

Biotypes of *Bemisia tabaci* and their relevance to the evolution and management of insecticide resistance

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ABSTRACT

In an effort to understand the factors that influence the dynamics of co-existing biotypes and how these impact upon the dynamics of insecticide resistance and the implementation of management strategies, we consider Mediterranean populations of *Bemisia tabaci*. These exist as a dynamic mix of 'B' and 'Q' biotypes. The published evidence suggests that these biotypes display different ecological and behavioral traits and different responses to insecticides and we consider how these might affect the spread and development of insecticide resistance. We present an overview of ongoing work that aims to characterize resistance in recently collected strains of 'B' and 'Q' biotypes from cotton fields, and that examines the ability of these forms to introgress (by measuring mating success rates, hybrid sex ratio and fecundity). We consider the impact that dispersal, introgression and the inheritance of resistant traits between biotypes might have on the development of insecticide resistance and describe large-scale laboratory studies on cotton, which aim to give empirical illustrations of these phenomena. The relevance of this research to resistance management is discussed.

Introduction

The increasing incidence of the cotton whitefly, *Bemisia tabaci* (Homoptera: Aleyrodidae) and its associated plant viruses ensures that the formulation and implementation of IPM strategies against this pest are a major priority for the global cotton industry. Both *B. tabaci* and some of the viruses that it transmits possess considerable evolutionary plasticity and consequently have the ability to adapt rapidly to any management tactic. A major complicating factor in understanding the dynamics of these adaptations is the global occurrence of several *B. tabaci* 'biotypes', which have the capacity to spread and supplant forms indigenous to particular regions (Brown *et al.*, 1995; Costa *et al.*, 1993; Moya *et al.*, 2001). These biotypes are morphologically identical but can be discriminated using biochemical and molecular markers.

In southern Europe and the Middle East, the two most widespread biotypes are referred to as the 'B' and 'Q' biotypes. These can be categorized by their enzyme banding patterns and although the presence of the 'B' band is associated with the hydrolysis of pyrethroids (Byrne *et al.*, 2000) the function of the esterases associated with 'Q' type banding pattern are unknown.

The literature is incomplete, but these distinct forms appear to show variation in their demography,

host plant specificity and virus transmission capability (e.g. Ishaaya and Horowitz, 1995; Muniz and Nombela, 2001; Jiang *et al.*, 1999; Sánchez-Campos *et al.*, 1999). The 'B' biotype has a broad geographical distribution and is considered to be a recent invader over much of its range. The 'Q' biotype was originally considered to be restricted to the Iberian Peninsula, but has recently been detected in Italy and, unexpectedly, to occur alongside the 'B' biotype in Israel (Horowitz *et al.*, 2000). The intra-population diversity of 'Q' biotype populations of the whole Mediterranean basin suggests that it is the indigenous biotype of the region (Moya *et al.*, 2001). A decade ago, it was not considered an important pest, but it is possible that highly competitive populations of the 'Q' biotype evolved and spread in response to current agricultural practices, and to the aggressive control measures adopted to control the novel 'B' biotype (which was originally considered a greater problem).

Monitoring of these biotypes has indicated that their distributions are not static, but change rapidly in response to unknown selection pressures (Beitia *et al.*, 1997; Beitia *et al.*, 1998). The impact that the dynamics of these biotypes might have on crop production and protection are difficult to predict but it is conceivable that they could lead to substantial changes in host plant range, geographical distribution, insecticide efficacy, severity of attack and virus incidence. An understanding of the biological characteristics of *B. tabaci* biotypes and their interactions may therefore be essential in the design and implementation of pest and resistance management strategies.

The potential importance of biotypes

A central hypothesis relating to the evolution of biotypes (and ultimately of species) is that specialization and divergence is driven by characteristics that encourage assortative mating. Thus the presence of discrete biotypes implies some ecological constraint to interbreeding. For example, host plant preferences in the pea aphid (*Acyrtosiphon pisum*) lead to *de facto* assortative mating despite the fact that there are no genetic barriers to introgression (Caillaud and Via, 2000). Such reproductive isolation can lead to biotypes with quite different biological characteristics and some of these may be of profound importance in pest management. For example, biotypes of the Hessian fly (*Mayetiola destructor*) and the greenbug (*Schizaphis graminum*) are partially categorized in terms of their resistance to wheat and sorghum cultivars (Patterson *et al.*, 1992; Beregovoy and Peters, 1994; Kindler *et al.*, 2001). Host plant preferences in *Aphis gossypii* appear to have led to insecticide resistance traits being linked to some biotypes and not others (Hosoda *et al.*, 1993; Saito, 1991). In *B. tabaci* itself, the 'B' biotype that emerged from the Americas in the 1980s has been associated with increased host range, plant pathogenic

effects and increased insecticide resistance (Cohen *et al.*, 1991; Costa *et al.*, 1993b; Costa *et al.*, 1993a).

Existing work on biotypes of *B. tabaci* around the Mediterranean basin has shown that their spatial and temporal distribution is dynamic. In many instances, both 'B' and 'Q' biotypes occur together (Guirao *et al.*, 1997b; Simón *et al.*, 2001; De Barro *et al.*, 2000) but the most detailed surveys have been made on the Iberian Peninsula. In 1993, biotype 'B' had a range that extended from the Algarve (Portugal) to Almeria (Spain), and was also found in Barcelona and Madrid (Arnó and Gabarra, 1994; Guirao *et al.*, 1997a). A non-'B' biotype (later named biotype 'Q') (Banks *et al.*, 1998) had an identical distribution and in certain cases was even found in the same sampling plots (Beitia *et al.*, 1997; Guirao *et al.*, 1997a). Later surveys (1998 and 2000) however, failed to detect biotype 'B' populations in Spain, except in the area of Barcelona. This change in the dominance of the two biotypes appears to have been mirrored in the Canary Islands (Beitia *et al.*, 1998).

It seems that not only does some barrier to introgression serve to maintain the distinctiveness of these biotypes, but that unknown factors are acting upon their distributions. Some studies have associated 'B' and 'Q' biotypes with specific host plants (Bosco *et al.*, 2001; Chermitti *et al.*, 1997) virus problems (Monci *et al.*, 2000) or particular types of insecticide resistance (Horowitz *et al.*, 2002). Any of these might serve to give one biotype an advantage over another. There is a growing literature that suggests that biotypes of *B. tabaci* do show distinct traits, although it is also true that many of these studies only refer to very specific comparisons between a single representative of each biotype studied (Table 1).

Biotypes and insecticide resistance

B. tabaci exhibits an alarming propensity to develop resistance not only to more conventional insecticides, but also to novel and environmentally compatible compounds such as buprofezin, pyriproxyfen and the neonicotinoids (Horowitz and Ishaaya, 1992; Horowitz *et al.*, 1998; Elbert and Nauen, 2000; Ishaaya and Horowitz, 1995). The distribution of such resistance, and the manner in which this is affected by insecticide use patterns, seasonal factors, host plants and the ecological differences that exist between biotypes are as yet unresolved. However, in other insect species, it has been proven that where assortative mating occurs, the associations of these traits can be complex (e.g. host-plant preference linked to different insecticide resistance profiles, even in the absence of insecticide selection pressure; Hosoda *et al.*, 1993; Saito, 1991).

It is simple to conceive that, once resistance has arisen in a particular biotype, its competitive advantage in insecticide-treated environments ensures that it

displaces other, more susceptible, biotypes. One of the explanations for the geographical expansion of the range of the 'B' biotype is that increasing use of pyrethroids gave resistant 'B' biotypes a competitive advantage (Costa *et al.*, 1993; Toscano *et al.*, 1998). The changing patterns of 'B' and 'Q' biotype occurrence in the Iberian peninsula over the course of the 1990s (Beitia *et al.*, 1997; Guirao *et al.*, 1997a) correlates with the increased use of neonicotinoids for whitefly control, and it was in Q-type strains that resistance to these compounds was first documented and characterized (Cahill *et al.*, 1996; Nauen *et al.*, 2002). In Israel, the presence of the 'Q' biotype seems to be associated with increased resistance to the IGR pyriproxyfen which, to date, is undetected in Israeli 'B' types (Horowitz *et al.*, 2002).

Inheritance of resistance

Work characterizing the inheritance of resistance using recently collected 'B' and 'Q' biotypes from Egypt, Israel and Spain show that resistance to many chemicals is inherited in a partially dominant manner (Devine and El Kady, unpublished; Horowitz, unpublished). This dominance level concurs with published studies on the inheritance of resistance in *B. tabaci* (e.g. bifenthrin) (Tan *et al.*, 1996). It is of note that the haplodiploid nature of this organism also means that any partially dominant or recessive traits are fully exposed in hemizygous males. In the presence of insecticide, this will serve to increase the speed at which resistance is selected (Denholm *et al.*, 1998).

Mating success between biotypes

In studies measuring mating success (number of single pairs producing female offspring) and hybrid sex ratio (female bias in those offspring), we have shown that not all biotype combinations hybridize effectively (Devine *et al.*, unpublished). The data produced to date suggests assortative mating in which homotypic crosses are more successful than heterotypic crosses. Some inter-biotype crosses do result in female offspring but the success rates are lower than for intra-biotype crosses. Other inter-biotype crosses are non-reciprocal (e.g. females of one biotype may not mate successfully with another biotype, whilst males do mate). Some inter-biotype crosses never produce females (in a haplodiploid, the presence of a female offspring denotes a successful fertilization event). It is still not understood if these apparent barriers to introgression occur before (e.g. behavioral effects) or after (e.g. incompatibility of gametes) fertilization. In general, our results show that homotypic crosses are more successful than heterotypic crosses but this has not yet been tested exhaustively. The data are in agreement with the general literature on biotype crosses (Table 2), which report examples of all possible outcomes (inviolate, non-reciprocal and full hybridization).

Large scale illustrations of effects of differential introgression

Such barriers to introgression between populations have profound consequences for the inheritance of insecticide resistance. Large-scale laboratory experiments at Rothamsted are in the process of illustrating the effects of dispersal and interbreeding between biotypes on the subsequent development of resistance. In large chambers, on whole plants, large populations of insecticide-susceptible or resistant biotypes are maintained. Limited dispersal between these biotypes is facilitated by connecting the chambers with tunnels. Temporal changes in response to insecticides are tested by removing whitefly from the chambers and testing them in standard bioassays.

Linked populations of non-interbreeding biotypes show gradual shifts in phenotypic response consistent with the gradual mixing of resistant and susceptible individuals through limited dispersal. In comparison, linked populations of fully interbreeding biotypes show shifts that are more rapid in phenotypic response consistent with the production of heterozygous females in addition to dispersal. Dispersal between non-reciprocal interbreeding biotypes (i.e. male x female crosses are differentially successful to female x male crosses) shows a more rapid shift in one chamber than in the other. This is probably because of the *de facto* dispersal rates of resistant or susceptible alleles (i.e. for a monogenic resistant trait in a haplodiploid insect, a successful cross involving RR x S will transfer twice as many resistant alleles as a successful cross involving SS x R).

Although these results are predictable, they serve to show empirically that full, partial or non-interbreeding between biotypes will alter the rates at which resistance develops. Moreover, the experiments show that where interbreeding is absent or non-reciprocal, the presence of susceptible refugia may not act to dilute the resistance inherent in another biotype.

Conclusions and implications for resistance management

B. tabaci exists as different biotypes, some of which have similar geographic distributions. Such sympatric differentiation must have occurred as a result of reproductive isolation mediated by unknown ecological or environmental factors. Although 'B' and 'Q' biotypes differ in a range of biological parameters, it is impossible to implicate, *a posteriori*, which of these might have been responsible for their original segregation. However, attempts to cross these biotypes illustrate that they do display a degree of reproductive isolation. Where crosses are successful, most resistant traits seem to be inherited in a partially dominant manner.

The implication of assortative mating between biotypes for resistance management is that, if one biotype carries a resistant trait and another does not, then the former will have a distinct advantage in an insecticide-treated environment. Moreover, their reproductive isolation may ensure that this trait is not easily passed to any other biotype. This may ensure that one biotype predominates. Given the ecological differences between biotypes that have been reported, it is clear that insecticides might select not only a particular resistant trait, but also a whole suite of biological characteristics.

When introgression is limited, it is also possible that the conservation of susceptible insects through the use of refugia may not decrease the speed at which rare and/or recessive resistance alleles are selected. In the absence of interbreeding, rare mutants or migrants are likely to be more rapidly selected than would be expected.

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Table 1. Summary of published work on comparative ecology of biotypes.

<i>B. tabaci</i> biotypes	Origin of biotypes	Parameters measured ^a			Reference
		H	D	V*	
B / A	USA	+	+		Cohen <i>et al.</i> , 1991
B / non-B	S. Europe	+	+		Bedford <i>et al.</i> , 1992
B / non-B	Hawaii	+			Costa <i>et al.</i> , 1993
B / A	USA	+		+	Liu <i>et al.</i> , 1993
B / non-B	Global			+	Bedford <i>et al.</i> , 1994
B / Q	Spain			+	Sanchez-Campos <i>et al.</i> , 1999
A / B	Brazil	+			Martinez <i>et al.</i> , 2000
B / Q	Spain	+	+		Muniz, 2000
B / Q	Spain		+		Nombela <i>et al.</i> , 2001

^a Parameters: host preferences (**H**), demography (**D**), virus specificity (**V**).

+ Differentiation tested for and observed

* The appearance of the 'B' biotype appears to have correlated with reports of new virus outbreaks (Isakeit *et al.*, 1994; Brown, 1994; Banks *et al.*, 2001).

Table 2. Summary of published work on interbreeding between biotypes.

<i>B. tabaci</i> biotypes crossed	Origin of biotypes	Outcome of reciprocal crosses		Reference
		Female x male	Male x female	
A/B	USA	±	±	Costa <i>et al.</i> , 1993
B /SUDS	Israel / Sudan	+	-	Byrne <i>et al.</i> , 1995
B/non-B	Global	-	-	Bedford <i>et al.</i> , 1994
B/non-B	Australia	+	+	Gunning <i>et al.</i> , 1997
B/non-B	Uganda	+	+	Maruthi <i>et al.</i> , 2001
B/EAN/WAN	Australia	-	-	De Barro and Hart, 2000
B/Q	Spain	±	±	Ronda <i>et al.</i> , 2000

+ Successful, - Unsuccessful, ± less successful than intra-biotype crosses