Biol Invasions (2009) 11:1059–1070
DOI 10.1007/s10530-008-9328-9

ORIGINAL PAPER

Differential invasion success among biotypes: case of *Bemisia tabaci*

Hélène Delatte · Pierre-François Duyck · Aurélie Triboire · Patrice David · Nathalie Becker · Olivier Bonato · Bernard Reynaud

Received: 28 October 2007 / Accepted: 25 July 2008 / Published online: 12 August 2008

Abstract Studies on success or failures of biological invasions by different insect biotypes are scarce and could provide interesting insights into the traits that determine greater or lower ability to invade. Life history traits of invasive whiteflies *Bemisia tabaci* of the B biotype (known as a worldwide invasive biotype) and of the indigenous biotype Ms (not known as an invader anywhere in the world), both from the island of La Réunion (Indian Ocean), were compared for this purpose. In our study we demonstrated that within a cultivated host plant (tomato), the B biotype differs from the Ms by a combination of several life-history traits. This combination gives the invasive biotype an advantage over the resident both in terms of rapid demographic growth (increased intrinsic rate of increase and associated traits such as short developmental times and high fecundity) and in terms of competition (large adult and offspring sizes), without any recorded trade off. However, in the field the resident biotype remains dominant on non-cultivated hosts (weeds) and in a particular climate (high humidity). This suggests that invasive biotypes are characterized by physiological, morphological and biological adaptations to a disturbed environment created by anthropic activities at different places in the world, while resident biotypes may persist in less altered habitats.

Keywords Life table · Host preference · Biological invasions · Demography · Resident and invasive biotypes · Whiteflies

H. Delatte (✉) · P.-F. Duyck · A. Triboire · N. Becker · B. Reynaud
CIRAD Pôle de Protection des Plantes, UMR C53 PVBMT CIRAD-Université de la Réunion, 7 Chemin de l'IRAT, Ligne Paradis, 97410 Saint Pierre, La Réunion, France
e-mail: delatte@cirad.fr

P.-F. Duyck
CIRAD PRAM, UPR Systèmes Bananes et Ananas, Quartier Petit-Morne, BP 214, 97285 Le Lamentin Cedex 2, Martinique, France

P.-F. Duyck
Department of Entomology, University of California, One Shields Avenue, Davis, CA 95616, USA

P. David
CEFE-CNRS, UMR 5175, 1919 Route de Mende, 34293 Montpellier Cedex 05, France

N. Becker
Muséum National d'Histoire Naturelle (MNHN), Département Systématique et Evolution, USM 601 & UMR 5202 CNRS, CP 50, 57 rue Cuvier, 75231 Paris Cedex 05, France

O. Bonato
IRD-CBGP, CS 30 016, 34988 Montferrier/Lez, France

Introduction

Biological invasions are a major agent of global change, often linked to emerging diseases (Fargette

et al. 2006; Vitousek et al. 1996), and increasingly recognized as a key threat to biodiversity (Mack et al. 2000). The negative effects of species invasions is often more pronounced in small and isolated regions, such as insular habitats (Gillespie and Roderick 2002), where invasive populations achieve high abundance and, hence, increased damage. Invaders are classically characterized by a high intrinsic rate of increase (Lodge 1993; Rejmanek and Richardson 1996) but often also prove able to withstand or win the competition with resident species (Case et al. 1994; Duyck et al. 2006; Juliano and Lounibos 2005). However traits that promote rapid population growth are usually assumed to trade-off with traits enhancing competitivity (Duyck et al. 2007; Kneitel and Chase 2004; Tilman 1994). Progress in understanding the link between life-history and invasiveness is possible through the accumulation of case studies comparing life-history traits and ecology between invasive and resident taxa. Pairs of closely related taxa offer the best opportunity of meaningful comparisons. Here we chose to compare an invasive and a resident strain (biotypes, see below) belonging to the same species of phytophagous insects, that currently co-occur in the island of La Réunion (Indian Ocean).

Insect populations morphologically similar to, but with different heritable characteristics from, other members of the species, are defined as biotypes (Diehl and Bush 1984). Biotypic variations within species have been extensively described in whiteflies and aphids. Biotypic variation has been related to insecticide resistance (Horowitz et al. 2005), host range (Dolatti et al. 2005; Hebert et al. 2006), plant physiological disorders induced by the insect (Yokomi et al. 1990) or differential fitness (Jyoti and Michaud 2005). These differences tend to persist when several biotypes are brought in sympatry, suggesting at least partial reproductive isolation among them; however the exact degree of isolation is usually unknown (Diehl and Bush 1984).

Some biotypes can be considered highly invasive compared to others. This is particularly the case in the whitefly *Bemisia tabaci* (Hemiptera: Aleyrodidae), a polyphagous pest causing severe losses on crops especially as vector of more than 111 viruses (Jones 2003). An increasing number of biotypes is being described in different parts of the world (Brown et al. 1995; Perring 2001). Population genetic studies have shown that the B biotype probably originated from the Mediterranean/Asia Minor/Africa region (Boykin et al. 2007; Frohlich et al. 1999) and biotype Q from the Mediterranean/North African region (Boykin et al. 2007; Brown 2000). Nowadays, both B and Q biotypes are defined as worldwide invasive biotypes on crops. The first major documented invasion by biotype B was in the USA in the 1980s (Costa and Brown 1991; Perring et al. 1993), where it displaced the indigenous biotype A. In Brazil also, an upsurge of biotype B was recorded in the 1990s (Lima et al. 2002) as well as in Australia (De Barro et al. 2006). In India biotype B was first reported in 1999 in the Kolar district of Karnataka State, South India, and has since then spread rapidly to other states in south India in 2 years (Rekha et al. 2005). Biotype B was also responsible for the displacement of the Turkey-cotton biotype in Turkey in 2000 (Bayhan et al. 2006) generating important damage to vegetable and cotton crops. Despite the worldwide dispersion of biotype B during the last 20 years, another biotype, Q, has started to re-invade regions where biotype B had established (Horowitz et al. 2003; Pascual and Callejas 2004; Shatters et al. 2006) (Zhang et al. 2005). Meanwhile, other biotypes such as A very moderately extended outside of their indigenous distribution.

Bemisia tabaci was reported on cassava from La Réunion, an island situated 700 km east of Madagascar, as early as 1938 (Bourriquet 1938) and later in 1953 (Luziau 1953). However there was no further upsurge or report of *B. tabaci* in La Réunion before the outbreak of the begomovirus *Tomato yellow leaf curl virus* (TYLCV) on tomato crops (*Lycopersicum* spp.) in 1997 with great economic losses (Peterschmitt et al. 1999; Reynaud et al. 2003). The invasion of a new biotype of *B. tabaci* in La Réunion and in the Indian Ocean (IO) was suspected and confirmed using cytochrome oxidase 1 (CO1) sequencing (Delatte et al. 2005). Two different genotypes were indeed found in La Réunion, one a newly described biotype (Ms biotype) indigenous in all the IO, the other being the worldwide invasive B biotype found in two islands of the IO: La Réunion and Mauritius (Delatte et al. 2005; Ganeshan and Abeeluck 2000). Both strains are genetically close and part of the same *B. tabaci* clad together with the Q biotype (Boykin et al. 2007; Delatte et al. 2005). Ms populations of *B. tabaci* induced silverleaf symptoms on *Cucurbita* sp. such as the B biotype populations, and both biotypes were

able to acquire and transmit TYLCV. Adult individuals of the Ms biotype were detected on several families of plants, *Convolvulaceae*, *Euphorbiaceae*, *Solanaceae*, *Fabaceae*, *Verbenaceae*, *Brassicaceae*, *Cucurbitacae*. Although local hybridisation between biotypes B and Ms has been reported at in La Réunion with a microsatellite study (Delatte et al. 2006), the two biotypes still form two separated genetic clusters.

Here, we attempt to identify the traits that have enabled the whitefly *B. tabaci* biotype B to be a successful invader (and to displace biotype Ms) in La Réunion. We first examine whether biotype B exhibits important differences in life-history, compared to Ms, in a common environment. We then examine field distribution patterns to assess whether biotype B seems to tolerate a wider (or different) range of environmental conditions (host plant and climate).

Experimental procedure

Insect rearing and plant material for laboratory studies

Whiteflies used in the whole study were from two laboratory cultures of *Bemisia tabaci*: biotype B and biotype Ms. These cultures originated from adults collected in La Réunion (Delatte et al. 2005). Both biotypes were reared in separate cages on tomato for more than 3 generations in separate climatic chambers (to avoid contamination) at 25 ± 1°C and 60 ± 10% relative humidity (RH) and a 12:12 h photoperiod. Tomato plants used in the longevity, fecundity and development trials were from the Nainemore cultivar (INRA, Fr).

Development of immature stages

We measured life-history traits under laboratory conditions. Two tomato plants (four leaves stage) were left 4 h in rearing cages of each biotype then, the number of eggs was counted per plant. Plants with equivalent amounts of eggs were introduced into separate chambers at five different temperatures: 15, 20, 25, 30, 35 ± 1°C and 60 ± 10% RH and a 12:12 h photoperiod. Two plants were used from 20 to 30°C. At the extreme temperatures: 15 and 35°C, four plants were used to obtain a larger number of eggs.

Every under-leaf of tomato plants with eggs was drawn and the position of each egg recorded. The same procedure was realized for larvae as only *B. tabaci* first instars are mobile. Observations were done daily under a stereoscopic microscope, till the emergence of adults. These drawings allowed us to follow individually each immature until adult emergence. When L4 larvae were observed on a specific plant, it was encaged under an insect-proof net in order to collect all the emerged adults. Eggs and immature stages survivorships were recorded at each temperature and for each biotype individually every day. This experiment was replicated twice.

The modified Logan model (Logan et al. 1976) was fitted to the reciprocal of mean developmental time in days for each temperature (Lactin et al. 1995). The nonlinear fitted line from the modified Logan model intercepted the *x*-axis and identified the lower developmental threshold, the temperature of 40.8°C was used as the maximum developmental temperature according to the literature for the B biotype (Muniz and Nombela 2001). The optimum temperature of development for each *B. tabaci* biotype was identified as the peak in the fitted line.

A one-way ANOVA test was performed to test the biotype effect on the length of each developmental stage and a Pairwise *T*-test was performed when significant values were obtained. All statistical analyses were processed using R (R Development Core Team 2004).

Longevity and fecundity tests

Three to 4 h-old pairs of *B. tabaci* of each biotype were inserted into clip-cages attached to the undersurface of tomato leaves (cv. Nainemore). The caged pairs were introduced into climatic chambers of different temperatures, 15, 20, 25, 30 or 35°C ±1°C at 60 ± 10% RH and a 12:12 h photoperiod. Ten to 25 clip cages per biotype per temperature were followed every 3 days. At that time, each *B. tabaci* pair was moved to a new under-leaf until the death of the female of the pair. The number of eggs laid and the survivorship of both insects per clip-cage were recorded every 3 days. An insect was declared dead when its body was found; otherwise it was not counted in our analysis. A One-way ANOVA was performed to test the biotype and temperature effects

on the fecundity. All statistical analysis were processed using R (R Development Core Team 2004).

Biotype assessment and field collection

Whiteflies were collected on the field on 12 different host plants in 18 different locations situated between 0 and 400 m all around the coast of La Réunion. Parts of the data used (567 whiteflies) came from the sampling described in the study of Delatte et al. (2006), the other part (137 whiteflies) comes from another sampling campaign (2005, unpublished data). For whiteflies of the second field collection, biotype differentiation was assessed by using microsatellite markers as described in Delatte et al. (2006). On the whole 699 *B. tabaci* of both biotypes were analysed. Samplings were done on several families of plants: *Convolvulaceae*, *Euphorbiaceae*, *Solanaceae*, *Fabaceae*, *Verbenaceae*, *Brassicaceae* and *Cucurbitacae*. Once all individuals were classified as B (344) or Ms (355) we analysed the spatial variation in relative frequency of the two biotypes in space. This was performed using a Poisson Log linear model (analysis of deviance with Poisson error), incorporating the effects of rainfall, temperature, host plant described as type (crop vs. weed) and interactions. The change in relative proportions of biotypes due to each effect is modelled as an interaction term between this effect and the "biotype" factor. For example, the interaction between rainfall and biotype models how the relative proportions of the biotypes change with rainfall. Tests of significance of particular effects were performed using standard model simplification procedures (Crawley 1993). Over dispersion was accounted for by using *F*-tests instead of chi-squares to evaluate the changes in deviance (Crawley 1993). All models were fitted using R (R Development Core Team 2004).

Calculation of demographic growth parameters

Demographic parameters were computed following standard methods (Carey 1982; Ebert 1999). Immature age-specific survivorship rates were interpolated as in Carey (1982). Confidence intervals for demographic parameters were estimated as the 2.5 and 97.5 percentiles of a bootstrap distribution resampled 1,000 times (Caswell 2001; Efron and Tibshirani 1993). For the demographic parameters the assumption of a 1:1 sex ratio was used (Ebert 1999).

Egg and adult sizes

Lengths of 100 randomly chosen eggs and adults (females and males) from biotypes B and Ms of the laboratory rearings on tomato plants were measured. Young adults of each biotype were captured and frozen, then laid on their back under a stereoscopic microscope, and their length was measured from the top of their head to the end of their abdomen. An analysis of variance was performed to compare the egg and adult sizes between biotypes B and Ms. A Pairwise *T*-test was performed to compare the size between males and females within and between biotypes using R (R Development Core Team 2004).

Results

Life table parameters and survivorship of immature stages

Life tables were constructed from the number of *B. tabaci* individuals from each biotype surviving at each stage and entering the following stage (Table 1). Temperature had a pronounced effect on the length of time from egg to emergence (ANOVA, $F = 995$, $df = 4$, $P < 0.001$), which was maximal at 15–20°C and minimal at 30°C. Biotype B had a slightly, but significant, shorter developmental time at all temperatures than biotype Ms (ANOVA, $F = 8.97$, $df = 1$, $P = 0.003$ and results of Pairwise *T*-tests are available in Table 1).

A complete logistic model on binomial data with over-dispersion (quasi-binomial), and then a chi-squared test on explicative variables sequentially added (temperature, biotype and interactions) were performed at 5% level of significance. It showed significant effects for the three factors tested (Null model: $df = 44$, temperature: $df = 4$, $P < 0.001$; biotype: $df = 4$, $P < 0.001$; interaction temperature-biotype: $df = 4$, $P = 0.01$). In order to compare the biotypes within each temperature an exact test of Fisher was performed on each temperature between biotypes. Immature survival rates in the temperature range from 20 to 30°C were not significantly different between biotypes B and Ms. A significant difference

Table 1 Durations of developmental immature stages of two biotypes of *Bemisia tabaci* from egg to adult at different temperatures

		Egg-1st instar			1st Instar–2d instar			2d Instar–3rd instar			3rd Instar–4th instar			4th Instar–pupae			Pupae–adult			Total instars	
T (°C)	Biotype	*n*	Duration	±SE	*n*	Duration	±SE	*n*	Duration	±SE	*n*	Duration	±SE	*n*	Duration	±SE	*n*	Duration	±SE	Duration	±SE
15	B	346	29.99	0.18	282	16.37	1.08	51	17.10	1.92	20	11.67	3.89	6	13.00		1	4.00	–	89.00	
	Ms	239	30.26	0.46	35	33.00	–	1	–	–	0	–	–	0	–		0	–	–	–	
20	B	260	12.93	0.09**	210	6.12	0.19	190	4.34	0.13	172	5.13	0.12	163	6.36	0.18	143	4.68	0.13	38.98	0.39**
	Ms	197	13.45	0.13	187	6.49	0.19	147	4.63	0.11	135	5.02	0.13	120	6.35	0.13	110	4.79	0.11	40.42	0.33
25	B	372	7.80	0.07***	263	3.90	0.08***	242	2.60	0.08***	228	3.21	0.08**	212	3.42	0.09*	192	2.69	0.06	23.22	0.18***
	Ms	301	7.37	0.06	250	4.92	0.10	234	3.17	0.09	209	2.92	0.07	185	3.73	0.11	179	2.71	0.07	24.64	0.20
30	B	192	5.81	0.05	178	3.33	0.11***	165	2.10	0.09	155	2.88	0.12***	135	3.02	0.11*	114	2.36	0.09	18.98	0.27***
	Ms	178	5.74	0.05	178	4.33	0.12	159	2.39	0.14	138	3.59	0.15	115	3.67	0.25	104	2.30	0.09	21.20	0.41
35	B	511	5.29	0.03	451	4.05	0.07***	375	2.64	0.08***	317	3.09	0.09*	266	3.78	0.13*	187	2.51	0.05	20.01	0.24***
	Ms	839	6.14	0.03	465	4.70	0.10	309	3.19	0.12	209	3.59	0.19	97	4.64	0.31	45	2.37	0.13	23.10	0.48

n, Number of individual observed; the length of each stage observed was measured in days

Chi-squared tests on the developmental length, significativity: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

between biotypes was reported at 35°C (odds ratio = 6.42, df = 1, $P < 0.001$) (Fig. 1). The difference was concentrated on extreme temperatures, especially 35°C where biotype B survived much better than Ms. Immatures of biotype Ms were not able to survive further than the 2d instar at 15°C, whereas immatures of biotype B were able to develop and reach the adult stage, but in a very low proportion (0.29%). Only 5.36% of biotype Ms total eggs studied reached the adult stage at 35°C, whereas 36.59% of the biotype B eggs did (Fig. 1).

Demographic parameters

The net reproductive rate (Ro) of biotype B was higher than biotype Ms at every temperature, especially at 25°C where the difference was twofold ($Ro_{(B)} = 29.69$; $Ro_{(Ms)} = 14.41$). Intrinsic rate of increase (r) recorded was positive for both biotypes at the different temperatures tested, except at 15 and 35°C. These values suggests a decrease of population for both biotypes at 15°C, and for the Ms biotype at 35°C and inversely an increase predicted for both biotypes at the other temperatures tested. Moreover, the r of biotype B was higher than that of biotype Ms at every temperature, the differential r ($r_B - r_{Ms}$) increasing at high temperatures (Table 2). The analysis of life tables, combining developmental rates, reproduction, mortality, suggested maximum population growth (r) at 30°C for both biotypes ($r_B = 0.128$, $r_{Ms} = 0.108$). These differences between the two biotypes mainly originate from the much higher adult fecundity and juvenile survival in biotype B, although its adult survival is slightly below that of biotype Ms.

The expectation of life at birth (eo) was almost the same for both biotypes for temperatures ranging from 20 to 30°C. However at the extreme temperatures (15 and 35°C), B biotype had a longer eo (almost twofold at 25°C, Table 2).

Temperature thresholds

A nonlinear model (Lactin et al. 1995; Logan et al. 1976) fitted to the data across the whole range of experimental temperatures. The optimum of development temperature was found to be virtually the same for the two biotypes: $T_{optB} = 31.9$°C for biotype B and $T_{optMs} = 31.2$°C for biotype Ms (Fig. 2).

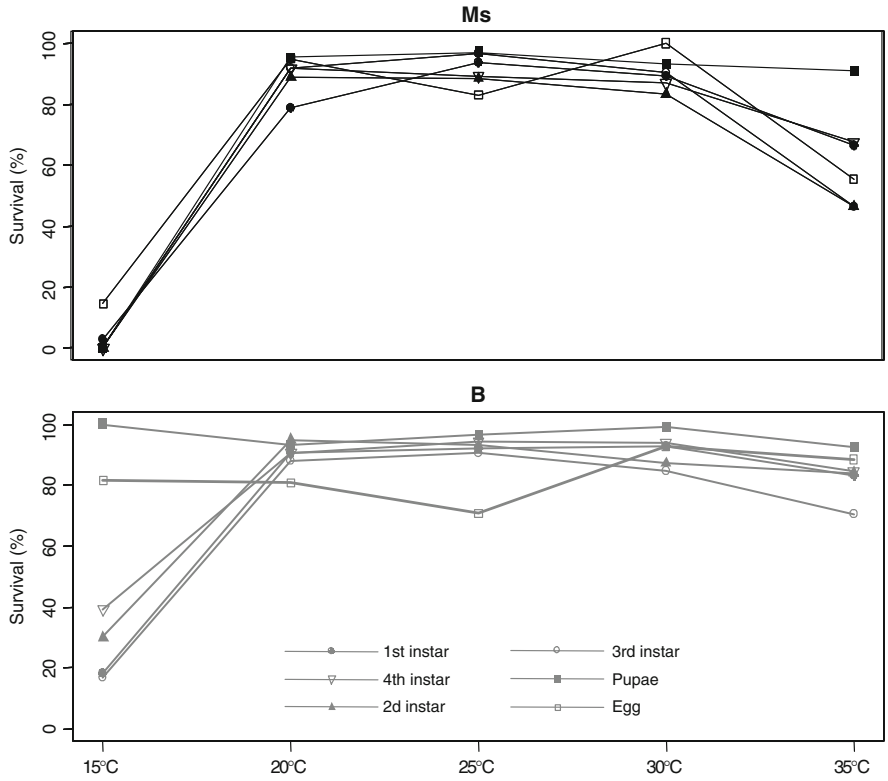

Fig. 1 Survival rates of immature stages in percentages at five constant temperatures for Ms and B biotypes

A linear relationship between larval stages survival of each biotype and temperatures in the range 15–35°C was used to estimate the lower temperature threshold for development. Biotype B had a minimal threshold temperature of development of 10.31°C. No Ms development was recorded at 15°C, so the minimal threshold temperature of development of biotype Ms was not estimated due to the too narrow temperature range observed to obtain a robust value.

Adult and egg sizes

Egg size was significantly larger in biotype B than in Ms (ANOVA, $F = 225$, df $= 1$, $P < 0.0001$), as were adult sizes within each sex (ANOVA, females: $F = 267$, df $= 1$, $P < 0.0001$, males: $F = 207$, df $= 1$, $P < 0.0001$) (Fig. 3).

Host preference and distribution

To assess the host preference and distribution of biotype B and Ms in La Réunion, an analysis of deviance was used as described in the "Experimental procedure" section. Temperature, rainfall and host-plant type significantly affected the relative abundance between the two biotypes (GLM with Poisson error: $F = 14.2$, df $= 2$, $P < 0.0001$; $F = 4.3$, df $= 2$, $P = 0.015$, $F = 22.2$, df $= 22.2$, $P < 0.0001$, respectively, while all interactions among these factors were non-significant ($P > 0.05$)). Relative abundance of the B biotype is higher on crops than on weeds and, higher in dry than in wet areas (Fig. 4, B Biotype frequencies: from 0.4 to 0.7 on crops and from 0.1 to 0.3 on weeds). The effect of temperature, though significant, is weak with a very slightly higher relative abundance of B in warm areas.

Discussion

In this study the invasive biotype B performed better (across the whole range of temperature) than the resident biotype Ms with respect not to a single, but to several life-history traits. The intrinsic rate of increase on tomato in laboratory conditions is higher for the invasive biotype than for the resident. Although a large intrinsic rate of increase is among the characteristics classically attributed to invasive

Table 2 Demographic parameters of biotypes B and Ms at five constant temperatures

	15 (°C)	20 (°C)		25 (°C)		30 (°C)		35 (°C)	
B. tabaci biotypes	B	B	Ms	B	Ms	B	Ms	B	Ms
Net reproductive rate (Ro)	0.02 [0.01;0.04]	17.03 [9.44;26.87]	9.69 [5.78;13.80]	29.69 [21.69;38.37]	14.41 [9.84;19.09]	29.48 [19.01;41.36]	20.22 [16.29;24.52]	2.53 [1.91;3.35]	0.40 [0.31;0.50]
Intrinsic rate of increase (r)	−0.034 [−0.048;−0.027]	0.056 [0.047;0.065]	0.044 [0.035;0.050]	0.101 [0.092;0.108]	0.086 [0.076;0.093]	0.128 [0.113;0.137]	0.108 [0.101;0.115]	0.039 [0.027;0.051]	−0.033 [−0.043;−0.025]
Gross reproductive rate (GRR)	24.3 [2.9;31.2]	61.5 [21.5;83.0]	25.0[12.3;36.9]	76.2 [59.1;90.3]	39.2 [28.0;45.0]	64.4 [37.0;85.0]	39.3 [32.4;47.3]	7.5 [5.6;9.9]	8.3 [6.3;10.4]
Intrinsic birth rate (b)	0.011 [0.006;0.013]	0.076 [0.067;0.084]	0.060 [0.051;0.065]	0.143 [0.133;0.151]	0.117 [0.107;0.124]	0.159 [0.142;0.169]	0.133 [0.126;0.140]	0.087 [0.076;0.099]	0.074 [0.066;0.081]
Intrinsic death rate (d)	−0.044 [−0.055;−0.040]	−0.020 [−0.020;−0.019]	−0.016 [−0.017;−0.015]	−0.042 [−0.043;−0.040]	−0.031 [−0.032;−0.030]	−0.031 [−0.032;−0.029]	−0.024 [−0.025;−0.024]	−0.048 [−0.050;−0.047]	−0.107 [−0.109;−0.105]
Finite rate of increase (λ)	0.97 [0.95;0.97]	1.06 [1.05;1.07]	1.05 [1.04;1.05]	1.11 [1.10;1.11]	1.09 [1.08;1.10]	1.14 [1.12;1.15]	1.11 [1.11;1.12]	1.04 [1.03;1.05]	0.97 [0.96;0.98]
Mean generation time (T)	115.4 [103.5;121.8]	50.6 [47.5;52.8]	51.1 [48.5;53.6]	33.5 [31.9;33.5]	31.0 [29.3;31.0]	26.4 [25.1;26.4]	27.8 [27.4;27.8]	23.8 [23.4;23.8]	27.5 [27.2;27.5]
Doubling time (DT)	20.7 [−25.3;−14.4]	12.4 [10.7;14.9]	15.6 [13.9;19.7]	6.8 [6.4;6.9]	8.1 [7.4;8.1]	5.4 [5.1;5.5]	6.4 [6.0;6.4]	17.7 [13.6;18.4]	21.0 [16.2;−21.4]
Average age in stable population (ā)	34.1 [31.9;40.9]	13.5 [12.4;14.7]	15.4 [14.5;17.2]	8.2 [7.8;8.3]	9.2 [8.8;9.2]	6.9 [6.6;7.0]	7.8 [7.4;7.8]	10.5 [9.5;10.6]	12.2 [11.3;12.2]
Expectation of life at birth (eo)	37.0 [37.0;37.0]	39.9 [36.2;44.5]	41.2 [39.3;43.1]	29.6 [26.6;29.6]	26.8 [24.1;26.8]	26.9 [24.6;27.0]	27.2 [25.7;27.2]	18.5 [17.8;18.5]	9.5 [9.4;9.5]

Confidence intervals were estimated as the 2.5 and 97.5 percentiles of a bootstrap distribution resample 1,000 times and presented into brackets

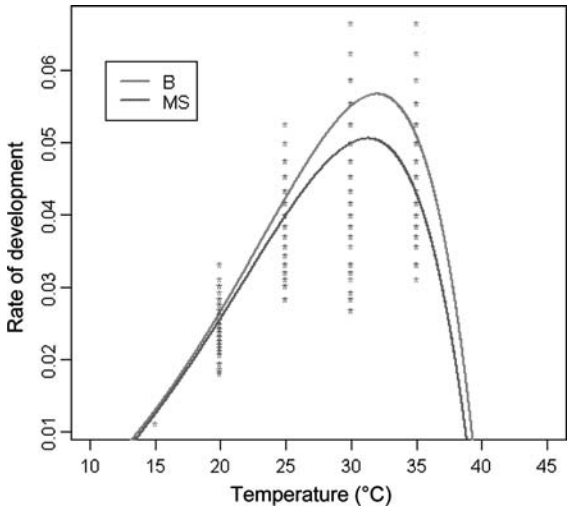

Fig. 2 Influence of temperature on development time of immature stages of *Bemisia tabaci* (B and Ms biotypes). Points indicate experimental values; curve simulated by the model of Logan modified by Lactin et al. (1995)

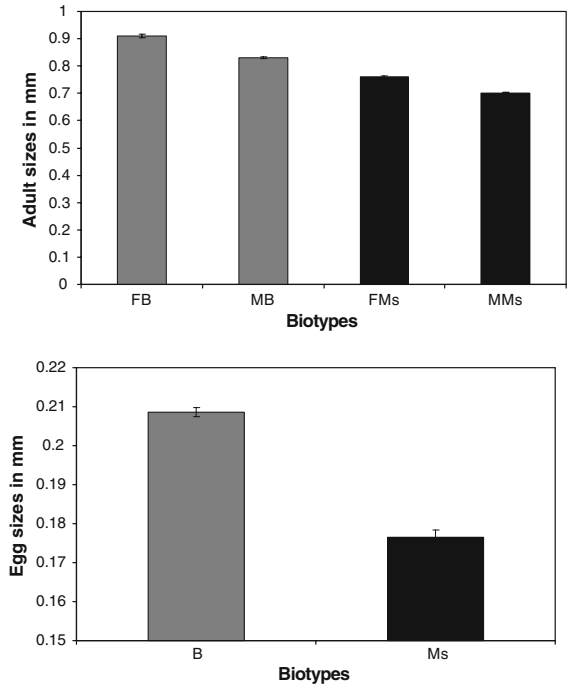

Fig. 3 Adult (females (F) and males (M)) and egg sizes (in mm) for 100 individuals per biotypes B and Ms reared on Tomato

species (Kneitel and Chase 2004) whether or not this population growth advantage could have been instrumental in the success of the B biotype in La Réunion (and worldwide) is not clear. This is because many other traits vary between B and Ms, without apparent trade-off. On the basis of current life-history theory, different traits are assumed to trade-off in such a way that advantages in some traits are balanced by disadvantages in others. For example, a trade-off between juvenile development time and size at maturity is a typical component of life-history models (Roff 1992). Current theory on optimal insect size typically involves a direct trade-off between the fitness advantages of large size, particularly high fecundity, and the disadvantage of a longer development time (Nylin and Gotthard 1998; Roff 1981). In the comparison between biotypes B and Ms, we see no such trade-off: B has shorter developmental times, larger egg and adult sizes, and higher adult fecundity. This was not compensated by survival differences either, because B and Ms had similar immature survival, and although the death rate of B adults was higher than that of Ms, this difference did not (by far) compensate for the higher fecundity.

As no trade-off was observed for biotype B on life-history traits and body sizes compared to Ms, a hypothesis for the size differentiation observed between the exotic invasive biotype and the indigenous one could be a better access to nutrients and ingestion of greater quantities of plant sap during feeding (Byrne and Miller 1990). This could explain how biotype B immature stages can grow to a larger size, and in less time, than Ms. A similar hypothesis has been put forward following observations realized on the honeydew excretion of biotype B (compared to biotype A, a resident biotype in America). Because B produced significantly more honeydew; it was assumed to process more phloem sap than the local biotype (Byrne and Miller 1990). Assuming that B is able to assimilate more energy per unit time in laboratory conditions than is the resident biotype (in our case, Ms), the question arises whether this difference is dependent on environmental factors, or, in other terms, whether Ms could have a symmetric advantage in habitats characterised by different temperatures, humidity and host plants. Up to now, no clear explanations are available on how environmental variation in temperature and diet quality is translated by the physiological and developmental program into phenotypic plasticity of body size in insects (Chapman 1998).

The two biotypes have roughly the same optimal temperatures (31.9 and 31.2°C, respectively), although

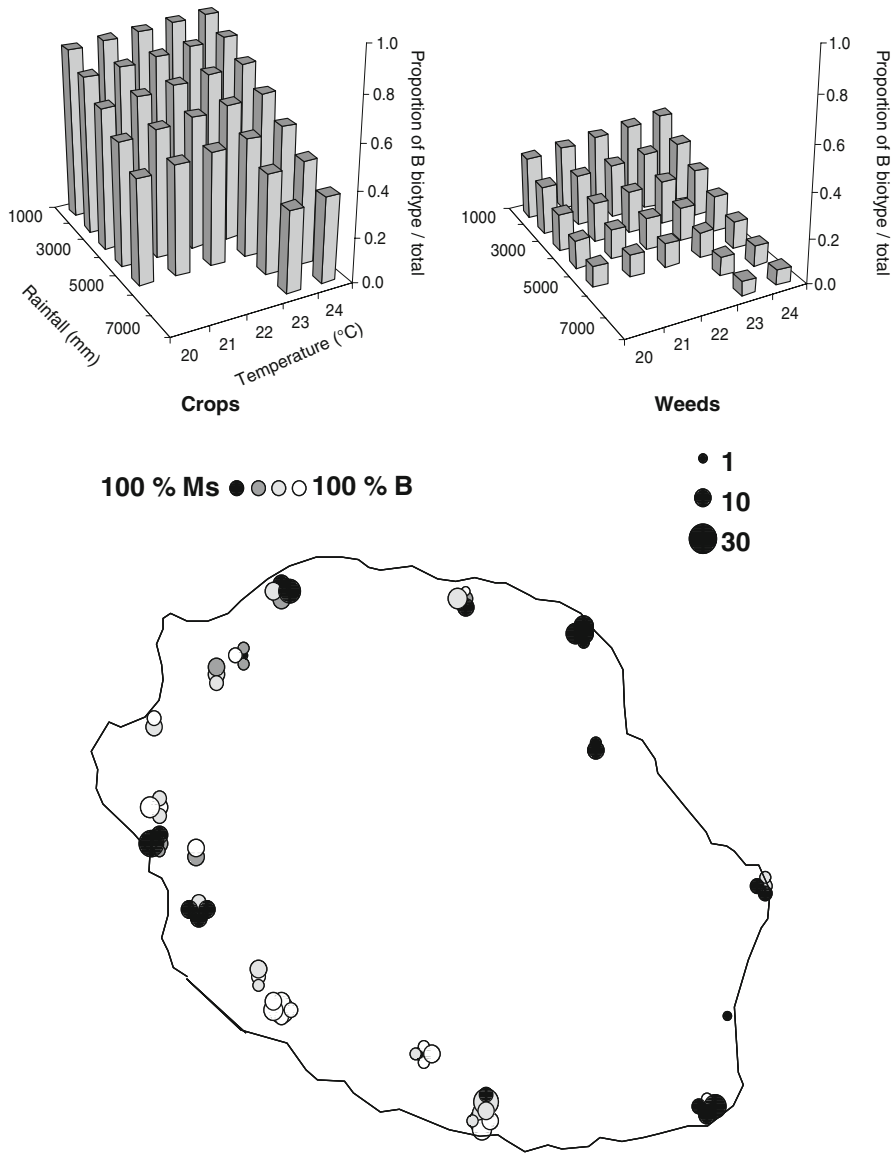

Fig. 4 *Bemisia tabaci* biotypes distribution over la Réunion with respect to rainfall, temperature and host plants. Graphs represent fitted abundances (with the proportion of biotype B over the total abundance) as a function of temperature and humidity in the two plant categories (crops and weeds). As no samples were found for the combination of climatic conditions, 20–23°C; 5,000–7,000 mm, fitted data are not represented for these ranges. Results of the analysis of deviance are given in the result section. The map represents raw data, each sample being represented by a circle, the size and color of which represent total numbers of whiteflies caught and proportions of the two biotypes, respectively

the tolerance of the invasive biotype B to extreme temperatures (in the range 15–35°C) seems higher than that of the resident Ms. The developmental threshold temperature we obtained for biotype B was of 10.3°C, which is quite similar to other thresholds found for biotype B in the literature such as in a study of Nombela et al. (2001) on sweet pepper ($T_{\min} = 9.7$°C). The optimum intrinsic rate of increase (r) at 30°C for both biotypes was also consistent with previous studies realised on tomato for biotype B of Taiwan (Yang and Chi 2006), or biotype Q of France (Bonato et al. 2007). Apart from extreme temperatures, variation in the range 20–30°C (which is the natural range of mean annual temperatures in La Réunion) has little effect on the relative demographic advantages of B observed in the laboratory on tomato. In agreement with these observations, the effect of temperature on relative abundance in the field is quite weak.

On the other hand, relatively dry climates (especially in the West coast) and a certain type of host plant (cultivated plants rather than weeds) seem to correlate with higher abundances of the B biotype relative to the Ms biotype in the field. The climatic effect observed is consistent with a study realised on feeding rate and metabolism of *B. tabaci* (Isaacs et al. 1998). Isaacs et al. demonstrated that biotype B

was able to exploit water-stressed host plants and a broad range of host plant that vary in nutritional quality, without its development being affected, because it was able to modify its physiology and behaviour in response to diets with different nutritional and physical properties (Isaacs et al. 1998).

It is interesting to compare the characteristics of B biotypes with those of another worldwide invasive biotype, biotype Q. We had access to preliminary data on Q, reared on tomato in the same conditions as biotypes B and Ms but in another laboratory (O. Bonato, unpublished data). Biotype Q seems intermediate between B and Ms in terms of adult and egg sizes (all Pairwise *T*-test between biotypes have $P < 0.0001$). Biotypes B and Q (Bonato et al. 2007) also seems to have a higher fecundity than biotype Ms (this study). Demographic and biological parameters differences on a similar host plant (tomato) between B and Q seem limited, at 25 and 30°C. However biotype Q has a better tolerance to extreme temperatures (Bonato et al. 2007). Those results might explain the invasive success of Q in temperate and subtropical area such as in Spain (Guirao et al. 1997) or China (Zhang et al. 2005). Two laboratory studies were carried out on aspects affecting competition between biotypes B and Q on tomato in mixed cultures (Pascual 2006; Pascual and Callejas 2004). Higher mortality for biotype Q and sex ratio favouring biotype B were observed; and different mating behaviours were also observed for B and Q biotypes favouring biotype B, suggesting reproductive interference between both biotypes. The results indicated that under laboratory conditions the studied biotype B should displace biotype Q. Nevertheless biotype Q is dominant in the field in Spain or in Israel, and this was explained by the higher susceptibility of biotype B to insecticides such as pyriproxyfen and neonicotinoids (Horowitz et al. 2005; Pascual 2006).

In conclusion, within a particular, cultivated, host (tomato), a combination of advantages on a series of life history traits might be responsible for the invasive success of biotype B over the resident Ms in La Réunion. On cultivated crops, the invasive biotype may have an advantage over the resident both in terms of rapid demographic growth (increased intrinsic rate of increase and associated traits such as short developmental times and high fecundity) and in terms of competition (large adult and offspring sizes), without any recorded trade off. Preliminary results show that similar characteristics are shared by another invasive biotype, Q, and that which invasive biotype becomes dominant depends on their tolerance to climatic conditions. Interestingly, in La Réunion, the resident biotype (Ms) can also remain dominant on a class of host plants (weeds) and a particular climate (high humidity). Thus coexistence among biotypes at the island scale may be maintained by niche partitioning for resource and climate. The presence of biotype Ms on cultivated plants would be explained by migration from its preferred niche. In addition, other mechanisms could promote coexistence, such as aggregative spatial and temporal distribution (Shorrocks et al. 1984; Wertheim et al. 2000). Disturbed environment created by anthropic activities may select traits favourable for invasive biotypes (Smith and Bernatchez 2008). Biotypes such as B and Q may owe their worldwide success as invaders to physiological, morphological and biological adaptations to these types of environment while resident biotypes may persist in less altered habitats. Highly disturbed habitats by human activities are common in most biome, and one of these consequences might be the loss of diversity such as in cropping systems where cultivated plants, cultural practices and molecules used for insecticide treatments are common to many countries. The globalisation of this kind of uniform disturbed environments plus the extensive exchange of material through international trade might enhance the invasion success.

Acknowledgments We would like to greatly thank Caroline Domerg and Frédéric Chiroleu for their help in the statistical analysis. This study was funded by CIRAD and the Conseil Régional of La Réunion.

References

Bayhan E, Ulusoy MR, Brown JK (2006) Host range, distribution, and natural enemies of *Bemisia tabaci* 'B biotype' (Hemiptera: Aleyrodidae) in Turkey. J Pest Sci 79:233–240. doi:10.1007/s10340-006-0139-4

Bonato O, Lurette A, Vidal C, Fargues J (2007) Modelling temperature-dependant bionomics of *Bemisia tabaci* (Q-biotype). Physiol Entomol 32:50–55. doi:10.1111/j.1365-3032.2006.00540.x

Bourriquet G (1938) Note concernant les maladies des plantes cultivées à La Réunion. Rev Agricole Reun 43:33–38

Boykin LM, Shatters RGJ, Rosell RC, McKenzie CL, Bagnall RA, De Barro PJ et al (2007) Global relationships of *Bemisia tabaci* (Hemiptera: Aleyrodidae) revealed using Bayesian analysis of mitochondrial COI DNA sequences.

Mol Phylogenet Evol 16:1306–1319. doi:10.1016/j.ympev.2007.04.020

Brown JK (2000) Molecular markers for the identification and global tracking of whitefly vector-Begomovirus complexes. Virus Res 71:233–260. doi:10.1016/S0168-1702(00)00221-5

Brown JK, Frohlich DR, Rosell RC (1995) The sweetpotato or silverleaf whiteflies: biotypes of *Bemisia tabaci* or a species complex? Annu Rev Entomol 40:511–534. doi:10.1146/annurev.en.40.010195.002455

Byrne D, Miller WB (1990) Carbohydrate and amino acid composition of phloem sap and honeydew produced by *Bemisia tabac*i. J Insect Physiol 36:433–439. doi:10.1016/0022-1910(90)90061-J

Carey JR (1982) Demography and population dynamics of the Mediterranean fruit fly. Ecol Modell 16:125–150. doi:10.1016/0304-3800(82)90005-9

Case TJ, Bolger DT, Petren K (1994) Invasions and competitive displacement among house geckos in the tropical Pacific. Ecology 75:464–477. doi:10.2307/1939550

Caswell H (2001) Matrix population models: construction, analysis and interpretation, 2nd edn. Sinauer Associates Inc Sunderland, Massachusetts

Chapman RF (1998) The insects: structure and function. Cambridge University Press, Cambridge

Costa HS, Brown JK (1991) Variation in biological characteristics and esterase patterns among populations of *Bemisia tabaci*, and the association of one population with silverleaf symptom induction. Entomol Exp Appl 61:211–219. doi:10.1007/BF00187724

Crawley MJ (1993) GLIM for ecologists. Blackwell, Oxford

De Barro PJ, Bourne A, Khan SA, Brancatini VAL (2006) Host plant and biotype density interactions—their role in the establishment of the invasive B biotype of *Bemisia tabaci*. Biol Invasions 8:287–294. doi:10.1007/s10530-005-1261-6

Delatte H, Reynaud B, Granier M, Thornary L, Lett JM, Goldbach R et al (2005) A new silverleaf-inducing biotype Ms of *Bemisia tabaci* (Hemiptera: Aleyrodidae) indigenous of the islands of the south-west Indian Ocean. Bull Entomol Res 95:29–35. doi:10.1079/BER2004337

Delatte H, David P, Granier M, Lett JM, Goldbach R, Peterschmitt M et al (2006) Microsatellites reveal the coexistence and genetic relationships between invasive and indigenous whitefly biotypes in an insular environment. Genet Res 87:109–124. doi:10.1017/S0016672306008135

Diehl SR, Bush GL (1984) An evolutionary and applied perspective of insect biotypes. Annu Rev Entomol 29:471–504. doi:10.1146/annurev.en.29.010184.002351

Dolatti L, Ghareyazie B, Moharramipour S, Noori-Daloii MR (2005) Evidence for regional diversity and host adaptation in Iranian populations of the Russian wheat aphid. Entomol Exp Appl 114:171–180. doi:10.1111/j.1570-7458.2005.00247.x

Duyck PF, David P, Junod G, Brunel C, Dupont R, Quilici S (2006) Importance of competition mechanisms in successive invasions by polyphagous tephritids in La Reunion. Ecology 87:1770–1780. doi:10.1890/0012-9658(2006)87[1770:IOCMIS]2.0.CO;2

Duyck PF, David P, Quilici S (2007) Can more K-selected species be better invaders? A case study of fruit flies in La Réunion. Divers Distrib 13:535–543. doi:10.1111/j.1472-4642.2007.00360.x

Ebert T (1999) Plant and animal populations—methods in demography. Harcourt Brace & Company, San Diego

Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman & Hall, London

Fargette D, Konate G, Fauquet C, Muller E, Peterschmitt M, Thresh JM (2006) Molecular ecology and emergence of tropical plant viruses. Annu Rev Phytopathol 44:235–260. doi:10.1146/annurev.phyto.44.120705.104644

Frohlich DR, Torres-Jerez I, Bedford ID, Markham PG, Brown JK (1999) A phylogeographical analysis of the *Bemisia tabaci* species complex based on mitochondrial DNA markers. Mol Ecol 8:1683–1691. doi:10.1046/j.1365-294x.1999.00754.x

Ganeshan S, Abeeluck D (2000) First record of the silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring (Hemiptera: Aleyrodidae), from Mauritius. Afr Entomol 8:303–304

Gillespie RG, Roderick GK (2002) Arthropods on islands: colonization, speciation, and conservation. Annu Rev Entomol 47:595–632. doi:10.1146/annurev.ento.47.091201.145244

Guirao P, Beitia F, Cenis JL (1997) Biotype determination of Spanish populations of *Bemisia tabaci* (Hemiptera: Aleyrodidae). Bull Entomol Res 87:587–593

Hebert C, Berthiaume R, Bauce E, Brodeur J (2006) Geographic biotype and host-associated local adaptation in a polyphagous species, *Lambdina fiscellaria* (Lepidoptera: Geometridae) feeding on balsam fir on Anticosti Island, Canada. Bull Entomol Res 96:619–627. doi:10.1017/BER2006464

Horowitz AR, Denholm I, Gorman K, Cenis JL, Kontsedalov S, Ishaaya I (2003) Biotype Q of *Bemisia tabaci* identified in Israel. Phytoparasitica 31:94–98

Horowitz AR, Kontsedalov S, Khasdan V, Ishaaya I (2005) Biotypes B and Q of *Bemisia tabaci* and their relevance to neonicotinoid and pyriproxyfen resistance. Arch Insect Biochem Physiol 58:216–225. doi:10.1002/arch.20044

Isaacs R, Byrne DN, Hendrix DL (1998) Feeding rates and carbohydrate metabolism by *Bemisia tabaci* (Homoptera: Aleyrodidae) on different quality phloem saps. Physiol Entomol 23:241–248. doi:10.1046/j.1365-3032.1998.233080.x

Jones D (2003) Plant viruses transmitted by whiteflies. Eur J Plant Pathol 109:195–219. doi:10.1023/A:1022846630513

Juliano SA, Lounibos LP (2005) Ecology of invasive mosquitoes: effects on resident species and on human health. Ecol Lett 8:558–574. doi:10.1111/j.1461-0248.2005.00755.x

Jyoti JL, Michaud JP (2005) Comparative biology of a novel strain of Russian wheat aphid (Homoptera: Aphididae) on three wheat cultivars. J Econ Entomol 98:1032–1039

Kneitel JM, Chase JM (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. Ecol Lett 7:69–80. doi:10.1046/j.1461-0248.2003.00551.x

Lactin DJ, Holliday NJ, Johnson DL, Craigen R (1995) Improved rate model of temperature-dependent development by arthropods. Environ Entomol 24:68–75

Lima LHC, Campos L, Moretzsohn MC, Navia D, Oliveira MRV (2002) Genetic diversity of *Bemisia tabaci* (Genn.) populations in Brazil revealed by RAPD markers. Genet Mol Biol 25:217–223

Lodge DM (1993) Biological invasions—lessons for ecology. Trends Ecol Evol 8:133–137. doi:10.1016/0169-5347(93)90025-K

Logan JA, Wollkind DJ, Hoyt SC, Tanigoshi LK (1976) An analytic model for description of temperature dependent rate phenomena in arthropods. Environ Entomol 5: 1133–1140

Luziau R (1953) Contribution à la prospection phytosanitaire de l'île de la Réunion. Phytoma 6:13–19

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl 10:689–710. doi:10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2

Muniz M, Nombela G (2001) Differential variation in development of the B- and Q-biotypes of *Bemisia tabaci* (Homoptera: Aleyrodidae) on sweet pepper at constant temperatures. Environ Entomol 30:720–727

Nombela G, Beitia F, Muniz M (2001) A differential interaction study of *Bemisia tabaci* Q biotype on commercial tomato varieties with or without the Mi resistance gene, and comparative host responses with the B biotype. Entomol Exp Appl 98:339–344. doi:10.1023/A:1018911114463

Nylin S, Gotthard K (1998) Plasticity in life-history traits. Annu Rev Entomol 43:63–83. doi:10.1146/annurev.ento.43.1.63

Pascual S (2006) Mechanisms in competition, under laboratory conditions, between Spanish biotypes B and Q of *Bemisia tabaci* (Gennadius). Span J Agric Res 4:351–354

Pascual S, Callejas C (2004) Intra- and interspecific competition between biotypes B and Q of *Bemisia tabaci* (Hemiptera: Aleyrodidae) from Spain. Bull Entomol Res 4:369–375

Perring TM (2001) The *Bemisia tabaci* species complex. Crop Prot 20:725–737. doi:10.1016/S0261-2194(01)00109-0

Perring TM, Cooper AD, Rodriguez RJ, Farrar CA, Bellows TS (1993) Identification of a whitefly species by genomic and behavioral studies. Science 259:74–77. doi:10.1126/science.8418497

Peterschmitt M, Granier M, Mekdoud R, Dalmon A, Gambin O, Vayssieres JF, Reynaud B (1999) First report of tomato yellow leaf curl virus in Réunion Island. Plant Disease 83:303

R Development Core Team (2004) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Rejmanek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77:1655–1661. doi:10.2307/2265768

Rekha AR, Maruthi MN, Muniyappa V, Colvin J (2005) Occurrence of three genotypic clusters of *Bemisia tabaci* and the rapid spread of the B biotype in South India. Entomol Exp Appl 117:221–233. doi:10.1111/j.1570-7458.2005.00352.x

Reynaud B, Wuster G, Delatte H, Soustrade I, Lett JM, Gambin O et al (2003) Les maladies à bégomovirus chez la tomate dans les départements français d'Outre-Mer. Phytoma 562:13–17

Roff DA (1981) On being the right size. Am Nat 118:405–422. doi:10.1086/283832

Roff DA (1992) The evolution of life histories: theory and analysis. Chapman & Hall, New York

Shatters RG, Boykin LM, Bagnall RA, Rosell RC, Frohlich DR, McKenzie CL (2006) Population genetics of *Bemisia tabaci* biotypes B and Q from the Mediterranean and the U.S. inferred using microsatellite markers. 4th International Bemisia workshop, Duck Key, Florida

Shorrocks B, Rosewell J, Edwards K, Atkinson W (1984) Interspecific competition is not a major organizing force in many Insect communities. Nature 310:310–312. doi:10.1038/310310a0

Smith TB, Bernatchez L (2008) Evolutionary change in human-altered environments. Mol Ecol 17:1–8

Tilman D (1994) Competition and biodiversity in spatially structured habitats. Ecology 75:2–16. doi:10.2307/1939377

Vitousek PM, D'Antonio CM, Loope LL, Westbrooks R (1996) Biological invasions as global environmental change. Am Sci 84:218–228

Wertheim B, Sevenster JG, Eijs IEM, Van Alphen JJM (2000) Species diversity in a mycophagous insect community: the case of spatial aggregation vs. resource partitioning. J Anim Ecol 69:335–351. doi:10.1046/j.1365-2656.2000.00396.x

Yang AC, Chi H (2006) Life tables and development of *Bemisia argentifolii* (Homoptera: Aleyrodidae) at different temperatures. J Econ Entomol 99:691–698

Yokomi RK, Hoelmer KA, Osborne LS (1990) Relationships between the sweetpotato whitefly and the squash silverleaf disorder. Phytopathology 80:895–900. doi:10.1094/Phyto-80-895

Zhang LP, Zhang YJ, Zhang WJ, Wu QJ, Xu BY, Chu D (2005) Analysis of genetic diversity among different geographical populations and determination of biotypes of *Bemisia tabaci* in China. J Appl Entomol 129:121–128. doi:10.1111/j.1439-0418.2005.00950.x