

IRAD Kumba/Barombi-kang Station, Cameroon

Effect of Fruiting Traits on the Field Resistance of Cocoa (*Theobroma cacao* L.) Clones to *Phytophthora megakarya*

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Abstract

The effects of some traits of field resistance (precocity and duration of the fruiting cycle, age of diseased fruit and vertical pod distribution on the tree) to *Phytophthora megakarya* of four known cocoa clones were studied in an on-station clonal plot planted in 1982 in the south-west of Cameroon. Weekly observations of fruit set and development, black pod and rainfall were carried out during three growing seasons (1999, 2000 and 2001). The study confirmed the previous field and laboratory assessments of resistance of these clones based on the mean percentages of rotten pods obtained annually. The present study has permitted the identification of fruit aged 2–3 months as the highly susceptible stage of development in the most susceptible clone. In addition, precocity and pod cycle duration varied significantly among the clones. The earlier the pod cycle began, the more susceptible was the clone: the most resistant clone started flowering 1 month after the most susceptible clone and therefore escaped the peak of disease severity. Rainfall intensity greatly modified the incidence of the disease in 2001, with high yield losses occurring in all four clones (70–93%), but their ranking remained stable over the 3 years. The spatial distribution of pods on the trees showed that pods on the trunk were more likely to become diseased than those on the branches, but its effect as a clone resistance component is variable among the four clones; the resistant clone producing more pods on the trunk and the susceptible clone more in the canopy.

Introduction

Cocoa production in Cameroon has remained stable over several decades (approximately 120 000 tons/year). This stability is due to several factors, the most important being black pod disease, due to *Phytophthora*

megakarya, which causes over 50% losses in central Africa. In Cameroon, losses can reach 100% if no control measures are taken (Despréaux et al., 1988).

Chemical control using copper-based contact or systemic fungicides remains expensive, restrictive and polluting. Selection of less susceptible planting material began in 1957 in Cameroon using local and introduced Trinitario clones (SNK and ICS, respectively). Different crosses between these materials, and slightly later with some Upper Amazonian clones introduced from Ghana, were carried out. Inoculation tests to evaluate resistance were carried out on pods (Blaha and Lotodé, 1976), but they involved a long selection cycle. An early screening test (Nyassé et al., 1995) using inoculations on leaves, gave significant correlations with resistance levels in the field (Nyassé, 1997; Tahi et al., 2000).

Research in the 1970s of cocoa collections in Cameroon revealed the existence of different levels of partial resistance to black pod based on polygenic systems (Partiot, 1975; Blaha and Lotodé, 1977). Partial resistance is an important factor in reducing severity by limiting the production of secondary inoculum (Van der Plank, 1963).

The influence of host conditions on the outcome of resistance is also a very important factor in disease development. Studies on cocoa tissue susceptibility have shown that the physiological stage of the fruit has an effect on the success of infection (Blaha and Lotodé, 1976).

As a component of field resistance to the disease, the duration of pod ripening may also be important in disease expression in the field, since the time pods are exposed to the pathogen is variable (Berry and Cilas, 1994a).

The field incidence of the disease is influenced by environmental factors. Rainfall provides favourable conditions for successful infection by the pathogen

(high humidity and low temperature). It is reported to increase field attacks in farmers' plots in different cocoa growing areas of Cameroon (Ndoumbè, 2002). Environmental and genetic correlations were calculated between the level of black pod and potential yield (total number of cherelles and pods produced) in an on-station diallel trial. The environmental correlation was positive, which showed that the more pods a tree bears, the more susceptible it is (Berry and Cilas, 1994b). In terms of disease propagation, rain splash (primary inoculum) has been shown to be responsible for infection on pods that grow near the soil surface (Meideros, 1976). Trajectory splash was found to disperse the spores up to a distance of 1.5–2 m, whereas wind-blown droplets could disperse the spores up to 12 m, but at lower frequencies (Gregory and Maddison, 1981).

The purpose of this study was to explore the existence of any genetic variability among cocoa clones in terms of starting date and duration of pod ripening (fruiting cycle), as components of field resistance to the disease (escape mechanisms). Moreover, the study also assessed differences within the following field resistance traits: susceptibility of pods related to their age, pod infections preferably at specific stages of their development; and spatial pod distribution on the tree.

Materials and Methods

Experimental site

The experiment was conducted on-station in a cocoa clonal plot (0.8 ha) at the Kumba/Barombi-kang Research Station belonging to the Institute of Agricultural Research for Development (IRAD) in the south-west region of Cameroon. The plot was established in 1982. Cocoa trees were planted in a randomly distributed design at 3 × 3 m spacing without shade trees, and had uniform and optimal cover (approximately 50% of the solar radiation pass through the canopy). No fertilizers were applied. Regular pruning was performed on the exceeding plagiotropic and orthotropic branches, along with the removal of parasitic epiphytes (*Lauranthus* spp.) and chupons. The four clones selected for this study were morpho-geographically distinct and grouped as follows:

- 1 Two local Trinitario selections (SNK10 and SNK413) and one Trinitario clone (ICS84) selected in Trinidad.
- 2 One upper Amazonian (UPA134) introduced from Ghana (West African Cocoa Research Institute, WACRI).

The clones were selected for their variable level of resistance to black pod rot disease in the field (Blaha and Lotodé, 1976; Despréaux et al., 1989; Berry and Cilas, 1994a): SNK10 (susceptible), ICS84 (moderately susceptible), SNK413 (moderately resistant) and UPA134 (resistant).

The plantation was chemically treated three times a year for weed control with Glyphosate (360 g/l) and

Paraquat (200 g/l) and fortnightly with Endosulfan (350 g/l) for mirid control. Ant nests were also treated locally with Chlorpyrifos (600 g/l), when they were considered to be damaging to the trees. Trees were replaced if they stopped producing or died (replacement rate < 10%).

Observations and disease assessment

A maximum of 50 fruit per tree was observed on 20 trees per clone during three growing seasons from 1999 to 2001. Each observed cherelle was marked after fruit set at the beginning of the flowering season (April). Observations of the following parameters were carried out for each pod on a weekly basis:

- 1 growing stage (1 = cherelle, 2 = young pod, 3 = green pod and 4 = ripe pod);
- 2 disease stage (0 = healthy, 1 = diseased, 2 = wilted and 3 = feeding damage).

The diseased, wilted, damaged (feeding) and ripened pods were weekly removed and rainfall data were also collected daily at the station.

The pod losses of a clone due to black pod were estimated in relation to potential production. The incidence of rotten pods in the study is expressed as the ratio between the rotten pods recorded and the total number of pods observed during the season, except wilted cherelles and pods with feeding damage.

The data recorded per week were used to calculate the sum of newly rotten pods per month (Figs 1–3). The duration of the fruiting cycle was estimated for a period of 3 years (1999, 2000 and 2001). The fruiting cycle started after fruit set, when cherelles were approximately 14 days old and had a maximum length of 20 mm.

The effect of spatial pod distribution on the incidence of the disease was also assessed. The number of pods on the trunk and on the branches was determined in each tree of a clone and expressed as percentage of the total production. In addition, the incidence (%) of rotten pods on the trunk and on the branches was determined for each clone.

Statistical analysis

The age of infected pods and the duration of the pod cycle of different clones were compared by ANOVA (SAS Institute Inc., 2001). We used a nested type ANOVA:

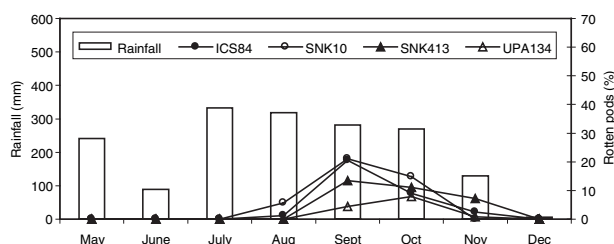


Fig. 1 Disease progress curve and monthly rainfall in 1999

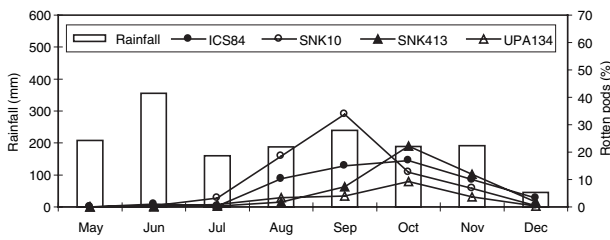


Fig. 2 Disease progress curve and monthly rainfall in 2000

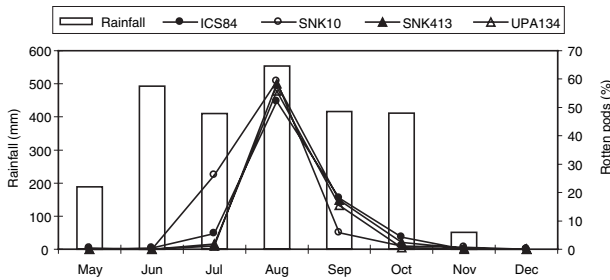


Fig. 3 Disease progress curve and monthly rainfall in 2001

$$a_{ijk} = \mu + c_i + t_{ij}(c_i) + e_{ijk}$$

μ , mean; c_i , effect of clones; $t_{ij}(c_i)$, effect of the trees within a clone; e_{ijk} , residual error.

The mean values for incidence of rotten pods, fruit age at disease appearance, fruiting cycle length and the total number of days required for the four clones to produce half their yield were separated for the four clones using the Newman and Keuls test (Cochran and Cox, 1957).

Results

Age of diseased fruit

Identification of the susceptible developmental stage was expressed as the mean age of rotten fruit for the four clones, and was estimated over the 3 years of the study. After fruit set, the clones differed significantly in the stage at which they were sensitive to the disease ($P < 0.0001$). The pods of clone SNK10 were the most susceptible at an earlier stage (around 71 days in 1999 as opposed to 90 days in SNK13) (Table 1). Susceptibility was also affected in the different years ($P < 0.0001$). Thus, when relatively high disease pressure followed high rainfall intensity (as in 2001), the disease began earlier and the exposure time was shortened. It should also be noted that observations in 1999 began 1 month after the start of pollination (June), which explains why symptoms on all the clones were seen at a younger pod stage (Table 1). The trees of the same clone also performed variably each year.

Duration of the fruiting cycle

From 1999 to 2001, the clones were ranked in the same order (Table 2), but the mean duration was relatively short due to an absence of the phase between pollination and fruit set (10–14 days) in the field observations. However, the production cycle of the individual trees

Table 1 Pod age at the occurrence of first symptoms for the four clones

Year	Source	F-value	CV (%)	Mean pod age (days)
1999	Clone	8.22**	20.03	S – SNK10: 70.8c
	Trees (clones)	2.47*		MS – ICS84: 76.92bc MR – SNK413: 89.40a R – UPA134: 81.33ab
2000	Clone	15.20**	20.47	S – SNK10: 97.96b
	Trees (clones)	2.43**		MS – ICS84: 111.60a MR – SNK413: 115.83a R – UPA134: 111.44a
2001	Clone	27.32**	17.02	S – SNK10: 76.24b
	Trees (clones)	3.10**		MS – ICS84: 91.11a MR – SNK413: 91.41a R – UPA134: 90.41a
Year		16.36**	–	–

Level of significance: * $P < 0.001$, ** $P < 0.0001$. CV, coefficient of variation; S, susceptible; MS, moderately susceptible; MR, moderately resistant; R, resistant. a,ab,b,bc,c : statistical groups.

Table 2 Mean duration and variation of the fruiting cycle for the four clones in 1999, 2000 and 2001

Year	Source	F-value	CV (%)	Mean length of pod cycle (days)
1999	Clone	19.26**	5.92	S – SNK10: 140.23b
	Trees (clones)	1.78*		MS – ICS84: 151.07a MR – SNK413: 155.04a R – UPA134: 138.83b
2000	Clone	85.28**	4.79	S – SNK10: 145.11c
	Trees (clones)	2.19**		MS – ICS84: 156.74a MR – SNK413: 148.49b R – UPA134: 147.2b
2001	Clone	10.28**	13.51	S – SNK10: 131.16b
	Trees (clones)	8.92**		MS – ICS84: 160.26a MR – SNK413: 135.26a R – UPA134: 142.52a
Year		40.52**	–	–

Level of significance: * $P < 0.05$, ** $P < 0.0001$. CV, coefficient of variation; S, susceptible; MS, moderately susceptible; MR, moderately resistant; R, resistant. a,b,c : statistical groups.

within a clone varied because of the length of the pollination period, which lasted 3 months (April–June). Consequently, the fruiting cycle of the trees per clone differed significantly ($0.03 < P < 0.0001$). The length of the cycle also varied from 1 year to another ($P < 0.0001$), but the levels of variation were limited ($5.92 < CV < 13.51$).

Disease progression analysis

The date first symptoms were observed was linked to the level of field resistance over the 3 years (Figs 1–3). The pods of the susceptible clone (SNK10) exhibited symptoms earlier (approximately 1 month before) compared with the resistant clone (UPA134). The other two clones were intermediate: whenever the disease on these clones was observed at almost the same period as on the most susceptible clone, it progressed relatively slower.

In addition, the earlier the disease occurred, the younger was the susceptible fruit stage and the earlier the fruiting cycle began. The production of clone SNK10 was observed beforehand, and compared with the others (Table 1).

Field-resistant (UPA134) and moderately resistant (SNK413) clones continued to flower during and after the disease peak and once disease pressure declined, most of the pods started ripening. In 1999, UPA134 escaped disease pressure by deferring the start of its flowering period and ripening occurred earlier while SNK413 had a longer maturation time and therefore was exposed to the disease for longer and its rotten pod rate rose at this stage.

Disease progress in the third year was greatly affected by rainfall intensity (Fig. 3). Rainfall levels obtained for the period of field data collection in the first year (1.668 mm) and the second year (1.577 mm) increased considerably in the third year (2.524 mm). Therefore, levels of disease were higher and similar in all clones in 2001.

The four genotypes were ranked according to the incidence of the rotten pods (%) registered for the 3 years (Table 3). As an indicator of the resistance component (disease escape), an assessment was also made according to the number of days (between the observation of the first fruit set and the ripening phase) required for one clone to produce half its total harvest a year (Table 3). UPA134, which had the smallest number of rotten pods over the 3 years of the study, took 151 days to achieve half its production, compared with 120 days of the susceptible clone SNK10. However, the moderately susceptible (ICS84)

and the moderately resistant (SNK413) were not very different from UPA134.

Effect of spatial pod distribution in the trees

The results of an analysis of pod rot incidence (%) on the different parts of the tree (trunk and branches) indicated that losses were higher on the trunk although in 2001 this trend was less marked (Table 4). Nevertheless, the rankings of the clones were the same and remained stable over the 3 years, based on percentage of pod losses on these two main parts of the trees. The lower section of a tree was relatively more susceptible to the inoculum of *P. megakarya* (Table 4). In contrast, pod production on the branches was relatively high, except for UPA134 in 2000 and 2001.

Discussion

Generally, development of a disease depends of three major factors: the host, the pathogen and the environment. In the case of *Phytophthora* pod rot in this study, the influence of each of these factors and their relative importance for disease development were sometimes unclear. Earlier studies have shown that conditions, which favour pod production, also coincide with conditions favourable to disease incidence (Meideros, 1976; Holderness, 1992). Many studies have been made to correlate the incidence of black pod disease with environmental factors. Such examples in West Africa include studies on black pod caused by *P. palmivora* in relation to rainfall, temperature and humidity (Thorold, 1967; Wood, 1974). Conflicting results have been obtained from the different cocoa regions, probably reflecting differences in weather patterns if not climate, and, possibly, variations within the pathogen (Maddison and Griffin, 1977).

In the present study, the different clones started their fruiting cycles at different times. The clone displaying the greatest precocity at the production phase (SNK10) lost more pods than the others due to the disease. In addition, its pods were infected at an earlier stage (2–3 months), when compared with the other clones. In contrast, for the trait 'pod age at disease appearance', studies to determine the relationship between pod age and susceptibility to witches' broom disease in Brazilian Amazon region have shown that differences were not detectable on inoculated pods older than 15 weeks (3–4 months) (Andebhran, 1984).

Table 3

Percentage of rotten pods for the four clones and estimation of the time taken to reach half the production in 1999, 2000 and 2001

Clone	Black pod (%)			Number of days needed for 50% of production (ripening)			Mean
	1999	2000	2001	1999	2000	2001	
SNK10	52.70a	69.14a	93.36a	85	185	91	120.33b
ICS84	26.33b	53.49b	80.20ab	126	212	111	149.66a
SNK413	25.06b	45.42c	79.56ab	99	212	111	140.66a
UPA134	13.15c	19.49d	79.69c	134	213	105	150.66a

a,b,ab,c,d: statistical groups.

Clone	Year					
	1999		2000		2001	
	Branches	Trunk	Branches	Trunk	Branches	Trunk
SNK10	52.7 ^a (72.5) ^b	71.4 (27.5)	58.8 (60.4)	74.9 (39.6)	94.4 (66.9)	91.3 (33.1)
ICS84	22.6 (66.7)	29.7 (33.3)	41.8 (61.0)	64.9 (39.0)	73.1 (55.7)	85.3 (42.3)
SNK413	24.8 (75.6)	25.6 (24.4)	32.9 (81.3)	61.8 (18.7)	78.2 (88.5)	82.1 (11.5)
UPA134	13.0 (57.5)	26.5 (42.5)	7.7 (36.7)	26.3 (63.3)	70.3 (39.7)	77.1 (60.3)

^aPercentage of rotten pods in the total amount of pods produced on the branches and trunk separately.

^bRelative frequencies (%) of the pods produced by a clone in the same year on the branches and trunk.

Table 4

Percentage of rotten pods and distribution of pod on the trunk and branches of the four clones in 3 years

Table 5
Mean duration (in days) of the fruiting cycle for the four clones in 1996 and 1997 (D. Bieysse, unpublished data)

Clone	1996			1997		
	Number of pods	Mean duration	SE	Number of pods	Mean duration	SE
UPA134	41	146.5	6.3	53	152.1	7.92
SNK10	36	159.8	9.9	43	158.3	8.87
SNK413	35	161.9	7.5	53	166.9	10.13
ICS84	65	165.0	9.8	43	172.0	7.04

In 1996 and 1997, the fruiting cycle of the same clones in the same plot was determined by taking into account the time between pollination and fruit set for the four genotypes (D. Bieysse, unpublished data). UPA134 had the shortest cycle with 146.5 and 152.1 days, respectively, and ICS84 had the longest with 165 and 172 days (Table 5). The difference between the two clones was 19 and 20 days, respectively. In 1997, the mean duration of the cycle differed slightly, with an increase of 6–7 days, except for clone SNK10.

In our study, the duration of the pod cycle within a year enabled us to understand how the four clones reacted to the pathogen as influenced by climatic conditions (mostly rainfall) in the area where they were planted: the beginning of the flowering period differed from one cocoa genotype to another, the fruit set and harvest periods were staggered throughout the cycle. The later the clone flowered, the slower the disease progressed (and the earlier was the harvest phase of resistant clone UPA134). The genetic effect of the cocoa trees on disease development was demonstrated by the substantial difference in disease incidence between clones SNK10 and UPA134. In terms of the cumulated number of rotten pods, UPA134 registered the lowest value over the 3 years of observations and also revealed an interesting delay to infection when compared with the other clones. This resistance ability was reported previously by Berry and Cilas (1994a) and was related to the short fruiting cycle, reducing the number of susceptible pods at the time of high disease pressure. Laboratory and field inoculations classified UPA134 as susceptible (Blaha and Lotodé, 1977), confirming that the resistance in this case was more due to the regulation of the flowering process than pod resistance. This clone is also susceptible under conditions of high rainfall. Studies on escape mechanisms of diseases caused by *Moniliophthora roreri* and *Crinepellis pernicioso* were carried out in the main cocoa-growing region of Ecuador (Maddison et al., 1995). For both diseases, the protracted dry season gives opportunity for pods to 'escape' disease by forming and maturing under much-reduced risk of attack. In addition, experiments have been established in Brazil to determine the infection cycle of *C. pernicioso* in relation to climatic factors (Evans and Bastos, 1979). Results have indicated that most

basidiocarps are produced during the latter part of the rainy season and correspondingly the highest disease incidence occurs early in the dry season.

The susceptibility of the clones was correlated to their fruiting precocity. The fungal cycle has been previously linked to the pod cycle (Muller, 1974). Susceptible clone (SNK10) started fruiting earlier (1 month before the most resistant clone) and its maximum pod production coincided with the phase most favourable to black pod incidence. At this critical point, the fruit were not fully developed which increased their susceptibility, and the pods of SNK10 were infected at a younger stage.

In morphogenetic terms, the duration of the fruiting cycle could contribute to the high susceptibility of most Trinitario clones in the field in Cameroon (Berry and Cilas, 1994b). Typical Trinitario clones, such as ICS, take 7 months to ripen whereas other types, such as Upper Amazon Forastero trees (e.g. UPA134), take only 4 months to ripen and are therefore less exposed to disease.

The inoculum of *P. megakarya* inside cocoa plantations is reported to survive in the soil and cocoa roots (Opoku, 1994) and in shade tree roots (Opoku et al., 2002). As the nearest part to the upper soil layer, the continuous splashing of rainfall droplets from the soil is a major source of inoculum for pods on the trunk. In addition, downward movement of water during rainfall increases the probability of inoculum being swept down the trunk leading to pod infection. Although this movement is more significant for *P. palmivora* as the primary source of inoculum, for *P. megakarya* in the soil.

In this study, vertical disease progression suggested that the lower section of a tree was relatively more susceptible to the inoculum of *P. megakarya*. Several factors could contribute to this including the main source of inoculum being in the soil and frequently, the shade density resulting from the canopy architecture is greater at the lower level of the tree and therefore favours the infection by the fungus.

As could be expected in areas with a greater incidence of *P. megakarya*, trees with a propensity for pod production on branches rather than on the trunk may exhibit greater field resistance due to the longer distance to the primary inoculum source in the soil. It tallies with results obtained from the basal pod suppression experiment carried out in Nigeria (Gregory and Maddison, 1981). However, pod production of the most resistant clone (UPA134) was lower in the branches compared with other clones in 2000 and 2001.

The role of rainfall in the host–pathogen interaction is critical. High rainfall is followed by high incidence of black pod, even in clones considered to have some level of field resistance. Whilst fruiting traits are certainly important in 'normal years', they are of secondary importance in wet years.

Cultural practices can affect the disease cycle for many pathogens. Weekly removal of diseased pods

(as performed here) interrupted the fungal cycle, and eventually lowered disease pressure, by reducing the secondary inoculum source inside the plantation (Ndoumbè, 2002). Yet studies in Ghana demonstrated that cultural control has little or no effect on the incidence of black pod due to *P. megakarya*, and even chemical control was ineffective (Opoku et al., 2000). In addition, the reaction of clones with different levels of resistance to variation in disease pressure has yet to be clearly elucidated although *P. megakarya* is known to be more aggressive in the field, and thus the effects of this variation on disease expression might be limited.

In conclusion, genetic variability exists in field resistance traits of cocoa clones. These traits, refer (in part) to disease escape during the favourable period of the fungal activity, and are linked to starting date and duration of the fruiting cycle, pod age and distribution of diseased fruit on cocoa trees. The earlier the start of the pod cycle of a clone, the higher is likelihood of its susceptibility to black pod in agro-ecological conditions prevailing at a given cocoa growing area. The study also identified pods aged 2–3 months as the susceptible stage of development, especially so in susceptible clones. For the spatial pod distribution, the ability of a clone to produce more pods in the canopy might not always raise its field resistance since other clones with propensity to produce on the trunk could record low disease incidence. This might therefore suggest that this resistance is not based on spatial distribution. Level of rainfall is a crucial factor in the field incidence of disease. Thus, it affects the field resistance of clones.

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