

ANTIXENOTIC AND ANTIBIOTIC COMPONENTS OF RESISTANCE TO THE CASSAVA MEALYBUG *PHENACOCCUS MANIHOTI* (HOMOPTERA: PSEUDOCOCCIDAE) IN VARIOUS HOST-PLANTS

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Abstract—Antixenotic and antibiotic components of resistance to the cassava mealybug, *Phenacoccus manihoti* Matt. Ferr. were evaluated in different varieties of cassava (*Manihot esculenta* Crantz), in Poinsettia (*Euphorbia pulcherrima* Wild), Talinum (*Talinum triangulare* Jack) and Faux-caoutchouc (hybrid of *M. esculenta* and *M. glaziovii* Mull. Arg.). Resistance, was estimated in the field on 25 varieties of cassava by means of varietal screening. Although we were unable to identify varieties of cassava totally resistant to *P. manihoti,* there was evidence of partial resistances. Thus the Incoza variety is the most resistant, followed by the Moudouma and Zanaga varieties. On the other hand we found very susceptible varieties, such as Dikonda, Kataoli, 3M8 and 1M20. Laboratory evaluations of the antibiotic component of resistance, made by estimating the intrinsic capacity for increase r_c, showed that the host-plants have a considerable effect on the multiplying capacity of the mealybug. Indeed r_c ranges from 0.038 (Poinsettia) to 0.160 (Ganfo cassava variety), i.e. a ratio of 1 to 4 between the two extreme values. If the cassava varieties alone are considered, the percentage of maximum variation is 20% between the Incoza ($r_c = 0.133$) and Ganfo ($r_c = 0.160$) varieties. The Incoza cassava variety is the most resistant, in terms of both antixenosis and antibiosis. Classification of the other cassava varieties, from the most to the least resistant, differs according to the resistant component under consideration. Poinsettia and Talinum both have a very strong antixenotic component, but their antibiotic component differs (r_c = 0.038 and 0.150 respectively). Our results suggest that the resistance mechanisms of the host-plants of *P. manihoti* intervening in the fixation of the pest (antixenosis), are different from those acting on the development of the mealybug (antibiosis). We established significant correlations between the size of the mealybugs and their demographic characteristics for all the plants studied: the duration of the prereproductive period is shorter and the net reproduction rate is higher when the mealybugs are large-sized. These results are discussed in the context of an integrated monitoring programme.

Key Words: *P. manihoti,* Pseudococcidae, cassava, varietal resistance, antibiosis, intrinsic capacity for increase, antixenosis

Résumé—Les composantes antixénotiques et antibiotiques de la résistance de différentes variétés de manioc (*Manihot esculenta* Crantz), du Poinsettia (*Euphorbia pulcherrima* Wild.), du Talinum (*Talinum triangulare* Jack.) et du Faux-caoutchouc (hybride de *M. esculenta* et *M. glaziovii* Mull. Arg.), vis-à-vis de la-cochenille farineuse du manioc *Phenacoccus manihoti* Matt. Ferr., ont ete évaluees. La résistance au champ a été estimée sur 25 variétés de manioc, au travers d'un criblage variétal. Ce dernier n'a pas permis d'identifier des variétés de manioc totalement résistantes vis-à-vis de *P. manihoti;* il a cependant permis la mise en évidence de résistances partielles. Ainsi, la variété Incoza est la plus résistante, suivie par les variétés Moudouma et Zanaga. A l'opposé, nous trouvons des variétés très sensibles telles que Dikonda, Kataoli, 3M8 et 1M20. L'evaluation au laboratoire de la composante antibiotique de la résistance, au travers de l'estimation de la capacité intrinsèque d'accroissement r_c, montre que les plantes-hotes exercent une forte influence sur le

pouvoir multiplicateur de la cochenille. En effèt, r_c est compris entre 0.038 (Poinsettia) et 0.160 (variété de manioc Ganfo) soit un rapport de 1 à 4 entre les deux valeurs extrêmes. Si nous ne considérons que les seules variétés de manioc le pourcentage de variation maximum est de 20% entre les variétés Incoza (r_c = 0.133) et Ganfo (r_c = 0.160). La variété de manioc Incoza est la plus résistante aussi bien en terme d'antixénose que d'antibiose. Le classement des autres variétés de manioc de la plus à la moins résistante est différent selon la composante de résistance considérée. Le Poinsettia et le Talinum dont la composante antixénotique est trés forte, s'opposent en terme de composante antibiotique (r_c = 0,038 et 0,150 respectivement). Nos résultats suggerent que les mécanismes de résistance des plantes-hôtes de *P. manihoti* qui interviennent dans la fixation du ravageur (antixénose) sont différents de ceux qui agissent sur le développement de la cochenille (antibiose). Nous avons pu établir des corrélations significatives entre la taille des cochenilles et leurs caractéristiques démographiques pour l'ensemble des plantes étudiées: la durée de la période préreproductive est d'autant plus rapide et le taux net de reproduction d'autant plus élevé que les cochenilles sont de grandes tailles. Ces résultats sont discutés dans la cadre d'un programme de lutte intégrée.

Mots Clés: *P. manihoti*, Pseudococcidae, manioc, variété résistante, antibiose, antixénose, capacite intrinséque d'accroissement

INTRODUCTION

The cassava mealybug, *Phenacoccus manihoti* Matile-Ferrero (Homoptera: Pseudococcidae) is one of the main enemies of cassava, *Manihot esculenta* Crantz, Euphorbiaceae in tropical Africa since the early 1970s (Silvestre, 1973; Herren, 1987). After a period of biological control, with the successful introduction from 1982 onwards of the South-American Encyrtidae, *Epidinocarsis lopezi* De Santis (Herren, 1987), research has focused on the study of the relationships existing between the cassava mealybug and its host-plants, with the aim of detecting eventual degrees of resistance among some of them. Indeed, one of the best ways of reinforcing the impact of agents in biological control, consists of selecting varieties relatively unfavourable to the proliferation of their pests (Van Emden and Wearing, 1965; Starks et al., 1972; Dreyer and Campbell, 1987; Auclair, 1988). This strategy has led, not only to limiting the reproduction of the pest, but has also lengthened its growth period, giving the insect-feeders more time to intervene.

Painter (1951) grouped the insect resistance mechanisms in plants into three large categories: non-preference (a term redefined by Kogan and Ortman in 1978 and given the new name of antixenosis), antibiosis and tolerance. These categories do not exclude each other for they can interact or be complementary (Horber, 1972). Practically no study has so far been made on the relationships between the cassava mealybug and its host-plants. Only Fabres and Le Rü (1988) in the Congo showed that the antibiotic resistance component in the M'Pembe variety of cassava is expressed better on old leaves and on plants maintained in a state of hydric stress, whereas in Nigeria, Schulthess et al. (1987) demonstrated that the "91934" and "ODONGBO" varieties of cassava exert a strong antibiotic action on the mealybug.

In this context, basing our investigations on the wealth of plant material available in the Congo, we set out to evaluate the resistance capacity of different host-plants of the cassava mealybug. Under natural conditions, *P. manihoti* colonizes the cassava plant and Faux-caoutchouc (a hybrid of *M. esculenta* and *M. glaziovii* Mull. Arg.) (Iheagwam, 1981); it has also been observed from time to time on Talinum (*Talinum triangulare* Jacq., Portulacacae) (Neuenschwander et al., 1986). Under laboratory conditions, it can likewise be maintained on Poinsettia (*Euphorbia pulcherrima* Wild., Euphorbiaceae) (Boussienguet, 1984).

The aim of the present study is to assess the first two resistance components, antixenosis and antibiosis, which have a depressive effect on pest populations. They were investigated in the field by two varietal screenings of collections from southern Congo, and in the laboratory, by determining the intrinsic capacity for increase r_c (Laughlin, 1965), integrating the different development components of the insect (duration of pre-reproductive and reproductive periods, survival rates and daily fecundity).

MATERIALS AND METHODS

Study on resistance in the field and the choice of varieties for the study of antibiosis under laboratory conditions

Resistance in the field was assessed by varietal screening of 25 varieties of the cassava plant with a high yield, chosen by those in charge of the Congolese National Cassava Programme, in order to initiate tests in many places throughout the Congo. These are congolese varieties cultivated for the most part in one of the territory of the Congo (M'Pembe, Moudouma, Incoza, Moutsiele, Ganfo, Gantza, Dikonda, Kataoli, ...), selected varieties (1M20, 59M2, MM96, MM78, ...) and foreign varieties (Oumbete from Benin;

Kinuani, Incoza and Kataoli from Zaire; MB38 and MB30 from IITA, Nigeria (Table 1).

Varietal screening was performed on two tested collections in September 1987 (end of the dry season), the period when the mealybug populations are most prolific. One was, planted at the ORSTOM Centre (Institut Francais de Recherche scientifique pour le Developement en Cooperation) of Brazzaville, in the Pool region, and the other at the State Agro-Industrial Complex of Mantsoumba (C.A.I.E.M.) in the Bouenza region, 250 km from Brazzaville. They had both undergone the usual agronomic treatment practiced at the C.A.I.E.M.: (1) preparation of the soil in May (end of the rainy season) and in October (beginning of the rainy season), (2) application of limestone to improve the soil in September (1.5 T/ha), (3) planting in mid-November 1986. (10,000 cuttings/ha), (4) addition of NPK fertilizers (200 kg/ha) and (5) weeding whenever necessary throughout the rainy season.

Each variety occupied an elementary plot of land (72 m^2). At the time of the varietal screening, the plants were 8 to 10 months old and between 1.5 and 2 m in height. On each elementary parcel of land, the presence or absence of mealybugs and the degree of infestation on 20 colonized stalks collected at random were noted. The infestation level was based on visual estimation and classified according to a density scale (1= very slight to slight infestation, 1–25 mealybugs; 2= slight to mean infestation, 26–50; 3= mean to dense infestation, 51–75; 4= dense to very dense infestation, > 75). These indices enabled the percentage of infestation on each elementary plot and the mean infestation level, to be calculated. The very diverse edaphic conditions of the plots studied meant we had to plant control plots, one for five elementary plots. They were planted with the M'Pembe variety at Brazzaville and the Moudouma variety at Mantsoumba, both considered by the experts of the National Cassava Programme to be the best adapted

Table 1. Results obtained in September 1987 in Brazzaville (Pool region) and Mantsoumba (Bouenza region) from varietal screening of 25 varieties of cassava

		Locality						
		Brazzaville			Mantsoumba			
Variety	Origin	% infested stalks	Mean infestation level	Classification	% infested stalks	Mean infestation level	Classification	Global classification
Incoza	Zaire	80	1,4	2	27	0,3	1	1
Moudouma	Congo	80	1,5	5	53	0,6	3	2
MM79 (Zanaga)	Congo	87	1,7	7	53	0,5	2	3
MB38	Nigeria	87	1,4	2	73	0,9	5	3
MM85 (Langourou)	Congo	87	1,3	1	*	*	*	5
MM89 (Imbama)	Congo	93	1,5	5	67	0,7	4	6
MM86 (Gantza)	Congo	100	1,4	2	67	1,2	12	6
MM 101 (Kiheta)	Congo	100	2,1	8	73	1	8	8
MB30	Nigeria	87	2,3	9	73	1	8	9
MM 100 (Maham'bana)	Congo	100	2,5	10	93	1,1	10	10
Kinuani	Zaire	93	3	–	76	0,9	5	11
Kataoli	Zaire	100	2,8	12	100	1,2	16	12
30M7	Congo	87	2,6	11	80	1,4	12	12
M'pembe	Congo	93	3	13	67	1,3	14	14
Oumbete	Benin	100	3	13	87	1,3	14	14
Moutsiele	Congo	100	4,1	19	60	0,9	5	16
MM178	Congo	100	3,9	18	83	1,1	10	16
1M20	Congo	100	3,6	17	93	1,7	22	18
Moukondzi	Congo	100	4,1	19	60	1,5	18	19
3M8	Congo	100	4,5	23	93	1,4	19	20
Dikonda	Congo	100	4,4	22	100	1,6	19	21
MM104 (Mbouaki)	Congo	100	4,6	24	73	1,6	16	22
MM 105 (Ganfo)	Congo	100	4,7	25	73	1,6	19	23
MM96	Congo	100	3,5	16	*	*	*	24
59M2	Congo	100	4,2	21	*	*	*	25

* Variety absent from the locality studied.

to the edapho-climatic conditions of their respective region. The mean percentage of infested stalks and the mean infestation level were calculated for all the control plots in the test and for the two controls in each group of five elementary plots. For each group of five elementary plots, we obtained a correcting factor (% of variation of the mean of both the corresponding control plots compared with the mean of all the control plots in the test). This enabled us to calculate the percentage of infested stalks in each variety and the mean degree of infestation, taking into account the heterogeneity of the soil of the different plots studied.

We were thus able, in both localities, to establish a hierarchy of the varieties in a decreasing degree of resistance by a simple classification of the mean increasing levels of infestation. Finally a global classification was obtained from the mean of the two average levels of infestation (Table 1).

Experimental study of antibiosis performed in the laboratory

Owing to the experimental conditions (it took over six months to obtain the plants and establish the life history of *P. manihoti),* we restricted the laboratory experiment on antibiosis to 7 varieties of cassava, chosen among the 25 which had been subjected to varietal screening. They were divided according to their field expression of resistance as high (Incoza, Moudouma and Zanaga), moderate (M'Pembe, 30M7) and slight (3M8, Ganfo) (Table 1). Practical factors also determined the selection such as a high yield, a thick layer of canopy soil, a low loss of foliar material during the dry season (Zanaga), a good experience of planting the varieties among the local peasants (M'Pembe, Moudouma, Ganfo) (Mabanza, pers. commun.). We also assessed antibiosis on faux-caoutchouc, Talinum and Poinsettia, taking into account their biological characteristics, as follows: (1) Faux-caoutchouc hosts large populations of *P. manihoti* throughout the year, unlike the cassava plant on which they are present for only 3–5 months; (2) Talinum is planted alongside cassava plots and often bears large populations of the cassava mealybug (Neuenschwander et al., 1986; Le Rü, unpubl.); (3) Poinsettia is sometimes used in the laboratory as a substitution plant for the multiplication of the mealybug (A. Panis and J. Boussienguet, pers. commun.) and in the Congo it is never attacked by the mealybug under natural conditions.

The plants were obtained from 30-cm cuttings, planted vertically up to two-thirds of their length in plastic bags (30 x 20 cm) filled with earth. The pots are placed in the shade for 2 weeks in conditions favourable for early growth. The plants are then exposed to the full light until the leaves reach stage 9–10 (i.e. when the plant is approximately 60 cm high, 9 to 10 weeks later). They are watered twice a week. The pots (five per host-plant) are then placed for 2 months in an air-conditioned shed at a mean temperature of 25°C (range 21–32°C) and a mean relative hygrometry of 70% (range 60%–80%). The photophase is 12 hours per day. At the end of 4 months under these experimental conditions, we obtained plants with 19 leaves, measuring 90–100 cm high. Under natural conditions in the Congo, mealybug attacks occur, at the beginning of the dry season, on plants 3 to 8 months old deriving from the propagation of cassava plants by cutting, mostly performed between November and April.

The *P. manihoti* line (a species reproducing by strict thelytocous parthenogenesis), used for the laboratory experimentation, was collected on the M'Pembe variety in the market-garden area around Brazzaville in October 1988. In order to limit the influence of parental trophic feeding, the mealybugs were reared for four generations (6 months) on each of the 10 host-plants during investigations on antibiosis.

The daily intrinsic rate of increase, r_m is a good indicator of antibiotic resistance of plants to Aphididae (Starks and Berry, 1976; Birch and Wratten, 1984; Di Pietro and Dedryver, 1986; Sumner et al., 1986). This parameter, defined by Birch (1948), with its increase capacity r_c defined by Laughlin (1965), which constitutes a good approximation for the cassava mealybug (Le Rü and Papierok, 1987), integrates the different development components of the insect (duration of development and larval mortality, survival rate and daily fecundity). An analysis of the values obtained by this parameter for different cassava plant-mealybug combinations, should allow us to establish, in terms of antibiosis, a classification of the plants in terms of the highest to the lowest resistance.

Development and embryonic mortality were estimated from about 100 eggs deposited by mealybugs which had been maintained for five generations on each of the host-plants. Development and larval mortality, were followed on the different host-plants on five cohorts, each with about 100 larvae, on an average of one cohort per cutting. Adult reproduction and mortality were studied on approximately 100 females per host-plant, i.e. 20 females per cutting. All the data collected in this way enabled us to calculate for each host-plant studied, the intrinsic capacity for increase r_c of five populations of mealybugs.

The size and weight of the young females (stage L4, just before the start of oviposition) were also estimated on each of the 10 host-plants. Indeed, certain studies on Homoptera Aphididae (Taylor, 1975; Dixon, 1987; Fereres et al., 1989) have revealed the existence of a clear positive correlation between

Table 2. Demographic and morphological characteristics of *P. manihoti* for the seven varieties of cassava (Incoza, Moudouma, Zanaga, 3M8, M'Pembe, Ganfo, 30M7), Faux-caoutchouc, Poinsettia and Talinum

Host-plant	N_1	Duration pre-reproductive period (days)	Mortality %	N_2	Duration reproductive period (days)	*Ro* %	r_c	Size (1) (mm)	Weight (2) (mg)
Poinsettia	417	41.1 ± 2.0 a*	30	45	35.4 ± 4.0	129.8 ± 19.8	0.038 ± 0.003 c	1.10 ± 0.04 d	0.92 ± 0.10 d
Incoza	423	33.9 ± 1.7 b	5	34	20.8 ± 3.8	295.6 ± 82.6	0.133 ± 0.003 b	1.30 ± 0.03 c	0.99 ± 0.03 d
Faux-caoutchouc	426	32.4 ± 0.5 bc	3	47	18.8 ± 2.1	401.0 ± 61.5	0.141 ± 0.003 b	2.02 ± 0.02 a	1.65 ± 0.11 b
Moudouma	480	32.2 ± 0.5 c	2.5	46	23.6 ± 5.5	356.3 ± 48.3	0.143 ± 0.002 b	1.50 ± 0.4 b	1.20 ± 0.16 cd
Zanaga	467	31.7 ± 0.3 cd	2	49	18.1 ± 4.9	299.1 ± 95.1	0.155 ± 0.009 a	1.50 ± 0.49 b	1.25 ± 0.18 cd
3M8	574	30.4 ± 1.1 de	3.5	20	20.0 ± 2.5	284.7 ± 76.9	0.141 ± 0.005 b	1.60 ± 0.06 b	1.26 ± 0.30 cd
Talinum	465	30.1 ± 0.7 de	2	64	20.4 ± 2.2	287.6 ± 38.6	0.150 ± 0.001 ab	2.00 ± 0.02 ab	1.65 ± 0.04 b
M'Pembe	520	30.1 ± 1.7 e	1.5	61	16.0 ± 4.3	249.0 ± 69.3	0.150 ± 0.003 ab	1.53 ± 0.06 b	1.34 ± 0.21 c
Ganfo	453	29.5 ± 1.3 e	1.5	58	20.8 ± 1.5	367.6 ± 37.4	0.160 ± 0.003 a	2.01 ± 0.07 a	1.97 ± 0.06 a
30M7	520	29.2 ± 2.0 e	2	48	21.3 ± 2.4	298.0 ± 51.5	0.150 ± 0. 011 ab	1.60 ± 0.06 b	1.10 ± 0.11 d

N_1 Number of repetitions for the pre-reproductive period
N_2 Number of repetitions for the reproductive period.
(1) Mean of repetitions. Mean of 50 repetitions.
(2) Mean of five repetitions.

*The ± means followed by similar letters are not significantly different at the 1% confidence level for the duration of the pre-reproductive period DPP (F^9 = 32.82), for the real net reproduction rate *Ro* (F^9 = 7.095), for r_c (F^9_{40} = 167.65), for size *T* (F^9_{40} = 46,37) and for weight (F^9_{40} = 30,38)

these parameters and the fecundity of the predator. Size was estimated on 50 females measured separately, i.e. 10 females collected from five cuttings per host-plant. Weight was deduced from five different weighings of batches of 10 mealybugs, i.e. 10 mealybugs collected from five cuttings per host-plant.

The mean values were treated statistically by a variance analysis (*F* test) at a confidence level of 1%, and by the PPDS method at a 1% confidence level. The link between the parameters observed and the antibiotic resistance of the 10 host-plants has been studied by a discriminating factorial analysis: 10 populations x five repetitions = 50 individuals; six variables = parameters (Dagnélie, 1975), and by simple correlation at a 5% confidence level.

RESULTS

All the results obtained are summarized in Table 2. The values for Poinsettia, obtained by the demographic parameters: duration of the pre-reproductive period (*DPP*), duration of the reproductive period (*DPR*), larval mortality and net reproductive rate (*Ro*) are very different from those observed on the nine other plants studied. Thus, the duration of the pre-reproductive period, which is 41.1 days on Poinsettia, ranges for the other plants from 33.9 to 29.2 days on the Incoza and 30M7 cassava varieties, respectively, i.e. a difference of 4.7 days between the two extreme values. Larval mortality, which is high on Poinsettia (30%), is very low for all the other host-plants, ranging from 4% (Incoza variety of cassava) to 1.5% (M'Pembe and Ganfo varieties of cassava), i.e. a difference of 2.5% between the two extreme values. The duration of the reproductive period, which is 35.2 days on Poinsettia, ranges for the other plants between 21.3 and 16 days on the 30M7 and M'Pembe cassava varieties, respectively, i.e. a difference of 5.3 days between the extreme values. Likewise, the net reproductive rate *Ro* is 129.8% on Poinsettia, whereas for the other plants, it is between 401.0% and 249.0% on Faux-caoutchouc and the M'Pembe variety of cassava, respectively.

The values obtained by the r_c parameter, which integrates the demographic parameters previously studied, confirm the rather unfavourable character of Poinsettia regarding the development of the mealybug (r_c = 0.038). Nine other plants studied, had r_c ranges from 0.160 to 0.133 for the Ganfo and Incoza cassava varieties respectively. The size and weight parameters of the mealybugs, varying greatly from one plant to another, are comprised between 2.0 mm (Faux-caoutchouc, Talinum and the Ganfo variety of cassava) and 1.1 mm (Poinsettia) for the former, and 1.97 mg (Ganfo) and 0.92 mg (Poinsettia) for the

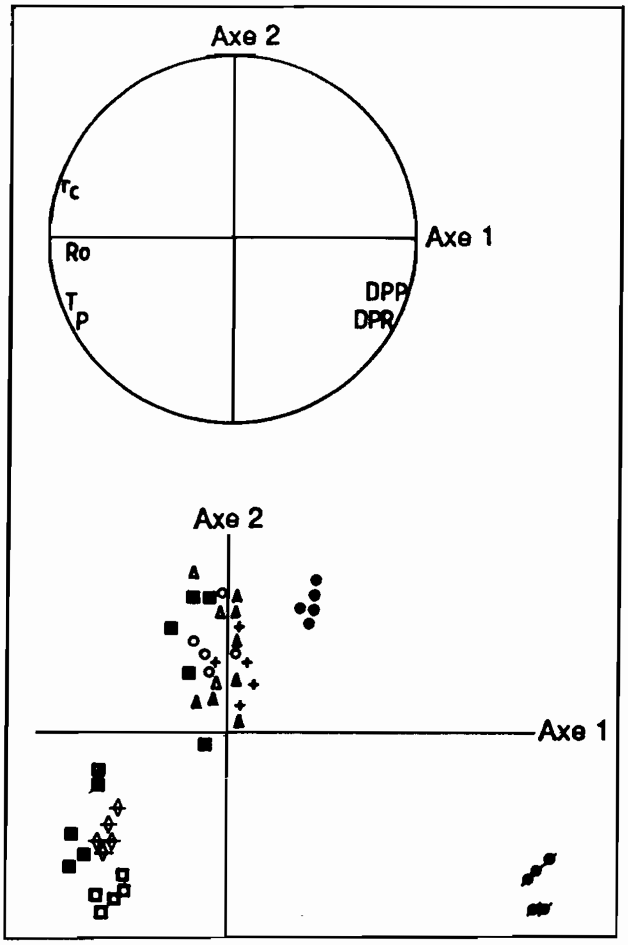

Fig. 1. First factorial plan of a discriminating analysis made on all the plants studied (seven varieties of cassava: Incoza (•), Moudouma (+), Zanaga (Δ), 3M8 (▲), M'Pembe (o), Ganfo ( ), 30M7 (■), Faux caoutchouc ( ), Poinsettia (ø) and Talinum (◊)) with repetitions (five per host plant), regarding the six parameters r_c, *DPP, DPR, Ro, T* and *P*.

Table 3. Simple correlations between the duration of the pre-reproductive period (*DPP*), the net reproductive rate (*Ro*), the intrinsic capacity for increase (r_c), size (*T*) and weight (*P*) of *P. manihoti* for the seven varieties of cassava (Incoza, Moudouma, Zanaga, 3M8, M'Pembe, Ganfo, 30M7), Faux-caoutchouc, Poinsettia and Talinum

	Ro	r_c	*T*	*P*
Ro				
r_c	0,770			
T	0,723	0,646		
P	-0,619	0,541	0,920	
DPP	-0,648	0,951	-0,674	-0,550

** $P < 0.05$; ddl = 9.

latter. Table 3 shows the correlations between the different demographic and morphological parameters studied. The size of the mealybugs is significantly correlated ($n = 10, P = < 5$ %) to the three demographic parameters, duration of the pre-reproductive period (*DPP*), net reproductive rate (*Ro*) and the intrinsic increase capacity (r_c) whereas the weight of the mealybugs is only significantly correlated to *Ro*.

Table 4. Varietal inter-group correlations between the parameters studied: Duration of the pre-reproductive period (*DPP*), duration of the reproductive period (*DPR*), net reproduction rate (*Ro*), intrinsic capacity for increase (r_c), size (*T*) and weight (*P*) and the discriminating variables 1 and 2

	Axe 1	Axe 2
DPP	0,8908	-0,3547
Ro	-0,849	-0,007
r_c	-0,901	0,433
P	0,809	-0,468
T	-0,912	-0,411
DPR	0,8086	-0,4529

The discriminating factorial analysis (Fig. 1) shows that the first two factors restitute almost 98% of the variability of the resistance indices studied. The projection of the statistical units on to the first factorial plan makes it possible to visualize the differences between the 10 host-plants studied. We note that the first discriminating variable is closely correlated to all the parameters studied (Table 4). It is negatively correlated with the r_c, *Ro, P* and *T* parameters, and positively correlated with the *DPP* and the *DPR* parameters. This discriminating variable can therefore be interpreted as being the expression of the capacity of plants to favour or retard the multiplication of *P. manihoti*. Thus, the first discriminating axis opposes the plants with a low multiplication rate, such as Poinsettia, to plants with a high multiplication rate, such as Faux-caoutchouc, Talinum and the Ganfo variety of cassava. Although the interpretation of the second discriminating variable is more complex, the combination of the first two discriminating axes makes it possible: (1) to demonstrate the peculiar situation of Poinsettia among the 10 plants studied, characterized by the longest *DPP* and *DPR*, the weakest *Ro* and r_c indices, and small-sized females (2) to separate the nine other plants studied into three groups ranked in a decreasing order of resistance to the mealybug: that of Incoza with low *Ro* and r_c indices, small-sized females, long *DPP* and *DPR;* that of Zanaga, 30M7, Moudouma, 3M8 and M'Pembe characterized by mean values of the parameters studied, and that of Ganfo, Talinum and Faux-caoutchouc with high *Ro* and r_c indices, large-sized females and the lowest *DPP* and *DPR*.

DISCUSSION AND CONCLUSION

From the results obtained by field selection in the collections tested at Brazzaville and Mantsoumba, the varieties of cassava were totally resistant to *P. manihoti*. They did however, reveal partial resistances. These results confirm those of Albuquerque (1976) and CIAT (1977) obtained from selections made in

Brazil and Colombia respectively, which did not lead either to the identification of varieties of cassava totally resistant to Pseudococcidae. Although they were carried out in two different places, classification of the varieties from the most to the least resistant (Table 1) are similar for most varieties. We have not succeeded, however, in determining whether the differences observed are due to different edapho-climatic or phytosanitary conditions in the two localities. In the field, the antixenotic resistance component, estimated by calculating the percentage of infested stems, seems to vary considerably from one variety to the next. The Incoza variety is resistant, followed by the Moudouma and Zanaga varieties. At the other end of the scale, we found highly sensitive varieties such as Dikonda, Kataoli, 3M8 and 1M20. Our protocol for evaluating resistance in the field did not allow us to determine, on its own, the antibiotic component of resistance. Indeed the mean level of infestation integrates both the antixenotic (% of infested apexes) and the antibiotic (level of infestation) components.

Our experimental results obtained in the laboratory concerning the antibiotic component of resistance, confirmed those of Schulthess et al. (1987), who have shown that the host-plants exert a strong influence on the increase capacity of the mealybug. In fact, r_c comprised between 0.038 (Poinsettia) and 0.160 (Ganfo variety of cassava), i.e. a ratio of 1 to 4 between the two extreme values. If we consider the cassava varieties alone, the percentage of maximum variation is 20% between the Incoza ($r_c = 0.133$) and Ganfo ($r_c = 0.160$) varieties. It is 2.5 times greater than that observed by Schulthess et al. (1987) in Nigeria, with only an 8% maximum variation between the 91934 (r_m = 0.1573) and EGE DUDU (r_m = 0.1704) cassava varieties.

The Incoza variety is the most resistant in terms of both antixenosis and antibiosis. Classification of the other varieties of cassava from the most to the least resistant, differs according to the resistance component considered. Thus, the Zanaga variety with a high antixenotic component has a low antibiotic resistance. On the other hand, the 3M8 variety with a low antixenotic resistance has a strong antibiotic component. Poinsettia is never colonized and Talinum is hardly ever colonized in natural conditions. Both have a very high antixenotic resistance component, the former is very antibiotic ($r_c = 0.038$), whereas the latter is not (r_c = 0.150, identical to that of the M'Pembe and 30M7 cassava varieties). These results suggest that the resistance mechanisms of the host-plants of *P. manihoti* which intervene in the fixation of the pest (antixenosis) are very different from those acting on the development of the mealybug (antibiosis). Similar conclusions have been reached by Dent (1986) and Firempong (1988) regarding Homoptera Aphididae, underlining the need for a study on both these components of resistance. Our results were obtained on plants of 4 to 6 months. Under natural conditions in the Congo, mealybug attacks occur, during the dry season until the beginning of the rainy season (July to October), on 3–12 months old plants issuing from propagation of the cassava plant by cutting, which is done mostly between November and April. One might ask if our results can be transposed to more advanced phenological state of the studied plants, cassava in particular. Various investigations made on Homoptera Aphididae have indeed revealed an influence of the phenologic stage of the plant on the expression of resistance (Kieckhefer, 1983; Di Pietro and Dedryver, 1986). From the practical point of view, in a programme for the varietal selection of the cassava plant, the estimation of antixenotic and antibiotic resistance components should be made at two phenologic stages at least, at 4–6 months as in our study, and at 10–12 months, in order to cover the whole period during which risks of infestation by the mealybug exist.

Among the demographic parameters studied, the duration of the *DPP* is the one which contributes most to the values obtained by r_c. In fact, the *DPP* is the best correlated parameter ($r = -0.951$, $P < 5$ %). Moreover, in a programme of varietal selection, a *DPP* estimation alone, which is simple and quick to perform, could well be a preliminary stage of the evaluation of antibiotic resistance. Comparable results have been obtained by Di Pietro and Dedryver (1986) who studied the resistance of winter wheat to attacks by the aphid, *Sitobion avenae* (F.) (Hom. Aphididae). We have been able to establish significant correlations between the size of mealybugs and their demographic characteristics for all the plants studied in our investigations. The developmental characteristics of *P. manihoti* are similar to those of Homoptera Aphididae (Lowe, 1974; Taylor, 1975; Ajayi and Dewar, 1983; Wellings and Dixon, 1987; Fereres et al., 1989). It is generally agreed that in Homoptera Aphididae the nutritional quality of the trophic substrate could be the origin (Mittler, 1958; Dixon, 1987). The selection of resistant varieties, by inducing a decrease in the size and weight of the pest, could well limit the efficiency of the parasitoid *E. lopezi*. In fact the sex ratio (%) of the latter increases when the size of its host decreases (Kraaijeveld and Van Alphen, 1986; Van Dijken et al., 1991). Furthermore, however incomplete it may be, the integration of the resistance of certain varieties of cassava in a programme of integrated control is likely to induce an important reduction in *P. manihoti* densities, as certain simulation models regarding cereal aphids in Europe have shown (Carter and Dixon, 1981; Acreman, 1984). Yet the sex ratio of *E. lopezi* is greatly affected by the density of its host (Van Dijken et al., 1991). In a programme of varietal selection in support of a programme of biological control, a detailed study of the interactions between plants, phytophagous species and parasitoids is essential. Special attention must be paid to the varietal incidence on the sex ratio of *E. lopezi,* owing to the importance of this parameter in biological control (Sinha and Singh,1979; Bhatt and Singh, 1991).

This is the first time that the different categories of resistance by plants to the cassava mealybug have been investigated, and we are now able to identify the varieties of the cassava plant which are partially resistant, in terms of antixenosis and antibiosis, to *P. manihoti.* However, the mechanisms of this resistance have still not been clearly defined. The pressure of selection exerted by the cassava pests appears to be low (cassava crops are widely dispersed, with very many local lines and traditional varieties all differing considerably in their susceptibility to pests and to disease), probably indicating a horizontal polygenic type of resistance (Belloti and Kawano, 1980). If this is confirmed, we may suppose that the cassava plant has numerous resistance mechanisms. Under natural conditions, mealybug infestation of cassava is considerable for only 3 months of the year. Sudden variations in the size of predator populations are observed, when important physiological changes take place in the plant (dessication of the summit of the cassava stalk in the dry season and a rise of sap at the beginning of the rainy season), related to variations in climatic factors (rainfall, temperature, hygrometry) (Le Rü et al., 1991). These observations indicate that modifications in the photosynthetic activity provoke temporary changes in the resistance of the plant, suggesting resistance mechanisms linked to biochemical factors, such as the composition of amino acids, carbohydrates and secondary substances (free cyanides, phenols, alkaloids) in phloem sap. Differences in biochemical composition among plants with different degrees of resistance to the cassava mealybug have yet to be studied.

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