3

Varietal Resistance

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The selection of plant material resistant to the various diseases that perennial tropical tree crops are confronted with is based on prior observations of the behaviour of this plant material under conditions of natural contamination. The differences in susceptibility among varieties or cultivars subjected to the same pathogen pressure help to establish the ground for this control strategy and at the same time conserve the agronomic qualities of the concerned crop.

Depending on the cases studied in this chapter, it could be a specific resistance system of a qualitative nature—where the reactions of the plant follow the 'all or nothing' rule—or a general or partial resistance system where the degree of susceptibility can be measured quantitatively. Ultimately it is varietal resistance which is the most satisfying procedure in a large number of cases. Its objective is to gradually obtain increasingly higher resistance levels so that the success of the crop depends less on other control methods, if at all they exist.

In most of the studies presented in this chapter, resistant plant material was selected by reproducing disease symptoms at an early stage in the vegetative growth on the seedling or on vulnerable parts in nature. Depending on the case, the symptoms were artificially induced by direct inoculation of the causal organism or by exposing the host to insect vectors (for example, swollen shoot of cocoa, coconut foliar decay, blast disease of oil palm). The pathogen can also be inoculated into plant parts that are easily accessible such as the leaf, which is not necessarily the targeted part. The reaction obtained should then be correlated with that of affected parts under natural conditions (brown pod rot of cocoa).

Furthermore, the search for resistant rootstocks is an interesting way, or even the only way, for crops which are amenable to it and obviously depends on the origin of the disease. Concrete results have been obtained with coffee and citrus plants and probably for some rot diseases of hevea.

COCOA

Swollen shoot

The swollen shoot virus (see the chapter on Insect vectors) can be inoculated into cocoa beans, thanks to the vectoring of scales (Legg and Lockwood, 1977). This test, which is used as an early test for resistance to the virus, initially gave extremely varying results. Improved knowledge on host-parasite relationships helped to demonstrate on the one hand the importance of the number of bugs and species and on the other that of the virus isolate and the efficiency of its transmission. Thus in Togo a study conducted by inoculating the larvae of *Planococcus citri* with the Agou isolate showed that the infection of a susceptible material (IFC5 × IFC5) was 28% with 3 scales per cocoa bean, 77% with 6 scales and 82% with 12 bugs. In the case of resistant material (T60/887 × IMC67), the infection rate varied from 4% with 3 scales per bean to 10% with 6 scales and 21% with 12 bugs (Dufour *et al.*, 1993).

Hence experiments were carried out in Togo with bugs of the species *Planococcus citri* at the rate of 6 larvae per bean on 13 hybrids popularised in the country (Paulin *et al.*, 1993). These hybrids were studied and compared with susceptible (IFC5 × IFC5) and more resistant (IMC67 × T60/887) controls. They showed varying degrees of infection, ranging from 3 to 65%, with an average of 33%. All the popularised hybrids showed lower susceptibility than the susceptible control (74%) and 2 hybrids showed lower susceptibility than the resistant control (12%). On the whole, the least susceptible hybrids came from Amazon Tall crosses. Moreover, a test-cross using a susceptible parent (IFC5) and a resistant parent (T60/887) showed transmission of susceptibility of the dominant type. Several plots situated in the zone infected by the virus and where the symptoms were detected were replanted with hybrids whose high resistance level had been demonstrated by the cocoa bean inoculation method. Field observations have confirmed the high resistance level of these selections (Paulin *et al.*, 1993).

Witches' broom disease

Selection of cocoa clones resistant to witches' broom disease caused by *Crinipellis perniciosa* is the only effective method for controlling this malady.

In Trinidad and Tobago the CRU (Cocoa Research Unit, University of West Indies) and CIRAD are jointly conducting researches to evaluate the resistance of nearly 2500 cocoa clones in the international collection of the IGC-T (International Germplasm Collection of Trinidad) to witches' broom disease. However, this evaluation can be made only for the B population of the pathogen, the only one present in the island of Trinidad. The clones thus selected should also be tested for their resistance to population A, which is the most aggressive; the second screening has to be developed in a country in South America where the disease is rampant, or at CIRAD in France.

Field observations on the 2500 clones helped to make a preliminary selection of plant material which did not show the infection in the field. In order to confirm this level of resistance, early evaluation tests were developed in the plant pathology laboratory of CRU. The leaf test has helped to evaluate more than 150 clones and to select a certain number of them showing high vegetative resistance to witches' broom disease such as TSH 919, Sca 6, P18 A, IMC 6, IMC 57 and IMC 67.

Furthermore, the selection of Gu clones obtained by CIRAD from a survey in French Guyana confirmed the interest of this wild material.

Within the framework of a preselection programme, the selected clones could be crossed among themselves with a view to cumulating the resistance genes. The descendants are being evaluated by the leaf test.

This test is also used to evaluate the vegetative resistance of seedlings obtained from the two crosses: IMC 57 (R) × Catongo (S) and Sca 6 (R) × Catongo (S). These progenies have also been biochemically mapped (by Rflp and Aflp) by CIRAD at CRU. The aim of this study is to further our knowledge of the genetic bases of resistance to witches' broom disease through QTL (quantitative trait loci) research.

An early test on cocoa beans has also enabled the selection of progeny showing good resistance: 92 from crosses between Thy and Ics clones and 125 from self-crossing of Ics clones.

Brown pod rot of cocoa (black pod rot)

Observations on naturally infested cocoa plants have enabled a preliminary classification of hybrid clones and families in terms of their behaviour towards brown pod rot of cocoa. The CIRAD selectors of cocoa lines have therefore veered, since the early 60s, towards direct experimentation on the fruits, in order to have a better understanding of the components of resistance and the hereditary mechanisms governing them, knowing that brown rot is a group of distinct diseases given the number of *Phytophthora* species involved and the nature of the reactions they induce on the cocoa plant.

The first breeding programme for tolerance was conducted by Besse (1964, 1969) in the Ivory Coast. He took into consideration the variations in the percentage of rot observed among clones and hybrid families the field, in collections and in comparative tests. Four years of observations, during which the fruits were harvested every 10 to 15 days, showed the susceptibility of Amelonado to be 30%, a susceptibility which is less thanks to the Amazon Tall (AT) in Amelonado × AT crosses (20 to 25%) and a more pronounced resistance in Trinitario × AT hybrids (less than 20%) and T38 × AT 605 hybrids (between 4 and 9%) hybrids. However, the heterogeneous nature of the distribution of the infection linked to climatic and environmental variations and to factors such as the density of the plantation and distribution of the production in time and space, led to the launching of a major programme of controlled evaluation of resistance in the early 60s. Various kinds of tests were performed on a pathosystem with *P. palmivora* in the Ivory Coast and later on another pathosystem with *P. megakarya* in Cameroon (Tarjot, 1964; Marticou and Muller, 1964; Lotodé and Muller, 1974).

Tests on pods

Artificial inoculations with *Phytophthora* spp. were first performed in the Ivory Coast on detached injured or uninjured pods in the laboratory and then on the still attached pods in plantations (Tarjot, 1965, 1967, 1969). The method on attached pods was taken up in Cameroon and strictly standardised. About a hundred clones from local selections and around 20 from introductions were thus classified based on two susceptibility criteria: resistance to entry through the epidermis, which expresses the percentage of successful infections and the rate of progress of the parasite in the inner cortical tissues (Blaha and Lotodé, 1976).

The comparison of 28 clones tested in two different ecologies in Cameroon showed that under conditions favourable for the disease, the percentage of successful infections is not sufficient to evaluate varietal resistance. On the other hand, the speed of colonisation of the cortex in the clones in the two sites showed similar variations ($r = 0.65$), thus confirming the stability of the intrinsic clonal resistance in geographically distinct sites (Nyasse *et al.*, 1996).

Tests on other plant parts

The pod test considerably delays the selection of plant material because of the time lapse of 4 to 5 years before the plants begin to yield fruits. The necessity of an early and non-destructive test led to testing on leaves. The abundance and renewal of leaves and especially the anatomical similarity of their lower surface to the epidermal surface of pods facilitated the selection of this part (Blaha and Paris, 1987). A simple recording of the severity of necrosis (from 0 to 5) twice successively (on the fifth and seventh day after inoculation) also makes this leaf test, which has been standardised to discs 15 mm in diameter, much faster. Only the age of the leaf has an extremely important influence on the expression of susceptibility and should be taken into consideration for obtaining a satisfactory reproducibility (Nyasse *et al.*, 1995). Moreover, this leaf test enables experiments to be performed outside the production zones.

Correlation between resistance tests and field resistance

The leaf test reproduced categories of extreme reactions (i.e., very high susceptibility or very high resistance) when pods were artificially inoculated in Cameroon and Latin America (Table 1). The test also took into account the significant influence of the plant in accordance with the high intrafamilial variability in cocoa plants (Nyasse *et al.*, 1995; Nyasse, 1997).

Table 1. Classification of 13 cocoa clones of various origins after inoculating leaf discs with two *Phytophthora* species: *P. palmivora* and *P. megakarya* (degree of susceptibility of the reference clones of both species being known for the fruits).

Clone		Observation of symptoms*			
		P. palmivora		*P. megakarya*	
IMC47		0.35	a	0.17	a
SNK413	(R)	0.90	ab	0.28	a
T85/799		1.10	abc	1.10	b
CC231	(LR)	1.13	abc	1.52	b
GU333		1.27	bcd	0.85	b
SNK10	(S)	1.35	bcd	1.08	b
SPEC138/8		1.48	bcd	0.90	b
R13	(LR)	1.55	bcd	1.52	b
EBC/10/401		1.63	bcd	1.02	b
UF667	(S)	1.85	bcd	2.40	c
LCTEEN37		1.90	cd	2.20	c
VEN4/4		2.17	d	2.20	c
OC77	(LS)	3.25	d	2.50	c

* The scale of observation of symptoms is from 0 (symptomless) to 5 (true necrosis). Mean values within a *Phytophthora* species followed by the same letter are not very different from the Neuman and Keuls test with a 5% threshold.
The reaction of fruits to artificial inoculations is given in parentheses (R and LR for more or less resistant, S and LS for more or less susceptible).

The test on attached pods brought out the influence of the plant on the clone and showed more clearly the influence of environmental factors on pods of the same genotype. This phenomenon could be responsible for the discordance between the inoculation test on the fruit and the losses in the field (Nyasse *et al.*, 1996). The influence of the genotype nevertheless dominates over the influence of the plant as long as the cultivation or experimental conditions are sufficiently uniform and hence individual selection for resistance can be done by inoculating the pods or leaves.

Inheritance of intrinsic resistance and field resistance

A study of the transmission of intrinsic resistance was undertaken in Cameroon, thanks to the test on attached pods, on 56 hybrid families obtained from clones of known behaviour. By cumulating the data of five years, tree by tree, it was observed that on the one hand there was a strong intrafamilial disjunction on the fruit and on the other a statistically higher proportion of less susceptible individuals in R × R crosses than in S × S crosses.

Different kinds of crosses were made in the various zones affected by the disease in order to define the genetic effects of the two characters targeted for selection under natural conditions of infection viz., production and resistance to brown pod rot (Cilas *et al.*, 1996). It is a 6 × 6 diallele in Cameroon, a factorial plan between 16 female Amazon Talls (AT) and 4 male Amazon Dwarfs (AD) parents in the Ivory Coast and a triangular triallel among 12 parents in Togo. An analysis showed the strong influence of Gca (general combining ability) compared to Sca (specific combining ability), Gre (general reciprocal effect) and Sre (specific reciprocal effect). This analysis also showed that the characters are transferred mainly by additive gene action because of the influence of female parents, the main variation factors in the factorial programme in the Ivory Coast.

TOWARDS A STRATEGY FOR EXPLOITING THE EFFECTS OF THE INTERACTION BETWEEN GENOTYPES AND THE ENVIRONMENT

The resistance of some clones is constant, whether as a function of time in the same country or some other geographic location: Africa (Ivory Coast, Togo, Cameroon), America (Trinidad and Tobago, Brazil, Costa Rica) or the southern islands (Papua New Guinea). The polygene governance of resistance forms of the horizontal or partial type in cocoa plants should ensure this stability and durability of resistance to the disease. Besides, the obligate saprophytic phase in the life-cycle of *Phytophthora* spp. between two cocoa sites appears to be an additional guarantee for the perpetuity of this resistance in the host (Chevaugeon, 1973).

The absence of interactions between a range of clones and isolates of the same species in the case of *Phytophthora palmivora*, as with *P. megakarya* (Nyasse *et al.*, 1993), would moreover signify that a selection can be made irrespective of the isolate used (Nyasse *et al.*, 1996) and that the groups obtained in one country could be used in other countries (Cilas *et al.*, 1996).

The various crossing programmes have helped to obtain a selection index after estimating the desired genetic gains in each of the quantitative characters taken into consideration, i.e., the production and rate of rot (Cilas *et al.*, 1994). Genotypes (individual, family) are now used in breeding programmes either directly as elite hybrid clones after validation through confirmation tests or as new parents in backcrossing programmes with the aim of accumulating the alleles favourable for the desired characters (Clément *et al.*, 1996).

The leaf test is a tool that can be used on leaves of seedlings (uniform environment, orthrotropic vegetative axis) for the early selection of newly created progeny because of its reliability. Nevertheless direct access to the genome is still preferred and a selection aided by molecular markers closely linked to the genes controlling the targeted character(s) represents the best, the quickest and the surest screening method. Thus a map saturated with genetic links was established with the help of isoenzymes and molecular markers (Rapd, Rflp, Aflp and microsatellites). Aflp markers and microsatellites were used to establish the genotype of 144 individuals studied in the Ivory Coast. Characters resistant to *Phytophthora palmivora* were evaluated by means of the leaf test and through analysis of the losses in yield over several years. A few Qtl could be identified, thus opening the path for using these techniques to aid selection (N'Goran, 1994; N'Goran *et al.*, 1996; Lanaud *et al.*, 1997).

At present it is the phenotypic, genetic and environmental correlations between the potential production (total number of pods formed) and degree of rot in the three African countries compared, viz., Cameroon, Togo and Ivory Coast, which seem to provide the most interesting information on the interactions between the genotypes and environment and their effects (Cilas *et al.*, 1996). Phenotypic correlations are very different from one country to another, especially in Cameroon where the effect of Trinitario in crosses is distinguished from the effects of Amazon Tall × Amazon Dwarf crosses (Berry and Cilas, 1994). The variability of the pathogen should not be minimised either. Genetic correlations show that parents good for production are also good for resistance to brown rot, the families which are attacked the most bearing less pods because the infection can take place on the young fruits or flowers. Environmental correlations between the degree of rot and potential production are systematically positive, a fact attributed by authors to fruit-to-fruit infection, which increases with the number of fruits present and also to the increased proximity between the fruits which are more numerous and the infection sources (on the tree itself, on the bark and cushion flowers).

Breeding programmes through recurrent selection programmes using genetically distinct populations even end by cumulating the minor genes in new elite hybrid clones that are agronomically acceptable, particularly their resistance to pod rot (Paulin and Eskes, 1995). However, genetic control alone is not sufficient and should be associated with other measures, especially adapted cultural practices for managing a veritable integrated control programme.

Muller (1974) reported the existence of a kind of escape detected in some clones which have the peculiarity of out-of-season flowering in the most extreme cases. In many other cases flowering is simply delayed or highly staggered, enabling a certain number of pods to escape infection. This kind of escape may be counted among the numerous factors intervening in field resistance, which expresses the actual impact of the disease. Selection from this notion of escape, eventually supported by adapted cultural methods such as irrigation, should not be given up.

COFFEE

Orange rust

Because of the seriousness of orange rust of coffee caused by *Hemileia vastatrix*, as well as the financial and technical difficulties in initiating a chemical control programme, development of resistant varieties became a priority for a number of coffee-growing countries. Selection of coffee plants resistant to orange rust was carried out mostly with the species *C. arabica*, the main varieties cultivated in the world (Bourbon, Typica, Mundo Novo, Caturra) being very susceptible to the most common races of the pathogen. Many species belonging to the genus *Coffea* were used as sources for gene resistance.

Specific resistance factors in *C. arabica*

Resistance factors present in the species *C. arabica* were used for the first time in India, with the Kent variety and its derivatives such as the K7 selection which possesses the SH2 gene. However, the resistance was quickly overcome because of the appearance of new races (Muller, 1984). A similar situation was observed after the introduction of resistance factors in the Ethiopian coffee plants Geisha and Dilla and Alghe which contain the SH1 factor and later in the Agaro genotype possessing the SH4 factor. Similarly, in Brazil, resistance of the multiline Iarana variety, constituted by lines with gene combinations associating SH1, 2, 4 and 5, was quickly overcome by the appearance of complex races. The distribution of this variety was thus interrupted because most of the plants were found to be attacked.

Specific resistance factors in *C. liberica*

The SH3 resistance factor was identified in the species *C. liberica*. In the past, interspecific hybrids with *C. arabica* had been created and the progenies of these plants were then backcrossed with the Kent variety. Resistance of these selections, such as S795, was maintained in the field for nearly twenty years (Muller, 1984). Resistance of advanced selection S1934, distributed especially in Indonesia, no longer seems to be effective except in new cultivating zones. In Brazil, as well as in other regions of Latin America, the field resistance conferred by SH3 seems to be operational but in an experimental way, as a race capable of overcoming this resistance has been described (Eskes, 1989).

Specific resistance factors in *C. canephora*

The species *C. canephora* is the most important source of resistance up to now (resistance factors SH6 to SH9 and probably S10). It was used through natural (Timor hybrid) or artificial interspecific crosses with *C. arabica*. The Timor hybrid, discovered in the middle of the century in the island of the same name, has not been commercially exploited directly but at the CIFC (Centro de Investigação das Ferrugens do Cafeeiro) in Portugal, its descendants (CIFC 832/1 and CIFC 832/2 in particular), which are resistant to all the known races of the parasite, were crossed with different commercial varieties; crosses with the Caturra dwarf variety gave rise to the Catimors.

In Brazil, a breeding programme of artificial hybridisation between *C. arabica* and *C. canephora* with repeated backcrossings with *C. arabica*, led to the distribution of the Icatu variety from 1980. In Colombia, it was through hybridisations between the Caturra variety and the CIFC.1343 progeny of the Timor hybrid that the Columbia variety was created. It is a composite variety containing different advanced selections of similar agronomic values but with different resistance factors. A similar selection programme resulted in the creation of the Ruiru 11 variety in Kenya (Van der Vossen and Walyaro, 1980; Walywaro *et al.*, 1982; Nyoro and Sprey, 1986).

Breeding programmes were therefore mainly based on the exploitation of specific resistant genes found in various species of *Coffea*. The resistance introduced by using the genes SH1 to SH5 present in the species *C. arabica* was overcome by the appearance of rust races accumulating the different virulent genes v1 to v5 through successive monogenic mutations. This has led to an erosion of the resistance genes SH1 to SH5 and hence they can no longer be used alone in breeding programmes for creating resistant varieties.

Selection programmes are now directed towards the exploitation of the resistance genes of *C. canephora*. However a diversification mechanism of the parasite towards the resistance genes present in the species *C. canephora* has also been observed. Pathogen races for the different genotypes of the Timor hybrid have been described in Timor (Gonçalves *et al.*, 1977), India, Sri Lanka and Angola, as well as in Brazil (Eskes, 1989). More recently, Holguin Melendez (1993) reported the presence of isolates, collected from Catimor in Indonesia attacking some plants issuing from the Timor hybrid, as well as Catimors and several differentials of *C. arabica*.

These elements pose a problem for the stability of the specific resistance in *C. canephora* and its derivatives. In order to obtain varieties showing a more durable resistance, researches were undertaken to try and find a non-specific type of resistance showing a quantitative character.

Incomplete resistance of coffee to rust

In Cameroon, investigations on 127 progeny of *C. arabica* from Ethiopia helped to demonstrate a wide variation in the average percentage of infection in the field and a highly variable defoliation rate depending on the origin (Tarjot and Lotodé, 1979). At the CIRAD in France, Leguizamon (1983) proposed a methodology for the quantitative evaluation of the development of symptoms under experimental conditions, integrating the various components of resistance. The results obtained with race II, which is the most represented in the world, showed the existence of incomplete resistance in Ethiopian coffee plants which is expressed by a low rate of sporulation and a long latent period. Fagioli (1988) confirmed this quantitative resistance in several races and showed that the accumulation of virulent genes in the pathogen could lead to a diminution in its aggressiveness. These results prove the existence of a source of incomplete resistance in the species *C. arabica* as emphasized by Eskes (1989).

Perspectives

The selection of varieties resistant to orange rust has been a major concern ever since this crop was introduced in the second half of the nineteenth century. Selections aimed at accumulating the resistance genes of *C. arabica* and *C. liberica* were overcome more or less quickly. The resistance obtained by the introgression of genes inherited from *C. arabica* in the Timor hybrid and resulting in the creation of Catimor appears to be a promising path.

However recent observations on the Catimor lines distributed in Asia which had lost their resistance indicate that the accumulation of SH6 to SH9 genes inherited from *C. canephora* can be overcome by isolates possessing a wide spectrum of virulent genes and showing a high degree of aggressiveness. It is therefore very important to prevent the gradual erosion of resistance in Catimor. At present although the strategy used for composite varieties, which possess different resistance factors in the different lines, appears to be satisfactory, exploitation of the incomplete resistance present in the species *C. arabica* should enable the selection of coffee plants showing a more durable resistance (Muller, 1984, 1985). However, this path is still to be investigated. We may particularly think of studying the sensitisation of the plant with age: no doubt, cultural corrections at an adult age would enable the expression of a resistance observed at a young age (see the chapter on Rational chemical control and cultural techniques).

Powdery rust

Concurrent with the investigations carried out on orange rust in Cameroon, Tarjot and Lotodé (1979) observed that the percentage of leaves attacked by *Hemileia coffeicola*, responsible for causing powdery rust, was distinctly higher in the Java variety than in the Jamaican variety, these two varieties then being the most widely grown in Arabica plantations. The study of collections showed that the number of cultivars infected by mealy rust was higher than that of cultivars affected by orange rust. However, an early test for evaluating the susceptibility could not be done. Wide differences in clonal susceptibility were observed in Robusta coffee plants. The level of susceptibility does not vary significantly from one ecology to another but the degree of infection shows variations which could be considerable.

Anthracnose of Arabica coffee berries

Evaluation of resistance

The resistance of Arabica coffee plants to anthracnose of berries (coffee berry disease) caused by *Colletotrichum kahawae* can be evaluated in the field under natural infection conditions. This is done mainly through the observation of the percentage of infected berries on the branches. However, this evaluation should take into consideration the variability in the susceptibility of the berries over time and requires several repetitions in order to appreciate the influence of climatic conditions and also take into account other factors which could have an incidence on the expression of the disease, such as the structure of the plantation (shading, spacing of coffee plants) and productivity of the trees.

Following the appearance of the disease in Kenya in 1922, differences were observed among the varieties in the field. A higher level of resistance was observed in Blue Mountain (Mac Donald, 1926). Later high levels of resistance were also observed by Firman (1964) in a wild population of coffee plants of West Sudanese origin (Rume Sudan) and by Vermeulen (1966) in the Timor hybrid, the natural hybrid of *C. arabica* and *C. canephora*.

In Ethiopia, where the disease was reported only in 1970, differences in the level of infection were observed in wild coffee populations and cultivated varieties (Robinson, 1974; Van der Graaf, 1981). In Cameroon, field observations revealed coffee plants showing different resistance levels in collections composed mainly of introductions of material of Ethiopian origin. These constitute the best source of variability of plant material and a good reserve of genes resistant to both orange rust and coffee berry disease (Bouharmont, 1992, 1995).

Resistance to coffee berry disease can also be evaluated by performing the artificial inoculation test. This is done by applying (spraying, drenching) a measured volume of a conidial suspension on different parts of the plant (hypocotyles of young seedlings, young shoots, berries); the inoculations can be done in the field or in the laboratory under controlled conditions on detached plant parts.

The test on hypocotyles of seedlings was developed by Cook (1973) in Kenya. It is still used for the identification and selection of resistant plant material. However, the results may vary depending on the test conditions (hypocotyle with or without roots and inoculation by drenching or spraying). It is therefore important that this test be standardised (controlled and homogeneous conditions for inoculation and incubation) in order to have a tool which would enable a reliable evaluation of the level of resistance.

In Ethiopia, Van der Graaf (1992) used the test on attached berries on a large scale. However, this test seemed to be too dependent on environmental conditions. Tests on detached berries inoculated in the laboratory apparently gave good results in Ethiopia but the results obtained in other countries are controversial. Ongoing researches in Cameroon indicate the importance of ensuring very rigorous and homogeneous experimental conditions as the expression of symptoms is highly influenced by them.

Resistance sources and characterisation of resistance

Studies on resistance to coffee berry disease actually began in Kenya, Ethiopia and Cameroon in the early 70s. Although the majority of the cultivated varieties were very susceptible to the disease, it was still possible to spot the varieties or wild coffee plants showing varying degrees of field resistance. However, the nature of this resistance has not been clearly established.

Resistant genotypes were observed in Kenya, especially in the Pretoria varieties (mutant of Typica) and K7, as well as in populations of Rume Sudan and Timor hybrid (a particularly interesting parent produced by the natural crossing between *C. arabica* and *C. canephora*), discovered on the island of Timor. Besides resistance to coffee berry disease, the Timor hybrid is interesting because it is also highly resistant to orange rust as well as nematodes.

A study of these populations helped to demonstrate that the resistance observed is of oligogenic nature. The hypothesis of a control by three genes located on three different loci was put forward (Van der Vossen and Walyaro, 1980): the recessive gene *k* present in the K7 and Rume Sudan varieties, gene *T* in the Typica variety and Timor hybrid and gene *R* in the Rume Sudan variety. Histological studies (Masaba and Van der Vossen, 1982) have shown that the resistance conferred by these genes is essentially mechanical in nature: the formation of a cork barrier has been observed.

Considering the supposed oligogenic nature of this resistance, the study of its specificity towards the pathogen is now a priority for the ongoing research programmes on this disease. Although some works have mentioned the possible existence of races in *Colletotrichum kahawae* (Rodrigues *et al.*, 1992), studies carried out within the framework of a European project on resistance to coffee berry disease tend to indicate the presence of a quantitative and nonspecific type of resistance. Nevertheless, a wide variability in aggressiveness has been systematically observed in the isolates tested (Bella Manga *et al.*, 1997).

In Ethiopia, the region of diversification of Arabica species, the appearance of the disease helped to demonstrate different levels of infection in wild populations of *C. arabica*. Van der Graaf (1981, 1992) showed that this resistance was quantitative in nature as immunity was not observed at all; the hypothesis of a polygenic type of resistance was proposed. In Cameroon, resistance to coffee berry disease was also demonstrated in introduced Ethiopian material (Bouharmont, 1995). Until now it has not been verified whether the genes *k*, *R* and *T* were also present in the Ethiopian material.

Selection for resistance

Breeding programmes were undertaken simultaneously with the search for resistance sources in the various countries affected by the disease.

In Kenya, the selection programme was defined with a view to combining the resistance observed in several varieties such as Rume Sudan and K7 with the organoleptic qualities of the best commercial varieties (SL28), especially through repeated backcrossings. The introduction of diverse Catimor lines during the period 1975-1977 enabled crosses between those showing resistance to both coffee berry disease as well as orange rust with the best known hybrids. This selection programme resulted in the creation of the Ruiru 11 variety; this is a mixture of hybrids with dwarf character which is now being distributed to the farming community (Van der Vossen and Walyaro, 1980); Walyaro *et al.*, 1982; Nyoro and Sprey, 1986). The resistance appears to be stable even after more than 10 years of use, although symptoms have been observed under some unfavourable environmental conditions. However, distribution of this plant material is being slowed down because of the low production of seeds which requires setting up manual pollination programmes.

A programme was launched in Ethiopia in 1973 to exploit the field resistance observed in wild coffee plants. The genotypes identified were thus integrated into a varietal breeding programme through mass selection. In 1986, this breeding programme resulted in the selection of hybrid varieties combining vigour and resistance to coffee berry disease (Van der Graaf, 1992).

In Cameroon, resistant trees were identified from collections containing cultivated varieties as well as those introduced from Ethiopia. Among the varieties evaluated, the Java variety was notable for its productivity, good vigour and degree of resistance to both orange rust and coffee berry disease (Bouharmont, 1992). This variety shows similarities with the Abyssinian variety introduced by Cramer at the beginning of the century in Java in Indonesia. The Java variety was released in Cameroon in the early 80s. However, it does not seem to be totally fixed (Cilas *et al.*, 1998) and recent studies have shown a variability among the trees (Berry, 1997), which may help to locate individuals that are more resistant than the mother population.

American disease of coffee

This disease is caused by *Mycena citricolor*, a highly polyphagous fungus. Moreover, it is of American origin and hence could not co-evolve with coffee. Consequently, the possibilities of finding specific resistance are practically non-existent. On the other hand there is a possibility, which cannot be ignored, of detecting a non-specific or incomplete resistance. Planters and some agronomists are of the opinion that Catimor is more susceptible than Catuaï.

Nuñez *et al.* (1995) have developed a methodology to estimate resistance in the laboratory: resistance to the entry of the pathogen and resistance to the fruiting bodies. The originality of this method is that the inoculations are done without causing injury. By using this methodology, it was found that Catimor appeared to be more resistant to entry but less resistant to the fruiting bodies than Catuaï. When these data are compared with field observations, it becomes evident that only resistance to the fruiting bodies could be responsible for the differences observed in susceptiblity. Later improvements in the methodology enabled evaluations under conditions very close to optimum for the fungus. Under these conditions, no difference could be observed between the susceptibility of Catimor and Catuaï. It therefore seems that incomplete resistance, if it exists, is useful only when environmental conditions are not exactly ideal for the fungus, i.e., when the disease is obviously not severe. Interest in this resistance is therefore quite diminished now.

Finally, it must be mentioned that differences in field resistance could also be due to architectural differences among the varieties. It is possible that certain architectures help to conserve a more humid ambience in the plantation and by the same token favour the disease. The capacity of water to adhere to leaves varies with the cultivars and this should not be ignored either.

Tracheomycosis

This disease is caused by the fungus *Fusarium xylarioides*. Observations made in the Republic of Central Africa in 1951 showed that Excelsa and neo-Arnoldiana were 100% susceptible to tracheomycosis (carbunculariosis), while the susceptibility of Robusta varied from 0 to 100% depending on the clones (Saccas, 1951). In the Ivory Coast, Kouilou (indigenous *C. canephora*) was found to be susceptible, Excelsa resisted better and Robusta showed clear resistance characterstics. Only Excelsa was affected in Cameroon. The disease was identified in Ethiopia in 1970. In future the selection of resistant clones or varieties should be done taking into account the wide diversity that the pathogenic species seems to be endowed with, since it does not attack the same varieties everywhere, and when they co-exist some may be more susceptible in one place and resistant elsewhere.

Nematode diseases

Grafting Arabica on Robusta

Highly pathogenic nematodes are very common in coffee plantations in Guatemala. Reyna (1968) therefore developed a grafting method in this country by using rootstocks of non-selected Robusta plants that had generally been observed to exhibit some resistance or tolerance to these pests. This hypocotyledonary type of grafting is done at the two-leaf cotyledonary stage using a bandage held in place by a thin plastic tape during cicatrisation. Cicatrisation and weaning are done in a seed-bed or directly in nursery bags. This technique is now commonly used by coffee planters in Guatemala, especially in regions with high nematode populations where nearly all the large plantations produce only grafted plants in the nurseries. Its success is due mainly to a good mastery of the technique: (*i*) 90 – 95% success in the nursery; (*ii*) a high degree of efficiency, as seen in Fig. 1, in controlling *Pratylenchus* sp., which is the most widespread nematode parasite of coffee in Guatemala and (*iii*) low cost compared to chemical control, which is more polluting and not very effective (Villain *et al.*, 1996).

This technique was introduced in Salvador where coffee plantations are also parasitised by highly pathogenic nematode populations (Hernandez *et al.*, 1995). Furthermore, major planters in Costa Rica also became interested in this technique. Lastly, it is very widely practised in Brazil.

Selection of *Coffea canephora* cv. Robusta rootstocks resistant to *Meloidogyne* spp.

Selection of plant material from the Robusta cultivar was done in Brazil. It

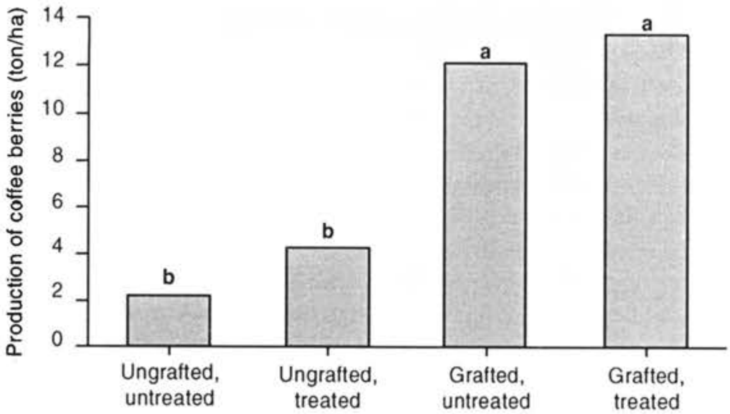

Fig. 1. Effect of grafting and Terbufos treatment to control *Pratylenchus* sp. on the average coffee production (from Villain *et al.*, 1996).

resulted in the creation of the Apoata variety (Fazuoli, 1986; Gonçalves and Ferraz, 1987) which is resistant to various pathotypes of *Meloidogyne incognita* that causes serious damage to coffee plants. On the other hand, in Central America no proper selection was carried out for resistance to nematodes. In the case of attacks by *Pratylenchus* sp. attacks, grafting on non-selected Robusta gave highly satisfactory results in Guatemala. However, it was necessary to make a selection for resistance to *Meloidogyne* spp. populations present in Central America, particularly for the populations in Guatemala and El Salvador which are highly pathogenic to coffee (Anzueto, 1993; Hernandez *et al.*, 1995). A project was therefore undertaken to evaluate and select genetic material for resistance to the important nematodes in Central America, with financial assistance from the European Union from 1993 to 1997. This search for resistance to nematodes has become one of the major criteria for selection in the regional coffee-breeding programme in Central America.

According to the studies carried out in several Central American countries (Decazy *et al.*, 1997), most of the Robusta lines tested were resistant to *M. exigua* populations in Costa Rica, a species which is also present in Nicaragua and the Honduras (Hernandez *et al.*, 1995). On the other hand, they are generally susceptible to the highly pathogenic *Meloidogyne* spp. populations in Guatemala and El Salvador. In fact, from this evaluation only two Robusta clones from the CATIE collection (Centro Agronomico Tropical de Investigación y Enseñanza) had transmitted a high level of resistance to *Meloidogyne* spp. populations collected from Central American countries (photo 94) to their progeny. These two clones are now being multiplied by CIRAD on a large scale through *in vitro* vegetative propagation in the CATIE laboratory. The vitroplants are being distributed to coffee establishments in the Central American countries to go through a phase of acclimatisation and weaning. They will then be planted in intercalation in isolated seedling fields with controlled fertilization in order to avoid contamination by pollen alien to these plots. The hybrid seedling resulting from the crossing of these two clones and constituting the rootstock of the Nemaya variety will be distributed to coffee growers from the year 2000 (Anzueto *et al.*, 1995). It must be pointed out that these two Robusta clones have also shown a good level of tolerance and resistance to the *Pratylenchus* sp. populations in Guatemala, which were found to be highly pathogenic to *C. arabica*.

SELECTION AND CREATION OF ARABICA CULTIVARS RESISTANT TO *MELOIDOGYNE* SPP.

A resistance to *M. exigua* populations was observed in some progenies of the Timor hybrid, Catimor and Sarchimor, but was not found in other varieties already distributed in Central America (Catuaï, Bourbon, Caturra), nor in the various varieties of Ethiopian origin that were tested (Decazy *et al.*, 1997; Hernandez, 1997). The IAPAR59 variety selected by the Agronomic Institute of Parana in Brazil was found to be resistant to the *M. exigua* populations in Costa Rica. Thanks to its good organoleptic property it is likely to be widely distributed in Costa Rica, as well as in the Honduras and Nicaragua where the same species seems to be present.

Tests carried out on a factorial hybridization programme with aggressive populations of *Meloidogyne* species from Guatemala (*M. incognita* or close to this species) showed that resistance was not transmitted by the two evaluated progeny of the Timor hybrid, viz., Catimor T8667 and Sarchimor T5296. On the other hand, two of the Ethiopian parents tested, ET59a2 and ET52a2, transmitted a good degree of resistance to all their descendants (Decazy *et al.*, 1997). Many other wild lines of Ethiopian origin also showed resistance to these Guatemalan populations (Anzueto, 1993; Hernandez, 1997), as well as to some of the *M. arenaria* populations from El Salvador and *M. arabicida* populations from Costa Rica (Hernandez, 1997). Hybridization using parents of Ethiopian origin therefore appears to be another interesting way of creating plant material resistant to certain populations of the genus *Meloidogyne* and could complement the selection of resistant rootstocks.

Hence, at present there are no commercial varieties that are resistant to the various species and types of nematodes at the regional level. Obtaining a universal resistant variety for the region appears to be very difficult because of the diversity of the pathogenicity (Hernandez, 1997). First of all, the plant material has to be selected in function of the populations present in each country. This solution would help to avoid grafting, especially in countries or regions where this practice is not common and where it increases the cost of production significantly, particularly in places where labour is expensive. Nevertheless, care should be taken to obtain a good organoleptic quality, which is now an important factor to be taken into consideration in genetic breeding programmes for coffee. The behaviour of these cultivars towards *Pratylenchus* sp. populations, which cause devastating economic losses in some countries, should also be studied. Lastly, transport of plant material should be strictly controlled in order to avoid the introduction of species which are pathogenic to the selected varieties.

COCONUT

At present varietal selection is not used much as a control method for coconut diseases. Nevertheless, often there are indications gathered from field observations that resistance or susceptibility appears to be linked to certain ecotypes. These indications are, however, fragile and can rarely be made use of by breeders.

Thus, in the case of foliar diseases in Brazil, the observation of the different ecotypes and hybrids of coconut present in this country helped to state that Dwarf coconut trees are less susceptible to *Phyllachora torrendiella*, causal organism of *lixa pequena*, than the Tall and hybrid coconut trees. The limited development of the perithecial stage of the fungus on the Dwarfs could be responsible for this better behaviour (IRHO, 1989).

Behavioural differences towards *queima das folhas* were observed among many coconut cultivars in Sergipe State in studies on the evolution of the size of lesions on the midrib of leaves, number of lesions and number of healthy leaves (Warwick *et al.*, 1991). When these criteria were considered, Equatorial Guinea Green Dwarf × West African Tall (EGD × WAT) and Cameroon Red Dwarf × West African Tall (CRD × WAT) hybrids showed the best performance under the studied conditions. These indices help to envisage using genetic diversity in coconut with a view to planting the best adapted plant material.

Coconut of Polynesian origin is susceptible to helminthosporiosis but it has been possible to identify cultivars that are more resistant than others and which could be used for producing Dwarf × Tall hybrids resistant to the disease. The West African Tall is particularly resistant and exhibits a hypersensitive reaction towards the parasite (Quillec and Renard, 1975).

On the other hand, neither hartrot nor cadang-cadang diseases seem to have been checked by the selection of such and such ecotype. Nevertheless, various fields screening trial towards hartrot have been planted and studied during the last twenty years, especially in French Guyana where four Dwarf varieties, eight Tall varieties and seven Dwarf × Tall hybrids were tested, but without success.

Better results were obtained for coconut foliar decay in Vanuatu (New Hebrides), lethal yellowing and *Phytophthora* rots.

Coconut foliar decay

All the varieties introduced in Vanuatu, whatever be their origin (Pacific, Asia, Africa), are susceptible to foliar decay of coconut. Only the local Tall, called Vanuatu Tall, is tolerant: the virus causing coconut foliar decay can multiply in it without affecting the growth or the yield of the tree (Calvez *et al.*, 1980).

Individual variations can be observed in some varieties. Although Rennell Tall can sometimes be quickly infected by foliar decay, it shows a high rate of remission. Besides, some trees of this variety seem to escape the disease even when they are situated in the middle of a focus. Isolated cases of remission could even be observed in one of the varieties reputed to be most susceptible to foliar decay, viz., the Malaysian Red Tall. In contrast, the local Red Dwarf (RD) is not very susceptible to the disease although it may sometimes show very strong symptoms leading to mortality. The VT × RD hybrid is very resistant.

It is possible to reproduce the disease on very young newly germinated coconut plants (one or two emergent-leaf stage) by introducing the insect vector *Myndus taffini* collected in the field from coconut trees, whether or not they are diseased. When insects were introduced at the rate of 200 per Malaysian Red Dwarf plant into a cage containing 25 of these young coconut seedlings, it resulted in 90–100% infection. These experiments help to quickly have an idea of the susceptibility of the varieties tested. They have helped to demonstrate a phenomenon of acquired resistance or resistance induced in certain varieties after being in a cage with *M. taffini* (Julia, pers. comm.). Some young coconut plants showed the typical symptoms of foliar decay after exposure to *M. taffini*. They harboured the virus but did not die and could be planted after they were taken out of the cage. This phenomenon is found in most of the varieties. Thus Brazilian Green Dwarf (BGD) crossed with Vanuatu Tall (VT) after passing through the cage with *Myndus* became tolerant to the disease. In an experiment on three rows of 25 BGD × VT trees including 8 controls which had not passed through the cage, the controls died or showed very strong symptoms followed by a long and difficult remission, whereas the trees exposed to *Myndus* in the cage survived. Experiments by reinfecting these trees with acquired resistance, at the rate of more than 10,000 vectors per tree, did not show signs of the disease. At present this property is not being used as a control method for fear of a high proliferation of the virus, but it could offer ways for disease control through genetic transformation of the coconut tree using viral genes.

Lethal yellowing

A high degree of resistance to lethal yellowing was observed in Malaysian Red Dwarf in Jamaica in the 50s. Later the Green Dwarf and Malaysian Yellow Dwarf were also found to be very resistant to these phytoplasma diseases and several fields screening trial were planted for evaluating varietal performance in various parts of the island during the 60s. In all these sites, an average survival rate of 96% after 10 to 18 years was obtained (Been, 1981).

However mortality rates of 10–11% were recorded for these Malaysian Dwarfs in some regions. Other ecotypes have been introduced since then. Some of them show good resistance, such as the Green Dwarf from Sri Lanka or the King coconut.

Some hybrids have been created: Malaysian Yellow Dwarf × Panama Tall (Maypan F1) hybrid has given good results with an acceptable level of resistance to lethal yellowing. By 1989, about ten million Maypan or Malaysian Dwarfs had already been replanted in Jamaica. However, after the hurricane of 1988, infection rates much higher than earlier were recorded (Been, 1995). The search for new resistant varieties has therefore been taken up once again.

In Tanzania, multilocation trials to evaluate varietal performance gave results that varied from one place to another, for example in Jamaica. On an average, the Dwarfs were more resistant than the Talls, and among the Dwarfs, the Cameroon Red Dwarf and the Equatorial Guinea Green Dwarf. On the other hand, it is quite surprising to see that some Local Talls of Tanzanian origin (from the Tanga region) seem to be quite resistant to the disease (Schuilling and Mpumani, 1990).

It was in Ghana that the CIRAD was particularly involved in setting up five fields screening trial, between 1981 and 1983 (Sangare *et al.*, 1992). For various reasons, especially with respect to the epidemiology of the disease, only two of these fields could be exploited for more than 10 years after their establishment. In fact the other fields, although situated in the disease zone or in its proximity, had not yet been affected. The results obtained in these two fields are summarised in Table 2 (Mariau *et al.*, 1996).

The results at present pertain to 10 varieties (5 Tall and 5 Dwarf) and 17 hybrids comprising 15 Tall × Dwarf and 2 Tall × Tall hybrids. Other causes for mortality were observed (infection by *Oryctes*, drought) and the missing plants were or were not replaced. Some of these replaced trees were affected by the disease, in which case they are placed in the 'mortality due to disease' column (M). Others had not grown enough to be affected by the disease and in such cases they remain in the R (replaced) column, giving rise to some heterogeneity in the results.

Despite the weakness of some plants, it was generally observed that the Dwarfs show greater resistance than the Talls, except for Vanuatu Tall whose level of resistance is, however, to be confirmed. All the other Talls tested were highly susceptible, especially the West African Tall. Among the Dwarfs, the Yellow Dwarf appears to be quite resistant. However, when disease pressure is strong, in other places it was observed that most of the trees ultimately succumbed to the disease. The apparent high resistance observed in the Sri Lankan Green Dwarf would probably be very interesting to use for crossing with a Tall, which could be the Vanuatu Tall. Other field resistance trials have been set up recently to test other varieties and hybrids. While waiting for the results, which will require many years, an initial regeneration programme for coconut plantations can be envisaged with the existing resistant material.

Table 2. Incidence of lethal yellowing disease on different varieties.

Varieties	Number of coconut trees				
	Initial number	Missing (M) or replaced (R)	Living	Died of the disease	Mortality rate (%)
WAT	37	7M + 5R	0	25	100
RLT	12	9M	0	3	100
MLT	12	6M	0	6	100
PYT	12	2M + 2R	2	6	75
VTT	6	1M	5	0	0
MYD	30	15M + 4R	10	1	9
SGD	36	11M	25	0	0
EGD	29	8M + 2R	10	9	47
MRD	36	16M + 1R	11	8	42
CRD	37	10M + 5R	6	16	78
MRD × WAT	35	4M + 3R	6	21	84
CRD × WAT	30	2M + 3R	4	21	84
MRD × PYT	28	0M + 1R	8	19	70
CRD × MLT	36	18M	7	11	61
RLT × WAT	48	8M + 2R	5	33	87
MYD × WAT	36	9M + 1R	4	22	84
MYD × PYT	9	4M	1	4	80
MYD × MLT	12	1M + 1R	6	4	40
MYD × RLT	12	7M	0	5	100
MYD × VTT	12	4M + 4R	1	3	75
SGD × WAT	11	5R	1	5	83
EGD × WAT	12	3M	0	9	100
EGD × VTT	12	3R	1	8	89
CRD × RLT	12	1M + 5R	0	6	100
CRD × VTT	12	3R	1	8	89
CRD × PYT	12	3M	1	8	89
VTT × MLT	12	4M + 1R	2	5	71

MLT: Malaysian Tall
RLT: Rennell Tall
SGD: Sri Lankan Green Dwarf
MRD: Malaysian Red Dwarf
VTT: Vanuatu Tall
WAT: West African Tall
PYT: Polynesian Tall
EGD: Equatorial Guinea Green Dwarf
CRD: Cameroon Red Dwarf
MYD: Malaysian Yellow Dwarf

Phytophthora rots

The most important works on the behaviour of coconut trees with respect to *Phytophthora* were carried out in the Ivory Coast, Indonesia and the Philippines (Renard, 1996). Characterisation of plant material is based on two kinds of information: the performance of cultivars planted in the field and the ability of nuts to develop lesions after artificial inoculation.

In the Ivory Coast, comparative tests on ecotypes and their hybrids under strong natural pressure of *Phytophthora katsurae* were performed for more than ten years for individual and systematic surveys of mortality due to bud rot and premature nutfall (Franqueville *et al.*, 1989). These observations enabled the classification of the various cultivars for each of these characters (Table 3; Renard, 1993).

Similarly in Indonesia and the Philippines, where parasite pressure from different species of *Phytophthora* is high, the results are most often from surveys made all over the country where numerous ecotypes and hybrids of coconut have been planted.

In Indonesia, among the most common ecotypes, the West African Tall, which is susceptible to bud rot wherever it is planted, confers a pronounced susceptibility to bud rot caused by *P. palmivora* to its hybrids. The local ecotypes (Bali, Tenga, Palu) are generally more resistant than the introduced ecotypes, except for Polynesian Tall and Rennell Tall which, moreover, show better resistance to bud rot than Bali Tall in northern Sumatra. These ecotypes, viz., Polynesian Tall and Rennell Tall, perform well in the presence of both *P. palmivora* and *P. katsurae*. In the Philippines the local ecotypes show a certain resistance: two hybrids, Camotes Green Dwarf × BayBay Tall and West African Tall × Rennell Tall, are unharmed by bud rot (Concibido-Manohar and Abad, 1994).

Table 3. Performance tests in Samo, Ivory Coast. Performance of plant material with respect to bud rot and nut fall caused by *Phytophthora katsurae*.

Plant material	Bud rot (%)	Nut fall (%)
MYD	5.0	1.3
MRD	28.3	2.4
CRD	13.3	4.2
MYD × WAT	8.3	21.5
MRD × WAT	20.0	14.2
CRD × WAT	20.0	36.6
EGD × WAT	31.7	37.2
MYD × RLT	5.0	11.2
MRD × RLT	15.0	6.9
CRD × RLT	6.7	11.0
WAT × RLT	8.3	7.7
MYD × VTT	6.7	2.0
VTT × VTT	5.0	1.9
MYD × MLT	0.0	4.7
CRD × MLT	8.6	12.8
VTT × MLT	5.0	1.9
MLT × MLT	1.8	3.3
MYD × PYT	0.0	2.3
MRD × PYT	3.3	5.3
WAT (Port Bouet)	25.0	8.8
WAT (Samo)	20.9	2.9

MYD: Malaysian Yellow Dwarf
EGD: Equatorial Guinea Green Dwarf
VTT: Vanuatu Tall
MRD: Malaysian Red Dwarf
WAT: West African Tall
MLT: Malaysian Tall
CRD: Cameroon Red Dwarf
RLT: Rennel Tall
PYT: Polynesian Tall

An attempt was made in Indonesia to detect resistant factors towards *Phytophthora* in the nut by artificially inoculating detached nuts (Kharie *et al.*, 1994). This method, in which an inoculum comprising a suspension of zoospores is deposited on the equatorial region of a large immature nut (in the 15-20 row), helped to establish a classification based on the size and rate of spread of the lesions, and also on the success of the infection. Among the Dwarf cultivars, the Bali Yellow Dwarf, Nias Yellow Dwarf, Malaysian Red Dwarf and Jombang Green Dwarf were found to be very susceptible to *P. palmivora*, *P. nicotianae* and *P. arecae* worldwide, despite some differences depending on the species of *Phytophthora* used. The nuts of Palu Tall and Bali Tall are also susceptible, as well as nuts of the Malaysian Yellow Dwarf × West African Tall hybrid.

Among the most resistant cultivars may be cited the Salak Green Dwarf, Tebbing Tinggi Green Dwarf, Rennell Tall, Polynesian Tall and Tall populations of Mapanget, KB 1, 2, 3 and 4.

These results have to be validated by their performance in the field; this was not always possible considering the low representation of some cultivars in the field. The field trials conducted within the framework of a programme funded by the European Union, set up in the central part of Balitka in northern Celebes (Indonesia), should be able to provide a solution in the future (Thévenin, 1994).

The precaution of comparing laboratory results with field performance becomes all the more important as the results obtained in the Ivory Coast with *P. katsurae* is an example of the pronounced differences in the response of the nuts depending on whether they were artificially inoculated or naturally contaminated in the field (Franqueville and Allou Kouassi, 1994). Such is the case, in particular with nuts of the Malaysian Yellow Dwarf × Polynesian Tall hybrid, which are not greatly affected by nut fall in the field, whereas detached nuts inoculated artificially are highly susceptible to *P. katsurae* and nuts of the Rennell × West African Tall hybrid to a lesser degree.

All the existing data on coconut behaviour should therefore help the concerned managers to make a rational selection of the plant material to be planted, i.e., material suitable for the region under consideration.

OIL PALM

All progeny of oil palm (*Elaeis guineensis*), irrespective of their origin, are very susceptible to the trypanosomas causing palm wilt (marchitez) from the age of two years. The *E. guineensis* × *E. oleifera* hybrid is also susceptible to it. Thus, at present there is no genetic solution for the intraphloem trypanosoma diseases, as in the case of hartrot disease of coconut. There do not seem to be any genetic solutions for dry bud rot, red ring and ring spot diseases either.

In the case of cercosporosis, a selection programme for resistance to it has not been developed, although it appears that certain genotypes are more susceptible to the disease than others. This is all the more true in the case of clones where a wider range of susceptibility was observed than in the commonly used sexual material. *Elaeis oleifera* and the *E. oleifera* × *E. guineensis* hybrids are much more susceptible than pure *E. guineensis* . Some cases of mortality may be recorded in this type of plant material, in the nursery or in the plantation. In any case the response that can be obtained against this disease, thanks to a rational chemical control strategy, does not justify considering this selection criterion.

On the other hand, three lethal diseases of oil palm illustrate the competition genetic control can give in varying degrees: blast disease, whose incidence on clones may be a limiting factor; bud rot in Latin America, against which selection strategies have to be formulated; and fusarium wilt, which is one of the most convincing examples of the efficacy of genetic control.

Blast disease

Blast disease was for long considered to be a disease whose development was not actually imputable to plant origin. This position was invalidated by the culture of oil palm clones, which showed a wide range of susceptibility under natural conditions. The disease symptoms can be easily reproduced by introducing *Recilia mica* Kramer, insect vector of the disease (see the chapter on Insect vectors), into insect-proof cages containing nursery stage oil palm seedlings (IRHO, 1992). During the course of an experiment conducted in cages, five clones selected for their performance (susceptible, resistant, intermediate) in the nursery were subjected to a high pressure of *R. mica* in the cage. The results, which conform to those observed in the nursery, are given in Table 4.

Table 4. Differences in the performance of oil palm clones with respect to blast disease.

Clone	Blast (%)	Remission (%)
LMC 104	96.0	27.0
LMC 051	74.0	32.0
LMC 056	70.0	44.0
LMC 096	20.0	100
LMC 044	16.0	100

These results show that a method for evaluating the performance of clones against the disease is now available. It has not been used in selection strategies, but the susceptibility of a given clone can be taken into consideration for the management of control methods practised in nurseries or at a young age in plantations.

Bud rot in Latin America

Environmental factors have an influence on the spread of the disease, which enables the application of some cultural practices destined to limit their impact. However, it is only through genetic control that this disease can be cured, thus considerably limiting the cultivation of oil palm in Latin America. Some variability in the susceptibility to this disease exists within the species *E. guineensis*, but it is probably weak. In contrast, *E. guineensis* × *E. oleifera* hybrids exhibit a high level of resistance. In a commercial plantation, in a 10-year old plot planted with a mixture of hybrids of this type, the percentage of diseased trees was observed to be 0.2%, whereas in neighbouring plots of the same age planted with *E. guineensis*, the disease rate was 15 to 20% (Mariau, 1992). Moreover, it could be observed that in almost all cases the infected hybrids did not die but re-established themselves after a few months. This kind of healing is quite exceptional in *E. guineensis*. Perhaps there is a variability even among these hybrids, but many research workers think that it is here that the solution to the problem can be found.

Fusarium wilt

When fusarium wilt began to spread in African oil palm plantations in the 1950s, it very quickly became apparent that like the other fusarium wilts, especially that of date palm (Pereau-Leroy, 1954), selection of plant material resistant to the disease could help to limit its spread (Bachy and Fehling, 1957). In fact, data collected on identified progenies from the field and from sampling plots in plantations have helped to show important differences in their performance which can be directly attributed to the origin and ancestry of these crosses.

Prendergast (1963) proposed conducting an early test to help evaluate the behaviour of plant material towards fusariosis by following an experimental process similar to the one carried out on the date palm (Laville, 1962). This test is based on the inoculation of *Fusarium oxysporum* f. sp. *elaeidis* into nursery seedlings. Renard *et al.* (1972) later improved this by passing from the nursery stage to the prenursery stage with a view to getting a quicker response on a larger number of crosses. Breeding for general resistance to fusarium wilts has become attractive since then.

Oil palm seedlings are about 1.5 to 2 months when they are inoculated with the pathogen. This is done in the collar region which has been cleared earlier to expose the base of the roots and the most superficial radicles. The inoculum is obtained by grinding a 5-day-old culture of *Fusarium oxysporum*. Each seedling receives 20 mm of this inoculum containing an average of 3.5×10^6 propagules. The crosses or clones are represented by 160 seedlings divided into 8 replications.

The test results are evaluated after 5 months by dissecting the pseudobulb of every seedling. Browning of the vascular fibres confirms the external symptoms.

The result of a cross or clone is expressed by an index representing the ratio between the percentage of wilted plants recorded for the cross or clone with the mean percentage of all the crosses represented in the inoculation series. An index of 100 is assigned to this average and the lower the index, the more resistant the cross.

A parent represented in several crosses will be characterised by the mean of the indices of the crosses where it is involved and also by the number of crosses with indices higher or lower than 100, which is the mean value of a series. Similarly, a type of determinant plant material can be characterised by grouping either the different crosses or the different trees belonging to this type of plant material.

The plant material tested for its reaction to the disease belongs to different selection programmes and particularly to the general oil palm breeding programme, which is based on the principle of recurrent reciprocal selection (Meunier and Gascon, 1972). Resistance to fusarium wilt constitutes an important selection criterion for material destined for Africa. Renard *et al.* (1980) have described resistance sources obtained from inoculation tests through a recurrent reciprocal selection programme on the one hand, and from new introductions such as those of Latin American origin derived from *Elaeis oleifera* and its hybridization with *E. guineensis* on the other. These results led Renard and Meunier (1983) to define the categories of plant material to be conserved or eliminated in regions affected by fusarium wilt.

The general validity of the tests has been demonstrated in the Ivory Coast (Renard and Meunier, 1983) as well as in the Democratic Republic of the Congo (Franqueville, 1984) under extremely varying conditions and with different genetic origins, by comparing the performance of young plant material with that expressed by the same material at an adult age, in replantations on fusarium wilt affected antecedents.

In-depth confirmation of the validity of these early tests was provided by Franqueville and Renard (1990) thanks to the study of the evolution of fusarium wilt in the 4000 hectare Robert Michaux experimental plantation in the Ivory Coast (Fig. 2). On an average, 20 to 30% of the oldest crops were infected by fusarium wilt, this percentage gradually diminishing during successive programmes until the incidence became almost negligible, despite the conditions of replantation confronting the plant material continuously with a high risk of fusarium infection. This evolution is directly related to the improvement in the level of resistance of the plant material discovered thanks to the introduction of the inoculation test.

The last is not limited to the characterisation of sexual material. Numerous clones of oil palm—about a hundred—have been introduced in early tests. The most promising were retained and have been planted in fusarium wilt infested zones since 1989 (Renard *et al.*, 1991). Evaluation tests were also

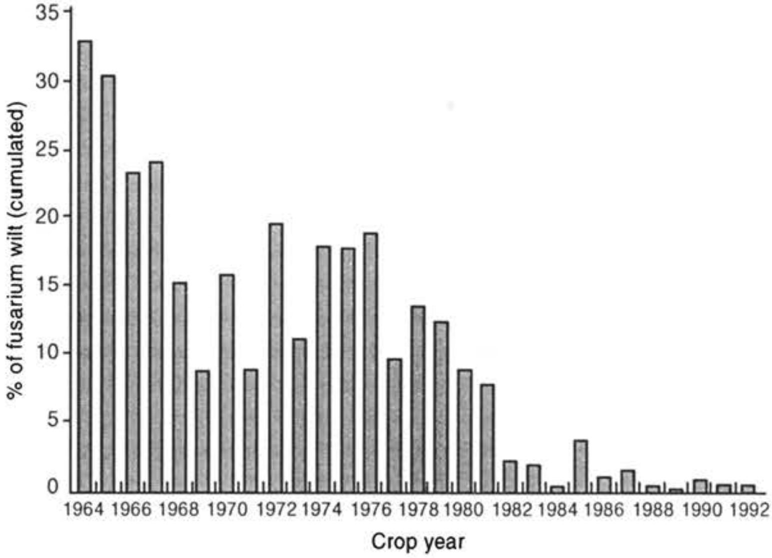

Fig. 2. Evolution of fusarium wilt in the Robert Michaux plantation (Ivory Coast; from Franqueville and Renard, 1990, updated by Franqueville and Diabate, 1995).

carried out by subjecting these clones to as high an inoculum pressure as possible.

The selection procedure adopted seems to be based on a polygenic type of resistance (Meunier *et al.*, 1979). There is no significant interaction between the geographic origin of the isolates of the pathogen and the performance of plant material inoculated with it. Grouping of the same range of crosses remains identical, irrespective of whether this range is compared with isolates from an old forest area or with a savanna precedent (Franqueville, 1991). This also seems to be the rule in all countries and the only differences observed are in the degree of aggressiveness of the pathogen (Mepsted *et al.*, 1994). Obviously this does not exclude a high variability of the pathogen, a variability that can be found using vegetative compatibility group techniques or with the help of molecular markers (see the chapter on Pathogens).

Selection techniques through inoculation no doubt give conclusive results, but they are costly in terms of time and number of oil palm seedlings. In order to have a better understanding of the mechanisms involved, the study of phenol metabolism, begun in the 80s (Taquet *et al.*, 1985), has helped to demonstrate the differences in the response depending on the genotype of oil palm attacked by the parasite (Diabate *et al.*, 1990; Ledeme *et al.*, 1992). Research efforts are therefore directed towards the optimisation of selection techniques.

HEVEA RUBBER

Genetic control of hevea diseases is a delicate application. This is particularly so in the case of rots, for example, *Fomes lignosus*, which attacks the rootstock. Researches are underway to find rootstocks resistant to the disease from different families of artificially infected seedlings. Plants which have survived a massive inoculation are selected for multiplication by shoot tip grafting. However chemical control methods and cultural techniques are also available.

For some foliar diseases such as the one caused by *Colletotrichum* in Central Africa, cultural techniques have helped to find a solution (see the chapter on Rational chemical control and cultural techniques). Genetic control is considered inevitable for the foliar disease, South American leaf blight of hevea (Salb), caused by *Microcyclus ulei*.

South American leaf blight

The Ford company was the first to launch a genetic breeding programme in 1937. Initially, selection was done mainly in Brazil and also in Costa Rica and Guatemala. However, the devastation caused by this disease in its plantations forced Ford to abandon its heroic enterprise in 1946. It was taken over in 1949 by the American company Firestone, which built up a network comprising Guatemala (Finca Clavellinas), Brazil (Fazenda Tres Pancadas in Bahia State), Florida (quarantine station) and Liberia.

The first resistance sources came from wild populations of *Hevea brasiliensis* found in the lower and middle Amazon basin and also in the upper Amazon basin where trees with high resistance levels were found: Acre (Brazil), Madre de Dios (Peru) and the region common to Brazil, Peru and Colombia between Leticia and Equitos. It is thought that it is in this vast region that highly resistant populations of *B. brasiliensis* are to be found (Holliday, 1970).

Two other species, *H. benthamiana* (Rio Negro) and *H. pauciflora*, were used for their high resistance level, especially the former and particularly the clone F 4542 (Ford 4542), which was used as the resistant parent in later crossing programmes. The latter, *H. pauciflora*, is totally resistant to the South American leaf blight but non-productive and is interesting because of its vigour and absence of wintering (Chee *et al.*, 1986).

Three other species, *H. guianensis*, *H. microphylla* and *H. spruceana*, have been used for producing interspecific hybrids with *H. brasiliensis*, but these hybrids were later discarded because they do not possess satisfactory agronomic characters (Pinheiro and Libonati, 1971).

The best results for improving the resistance of hevea to the disease were obtained by interspecific crosses between *H. brasiliensis* and *H. benthamiana*. However the genetic base for resistance is essentially limited to the clone F 4542 (*H. benthamiana*) mainly because of its resistance to *Phytophthora* leaf disease (Holliday, 1970).

The primary sources of resistance in *H. brasiliensis* for conducting the preceding crosses came from Acre (Brazil) and were limited to the clones F 351, F 409 and FA 1717 (Ford selections).

A large number of primary crosses were also carried out with highly productive clones from the east, such as Pb 86-186 (Malaysia), Tjir 1, Tjir 16 (Java) and Avros 49-183-363 (Sumatra). The best progenies were then backcrossed or crossed with the same eastern clones.

These last are generally extremely susceptible to *M. ulei*, because they were produced away from all pressure exerted by this parasite. It is also acknowledged that their common genetic base has been limited to only 22 trees in about a century of hevea culture and that millions of trees now planted have these individuals as their ancestors. Although repeated crossings have helped to increase the productivity to a level almost equal to that of the eastern clones of the 60s, it is a matter of regret that nearly all the South American selections obtained from these crossing programmes have only the clone F 4542 as the common parent and a source of resistance to *M. ulei* (Pinheiro and Libonati, 1971).

Further, Townsend (1960) reported a poor transfer of resistance from clone F 4542 to the F_2 and F_3 generations obtained by backcrossing with a susceptible eastern parent. This may explain the fact that the clones recommended and most widely planted in South America are clones of the first generation (F_1) including the following:

H. brasiliensis × *H. benthamiana* = FX (Ford cross) 3810-3899-3925, IAN 717 (Belém);

H. brasiliensis × *H. brasiliensis* = FX 25-3864-4098, IAN 710-713-873 (Holliday, 1970; Chee *et al.*, 1986).

These clones are still being planted on a commercial scale in places where *Microcyclus* does not allow the cultivation of eastern clones.

Hevea cultivation in South America is therefore confronted by the double problem of variability of the parasite, which is still not clearly known and a reduced genetic base on which the resistance of the plant material now planted depends. Besides, the production potential of this material is now surpassed by modern clones.

Considering the capacity of the pathogen to adapt to modifications in the host population, it is now necessary to be concerned not only about resistance of the specific or total type, but also with another kind of resistance called partial, which is more durable in nature because it is non-specific (Simmonds, 1982).

New resistance sources should therefore be found. Two surveys were made in the Amazon in 1974 and 1981. They helped to enrich the gene pool of hevea significantly and a fund of resistance to foliar maladies could be observed (Nicolas *et al.*, 1994). This new material was selected to constitute a core collection in which certain clones could serve as parents for creating clones (Clément-Demange *et al.*, 1995).

Researches have been carried out in French Guyana since 1982 (Rivano *et al.*, 1989), on the one hand to evaluate the degree of genetic variability of the parasite and on the other, to identify some components of partial resistance among the available clones (old and new) that could serve as the base in a new genetic breeding programme for hevea in Latin America (Rivano, 1992).

These researches are directed mainly to the study of the performance of species of the genus *Hevea*, their hybrids and clones with good agronomic characters under ecological and climatic conditions that are very favourable for South American leaf blight.

Collections were constituted and are being continuously enriched since nearly fifteen years. Fields with experimental clones were set up on a small scale (large number of clones, number of individuals reduced to less than 50 per clone) as well as on a larger scale (smaller number of clones, number of trees more than 300 per clone). These sampling plots are complemented by a plant pathology laboratory where a large collection of isolates of the fungal parasite is cultivated.

These experiments have helped to collect information on the adaptation of plant material to the environment and especially on its susceptibility to *M. ulei* and other leaf parasites. They have helped to distinguish between the effects of host-climate interactions through the phenology of the tree from those due to parasite-climate interactions in the complex relationship which links the plant to the pathogen. A first fall-out of these basic studies is in the development of a method for evaluating the general field resistance of hevea to foliar diseases and especially to *M. ulei* (Rivano, 1997).

The principal manifestations of the disease that can be quantitatively evaluated in the field are the abscission rate of leaves, intensity of distortion of young leaves and percentage of necrotic leaf area on adult leaves. The clones tested could be classified into three statistically homogeneous groups for each of these three expressions of the disease. Apart from a few exceptions, clones of South American origin were significantly more resistant than Asian materials; some of them were even totally resistant to the disease from more than ten years (Fig. 3).

Furthermore, the preponderant role of phenology, the natural phenomenon of defoliation and refoliation manifested every year during the dry season from the fifth year of planting, in protecting trees confronted by fungal attacks was demonstrated. It is a reflection of the adaptation of clones to the ecological and climatic conditions under which they are planted. In favourable cases this is expressed by a homogeneous and rapid refoliation of all the trees during a period of the year when the climatic conditions are unfavourable for the growth of the fungus. Given that only leaves less than 15 days old are susceptible to *M. ulei*, this natural phenomenon would enable certain clones to escape the disease by reconstituting their foliage during the dry season and would thus restrict the development of epidemics to the rainy season (Rivano, 1992).

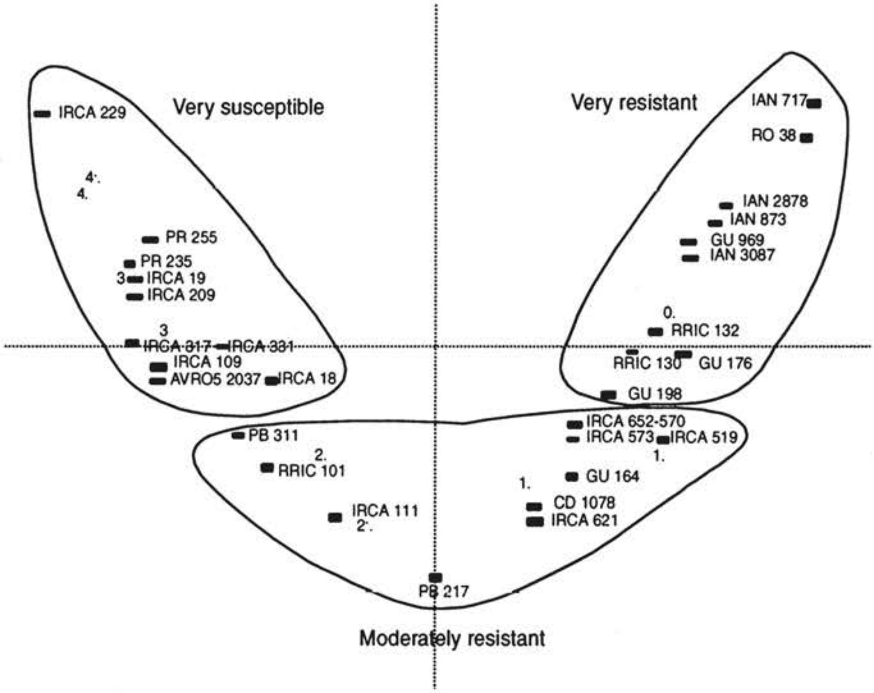

Fig. 3. Distribution of clones based on factorial correspondence analysis (fca) from observations of intensity of *Microcyclus ulei* infection on young (0 to 4) and old (0' to 4') leaves (from Rivano, 1997).

A complementary approach is to study about a dozen components of partial resistance to hevea under controlled conditions by artificially inoculating potted plants with *M. ulei*. This enables a comparison of clones on a quantitative basis and at the same time helps to consolidate the results obtained in the field (Rivano, 1992).

The results of these inoculations have very often revealed interactions of a quantitave nature between the clones and strains, which do not allow a global and final judgement of the level of partial resistance of a clone or the degree of aggressiveness of a pathogenic strain. In fact, we cannot rely on the inoculation of a single strain to appreciate the partial resistance of a clone and vice versa.

These interactions forbid us to state that partial resistance does not exercise any pressure on the aggressiveness of the pathogen population and that it is durable in nature. Contrary to Van der Plank's hypothesis (1968), it must be acknowledged that aggressiveness could evolve in function of the force exercised on it by the resistance mechanisms brought into play by the host.

The display could reside in the association of various defence mechanisms in the same genotype of hevea, but this implies that we have a fairly good knowledge of these mechanisms in the plant.

We can no more envisage making the best use of reinforced partial resistance without using it as a strategy conceived for prolonging its durability and efficiency. When hevea cultivation is introduced in a new region where *M. ulei* is still absent, we can plan to bring together in the same clone forms of efficient partial and total resistance whose circumvention would be judged as least probable. Total resistance would ensure efficient protection at least during the juvenile phases of the tree's growth, a period during which the absence of a defoliation-refoliation rhythm makes it particularly vulnerable. Partial resistance would then take over by slowing down the progress of the damage.

A separate study on the components of partial resistance under controlled conditions of infection also revealed that none of the clones in the experiment showed the best characteristics for all the manifestations of partial resistance. From this point of view, everything looks as if the selections made in South America in the presence of the disease and included in our experiments had been carried out partly blindly. A material may show very good characters associated with others which are less so.

These results have helped to launch a new genetic breeding programme for hevea in Brazil for creating material that is resistant to South American leaf blight by associating several elements of partial resistance, now dispersed in different clones, in the same genotype and at the same time raising its production level.

FRUIT CROPS

Citrus gummosis caused by *Phytophthora*

Genetic control of citrus gummosis caused by *Phytophthora* appeared to be very interesting right from the beginning. It quickly became universal mainly because of the choice of resistant varieties, which could be used as rootstocks (Boccas and Laville, 1978; Laville, 1984).

Their selection depends on several factors. First of all, the association of rootstocks with the commercial varieties should be compatible with the presence of viral diseases of citrus, especially tristeza. The rootstocks should also be well adapted to the soil and climate so that the fruit harvest is of a good quality. This is why the majority of clementine orange orchards are grafted either on Seville orange or *Poncirus trifoliata* or Troyer citrange.

With respect to *Phytophthora* infections, Seville orange is still considered to be correctly resistant on condition the trunks and roots are not injured, because it is known that any change in the bark and cortical zones of the roots considerably diminishes the resistance of this rootstock variety.

Poncirus trifoliata is clearly more resistant to both insidious attacks on roots as well as attacks on the base of the trunk. Wounds do not alter its resistance and cicatrisation takes place without secondary infection by *Phytophthora* (Laville and Blondel, 1979; Jacquemond and Blondel, 1986).

Resistance in Troyer citrange is also of a good level but the association of this rootstock with clementine posed a few problems in some orchards in Corsica. In fact, some cracks were observed in the bark on the outgrowth of the graft, near the union of the scion and rootstock. These injuries are often due to gummosis, which then quickly spreads to the susceptible clementine part. As these cankers appear on the trunk very close to the ground, they rapidly invade the base of the low branches. Hence despite appearances, it cannot be said that Troyer citrange is susceptible to gummosis, but this type of infection on the graft is found to be more common in Troyer citrange-clementine associations (Boccas and Laville, 1978).

This kind of attack as well as direct infections on the low branches on the grafted part of the trunk (very low plantations) or on roots can only be treated chemically.

Researches on the nature of host-parasite relationships indicate that in the citrus-*Phytophthora* pair, two categories of relationships are in play: one is the polygenic type and the other is oligogenic (Laville, 1975; Vallavieille, 1983). The latter type is more easily detected in a relatively susceptible host population belonging to the same group as in the case of orange, or when only the grafted variety is different. In contrast, the former seems to be preponderant on the one hand when all the citrus varieties are compared, from the most susceptible to the most resistant, and on the other within resistant host groups such as *Poncirus*.

These results indicate that it is clearly preferable to select new resistant varieties from hybrid populations obtained by interspecific crossings. In fact when the main characteristics of *Phytophthora* diseases of citrus are compared, we observe a high potential variability of the parasites, a low variability of the hosts and a strong selection pressure on parasite populations. Therefore, using horizontal resistance (high partial resistance) is undoubtedly the best guarantee for durability and efficiency in the different geographic zones.

Cercosporiosis of citrus

Evaluation of citrus cercosporiosis, caused by *Phaeoramularia angolensis* in the field, had been carried out for several years in Cameroon. About 120 citrus accessions were evaluated and none of them was found to be totally resistant (Bella Manga *et al.*, 1991; Rey *et al.*, 1986; Kuate, 1993; Kuate *et al.*, 1994). These different studies nevertheless suggest a considerable variation in varietal performance, ranging from a more or less pronounced partial resistance (lime, lemon, pampelmouse and some mandarin trees) to high susceptibility (pomelo, sweet lime and other mandarin trees). However, there is no information on the components which are in play during these interactions between the host and parasite and which could modulate the level of partial resistance. Analyses of these interactions, which should be done under standardised conditions (for both host and inoculum pressure), can be done by using experimental inoculation techniques that have already been perfected (Nzoumba, 1985). These data are indispensable for directing the work of varietal screening for which resistance to *P. angolensis* is the biggest challenge. Exploitation of resistance sources present in the species complex requires a good knowledge of genetic determinism and inheritability of partial resistance. This aspect will be studied in the near future for the two main methods of creating varieties which have now been perfected for citrus, viz., sexual recombination and somatic hybridization (Ollitrault *et al.*, 1944a, 1944b).

Bacterial citrus canker

The susceptibility of citrus and more broadly of the family Rutaceae, to bacterial or Asian canker, is generally quite similar in all the cultivars that comprise the plant species. However, there are some distinct differences in the susceptibility in the true cultivars of sweet lime and pampelmouse. The susceptibility of the major citrus species is summarised in Table 5 (Vernière, 1992).

Black spot disease of mango

A large collection of mango trees has been established in Réunion since the 1960s. The cultivars in this collection are mainly from Florida and the Mascarene archipelago (most of these or their parents were probably introduced from India during the massive migrations in the nineteenth century). Observations made over a decade indicated that the majority of these cultivars were very susceptible to the black spot disease caused by *Xanthomonas* sp. *mangiferaeindicae*. Following these observations, three cultivars, viz., José, Auguste and Early Gold, were distributed to growers from the early 1980s: The José and Early Gold cultivars were distributed in Réunion as there is a high local demand for Indian type fruits. These were selected because they were the least susceptible among cultivars of this type and their fruiting periods are spread over four to six weeks. Hence these two cultivars are already harvested by the time the rainy season begins in Réunion. Data gathered since the 80s have helped to verify the good global performance of the Auguste cultivar. The José cultivar, which is very late, is often subject to severe infections linked to the heavy rains of the cyclonic season.

The good performance of the Early Gold cultivar in Réunion could be verified in a large number of commercial orchards established since the early 1980s. Studies have helped to demonstrate the following points:

— the intrinsic susceptibility of fruits of the Early Gold cultivar to the disease is high, whether the infection takes place through injuries or through lenticels (Pruvost and Luisetti, 1991);

Table 5. Susceptibility of citrus to *Xanthomonas axonopodis* pv. *citri*.

Susceptibility classes of fruit crops

Very susceptible	Susceptible	Slightly susceptible	Resistant
C. paradisi (Pomelo)	*C. latifolia* (Tahiti lime)	*C. medica* (citron)	*C. madurensis* (calamondin)
C. aurantifolia (Mexican lime)		*C. limon* (lemon)	*C. unshiu* (Satsuma mandarin)
C. hystrix (combava)			*C. reticulata* (mandarin)
		C. grandis (Pampelmouse)	
	C. sinensis (sweet lime)		
	Tangelo*	Tangor*	*Fortunella* spp. (Kumquat)

* Hybrid cultivars Tangelo: *C. reticulata* × *C. paradisi*;
Tangor: *C. sinensis* × *C. reticulata*

Susceptibility classes of rootstocks

Very susceptible	Susceptible	Slightly susceptible	Resistant
Poncirus trifoliata (Trifoliate orange)	*C. macrophylla*		
Citrange*	*C. limonia* (Rangpur lime)		
Citrumelo*	*C. jambhiri* (rough lime)		
C. aurantium (Seville orange)			
C. reshni (Cleopatra mandarin)			

* Hybrid cultivars Citrange: *C. sinensis* × *Poncirus trifoliata*; Citrumelo: *Poncirus trifoliata* × *C. paradisi* cv. Swingle

— in producing orchards it was observed that trees of this cultivar have very few lesions on the leaf when compared to highly susceptible cultivars. Moreover, in the case of several cultivars in Réunion and South Africa, it was shown that there exists a clear relationship between the disease level recorded on leaves during the winter season and the percentage of infected fruits at the time of harvesting (Manicom, 1986; Pruvost *et al.*, 1990). The low susceptibility of leaves of the Early Gold cultivar was verified by comparing it with the more susceptible Maison Rouge, Haden and Irwin cultivars.

— the presence of water is indispensable for infection to take place.

If the lower foliar susceptibility plays a role in the global performance of the Early Gold cultivar, it is important to emphasise that it is among the earliest cultivars of the initial collection. Hence in Réunion most of the harvesting is done every year before the onset of the rainy season. This case is thus a good example of the adaptation of a cultivar to ecological conditions.

In South Africa, where the rainy season commences at the beginning of November, the performance of the Early Gold cultivar is relatively mediocre.

Several other cultivars show interesting levels of resistance. The Sensation cultivar, although very late, has been described in literature as resistant to the disease. It has not been distributed in Réunion because in view of the difficulties encountered with the José cultivar, the emphasis was on the distribution of early cultivars. However its resistance level, confirmed by several research teams, makes it a potentially interesting cultivar. It has been widely used in breeding programmes in Australia and South Africa for creating varieties with a view to obtaining resistant lines (Du Plooy, 1991; Whiley *et al.*, 1993). Researches carried out in South Africa have led to the recent distribution of four cultivars selected for their resistance to black spot disease in South Africa: Ceriese, Heidi, Neldica and Neldawn (Du Plooy, 1991). The resistance mechanisms are still not known. The agronomic performance of the Sensation, Heidi and Neldawn cultivars and their susceptibility to this disease are currently being evaluated in Réunion.

Black spot disease of mango probably originated in the Indian subcontinent. The typical symptoms were observed on herbarium specimens collected in 1880. It is probably in this region that the longest confrontation between the host and pathogen has taken place. The genetic diversity of the pathogen among the Indian sources is distinctly wider than the genetic diversity in strains originating from other countries (Gagnevin *et al.*, 1997). It would therefore be interesting to prospect for sources resistant to the disease in this region. Furthermore, until now there is no information available on the susceptibility of other species of the genus *Mangifera* to the disease. Resistance sources could exist in this material.

Recent works have shown the existence of a fairly wide phenotypic and genetic variability in *Xanthomonas* sp. *mangiferaeindicae* (Gagnevin *et al.*, 1997). It is important to take this variability into consideration while evaluating the susceptibility of mango cultivars to bacterial black spot disease.

Citrus tristeza

Host plants of citrus tristeza virus

By host plant we mean plants capable of multiplying the citrus tristeza virus in their tissues, irrespective of the expression of symptoms. This capacity is usually tested by injecting the plants with an Elisa dose of the viral antigen.

The host range of the citrus tristeza virus is essentially restricted to the family Rutaceae. Nevertheless more than 100 species belonging to 38 other families have been found to be unharmed by the citrus tristeza virus after mechanical inoculation or after exposure to insect vectors. Only a few Passifloraceae species could be infected experimentally. However in Réunion, where the disease is efficiently transmitted by a vector, passifloras are very rarely infected by the citrus tristeza virus under natural conditions. Thus after two years of exposing 400 lianes (mainly *Passiflora edulis*) to natural vector populations, only one was found to be infected.

Resistance and tolerance sources in Rutaceae

The striking form of tristeza (quick decline) attacks especially sweet lime and mandarin orange trees when they are associated with certain rootstocks, particularly Seville orange. This is due to an incompatibility between the rootstock and scion provoked by the virus and has resulted in the loss of millions of trees grafted on Seville orange throughout the world. In the case of sweet lime and mandarin orange, the damage can be remedied by using rootstocks which can confer a tolerance or resistance to the association. About 20 lines of rootstock were tested with the Beauty mandarin. These associations, which were screened in Réunion in the presence of severe viral strains, helped to identify different rootstocks showing a good degree of resistance to the virus and at the same time possessing satisfactory agronomic characters (Grisoni, 1995; Grisoni *et al.*, 1989). On the other hand, several hybrids with Seville orange and *P. trifoliata* as parents proved to be deceptive. The natural hybrid of Gao-Tao Seville orange shows a good degree of resistance to quick decline but it was found to be susceptible to stem pitting under the conditions prevailing in the island of Réunion.

The resistance in *P. trifoliata* to citrus tristeza virus has already been put to use for producing rootstocks. Other sources resistant to the virus could be found in some Rutaceae and used in varietal breeding programmes.

The Carrizo citrange (hybrid of *P. trifoliata* and *Citrus sinensis*) has been retained for development programmes in the nurseries in Réunion Island. The same rootstock had also been selected in French West Indies long before the recent introduction of citrus tristeza virus and the aphid *Toxoptera citricidus* (Kirkaldy), which has helped to considerably reduce the impact.

Protection of directly susceptible species

Several species are themselves susceptible to the citrus tristeza virus (irrespective of the rootstock used). This is especially so with sour *Citrus* species such as lime, combava and pomelo. This susceptibility is expressed by symptoms of stem pitting, which is often accompanied by a more or less drastic reduction in the vigour of the plants. The intensity of symptoms varies greatly depending on the nature of the viral strains. This variability and the presence of interactions among viral isolates help to protect susceptible species from damage caused by severe strains by preinoculating the plants with a mild isolate. The protecting isolates for combava were selected in Réunion

Island (Aubert and Bové, 1984, Grisoni, 1995). Protection provides a lasting guarantee for the productivity of combavas in an environment where severe strains of tristeza virus are prevalent (Fig. 4).

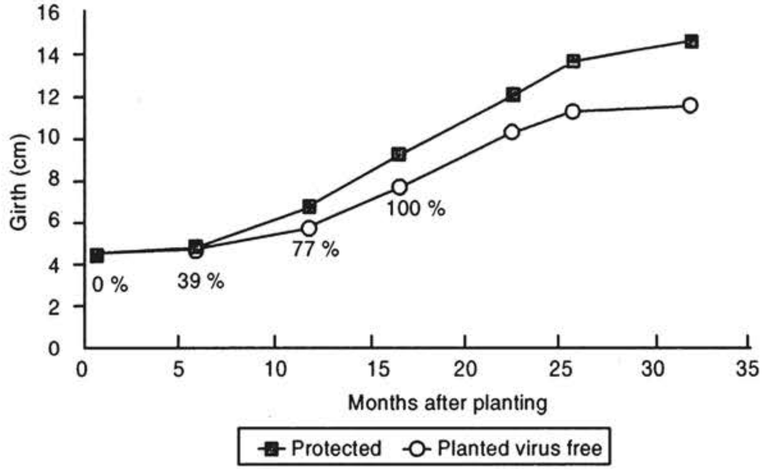

Fig. 4. Growth of grafts between combava, planted free of CTV and plants protected by the TR 26 isolate. Rate of contamination in plants planted free of the virus (from Grisoni, 1995).

CONCLUSION

The studies described in this chapter have often helped to jugulate diseases of tropical tree crops thanks to a profound knowledge of the evolution of the plant in its environment and thus helping to define selection strategies integrating the different parameters of economic interest.

However, these researches faced, or are still facing, several hurdles that cannot be ignored. Firstly, they concern the very nature of the tree crops because their reproductive and cultivation cycles generally impose long delays before results can be obtained and exploited.

Consequently it is necessary to develop early tests that are reliable, quick and reproducible. In most cases, knowledge of the causal organism or its vector has led to developing screening methods whose results can now be observed in full force. Nevertheless precautions have to be taken by adapting appropriate strategies against risks related to the development of resistance which is quickly overcome by the pathogen (for example, orange rust of coffee, South American leaf blight of hevea). Similarly, the plant material that is distributed should not depend on a very narrow genetic base, which is still the case with vascular wilt of oil palm in West Africa. The appearance of new pathogens may then prove to be disastrous.

Recent advances in biotechnology give reason to hope for new developments in the domain of breeding for varietal resistance. It is thus that analysis of plant pathogen populations and their diversity, characterised with the help of molecular markers, has helped to target isolates that are most representative of the different production zones. This progress should lead to a better evaluation of resistance and help in defining new breeding strategies based on selection aided by markers. The genetics of resistance, whose study is related to genome mapping of plants and identification of resistance genes, helps increasingly to plan a better management of host-parasite relationships and the mechanisms governing them.

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