Life History Traits of Three Cryptic Species Asia I, Asia II-1 and Asia II-7 of Bemisia tabaci (Hemiptera: Aleyrodidae) Reconfirm Their Genetic Identities

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Life history traits of three cryptic species Asia I, Asia II-1 and Asia II-7 of *Bemisia tabaci* (Hemiptera: Aleyrodidae) reconfirm their genetic identities

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**Abstract**

The *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is a pest of agricultural and horticultural crops. It is a species complex consisting of 34 cryptic species. For the distinction of these cryptic species molecular data is extensively used, but corroboration of these with life history traits has been inadequate. In the present study life history traits of 3 cryptic species Asia I, Asia II-1 and Asia II-7 were compared to verify whether biology data of these coincide with molecular data and genetic identities. The results revealed that developmental periods of Asia I, Asia II-1 and Asia II-7 groups ranged from 23.65 to 25.75 days and these were longer in Asia I than Asia II. Survivorships were nearly equal in all these varying from 68.23 to 69.12% with the variations being statistically insignificant. However, the durations of the preoviposition period, egg stage, fourth instar and longevity were observed to be significantly varying (P ≤ 0.001). Multivariate analysis of the life history parameters through principal component analysis (PCA) revealed that the first 4 principal components (PCs) account for 49.5% of total variation. Separate clusters were observed for the Asia I, Asia II-1 and Asia II-7 with slight overlapping. Overall 70% of the classifications got correctly attributed through canonical discriminant analysis (CDA) and the clustering confirmed the groups revealed by principal component analysis (PCA). These clusterings were reconfirmed in the genetic identity of the 3 cryptic species Asia I, Asia II-1 and Asia II-7 determined through molecular characterization. Thus this study adds to the knowledge on the life history traits of the *B. tabaci* and its cryptic species complex in India.

Key Words: canonical discriminant analysis; cotton life history parameters; multivariate analysis; principal component analysis

**Resumen**

*Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) es una plaga de cultivos agrícolas y hortícolas. Su complejo de especies consta de 31 grupos genéticos o especies putativas. Para la distinción de los grupos genéticos de este complejo, los datos moleculares son utilizados ampliamente, pero la corroboración con las características de la historia de vida ha sido inadequada. En este estudio se compararon las características de la historia de vida de los grupos genéticos Asia I, Asia II-1 y II-Asia 7. El período de desarrollo de Asia I, Asia II-1 y Asia II-7 fue desde 23.65 a 25.75 días, y fue mas largo en Asia I que en los grupos genéticos de Asia II. La sobrevivencia fue casi igual en todos los 3 grupos genéticos, que fue de 68.23 a 69.12% y la variación no fue estadísticamente significativa. Pero la duración del período de preoviposición, estadio de huevo, cuarto estadio y la longevidad de los 3 grupos genéticos observados fueron significativamente diferente (P < 0.001). El análisis multivariante de los parámetros de historia de vida a través de un análisis de componentes principales (ACP) reveló que los primeros 4 componentes principales (PC) representan el 49.5% de la variación total y se observaron grupos separados para los grupos genéticos Asia I, Asia II-1 y Asia II-7 con un poco de solapamiento. En general, el 70% de las clasificaciones se atribuyeron correctamente por el análisis discriminante canónico (CDA) y la agrupación confirmó los grupos revelados por el análisis de componentes principales (ACP). Estos grupos fueron idénticos a los grupos genéticos determinados por la caracterización molecular. Así, este estudio añade a los conocimientos sobre las características del ciclo vital de complejo de especies de *B. tabaci* y de sus grupos genéticos en la India.

Palabras Clave: análisis discriminante canónico; parámetros de historia de vida de algodón; análisis multivariante; análisis de componentes principales

*Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae) is a haplodiploid, sap-sucking hemipteran pest in field crops of warm to hot climates between 30° N and 30° S of the equator. It is polyphagous and has been reported reproducing on more than 900 host plant species (Hsieh et al. 2006). In the last 2 decades, it has become a serious pest on short-lived herbaceous hosts including numerous dicotyledonous crops of agricultural and horticultural importance (Ahmed et al. 2010). The genetic complexity of *B. tabaci* was first recognized in the late 1950’s (Bird 1957). Several populations were observed to be morphologically indistinguishable but differing in host range, host plant adaptability and...
their ability to transmit plant viruses (Perring 2001; Boykin et al. 2007).

De Barro et al. (2011) stated that *B. tabaci* is a species complex of 11 well-defined high level groups containing at least 24 morphologically indistinguishable species. These were later concluded to consist of 34 cryptic species with differences in genetic structure, host plant preferences, bacterial symbionts and interbreeding capabilities (Hu et al. 2011; Liu et al. 2012; Boykin et al. 2012; Lee et al. 2013; Boykin, 2013; Boykin et al. 2013; Boykin & De Barro, 2014).

In India *B. tabaci* was first reported from cotton fields of Punjab in 1905 (Misra & Lambda 1929). Banks et al. (2001) reported the presence of invasive biotype B (now referred as Middle East Asia Minor 1, aka MEAM 1) from the fields of Kolar and Bangalore. Boykin et al. (2007) differentiated the Asian *B. tabaci* populations into Asia I, Asia II and China groups. Ahmed et al. (2011) reported Asia I, Asia II-1 and MEAM 1 from Punjab and Sindh province of Pakistan. Reddy et al. (2012) further resolved these and showed that Asia I, Asia II-1, Asia II-5, Asia II-7, Asia II-8 and MEAM1 groups are present in the Indian subcontinent and Asia.

Numerous studies elaborate the biology, ecology and developmental characteristics of *B. tabaci* and its biotypes, i.e., B biotype (Perring 2001; Brown & Czosnek 2002; Jones 2003; Horowitz et al. 2005; Liu et al. 2007), Cv biotype (Qiu et al. 2011), Q biotype (Drost et al. 1998; Muniz & Nombella 2001) and Asia II-1 and MEAM 1 cryptic species (Ahmed et al. 2014). Biological variations of *B. tabaci* had also been reported according to host plants, viz., cotton (Bethke et al. 1991; Thomas et al. 2011), sweet pepper (Muniz & Nombella 2001), eggplant and tomato (Tsai & Wang 1996), and soybean and garden bean (Mansaray & Sundufu 2009). But corroboration of life history traits with molecular data and genetic grouping had been largely inadequate. In the present study, we compare the life history traits of 3 cryptic species Asia I, Asia II-1 (formally referred to as ZH2 biotype) and Asia II-7 (formally referred to as Cv biotype) collected from the agroclimatic zones of India, and reared on cotton under controlled environmental conditions.

**Materials and Methods**

**WHITEFLY POPULATIONS**

Populations of *B. tabaci* were collected from 5 locations (Amravati, N 21°01'60°4", E 77°55'00°4", 367 m; Kalyani, N 23°37'36.2° E 87°44'09.4", 38 m; Ludhiana, N 30°53'93.2° E 75°48'22.9", 240 m; Sriganganagar, N 29°45'205° E 74°04’ 854°", 171 m and Delhi, N 28°38’28.1" E 77°10'12.2", 213 m asl) in various agroclimatic zones of India from their host plants viz., cotton (*Gossypium* spp.; Malvales: Malvaceae), brinjal (*Solanum melongena* L.; Solanales: Solanaceae) and leucaena (*Leucaena* spp.; Fabales: Fabaceae). These were reared for 6 generations on line ‘RCH138 BGI’ of hybrid cotton in an insect proof climate control chamber at the Indian Agricultural Research Institute, New Delhi, India. The methodology for maintaining pure colonies followed was as described by Luan et al. (2008). Briefly each *B. tabaci* population was maintained in a separate insect proof climate control chamber in an acrylic cage (61 x 61 cm) on line ‘RCH138 BGI’ of hybrid cotton at 28 ± 2 °C, 60 ± 5% RH and 10:14 h L:D. The purity of each of the 3 cryptic species was monitored every alternate generation using mitochondrial cytochrome oxidase 1 (mtCO1) gene sequence analysis. The samples drawn from these cultures were used for the molecular analyses on the above line of hybrid cotton as well as for molecular confirmation of their genetic identities.

**DNA EXTRACTION**

Genomic DNA was extracted from the whole adult female body as described by De Barro & Driver (1997). The PCR primers were employed to amplify a mtCO1 gene fragment (800-820) of *B. tabaci* (Frohlich et al. 1999) with the following PCR conditions: initial denaturation at 95 °C for 4 min followed by 35 cycles of 94 °C for 30 s, 47 °C for 40 s and 72 °C for 1 min with final extension of 72 °C for 10 min. The PCR products were purified and sequencing was performed by Scigenomics Pvt. Ltd. (Cochin, India).

The mtCO1 sequences obtained here were compared with those of the *B. tabaci* species complex from GenBank (Dinsdale et al. 2010; Hu et al. 2011). The sequences were aligned with the CLUSTAL W algorithm (Thompson et al. 1994) and distances were calculated with the Kimura 2-parameter model of MEGAS (Tamura et al. 2013). The NJ (Neighbour-Joining) program available in MEGA6 (Tamura et al. 2013) was used to infer phylogenetic relationships, using *B. afer* (Priesner & Hosny) as an outgroup. One thousand bootstrap replicates were performed for each analysis.

**DEVELOPMENT**

To determine the duration of the various developmental stages, males and females were confined on the abaxial surface of a fully expanded leaf in micro-cages, as described by Zang et al. (2005) and Xu et al. (2010). The eggs laid were observed at 24 h intervals. Transitions not directly observed were inferred from changes in morphology and size, or from the presence of exuviae. A Leica E52 stereozoom microscope was used to observe the life cycle stages and observations were replicated 20 times for each genetic group.

**SEX RATIO AND PREOVIPOSITION PERIODS**

To evaluate the sex ratio, the adults emerging from the puparia were collected cage by cage and anaesthetized with carbon dioxide for 15–20 s; and their sexual gender was determined while these were inactive under the Leica E52 stereozoom microscope taking into account their genitalia (Gill 1990). Twenty pairs of newly emerged adults (<2 h) from each genetic group were randomly selected and confined in 20 clip cages for periodical observations on the preoviposition period.

**LONGEVITY AND FECUNDITY**

To analyse longevity and fecundity, newly emerged males and females were confined in pairs in clip cages having minute holes on both sides (3 x 3 mm), on leaves of 5 to 10 day-old plants. Longevities of males and females, and numbers of eggs laid were recorded daily from 20 such pairs.

**CLUSTERING OF CRYPTIC SPECIES**

Univariate one way single factor ANOVA was performed individually for all the observations on life cycle stages to find out the significant variables (Kalaisekar et al. 2012). After this the pattern of clustering was analyzed using multivariate statistical techniques (Tabachnick & Fidell 2007). The Principal Component Analysis (PCA; SAS procedure; PRINCOMP; SAS version 9.1.3, SAS Institute Inc., Cary, NC, USA) was used without any prior assumption of grouping, and which assesses the components for total variation among the specimens by calculating linear combinations of variables that explain the maximum of the total variation. Canonical Discriminant Analysis (CDA; SAS procedure; CANDISC) was used for calculating the linear combinations of variables that maximize the separation of means of previously defined classes. Contributions of the variables best summarizing the differences between classes are revealed by this technique. Since, Discriminant Func-
tion Analysis (DFA; SAS procedure; DISCRIM) maximizes the variation among groups, it was used to separate cryptic species of *B. tabaci* based on life history data.

**Results**

**GENETIC IDENTITY**

The PCR amplification of mtCO1 gene sequence was edited to remove PCR primer sequences, which yielded a ~750-bp fragment for each *B. tabaci* populations from the Amravati (KF298442), Kalyani (KF298441), Ludhiana (KF298443), Sriganganagar (KF298439) and Delhi (JQ023501) and these were compared with sequences assigned members of *B. tabaci* species complex. Analysis of mtCO1 revealed that these were assignable to the Asia I, and Asia II groups namely Asia II-1 (formally referred to as the Zhu2 biotype) and Asia II-7 (formally referred to as the Cv biotype). The Amravati and Kalyani populations clustered with Asia I, those of Ludhiana and Sriganganagar with Asia II-1, while the Delhi populations clustered with Asia II-7 cryptic species complex. All these populations showed 100% similarity with their respective sequences of assigned members of *B. tabaci* species complex.

**DEVELOPMENT**

The developmental periods of the 3 cryptic species of *B. tabaci* are shown in Table 1. The total developmental periods of Asia I, Asia II-1 and Asia II-7 ranged from 23.80 to 25.75 days. This period was slightly longer in Asia I than in the Asia II. Statistical analysis showed a significant difference in the total developmental period (*F* = 6.6246, df = 4, *P* < 0.001). The developmental periods of the egg, and the first, second, third and fourth instars were longer in Asia I than in Asia II, among which the durations of the egg and the fourth instar periods were significantly varying (*F* = 14.6818, df = 4, *P* < 0.001; *F* = 4.8298, df = 4, *P* < 0.001 respectively).

**SEX RATIO AND PREOVIPOSITION PERIOD**

Results given in Table 1 indicate that females are always more numerous than males regardless of cryptic species. The highest sex ratio was recorded in Asia II-7 followed by Asia II-1 and lastly by Asia I, however the differences were not significant (*F* = 1.8496, df = 4, *P* = 0.05423). The preoviposition period, i.e., the period between adult emergence and egg deposition was the longest in Asia II-7 followed by Asia I and shortest in Asia I, and these differences were statistically significant (*F* = 3.8298, df = 4, *P* < 0.001).

Table 1. Developmental parameters of the genetic groups of *Bemisia tabaci* (mean ± SE in days, *n* = 20).

| Developmental stage/ Component | Asia I     | Asia II-1   | Asia II-7   |
|-------------------------------|------------|-------------|-------------|
| Egg (days)                    | 8.25 ± 0.18| 7.35 ± 0.13 | 6.65 ± 0.21 |
| First instar (days)           | 4.80 ± 0.16| 4.65 ± 0.13 | 4.25 ± 0.12 |
| Second instar (days)          | 3.45 ± 0.11| 3.55 ± 0.13 | 3.85 ± 0.10 |
| Third instar (days)           | 3.60 ± 0.17| 3.30 ± 0.11 | 3.20 ± 0.09 |
| Fourth instar (days)          | 5.65 ± 0.16| 5.20 ± 0.09 | 5.85 ± 0.15 |
| Total dev. period (days)      | 25.75 ± 1.60| 24.05 ± 2.10| 23.80 ± 0.99|
| Preoviposition periods (h)    | 62.3 ± 0.03| 65.9 ± 0.00 | 68.2 ± 0.08 |
| Longevity (male) (days)       | 13.5 ± 0.05| 12.3 ± 0.07 | 13.9 ± 0.07 |
| Longevity (female) (days)     | 17.6 ± 0.05| 16.7 ± 0.05 | 16.5 ± 0.06 |
| Fecundity (no. of eggs)       | 54.04 ± 3.40| 62.3 ± 4.20 | 64.3 ± 2.40 |
| Survivorship (%)              | 68.49 ± 1.02| 68.94 ± 0.59| 69.12 ± 0.56|
| Sex ratio (male: female)      | 1:2.3      | 1:2.8       | 1:3.1       |

**LONGEVITY, FECUNDITY AND SURVIVORSHIP**

The longevity and fecundity data of the cryptic species are shown in Table 1. Male longevity was in the following declining order: Asia II-7 > Asia I > Asia II-1, and the differences were statistically significant (*F* = 8.4029, df = 4, *P* < 0.001). The female longevity was in the following declining order: Asia I > Asia II-1 > Asia II-7, and these differences too were statistically significant (*F* = 5.7036, df = 4, *P* < 0.001). Mean fecundity was in the following declining order: Asia II-7 > Asia II-1 > Asia I. However, variations in fecundity among the 3 cryptic species were statistically insignificant (*F* = 1.8496, df = 4, *P* = 0.1257). The mean percentage of survivorship was found nearly equal in all the 3 cryptic species, and these ranged from 68.49 to 69.12% and the variations were statistically insignificant (*F* = 2.4651, df = 4, *P* = 0.1638).

**CLUSTERING OF CRYPTIC SPECIES**

Life history data such as developmental periods of eggs and instars, longevity, fecundity, preoviposition period and sex ratio were subjected to PCA, which resulted in a reduction of dimensions and in the identification of the sources of variation. The first 4 principal components (PCs) each with an eigenvalue >1 were observed to account for 49.5% of total variation (Table 2). PC1 explained about 25% of the total variation and had a positive loading for 3 variables, i.e., egg, and first and third instars. PC2 explained about 19% of total variation having positive loading for 2 variables, i.e., second instar and the longevity of the male. The plot for first 2 PCs i.e., PC1 and PC2 shown in Fig. 1 brings out the grouping of the cryptic species. These reveal that separate clustering was observed for Asia I, Asia II-1 and Asia II-7 with slight overlap. Canonical discriminant analysis (CDA) was carried out with prior grouping and use of the life history data as classification variables. The statistics namely Wilks’ λ, Pillai’s trace, Hotelling-Lawley Trace and Roy’s greatest root (Table 3) were found to be significant at *P* < 0.0001. These statistics clearly depict the significant contribution towards the model with a lower Wilks’ λ (0.2900), and which held true for all of the other statistics. The projection of biological data onto the first 2 canonical discriminant axes is shown in Fig. 2. The analysis was able to extract differences between the 3 cryptic species with slight overlap among them. The first canonical root clearly discriminates the cryptic species with the main contributions from the egg stage duration and the longevity of the female, while second canonical root was able to discriminate from the fourth instar and the longevity of the male (Table 2). This clustering obtained from CDA confirmed the grouping brought out by PCA. A cross validation of group membership was performed identifying the misclassification of specimens and assessing the utility of selected observations. Overall 70% of the classifications were correctly attributed with a relatively less misclassification. The result of cross validation accurately classified 85% of Asia II-1 populations followed by 75% of those of Asia I and 50% of Asia II-7 (Table 4).

**Discussion**

The range of host plants and host plant suitability are considered as 2 major factors affecting the spread and damage of *B. tabaci*. Host plant suitability and biology had been earlier studied in detail (Bethke et al. 1991; Lin & Ren 2005; Lida et al. 2009; Oriani et al. 2011). The life history traits of Asia I, Asia II-1 and Asia II-7 reported herein add to the existing knowledge on the variations in *B. tabaci* species complex. In the present study, we found significant variations in the total developmental time, egg period and duration of the fourth instar. These are similar to the results obtained on cotton earlier (Bethke et al. 1991; Thomas et al. 2011). The developmental time from egg to adult of the 3 cryptic species ranged from 23.80 to 25.75 days when these were
reared on cotton, which was longer than those reported for Asia II-1 from Pakistan (Ahmed et al. 2014) and for B biotype (now referred as MEAM1) (Lida et al. 2009) on different hosts, but nearly similar to the Cv biotype (now referred as Asia II-7) on cucumber and tomato (Qiu et al. 2011). This variation might be due to host plant because time required for *B. tabaci* to complete development from egg to adult was influenced by the host plant on which it fed (Coudriet et al. 1985; Mansary & Sundufu 2009).

The largest sex ratio was recorded in Asia II-7 followed by Asia I and Asia II-1. The host plant was demonstrated to have a significant effect on the longevity and fecundity of *B. tabaci* (Qiu et al. 2003; Lin & Ren 2005; Qiu et al. 2011; Ahmed et al. 2014). Herein, we found that the longevity of both the male and the female varied significantly, ranging from 12.3 to 17.6 days despite being on the same host plant, i.e., cotton. The longevities of Asia I and Asia II-7 were similar to that of the Cv biotype on tomato, but differed from that of the B biotype (Qiu et al. 2011), which was in the range (10–15 days) reported by Gerling et al. (2001) for *B. tabaci* in the field at temperatures in the higher 20 °C. However the longevity of Asia II-1 was lesser than that reported by Ahmed et al. (2014), which was 28.8 ± 0.5 days. The fecundity variations were statistically insignificant, and fecundity was less than the reported fecundity of B biotype and Cv biotype on other hosts (Qiu et al. 2011) and of Asia II-1 on cotton (Ahmed et al. 2014), but nearly similar to the fecundity of B biotype on laurel and Cv biotype on poinsettia (Qiu et al. 2011).

![Fig. 1. Component analysis (PCA) showing the clustering of genetic groups of *Bemisia tabaci* species complex.](https://bioone.org/journals/Florida-Entomologist)

![Fig. 2. Canonical discriminant functional analyses showing 3 genetic groups of *Bemisia tabaci* species complex.](https://bioone.org/journals/Florida-Entomologist)

| Variable          | Component 1 | Component 2 | Component 3 | Canonical axis 1 | Canonical axis 2 |
|-------------------|-------------|-------------|-------------|-----------------|-----------------|
| Egg               | 0.4503      | -0.0627     | 0.3449      | 0.8932          | -0.2077         |
| First instar      | 0.5220      | -0.3443     | 0.0831      | 0.0194          | -0.0388         |
| Second instar     | -0.0685     | 0.4449      | 0.5260      | -0.3127         | 0.3555          |
| Third instar      | 0.5472      | -0.0194     | 0.3980      | 0.1413          | -0.2016         |
| Fourth instar     | 0.1675      | -0.1238     | 0.5355      | 0.2161          | 0.7661          |
| Longevity         | 0.0578      | 0.6077      | 0.0878      | 0.3331          | 0.7829          |
| Longevity$^2$     | 0.3083      | 0.4238      | -0.2949     | 0.4076          | -0.0950         |
| Fecundity         | -0.3069     | -0.3391     | 0.2400      | -0.2617         | 0.0011          |
| Eigen values      | 2.0491      | 1.5247      | 1.1416      |                 |                 |
| Proportions of variation | 25% | 19% | 14% | |

Table 2. Proportion of variation and variable coefficients for the life history data of *B. tabaci* species complex PC1, PC2, PC3 of PCA and standardized canonical coefficients (CDA)

| Statistic          | Value  | F Value | Num DF | Den DF | Pr > F |
|--------------------|--------|---------|--------|--------|--------|
| Wills’ Lambda      | 0.29000 | 4.07    | 32     | 326.12 | < .0001 |
| Pillai’s Trace      | 0.94127 | 3.50    | 32     | 364    | < .0001 |
| Hotelling-Lawley Trace | 1.68882 | 4.58   | 32     | 219.69 | < .0001 |
| Roy’s Greatest Root | 1.00983 | 11.49   | 8      | 91     | < .0001 |

Table 3. Multivariate statistics and F approximations for the life history data of the *Bemisia tabaci* species complex.
be in agreement with the present study. DFA with a higher classification (85%, 75% and 50%) values helps to establish the probable validity of these life history traits variations. Thus the biological data with the help of PCA and CDA might provide additional knowledge on the B. tabaci cryptic species complex known from India.

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References Cited

Ahmed MZ, De Barro PJ, Greeff JM, Ren SX, Naveed M, Qiu BL. 2011. Genetic identity of the Bemisia tabaci species complex and association with high cotton leaf curl disease (CLCuD) incidence in Pakistan. Pest Management Science 67: 307-313.

Ahmed MZ, Naveed M, Ane MN, Ren SX, De Barro PJ, Qiu B. 2014. Host suitability comparison between the MEAM1 and Asia I1 cryptic species of Bemisia tabaci in cotton-growing zones of Pakistan. Pest Management Science 70: 1531-1537.

Ahmed MZ, Ren SX, Mandour NS, Marathi MN, Naveed M, Qiu BL. 2010. Phylogenetic analysis of Bemisia tabaci (Hemiptera: Aleyrodidae) populations from cotton plants in Pakistan, China and Egypt. Journal of Pest Science 93: 135-141.

Banks GK, Colvin J, Chowda RV, Maruthi MN, Munipappa V, Venkatesh KM, Kiran KM, Padmaja AS, Beita FI, Seal SE. 2001. First report of the Bemisia tabaci B biotype in India and an associated tomato leaf curl virus disease epidemic. Plant Diseases 85: 231.

Bethke JA, Paine TD, Nuessly GS. 1991. Comparative biology, morphometrics, and development of 2 populations of Bemisia tabaci (Homoptera: Aleyrodidae) on cotton and poinsettia. Annals of the Entomological Society of America 84: 407-411.

Bird J. 1957. A whitefly transmitted mosaic of Jatropha gossypifolia. Technical Paper, University of Puerto Rico, Agricultural Experiment Station 22: 1-35.

Boykin LM, De Barro P. 2014. A practical guide to identifying members of the Bemisia tabaci species complex: and other morphologically identical species. Frontiers in Ecology and Evolution 2: 45. doi:10.3389/fevo.2014.00045.

Boykin LM, Shatters RG Jr, Rosell RC, Mckenzie CL, Bagnall RA, De Barro P, Bird J. 1957. A whitefly transmitted mosaic of Bemisia tabaci (Hemiptera: Aleyrodidae) species complex and distribution in Eastern Asia based on mitochondrial DNA markers. Molecular Ecology 8: 1683-1691.

Gerling D, Alomar S, Arno J. 2001. Biological control of Bemisia tabaci using predators and parasitoids. Crop Protection 20: 779-799.

Gill RJ. 1990. The morphology of whiteflies. Whiteflies: Their Bionomics, Pest Status and Management. Intercept, Andover. 1346 pp.

Hsieh CH, Wang CH, Ko CC. 2006. Analysis of Bemisia tabaci (Hemiptera: Aleyrodidae) species complex and distribution in Eastern Asia based on mitochondrial DNA markers. Annals of the Entomological Society of America 99: 760-775.

Hu J, De Barro PJ, Zhao H, Wang J, Nardi F, Liu SS. 2011. An extensive field survey combined with a phylogenetic analysis reveals rapid and widespread invasion of two alien whiteflies in China. PLoS One, 6 (1): e16061. doi:10.1371/journal.pone.0016061.

Jones DR. 2003. Plant viruses transmitted by whitefly. European Journal of Plant Pathology 109: 195-219.

Kalaiselvam A, Ramamurthy VI, Patil JV, Dhandapani A, Azad Thakur NS. 2012. Multivariate morphometrics of elytral colour polymorphism in seven-spotted ladybird beetle, Coccinella septempunctata L. (Coleoptera: Coccinellidae). Current Science 102(10): 1418-1425.

Lee W, Park J, Lee GS, Lee S, Akimoto S. 2013. Taxonomic status of the Bemisia tabaci complex (Hemiptera: Aleyrodidae) and reassessment of the number of its constituent species. PLoS ONE 8(5): e63817. doi:10.1371/journal.pone.0063817.

Lida H, Kitamura T, Honda K. 2009. Comparison of egg-hatching rate, survival rate and development time of the immature stage between B- and Q-biotype of Bemisia tabaci (Gennadius) (Homoptera: Aleyrodidae) on various agricultural crops. Applied Entomology and Zoology 44: 267-273.

Lin L, Ren SX. 2005. Development and reproduction of ‘B’ biotype Bemisia tabaci (Gennadius) (Homoptera: Aleyrodidae) on four ornamentals. Insect Science 12: 1-9.

Liu SS, Colvin J, De Barro PJ. 2012. Species concepts as applied to the whitefly Bemisia tabaci systematics: how many species are there? Journal of Integrative Agriculture 11: 176-186.

Liu SS, De Barro PJ, Xu J, Luan JB, Zang LS, Ruan YM, Wan FH. 2007. Asymmetric mating interactions drive widespread invasion and displacement in a whitefly. Science 318: 1769-1772.

Luan JB, Ruan YM, Zang L, Liu SS. 2008. Pre-copulation intervals, copulation frequencies, and initial progeny sex ratios in two biotypes of whitefly, Bemisia tabaci. Entomologia Experimentalis et Applicata 129: 316-324.

Mansaray A, Sundufu AJ. 2009. Oviposition, development and survivorship of the sweetpotato whitefly Bemisia tabaci, on soybean, Glycine max, and the garden bean, Phaseolus vulgaris. Journal of Insect Science 9: 1-6.

Misra CS, Lamba SK. 1929. The cotton whitefly (Bemisia gossypiperda sp.). Bulletin of Agricultural Research Institute Pusa 196: 1-7.

Muniz M, Nombella G. 2001. Differential variation in development of the B and Q biotypes of Bemisia tabaci (Homoptera: Aleyrodidae) on sweet pepper at constant temperature. Environmental Entomology 30: 720-727.

Oriani MAG, Vendramim JD, Vasancones CJ. 2011. Biology of Bemisia tabaci (Genn.) B biotype (Homoptera, Aleyrodidae) on tomato genotypes. Scientia Agriculturae 68(1): 37-41.

Perring TM. 2001. The Bemisia tabaci species complex. Crop Protection 20: 725-737.

Qiu BL, Deng F, Li SJ, Ahmed MZ, Jin FL, Ren SX, Cuthbertson AGS. 2011. Comparison of biological parameters between the invasive B biotype and a new defined Cv biotype of Bemisia tabaci (Homoptera: Aleyrodidae) in China. Journal of Pest Science 84: 419-427.

Qiu BL, Ren SX, Lin L, Musa PD. 2003. Effect of host plants on the development and reproduction of Bemisia tabaci (Hemiptera: Aleyrodidae). Acta Ecologica Sinica 23: 1206-1211.

Reddy RVC, Kirankumar M, Susan ES, Munipappa V, Veland GB, Govindappa MR, Colvin J. 2012. Bemisia tabaci phylogenetic groups in India and the relative transmission efficacy of tomato leaf curl Bangalore virus by an indigenous and an exotic population. Journal of Integrative Agriculture 11(2): 235-248.

Tabachnick BG, Fidell LS. 2007. Using multivariate statistics, 2nd Edition. Allyn and Bacon, Boston, MA, USA.
Chaubey et al. Life history traits of three cryptic species of *Bemisia tabaci*

Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2013. MEGA6: Molecular Evolutionary Genetics Analysis version 6.0. Molecular Biology and Evolution 30: 2725-2729.

Thomas A, Chaubey R, Kar A, Naveen NC, Ramamurthy VV. 2011. *Bemisia tabaci* (Gennadius) on *Leucaena leucocephala*: new host record from India and a comparative study with cotton populations. International Journal of Tropical Insect Science 31: 235-241.

Thompson JD, Higgins DG, Gibson TJ. 1994. Clustal W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research 22: 4673-4680.

Tsai JG, Wang KH. 1996. Development and reproduction of *Bemisia argentifolii* (Homoptera: Aleyrodidae) on 5 host plants. Environmental Entomology 25: 810-816.

Xu J, De Barro PJ, Liu SS. 2010. Reproductive incompatibility among genetic groups of *Bemisia tabaci* supports the proposition that the whitefly is a cryptic species complex. Bulletin of Entomological Research 100: 359-366.

Zang LS, Liu YQ, Liu SS. 2005. A new clip cage for whitefly experimental studies. Chinese Bulletin of Entomology 42: 329-331.