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Review

Levels of resistance to *Phytophthora* pod rot in cocoa accessions selected on-farm in Côte d'Ivoire

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Abstract

Resistance to *Phytophthora* pod rot (Ppr) is becoming an increasingly important criterion for selection of new cocoa cultivars in Côte d'Ivoire. The predominant species of the pathogen, *Phytophthora palmivora*, causes pod losses of 10–15% but the more aggressive *Phytophthora megakarya* present in the eastern part of the country causes losses of 40–60%. The latter species is expected to continue its spread to the main cocoa belt in Côte d'Ivoire over the next decade. Since 2000, the Centre National de Recherche Agronomique has been selecting new cocoa cultivars with direct involvement of farmers. More than 250 farmers were visited and their knowledge is being used to collect accessions with high yield potential, with low pest (mirids) infestation or with low Ppr incidence. Farmers were capable of identifying mother trees with low Ppr incidence only in regions with high disease pressure (Abengourou and Aboisso). Open-pollinated seedling progenies obtained from 226 promising trees in farmers' fields were screened for resistance to Ppr by inoculating leaf discs from nursery plants with spores of a *P. palmivora* isolate. Three clones (SCA6, PA150 and NA79) and three recommended hybrids were used as control cultivars. The results of the leaf disc test confirmed the known variation of resistance of the control cultivars. The relative level of resistance of the farm accessions varied mainly between moderately resistant and susceptible, but several accessions could be considered as resistant, in relation to the control cultivars. The major part of the 15% most resistant farm accessions came from the Abengourou and Aboisso regions in the eastern part of the country. Progenies from mother trees that farmers had selected as showing low Ppr incidence in their fields also appeared to be more resistant in the leaf disc test. This suggests that the resistance identified to *P. palmivora* in the leaf disc test may be efficient in the field in areas infected with *P. megakarya*. It is recommended that the genetic diversity identified through participatory selection of promising mother trees in farmers' fields be further exploited in breeding to obtain new hybrid or clonal cocoa cultivars with low incidence of Ppr, good yield and low mirid damage.

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Keywords: *Theobroma cacao*; Farmers' knowledge; *Phytophthora megakarya*; *Phytophthora palmivora*; Black pod; Breeding; Leaf disc test

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1. Introduction

The cocoa tree (*Theobroma cacao*) originates from the tropical forests in South America. The species is generally highly susceptible to diseases and pests, although to different degrees. Globally, the most widespread disease is *Phytophthora* pod rot (Ppr), also called black pod, which is caused by four species of *Phytophthora*. The most common worldwide is *Phytophthora palmivora*. The more aggressive *Phytophthora megakarya* is an African species that predominates in Cameroon, Nigeria and Ghana, where losses due to Ppr reach 50–80% if no control measures are taken (Despréaux, 2004). In Ghana, the predominating *P. palmivora* species is currently being replaced by *P. megakarya* that has been spreading northwards and westwards over the last 20 years (Opoku et al., 2000). In Côte d'Ivoire, *P. palmivora* is still predominant but *P. megakarya* was detected in the eastern part of the country by the end of the 1990s (Koné, 1999). In areas near the border with Ghana invaded by *P. megakarya*, the pod losses have increased from an average of 15%, in the presence of *P. palmivora*, to an average of 30–35%. Chemical control of Ppr is possible but expensive in relation to the low average productivity by smallholder cocoa growers in Africa (Kébé, 1994). The majority of cocoa cultivars grown worldwide are highly susceptible to Ppr disease (Eskes and Lanaud, 2001). Although significant variation for genetic resistance has been observed in germplasm collections and breeding trials (e.g. Blaha and Lotodé, 1976; Despréaux et al., 1989; Iwaro et al., 2003), the percentage of resistant accessions is generally low. Considerable efforts have been undertaken over the last 10 years to develop and/or improve resistance evaluation methods, using inoculations of detached or attached pods, leaves and leaf discs (Nyassé et al., 1995; Cilas and Despréaux, 2004; Iwaro et al., 2003; Nyassé et al., 2002; Tahi et al., 2000, 2006). Inoculation of leaf discs of many cocoa accessions and different pathogen isolates suggests that resistance to *P. megakarya* can be correlated with resistance to *P. palmivora* (Nyassé et al., 1995; Paulin et al., 2005). The results of the leaf disc and detached pod inoculation tests, when carried out under standardised conditions, have been shown to be significantly correlated with field level of infection (Iwaro et al., 2005; Tahi et al., 2000, 2006).

Selection for Ppr-resistant cocoa cultivars has become a priority for the Centre National de Recherche Agronomique (CNRA) from 1990. In Côte d'Ivoire, good repeatability and highly positive correlations with natural infection in the field have been demonstrated by using inoculations of leaf discs (Tahi et al., 2000, 2006). This method has been applied routinely from 2000 to evaluate resistance to Ppr in

the CNRA breeding programme, which includes a recurrent selection approach of two separate base populations (Upper Amazon and Lower Amazon). Among 55 parental clones of the recurrent selection programme, only 12 had good levels of resistance (Lachenaud et al., 2001). Two of the most resistant accessions used in the breeding programme are PA150 and SCA6. So far, little is known about the variation for resistance to Ppr in farmers' fields in Côte d'Ivoire.

In 2000, the CNRA included a farmers' participatory approach in the cocoa breeding programme. The objective is firstly to make use of farmers' knowledge to select promising accessions in farmers' fields and to compare in on-farm trials the best cultivars selected by breeders with farmers' selections. The programme started with a farm survey carried out in the 2001/2002 main harvesting period, during which pods were collected from trees that were considered by the farmers as promising for high yield, low Ppr and/or low mirid incidence (Pokou et al., 2005). Results are presented here on the level of resistance to *P. palmivora*, evaluated with the leaf disc test, of 226 accessions selected in a participatory manner in farmers' fields from the main cocoa-growing regions in Côte d'Ivoire.

2. Materials and methods

2.1. Plant materials

During the 2001/2002 main harvesting period (e.g. October 2001–January 2002), visits were carried out by the first author to 280 representative farms (2–10 ha cocoa plots) in the main cocoa-producing regions in Côte d'Ivoire: Abengourou (AB), Aboisso (A), Divo (D), Daloa (DA), Gagnoa (G) and Soubré (S) (Fig. 1). The oldest cocoa regions are located near the Ghanaian border (Abengourou and Aboisso), where cocoa was established mainly between 1950 and 1970. The youngest cocoa region is Soubré, with strong cocoa development after 1980. Farmers were asked whether they knew of trees that over the last years had consistently produced high yield, low Ppr incidence or low insect infestation (infestation of mirids on pods), without asking them to quantify absolute production or damage levels. Farmers in all regions recognised a few trees in their plots as "high yielding" and/or with "low mirid infestation". But farmers recognised significant variation between trees in Ppr incidence only in the Abengourou region, where pod losses are higher due to the presence of *P. megakarya*. Trees preferred by farmers for the above-mentioned criteria were observed by the first author for their growing conditions and environment. When collecting farm accessions for the present study, trees

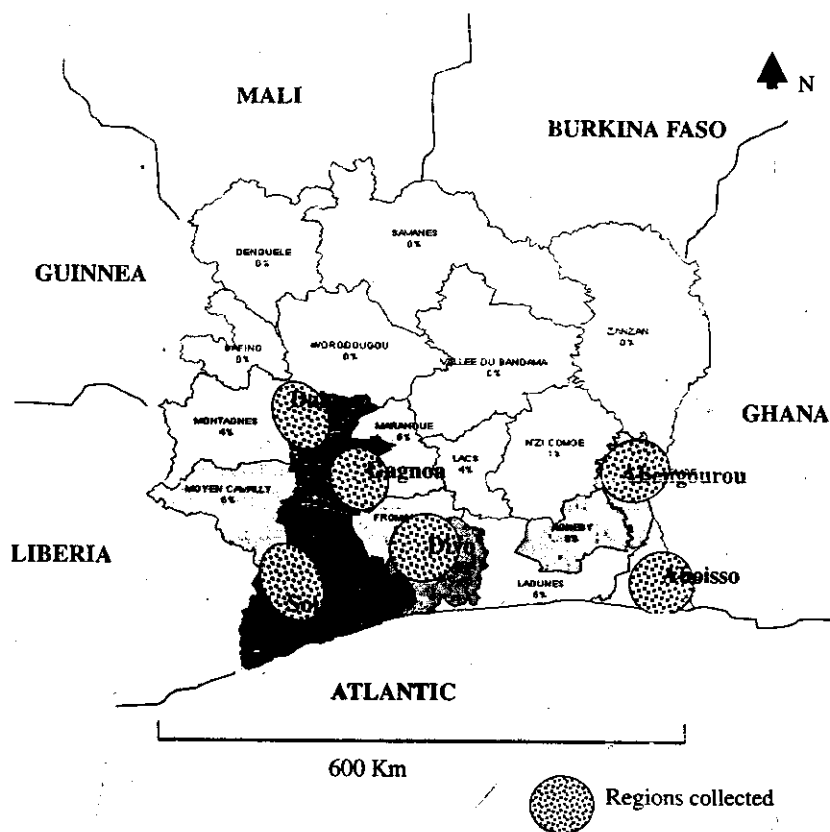


Fig. 1. Main cocoa-producing regions in Côte d'Ivoire where cocoa farm accessions were collected.

were avoided that were considered to be growing under very favourable conditions (e.g. isolated trees or near farm houses).

A sample of 10 beans was taken at random from two to five pods of each of the 226 mother trees and sown in plastic bags in a nursery at the Adiopodoumé centre of the CNRA in Abidjan between October 2001 and January 2002. The seedlings of each progeny (called hereafter "farm accession") were placed together in lines of 10 plants and the nursery was uniformly shaded with palm leaves.

Ten seedlings of each of the three hybrid cultivars (UPA409 × POR, NA32 × IFC5 and T79/501 × IFC5) recommended for commercial planting in Côte d'Ivoire (Clement et al., 1999) were planted in the same nursery as the farm accessions. Based on the resistance of the parental genotypes (Tahi et al., 2000; Lachenaud et al., 2001) and field observations (Clement et al., 1999), the first two hybrids can be considered as susceptible and the last one as moderately susceptible. The seeds of these hybrids were obtained by hand-pollinations carried out at the CNRA station in Divo. Two clones with known Ppr resistance (SCA6 and PA150) and one susceptible control clone (NA79) (Tahi et al., 2000; Lachenaud et al., 2001) were used. Leaves of adult trees of these clones growing at the CNRA station in Bingerville (near Abidjan) were harvested and used for each leaf disc inoculation series.

2.2. Fungal isolate

Due to the restricted presence of *P. megakarya* in Côte d'Ivoire, only near the border with Ghana, it was not possible to use an isolate of this species for the resistance tests. Therefore, an isolate of *P. palmivora* (M3-7.2) commonly used before in resistance tests in Côte d'Ivoire (Tahi et al., 2000, 2006) was chosen for the leaf disc inoculation test. It has an average level of aggressiveness, with disease severity scores in the leaf disc test varying generally between 3 and 4 for susceptible cocoa genotypes. The pathogenicity of the isolate was maintained by regular inoculation in the laboratory of green mature cocoa pods and by re-isolation afterwards on pea agar medium in tubes placed at 26 °C in the dark. Zoospore suspensions were obtained after incubation of culture flasks for 6 days in darkness followed by 10 days with alternating 12 h darkness and fluorescent light (Tahi et al., 2000). To obtain zoospore release, cultures were flooded with distilled water at 4 °C and incubated with incandescent light for at least 40 min.

2.3. Leaf disc test

One leaf of approximately 2 months of age, when the peduncles change from green to brown (Tahi et al., 2006), was collected between 07:00 am and 09:00 am from each of

the 10 nursery plants for each farm accession and control hybrid cultivars. For the clone control cultivars, four leaves of the same age were collected from each of the three trees in the germplasm collection of Bingerville. The leaves were placed in humidified plastic bags and conserved for 24 h in the dark in the laboratory at approximately 26 °C. The next morning, the leaves were cleaned with a towel wetted with distilled water and three leaf discs were obtained from each leaf by using a cork borer of 1.5 cm diameter. Seven leaf discs of each accession or control cultivar were placed upside down on wetted plastic foam in each of the four trays of 70 cm × 60 cm × 10 cm (length × width × height), totalling 28 discs per accession for one inoculation series. The trays were covered with a plastic sheet until inoculation was done later on the same day.

The leaf discs were inoculated by placing 10 µl droplets of a suspension of 300,000 zoospores per ml in the centre of each leaf disc. After inoculation, the trays were covered with a plastic sheet and incubated in the dark at 26–28 °C. Scoring of disease severity was done 7 days after inoculation by applying a 0–5 scale for increasing size and intensity of symptoms (Nyassé et al., 1995), with 0 = no symptoms, 1 = small necrotic flecks and 5 = large necrotic lesions expanding outside the area covered by the inoculation droplet.

Not all 226 farm accessions could be inoculated at once. Therefore, they were divided into four batches, containing 63, 61, 41 and 61 accessions. These batches were each inoculated twice between October 2002 and December 2002. In each of the eight inoculations carried out, the three clonal control cultivars were also inoculated in the same way as the farm accessions. The hybrid control cultivars were only tested twice, together with the second group of farm accessions.

2.4. Statistical analyses

The statistical unit used for the analyses of variance (ANOVA) was the average disease score of the seven leaf discs for each farm accession or for each control cultivar present in one inoculation tray. Normality of the residuals and homogeneity of variances was verified. ANOVAs were

carried out using the general linear model of SAS V8 (1999–2001) statistical package. The repeatability of the leaf disc test results was assessed by calculating the coefficient of linear correlation between the results of the two inoculation series carried out for each of the four batches of genotypes. The effects of the control genotypes, of the inoculation series (within batches) and of the trays (replicates within inoculation series) were analysed using all data for the control clones. In order to be able to analyse all results together, the average disease scores for each genotype in each tray were corrected by multiplying with the average disease score for the three control clones (over all inoculation series) divided by the average scores for the same control clones in the inoculation series. All corrected data (eight replicates, i.e. average scores for each of the farm accessions or control cultivars) were analysed together in a one-way ANOVA. Comparison between corrected means was done by the Student Newman and Keuls method with a probability of 5%. The effect of the criteria used by the farmers to select the mother trees (yield, black pod incidence and mirid infestation) on the disease scores of the farm accessions was analysed by using the average scores for each accession within each of the treatments.

3. Results

The number of selected mother trees varied according to the region and according to the farmers' knowledge on the existence of trees with high yield, low mirid infestation and/or low Ppr incidence. Trees that were favoured due to their growing conditions were avoided in the selection process. In total, 106 trees were selected for high yield, 101 for low mirid infestation and 19 for low Ppr incidence (Table 1). In all regions visited during the survey, farmers were generally able to identify trees in their plantations with high yield or low insect infestation (they mainly referred to infestation of mirids on pods and borer on stem). However, they were able to identify trees with low Ppr incidence only in regions where the disease pressure was high, i.e. in the eastern part of the country (Abengourou and Aboisso regions). Eighteen of the 19 mother trees selected for low Ppr

Table 1
Number of cocoa trees selected according to three selection criteria applied by the farmers in six cocoa-growing regions in Côte d'Ivoire, and the number of accessions showing superior Ppr resistance level in the leaf disc test (belonging to 15% of the most resistant accessions)

Selection criterion	Cocoa-growing region						Total	Accessions with superior resistance
	AB	A	D	G	DA	S		
Yield potential	27	6	3	10	23	37	106	10 (9.4%)
Insect infestation	25	2	4	15	25	30	101	12 (11.9%)
Ppr incidence	14	4			1		19	12 (63.2%)
Total	66	12	7	25	49	67	226	
accessions with superior resistance	13 (20%)	7 (58%)	1 (14%)	3 (12%)	3 (6%)	7 (10%)	34 (15%)	

AB: Abengourou; D: Divo; G: Gagnoa; A: Aboisso; DA: Daloa; S: Soubré.

Table 2
Coefficients of linear correlation between average disease scores obtained in two inoculations of 226 farm accessions and control genotypes tested in the leaf disc test in four batches

Statistical parameter	Batch			
	1	2	3	4
Coefficient of correlation	0.27	0.63	0.51	0.45
Stability	0.03	<0.001	<0.001	<0.001

ence came from these regions. Some farmers identified that combined more than one favourable trait: high yield and low insect or Ppr incidence. In such cases, farmers were asked what they considered as the most important trait and the tree was labelled according to that criterion.

The coefficients of linear correlation between average disease scores of the genotypes tested in the two inoculation series of each batch of genotypes were highly significant ($P < 0.001$) for batches 2, 3 and 4 (with 0.63, 0.51 and 0.45, respectively). The coefficient of correlation was lower for batch 1 ($r = 0.27$) but still significant at $P = 0.03$ (Table 2).

The ANOVAs for the three control clones tested in each of the two inoculation series in each of the batches of farm accessions showed highly significant effects (at $P < 0.0001$) for the genotypes (control clones), for the inoculation series and for the interaction between clones and inoculation series. The effect of the inoculation series (within batches) was also significant ($P = 0.03$), but not the effects of the inoculation trays (within inoculation series, $P = 0.38$) and of the interaction between genotypes and trays ($P = 0.61$). The interaction between inoculation series and genotypes was also not significant ($P = 0.16$).

The raw data were then corrected for by the effect of inoculation series, which made it possible to carry out a combined one-way ANOVA based on eight scores for each farm accession (average scores for each of the four inoculation trays in the two inoculation series). The analysis of the corrected data indicated a highly significant genotype effect at $P < 0.0001$ (Table 3). The average corrected disease scores for the 226 farm accessions varied between 1.44 and 3.33 (Table 4). The distribution was highly skewed towards the lower scores (Fig. 2). The coefficient of variation of the averages scores was 23%.

As expected, the scores of the resistant (SCA6 and PA150) and susceptible (NA79) control clones varied between 1.56, 1.79 and 4.10, respectively, while the variation of the averages for each of these clones obtained in the four batches was relatively small (Table 4). This indicated the relatively good stability of the results obtained for the control clones in the four inoculation batches. The most susceptible control clone was significantly more susceptible than any of the farm accessions.

The average corrected scores for three control hybrid genotypes varied between 2.59 (T79/501 × IFC5) and 3.32

Table 3
Analysis of variance (ANOVA) for the disease scores in the leaf disc test of the three control clones, tested in each of the two inoculation series for the four batches of farm accessions (A), and a combined ANOVA for the scores of 226 farm accessions and control cultivars, after correction for the effect of inoculation series (B)

Source of variance	DF	MS	F	P
(A)				
(a) ANOVA of the control cultivars (clones)				
Genotypes (control clones)	2	63.64	680.53	<.0001
Batches	3	1.52	16.27	<.0001
Inoculation series (within batches)	2	0.30	3.19	0.03
Trays (within inoculation series)	6	0.10	1.08	0.38
Genotypes × batches	6	0.07	0.75	0.61
Genotypes × inoculation series	8	1.27	13.53	<.0001
Inoculation trays × genotypes	6	0.14	1.57	0.16
CV (%)	12.7			
(b) ANOVA of the farm accessions and control hybrid cultivars				
Genotypes	228	1.67	6.04	<.0001
CV (%)	20.4			
(B)				
(a) ANOVA of the control cultivars (clones)				
Genotypes (control clones)	2	63.64	680.53	
Batches	3	1.52	16.27	<.0001
Inoculation series (within batches)	2	0.30	3.19	<.0001
Trays (within inoculation series)	6	0.10	1.08	0.38
Genotypes × batches	6	0.07	0.75	0.61
Genotypes × inoculation series	8	1.27	13.53	<.0001
CV (%)	12.7			
(b) ANOVA of the farm accessions and control hybrid cultivars				
Genotypes	228	1.67	6.04	<.0001
CV (%)	20.4			

Table 4
Variation for corrected disease scores for farm accessions and for the control cultivars (clones and hybrids) tested in four inoculation series

Genotypes tested	Mean score	Range	CV (%)
<i>Farm accessions</i>	2.58	1.44–3.33	23.34
<i>Control clones</i>			
SCA 6	1.56a*	1.26–1.87**	–
PA150	1.79ab	1.64–1.94	–
NA79	4.10c	3.70–4.45	–
<i>Control hybrid cultivars</i>			
T79/501 × IFC5	2.59b	–	–
NA32 × IFC5	2.84b	–	–
UPA409 × POR	3.32b	–	–

*Means with different letters are significantly different at $P = 0.05$ according to the SNK test.

**Variation for average scores of the control clones observed in the four inoculation batches.

(UPA409 × POR), and were all significantly different from the most susceptible (NA79) and most resistant control clone (SCA6).

Combined analyses for all regions showed that accessions collected from mother trees selected by the farmers

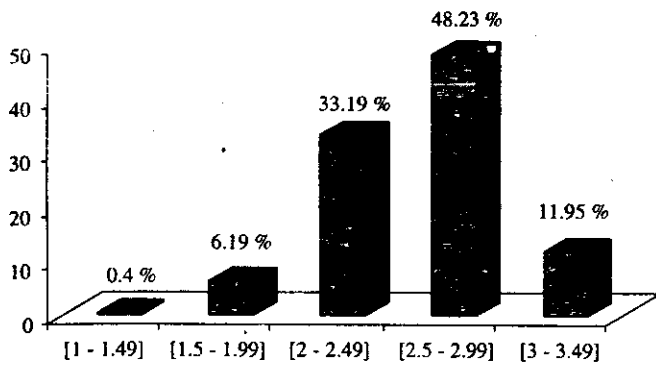


Fig. 2. Distribution of average scores of the 226 farm accessions evaluated in the leaf disc test for resistance to *P. palmivora*.

Table 5

Mean disease scores for farm accessions from regions with high and low Phytophthora pod rot (Ppr) disease pressure and according to three criteria for mother tree selection (high yield potential, low insect infestation and low Ppr incidence)

Selection criteria	Regions with high Ppr disease pressure (Abengourou, Aboisso)	Other regions (Divo, Gagnoa, Daloa and Soubre)	Average (all regions)
Yield potential	2.52b*	2.66b	2.59b
Low insect infestation	2.66c	2.55a	2.58b
Low Ppr incidence	2.28a	—	2.28a

*Means with different letters indicate significant differences between accessions selected according to different criteria within groups of regions at $P = 0.05$ according to the Bonferroni test.

for high yield potential and low insect infestation had higher average disease scores (2.59 and 2.58, respectively) than those selected for low Ppr incidence (2.28) (Table 5). In regions with a high pressure of Ppr progenies from trees selected for high yield potential also appeared to be more resistant than progenies from trees with low insect infestation. The opposite appeared to be the case in the other regions.

Twenty out of the 34 accessions with highest level of resistance (belonging to the 15% most resistant accessions) originated from the Abengourou and Aboisso regions (Table 1). This represents 20% and 58%, respectively, of the total number of farm accessions tested from these regions. For the other regions, the percentage of resistant accessions varied between 6% and 14%. With regard to the farmers' selection criterion, 12 out of the 19 mother trees (63.2%) selected for low Ppr incidence showed high levels of resistance, whereas the percentage of resistant accessions was much lower for the mother trees selected for yield (9.4%) or for low insect incidence (11.9%).

4. Discussion

The results in Table 1 show that the farmers in Côte d'Ivoire only recognised promising trees for low Ppr incidence in regions where the disease pressure was high. In the Abengourou region, the high disease pressure appeared to be related to the presence of *P. megakarya* (Koné, 1999). There is no indication that *P. megakarya* was also present in the Aboisso region at the time of the survey; therefore, the high disease pressure mentioned by the farmers in that region could rather be due to the high relative humidity in this region, favouring Ppr epidemics. Further surveys aiming at finding more resistant accessions in farmers' fields should best be directed to areas with high disease pressure due to *P. megakarya*.

The farmers more easily recognised promising trees for yield and low mirid infestation. This is not so surprising for yield, as this is the criterion of major interest to the farmers. However, the fact that farmers also easily recognise trees with low infestation of mirids on pods is interesting. Firstly, this may indicate that there is a genetic factor related to mirid infestation on pods that can possibly be explored in breeding. Secondly, whereas researchers tend to pay more attention to mirid damage that is expressed as die-back of young branches, farmers do not apparently easily recognise trees with low levels of damage in the canopy. Further research needs to be done to verify whether accessions selected for low mirid damage on pods may also be more resistant to mirid attack on the branches.

The linear coefficients of correlation between all genotypes tested in two different inoculation series were significant, but varied quite considerably (0.27–0.63). Furthermore, the effect of the interaction between the control genotypes and inoculation series (Table 3) was significant, suggesting that some degree of residual variation occurred in the experimental conditions between the replicate inoculations. This might possibly be ascribed to slight variations in leaf age or light intensity (Tahi et al., 2006, 2007). However, the effect of the genotypes (farm accessions), based on data corrected for the effect of the inoculation series, was highly significant (Table 3B). Furthermore, the reaction of the control clones and hybrids tested in all inoculation series was stable (Table 4) and well related to their known level of field resistance (Clement et al., 1999) and to earlier leaf disc test results (Tahi et al., 2000; Lachenaud et al., 2001). This suggests that the variation in resistance of the farm accessions (Fig. 2) can be successfully exploited to obtain cultivars with increased field resistance to Ppr.

The average disease score in the leaf disc test of farm accessions selected for low Ppr incidence was 0.3 points lower than that of the accessions selected for yield or for low mirid infestation (Table 5). Furthermore, the percentage of accessions classified as more resistant in the leaf disc test was much higher (63%) for accessions derived from mother trees selected for low Ppr incidence than of those

selected for other criteria (9–12%) (Table 1). These results appear to confirm that the trees recognised by the farmers as presenting lower Ppr incidence have a higher level of genetic resistance to Ppr infection. This is not self-evident, as low infection in the field may also be related to escape mechanisms (Cilas and Despréaux, 2004). Our results are in agreement with recent results obtained from a similar farm participatory selection programme in Cameroon (Efombagn et al., in press).

In relation to the control cultivars, most of the farm accessions appeared to be moderately resistant, moderately susceptible or susceptible to Ppr in the leaf disc test, with a majority of disease scores between 2.0 and 3.5. No farm accession was as susceptible, or more susceptible, than the most susceptible control clone (NA79). On the other hand, approximately 6.5% of the farm accessions (15 out of 226) had average scores below 2 and two accessions had scores even lower than that of the most resistant control clone (SCA6). Considering that the farm accessions were obtained from open pollinated pods, this means that further progress can be expected if the variation within the farm accessions is exploited. This could be done by testing the Ppr resistance of individual trees of the 10–15% most resistant accessions, which were planted at the CNRA research station in Divo in 2003.

A study is currently under way by the first author on the genetic diversity of the same farm accessions studied in this publication, by using microsatellite markers and morphological traits (Pokou et al., 2005). Comparison of the genetic variation and of the origin of the most resistant accessions, together with the phenotypic evaluation of the most resistant farm accessions, would guide the further use of these accessions in the CNRA breeding programme. For example, promising homozygous accessions could be used as parents to create new hybrid cultivars, and resistant productive accessions of Lower or Upper Amazon origin could be introduced in the third cycle of the recurrent selection programme that has been carried out by the CNRA from 1990 (Lachenaud et al., 2001).

5. Conclusion

The results of this study showed the usefulness of farmers' participation in the identification of trees resistant to Ppr. Indeed, without farmers' contributions, the percentage of resistance accessions is about 9–12%, whereas 63% of trees selected by farmers for low Ppr incidence have been confirmed as such by the leaf disc test. Although the study used a *P. palmivora* isolate, the identified correlation with resistance to *P. megakarya* (Nyassé et al., 1995; Paulin et al., 2005) suggests that the results obtained can be successfully exploited to also select more resistant cultivars to the more aggressive *P. megakarya* species, which is threatening to spread to the major cocoa belt in Côte d'Ivoire.

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