Crop Protection 67 (2015) 91–95

Contents lists available at ScienceDirect

Crop Protection

journal homepage: www.elsevier.com/locate/cropro

The "Guiana" genetic group: A new source of resistance to cacao (*Theobroma cacao* L.) black pod rot caused by *Phytophthora capsici*

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ARTICLE INFO

Article history:
Received 3 July 2014
Received in revised form
22 September 2014
Accepted 23 September 2014
Available online

Keywords:
Cocoa
Resistance
Phytophthora capsici
Black pod
French Guiana

ABSTRACT

Black pod rot, caused by Stramenopiles of the genus *Phytophthora*, leads to serious production losses in all cocoa growing zones. In order to reduce the impact of these pests, preference is given to genetic control using resistant varieties, and sources of resistance are actively being sought, particularly in wild cacao trees. Surveys were undertaken in the natural cacao tree populations of south-eastern French Guiana between 1985 and 1995 and an abundant amount of plant material belonging to a particular genetic group, the "Guiana" group, was collected. A great deal of work has shown the merits of this genetic group as a source of resistance to *Phytophthora palmivora* and *megakarya*. We describe here the results of a global study to assess the resistance of the 186 clones in the "Guiana" group "core collection" to a Guianese strain of *Phytophthora capsici* (strain Reg 2-6). This study, which used an efficient methodology (fifteen series of tests on leaf discs and a statistical test adapted to the ordinal nature of the basic data), showed that the "Guiana" genetic group is a major source of resistance to *P. capsici*. Strain Reg 2-6 proves to be particularly virulent, as the Scavina 6 control, an international reference for resistance to *Phytophthora*, is not resistant to it. However, 24 clones of the "Guiana" group are, and 92 have proved to be more resistant than Scavina 6, thereby showing the interest of the group in genetically controlling *P. capsici*.

Thus, of the clones in the Guiana group that are more resistant to *P. capsici* than Scavina 6, some, which are also resistant to *P. palmivora* and/or *Phytophthora megakarya*, and also displaying some other notable qualities, could be incorporated into cocoa genetic improvement programmes in countries where *P. capsici* is rife on cacao trees.

1. Introduction

Black pod rot, caused by several species of Stramenopiles of the genus *Phytophthora*, lead to serious damage in all cocoa growing zones. For sustainable, ecological and economical control, genetic control using resistant varieties is essential; breeders are therefore seeking sources of resistance, particularly in wild cacao trees, in the species' zones of origin. For instance, certain wild cacao trees of south-eastern French Guiana, belonging to the "Guiana" genetic group (Motamayor et al., 2008), collected between 1985 and 1995 (Lachenaud and Sallée, 1993; Lachenaud et al., 1997), have undergone early *Phytophthora palmivora* and *Phytophthora megakarya* resistance tests in various countries. For resistance to *P. palmivora*, after many one-off results (Anonyme, 2004; Paulin et al., 2005; Lachenaud et al., 2007; Paulin et al., 2007, 2010) regarding the merits of GU clones from the Camopi and Tanpok river basins, the in-terest of the group as a whole has been shown (Thevenin et al., 2012). Likewise, for *P. megakarya*, which is only present in Africa, some tests carried out by CIRAD in Montpellier showed the exceptional merits of these cacao trees (Paulin et al., 2008, 2010). In tropical America, another species judged to be predominant (Lawrence et al., 1982; Ducamp et al., 2004) causes black pod rot, *Phytophthora capsici*.

This species has been acknowledged to consist of three close genetic groups, CAP1, 2 and 3 (Ducamp et al., 2004), but some authors have proposed that part of the CAP2 and 3 strains, derived from perennial plants, and especially the cacao tree, is a new species, *Phytophthora tropicalis* (Mchau and Coffey, 1995; Aragaki and Uchida, 2001; Donahoo and Lamour, 2008; Kroon et al. 2012).

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http://dx.doi.org/10.1016/j.cropro.2014.09.015
0261-2194/

However, the situation concerning this new species seems still controversial (Bowers et al., 2007).

As the species *P. capsici* exists in French Guiana, it was possible, and important, to test all the "Guiana" clones in the core collection at Paracou-Combi (Sinnamary, French Guiana) and to select some resistant clones there that can be used directly or as parents in breeding programmes.

2. Material and methods

2.1. Plant material

One hundred and eighty-nine clones were studied: 186 "Guiana" clones and three clones from other groups already used as controls in an earlier study (Thevenin et al. 2012). The "Guiana" clones came from wild mother-trees in the Oyapok, Camopi, Euleupousing, Yaloupi and Tanpok river basins surveyed and collected between 1987 and 1995 (Lachenaud and Sallée, 1993; Lachenaud et al., 1997). The 186 clones represented 17 demes of natural populations, plus one subspontaneous clone (Table 1). All the official authorizations required were obtained for the surveys, as mentioned in earlier work on the same genetic material (Thevenin et al. 2012).

The resistance control was the Scavina 6 clone (= SCA 6), the usual reference in tests on *P. palmivora* (Tahi et al., 2000; Lachenaud et al., 2001; Anonyme, 2001; Pokou et al., 2008; Akaza et al., 2009; Thevenin et al., 2012) and known to be resistant to *P. capsici* in Brazil (Lawrence et al., 1982; Luz et al., 1996). Clone T60/887, which is moderately resistant to *P. palmivora* (Tahi et al., 2006b) was included in the tests. Four clones from French Guiana were used as "susceptibility indicators" to check that the inoculation tests went ahead properly: 3 "Guiana" clones, ELP 40-B, OYA 2-B (highly susceptible to *P. megakarya*; Paulin et al., 2008) and GU 138-A (highly susceptible to *P. palmivora*; Paulin et al., 2010), along with a clone selected from cacao trees formerly grown in French Guiana, GF 24, susceptible to *P. palmivora* (Paulin et al. 2007). All these "susceptibility indicator" clones were confirmed to be susceptible to *P. palmivora* in an earlier study (Thevenin et al. 2012).

The 191 objects (i.e. 189 clones, of which 2 were replicated twice, Scavina 6 and ELP 40-B) all came from the same phenotyping platform, a plot kept under artificial shade (Thevenin et al. 2012) to ensure uniform environmental conditions essential for the tests (Tahi et al., 2007).

Table 1
Distribution by deme of the 186 "Guiana" clones studied (the "Camopi 0" clone is a subspontaneous clone of indeterminate deme but of local origin).

Deme	Nomenclature	Number	% Of total
Borne 7	B7	7	3.8
Camopi 1	GU	27	14.5
Camopi 2	GU	1	0.5
Camopi 3	GU	16	8.6
Camopi 6	GU	1	0.5
Camopi 7	GU	19	10.2
Camopi 8	GU	2	1.1
Camopi 9	GU	40	21.5
Camopi 10	GU	1	0.5
Camopi 12	GU	5	2.7
Camopi 13	GU	10	5.4
Euleupousing	ELP	25	13.4
Kérindioutou	KER	19	10.2
Oyapok	OYA	3	1.6
Pina	PINA	1	0.5
Tanpok	GU	3	1.6
Yaloupi	YAL	5	2.7
Camopi 0	GU	1	0.5
Total		186	100.0

2.2. Fungal material

The strain of *P. capsici* used, Reg 2-6, was isolated from a pod harvested in an old plot near Régina, in the remnants of some 18th century plantations. It was classed specifically by studying ITS sequences (Vasseur, 2010; Thevenin et al., 2012). The upkeep of the strains and maintenance of their pathogenicity were described by Thevenin et al. (2012).

In order to obtain the inoculum (formation of sporocysts and zoospores), the strains were grown at 24 °C on V8 1/5 + Beta sitosterol medium for 3 days in total darkness, then 7 days in the light. Zoospores were released after thermal shock (cold water + 20 min at 4 °C), then the suspension was calibrated with a Malassez cell. During preliminary tests in the study, the local strains of *P. capsici* proved to be clearly more aggressive than those of *P. palmivora*, involving a concentration of 100,000 zoospores/mL maximum rather than the 300,000 used for *P. palmivora*.

2.3. Experimental protocol

The leaf disc test (Nyassé et al. 1995; Tahi, 2003; Tahi et al. 2000, 2006a,b, 2007) was used, for its good correlation with black pod rot losses in the field. The performance of the clones was estimated by the appearance and area of necrotized patches on the underside of the leaf discs, after depositing 10 μL of a calibrated suspension of zoospores.

The inoculated discs were placed in trays and incubated in the dark at 25 °C. Symptoms were scored after 5 days of incubation, using the scale of Nyassé et al. (1995): Highly Resistant (HR: $0 < \text{score} \leq 1$), Resistant (R: $1 < \text{score} \leq 2$), Moderately Resistant (MR: $2 < \text{score} \leq 2.5$), Susceptible (S: $2.5 < \text{score} \leq 3.5$), Highly Susceptible (HS: $3.5 < \text{score} \leq 5$).

Fifteen series of tests were carried out between February 2011 and November 2013, covering all local seasonal variations, with 10 incubation trays per series, each comprising one leaf disc per. The numbers per series varied from 155 to 191 objects, with an average of 179.4, i.e. 94% of the objects. The series were therefore the equivalent of incomplete blocks.

Details about the sampling of the leaves used in the tests (stage and times) can be found in earlier work (Thevenin et al., 2012).

2.4. Statistical methods

The statistical methods used were the same as those used in similar work on *P. palmivora* (Thevenin et al., 2012). We modelled the link between the scores assigned to each disc by a generalized linear model (GLM, McCullagh and Nelder, 1989) using an ordinal probit link (Agresti, 2002). This model respected the ordinal qualitative nature of the scores. The significance of clone and tray effects was assessed by likelihood ratio tests ($pv = 0$ for each of the effects).

In order to assess clonal differences and construct homogeneity groups, we carried out paired likelihood ratio tests. For each pair of clones, we compared the likelihoods of the probit GLM, assuming successively that the 2 clones had some different and identical effects. Statistical processing was carried out with R software (R Development Core Team, 2011).

3. Results

The general mean after 15 series of tests was 2.69, corresponding to overall "Low Susceptibility". The "susceptibility

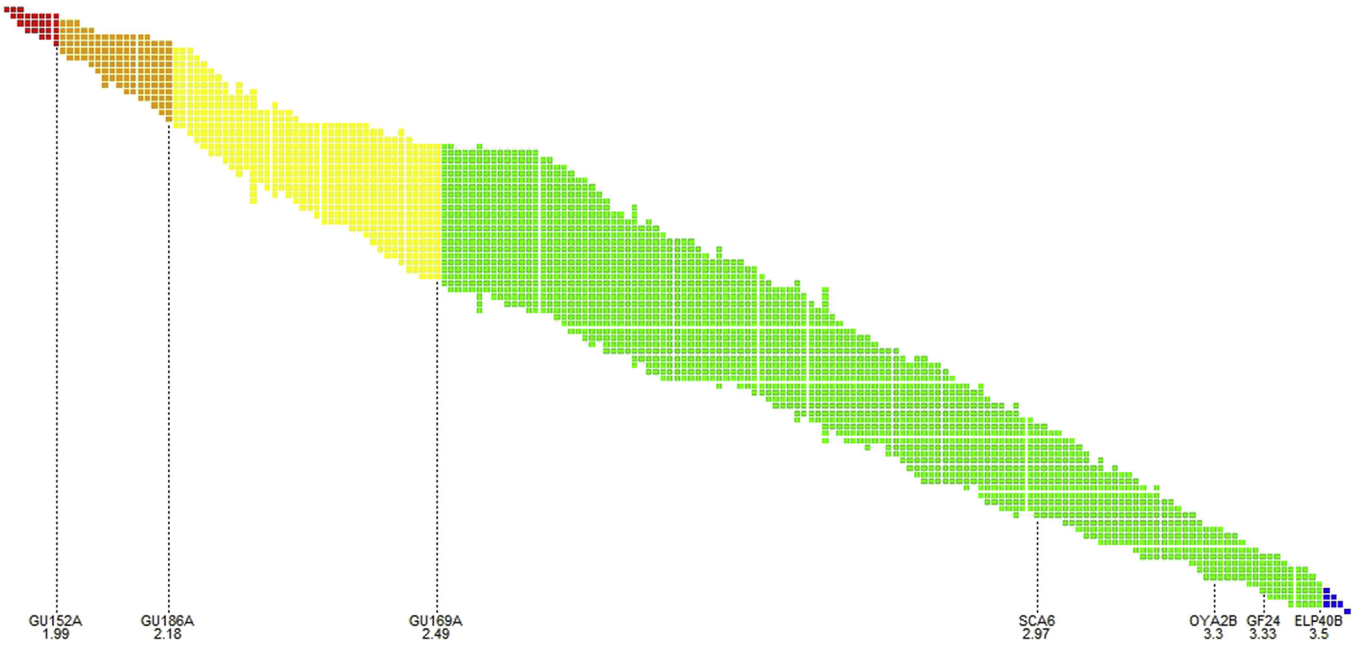

Fig. 1. Cross-representation of the clones and homogeneity groups. Each column corresponds to a clone and each row corresponds to a homogeneity group. 5 groups are represented, from left to right: strictly resistant clones (R, with a mean ≤ 2, in red); resistant clones = homogeneous with the previous ones (R, orange); moderately resistant clones (MR, with a mean ≤ 2.5, in yellow); susceptible clones (S, with a mean > 2.5 and ≤ 3.5, in green) and highly susceptible clones (HS, with a mean > 3.5, in blue). The indicated clones, with their average score, are the controls (SCA 6, ELP 40-B, OYA 2-B, GF 24) and those on the edges of groups (GU 152-A, GU 186-A and GU 169-A).

indicator" clones confirmed their susceptibility to *P. capsici* with average scores of 2.96 for GU 138-A, 3.30 for OYA2-B, 3.33 for GF24 and 3.48 for ELP 40-B (Fig. 1). Scavina 6, with an average score of 2.97, also proved to be susceptible, which was not expected, given the results acquired in Brazil (Lawrence et al., 1982; Luz et al., 1996). Clone T 60/887 was susceptible too, but moderately and statistically less so than Scavina 6, with an average of 2.56.

The raw averages were distributed as follows: 8 objects (all Guiana clones) had a score below or equal to 2, 54 objects had a score of between 2 and 2.5 (all Guiana) and 129 objects (of which 125 Guiana) had a score over 2.5.

The analysis based on the ordinal probit model showed 89 homogeneity groups (Fig. 1). Eight clones were strictly resistant (SR, mean ≤ 2) and 16 (means of 2.03–2.18) were homogeneous with the first 8, and therefore considered resistant (R) (Table 2, Fig. 1). The other clones were therefore moderately resistant (MR), with scores of 2.22–2.49 (i.e. 38 clones), susceptible (S), with means of 2.51–3.50 (i.e. 125 clones, of which 122 Guiana) and highly susceptible (HS, i.e. 3 clones, including ELP 25-A, alone in its homogeneity group, with a score of 4.01). Thus, 62 Guianese clones out of 186 were "Resistant", and "Moderately Resistant", corresponding to a "resistance index" (IRBP, Akaza et al., 2009) of 33.3%.

The distribution of the 24 resistant clones by deme (Table 2) showed that some demes were not represented, such as Camopi 2, 6, 12, 13, 10, KER, OYA, Pina, YAL, which nonetheless represented a cumulative 25% of the clones tested. Conversely, some demes were largely over-represented, such as ELP (29% of resistant clones as opposed to 13.4% of the clones tested) and Camopi 1 (24% and 14.5% respectively), while some others seemed under-represented, such as Camopi 9 (16.7% as opposed to 21.5%). Compared to our previously published results on the resistance of the same clones to *P. palmivora* (Thevenin et al., 2012), the clones of the Camopi 1 deme thus confirmed their merits.

4. Discussion

In relation to our Guianese strain of *P. capsici*, Reg 2-6, the Scavina 6 clone, while being the international reference for *Phytophthora* resistance tests and resistant to certain Brazilian strains, proved susceptible. When exposed to this particularly virulent strain, 8 "Guiana" clones proved to be strictly resistant and 16 could be considered as resistant, as they were homogeneous with these 8

Table 2
The 24 clones resistant to *P. capsici*, ordered according to their effect in the ordinal probit model. The strictly resistant clones (score ≤ 2) are in bold and the others are homogenous with them (same homogeneity groups).

Clone code	Clone name	Mean	Deme
139	**GU 265-V**	**1.68**	**CAM 1**
55	**ELP 9-A**	**1.84**	**ELP**
87	**ELP 11-A**	**1.83**	**ELP**
15	**GU 161-A**	**1.90**	**CAM 1**
58	**ELP 18-A**	**1.90**	**ELP**
137	**GU 262-A**	**1.93**	**CAM 1**
97	**ELP 8-A**	**1.94**	**ELP**
11	**GU 152-A**	**1.99**	**CAM 7**
3	GU 129-A	2.03	CAM 7
109	GU 156-B	2.09	CAM 1
168	ELP 15	2.08	ELP
185	B7–B3	2.08	Borne 7
156	GU 353-V	2.13	CAM 9
99	GU 123-V	2.13	TAN
57	ELP 16-A	2.12	ELP
138	GU 263-V	2.13	CAM 1
148	GU 303-B	2.14	CAM 9
68	GU 100-A	2.14	CAM 3
123	GU 225-B	2.15	CAM 3
60	ELP 22-A	2.17	ELP
12	GU 153-A	2.15	CAM 8
150	GU 309-A	2.16	CAM 9
32	GU 264-A	2.18	CAM 1
18	GU 186-A	2.18	CAM 9

clones (scores < 2.18). In addition, 92 "Guiana" clones proved to be more resistant than Scavina 6, thereby showing the potential merits of this group against "normally" virulent strains of *P. capsici*. In fact, *P. capsici* is reputed to be less virulent than *P. palmivora*, as is the case in Brazil (Lawrence et al., 1982) and our Guianese situation, where, on the contrary, *P. capsici* proved to be much more virulent than *P. palmivora*, seems exceptional and argues in favour of taking a closer look at its specific status, as it could correspond to the species *P. tropicalis* (Decock, pers. comm.).

Table 3 shows that, of the 24 clones found to be resistant to *P. capsici* in this study, 9 were also resistant (or highly resistant in one case) to *P. palmivora* and *P. megakarya*. These were clones ELP 9-A, ELP 8-A, ELP 15, ELP 16-A, ELP 22-A, GU 123-V, GU 156-B, GU 263-V and GU 303-B, i.e. 5 clones of the ELP deme, 2 of the Camopi 1 deme, 1 of the Camopi 9 deme and 1 of the Tanpok deme. The ELP and Camopi 1 demes therefore confirmed their great merits as sources of resistance in controlling cacao black pod rot diseases caused by *Phytophthora*.

When studying Spearman's coefficient of correlation between the average *P. capsici* resistance scores for the 186 wild Guianese objects in this study, and their average *P. palmivora* resistance scores already published (Thevenin et al., 2012), a very highly significant ($p = 0.0001$) and positive R value of 0.582 was obtained, i.e. an R^2 of 0.34. Thus, at least in this genetic group, resistance to the two species was positively correlated with an average R^2 value.

5. Conclusion

Our results confirmed that the "Guiana" group, which is already a source of resistance to *P. palmivora* (Thevenin et al. 2012) and *P. megakarya* (Paulin et al. 2008, 2010) is also a major source of resistance to *P. capsici*. Twenty-four clones are resistant (8 proving to be strictly resistant), while 38 are moderately resistant. Very many clones (92) proved to be statistically more resistant than the Scavina 6 reference, which proved to be susceptible to our strain of *P. capsici*.

Of the resistant clones, and particularly the 9 also resistant to the other two species, *P. palmivora* and *megakarya*, some could be incorporated into numerous cacao breeding programmes, especially those displaying other notable agronomic qualities (Lachenaud et al., 2007). They can be available after ordering from the first author, the establishment of a Material Transfer Agreement (MTA) and two years' quarantine in a temperate zone.

Table 3
The 24 clones resistant to *P. capsici*, and their reaction to *P. palmivora* (PP) and *P. megakarya* (PM), according to the work by Thevenin et al., (2012), Paulin et al. (2008, 2010) and Lachenaud et al. (2007), where HR = highly resistant, R = resistant, MR = moderately resistant, S = susceptible, ? = contradictory results and – = not tested.

Clone code	Clone name	PP	PM
139	GU 265-V	R	?
55	ELP 9-A	R	R
87	ELP 11-A	R	–
15	GU 161-A	R	–
58	ELP 18-A	R	–
137	GU 262-A	R	–
97	ELP 8-A	R	R
11	GU 152-A	R	–
3	GU 129-A	R	–
109	GU 156-B	R	R
168	ELP 15	R	R
185	B7–B3	MR	R
156	GU 353-V	S	R
99	GU 123-V	R	HR
57	ELP 16-A	R	R
138	GU 263-V	R	R
148	GU 303-B	R	R
68	GU 100-A	MR	–
123	GU 225-B	R	–
60	ELP 22-A	R	R
12	GU 153-A	S	–
150	GU 309-A	MR	–
32	GU 264-A	MR	–
18	GU 186-A	R	–

Acknowledgements

This study was carried out under an ERDF project (European Regional Development Fund) 2009-2012: "Dicacao" (Diversity of wild cacao trees in French Guiana and associated endophytes. Merits and use in disease control). Our thanks to Peter Biggins for translating the text, and Virgile Condina for help during the tests.

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