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Recent lethal yellowing outbreak: why is the Malayan Yellow Dwarf Coconut no longer resistant in Jamaica?

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Abstract In Jamaica, the Maypan, a hybrid of Malayan Yellow Dwarf (MYD) and Panama Tall coconut, previously considered highly resistant, is currently being devastated by an epidemic outbreak of lethal yellowing disease. There are several possible causes for this change. In this study, we checked that affected planting material in Jamaica is genetically the same as the material shown to be resistant. We compared the deoxyribonucleic acid (DNA) of MYD sampled in four locations in Jamaica with a reference DNA of the same cultivar collected in five different countries. The results of our analyses showed more variation at 34 simple sequence repeat loci in Jamaica than in the rest of the world providing clear evidence for the presence of about 16% of alleles that do not match the usual typical MYD genotype. These alleles appear to have already been present in the introduced germplasm. This rules out a possible cause of the new outbreak: The observed hetero-

geneity may have caused some loss of resistance but is insufficient to explain a massive outbreak of the disease.

Keywords Lethal yellowing · Phytoplasma · SSR · Cultivar identification · Molecular markers · Disease resistance

Introduction

A new outbreak of lethal yellowing (LY) is devastating the coconut palm grove in Jamaica. Affected varieties include the Malayan Yellow Dwarf (MYD) and its hybrid with the Panama Tall or Maypan, which had been recommended as resistant. This raises several questions:

- Did the virulence of the pathogen change through mutation and/or selection of virulent types?
- Did a change occur in the nature or in the behaviour of the vector?
- Is the planting material that is affected today the same as the one that was declared resistant two decades earlier?
- Are the populations used in Jamaica representative of the cultivar they are supposed to belong to?

Answering these questions is essential for establishing a sound control strategy. Molecular markers can now answer the last two questions. We propose to show how assignment methods can be used to assess the trueness-to-type of genetic material used in genetic trials and in seed production. We will concentrate here on the MYD found at different locations in Jamaica and how it differs from those found in other countries.

MYD is a genetically uniform cultivar because it has a strong tendency to self-pollinate under natural conditions.

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The resulting natural tendency of the MYD towards homozygosity is further increased by human selection based on the distinctive yellow colour of the sprout. Bourdeix (1988) showed that this colour is determined by two recessive genes. Selection based on colour is very efficient in discarding out-crossed seedlings.

Jamaican MYD represents an exception among MYDs in that it is visually more heterogeneous than populations from other countries (Fig. 1).

This cultivar was introduced to Jamaica at different periods. The seeds never came directly from Malaysia. Whitehead 1966 reported that first importations of MYD and Malayan Red Dwarf (MRD) from Miami took place in 1939 and in 1940. Only four individuals survived and had progenies living in 1966. In the second case, MYD was introduced from Sri Lanka or Malaysia via Trinidad. There were two survivors and 15,000 progenies existed in the West End in 1966. However, the majority of the MYD present on the island resulted from later importations from Santa Lucia after serious hurricanes in 1944 and in 1951. Some 70,000 Malayan Dwarfs were imported before 1951. The initial source material in Santa Lucia consisted in 18 Malayan Dwarfs (six Green, six Red and six Yellow), imported from Malaysia (then the Federated Malayan States).

Hurricanes were not the only cause of losses of coconut trees. LY, a coconut palm disease, is currently devastating the Caribbean region, including Jamaica. The first reports of the presence of the disease in Jamaica appeared in 1884 (Coconut Industry Board 1971). Mycoplasma-like organisms (now known as phytoplasma) were observed by

electron microscopy and found specifically associated with LY syndromes in Florida and in Jamaica (Beakbane et al. 1972; Heinze et al. 1972a, b; Plavšić-Banjac et al. 1972). In 1983, Howard et al. showed that *Mindus crudus*, a plant hopper, is the vector of the disease in Florida. LY took 10 years, from 1961 to 1970, to invade all of Jamaica. By 1980, the disease had been responsible for the death of more than 7 million coconut palms in Jamaica. Malayan Dwarf, then Maypan (cross of Panama Tall and Malayan Dwarf), were replanted across the island because they were considered at that time as the most resistant varieties (Been 1981). However, Howard et al. 1987 reported losses because of LY in the MYD as early as 1987. At various locations along the coastal areas of the northern region, mortality levels among stands of MYD and Maypan were observed to be consistently higher than anticipated (Myrie 2005). This pattern continued into the 1990s, and in certain locations, the disease has started to move away from the coastal areas. The infection rate of the disease was increasing significantly. It was clear that LY re-emerged as the single most important plant disease affecting the coconut industry of Jamaica. In total, this new outbreak destroyed 1.3 million coconut trees.

Among the possible reasons cited to explain this apparent change of behaviour is that the MYD dying from the disease could differ genetically from those that were tested in the resistance trials. To check this hypothesis, we examined the diversity of the MYD presently found in Jamaica and compared it with degree of variation observed in the same cultivar in various countries.

Fig. 1 Map of Jamaica showing the major coconut growing areas and locations where samples were collected



Materials and methods

International reference for MYD

The reference samples we used to characterize the MYD were collected in five different countries. The 20 individuals from Côte d'Ivoire were taken from two accessions: One was imported from Malaysia (13 individuals) and the other one from Ghana (seven individuals) and is also known as the Ghana Yellow Dwarf. The other countries were the Philippines, India, Mexico and Malaysia itself (Table 3 below).

Eleven MRD and five Malayan Green Dwarf (MGD) samples from the Marc Delorme Research station were also analyzed for the same loci.

Jamaican MYD germplasm

The Jamaican MYD germplasm came from four locations (Table 1 and Fig. 2). The samples were collected between February 2, 2005 and May 26, 2005 at the location shown on the map. Among the samples from Barton Isles, we distinguished two sets, which were visually identified as “true to type” or “off type” based on the presence or absence of a bole and on height growth.

Microsatellite markers

The molecular markers used for this study were 14 microsatellite (simple sequence repeat, SSR) markers from the “microsatellite kit for coconut cultivar identification” (Baudouin and Lebrun 2002; Lebrun et al. 2005) and 20 additional markers. The selection criteria for these markers were that they should be easy to implement and to score. Table 2 lists some details on the 34 SSR markers.

SSR genotyping

SSR analyses were performed on an automatic sequencer Li-Cor IR2 (Lincoln, NE). All technical conditions are described in Baudouin et al. (2005).

Table 1 list of samples studied in Jamaica

Place of collection	Planting date	Code	Visual appearance	Number
Fair Prospect	Around 1960	FP	n.a.	5
Barton Isles	1973–1974	BI	n.a.	31
Barton Isles, Yard Piece	1973–1974	YPt	True-to-type (Yard Piece)	7
Barton Isles, Yard Piece	1973–1974	YPo	Off-type (Yard Piece)	5
Hermitage	Around 1960	H	n.a.	11
Ballards Valley	Around 1960	BV	n.a.	10



Fig. 2 An off-type coconut MYD with a bole at the base of the trunk. Trees in the background have the typical phenotype (without bole)

Statistical analyses

We grouped the genotypes at each locus into four categories: (A) homozygote for the most frequent allele (described below as “the typical MYD genotype”), (B) homozygote for another allele, (C) heterozygote possessing the most frequent allele and (D) heterozygote for two rare alleles (see Table 3). This made it possible to calculate two further parameters: observed heterozygosity as $(C+D)/N$ and occurrence of non-typical alleles as $1-(A+C)/N$ with A , B , C and D being the number of genotypes in each category and $N=A+B+C+D$ being the total number of genes scored. In addition, we estimated Nei's diversity index $h=2n(1-\sum x_i^2)/(2n-1)$ (Nei 1978) where x_i is the frequency of the i th allele of the considered locus and n is the number of individuals.

Results

Reference samples

Excluding Jamaica, we scored 55 MYD individuals at 34 loci. Of the $55 \times 34 \times 2 = 3,740$ resulting allelic observations,

Table 2 List of SSR markers used for assessing the trueness-to-type of MYD individuals

Number	SSR clone	5'...3' Forward primer	5'...3' Reverse primer	Linkage group ^a	EMBL access. number	Detection power ^b	Size of MYD (or MRD) typical allele (bp) ^c
Markers from the microsatellite kit							
1	CnCir A3	AATCTAAATCTACGAAAGCA	AATAATGTGAAAAAGCAAAG		AJ458309	21	240
2	CnCir A9	AATGTTGTGCTTTGTGGTGTGT	TCCCTAATTTTCTCCCTTCCTCA		AJ458310	6	89
3	CnCir B6	GAGTGTGAGCCAGCAT	ATTGTTACAGCTTCCA		AJ458311	39	202
4	CnCir B12	GCTCTTCAGTCTTCTCAA	CTGTATGCCAATTTTCTA	3	AJ458312	46	169
5	CnCir C3'	AGAAAGCTGAGAGGGAGATT	GTGGGGCATGAAAAAGTAAAC		AJ458313	15	174
6	CnCir C7	ATAGCATATGTTTTCTCT	TGCTCCAGCGTTCATCTA		AJ458314	17	161–(163)
7	CnCir C12	ATACCACAGGCTAACAT	AACCAGAGACATTTGAA		AJ458315	22	183
8	CnCir E2	TCGCTGATGATGCTTGGCT	GGGGCTGAGGGATAAACCC		AJ458316	3	135
9	CnCir E10	TTGGTTCATTTCTTCTCTAIC	GCTCTTATAGGGTTCGTTTCTTAG		AJ458317	13	238–(232)
10	CnCir E12	TCACGCAAAAGATAAAACC	ATGGAGATGGAAAAGAAAGG		AJ458318	3	164
11	CnCir F2	GGTCTCTCTCCCTCTTATCTA	CGACGACC AAAACTGAAACAC		AJ458319	13	205
12	CnCir G11	AATATCTCCAAAATCATCGAAAAG	TCATCCCACCCCTCTCT		AJ458320	33	194
13	CnCir H4'	TTAGATCTCTCCCAAAG	ATCGAAAAGAACAGTCAAG	3	AJ458321	23	230
14	CnCir H7	GAGATGGCATAACACCTA	TGCTGAAAGCAAAAAGAGTA		AJ458322	5	139
Additional markers							
15	CnCir A4''	GTTGGTTACTGGAATCTT	CATGACATACGGACTAGC		AJ865089	44	200
16	CnCir B3	CACTTGTCTTTACCATCC	AATACTGTGGGTTTTGGCTT	3	AM113713	10	293
17	CnCir B4'	TTTCATTCGAAGAGCCTAC	TTTCAAGCATCATTTCAAAT		AJ865091	8	196
18	CnCir B11'	TCTGCATCCCTCTTTAATA	TCTGCATCCCTCTTTAATA	10	AJ865093	34	110
19	CnCir C5	ACCAACAAAAGCCAGAGC	GCAGCCACTACTAAAAG		AJ865094	17	132
20	CnCir C9	CAGAAAGGAGAAAAGGAAAT	CTACGATAGAGGAATGAGC	4	AJ865095	25	214
21	CnCir C11	TGTTAATTTGTTAATTTACAGG	TCACCAATCTTCTCAGTTTC		AJ865096	10	221
22	CnCir D1	GGGAGGGAGGAGACTATG	AATTCAGGCCAACACAGACC	4	AJ865097	15	204
23	CnCir D8	GCTCTTGTATGGCTGCT	AGGGGTGTTGAGATTGTGA		AJ865098	44	251–(245)
24	CnCir E1	CTTGTATGTCGTTTGTG	CTGAGACCCTGTTGATGT	4	AJ865099	8	227
25	CnCir E4'	GCAATGGTATTCGGATTTG	ATGGTTACAGATTGGACAGT		AJ865100	3	187
26	CnCir E7	AACTACAACAAGAAAACAG	AGAGAAAGGAAAAGGATA		AJ865101	55	216
27	CnCir E11	CAGAAACAGCCAATCAAGCAATA	ATCCATAATAGCCACTCAACAAAAA		AJ865102	25	200–(196)
28	CnCir F3'	CCCTACTCTCCCTCAT	TGCCTAGTCAATCAATAC	4	AJ865103	22	172
29	CnCir G4	AGTATAGTACGCCAGAAAA	AAACCCATAACCAGCAAG		AJ865104	22	168
30	CnCir H11	TCATTCAGAGGACAAAAGTT	TAAAAATTCATAAAGGTAATAA	5	AJ865105	25	173–(193)
31	CnCir I4	TCCTAGTCTATGCTTGAC	TTGATGGTTTGATTTGAA	15	AJ865106	0	285
32	CnCir J2	CCATTTGCAATGTTAATTTG	GTCACCATCTTCTCAGTTTC	15	AJ865107	6	232
33	CnCir J10	GAGGGTATGGTCTGCTTG	ATCCTTCATGTGGCTCGTC	10	AJ865108	6	150
34	CnCir K8	CCAGACATGAAACAAACA	CATGGCACATAGGAAGAAC	13	AJ865114	20	162

^a See Baudouin et al. 2005^b Number of occurrences of “outsider” alleles detected in the Jamaican accessions using the locus^c The typical allele size for the MRD is given in parentheses when it differs from the MYD allele

Table 3 Summary results of genotyping of the MYD in reference samples and in Jamaica

Collected country	Number	Homozygotes (%)		Heterozygotes (%)		Heterozygosity rate (%)	Percentage of non-typical alleles (%)
		For MYD	For non-typical alleles	With 1 MYD allele	With 2 non-typical alleles		
		A	B	C	D		
Côte d'Ivoire	20	100.0	0.0	0.0	0.0	0.0	0.0
Mexico	3	100.0	0.0	0.0	0.0	0.0	0.0
Philippines	10	99.4	0.6	0.0	0.0	0.0	0.6
India	10	92.6	2.4	5.1	0.0	5.1	5.0
	9	<i>97.1</i>	<i>2.6</i>	<i>0.4</i>	<i>0.0</i>	<i>0.4</i>	<i>2.8</i>
Malaysia	12	99.7	0.0	0.3	0.0	0.3	0.1
Average							
All data	55	98.5	0.5	1.0	0.0	0.96	1.10
Without F ₁ hybrid	54	<i>99.4</i>	<i>0.5</i>	<i>0.1</i>	<i>0.0</i>	<i>0.12</i>	<i>0.58</i>
Jamaica							
Fair Prospect (FP)	5	86	5	9	0	9	14
Barton Isles (BI)	31	86	9	4	1	5	13
True type (Ypt)	7	94	3	3	0	3	6
Off type (Ypo)	5	76	8	15	2	17	23
Hermitage (H)	11	74	9	15	1	17	25
Ballard Valley (BV)	10	72	13	13	3	16	27
Average							
All data	69	82	9	8	1	9	17
Without F ₁ hybrids	67	<i>84</i>	<i>9</i>	<i>6</i>	<i>1</i>	<i>7</i>	<i>16</i>

Average values are given in bold. Figures in italics are averages obtained after removing the obvious hybrids

3,536 were scorable, and 3,501 corresponded to the most frequent allele at their respective locus, i.e. the “typical allele” of the MYD. Of the remaining 35 occurrences of rare alleles, 15 were found at heterozygous loci in a single individual from India. This individual was thus not a MYD but a hybrid (possibly a F₁ hybrid or a backcross with an undetermined local cultivar). Five individuals were homozygous for a rare allele at a single locus and two other at two loci. Finally, two individuals heterozygous at a single locus accounted for the remaining cases.

CnCirE7 and CnCirC7 were the two most polymorphic markers. CnCirE7 deviated from the typical genotype in five homozygous individuals. Three of the five individuals came from India and shared the same rare allele. The two remaining individuals were from the Philippines and had a rare allele in common, different from the one observed in

the Indian germplasm. At locus CnCirC7, the three Indian variants were also homozygous for the same allele, suggesting that the variant individuals from the same country are related.

Among the 11 MRD samples, eight had exactly the same genotype, differing from the MYD genotype at only five loci. One had the typical MRD genotype except that it had the MYD allele at one locus. The remaining two differed from the typical genotype at, respectively, six and seven loci. The genotype of the MGD was more complex: The most frequent allele was generally the same as in the MYD, but polymorphism was found at 21 loci. Moreover, observed heterozygosity was 10%. It is worth noting that the MGD is much less homogeneous phenotypically than either the MYD or the MRD. The tendency to self-pollinate is less pronounced in the MGD than in the other Malayan Dwarfs.

Table 4 Status of the Jamaican MYD samples according to their microsatellite genotype

	Number	True to type	2 non-typical alleles or less	F1 hybrids	2e generation hybrids	Others
Fair Prospect (FP)	5	0	0	0	1	4
Barton Isles (BI)	31	9	2	0	1	19
True type (YP) (Ypt)	7	2	3	0	0	2
Offtype (YP) (Ypo)	5	0	0	0	2	3
Hermitage (H)	11	0	1	1	2	7
Ballard Valley (BV)	10	0	1	1	1	7
Overall	69	11	7	2	7	42

Jamaican MYD

Among the 69 individuals collected in Jamaica, only ten had the typical MYD genotype at all loci; six further individuals differed at no more than two loci. On the other hand, two individuals were obviously recent hybrids as suggested by the high level of heterozygosity (>50%) and the large number non-typical alleles observed. One of the hybrids (from Ballard) is likely a F_1 hybrid with the Panama Tall while the other (from Hermitage) appears to be a hybrid with the local cultivar Jamaica Tall. Seven more individuals had a heterozygosity rate between 0.35 and 0.20 and were possible backcrosses or F_2 hybrids. The majority of the analyzed individuals did not fall into the previous categories and had several non-typical alleles (presumably “outsiders”) and a moderate rate of heterozygosity (Table 4).

The percentage of non-typical MYD alleles per individual varied from 0 to 74% (average=17%). Excluding the apparent F_1 hybrids, the heterozygosity rate was moderate (7%) and substantially lower than the Nei’s diversity index (0.22), yielding a F_{IS} close to 0.66. This indicates a high rate of inbreeding and suggests that the MYD from Jamaica is highly self-pollinating, like any other Dwarf (Table 3). If we consider samples separately, the sample with the fewest non-typical MYD alleles (6%) and the lowest observed heterozygosity (3%) was the true-to-type Yard Piece sample from Yard Piece. At the other end of the scale, the Ballards Valley, Hermitage and off-type Yard Piece samples had about 25% of non-typical MYD alleles and about 17% observed heterozygosity. Finally, comparing the three samples from Barton Isles (Barton Isles, true-to-type Yard Piece and off-type Yard Piece), the visually true-to-type individuals (true-to-type Yard Piece) had fewer non-typical MYD alleles than either the “off-types” (off-type Yard Piece) or random sample (Barton Isles). They were however not all “pure” MYD: The percentage of non-typical alleles was still ten times larger than in the reference samples.

Detection power of the markers

The low degree of polymorphism expected from this highly self-pollinating cultivar required a large marker set. For example, it would not have been possible to detect heterogeneity in the Philippines with the 14 markers of the “coconut cultivar identification kit” alone. In this case, the whole 34-marker set proved to be necessary. However, we could reduce this number in further studies based on the experience acquired here. In effect, the markers used were not equally able to detect polymorphism. The number of non-typical MYD alleles detected in Jamaica (Table 2, seventh column) varied from 0 to 55 (or 40%) according to the marker, and 50% of this polymorphism was detected with only nine markers (CnCirE7, CnCirB12, CnCirA4”,

CnCirD8, CnCirB6, CnCirB11’, CnCirG11, CnCirE11 and CnCirH11). To detect 90% of the heterogeneity, 13 additional markers would be necessary, thus saving 35% of the genotyping effort required. Finally, we note that although they were selected under somewhat different conditions, there is virtually no difference regarding polymorphism detection between the 14 usual and the 20 additional markers: The average value is 18.5 and 20, respectively.

Conclusion

The issue of varietal identity in the MYD in Jamaica is critical because this cultivar was claimed to be resistant to LY and has been extensively used to control the disease as a pure variety or as the female parent of the Maypan. Obviously, such a claim is meaningful only if the distributed planting material corresponds to what was tested. This had to be questioned because both the MYD and the Maypan are presently being devastated by the disease. The present study shows that the Jamaican MYD is only partially true to type. This heterogeneity may have some adverse effect on its degree of resistance but is not sufficient to account for the “massive” losses described by Broschat et al. 2002. Moreover, heterogeneity in the Jamaican MYD is not a recent phenomenon, as the oldest stands (Hermitage and Ballard Valley) are among the most heterogeneous. We are thus forced to conclude that MYD itself is no longer (if it has ever been) fully resistant to the current strains of LY phytoplasma.

We obtained for the first time a rough but quantitative evaluation of the normal degree of variation in a Dwarf coconut: The rates of non-typical alleles and of heterozygosity are, respectively, close to 0.5 and 0.1% heterozygous loci in the MYD. These values are rather conservative if we remark that accessions from Côte d’Ivoire and Mexico were identical at all 34 loci. This confirms that both its self-pollinating habit and human selection tend to make the MYD a highly uniform cultivar (Sangaré et al. 1978; Sangaré 1981). The presence of a small proportion of non-typical alleles can be explained by the fact that they were not yet eliminated by the selfing process. In theory, their frequency is reduced by half at each subsequent generation (Falconer and Mackay 1996). In addition to mutation, occasional crosses with closely related genotypes may also contribute to diversity, provided that their progenies are phenotypically close enough to the MYD.

Polymorphism in Jamaica is far beyond the normal range for the MYD. The rate of non-typical alleles and of heterozygotes were, respectively, 7 and 16% (excluding the two obviously hybrid genotypes). Only 16% of the Jamaican genotypes were true to type (26% if we allow for

two non-typical alleles). The account of MYD introduction by Whitehead 1966 supports the hypothesis that heterogeneities in the MYD have been there since the beginning: The most likely origin of the majority of the tested samples is the introduction from Santa Lucia, which comprised all three Malayan Dwarfs. In addition, the MGD is more heterogeneous than the other two, partly because the nursery selection criterion based on colour is no longer available. It is thus more likely to harbour alleles originating from another cultivar because of occasional intercrossing. Crosses among these initial introductions have probably created the observed diversity.

The structure of diversity in the Jamaican MYD seems to illustrate a possible mechanism of evolution in Dwarf coconuts. In effect, we observed a combination of a rather high proportion of non-MYD alleles with a moderate degree of heterozygosity. Although they are not all true to type, most Jamaican MYDs may be considered as “normal” Dwarfs as far as their reproductive behaviour is concerned. They are presently slowly returning to a homozygous state, thus producing a bundle of closely related pure lines, differing by the varying fraction of non-MYD alleles they incorporated. During this process, natural selection is at work: Besides LY, the strongest selection pressure is probably due to hurricanes, to which the MYD is highly susceptible. This probably leads to a selection in favour of non-MYD alleles in the chromosomal regions that are involved with a strong rooting system and reduced precocity. Finally, visual selection of true-to-type MYDs was probably less stringent than elsewhere in the world owing to the lack of a “pure” reference population. The observations made at Barton Isles confirm that visual selection, although effective, is insufficient to restore the original MYD genotype.

For germplasm conservation and seed production, it is important to keep the original MYD germplasm in Jamaica. This could be done through new importation; however, an acceptable method would be to collect nuts from the (molecularly as well as visually) true-to-type material identified at Yard Piece (Barton Isle). Combining this collection with nursery selection and emasculation of the off types will ensure a high degree of purity. This is not to say that the diversity that was involuntarily created in the Jamaican MYD should be discarded right away. Its interest lies in the fact that it is partly fixed, thus making family-based selection easier. As an example, such selection, monitored by molecular genotyping, could rapidly arrive at “improved” MYD lines, showing improved resistance to hurricanes.

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