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Insecticide resistance in *Bemisia tabaci* biotype Q (Hemiptera: Aleyrodidae) from China

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ABSTRACT

Dispersion of invasive biotypes of the tobacco whitefly, *Bemisia tabaci*, has led to protracted crop protection constraints in numerous countries over recent decades. These polyphagous, highly efficient vectors of plant viruses present an intractable problem as they frequently carry a diverse suite of insecticide resistance mechanisms. In many areas of China, native biotypes have been supplanted by the invasive and globally widespread biotype B since the 1990s. More recently, biotype Q has established, posing a new and more potent threat to agricultural production systems throughout the country. Insecticide resistance profiles for a range of Chinese *B. tabaci* strains covering biotypes B and Q were examined, to establish the potential for insecticides to play a pivotal role in biotype competition and ultimate displacement. Commonly used compounds including pyrethroids, neonicotinoids, abamectin and pyriproxyfen were targeted as widespread use is pre-requisite to drivers of population dynamics on a national scale.

It was found that across several strains, both biotypes responded similarly against pyrethroids, abamectin and pyriproxyfen. However, their responses to three commercially available neonicotinoids were consistently contrasting. Biotype B strains remained largely susceptible to acetamiprid, imidacloprid, and thiamethoxam, whereas biotype Q strains expressed 20–170 fold resistance to these insecticides. It appears that in China the use of neonicotinoid insecticides has the potential to select for biotype Q within mixed biotype areas, contributing to the establishment and prevalence of this relatively recent introduction.

1. Introduction

The tobacco whitefly, *Bemisia tabaci* (Gennadius), is considered a taxonomically complex and intractable pest of vegetable, ornamental and commodity crops (Brown et al., 1995; Denholm et al., 1998). Conventional practice is to divide the species into biochemically distinct but morphologically inseparable biotypes, two of the most prevalent being biotype B and biotype Q. Biotype B is distributed throughout the world, following a dramatic expansion in range that commenced in the late 1980s (Guirao et al., 1997; Rosell et al., 1997). Biotype Q, which is thought to originate from the Iberian Peninsula (de la Rua et al., 2006), has spread throughout the Mediterranean region and has more recently become established in China (Chu et al., 2006), Japan (Ueda and Brown, 2006), Mexico (Martinez-Carrillo and Brown, 2007), the USA (Boykin et al., 2007) and New Zealand (Scott et al., 2007). Both biotypes exhibit broad host ranges, rapid population growth, and a marked ability to develop strong resistance to insecticides (Horowitz et al., 2005).

B. tabaci was first recorded in China in 1949 (Zhou, 1949) but was not considered a significant pest until the 1990s (Xu, 1996). Since then biotype B has been found to be widely distributed in China on vegetable and cotton crops (Luo et al., 2002; Wu et al., 2002; Qiu et al., 2007; Ma et al., 2007). Following suspected importation on ornamental plants, biotype Q was first found in China in 2003 (Chu et al., 2005; Zhang et al., 2005) and subsequently in new regions in 2004 (Chu et al., 2006). A further infestation of biotype Q occurred at the 2006 Shenyang International Horticultural Show (Fang et al., 2008). The exact contemporary distributions of biotypes B and Q remains unclear but it is known that Q has substantially supplanted B on outdoor crops in Hubei province (Qiong Rao, unpublished data), where reported crop losses due to *B. tabaci* in 2007 were in excess of US$ 600 million (data supplied by Hubei Plant Protection Service, 2008).

Insecticides are the primary means of controlling *B. tabaci* in China and resistance is a constant threat. Resistance can be selected *de novo* through over-reliance on particular chemicals or, more

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perversely, may already be present when pests invade new cropping systems (Denholm et al., 1998). This is a particular concern with biotype Q, which shows a frequent association with resistance to IPM-compatible insecticides including neonicotinoids and the juvenile hormone analogue, pyriproxyfen (Horowitz et al., 2005). We report here for the first time on resistance profiles of biotype Q insects collected in China, compare these with contemporary biotype B collections, and discuss the implications for biotype dynamics and the potential displacement of one biotype by another.

2. Materials and methods

2.1. B. tabaci strains

Five samples of *B. tabaci* were collected in 2007/2008 from Xinjiang (XJ), Beijing (BJ), Zhejiang (ZHJ), Jiangsu (JS) and Hubei (HB) provinces (Fig. 1). Each consisted of numerous leaves collected at random from the crop canopy, containing a minimum of 100 adults or nymphs per sample. Of the compounds tested, the neonicotinoids (imidacloprid, thiamethoxam and acetamiprid), pyrethroids (cypermethrin, bifenthrin) are being widely used for control of *B. tabaci* outbreaks on vegetable crops in China. Abamectin is primarily used as an acaricide targeted at spider mites, although applications targeting both spider mites and *B. tabaci* that coexist as a pest complex are common. Pyriproxyfen has been registered in China since the 2006–2007 season, as it was little used within vegetable cropping systems at the time of collection.

Three additional laboratory strains were used as reference material; BTB as a biotype B standard, BTQ as a biotype Q standard, and BTS provided insecticide-susceptible baselines. The collection details for all strains are summarised in Table 1. All strains were maintained on cotton plants (*Gossypium hirsutum* L. var. 'Linda') without exposure to insecticides, under a 16 h photoperiod at 28 °C. Adult individuals were used for biotype determination, and all adults used in bioassays were less than 7 days old.

2.2. Biotype determination

Direct sequencing of mitochondrial cytochrome oxidase I (COI) genes was used to diagnose biotypes. DNA was extracted from adult *B. tabaci* individuals and Taqman® allele-specific PCR (Jones et al., 2008) used to confirm biotype status. For each strain, 18 adults were individually homogenised in wells of a 96-well microplate containing 60 μL of sucrose solution (10% sucrose, 1.75% NaCl, 0.8% Tris–HCl). Thirty microliters of homogenate were transferred to a PCR plate and maintained at 99 °C for 9 min. Each subsequent PCR reaction comprised of gDNA (1 μL), SensiMix DNA kit (12.5 μL; Quantace Ltd, Neutral Bay, Australia), 900 nM of forward and reverse primers (BEMBQ-SNP1F 5′-GCCTTTGATTTACAG-GATTTTTATTTTTATTTACTATAGGT-3′ and BEMBQ-SNP1R 5′-GAAATCAAT-AGATAACTCCTCCTACAATAGCA-3′, respectively) and 200 nM of each of two probes (SNP1V2: 5′-ATGCAGA-CACACATC-3′ and SNP1M2: 5′-ATGCAAACACACATC-3′). The total volume was made up to 25 μL with sterile water. Sterile water (1 μL) was used for negative controls. Real-time PCR was performed on a Rotor-Gene 6000™ (Corbett Research) using temperature cycling conditions of 10 min at 95 °C, followed by 40 cycles at 95 °C for 10 s, and 60 °C for 45 s. The increases in VIC and FAM reporter dyes, representing biotype B and Q sequences, respectively, were monitored in real time using the Rotor-Gene software. Scatter plots of the resulting fluorescence were used to assign individuals to biotype-specific clusters.

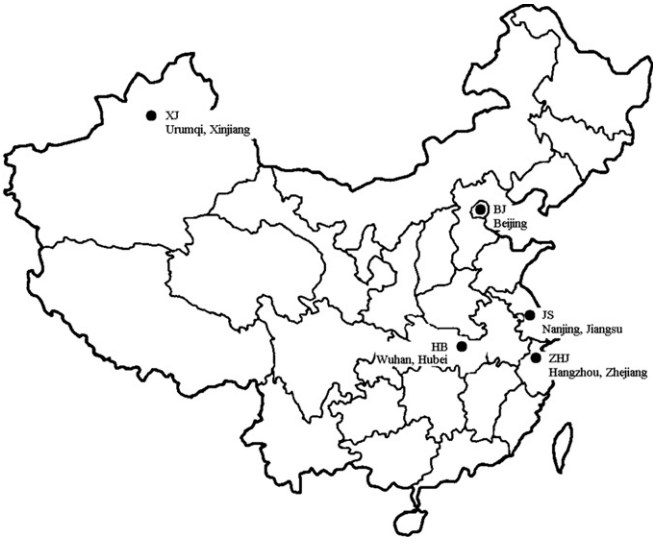

Fig. 1. Map of China detailing the strain names, towns, and provinces of *B. tabaci* collection sites.

Table 1
Origins and host plants of *B. tabaci* strains.

Strain	Date of collection	Country of origin	Host	Biotype
BTS	1978	Sudan	Cotton	–
BTB	1996	USA	Cotton	B
BTQ	2007	Spain	Tomato	Q
XJ	June 2007	Urumqi	Cotton	B
BJ	June 2008	Beijing	Tomato	B
ZHJ	November 2007	Hangzhou	Capsicum	Q
JS	June 2008	Nanjing	Cotton	Q
HB	June 2008	Wuhan	Cotton	Q

–, Neither biotype B nor Q.

2.3. Insecticides

Formulated insecticides used for bioassays were the pyrethroids cypermethrin (Toppel 10 EC) and bifenthrin (Capture 25 EC), the neonicotinoids imidacloprid (Confidor 20 SL), thiamethoxam (Actara 25 WG) and acetamiprid (Gazelle 20 SP), the juvenile hormone analogue pyriproxyfen (Knack 10 EC), and the avermectin derivative abamectin (Dynamec 1.8 EC). All dilutions were made using a diluent of distilled water containing a 0.01% concentration of the non-ionic wetter Agral®. Control treatments used the diluents only.

2.4. Bioassays

Adult *B. tabaci* were tested with cypermethrin, bifenthrin, imidacloprid, thiamethoxam, acetamiprid and abamectin using a leaf-dip bioassay based on Cahill et al. (1995). Leaf discs (39 mm diameter) cut from fully expanded cotton leaves were dipped into serial dilutions of insecticide for 20 s and laid abaxial side down on a bed of agar (2%) within the base of a plastic Petri-dish (40 mm diameter). After drying, approximately 20 females were aspirated into a small vial and placed onto each treated leaf disc. Petri-dishes were covered with an absorbent cellulose pad (45 mm diameter) and sealed with a lid. Petri-dishes were inverted and held in a 16 h photoperiod at 28 °C for 48 h, after which, mortality was assessed using a binocular microscope. Adults showing no sign of movement were scored as dead. Bioassays consisted of 3 replicates at a minimum of 5 concentrations.

B. tabaci eggs were tested with pyriproxyfen using a method based on Horowitz et al. (2003). Cotton leaves on whole plants were

trimmed into squares (approximately 40 × 40 mm) and inoculated with at least 20 whiteflies per leaf. Adults were removed 24 h later. After a further 24 h, leaves containing eggs were dipped for 20 s into the required concentrations of serially diluted insecticide. Plants were maintained under a 16 h photoperiod at 28 °C for a total of 2 weeks, until all surviving eggs had hatched and mortality could be accurately recorded. Endpoint readings include the number of dead nymphs and number of live nymphs/pupae, the sum of which provides the total sample tested (n). Bioassays consisted of 3 replicates at a minimum of six concentrations.

2.5. Statistical analysis

Probit analyses of the concentration-dependent mortality data were calculated using PoloPlus (LeOra software, Berkley, California). Resistance factors (RFs) were obtained by dividing LC_{50} values by the corresponding value for the susceptible (BTS) reference strain.

3. Results

3.1. Biotype determination

All individuals from the biotype reference strains scored correctly. Negative controls did not induce fluorescence of either reporter dye; positive controls demonstrated differential fluorescence rates. Biotypes B and Q positive controls increased fluorescences of VIC and FAM reporter dyes, respectively. All individuals from the five Chinese strains fell unambiguously into one of two clusters on a bivariate scatter graph (Fig. 2). All the strains were single biotype, i.e. different biotypes were not found in coexistence. Using this approach, strains ZHJ, HB, and JS were diagnosed as biotype Q and strains XJ and BJ were diagnosed as biotype B (Table 1). None of the strains contained individuals of any biotype other than B or Q.

3.2. Resistance profiles

Chinese strains referable to biotypes B and Q differed markedly in response to the neonicotinoids acetamiprid, imidacloprid and thiamethoxam (Table 2). With one exception (BJ vs. acetamiprid), LC_{50} values for the biotype B strains (XJ and BJ) were similar to those for the susceptible reference strain (BTS). LC_{50} values for biotype Q strains to all three neonicotinoids were significantly greater than for the reference or biotype B strains. ZHJ was the most resistant to all three compounds with resistance factors of 33, 83.8 and >166 for acetamiprid, imidacloprid and thiamethoxam, respectively.

All five field strains exhibited significant resistance to the pyrethroid insecticides, bifenthrin and cypermethrin (Table 3). Resistance factors varied between 7 and 86 for bifenthrin, and between 20 and 246 for cypermethrin. However, there was no apparent associated between biotype and pyrethroid-resistant phenotype.

There was limited variation between responses of strains to abamectin, although two strains (ZHJ and BJ, representing biotypes Q and B, respectively) gave significantly higher LC_{50} values than BTS yielding resistance factors of 3.75 (Table 3). Responses to the juvenile hormone analogue pyriproxyfen were broadly similar. Two biotype Q strains (JS and HB) gave significantly higher LC_{50} values than that of the susceptible reference strain (based upon overlap of 95% fiducial limits at LC_{50}), although these low levels of resistance are unlikely to have impaired control at recommended application rates (Table 3).

4. Discussion

Factors influencing the invasiveness and subsequent establishment of biotypes of *B. tabaci* are likely to be complex and dependent, in large part, on regional differences in climate, cropping systems and control practices. In China, the appearance and spread of biotype B in the late 1990s led to a substantial expansion in the geographical and host ranges of *B. tabaci*, and in its status as an agricultural pest. Use of insecticides against this species increased accordingly with strong reliance on neonicotinoids to replace older products such as pyrethroids already compromised by resistance. In retrospect, the global expansion of biotype B has been linked in part to its propensity to develop pyrethroid resistance, especially through the involvement of a characteristic biotype B esterase ($E_{0.39}$) in pyrethroid metabolism (Byrne et al., 2000). The presence of pyrethroid resistance in our biotype B strains is consistent with other studies on this biotype from China (He et al., 2007; Kang et al., 2006; Ma et al., 2007; Wang and Wu, 2004), although the relative contribution of metabolic and target-site mechanisms (Alon et al., 2006; Byrne et al., 2000; He et al., 2007; Morin et al., 2002; Wang and Wu, 2004) to these resistance phenotypes remains to be

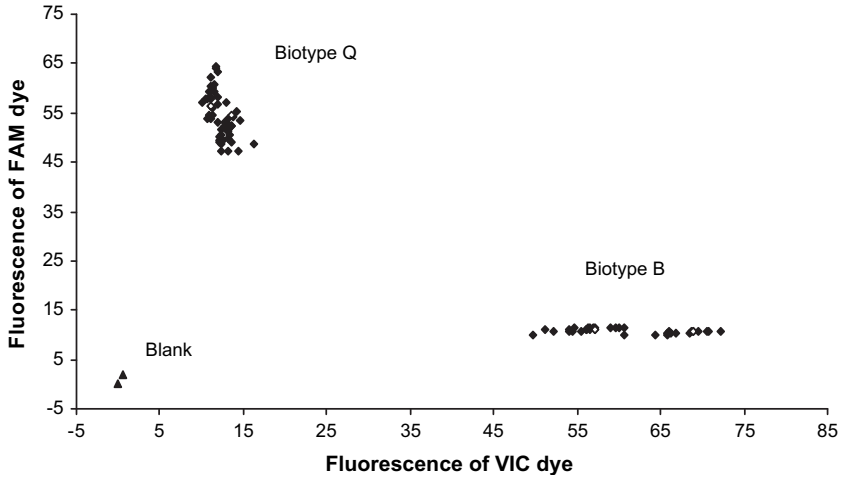

Fig. 2. Scatter plot analysis of fluorescence data for 18 individuals of each Chinese *B. tabaci* strain. All samples group clearly into either biotype B or biotype Q clusters. Two water controls (blank), two known biotype B (open diamonds) and two known biotype Q (open diamonds) standards were also included.

Table 2
LC_{50} values (mg ai L^{-1}), fiducial limit (FL), slopes and RF values for Chinese and insecticide-susceptible reference strains of *B. tabaci* against three neonicotinoid insecticides.

Compound	Strain	Biotype	*n*	LC_{50}	FL (95%)	Slope ± SE	RF
Acetamiprid	BTS	-	218	8.48	3.87–16.8	1.63 ± 0.25	1
	BJ	B	344	61.0	40.8–83.2	2.23 ± 0.45	7.20
	XJ	B	212	3.64	2.29–5.82	1.10 ± 0.12	0.43
	ZHJ	Q	214	280	190–423	2.01 ± 0.27	33.0
	JS	Q	244	248	147–390	2.46 ± 0.35	29.3
	HB	Q	243	167	68.8–339	1.33 ± 0.20	19.7
Imidacloprid	BTS	–	250	4.13	2.37–7.18	0.94 ± 0.13	1
	BJ	B	236	4.11	2.56–6.66	1.11 ± 0.15	1.00
	XJ	B	187	5.69	2.36–14.7	0.95 ± 0.11	1.38
	ZHJ	Q	318	346	238–520	1.28 ± 0.18	83.8
	JS	Q	223	96.7	53.5–151	1.18 ± 0.18	23.4
	HB	Q	265	220	124–339	2.61 ± 0.32	53.3
Thiamethoxam	BTS	–	192	6.00	2.99–11.8	1.44 ± 0.17	1
	BJ	B	249	6.45	2.33–14.6	1.48 ± 0.18	1.08
	XJ	B	338	6.89	3.36–15.0	1.00 ± 0.09	1.15
	ZHJ	Q	202	>1000	>1000	0.55 ± 0.16	>166
	JS	Q	262	169	37.8–342	1.38 ± 0.26	28.2
	HB	Q	270	267	158–432	2.08 ± 0.31	44.5

resolved. Similarly, although biotype Q strains from China are shown to have comparable profiles of pyrethroid resistance, parallels in the genetic and biochemical basis of this trait in B and Q insects is yet to be investigated.

Evidence for the extent of the more recent invasion of biotype Q into China is still rather piecemeal or anecdotal. However, a comprehensive survey of biotype composition in Hubei province has shown Q to be by far the most widespread biotype on major field crops (Qiong Rao, unpublished data). In addition, data suggest that biotype Q outbreaks in China are frequently associated with major transportation routes and agricultural areas. In such a case it is intriguing to hypothesise that biotype Q, unrecorded in China before 2003, has very rapidly supplanted biotype B under conditions where insecticide use is most intense. Given the current scale of neonicotinoid use against *B. tabaci*, the differential responses of B and Q insects to these chemicals would have been a powerful driver promoting the survival and spread of the latter. The occurrence of broad-spectrum resistance to neonicotinoids in all our strains of biotype Q suggests that such resistance was already present at the time of its first introduction to China. High levels of neonicotinoid resistance have become a relatively consistent feature of biotype Q insects from around the world (Boykin et al., 2007; Chu et al., 2006; Nauen and Denholm, 2005; Prabhaker et al., 2005), mediated largely or wholly through over-expression of a cytochrome P450-dependent monooxygenase enzyme, CYP6CM1 (Karunker et al., 2008). The recently documented age-specificity of this mechanism (Nauen et al., 2008) was demonstrated in biotypes B and Q, therefore it is considered unlikely to be contributing to displacement at present. However, the presence/development of additional mechanisms that are biotype-specific could have a significant impact on the dynamics of these and other competing biotypes.

Table 3
LC_{50} values (mg ai L^{-1}), 95 % fiducial limit (FL), slopes and RF values for Chinese and insecticide-susceptible reference strains of *B. tabaci* against four commonly used insecticides.

Strain	Strain	Biotype	*n*	LC_{50}	FL	Slope ± SE	RF
Abamectin	BTS	–	340	0.12	0.09–0.19	1.78 ± 0.17	1
	BJ	B	279	0.45	0.38–0.53	4.13 ± 0.53	3.75
	XJ	B	255	0.08	0.06–0.10	2.13 ± 0.25	0.67
	ZHJ	Q	239	0.12	0.06–0.35	1.61 ± 0.18	1.0
	JS	Q	204	0.45	0.29–0.66	1.96 ± 0.31	3.75
	HB	Q	230	0.24	0.09–0.48	1.05 ± 0.16	2.0
Bifenthrin	BTS	–	183	1.80	1.15–2.82	1.37 ± 0.16	1
	BJ	B	231	82.7	16.9–199	1.06 ± 0.19	45.9
	XJ	B	287	60.9	44.3–89.8	1.64 ± 0.22	33.8
	ZHJ	Q	305	155	39.9–9270	0.66 ± 0.12	86.1
	JS	Q	221	12.2	7.18–18.7	1.70 ± 0.28	6.78
	HB	Q	296	21.5	10.5–42.1	1.20 ± 0.12	11.9
Cypermethrin	BTS	–	223	4.67	0.67–10.6	0.82 ± 0.19	1
	BJ	B	294	171	123–249	2.81 ± 0.43	36.6
	XJ	B	297	1150	501–8230	1.01 ± 0.22	246
	ZHJ	Q	286	160	123–211	2.01 ± 0.36	34.3
	JS	Q	267	94.3	58.5–139	1.42 ± 0.19	20.2
	HB	Q	300	168	86.7–310	1.34 ± 0.16	36.0
Pyriproxyfen	BTS	–	2220	0.01	0.00–0.02	1.16 ± 0.06	1
	BJ	B	3100	0.02	0.01–0.03	0.89 ± 0.04	2.0
	XJ	B	1330	0.07	0.02–0.19	1.24 ± 0.07	7.0
	ZHJ	Q	571	0.02	0.01–0.03	1.32 ± 0.14	2.0
	JS	Q	1430	0.09	0.06–0.13	0.95 ± 0.04	9.0
	HB	Q	670	0.11	0.04–0.30	0.83 ± 0.05	11.0

The presence of neonicotinoid resistance in biotype Q strains is of obvious practical concern. Further selection pressure exerted by continued applications may widen the gap in response between biotypes, exacerbating the current situation and reinforcing biotype displacement. Alternatively, there are now cases of strong resistance to neonicotinoids in biotype B (Byrne et al., 2003; Karunker et al., 2008) and it is interesting to speculate about the consequences of this being selected *de novo* in China. Without differences in resistance playing a dominant role in population dynamics, numerous other biological factors influencing the competitive ability of co-existing biotypes (Bonato et al., 2007; Liu et al., 2007; Nombela et al., 2001; Pascual and Callejas, 2004) would come more into play. In the short-term, our bioassays have identified compounds (abamectin and pyriproxyfen) that retain efficacy against both biotypes, although both are vulnerable to resistance (Horowitz et al., 2003; Wang and Wu, 2007) and use should always be in accordance with a pre-planned resistance management strategy. In particular, the susceptibility to pyriproxyfen in biotype Q is likely to be fragile as this biotype has frequently been associated with high pyriproxyfen resistance (e.g. Fernandez et al., 2009). The levels of susceptibility observed may have been a consequence of the limited pyriproxyfen use within Chinese vegetable cropping systems at that time. Monitoring of susceptibilities to pyriproxyfen in biotype Q collections showed a relatively rapid reversion of highly resistant populations in Israel's Ayalon Valley, after pyriproxyfen use had stopped due to loss of control (Horowitz et al., 1999). Continued and co-ordinated monitoring of events in China will not only help with optimising control measures, but will also cast further light on important interactions between systematic and population biology of pests on the one hand, and prevailing agricultural practices on the other.

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