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Biological Parameters of *Bemisia tabaci* (Gennadius) Biotype B (Hemiptera: Aleyrodidae) on *Jatropha gossypiifolia*, Commercial (*Manihot esculenta*) and Wild Cassava (*Manihot flabellifolia* and *M. carthaginensis*) (Euphorbiaceae)

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ABSTRACT - *Bemisia tabaci* (Gennadius) is one of the most important pests of cassava in Africa and several countries of Asia due to the damage caused by direct feeding, the excretion of honeydew, and its capacity as a vector of cassava mosaic geminivirus. There is a general consensus that *B. tabaci* is a complex of morphologically indistinguishable populations with different biotypes. In the Americas, the polyphagous biotype B does not appear to feed on cassava. Recent studies indicate that it is possible, however, for biotype B to gradually adapt to cassava using phylogenetically related hosts. Therefore, the possibility that some wild species of cassava constitute intermediate hosts in the adaptation process may lead to the establishment of biotype B on commercial varieties of *Manihot esculenta*. In here, we evaluated *Jatropha gossypiifolia*, two wild species of cassava (*Manihot flabellifolia* and *M. carthaginensis*) and a commercial cassava variety (MCol 2063) as hosts of biotype B. The highest oviposition rate (2.7 eggs /two days) occurred on *M. esculenta*, although the development time (44 d) was the longest when compared to *M. carthaginensis* and *J. gossypiifolia*. About 60% of the population could reproduce on the wild cassava species vs. 55% on *J. gossypiifolia* and 27.5% on the commercial variety. Our data suggest that *J. gossypiifolia* is a suitable host and the wild species *M. carthaginensis* can constitute a potential intermediate host in the adaptation of biotype B to commercial varieties of cassava.

KEY WORDS: Adaptation, trophic relationship, whitefly

Cassava, *Manihot esculenta*, is the third largest source of carbohydrates for humans in the Tropics, particularly in Africa and Asia (Fauquet & Fargette 1990, Legg *et al* 2002). In Africa, the most limiting factor and utmost economic importance for cassava production is the cassava mosaic disease (CMD), caused by a complex of cassava mosaic geminivirus (CMGs) (Geminiviridae: *Begomovirus*) (Legg *et al* 2002). There is a strong overlap between the geographic ranges of distribution of the African cassava mosaic virus (ACMV) and its only known vector, the sweet potato whitefly, *Bemisia tabaci* (Gennadius) (Robertson 1987, Fauquet & Fargette 1990).

Bemisia tabaci is a complex of morphologically indistinguishable biotypes and depending on the host, cultivar, environmental conditions and pathogen involved, they can cause until 95% of yield losses (Legg 1999). Although monophagous and oligophagous populations of *B. tabaci* have been reported, e.g., *Jatropha* (Brown *et al* 1995) and the cassava biotype (Abdullahi *et al* 2003), respectively, the complex is formed mainly by polyphagous populations (Mound 1983). Among them, the biotype B appears to have the widest host range (Brown *et al* 1995). On this respect, it is suggested that there is a wide range of genetic differences among the *B. tabaci* populations that permit them to adapt to new hosts and climates in different geographic regions (Basu 1995).

The distribution of biotype B into new areas in the Americas and the Caribbean is often associated with the movement of plants and the ability of some *B. tabaci* populations to adapt to a broad spectrum of new hosts (Bedford *et al* 1994). In Latin America, the biotype B is displacing biotype A and becoming adapted to new hosts such as cassava (*M. esculenta*) (Lima *et al* 2002, Rodríguez *et al* 2005). Indeed, very soon after being firstly reported on this crop in the Dominican Republic (Brown *et al* 1995), it was found in Cuba (Vásquez *et al* 1995) and, more recently, in Colombia and Ecuador (Anderson *et al* 2005). It is important to bear in mind that the *B. tabaci* complex includes vectors of viruses to crops often grown in association with cassava (e.g., common beans, sweet potatoes, tomatoes, cotton and soybeans) (Costa & Russell 1975, Bellotti & Arias 2001). In addition, studies in India revealed that *B. tabaci* could

transmit CMV (Matew & Muniyappa 1993). All of these point to the possible circulation of viral diseases between cassava and other hosts and/or the possibility of acquirement and transmission of new viruses.

Unfortunately, there are few historic events that would allow to reconstruct or to explain the entry and subsequent colonization of hosts by *B. tabaci* in different areas of the world. In the case of *M. esculenta*, for instance, the *B. tabaci* populations that feed on this host in Africa and Asia are included within the cassava biotype (unlike the biotype B). The origin of this biotype, regarded as oligophagous, is unknown but it is able to develop in the wild on *M. esculenta*, *Solanum melongena* and *S. aethiopicum* (Legg *et al* 1994). The reproductive capacity of the cassava biotype has been demonstrated on *Nicotiana debneyi* (Thompson 2003), *Manihot glaziovii* (Legg *et al* 1994), *Lycopersicon esculentum* and *Vigna unguiculata* (Omondi *et al* 2005). Therefore, the hypothesis that polyphagous populations of *B. tabaci* (biotype B) from the Americas could become adapted to cassava should not be disregarded (Carabalí *et al* 2005). Using the concept of gradual adaptation on a series of intermediate hosts in the genus *Manihot* (comparing reproduction rates), these authors successfully bred a line of the biotype B of *B. tabaci* able to develop on *M. esculenta*.

Hence, it is plausible to postulate that the wild *Manihot* species could be key hosts in which *B. tabaci* could increase its biotic potential in the process of adaptation to *M. esculenta*. The objective of this study was to evaluate the potential of adaptation of *B. tabaci* to alternative species of *Manihot*. We have compared the development of Colombian biotype B populations on *J. gossypiifolia*, two wild cassava species (*M. flabellifolia* and *M. carthaginensis*) and commercial cassava variety (MCol 2063) (*M. esculenta*).

Material and Methods

***Bemisia tabaci* and wild cassava (*Manihot* spp.).** The biotype B strain of *B. tabaci* came from a colony established on *Phaseolus vulgaris* var. ICA-Pijao at the CIAT Common Bean Project, originated near Dapa (Cauca Valley Province, Colombia). The colony was reared for five generations on *J. gossypiifolia* (Carabalí *et al* 2005) under controlled conditions (25 ± 2°C; 70 ± 5% RH; LD12: 12), in 1 m^3 cages made of cotton mesh and wood. The purity of the strain was verified periodically by testing adults using RAPD-PCR analysis (Quintero *et al* 2001). Ten 40-d-old plants of *J. gossypiifolia*, *M. flabellifolia* and *M. carthaginensis* were supplied by CIAT`s Genetic Resources Unit.

Longevity and fecundity. These life history traits were studied using forty newly emerged and previously sexed pairs (males; females) of *B. tabaci* coming from *J. gossypiifolia*. Adults were introduced into insect clip cages (diameter = 2.5 cm; depth = 2.0 cm) using a manual aspirator by placing them on the underside of the leaves of ten plants of each host (*J. gossypiifolia, M. flabellifolia*, *M. carthaginensis* and *M. esculenta*). Every 48h, the adults in the insect clip cage were transferred to a new leaf area. This process was continued until natural death of the females; males were replaced as they died. Fecundity was estimated as the number of eggs oviposited by females every 48h (in order to minimize disturbance and mortality).

Development time, survival rate and sex ratio. Fifty unsexed, 2-day-old adults of *B. tabaci* were taken from the apical leaves of *J. gossypiifolia* with an aspirator and transferred to insect clip cages (see above) on the underside of the leaves of *J. gossypiifolia, M. flabellifolia, M. carthaginensis* and *M. esculenta*. Adults were allowed to oviposit for 6h and 200 eggs were selected at random with the aid of a binocular (40 x) stereomicroscope. Development time from egg to adult, survival rate of the immature stages and sex ratio were recorded under the same laboratory conditions as above.

Demographic parameters. The data on the development time, the survival rate of the immature stages and the proportion of females were combined with the experimental data on reproduction (lx-mx) to generate life tables. For each experiment, the following parameters were calculated (Price 1975):

The net reproduction rate (Ro) (defined as the average number of female progeny that a female had during a generation), the generation time (T) (equivalent to the period between the eclosion of the parents and that of the progeny), the intrinsic growth rate of the population (r_m) (represents the daily contribution of each individual to population development). The intrinsic growth rate of the population (r_m) was estimated using the equation (Carey 1993):

$$\sum \exp(-r_m x)\, lxmx = 1,$$

where *x*, is the age of the female; lx is the specific age of survival and mx is the proportion of females of the progeny of a female at age x.

To calculate the r_m values, the corrected age (X+0.5) and the equation ln 2/ r_m for estimating the necessary days to double the population were used (Carey 1993).

Statistical analyses. Kaplan-Meier statistical package which includes four statistical tests (i.e. Gehan-Wilcoxon, Cox-Mantel, Peto-Wilcoxon and Logrank-tests) was used to compare survivorship of females among host species from median survival times (Lee 1992) (Statistix 8.0). Differences between the mean values of longevity, fecundity, oviposition rate and development time were analyzed using one-way ANOVA. Student-Newman-Keuls was used for the multiple-comparison tests. The survival rates of the immature stage were compared using χ^2 test (SAS Institute 1989). The life table parameters were estimated by Jackknife technique and means were compared by ***t*** test using the LIFETABLE.SAS software developed by Maia *et al* (2000).

Results and Discussion

Female longevity, fecundity and oviposition rate. According to the conservative Cox-Mantel and Logrank-tests, survival time was similar on all plant hosts (Table 1).

Table 1 Median survival time (days) test of *Bemisia tabaci* on *Manihot carthaginensis*, *M. esculenta*, *M. flabellifolia* and *Jatropha gossypiifolia* (n = 40).

Host	Gehan-Wilcoxon	Cox-Mantel^{ns}	Logrank test^{ns}	Peto-Wilcoxon
J. gossypiifolia	8.0 (8-10) a	8.0 (8-10)	8.0 (8-10)	8.0 (8-10) a
M. esculenta	5.0 (4-6) c	5.0 (4-6)	5.0 (4-6)	5.0 (4-6) b
M. flabellifolia	6.0 (6-6) b	6.0 (6-6)	6.0 (6-6)	6.0 (6-6) b
M. carthaginensis	6.0 (6-8) b	6.0 (6-8)	6.0 (6-8)	6.0 (6-8) a

Medians followed by different letters within a column differ significantly; ^{ns}non significant.
ANOVA $P < 0.0001$ Kaplan-Meier Survival test $P < 0.05$.

However, the same *B. tabaci* survival on *J. gossypiifolia* and *M. carthaginensis* were statistically different when compared with *M. esculenta* and *M. flabellifolia* when analyzed with the Peto-Wilcoxon test. Further, a significant trend was observed with the Gehan-Wilcoxon test. The later is more suitable to explain the biological significance of our results as it indicates that any female reared on *J. gossypiifolia* survived, in average, three days (see Table 1) longer than those on *M. esculenta* and two days more compared with *M. flabellifolia* and *M. carthaginensis*. These differences can be observed in the survival curves (Fig 1). The survival curves also show that, the percent live females was reduced to 28, 65, 82.5 and 90% on *J. gossypiifolia*, *M. carthaginensis*, *M. esculenta* and *M. flabellifolia*, respectively, on the sixth day.

The mean longevity of *B. tabaci* females was higher (nine days) on *J. gossypiifolia* ($P < 0.0001$, followed by Student-Newman-Keuls $P < 0.05$), with females living four to six days longer on the other host plants tested (Table 2). Our data on female longevity on *J. gossypiifolia* was similar to that obtained when *B. tabaci* was reared on a suitable hosts, such as garden bean (Musa & Ren 2005).

Bemisia tabaci fecundity varied among host species (Table 2). The average number of eggs per female was 1.5, three and two times higher on *J. gossypiifolia* as compared with *M. esculenta*, *M. flabellifolia* and *M. carthaginensis*, respectively. The highest oviposition rate (2.7 eggs/female/2 days) was found on *M. esculenta*, being significantly higher than in the wild cassava species and *J. gossypiifolia* (ANOVA $P < 0.0001$ followed by Student-Newman-Keuls $P < 0.05$). In all four species, females began oviposition during the first 48h, obtaining 71% and 67% of the total fecundity on *M. esculenta* and *M. flabellifolia*, respectively; whereas on *M. carthaginensis* and *J. gossypiifolia* it reached only 36% and 12%, respectively (Fig 2). The highest number of eggs was obtained during the first 6 d of oviposition on the four hosts, with maximum values on the second day for *M. esculenta* and *M. flabellifolia*, and on the fourth day for *M. carthaginensis* and *J. gossypiifolia*. Data analyses indicated that when populations of *B. tabaci* were reared for some generations on *J. gossypiifolia* they had higher oviposition capacity and longevity.

Development time, survival rate and sex ratio. The development time of *B. tabaci* on *J. gossypiifolia* was significantly different when compared to wild *Manihot* species (Table 3). The survival rates of the immature stages was also affected by the host plant ($\chi^2 = 127.2$, 2 d.f., $P < 0.0001$; Table 3). From a total of 200 eggs, 120 reached the adult stage on *M. carthaginensis*, compared with 101, 55 and 16 adults on *J. gossypiifolia*, *M. esculenta* and *M. flabellifolia*, respectively. This parameter can be a good indicator of the potential capacity that *B. tabaci* has for developing on the wild cassava species *M. carthaginensis* and on the cultivated variety. Although survival was lower on *M. flabellifolia*, this

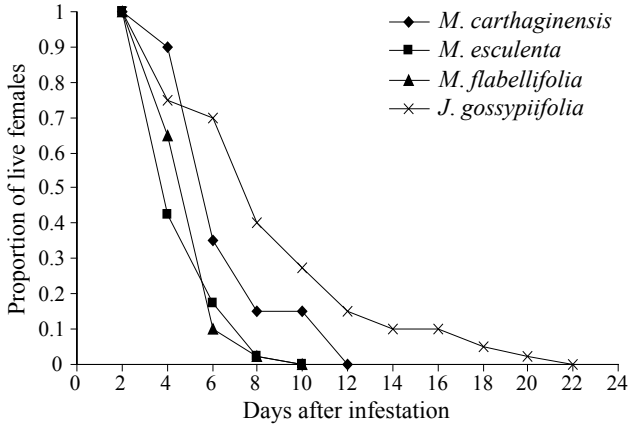

Fig 1 Survival curves of females of biotype B of *Bemisia tabaci* on *Manihot carthaginensis*, *M. esculenta, M. flabellifolia* and *Jatropha gossypiifolia*

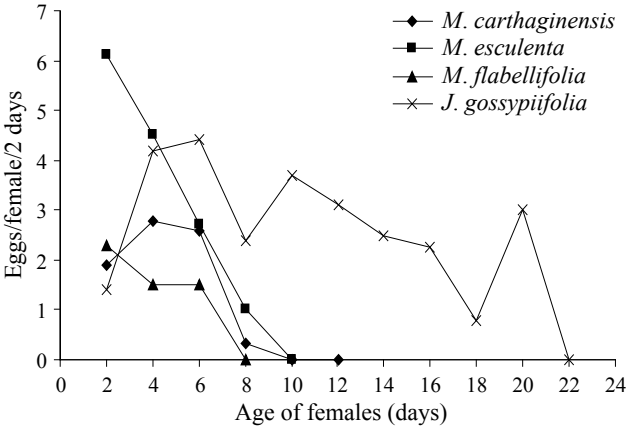

Fig 2 Oviposition curves of biotype B of *Bemisia tabaci* on *Manihot carthaginensis*, *M. esculenta*, *M. flabellifolia* and *Jatropha gossypiifolia*.

result has important implications, given that it constitutes a new host on which *B. tabaci* was able to feed, reproduce and complete its life cycle.

The sex ratio (0.5) was not affected when *B. tabaci* was reared on *J. gossypiifolia*, *M. carthaginensis* and *M. esculenta*, but had a slight difference on *M. flabellifolia* (0.56: 0.5) (Table 3).

Demographic parameters. The net reproductive rate of *B. tabaci* on *J. gossypiifolia* was significantly different when compared to *M. esculenta* and wild *Manihot* species ($P < 0.05$). Data on the net reproductive rate (Ro) allowed the estimation of a population growth of 4.3 times at each generation on *J. gossypiifolia*. The population growth on this host plant was two times higher than that on *M. esculenta* and *M. carthaginensis* (Table 4). Females of *B. tabaci* had the lower values of Ro (0.2) when reared on *M. flabellifolia*. This variability can be explained by the lower rate of fecundity reached on *M. esculenta* and wild *Manihot* species.

The generation time (T) was also affected by the rearing host, developing faster on *J. gossypiifolia*, with *M. flabellifolia* being the host in which the insect took the longest period to develop (Table 4).

The intrinsic growth rate (r_m) was 0.055 on *J. gossypiifolia* and 0.033 on *M. carthaginensis* (Table 4). Both values were statistically different from those

Table 2 Longevity (days), fecundity (eggs/female) and oviposition rate (eggs/female/2 days) of *Bemisia tabaci* on *Manihot carthaginensis*, *M. esculenta*, *M. flabellifolia* and *Jatropha gossypiifolia* (n = 40).

Parameter	*M. carthaginensis*	*M. esculenta*	*M. flabellifolia*	*J. gossypiifolia*
Mean longevity	5.1b	3.1c	3.6c	9a
Range	2 - 12	2 - 10	2 - 8	2 - 22
Mean fecundity	5.4b	8.2b	3.9b	12.1a
Range	1 - 35	1 - 41	1 - 16	1 - 39
Oviposition rate				
Mean	0.9b	2.7a	1.2b	1.4b
Range	0.25 - 3.6	0.5 - 8	0.25 - 4	0 - 39

Means within a row followed by the same letter are not significantly different at the 5% level. ANOVA $P < 0.0001$ followed by Student-Newman-Keuls, $P < 0.05$.

Table 3 Development time (days), survival rate and proportion of females of *Bemisia tabaci* on *M. carthaginensis*, *M. esculenta, M. flabellifolia* and *Jatropha gossypiifolia*.

Parameter	*M. carthaginensis*	*M. esculenta*	*M. flabellifolia*	*J. gossypiifolia*
Time development	33.3 a	44.4 a	47.2 a	27.5 b
Nº. insects	120	55	16	101
Survival rate	0.6 a	0.275 c	0.08 d	0.55 b
Nº. insects	200	200	200	200
Proportion of females	0.50	0.50	0.56	0.50
Nº. insects	120	55	16	113

Means within a row followed by the same letter are not significantly different at the 5% level. ANOVA $P < 0.0001$ followed by Student-Newman-Keuls, $P < 0.05$. Chi square = 141.6, 3 d.f., $P < 0.0001$.

Table 4 Life table parameters of *Bemisia tabaci* on *Manihot carthaginensis*, *M. esculenta*, *M. flabellifolia* and *Jatropha gossypiifolia*.

Parameter	*M. carthaginensis*	*M. esculenta*	*M. flabellifolia*	*J. gossypiifolia*
Net reproductive rate (Ro)	2.3 b	1.56 b	0.2 c	4.3 a
Intrinsic growth rate (r_m)	0.033 b	0.014 b	-0.028 c	0.055 a
Generational time (T)	29.8 c	37.9 b	60.8 a	28 d
Duplication time (TD)	21 b	49.5 a	-24.7 c	12.6 b

Means within a row followed by same letter are not significantly different at the 5% level.
ANOVA $P < 0.0001$ followed by Jackknife method $P < 0.05$.

obtained for populations reared on *M. esculenta* and *M. flabellifolia* ($P < 0.05$). However, *B. tabaci* had the highest growth rate on *J. gossypiifolia,* surpassing those reared on *M. carthaginensis* and *M. esculenta* by 40% and 75%, respectively. In case of individuals reared on *M. flabellifolia*, the r_m value was negative (-0.028), suggesting the wild host species had a negative impact on insect development and reproduction, reducing the population capacity to increase in number. Our data suggest that there are differences in the biotic potential of the insect reared on *J. gossypiifolia* and *M. carthaginensis* as compared with *M. esculenta* and *M. flabellifolia*.

Fecundity and longevity of *B. tabaci* were the biological traits most affected by wild *Manihot* species and *M. esculenta*. Similarly, the results show that of the four hosts evaluated, *J. gossypiifolia* was the most favorable for the adaptation of biotype B. The high survival rate in the immature stage, lower development time, and the highest intrinsic growth rate of the population represent unmistakable indicators of the suitability of *J. gossypiifolia* for the development of this biotype. Nevertheless, the percentage of whitefly immatures that survived on *M. carthaginensis* was similar to those obtained by Tsai &Wang (1996) with *B. tabaci* on suitable hosts such as tomato (*Lycopersicon esculentum*) and potato (*Ipomoea batatus*).

The reproductive success (high fecundity and reproductive rate) obtained by *B. tabaci* on *M. esculenta* was not evident later in the development of the immature stages (survival rate). These results concur with those reported by Costa *et al* (1991), who did not found a direct correlation between the number of eggs deposited by *B. tabaci* and the survival rates on different hosts. This suggests that oviposition of *B. tabaci* can be a phenomenon that is not mediated by evaluating the potential quality of the host plant.

Despite the polyphagous nature of populations of *B. tabaci* found in the Americas and the sporadic records of whitefly on cassava (Brown *et al* 1995, Vásquez *et al* 19950, Anderson *et al* 2005), this crop does not appear to be an important host. Nonetheless**,** after a process of pre-adaptation on species phylogenetically related to the genus *Manihot* (*Euphorbia pulcherrima* and *Jatropha gossypiifolia*), Carabalí *et al* (2005) were able to show that *B. tabaci* found in Colombia was able to develop and reproduce on commercial cassava, thereby confirming the potential of this biotype to become adapted to this host. Moreover, *J. gossypiifolia*, the bridge host used in this study, still continues to support high populations of *B. tabaci* under laboratory rearing conditions. In contrast, *J. gossypiifolia* has been reported as hosting monophagous populations of the biotype known as "Jatrofa" in Puerto Rico (Brown *et al* 1995, Perring 2001).

These variations confirm the constant dynamics or the plasticity of the variations of populations of *B. tabaci* and reveal the complexity of establishing a permanent boundary between them. Taken together, these facts suggest a possible explanation for the emergence of different populations, which in relatively short periods of time acquire the status of host races or biotypes.

Our data demonstrate for the first time that the biotype B of *B. tabaci* can feed and reproduce on *J. gossypiifolia* and on two wild cassava species, closely related to *M. esculenta*. At the same time, it is possible that the adaptation of this biotype on *M. esculenta* in Colombia is favored by the existence of hosts such as *J. gossypiifolia* or *M. carthaginensis* on which *B. tabaci* can develop successfully. In addition, this issue is particularly valid and key at moments when several developing countries, such as Colombia, Brazil and Central American countries, are adopting strategies to increase the areas to be cultivated with *Jatropha* spp. (especially *J. curcas* (Foidl *et al* 1996), as they have multiple uses. However, our results recall for prudence. Despite the fact that *Jatropha* could yield major potential economic and environmental benefits for these countries, helping to combat soil erosion, create additional income for the rural poor, and alleviate countries' balance of payment constraints (van Eijck & Romijn 2008), at the same time they represent a risk to cassava growers as *Jatropha* may work as a bridge for *B. tabaci* to become adapted to *Manihot* species. This would certainly require a reevaluation of the expansion of the areas cultivated with *Jatropha*, as cassava crop is a primary food source for many people in the third world, and may represent the sole food source in many African and Latin American countries.

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