International Journal of Tropical Insect Science Vol. 33, No. 2, pp. 99–106, 2013
doi:10.1017/S1742758413000040

Dynamics of the invasive *Bemisia tabaci* (Homoptera: Aleyrodidae) Mediterranean (MED) species in two West African countries

Olivier Gnankine[1]*, Guillaume Ketoh[2] and Thibaud Martin[3]

[1]Université de Ouagadougou, Unité de Formation et de Recherche en Sciences de la Vie et de la Terre (UFR-SVT), Laboratoire d'Entomologie Fondamentale et Appliquée, 09 BP 848, Ouagadougou 09, Burkina Faso;
[2]Faculté des Sciences, Université de Lome, BP 1515, Lome, Togo;
[3]UR Hortsys, CIRAD, 34398 Montpellier Cedex 5, France

(Accepted 8 February 2013)

Abstract. *Bemisia tabaci* Gennadius is a major pest on cotton and vegetable plants in Africa. It is considered as a cryptic species complex. Identification of the most damaging species such as the Middle East–Asia Minor 1 (B biotype) and Mediterranean (MED) (which contains the Q and Africa silverleaf (ASL) biotypes) species represents an important step towards the management of *B. tabaci*. Some data on the geographical distribution of the *B. tabaci* species complex exist in Burkina Faso, Benin and Togo, but data on the pest's invasion and displacement dynamics, in relation to time, are lacking. Here, molecular markers (mitochondrial cytochrome oxidase, *mtCO1*) were used to determine the identity of *B. tabaci*. Our results illustrate population dynamics on cotton and vegetable plants between 2007, 2009 and 2010. On cotton in southern Togo, ASL was predominant and found in sympatry with Q1. Its frequency decreased slightly over time, i.e. from 92% in 2009 to 90% in 2010. In Burkina Faso, Q1, Q3 and ASL biotypes showed different temporal and spatial distribution patterns. There, Q1 dominated on cotton plants throughout the study. This work provides relevant information about the population dynamics of *B. tabaci* MED species in two West African countries, Burkina Faso and Togo, in connection with pest management programmes.

Key words: *Bemisia tabaci*, Mediterranean species, Q populations, ASL populations, pest management programmes

Introduction

Bemisia tabaci Gennadius (Homoptera: Aleyrodidae) is an invasive and destructive pest of cotton and vegetable crops worldwide and particularly in Africa. It has a global distribution, and its members are major pests of agricultural crops, causing damage directly by feeding and indirectly by transmitting many plant viruses (Jones, 2003). Many factors contribute to its population growth such as climatic conditions, host plant preference (Musa and Ren, 2005), elimination of beneficial species (Gnankiné *et al.*, 2004) and selection of insecticide-resistant populations (Dittrich *et al.*, 1990; Byrne and Devonshire, 1997; Byrne and Toscano, 2002; Roditakis *et al.*, 2006; Roditakis *et al.*, 2009). Its propensity to develop insecticide resistance, in combination with high genetic variability, makes its control problematic

*E-mails: olgnankine@hotmail.com; olivier.gnankine@univ-ouaga.bf

(Tsagkarakou *et al.*, 2012). *Bemisia tabaci* is considered as a complex of morphologically indistinguishable species (Boykin *et al.*, 2007; McKenzie *et al.*, 2009; De Barro and Ahmed, 2011; De Barro *et al.*, 2011; Hu *et al.*, 2011; Liu *et al.*, 2012). Here, we refer to the Middle East–Asia Minor 1 (MEAM1) species (known commonly as biotypes B and B2) and to the Mediterranean (MED) species (known as biotypes Q, J, L and sub-Saharan Africa silverleaf (ASL) biotypes) (Dinsdale *et al.*, 2010). The MEAM1 and MED species belong to the same Africa/Middle East/Asia Minor major group of *B. tabaci* identified by Dinsdale *et al.* (2010). Another group from sub-Saharan Africa is composed of four species (sub-Saharan Africa 1, 2, 3 and 4) (Liu *et al.*, 2012). It is known that the MEAM1 species originates from the Middle East/Asia Minor region, whereas the MED species has its home range in the Mediterranean basin area and sub-Saharan Africa. The invasive non-silverleafing *B. tabaci* populations come from the Mediterranean basin (De Barro and Ahmed, 2011).

Life-history traits such as resource exploitation and resistance to insecticides may affect the distribution and frequency of the different members of the *B. tabaci* species complex (Pascual and Callejas, 2004; Horowitz *et al.*, 2005; Crowder *et al.*, 2010). These traits can also contribute to the exclusion or coexistence between different *B. tabaci* species (Pascual and Callejas, 2004; Crowder *et al.*, 2010). In Israel, Q populations replaced B biotypes when insecticides were used, whereas B populations rapidly evolved resistance to insecticides in the USA (Horowitz *et al.*, 2005; Khasdan *et al.*, 2005).

In West Africa (Burkina Faso and Benin), Houndété *et al.* (2010) showed resistance of the MED species to pyrethroids (PY; deltamethrin and bifenthrin), organophosphates (OP; dimethoate and chlorpyrifos) and neonicotinoids (acetamiprid and thiamethoxam). In this part of Africa, the MED species is present in two distinct populations, one that is able to induce silverleafing symptoms in squash (referred to as sub-Saharan ASL) and the other that is unable to induce these symptoms (referred to as Q). De Barro and Ahmed (2011) showed that the MED species evolved in sub-Saharan Africa and then spread from there to the Mediterranean basin, a process that led to a loss of capacity to induce silverleafing. In more recent times, this Mediterranean population has reinvaded West Africa. Sequence analyses showed the presence of two genetic subgroups or haplotypes of the Q population recently detected in West Africa: Q1 and Q3 (Gueguen *et al.*, 2010; Gnankiné *et al.*, 2012). Q1 is predominant on cotton and reaches a very high frequency of up to 100%, but on vegetables such as tomato, eggplant and tobacco, it coexists with ASL (Gnankiné *et al.*, 2012). We know that Q1 is associated with high levels of resistance to some insecticides (Gnankiné *et al.*, 2012), but nothing is known on the insecticide resistance profile of ASL.

Here, we describe the distribution of *B. tabaci* MED species in two West African countries, Burkina Faso and Togo, as influenced by host plants and pest management programmes.

Materials and methods

Pest control strategies

Four pest management strategies were used according to the host plants and study areas: (1) two to four treatments with PY plus OP and two other treatments with neonicotinoids (conventional treatment); (2) two to four treatments with PY plus OP; (3) one to two treatments of OP or PY depending on pest infestation; and (4) untreated, where no chemical was used (Table 1).

Origin of the whiteflies

Live adult *B. tabaci* (males and females) were collected in Burkina Faso and Togo (Fig. 1) and individually placed in 1.5 ml tubes containing 95% ethanol, and conserved at −20°C until DNA extraction. A total of 531 individuals collected from nine localities, on two cultivated host plants (cotton and tomato) and the invasive weed *Lantana camara* L. (Verbenaceae), were sampled during 2007, 2009 and 2010 (Table 1).

DNA extraction

Total DNA was extracted from each individual in 26 µl of an extraction buffer containing 50 mM KCl, 10 mM Tris–base (pH 8), 0.45% Nonidet P-40, 0.45% Tween-20 and 50 mg proteinase K/ml. The extraction buffer was added to the crude extract, incubated at 65°C for 3 h and then incubated at 100°C for 15 min. A volume of 35 µl of pure water was added to this extract, which was then stored at −20°C until use.

Identification of B. tabaci *species and genetic subgroups*

Genomic DNA was extracted from each individual adult *B. tabaci* in 26 µl of Nonidet extraction buffer (Delatte *et al.*, 2005) and stored at −20°C. Biotypes were identified using a polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) based diagnostic assay. Briefly, in this method, a fragment of the mitochondrial marker *CO1* (cytochrome oxidase 1 gene sequences, *mtCOI*) gene was amplified by PCR (Frohlich *et al.*, 1999)

Table 1. Climatic zones and pest management strategies for various populations of *Bemisia tabaci* in Burkina Faso and Togo during 2007, 2009 and 2010

Country	Localities	Geographic co-ordinates		Climatic zones	Insecticide control[1]	Q1[2]	Mutation ASL[3]	Q3
Burkina Faso	Sidéradougou	4°15′12.6″W	10°40′30″N	Sudano-Guinean	T1	*kdr* and *ace-1* ^{R}	–	–
	Pô	1°8′42″W	11°9′54″N	Sudano-Guinean	T1	*kdr* and *ace-1* ^{R}	–	–
	Kompienga	0°46′14.04″E	11°31′03.95″N	Sudanian	T1	*kdr* and *ace-1* ^{R}	*ace-1* ^{R}	–
	Bobo/Kuinima	4°17′48.12″W	11°10′6.24″N	Sudano-Guinean	T3	*kdr* and *ace-1* ^{R}	*ace-1* ^{R}	–
	Leguema	4°09′43.74″W	11°14′01.27″N	Sudano-Guinean	T3	*kdr* and *ace-1* ^{R}	*ace-1* ^{R}	–
	Soumousso	4°01′46.18″W	11°01′07.02″N	Sudano-Guinean	T3	*kdr* and *ace-1* ^{R}	*ace-1* ^{R}	–
	Toukoro	4°14′45.04″W	11°26′02.55″N	Sudano-Guinean	T3	*kdr* and *ace-1* ^{R}	–	–
	Ouagadougou	1°31′54.48″W	12°21′36″N	Sudanian	UT	–	–	–
Togo	Tové	1°14′59.02″E	6°43′03.23″N	Guinean	T2	*ace-1* ^{R}	–	–

[1] T1: two to four treatments with PY plus OP and two other treatments with neonicotinoids (conventional); T2: two to four treatments with PY plus OP; T3: one to two treatments of OP or PY; UT: untreated.
[2] Q1 populations have two mutation (*kdr* and *ace-1*^{R}) alleles (Gnankiné, 2011).
[3] ASL populations have only the *ace-1*^{R} allele (Gnankiné, 2011).

using the universal COI primers C1-J-2195 (5′-TTGATTTTTTGGTCATCCAGAAGT-3′) and TL2-N-3014 (5′-TCCAATGCACTAATCTGCCATATTA-3′) (Khasdan *et al.*, 2005). The PCRs were composed of a 25 µl Platinum® PCR SuperMix, a 0.5 µl forward primer (10 pmol/µl), a 0.5 µl reverse primer (10 pmol/µl) and a 2 µl DNA template. The PCR products were then digested by the restriction endonucleases *Xap* I (Fermentas) and/or *Bfm* I (Fermentas), which generated clear polymorphism between the populations B, MS, Q and the Q1, Q2 or Q3 genetic group. *Bfm* I was used to separate Q2 to Q3 groups. The PCR products were incubated with 10 U *Xap* I/µl (Fermentas) at 37 °C for 3 h before loading onto agarose gel.

Statistical analyses

Data collected on the frequencies of *B. tabaci* populations and pest control strategies were subjected to Fisher's exact test using Statview 5.0 software (SAS, 1991–1998). The significance threshold was 5%.

Results

Among the 531 individuals sampled from nine localities in Burkina Faso and Togo, the Q and ASL biotypes of the MED species were identified (Tables 1 and 2; Figs 1 and 2A and B). The Q1 and Q3 genetic groups or haplotypes of Q populations were recorded in our sampling.

Dynamics of biotypes on cotton plants

In Tové (southern Togo), ASL was always found on cotton in sympatry with Q1 and at a high frequency. ASL frequency was 92 and 90% in 2009 and 2010, respectively (Fig. 1). In Burkina Faso, Q1 dominated in most of the sites sampled. Q1 and ASL showed a different distribution pattern in Burkina Faso both in terms of spatial and temporal variability. The ASL biotype occurred at a low frequency and always in sympatry with Q1 on cotton in Kompienga (eastern) and Pô (middle-east), respectively. In Sidéradougou (south-western Burkina Faso) Q1 was predominant. In this area, from 2007 to 2010, Q1 frequency stood at 100% (Fig. 1).

Dynamics of biotypes on vegetables and L. camara

On tomato plants in Burkina Faso, the ASL biotype was found in sympatry with Q1 in populations from Bobo/Kuinima, Leguema and Soumousso throughout the study. From 2007 to 2009, in Bobo/Kuinima, ASL prevalence decreased from 58 to 24%, but increased again to 40% in 2010. Q1 frequency rose from 42% in 2007 to 60% in 2010 in the same locality, whereas Q3 was detected in Bobo/Kuinima only on tomato in 2009 (Tables 1 and 2). The dynamics in Leguema and Soumousso were similar with Q1 frequency on tomato (58 and 67% in 2009 and 60 and 59% in 2010, respectively).

In Toukoro, Q1 populations were only found between 2009 and 2010, and all individuals were collected on tomato. As for Q3, it was only observed on *L. camara* in Ouagadougou, year after year.

Impact of pest control strategies on the distribution of biotypes

A significant relationship was found between pest control strategies and the distribution of *B. tabaci* populations ($P = 0.0005$). In particular, on cotton in the Kompienga, Sidéradougou and

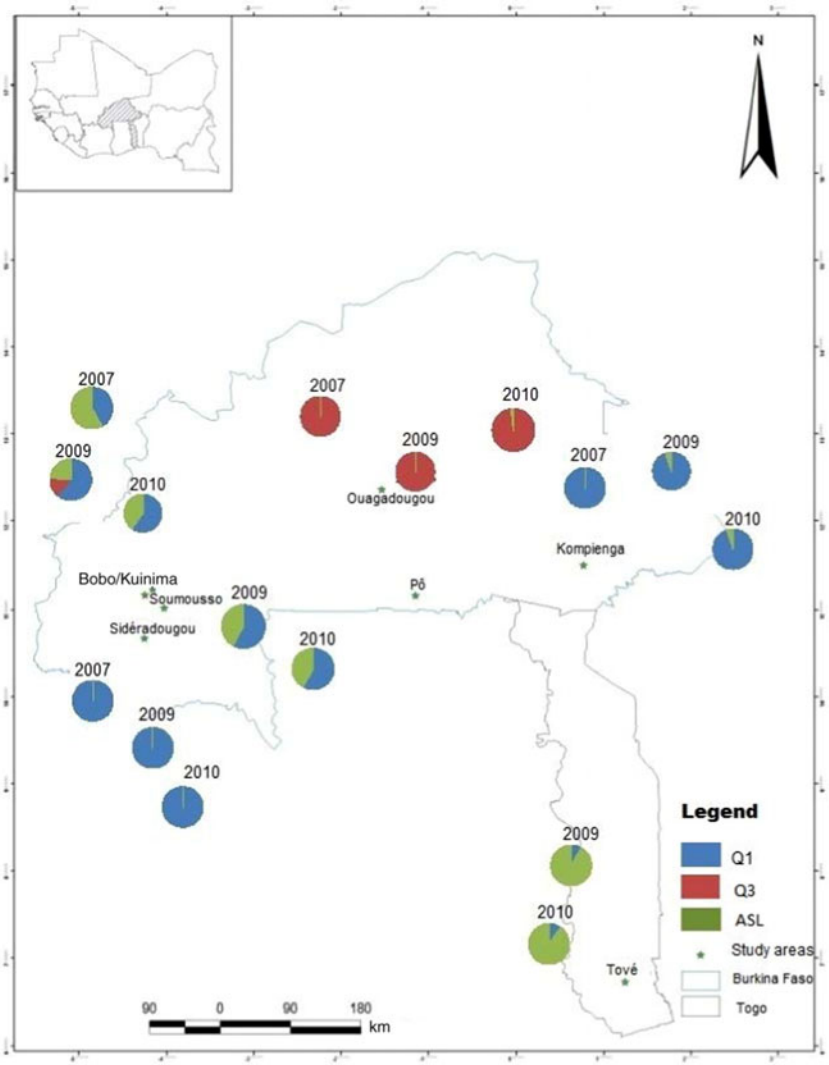

Fig. 1. MED species of the *Bemisia tabaci* complex in localities in Burkina Faso and Togo (2007, 2009 and 2010) (a colour version of this figure can be found online at http://journals.cambridge.org/jti)

Pô, areas where insecticide applications were intense, Q1 was predominant ($P = 0.0005$; Tables 1 and 2). On vegetables, where insecticide pressure was lower than on cotton, ASL was detected together with Q1, but their occurrence was not significantly related to pest control strategies ($P = 0.70$). In Toukoro, however, all individuals proved to be Q1 (Tables 1 and 2). Q3 was only found on tomato in Kuinima and was largely predominant on *L. camara*. Its occurrence was significantly influenced by pest control strategies ($P = 0.003$) and was only found on either untreated fields or in areas with few insecticide applications (Tables 1 and 2).

Discussion

Our results illustrate the dynamics of invasion and displacement between the MED species of *B. tabaci* over time in eight localities in Burkina Faso and one in Togo. As previously described, Q1 and Q3 showed a different distribution in Burkina Faso in terms of geographical position and host plant species. Q3 was only observed in the western part of the country and only on *L. camara* and tobacco, while Q1 occurred in most sampling sites and on most host plants (Gnankiné *et al.*, 2012). Our results confirm that population identity on cotton is stable between the years.

The occurrence of the Q1 population raises the question of pest management and the risk of spread to other countries in West Africa. Q1 has so far been found in Mediterranean countries such as Morocco, Spain, Algeria, Portugal, Greece and France, as well as in The Netherlands, China, Japan, the USA and South Korea (Chu *et al.*, 2008). De Barro and Ahmed (2011) showed that non-silverleafing MED species

Table 2. Frequencies of the *Bemisia tabaci* MED species complex related to host plants, localities and various years

Country	Locality	Host plant	n[1]	Collection year	Duration of cycle	Area	Agricultural practice[2]	Biotypes (%)[3]
Burkina Faso	Kompienga	Cotton	30	2007	Humid season	Wide	Treated	Q1 (100)
	Kompienga	Cotton	30	2009	Humid season	Wide	Treated	Q1 (97), ASL (3)
	Kompienga	Cotton	29	2010	Humid season	Wide	Treated	Q1 (96), ASL (4)
	Bobo/Kuinima	Tomato	30	2007	Humid and dry seasons	Small	Treated	Q1 (42), ASL (58)
	Bobo/Kuinima	Tomato	30	2009	Humid and dry seasons	Small	Treated	Q1 (62), ASL (24), Q3 (14)
	Bobo/Kuinima	Tomato	30	2010	Humid and dry seasons	Small	Treated	Q1 (60), ASL (40)
	Leguema	Tomato	20	2009	Humid and dry seasons	Small	Treated	Q1 (58), ASL (42)
	Leguema	Tomato	20	2010	Humid and dry seasons	Small	Treated	Q1 (60), ASL (40)
	Soumousso	Tomato	21	2009	Humid and dry seasons	Small	Treated	Q1 (67), ASL (33)
	Soumousso	Tomato	21	2010	Humid and dry seasons	Small	Treated	Q1 (59), ASL (41)
	Sidéradougou	Cotton	23	2007	Humid and dry seasons	Small	Treated	Q1 (100)
	Sidéradougou	Cotton	15	2009	Humid and dry seasons	Small	Treated	Q1 (100)
	Sidéradougou	Cotton	15	2010	Humid and dry seasons	Small	Treated	Q1 (100)
	Toukoro	Tomato	22	2009	Humid and dry seasons	Small	Treated	Q1 (100)
	Toukoro	Tomato	15	2010	Humid and dry seasons	Small	Treated	Q1 (100)
	Pô	Cotton	15	2009	Humid season	Wide	Treated	Q1 (85), ASL (15)
	Pô	Cotton	30	2010	Humid season	Wide	Treated	Q1 (97), ASL (3)
	Ouagadougou	*Lantana camara*	30	2007	Humid and dry seasons	Small	Untreated	Q3 (100)
	Ouagadougou	*L. camara*	30	2009	Humid and dry seasons	Small	Untreated	Q3 (100)
	Ouagadougou	*L. camara*	30	2010	Humid and dry seasons	Small	Untreated	Q3 (98), ASL (2)
Togo	Tové	Cotton	30	2009	Humid season	Wide	Treated	ASL (92), Q1 (8)
	Tové	Cotton	15	2010	Humid season	Wide	Treated	ASL (90), Q1 (10)

[1] Number of individuals in the sample.
[2] This column indicates whether pesticides were used or not.
[3] Percentage of each population found at the collecting site.

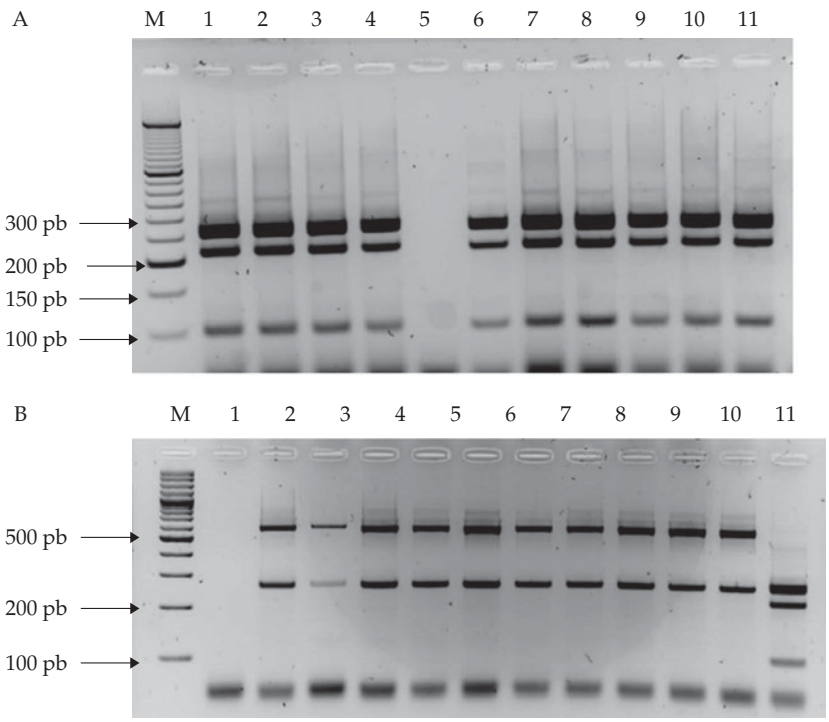

Fig. 2. A, representative gels showing Q populations (Q1 group) collected in Burkina Faso. Lanes 1, 2, 3, 4: Q1; lanes 6, 7, 8, 9, 10, 11: Q1, digested with *Xap*I. M: 50 bp DNA ladder. B, representative gels showing the ASL and Q1 populations collected in Togo. Lanes 2, 3, 4, 5, 6, 7, 8, 9, 10: ASL; lane 11: Q1, digested with *Xap*I. M: Hyperladder IV.

found in sub-Saharan Africa are all closely related to the haplotype of MED (MCh1), Q1 in our study. The most likely origin of Q in sub-Saharan Africa is the western Mediterranean (De Barro and Ahmed, 2011).

In addition, the parsimonious structure for MED established by De Barro and Ahmed (2011) supports two home range distributions. The first is a sub-Saharan Africa and the second a Mediterranean range. For appropriate pest management, it is important to understand the invasion history. According to De Barro and Ahmed (2011), one possible explanation is that MED evolved in sub-Saharan Africa and then extended to the eastern and western Mediterranean, respectively. Moreover, MED has recently moved back to sub-Saharan Africa from the Mediterranean region, possibly via Sudan (De Barro and Ahmed, 2011).

How did this population colonize West Africa? Its occurrence seems to be related to trade in ornamental plants during the last 10 years from the Maghreb. Another possibility would be migration, as the effective localized migrational range of *B. tabaci* could be 2.7 km or more, carried up by high winds (Byrne and von Bretzel, 1987; Byrne, 1999).

High insecticide pressure due to frequent and persistent applications over time in cotton might have contributed to the selection of the invasive Q1 population on cotton plants. Gnankiné (2011) already showed on cotton fields the presence of both mutations (*kdr* and *ace-1*^{R}) in Q populations from Burkina Faso in 2009. The substitution of leucine by isoleucine at position 925 (L925 I) in the para-type voltage-gated sodium channel (*kdr*) is implied in pyrethroid resistance (Alon *et al.*, 2006; Tsagkarakou *et al.*, 2009). The replacement of phenylalanine by tryptophan (F331 W) in the acetylcholinesterase enzyme *ace1*, which is implicated in organophosphate resistance (Alon *et al.*, 2008; Tsagkarakou *et al.*, 2009), has also been recorded in Q1 populations (Gnankiné, 2011).

In the USA, B populations often rapidly adapt to insecticide pressure because of the presence of these resistance alleles (Dennehy *et al.*, 2004; Crowder *et al.*, 2008). On the contrary, in Israel, B populations show relatively little genetic variation for resistance to insecticides due to the scarcity of resistance alleles (Horowitz *et al.*, 2005).

On vegetables, ASL and Q1 were found sympatrically with more or less the same prevalence over the years. The ASL biotype has already been discovered in Togo, Benin, Burkina Faso, Ivory Coast, Cameroon and Ghana (Gueguen *et al.*, 2010; De Barro and Ahmed, 2011). Ecological traits and agricultural practices may affect the distribution and frequency of the different members of the *B. tabaci* species complex (Gnankiné *et al.*, 2013). In West Africa on tomato, the frequency of

insecticide applications is lower than that on cotton and most of the pesticides are derived from the cotton sector (Ahouangninou *et al.*, 2011). Farmers use insecticides only when the level of pest populations is very high. Nevertheless, Gnankiné *et al.* (2012) revealed *ace-1* ^{R} but no *kdr* mutations in ASL individuals. The co-occurrence of the two sympatric populations raises questions on their management.

Conclusion

A better knowledge of Q1 and ASL seasonal dynamics will provide crucial information on their biology and might reveal the replacement of ASL by Q1 in areas with high insecticide pressure. Agricultural practices associated with the negative effects of chemicals such as PY and OP raise the question of their use in the management of pests. In addition, insecticides are expensive and have only a limited effect on whiteflies. Thus, the search for alternatives to limit significantly the quantities of insecticide used remains a main priority.

Acknowledgements

This study was partly funded by CORUS 6015. The authors would like to thank Yé Moumine and Handé Samou who supplied us with samples.

References

Ahouangninou C., Fayomi B. E. and Martin T. (2011) Évaluation des risques sanitaires et environnementaux des pratiques phytosanitaires des producteurs maraîchers dans la commune rurale de Tori-Bossito (Sud-Bénin). *Cahiers Agricultures* 20, 216–222.

Alon M., Alon F., Nauen R. and Morin S. (2008) Organophosphates' resistance in the B-biotype of *Bemisia tabaci* (Hemiptera: Aleyrodidae) is associated with a point mutation in an *ace1*-type acetylcholinesterase and overexpression of carboxylesterase. *Insect Biochemistry and Molecular Biology* 38, 940–949.

Alon M., Benting J., Lueke B., Ponge T., Alon F. and Morin S. (2006) Multiple origins of pyrethroid resistance in sympatric biotypes of *Bemisia tabaci* (Hemiptera: Aleyrodidae). *Insect Biochemistry and Molecular Biology* 36, 71–79.

Boykin L. M., Shatters R. G., Rosell R. C., McKenzie C. L., Bagnall R. A., De Barro P. and Frohlich D. R. (2007) Global relationships of *Bemisia tabaci* (Hemiptera: Aleyrodidae) revealed using Bayesian analysis of mitochondrial *COI* DNA sequences. *Molecular Phylogenetics and Evolution* 44, 1306–1319.

Byrne D. N. (1999) Migration and dispersal by the sweet potato whitefly, *Bemisia tabaci*. *Agricultural and Forest Meteorology* 97, 309–316.

Byrne D. N. and von Bretzel R. K. (1987) Similarity in flight activity rhythms in coexisting species of Aleyrodidae, *Bemisia tabaci* and *Trialeurodes abutilonea*. *Entomologia Experimentalis et Applicata* 43, 215–219.

Byrne F. J. and Devonshire A. L. (1997) Kinetics of insensitive acetylcholinesterases in organophosphate-resistant tobacco whitefly, *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae). *Pesticide Biochemistry and Physiology* 58, 119–124.

Byrne F. J. and Toscano N. C. (2002) Evaluation of peracid activated organophosphates in studies of insecticide resistance conferred by insensitive acetylcholinesterases. *Journal of Economic Entomology* 95, 425–429.

Chu D., Wan F. H., Tao Y. L., Liu G. X., Fan Z. X. and Bi Y. P. (2008) Genetic differentiation of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) biotype Q based on mitochondrial DNA markers. *Insect Science* 15, 115–123.

Crowder D. W., Ellers-Kirk C., Yafuso C., Dennehy T. J., Degain B. A., Harpold V. S., Tabashnik B. E. and Carrière Y. (2008) Inheritance of resistance to pyriproxyfen in *Bemisia tabaci* (Hemiptera: Aleyrodidae) males and females (B biotype). *Journal of Economic Entomology* 101, 927–932.

Crowder D. W., Horowitz A. R., De Barro P. J., Liu Shu S, Showalter A. M., Kontsedalov S., Khasdan V., Shargal A., Liu J. and Carrière Y. (2010) Mating behaviour, life history and adaptation to insecticides determine species exclusion between whiteflies. *Journal of Animal Ecology* 79, 563–570.

De Barro P. and Ahmed M. (2011) Genetic networking of the *Bemisia tabaci* cryptic species complex reveals pattern of biological invasions. *PLoS One* 6, e25579.

De Barro P. J., Liu S.-S., Boykin L. M. and Dinsdale B. (2011) *Bemisia tabaci*: a statement of species status. *Annual Review of Entomology* 56, 1–19.

Delatte H., Reynaud B. and Granier M. (2005) A new silverleaf-inducing biotype Ms of *Bemisia tabaci* (Hemiptera: Aleyrodidarum) indigenous to the islands of the south-west Indian ocean. *Bulletin of Entomological Research* 95, 29–35.

Dennehy T. J., DeGain B. A., Harpold V. S., Brink S. A., Nichols R. A. (2004) Whitefly resistance to insecticides in Arizona: 2002 and 2003 results, pp. 1926–1938. In *Proceedings of the Beltwide Cotton Conference*, 5–9 January 2004, San Antonio, TX, USA. National Cotton Council, Memphis, Tennessee.

Dinsdale A., Cook L., Riginos C., Buckley Y. M. and De Barro P. (2010) Refined global analysis of *Bemisia tabaci* (Hemiptera: Sternorrhyncha: Aleyrodoidae: Aleyrodidae) mitochondrial cytochrome oxidase 1 to identify species level genetic boundaries. *Annals of the Entomological Society of America* 103, 196–208.

Dittrich V., Ernst G. H., Ruesch O. and Uk S. (1990) Resistance mechanisms in sweet-potato whitefly (Homoptera: Aleyrodidae) populations from Sudan, Turkey, Guatemala and Nicaragua. *Journal of Economic Entomology* 83, 1665–1670.

Frohlich D. R., Torres-Jerez I. I., Bedford I. D., Markham P. G. and Brown J. K. A. (1999) Phylogeographical analysis

of the *Bemisia tabaci* species complex based on mitochondrial DNA markers. *Molecular Ecology* 8, 1683–1691.

Gnankiné O. (2011) Caracterisation moleculaire des populations de *Bemisia tabaci* (Homoptera: Aleyrodidae) et diffusion de la résistance aux insecticides en Afrique de l'ouest. Rapport de stage, Nov 2010–Mars 2011, Université Claude Bernard de Lyon 1, UMR-CNRS, 22 pp.

Gnankiné O., Mouton L., Henri H., Terraz G., Houndeté T., Martin T., Vavre F. and Fleury F. (2012) Distribution of the *Bemisia tabaci* (Homoptera: Aleyrodidae) biotypes and their associated symbiotic bacteria on host plants in West Africa. *Insect Conservation and Diversity*. doi: 10.1111/j.1752-4598.2012.00206.x

Gnankiné O., Mouton L., Savadogo A., Martin T., Sanon A., Vavre F., Dabire K. R. and Fleury F. (2013) Biotype status and resistance to neonicotinoids and carbosulfan in *Bemisia tabaci* (Hemiptera: Aleyrodidae) in Burkina Faso, West Africa.

Gnankiné O., Traoré D., Sanon A. and Ouedraogo A. P. (2004) Impact des traitements insecticides sur les ennemis naturels de *Bemisia tabaci* au Burkina Faso. *Annales de l'Université de Ouagadougou* 2, 225–242.

Gueguen G., Vavre F., Gnankine O., Peterschmitt M., Charif D., Chiel E., Gottlieb Y., Ghanim M., Zchori-Fein E. and Fleury F. (2010) Endosymbiont metacommunities, *mtDNA* diversity and the evolution of the *Bemisia tabaci* (Hemiptera: Aleyrodidae) species complex. *Molecular Ecology* 19, 4365–4378.

Horowitz A. R., Kontsedalov S., Khasdan V. and Ishaaya I. (2005) Biotypes B and Q of *Bemisia tabaci* and their relevance to neonicotinoid and pyriproxyfen resistance. *Archives of Insect Biochemistry and Physiology* 58, 216–225.

Houndété T. A., Kétoh G. K., Hema O. S. A., Brévault T., Glitho I. A. and Martin T. (2010) Insecticide resistance in field populations of *Bemisia tabaci* (Hemiptera: Aleyrodidae) in West Africa. *Pest Management Science* 66, 1181–1185.

Hu J., De Barro P., Zhao H., Wang J., Nardi F. and Liu S.-S. (2011) An extensive field survey combined with a phylogenetic analysis reveals rapid and widespread invasion of two alien whiteflies in China. *PLoS One* 6, e16061. doi:10.1371/journal.pone.0016061

Jones D. R. (2003) Plant viruses transmitted by whiteflies. *European Journal of Plant Pathology* 109, 195–219.

Khasdan V., Levin I., Rosner A., Morin S., Kontsedalov S., Maslenin L. and Horowitz A. R. (2005) DNA markers for identifying biotypes B and Q of *Bemisia tabaci* (Hemiptera: Aleyrodidae) and studying population dynamics. *Bulletin of Entomological Research* 95, 605–613.

Liu S.-S., Colvin J. and De Barro P. J. (2012) Species concepts as applied to the whitefly *Bemisia tabaci* systematics: How many species are there? *Journal of Integrative Agriculture* 11, 176–186.

McKenzie C. L., Hodges G., Osborne L. S., Byrne F. J. and Shatters R. G. Jr (2009) Distribution of *Bemisia tabaci* (Hemiptera: Aleyrodidae) biotypes in Florida – investigating the Q invasion. *Journal of Economic Entomology* 102, 670–676.

Musa D. P. and Ren S. X. (2005) Development and reproduction of *Bemisia tabaci* (Homoptera: Aleyrodidae) on three bean species. *Insect Science* 12, 25–30.

Pascual S. and Callejas C. (2004) Intra- and interspecific competition between biotypes B and Q of *Bemisia tabaci* (Hemiptera: Aleyrodidae) from Spain. *Bulletin of Entomological Research* 94, 369–375.

Roditakis E., Grispou M., Morou E., Kristoffersen J., Roditakis N., Nauen R., Vontas J. and Tsagkarakou A. (2009) Current status of insecticide resistance in Q biotype *Bemisia tabaci* populations from Crete. *Pest Management Science* 65, 313–322.

Roditakis E., Tsagkarakou A. and Vontas J. (2006) Identification of mutations in the para sodium channel of *Bemisia tabaci* from Crete, associated with resistance to pyrethroids. *Pesticide Biochemistry and Physiology* 85, 131–166.

SAS Institute, Inc. (1992–1998) *Statview for Windows. Version 5.0*. SAS Institute, Cary, North Carolina.

Tsagkarakou A., Mouton L., Kristoffersen J. B., Dokianakis E., Grispou M. and Bourtzis K. (2012) Population genetic structure and secondary endosymbionts of Q *Bemisia tabaci* (Hemiptera: Aleyrodidae) from Greece. *Bulletin of Entomological Research* 102, 353–365.

Tsagkarakou A., Nikou D., Roditakis E., Sharvit M., Morin S. and Vontas J. (2009) Molecular diagnostics for detecting pyrethroid and organophosphate resistance mutations in the Q biotype of the whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae). *Pesticide Biochemistry and Physiology* 94, 49–54.