMB2x5105-1 was M. a. ssp. m. malaccensis ‘Pisang Lili’ and the male parent was M. a. ssp. barmanicoides ‘Calcutta 4’. TMB2x9128-3 had M. a. ssp. microcarpa ‘Tjau Lagada’ as the female parent and ‘Pisang Lili’ as the male parent.

The accession ‘Pisang Lili’ originated in Myanmar (Stover and Simmonds, 1987) and is described as a translocciated clone with edible parthenocarpic fruits and high resistance to black Sigatoka. It is moderately female fertile, but highly male fertile and known to frequently produce 2n or 4n pollen, depend-
ing on the season (Ortiz, 1997b). ‘Calcutta 4’ is a nonedible wild accession from Myanmar (De Langhe and Devreux, 1990) that produces many true-seeded fleshless fruits because it lacks one of the three dominant complementary genes for parthenocarpy (Simmonds, 1953). ‘Calcutta 4’ produces large quantities of fertile pollen and is resistant to black Sigatoka and several nematode species including R. similis and P. coffeae (Viaene et al., 2000). ‘Calcutta 4’ has been considered morpho-taxonomically related to plantain (De Langhe, 1969), justi-
fying its extensive use in crosses to improve plantain germplasm (Swennen and Vuylsteke, 1993; Vuylsteke et al., 1993; Vuylsteke and Ortiz, 1995). Both ‘Pisang Lili’ and ‘Calcutta 4’ are reference accessions of the International Musa Testing Program (Orjeda, 2000). ‘Tjau Lagada’ was originally collected in the Java island of Indonesia (Stover and Simmonds, 1987), is moderately female and male fertile, produces a long bunch with many hands, and the fruits are moderately parthenocarpic. Com-
pared to ‘Calcutta 4’, the resistance of ‘Tjau
lished in early evaluation trials (EETs) from hybrids from other crosses were field established at flowering and at harvest, as described by Swennen and De Langhe (1985).

The crosses and initial field evaluations were carried out at the IITA High Rainfall Station located at Onne (lat. 4°43′N, long. 7°01′E, 10-m altitude above sea level), in the humid forest zone and plantain growing area in southeastern Nigeria. The station is located in a degraded rainforest-swamp characterized by an Ultisol/Acrisol (U.S. Dept. of Agriculture (USDA) taxonomy/WRB) derived from coastal sediments and 2400 mm unimodal annual rainfall. The soil is a deep and freely drained Typic Paleudult/Haplic Acrisol of the coarse-loamy, siliceous isohyperthermic family, with poor nutrient status and low pH (pH 4.3 in 1:1 H₂O in the upper 15 cm). Detailed characteristics of the Onne station have been described elsewhere (Ortiz et al., 1997).

Subsequent evaluations of the TMB2x hybrids were carried out at Onne and at a second location, Namulonge (lat. 0°32′N, long. 32°34′E, 1128-m altitude above sea level) within the main banana-growing region of Uganda. This site is classified as an isohyperthermic Rhodic Kandiudalf/Rhodic Nitisol (USDA taxonomy/WRB) with slope averaging 4% and pH ranging from 5.4 to 6.4 in the upper 20 cm. Rainfall at Namulonge averages 1200 mm annually with bimodal distribution. At both locations, cultural practices were similar to those described by Swennen (1990). Nematode-resistance screening was carried out using a method that is based on the inoculation of individual roots (De Schutter et al., 2001). Screening trials included two reference cultivars with known responses to *R. similis*, namely, ‘Valery’ (Musa AAA, Cavendish subgroup), which is very susceptible to *R. similis* and ‘Yangambi Km 5’ (Musa AAA-group), which is resistant to *R. similis* (Sarah et al., 1992; Price, 1994; Fogain and Gowen, 1998). ‘Yangambi Km 5’ is also used as a reference cultivar of the International Musa Testing Program (Orjeda, 2000). Suckers of test and reference genotypes were selected for absence of weevil damage, pared to remove nematode-infected roots and corn tissue, and treated with hot water (53°C to 55°C) for 20 min (Colbran, 1967) before planting. Three suckers of each genotype were disposed in wooden boxes (0.5 × 0.5 × 0.5 m) containing heat-sterilized sawdust. Four weeks after planting, a small plastic cup was placed on an 8-cm-long decimated segment of three primary roots at ±5 cm from the corn for each sucker. Two days later, the roots were inoculated by pouring a 4 mL aqueous suspension containing 50,000 nematodes directly onto the number of standing leaves (NSL), the index of non-spotted leaves (INSL) was calculated as INSL = 100 (YLS-1) / NSL. Both ‘Calcutta 4’ and ‘Pisang Lilin’ are routinely included in the EETs as resistant controls. Also included in the EETs as a partially resistant control is ‘SH3362’, a high-yielding diploid hybrid from the Fundacion Hondurena de Investigacion Agricola (FHIA, Honduras). The most popular plantain landraces ‘Agbagba’ and ‘Obino l’Ewai’ serve as susceptible controls in the EETs. Growth and yield variables were evaluated at flowering and at harvest, as described by Swennen and De Langhe (1985).

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Fig. 1. Bunch characteristics of TMB2x5105-1, its parents and its progeny. From left to right: (A) Obino l’Ewai; (B) TMPx4698-1 (Obino l’Ewai x Calcutta 4); (C) Calcutta 4; (D) TM3x 25502-S4 (TMPx4698-1 x TMB2x5105-1); (E) Pisang Lilin; (F) TMB2x5105-1; and (G) Calcutta 4.

Fig. 2. Bunch characteristics of TMB2x9128-3 (center), an improved diploid hybrid from a cross between ‘Tjau Lagada’ (maternal parent, left) and ‘Pisang Lilin’ (paternal parent, right). TMB2x9128-3 has a large number of hands and fruits (inherited from its maternal parent), resistance to black Sigatoka and resistance to the burrowing nematode (*Radopholus similis*).
8-cm-long root segment before covering it with heat-sterilized soil (De Schutter et al., 2001). In Nigeria, nematode inoculum was obtained by hand-picking *R. similis* from an aqueous suspension containing nematodes extracted from infected ‘Valery’ roots using a modified Baermann funnel technique (Speijer and De Waele, 1997). In Uganda, nematode inoculum was obtained from carrot disc cultures (Pinochet et al., 1995) whereby petri dishes containing the carrot discs were rinsed with sterile distilled water and the nematodes were collected in a test tube. Eight weeks after inoculation, the plastic containers with the root segments were excavated and the 8-cm-long root segments were removed, washed with tap water, chopped into 0.5-cm pieces, thoroughly mixed and macerated in a kitchen blender during two periods of 10 s separated by a 5-s interval (De Schutter et al., 2001). All nematodes were collected in 25 mL and the counts of all vermiciform developmental stages and sexes were repeated three times using 2 mL aliquots. The method is based on the assumption that susceptible plants allow a higher reproduction ratio than resistant plants. The reproduction ratio (Rr) of each genotype was calculated as the square root transformed mean reproduction using 2 mL aliquots. The method is based on the assumption that susceptible plants allow a higher reproduction ratio than resistant plants. The reproduction ratio (Rr) of each genotype was calculated as the square root transformed mean reproduction ratio (<1) observed on the resistant reference cultivar ‘Valery’, representing >50-fold population increase (De Schutter et al., 2001) and contrasting with the low reproduction ratio (<1) observed on the resistant reference cultivar ‘Yangambi Km 5’ in both Nigeria and Uganda (De Schutter et al., 2001). In comparison, the reproduction ratios observed for ‘TMB2x5105-1’ and ‘TMB2x9128-3’ were <1 and not significantly different from that of ‘Yangambi Km 5’ (De Schutter et al., 2001; De Schutter et al., 2001), which was taken as evidence of their nematode resistance status.

Agronomic performance. The most distinctive phenological features of the diploid hybrids are their longer growth cycle, longer fruit filling time, and taller stature compared to their female parents (Table 2). The TMB2x hybrids also expressed increased yield per plant when compared with their parents (Table 3). In Nigeria, high parent heterosis was 175% in ‘TMB2x5105-1’ and 30% in ‘TMB2x9128-3’, while mid-parent heterosis was 238% and 81%, respectively. In Uganda, ‘TMB2x5105-1’ expressed heterotic values of 114% for the high parent and 226% for the mid-parent (Table 3).

Higher yield resulted from a shift towards increased fruit number (Table 3), confirming that genetic improvement of yield can be achieved by gradual accumulation of favorable alleles with additive effects associated with yield components (Ortiz, 1997c). As indicated by Ortiz and Vuyyleste (1994b), deleterious alleles (genetic load) are maintained in diploid gene pools through highly heterozygous germplasm and vegetative propagation. Breeding advances through phenotypic recurrent selection in diploid banana populations are made by selecting against these deleterious alleles, although the most promising selections appear to be highly heterozygous. Therefore, further improvement of the TMB2x hybrids can be achieved through recurrent selection with breeding values assessed prior to utilization as progenitors. Both ‘TMB2x5105-1’ and ‘TMB2x9128-3’ exhibit a regulated suckering, i.e., only a few suckers escape from apical dominance and develop into the ratoon crop. They also produce suckers escape from apical dominance and develop into the ratoon crop. They also produce

### CULTIVAR & GERMPLASM RELEASES

**Description and performance**

Resistance to black Sigatoka and nematodes. The TMB2x clones are identified by their original cross (progeny) numbers. Both hybrids expressed resistance to black Sigatoka under natural conditions, as evidenced by INSL scores of 65% or more, significantly greater than those of the traditional cultivars (<50%), but less than the scores of the resistant controls which had scores in excess of 75% (Table 1). The TMB2x hybrids expressed similar levels of resistance than ‘SH3362’, a high-yielding and partially resistant diploid hybrid from FHI (Honduras) that we routinely use as a control in our diploid breeding scheme. Host response causes low pressure on pathogen populations, resulting in more durable resistance (Ortiz and Vuyyleste, 1994a).

In addition to their resistance to black Sigatoka, both hybrids also expressed resistance to the burrowing nematode *R. similis*. No significant differences in root necrotic index, fresh weight of roots, percentage of dead roots, and plant height of infected vs. noninfected plants were noted. Single root inoculation using the method of De Schutter et al. (2001) resulted in ~2500 nematodes recovered from the root segments of the susceptible reference hybrid cultivar ‘Yangambi Km 5’, in both Nigeria and Uganda (Auwerkerken et al., 2001; De Schutter et al., 2001). In comparison, the reproduction ratios observed for ‘TMB2x5105-1’ and ‘TMB2x9128-3’ were <1 and not significantly different from that of ‘Yangambi Km 5’ (Auwerkerken et al., 2001; De Schutter et al., 2001; De Schutter et al., 2001). The TMB2x hybrids expressed similar levels of resistance than ‘SH3362’, a high-yielding and partially resistant diploid hybrid from FHI (Honduras) that we routinely use as a control in our diploid breeding scheme. Host response causes low pressure on pathogen populations, resulting in more durable resistance (Ortiz and Vuyyleste, 1994a).
pendulous bunches, which is an economically important characteristic because pendulous bunches are more symmetrical and, therefore, better adapted to transportation.

### Breeding potential and combining ability.

Both ‘TMB2x5105-1’ and ‘TMB2x9128-3’ are female and male fertile and can be used as seed or pollen parents in crosses. The breeding potential of the TMB2x clones may be determined as the relative performance of their offspring. Hence, the general combining ability (GCA), i.e., the mean deviation of the progeny from the overall mean of the population (Wricke and Weber, 1986), was calculated for their offspring. Hence, the general combining ability (GCA) was calculated as the relative performance of the breeding potential of the TMB2x clones may be determined as the relative performance of their offspring. Hence, the general combining ability (GCA), i.e., the mean deviation of the progeny from the overall mean of the population (Wricke and Weber, 1986), was calculated for both ‘TMB2x5105-1’ (in 4x-2x crosses) and ‘TMB2x9128-3’ (in 4x-2x and 2x-2x crosses).

The GCA values associated with the INSL were negative, reflected in lower resistance to black Sigatoka in progenies derived from both hybrids. Both ‘TMB2x5105-1’ and ‘TMB2x9128-3’ are now routinely used as progenitors in IITA’s crossing programs to generate superior secondary triploid or diploid stocks, several of which are now in advanced stages of evaluation (IITA, 2000).

### Availability

Limited numbers of in vitro plantlets are available upon request. Researchers interested in using TMB2x hybrids for development of improved Musa populations in their breeding programs should write to the International Institute of Tropical Agriculture (IITA), c/o Dr. C. Pasberg-Gauhl, and R. Swennen. 1993. Yield loss in plantain from black Sigatoka leaf spot and field resistance of resistant hybrids. Field Crops Res. 35:35–42.

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