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Host plant and biotype density interactions – their role in the establishment of the invasive B biotype of *Bemisia tabaci*

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Abstract

Bemisia tabaci is a complex of closely related genetic types of whiteflies, few of which are invasive. One of these, B biotype, has proven to be particularly adapted to invading new areas, but the underlying reasons as to why it has a well-developed capacity to invade is not known. To develop an understanding of factors that may be contributing to B's invasive capacity, inter-biotype mating interactions and host plant suitability for the exotic B (*B. tabaci* Mediterranean/Asia Minor/Africa) and the indigenous Australian (AN) biotype (*B. tabaci* Australia) were examined. The results suggest that when confined to a mutually acceptable host, B cannot establish when the ratio of AN : B exceeds 20 : 1. However, when simultaneously provided with a host that only it prefers, B is able to establish even at 50 : 1 (AN : B). Further, when both biotypes occur together the number of progeny per female increases (relative to the number produced when only one biotype is present). The response is observed for both biotypes, but is considerably greater in the case of B. In addition, B performs better in the presence of the AN biotype B. tabaci Australia while AN perform worse in coexistence with B, but only if the demographics allow B to mate without significant interference. This leads to the prediction that B will invade in circumstances where its unique hosts are of sufficient number to escape the full negative impact of inter-biotype mating interactions and reduced competitiveness in terms of reproductive rate, while exposing the indigenous biotype to the full effects of the interaction.

Abbreviation: DNA-polymerase chain reaction; RAPD-PCR – random amplified polymorphic

Introduction

Bemisia tabaci (Gennadius) (Hemiptera : Aleyrodidae), a haplo-diploid species of whitefly, is composed of numerous genetically distinct populations often, although perhaps incorrectly, referred to as biotypes (Frohlich et al. 1999; De Barro et al. 2000). At present there are 20 distinct genetic types (Perring 2002), of which few have, at least in recorded history, proven to be invasive. A distinctive feature of the global distribution of these genetic types is the strong geographic delineation of their distributions (Frohlich et al. 1999; De Barro et al. 2000, 2005). The clear exception has been the B biotype (sometimes referred in the literature to *B. argentifolii* (Bellows & Perring)), which in the past 20 years has spread rapidly around the world to become a considerable pest of agriculture in the Americas, Australia, Mediterranean Basin and the Middle East (see De Barro 1995 for review). Why this biotype, and not others, has become such a successful invader is unclear.

Part of the explanation may lie in the curious biology stemming from mating interactions between different biotypes (De Barro and Hart 2000; Pascul and Callejas 2004). Using the interaction between the B and Australian (AN)

biotypes as a model, DeBarro and Hart (2000) found that the interaction between the two biotypes reduced overall population increase through a marked increase in the proportion of male progeny, production of no fertile hybrid females, and the laying of fewer eggs by females paired with males of the different biotype (compared with females paired with males of the same biotype). Further, their data suggested that a threshold existed that required a minimum number of the invading biotype adults relative to the indigenous biotype before establishment could occur. That is, in situations where the existing biotype was abundant, incursions involving exotic biotypes were likely to be at a relative numerical disadvantage. Consequently, exotic biotypes, given their inability to distinguish between conbiotypes (Li et al. 1989), were more likely to encounter and attempt to mate with individuals from the established biotype resulting in fewer eggs being laid, no fertile female progeny and a slow rate of population growth. Together, these were likely to reduce the likelihood of establishment.

Invasions by exotic species generally involve a small number of individuals. If the above were the sole determinants for an invasion success, then one would not expect B's success as an invader, as it would nearly always be at a numerical disadvantage to the indigenous biotype in terms of any mating interaction. This suggests that B has the capacity to escape the negative interactions and increase the prospect for same-biotype matings. This study, explores this possibility by extending the study on biotype interactions to include the role that host plant availability plays in establishment and tests the hypothesis that the relative suitability of host plants to different biotypes of *B. tabaci* contributes to the capacity to establish.

Materials and methods

Whitefly cultures and adult collection

Whiteflies of both biotypes were maintained in separate cultures on painted spurge, *Euphorbia cyathophora* Murray (Euphorbiaceae) in separate screened glasshouses. Cultures were screened for purity using random amplified polymorphic DNA-polymerase chain reaction (RAPD-PCR) according to the protocol outlined in De Barro and Driver (1997) and De Barro and Hart (2000). Whiteflies used in the experiments were collected from cultures as fourth instar red eye pupae and placed in emergence cages. As *B. tabaci* adults < 12 h old do not mate (Li et al. 1989), only those that had emerged within this period were used to ensure their virginity. Adults used in the experiment were collected into glass vials, to assess starting sex ratios and confirm biotype purity. The identity of whiteflies collected during the course of the experiment was also determined.

Cage experiment

To study the interaction threshold between the two biotypes and the role of host plant in biotype establishment, a field cage experiment was set up using 18 test cages and six control cages, each measuring $1 \times 1 \times 2$ m and covered with fine mesh screen. Two host plants were used: spurge (*E. cyathophora*), a species on which both biotypes perform well and cotton (*Gossypium hirsutum* L.; Malvaceae), a host on which the AN biotype does poorly in contrast to the B biotype. Two spurge plants were placed into each of six test cages. In each of another six test cages two cotton plants were placed while in the third set of six test cages, one cotton and one spurge were placed. Cotton and spurge plants have different numbers and sizes of leaves. To account for this, an assessment was made of leaf area using the length and breadth of leaves. Plants were then selected so that the difference in total leaf area was within 5%. For each host plant combination, three ratios of B to AN females were tested, 1 : 10, 1 : 20 and 1 : 50, with a starting population of either one (plus one B male) or five (plus three B males) B females. Male AN whiteflies were also added with the numbers being 50% of the number of AN females added. Samples were taken at the end of the first and second generations. In each generation, 15 leaves were collected from each cage at random from across each plant. A 24 mm diameter disk was cut from each leaf and the total number of nymphs on the disk counted. Six control field

cages were also set up using either 10, 20 or 50 adult females belonging to each of the two biotypes, plus half the number of males, and provided with two spurge plants. In addition to the leaf samples, 100 adults were collected from each cage and preserved in 95% ethanol for sex determination and biotyping.

Statistical analysis

Analysis of variance was used to test differences in factors and their interactions using the three-factor interaction term as the error. The mean nymph density for each generation was log transformed prior to analysis. The difference between the log estimates when back transformed provides an unbiased estimate of the proportional increase or decrease within and between treatments. The difference between the two log densities for the two generations was also analysed to yield estimates of the proportional increase per generation.

Two analyses were performed, one with three plant combinations (cotton, spurge and cotton plus spurge) and the other with four plant combinations (separating the cotton plus spurge treatment to cotton in the presence of spurge and spurge in the presence of cotton with the sample size halved for these combinations). The percentage males and the percentage B individuals were also analysed by combining both generations and then using generation as another factor.

Results

All means and LSDs are presented as log-transformed data. Where appropriate, back-transformed data are presented in parentheses for ease of comparison.

Nymph density – first generation

The overall mean density of nymphs was significantly affected by the initial B type density ($F = 2374$, df = 1, 6, $P < 0.001$) with no interactions with the other factors (estimate of lower density, 0.029; higher density, 0.718 sed 0.0205). After back transformation, the highest density was 4.9 times higher (nymphs/cm^2) than the lowest density (95% confidence interval 4.0–6.0). The plant types (plant types, $F = 1081$, df = 3, 6, $P < 0.001$) and initial density of AN ($F = 962$, df = 2, 6, $P < 0.001$) both also had significant effects on nymph density and there was a significant interaction ($F = 214$, df = 6, 6, $P < 0.001$) (Table 1). Overall, nymph density on spurge was greater with cotton in the cage than on spurge alone. In contrast, the density on cotton when spurge is in the cage was less than with cotton alone. The density on spurge alone was greater than on cotton alone.

The interaction (Table 1) shows that as more AN females were added to the cage, the increase in nymph density was much greater on spurge than on cotton. With spurge the proportional increase from 1 : 10 to 1 : 20 was 5.2-fold and from 1 : 20 to 1 : 50, 5.7-fold. When cotton was present with the spurge the increases were 5.8- and 3.1-fold. With the cotton and cotton plus spurge treatments the increases from 1 : 10 to 1 : 20 and from 1 : 20 to 1 : 50 were both 1.2-fold.

As the analysis of nymphs of the second generation was very similar to the first generation it is redundant to present it here. It is more useful instead to analyse on the log scale, the difference between generations so as to give the proportion increase per generation.

Rate of increase between generations

The difference in log nymph densities between the two generations for each of the factors was calculated for the 36 observations. In the analysis, the effect of the initial number of B females was not significant. The effects of host combination ($F = 302$, df = 2, 8, $P < 0.001$), initial AN numbers ($F = 142$, df = 2, 8, $P < 0.001$), and

Table 1. Estimates of the log nymph density (nymphs/cm^2) for the interaction of host plant and biotype ratio using four plant treatments, LSD 0.111 (for the first generation).

Host combination	1 : 10	1 : 20	1 : 50
Cotton	−0.025	0.040	0.128
Cotton plus spurge	−0.138	−0.066	0.004
Spurge	−0.141	0.582	1.337
Spurge plus cotton	0.246	1.008	1.507

Table 2. The mean difference in log nymph densities between the two generations for each host combination and each initial ratio of B to AN.

Host combination	1 : 10	1 : 20	1 : 50
Cotton	0.82 (6.6)	0.81 (6.5)	0.83 (6.8)
Spurge	0.36 (2.3)	0.39 (2.5)	0.84 (6.8)
Cotton plus spurge	0.58 (3.7)	0.62 (4.1)	0.66 (4.5)

The LSD was 0.16. Also shown in parentheses is the back transformation giving the proportional increases in nymph densities per generation.

their interaction ($F = 89$, df = 4,8, $P < 0.001$) were all significant (Table 2).

Percentage males

The percentage of males in the 18 cages for both generations was obtained from a sample of 100 adults collected from each cage. In the analysis, the effects of the initial number of B females, generation and their interactions were not significant, i.e., results were not different between the first and second generation, nor when one or five B females were used. However, the effects of host combination ($F = 138$, df = 2, 25, $P < 0.001$), the initial density of AN females ($F = 29$, df = 2, 25, $P < 0.001$) and their interaction ($F = 22$, df = 4, 25, $P < 0.001$) were all significant (Table 3). The percentage of males was greatest in the spurge treatments, except for the starting ratio of 1 : 50 where B failed to establish, intermediate in the cotton plus spurge treatments and lowest in the cotton treatments where AN where numbers were close to zero.

Table 3. The mean percentage of male whiteflies in each of treatment combination, pooled over levels of starting density of B which had no significant effect.

	Starting ratio of B : AN		
Host combination	1 : 10	1 : 20	1 : 50
Cotton	23.3 ± 3.7	21.3 ± 1.4	19.3 ± 3.3
Spurge	69.8 ± 1.7	77.5 ± 2.1	21.3 ± 2.8
Cotton plus spurge	48.8 ± 1.3	48.8 ± 4.5	47.3 ± 2.8

The LSD is 8.0.

Percentage B individuals

Similarly, the percentage of B individuals in the samples was analysed. Again, neither the initial numbers of B females, nor generation had any effect in the analysis whereas host combination, the initial AN density and their interaction all had strongly significant effects ($P < 0.001$, LSD 5.3) (Table 4). In the case of cotton, virtually no AN established while on spurge, B failed to establish when the initial starting ratio was 1 : 50.

Derivation of progeny per female in the first generation

Table 5 shows the percentage of males and females of both biotypes in each of the nine treatment combinations. This enabled the nymph density for each combination to be partitioned. Using nymphs/cm^2 as a measure of progeny and knowing the initial number of females of both species for the first generation, it is possible to derive the progeny per female for each host combination and the starting ratio for both biotypes.

The densities of nymphs derived from the untransformed data for the treatments are shown in Table 6. Where five B females were added, the results were divided by five and pooled with the data where a single one B female was added to give an overall estimate. This was possible for all treatments combinations as five B females gave five times the nymphal density produced from a single B.

The data (Figure 1) indicates that in the cotton treatments where B made up more than 99% of the whiteflies present, the density per female ranged from 0.41 to 0.61 per cm^2 indicating a small increase in density per female across the three

Table 4. Estimates of the percentage of B individuals in each treatment for the interaction of host plant and biotype ratio.

	Starting ratio of B : AN		
Host combination	1 : 10	1 : 20	1 : 50
Cotton	96.5 ± 2.4	99.8 ± 0.2	99.0 ± 0.7
Spurge	25.0 ± 4.3	29.3 ± 3.9	0
Cotton plus spurge	38.3 ± 5.8	34.0 ± 4.7	27.0 ± 3.8

The LSD is 5.3.

Table 5. The percentage of males and females of each biotype in the 1st generation for each host combination and starting ratio of B : AN.

Host combination	1 : 10				1 : 20				1 : 50			
	B♂	B♀	AN♂	AN♀	B♂	B♀	AN♂	AN♀	B♂	B♀	AN♂	AN♀
Cotton	21.5	75.0	1.8	1.8	21.5	78.5	0	0.3	19.3	79.8	0	1.0
Spurge	19.3	5.8	50.5	24.5	25.0	4.3	52.5	18.3	0	0	31.5	68.5
Cotton plus spurge	23.3	15.0	25.5	36.3	21.3	12.8	27.5	38.5	15.3	11.8	32.0	41.0

Table 6. The mean density (nymphs/cm^2) of nymphs (both biotypes combined) derived from the untransformed data for each treatment .

Host combination	1 : 10	1 : 20	1 : 50
Cotton	0.42	0.49	0.61
Spurge	0.32	1.71	9.40
Cotton plus spurge	0.56	2.46	7.44
Spurge, AN only control	2.84	5.04	12.87
Spurge, B only control	4.33	9.83	24.67

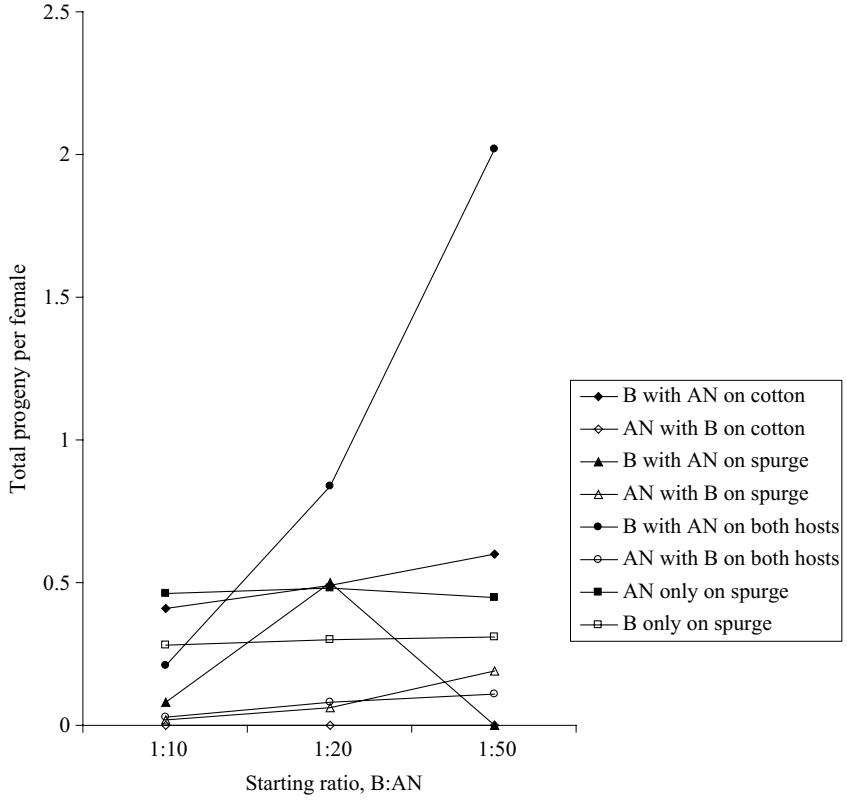

Figure 1. The estimated total progeny per female for each biotypes for each host combination and starting ratio of B : AN.

initial densities. However, when both biotypes were present in the cotton plus spurge combination, the estimated density of B increased from 0.21 to 2.02, representing an approximately 4-fold increase between 1 : 10 and 1 : 20 and 2-fold between 1 : 20 and 1 : 50 whereas the

estimated increase in AN was only 2-fold between 1 : 10 and 1 : 20 and remained virtually unchanged between 1 : 20 and 1 : 50. Similarly, in the spurge treatments, the estimated increase in B between 1 : 10 and 1 : 20 was approximately 6-fold while AN increased 3-fold. In the total absence of either AN or B (Figure 1), females on spurge showed no increase in the number of offspring per female across the starting densities.

Discussion

Many of the elements of the interaction noted in De Barro and Hart (2000) (see introduction) were again observed here, but host plant emerged as an additional important factor in mediating the overall interaction between the two biotypes in terms of the capacity of biotypes to establish in a given space. This was borne out in four dependent variables of the study : density of nymphs, increase in numbers between generations, percentage of males produced, and the ratio at which the B biotype established. The nymphal density was greatest in treatments where only one biotype established, lowest when both biotypes were forced together on a mutually acceptable host and intermediate when presented with a mix of hosts – one suitable to both biotypes and the other, cotton, to only one of the biotypes. Similarly, the rate of increase between the two generations mirrored the above patterns. Further, the percentage of males produced was greatest when both biotypes co-occurred on the same host, was intermediate when one of the two available hosts was suitable to only one of the biotypes and lowest when both hosts were suited to only one biotype. The consequence of these interactions was that B established best when able to exploit a space containing hosts unfavourable to the indigenous biotype and the capacity to establish increased as the proportion of these hosts also increase from 50 to 100%. Further, when confronted by hosts suitable to both biotypes, B established only when the numbers of invading individuals were not so diluted by the indigenous biotype as to preclude intra-biotype courtship and mating, i.e. did not exceed the threshold of establishment which in this study was between 1 : 20 and 1 : 50 B to AN individuals. This is supported by the observation that AN adults do not readily move onto non-preferred hosts when suitable healthy preferred hosts are also available (P.J. De Barro, unpublished data). Under these circumstances, adults straying onto non-preferred hosts are unlikely to settle sufficiently long to engage in courtship activities which take on average 21 min (Li et al. 1989). The biotype is therefore best able to establish when the space it invades includes a host that only it can exploit. This enables it to avoid inter-biotype interactions and the proportion of space occupied by the host governs the extent of the avoidance.

The broad host range of the B biotype (see De Barro 1995 for review) enables it to utilise a number of non-indigenous ornamental and crop host species that are not hosts of the potentially competing indigenous biotypes. This is indicative of invasional meltdown (Simberloff and Von Holle 1999). The concept of invasional meltdown proposes that successive non-indigenous species facilitate the establishment and spread of subsequent invaders. Here we extend that idea to include agricultural and ornamental species which, through the actions of humans become widespread and moderate the interaction between biotypes.

A further element of the interaction was the difference in the deduced numbers of progeny per female in the first generation in single biotype and mixed biotype treatments. The number produced remained either constant or showed a very slight increase across the three densities when all individuals belonged to the same biotype. In contrast, when two biotypes were present, relative fecundity increased markedly in most cases as overall density increased, with the B biotype exhibiting the stronger response. These observations suggest that the presence of feeding by two biotypes rather than one biotype influences the host in ways that benefit the whiteflies. Further, the magnitude of the response observed in the B biotype suggests it benefits from the interaction to a greater extent than the AN biotype. The only exception to this was the 1 : 50 on the mutually acceptable host, spurge, where the B biotype failed to establish, presumably due to the negative outcome of the inter-biotype mating interaction.

Feeding by herbivorous insects is known to induce a range of chemical responses in plants (Walling 2000; Gatehouse 2002). In most cases, these responses act to protect the plant from further attack by either the same or different species (Moran and Whitham 1990; Alla et al. 2001; Petersen and Sandstrom 2001; Messina et al. 2002). However, in some cases feeding by one species acts to reduce the host's capacity to deter feeding by the same or different species (Gange and Brown 1989; Underwood 1998; Agrawal and Sherriffs 2001). The effect of whiteflies in this regard is unknown, but feeding by other phloem feeders, in particular aphids, can significantly improve the fitness of subsequent infestations. Aphids such as *Elatobium abietinum* (Walker) (Fisher 1986) and *Pemphigus betae* Doane (Larson and Whitham 1991) were able to induce changes in the host that favoured subsequent reinfestation. In the case of gall forming species such as *P. betae*, this was via the mechanism of altered source–sink relationships in the leaves (Larson and Whitham 1991; Burstein et al. 1994). As well as benefits to con-specifics, Kidd et al. (1985) demonstrated that feeding by *Schizolachnus pineti* (Fabr.) enabled a second species, *Eulachnus agilis* (Kalt.) to improve its overall fitness by feeding on the same leaves as *S. pineti*. The response we have observed, while suggesting a possible change in source–sink relationships, is perhaps a less likely explanation, as the effect was not apparent when only a single biotype was present.

Whiteflies, specifically *Trialeurodes vaporariorum* (Westwood) and *B. tabaci*, induce a range of genes associated with plant defences (Jimenez et al. 1995; Mayer et al. 1996; Walling 2000; Mayer et al. 2002). Further, different biotypes of *B. tabaci* can induce plant gene responses that vary in level depending on the biotype and the life stage involved in the attack (van de Ven et al. 2000; Walling 2000). While the function of these various induced responses is not fully understood, prior feeding by the B biotype has recently been shown to affect the fitness of potential competing herbivores negatively (Mayer et al. 2002). These studies suggest that it is more likely that the combined feeding by two biotypes reduces the impact of plant defences either by direct detoxification or the down-regulation of wound responses. In our study, the magnitude of the response decreased as the ratio of B to AN increases such that as the increase from 1 : 20 to 1 : 50 saw no improvement in production per AN female and a much weaker increase for B females. This indicates that the response needs the presence of a sufficient number of both biotypes before it can take effect, suggesting that not only the mix, but the relative numbers of each is important in understanding the impact of inducible plant defences on a community of herbivores (Stout et al. 1999; Thaler et al. 2001, 2002).

Our research provides a useful insight into why the B biotype is such a good invader. The data suggest that the B biotype will perform better (based on nymphs/female data) in the presence of the AN biotype (mixed cultures compared to alone), that the AN biotype will selectively perform worse in coexistence with the B biotype (mixed cultures compared to alone), but only if the demographics allow B to mate successfully. This would lead to the prediction that the B biotype would be a serious invader in circumstances where its unique hosts outnumber those of the native thereby enabling it to escape the full negative impact of the mating interaction. In contrast, if the indigenous biotype has a host range that is entirely acceptable to B, it will not be able to escape and so will be more susceptible to the mating interaction. One would therefore predict that those regions successfully invaded by the B biotype are populated with indigenous biotypes that possess host ranges that do not overlap completely B's whereas, those where B has yet to invade have biotypes with host ranges equivalent in composition to that of the B biotype.

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