Temporal Changes in the Aphid–Natural Enemy Complex in Tunisian Citrus over Two Decades[1]

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Abstract Aphid species and their natural enemies were identified in a citrus orchard in the Cap Bon region of Tunisia in 2014–2016. Aphids within the same orchard had previously been studied in 1991–1992, allowing a comparison of the populations over the 20+ yr. Ten aphid species were identified in 1991–1992, while only four were observed in 2014–2016. This reduction in aphid diversity could be linked to observed temperature and rainfall changes attributed to climate change, interspecific competition, increased occurrence of hyperparasitoïds, or any combination of these and other factors. *Aphis spiraecola* Patch and *Aphis gossypii* Glover increased in abundance and occurrence, which is of special concern because they are known as vectors of *Citrus tristeza virus*. Four species of parasitoids and two of predators were identified in 2014 samples, while an increase of hyperparasitism occurred.

Key Words aphids, natural enemies, species composition, population dynamics, citrus

Citrus is an economically important fruit crop that has been cultivated worldwide for over 4,000 yr (Ayazpour et al. 2011, Mukhopadhyay et al. 2004, Olivares-Fuster et al. 2003). It is an especially important crop in the Mediterranean region (Comité de Liaison de l'Agrumiculture Méditerranéenne 2007). In Tunisia alone, where 69% of the country's citrus orchards are in the Cap Bon region (Governorate of Nabeul), production reached a historic high in 2016–2017 with 560,000 metric tons of oranges, clementines, mandarins, and lemons (Tunisian Ministry of Agriculture 2017). This important crop is threatened by aphid pests, which reduce yield by direct feeding (Hermoso De Mendoza et al. 2012) and by vectoring viruses such as *Citrus tristeza virus* (Komazaki 1991), which is recognized as the most important viral disease of citrus in most citrus-producing areas of the world (Rocha-Peña et al. 1995).

The major aphid species encountered in Tunisian citrus orchards are listed by Ben Halima-Kamel et al. (1994) and Boukhris et al. (1996). Those are *Aphis spiraecola* Patch, *Aphis gossypii* Glover, *Toxoptera aurantii* Boyer de Fonscolombe, *Myzus persicae* (Sulzer), *Aphis craccivora* Koch, *Brachycaudus helichrysi* Kaltenbach, *Aphis nerii* Boyer de Fonscolombe, *Macrosiphum euphorbiae*

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(Thomas), and *Aphis fabae* Scopoli. Natural enemies of these aphids were also identified and include representatives of the Coccinellidae, Cecidomyidae, Syrphidae, Chrysopidae, and Braconidae, with the most abundant and conspicuous being coccinellids and cecidomyids (Boukhris-Bouhachem 2011). Gomez-Marco et al. (2016) found many of the same natural enemies attacking *A. spiraecola* in citrus. However, they found that they lacked sufficient efficacy to regulate the aphid populations. In fact, natural control by parasitoids was limited by hyperparasitism (Boukhris-Bouhachem 2011, Gomez-Marco et al. 2015) and the lag time of natural enemy appearance after the aphid population reach damaging levels (Gomez-Marco et al. 2016). Yet, understanding the population dynamics of aphids and their natural enemies is important for proper management of aphid pests of citrus.

In addition, recent studies have demonstrated the impact of climate change on crop pests, especially aphids (Ladànyl and Horvàth 2010) and their natural enemies (Thomson et al. 2010). This impact was related to the increase of atmospheric temperature that regulates insect development. Rainfall also affects the insect metabolism and biology (Andrewartha and Birch 1954). Bale et al. (2002) showed the extreme sensitivity of foliar pests to warming temperatures. Bezemer et al. (1998) reported an increase in *M. persicae* populations due to increases in atmospheric temperature and CO_2. Furthermore, the period during which migration of certain aphid species occurs is increased from 4 to 19 d with an increase of only 1°C in the average winter temperature (Harrington et al. 2007, Zhou et al. 1995). This extended migration allows for the early arrival of aphids to cause increased crop damage by feeding and vectoring viruses (Harrington and Clark 2010). On the other hand, the lack of rain concentrates the carbohydrates in the plant sap making it more attractive to insects (Ziska and Runion 2007). Moreover, several mathematical models demonstrate a change in the species distribution (migration from south to north or at altitude) as a result of climatic change (Jeffree and Jeffree 1996). Overall, these studies suggest a possible shift in aphid species and their natural enemies because of climate changes.

In the study reported herein, we had the relatively unique opportunity to examine the aphid and natural enemy species composition in a citrus orchard that had been previously studied in 1991–1992. We thus investigated the population dynamics of aphids and their natural enemies in the same orchard 23 yr later. Our objective was to detect what changes, if any, had occurred over time.

Materials and Methods

Insect sampling. Aphid samples were collected from a conventionally-managed citrus orchard in the Cap Bon region (N37°05′15″, E11°02′07″) of Tunisia. The orchard had been planted with orange trees, *Citrus* sp., approximately 40 yr earlier. Sampling was conducted weekly from 2014 through 2016. For each sample, aphids were counted on randomly selected 1-m lengths of young shoots (20 shoots × 50 trees). Shoots were removed from the trees and transported to the laboratory where aphids were brushed into a container using 70% ethanol and a fine brush. Counts were made with the aid of a binocular microscope. Aphid species and stages were identified according to the key of Blackman and Eastop (1985). The same orchard and sampling method had been employed in the 1991–1992 study reported by Boukhris-Bouhachem (2011).

Natural enemies of aphids were sampled in 2014 using the same young shoots sampled for aphids. Mummies encountered in these samples were placed separately into small boxes and held under controlled conditions (22°C, 70% relative humidity) until emergence. Parasitoids with open mummies were transferred to Eppendorf tubes to be preserved in 70% ethanol and later mounted in Canada balsam on slides for identification. Any adults of predators found in the samples were collected and identified.

Weather data. Weather data, namely rainfall, mean minimum temperature (T_{min}), and mean maximum temperature (T_{max}), for the 1991–1992 and 2014–2016 periods were obtained from the Meteorological Institute of Tunisia.

Statistical analysis. Data were analyzed with SPSS software (version 2.0). The weather data recorded in the 1991–1992 and 2014–2016 periods were compared by analysis of variance ($\alpha = 0.05$). Aphid and parasitoid occurrences from both periods were compared by χ^2 test. A simple linear regression analysis was used to predict the relationship between total number of aphids and T_{max} recorded in 1991–1992 versus 2014–2016.

Results

Aphid species. Boukhris-Bouhachem (2011) found 10 aphid species in the target citrus orchard in the Cap Bon region in their 1991–1992 study. Those were placed in four groups according to their abundance and timing of occurrence (Table 1) with Group 1 being abundant and present in all seasons (e.g., *A. spiraecola* and *T. aurantii*), Group 2 being abundant during limited periods of the year (e.g., *A. gossypii*), Group 3 being present in low numbers during limited periods (e.g., *A. fabae* and *M. euphorbiae* only in spring season, *M. persicae* from spring to the beginning of the summer, *A. craccivora* from January to June), and Group 4 being winged aphids (e.g., *A. nerii, Lipaphis erysimi* [Kaltenbach], and *Rhopalosiphum maidis* [Fitch]). In that study, *A. spiraecola* and *T. aurantii* (Group 1) were found in mixed colonies with different numbers depending on the sampling period, recorded temperatures, and rainfall. The maximum numbers of *A. spiraecola* and *T. aurantii* were recorded in the spring and autumn when the T_{min} was 10°C and 14°C, respectively, T_{max} was 20°C and 25°C, respectively, and rainfall was 6.5 and 21 mm, respectively. *Toxoptera aurantii* numbers also increased during the summer when only some scattered colonies of *A. spiraecola* were encountered (Fig. 1A). In terms of abundance, *A. gossypii* was third in abundance of colonizing species on citrus with population peaks in late spring and in the autumn.

In our 2014–2016 study, we found only four aphid species in the same orchard. The numbers of *A. spiraecola* and *A. gossypii* significantly increased, but other species that occurred 23 yr earlier, such *T. aurantii*, were absent. The aphids identified in this current survey could be grouped into Group 1 (*A. spiraecola*), Group 2 (*A. gossypii*), and Group 3 (*A. craccivora* observed from April to September; *M. persicae* found only in spring). Aphids (all stages) were present almost the entire year with maximum aphid infestations in the spring and autumn when below average rainfall (40 and 37 mm, respectively) and T_{max} (22°C and

Table 1. Comparison of the aphid species composition and occurrence in Cap Bon (Tunisia) citrus orchard in 1991–1992 and 2014–2016. (χ^2 test: $P < 0.05$).

	1991–1992		2014–2016	
Aphid species	**Percentage**	**Occurrence**	**Percentage**	**Occurrence**
Aphis spiraecola	55.16 a	All year	87.99 b	All the year except Jan.–Feb. and Aug.
Toxoptera aurantii	37.26 a	All year	0 b	—**
Aphis gossypii	5.84 a	All year	11.76 b	All the year except Jan.–Feb. and Aug.
Aphis craccivora	2.63 a	Jan.–June	0.06 b	Apr.–Sept.
Aphis fabae	2.03 a	Apr.	0 b	—**
Macrosiphum euphorbiae	0.13 a	Apr.	0 b	—**
Myzus persicae	0.13 a	Apr.–June	0.03 b	Apr.
Other	0.01 a	Limited periods	0 b	—**

* Percentages within a row and followed by different lowercase letters are significantly different ($P < 0.05$).
** Dash (—) denotes absence of that species.

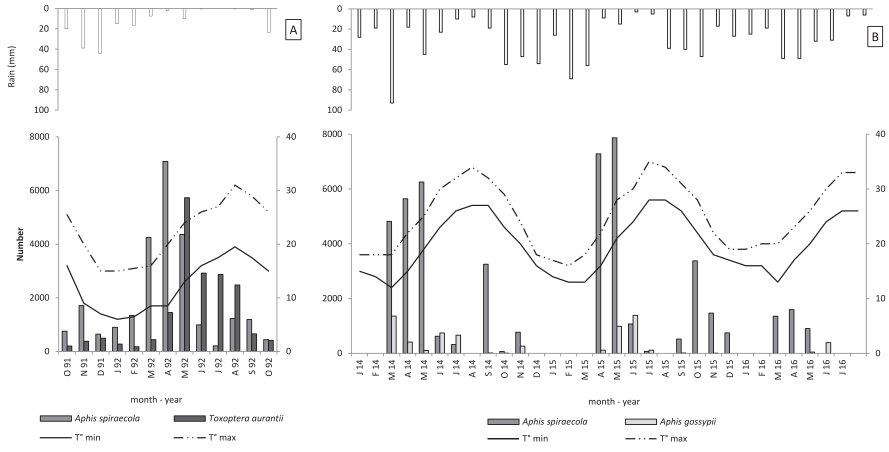

Fig. 1. Aphid species composition in 1991–1992 (A) and 2014–2016 (B) associated with temperatures and rainfall data.

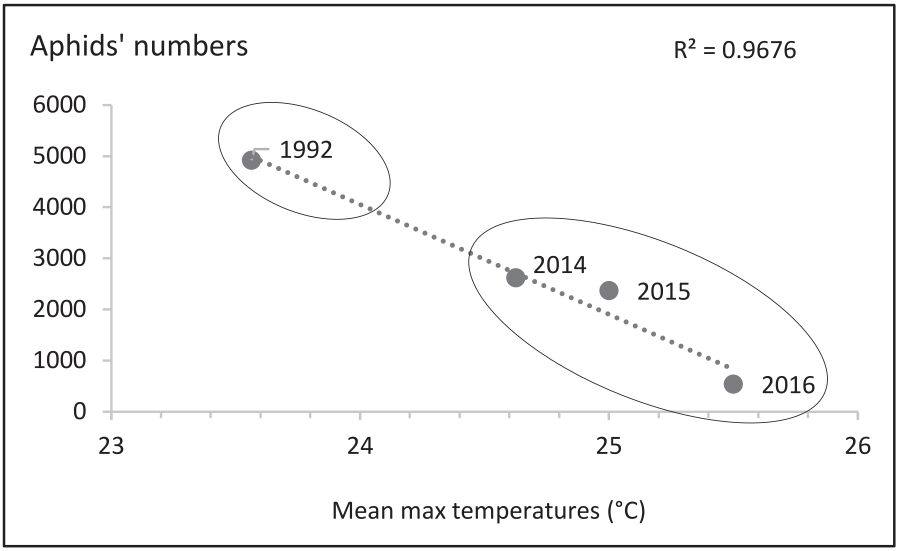

Fig. 2. Linear regression between mean maximum temperatures (°C) (X-axis) and aphid abundances (Y-axis) during 1992 and 2014–2016 in Cap Bon citrus orchard ($R^2 = 0.967$; $y = -2148.7x + 55624$).

28°C, respectively) favorably impacted aphid numbers on citrus. During the winter and summer, the conditions were unfavorable to aphid colonization (T_{min} reached 13°C in winter and T_{max} reached 39°C in summer), and the absence of young shoots on trees during those times likely did not provide aphids adequate refuge and food (Fig. 1B). Mean T_{min} was 20°C and mean T_{max} was 25°C during 2014–2016, which were both significantly higher than in 1991–1992, when mean T_{min} was 12°C and mean T_{max} was 22°C. These are increases of 8°C and 3°C, respectively. Then, mean T_{max} temperatures recorded between January and August in 1991–1992 (23.5°C) were significantly lower than those over the same months in 2014–2016 (25°C). Total rainfall was 17 mm higher in 2014–2016 than in 1991–1992.

Total number of aphids, all species combined, was lower in 2014–2016 in comparison to 23 yr prior. Temperature, and perhaps climate change, could be the cause. According to regression analysis, there is a strong relationship ($R^2 = 0.9676$) between aphid abundance and mean T_{max}, and aphid abundance was distinctly different between the two studies (Fig. 2).

Aphid populations. Numbers of immatures and adults (winged and wingless) of the major aphid species encountered in both studies show that young shoots of citrus are colonized by aphids in March or April, according to the aphid species, in Tunisia (Fig. 3). Thereafter, the total aphid population increases exponentially with a first peak in population density observed in May and a second one of lesser density in September–October.

In 1991–1992, *A. spiraecola* and *T. aurantii* were continuously present on citrus throughout the year, but the numbers of immatures and adults fluctuated depending on the time of the year. Winged *A. spiraecola* females first appeared in January

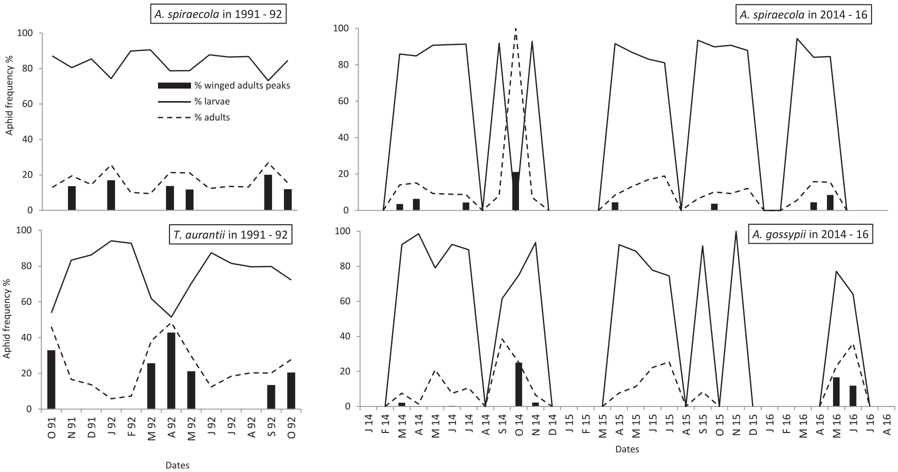

Fig. 3. Population structures of key aphid species *Aphis spiraecola* and *Toxoptera aurantii* in 1991–1992 and *A. spiraecola* and *Aphis gossypii* in 2014–2016.

1992, and *T. aurantii* winged females appeared in March. These initial infestations corresponded with observed increases in numbers of wingless individuals that rapidly reproduced by parthenogenesis resulting in the highest density of the two species in May 1992. Peaks of *T. aurantii* winged females occurred in March–April–May of 1992, while the highest population peaks of *A. spiraecola* winged adults occurred in April–May 1992. Those peaks corresponded with periods of flight and migration for both species, after which crashes in the populations of both species were noted in late summer.

In 2014–2016, the population abundance and structure were characterized by a discontinuity of aphid colonization. All generations of *A. spiraecola* and *A. gossypii* were simultaneously present in mixed colonies in the samples. Population peaks of winged females of *A. spiraecola* were observed in April and October of 2014 and 2015 and in May 2016. For *A. gossypii*, the peaks of winged females occurred in March and October 2014; in March, September, and October 2015; and in May 2016. The spring peaks were followed by high winged aphid productions for both species with a maximal abundance recorded in May 2014 and 2015 for *A. spiraecola* and in March 2014, May–June 2015, and May–June 2016 for *A. gossypii*. In summer, both species disappeared, with the departure of *A. gossypii* occurring later than *A. spiraecola*, which migrated few weeks earlier.

Natural enemies. In 2014, the most abundant and prominent parasitoids that emerged from aphid mummies were *Lysiphlebus testaceipes* (Cresson) followed by *Lysiphlebus fabarum* (Marshall), *Binodoxys angelicae* (Haliday), and *Aphidius matricariae* Haliday. *Lysophlebus testaceipes* emerged primarily from *A. gossypii* (85%) and rarely from *A. spiraecola* (15%). Similarly, *L. fabarum* primarily parasitized *A. gossypii* (75%) and occasionally *A. spiraecola* (25%). *Binodoxys angelicae* and *A. matricariae* were parasitized by *A. spiraecola*, but parasitism was minor.

Table 2. Comparative percentages of parasitoids and hyperparasitoids observed on aphids in Cap Bon (Tunisia) citrus orchard in 2001 and 2014. (χ^2 test: $P < 0.05$).*

Species	2001**	2014
Lysiphlebus testaceipes	6.5 a	30 b
Lysiphlebus fabarum	10 a	6 b
Binodoxys angelicae	9 a	3 b
Aphidius matricariae	14.5 a	2 b
Pachyneuron sp.	38.5 a	56 b
Asaphes sp.	0 a	3 b
Other	21.5 a	0 b

* Percentages within the same row and followed by different lowercase letters are significantly different ($P < 0.05$).

** From Boukhris-Bouhachem (2011).

Of note, 59% of the parasitoids that emerged were hyperparasitoids from the genus of *Pachyneuron* Walker and *Asaphes* Walker (Table 2). Furthermore, the ladybird beetle *Scymnus subvillosus* (Goeze) with the cecidomydid *Aphidoletes aphidimyza* (Rondani) were the most abundant aphid predators found in the samples.

Discussion

Aphid species composition in the Cap Bon citrus orchard in Tunisia was diversified and consisted of 10 species in 1991–1992. More than two decades later, the aphid composition in the same orchard was less diversified; only four species were collected, with *A. spiraecola* and *A. gossypii* being the key species, accounting for 99.75**%** of the total aphids sampled during this study.

In the Mediterranean Basin, Franco et al. (2006) listed nine aphid species in Algerian citrus orchards, seven in France, eight in Greece, one in Israel, five in Italy, six in Morocco, and five in Turkey. In Egypt, only *A. gossypii* was reported on citrus trees (Kamel 2010). Furthermore, eight species were reported in Spain (Hermoso De Mendoza and Moreno 1987, Hermoso De Mendoza et al. 1997), nine in Japan (Komazaki 1981) and 14 worldwide on citrus (Blackman and Eastop 2006).

The predominance of *A. spiraecola* and *A. gossypii* also was observed in Morocco by El-Haddad et al. (2016) who reported that 60–100**%** of total aphids were *A. spiraecola* and *A. gossypii*. In Spain, the most abundant aphid species were *A. spiraecola* (77**%**) and *A. gossypii* (15**%**) with only a few colonies of *T. aurantii* and *M. persicae* (García-Prieto et al. 2005).

The disappearance of *T. aurantii* (the second most abundant aphid species recorded in the 1991–1992 study), *A. fabae*, and *M. euphorbiae* from the orchard coupled with the reduction of *A. craccivora* and *M. persicae* populations occurring during shorter periods of time may be the result of repetitive prophylactic pesticide treatments and/or climatic changes (increase of 3°C in mean T_{max} over the two decades). Giorgi and Lionello (2007) found that pronounced atmospheric warming in the Mediterranean region has affected aphid diversity. Additional studies have reported that temperature impacts aphid population composition (Campbell et al. 1974; Komazaki 1982; Nowierski et al. 1983; Wang and Tsai 2000, 2001).

Inter- and intraspecific competition also may have played a role in the disappearance of *T. aurantii*, *A. fabae*, and *M. euphorbiae* from the citrus orchard and the accompanying dominance of aphid populations by *A. spiraecola* and *A. gossypii* in 2014–2016. In fact, Hermoso De Mendoza et al. (2012) found that in Spain since the 1980s, *A. spiraecola* has displaced *A. gossypii* as the most abundant aphid on citrus. They postulated that this was due to the low efficacy of the natural enemies against *A. spiraecola*. Muller and Godfray (1997) further demonstrated that *Microlophium carnosum* Buckton and *Rhopalosiphon padi* L. populations on nettle were affected by an indirect interspecific competition. Yet, Petersen and Sandström (2001) demonstrated that indirect competition between two aphid species can influence aphid performance (e.g., nymph production and feeding behavior), resulting in the disappearance of one species and, in return, the increase in number of the other.

The disappearance of *T. aurantii* from the orchard was accompanied by *A. gossypii* becoming the second most abundant aphid in the orchard. A similar situation was observed in Calabria (Spain) where 3 yr of monitoring of aphid populations in citrus revealed the disappearance of *Toxoptera citricidus* Kirkaldy, replaced in number and frequency by *A. gossypii* (Albanese et al. 2010). This also underscores that *A. gossypii* is increasing in worldwide importance in threatening citrus production. Unfortunately, *A. spiraecola* and *A. gossypii* are well known as polyphagous pests, vectors of *Citrus tristeza virus*, *Cucumber mosaic virus* (CMV), and *Potato virus Y* (PVY) (Hermoso De Mendoza et al. 1984, Hullé et al. 2012, Maroquin et al. 2004, Norman and Grant 1953) and are reportedly developing resistance to chemical insecticides (Smirle et al. 2010).

Moreover, during 1991–1992, *A. spiraecola* and *T. aurantii* were continuously present in the Cap Bon citrus orchard while in Japan, Komazaki (1981) found *T. aurantii* in citrus from spring to the start of the summer. On the other hand, Boukhris-Bouhachem (2011) reported *A. fabae* from the Cap Bon orchard only in the spring of 1992. Sekkat (1987) observed *A. fabae* occurring over a longer period from spring to the start of the summer in Morocco. By contrast, Komazaki (1981) and Aroun (1985) did not report *A. fabae* in their studies. Boukhris-Bouhachem (2011) reported *M. euphorbiae* in May while, in Algeria, Aroun (1985) reported the species during the spring and autumn. Observations of all other aphid species identified in the 1991–1992 study (Boukhris-Bouhachem 2011) corroborated the observations and reports from Algeria (Aroun 1985), Morocco (Sekkat 1987), Spain (Hermoso De Mendoza and Moreno 1987, Hermoso De Mendoza et al. 1997), and Japan (Komazaki 1981).

On the other hand, initial infestations of *A. spiraecola* and *T. aurantii* within the Cap Bon orchard appeared in January and March, respectively. These populations then spread throughout the orchard in midspring for *A. spiraecola* and spring and autumn for *T. aurantii*. This dynamic is characteristic of tree-dwelling aphids, which exhibit an exponential increase in populations in the spring followed by a sudden and total collapse of the population in the summer (Karley et al. 2004). Frequently, this summer population crash is followed by a secondary peak, of lesser magnitude, in the late summer. Aphid population dynamics also depend on their competitors (Kaneko 2003, Stadler 2004), the quality of the host plant tissues (Dixon and Glen 1971) (in this case the flushing shoots), migration (Kindlmann and Dixon 1996), and weather conditions (Karley et al. 2004).

Over two decades after the initial study, *A. spiraecola* and *A. gossypii* became the most abundant species and were highly active in spring. They reproduced continuously by parthenogenesis and spread throughout the orchard in early summer, a phenomenon also reported by Van Emden and Harrington (2007). In general, high aphid populations were observed in April–June, a cool and wet period of the year, when host plant growth is characterized by heavy and active flush development of shoots and foliage, thus providing food resources to support aphid population increase as described by Southwood and Way (1970). Lower numbers of aphids occurred between September and November, the hot and dry months of the year, characterized by a relative lack of flush host plant growth.

Parasitoids collected from 2014 have been previously reported in Greece (Katsoyannos 1993), Italy (Tremblay et al. 1980), Spain (Llorens and Jose 1990), and Tunisia (Limam Sallemi et al. 2013). *Lysiphlebus testaceipes* increased in occurrence and abundance, as cited by Limam Sellami et al. (2013), and replaced *A. matricariae*, *L. fabarum*, and *B. angelicae* reported in 2001 by Boukhris-Bouhachem (2011). *Lysiphlebus testaceipes* is a competitive and dominant endophagous species of *T. aurantii* and *A. gossypii*. However, it is unable to complete its development on *A. spiraecola* (Tremblay and Barbagallo 1983). Consequently, high numbers of *A. spiraecola* might be attributed to the low parasitism rate by this parasitoid. Moreover, *B. angelicae*, its unique primary parasitoid (Gomez-Marco et al. 2015), is significantly decreasing in abundance over time in Tunisian citrus orchards. This may be due to the hyperparasitoid activities as cited by Gomez-Marco (2016).

Biological control exerted by natural enemies of aphid pests of citrus is thus not sufficient to provide management of aphid infestations, but it may prove promising as a component of an overall pest management program for aphids in citrus. Predation was basically nonexistent in our study, but it should not be discounted for future consideration and development. Interestingly, Wu et al. (2011), relying on the results of Walters and Hassall (2006), who demonstrated that insect body size is inversely related to temperature, concluded that parasitoids took longer to handle large aphids than small ones. Furthermore, the attack rate of the predator *Harmonia axyridis* (Pallas) and the parasitoid *Aphidius picipes* Nees on *Sitobon avenae* F. increased in elevated CO_2, resulting in substantially suppressed aphid abundance (Chen et al. 2007). Yet, Schmidt et al. (2003) showed that hymenopteran parasitoids provided important suppression of aphids and are more effective natural enemies than predators. However, Gomez-Marco et al. (2016) observed that, when abundant sufficiently early in the target host population development, predators are capable to lowering aphid populations below economic threshold levels. Potts and Vickermam (1974) attributed low levels of coccinellids in aphid-infested crops to insecticide use, while Vickerman and Wratten (1979) postulated that coccinellids require certain threshold densities of target prey to remain and reproduce in cereal grains. Hence, these factors demonstrate the possibility of using natural enemies for the biological control of aphids. The response of these fauna to climate change should be considered as coccinellids, and possibly others, are more resistant to predicted climate conditions (Thomson et al. 2010). All these factors should be continually assessed and evaluated for a better understanding of the natural enemy behavior.

In conclusion, the aphid species composition and their natural enemies in the Cap Bon citrus orchard changed over the two decades. Two pest species, *A. spiraecola* and *A. gossypii*, emerged as the most abundant and occurred throughout the year. Other species, such as *T. aurantii*, *A. fabae*, and *M. euphorbiae*, were not found in the orchard in 2014–2016. Increased abundance of *A. spiraecola* in Tunisia and Mediterranean area orchards may be due to climate changes and interspecific competition. In addition, *A. spiraecola* is tolerant of high proline content in citrus trees, and this species efficiently converts foliar energy metabolites (Mostefaoui et al. 2014), which may explain their high numbers in comparison to other aphid species in citrus. The parasitoid *L. testaceipes* was observed at higher levels in 2014 than in 2001, which could account for the increasing numbers of its targeted prey *A. gossypii*.

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References Cited

Albanese, G.R., R. Schimio, A. Fontana, L. Ferretti, V. Palmeri, O. Campolo and M. Barba. 2010. Assessment of *Citrus tristeza virus* (CTV) incidence in Calabria, southern Italy: Results of a three-year survey. Phytopathol. Mediterr. 49: 27–34.

Andrewartha, H.G. and L.C. Birch. 1954. The Distribution and Abundance of Animals. Univ. Chicago Press, Chicago, IL.

Aroun, M.E.F. 1985. Les aphides et leurs ennemis naturels dans un verger d’agrumes de la Mitidja (Algérie). Thèse de magister. Institut National Agronomique, El Harrach, Algeria.

Ayazpour, K., K. Sijam, G. Vadamalai and H. Jaafar. 2011. Molecular characterization of *Citrus tristeza virus* strains in Peninsular Malaysia. Afr. J. Microbiol. Res. 5: 2838–2846.

Bale, J.S., G.J. Masters, I.D. Hodkinson, C. Awmack, T.M. Bezemer, V.K. Brown, J. Butterfield, A. Buse, J.C. Coulson, J. Farrar, J.E.G. Good, R. Harrington, S. Hartley, T.H. Jones, R.L. Lindroth, M.C. Press, I. Symrnioudis, A.D. Watt and J.B. Whittaker. 2002. Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. Glob. Change Biol. 8: 1–16.

Ben Halima-Kamel, M., J.M. Rabasse and M.H. Ben Hamouda. 1994. Les pucerons des agrumes et leurs ennemis en Tunisie. Tropicultura 12 (4): 145–147.

Bezemer, T.M., T.H. Jones and K.J. Knight. 1998. Long-term effects of elevated CO_2 and temperature on populations of the peach potato aphid *Myzus persicae* and its parasitoid *Aphidius matricariae*. Oecologia 116: 128–135.

Blackman, R.L. and V.F. Eastop. 1985. Aphids on the World’s Crops. An Identification Guide. John Wiley and Sons, Chichester, MA.

Blackman, R.L. and V.F. Eastop. 2006. Aphids on the World’s Herbaceous Plants and Shrubs. John Wiley and Sons, Chichester, MA.

Boukhris, S., A. Jerraya and H. Boudhir. 1996. Etude préliminaire sur la présence des espèces aphidiennes en verger d'agrumes (Cap Bon, Tunisie). Ann. Institut Nat. Rech. Agro. Tunisie 69: 55–72.

Boukhris-Bouhachem, S. 2011. Aphid enemies reported from Tunisian citrus orchards. Tunisian J. Plant Prot. 6: 21–27.

Campbell, A.B.D., B.D. Frazer, N. Gilbert, A.P. Gutierrez and M. Mackauer. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431–438.

Chen, F.J., G. Wu, M.N. Parajulee and F. Ge. 2007. Impact of elevated CO_2 on the third trophic level: A predator *Harmonia axyridis* and a parasitoid *Aphidius picipes*, Biocontrol Sci. Technol. 17: 313–324.

Comité de Liaison de l'Agrumiculture Méditerranéenne. **2007.** Les exportations d'agrumes du basin Méditerranéen. Statistiques, évaluations, répartitions, situation 2006–2007.

Dixon, A.F.G. and D.M. Glen. 1971. Morph determination in the bird cherry-oat aphid *Rhopalosiphon padi* L. Ann. Appl. Biol. 68 (1): 11–21.

El-Haddad, A., A. El-Amrani, A. Fereres and A. Moreno. 2016. Spatial and temporal spread of *Citrus tristeza virus* and its aphid vectors in the north western area of Morocco. Insect Sci. 23: 903–912.

Franco, J.C., F. Garcia-Marí, A.P. Ramos and M. Besri. 2006. Survey on the situation of citrus pest management in Mediterranean countries. Intern. Org. Biol. Integr. Contr., West Palaearctic Reg. Sec. Bull. 29 (3): 335–346.

García-Prieto, F., A. Tinaut-Ranera, N. Pérez Hidalgo and J.M. Nieto Nafría. **2005.** Apéndice 3. Relaciones pulgón/hormiga y hormiga/pulgón, Pp. 345–350. *In* Nieto Nafría, J.M., M.P. Mier Durante, F. García Prieto and N. Pérez Hidalgo (eds.), Fauna Ibérica. Vol. 28, Hemiptera, Aphididae III. Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid.

Giorgi, F. and P. Lionello. 2007. Climate change projections for the Mediterranean region. Glob. Planet Change 63: 90–104.

Gomez-Marco, F., A. Tena, J. A. Jacques and A. Urbaneja García. 2016. Early arrival of predator controls *Aphis spiraecola* colonies in citrus clementines. J. Pest Sci. 89: 69–79.

Gomez-Marco, F., A. Urbaneja, J.A. Jacques, P.F. Rugman-Jones, R. Stouthamer and A. Tena. 2015. Untangling the aphid–parasitoid food web in citrus: Can hyperparasitoids disrupt biological control? Biol. Contrik 81: 111–121.

Harrington, R. and S. Clark. 2010. Trends in the timings of the start and end of annual flight periods, Pp. 41–54. *In* Kindlmann, P., A.F.G. Dixon and J.P. Michaud (eds.), Aphid Biodiversity Under Environmental Change: Patterns and Processes. Springer, Dordrecht, Netherlands.

Harrington, R., S.J. Clark, S.J. Welham, P.J. Verrier, C.H. Denholm, M. Hullé, D. Maurice, M.D. Rounsevell and N. Cocu. 2007. European Union Examine Consortium: Environmental change and the phenology of European aphids. Glob. Change Biol. 13: 1550–1564.

Hermoso de Mendoza, A., J.F. Ballester-Olmos and J.A. Pina-Lorca. 1984. Transmission of *citrus Tristeza virus* by aphids (Homoptera, Aphididae) in Spain, Pp. 23–27. *In* Garnsey, S.M., L.W. Timmer and J.A. Dodds (eds.), Proc. 9th Conf. Intern. Org. Citrus Virol. (IOCV), Riverside, CA.

Hermoso de Mendoza, A., R. Esteve, J.M. Llorens and J.M. Michelena. 2012. Evolución global y por colonias de los pulgones (Hemiptera, Aphididae) y sus enemigos naturales en clementinos y limoneros valencianos. Bol. San. Veg. Plagas 38: 61–72.

Hermoso de Mendoza, A. and P. Moreno. 1987. Cambios cuantitativos en la fauna afidica de los cítricos valencianos. Bol. San. Veg. Plagas 15: 139–142.

Hermoso de Mendoza, A., E. Pérez and V. Real. 1997. Composición y evolución de la fauna afídica (Homoptera, Aphidinea) de los cítricos valencianos. Bol. San. Veg. Plagas 23: 363–375.

Hullé, M., E. Turpeau and B. Chaubet. 2012. Encyclop'aphid, tout savoir sur les pucerons. Institut National Recherche Agronomique Mag. 21: 21–31.

Jeffree, C.E. and E.P Jeffree. 1996. Redistribution of the potential geographical ranges of mistletoe and Colorado beetle in Europe in response to the temperature component of climate change. Funct. Ecol. 10: 562–577.

Kamel, A.S. 2010. Insects attack citrus trees in Al-Qalyubiyah Governorate, Egypt. Egypt. Acad. J. Biol. Sci. 3 (2): 107–117.

Kaneko, S. 2003. Different impacts of two species of aphid-attending ants with different aggressiveness on the number of emerging adults of the aphid's primary parasitoid and hyperparasitoids. Ecol. Res. 18: 199–212.

Karley, A.J., W.E. Parker, J.W. Pitchford and A.E. Douglas. 2004. The mid-season crash in aphid populations: Why and how does it occur? Ecol. Entomol. 29: 383–388.

Katsoyannos, P. 1993. Integrated pest management for citrus insect pests in Northern Mediterranean countries. Food and Agriculture Organization of the United Nations, Plant Prot. Bull. 41: 177–197.

Kindlmann, P. and A.F.G. Dixon. 1996. Population dynamics of a tree-dwelling aphid: Individuals to populations. Ecol. Model. 89: 23–30.

Komazaki, S. 1981. Life cycles and population fluctuations of aphids on citrus, Pp. 692–695. Proc. Intern. Soc. Citricult. Tokyo.

Komazaki, S. 1982. Effects of constant temperatures on population growth of three aphid species, *Toxoptera citricida* (Kirkaldy), *Aphis citricola* Van der Goot and *Aphis gossypii* Glover (Homoptera: Aphididae) on citrus. Appl. Entomol. Zool. 17: 75–81.

Komazaki, S. 1991. Studies on the biology of the spirea aphid, *Aphis spiraecola* Patch, with special reference to biotypic differences. Bull. Fruit Tree Res. Stn. (Suppl. 2).

Ladànyl, M. and L. Horvàth. 2010. A review of the potential climate change impact on insect populations—General agricultural aspects. Appl. Ecol. Environ. Res. 8: 143–152.

Limam Sallemi, E., G. Delvare and B. Chermiti. 2013. Parasitoids and hyperparasites of citrus aphids in northern east of Tunisia (Cap Bon). IOBC-WPRS Bull. 95: 131–139.

Llorens, C. and M. Jose. 1990. Pulgones de los Citricos y su Control Biológico. 1st edition. Valencia, Spain.

Maroquin, C., A. Olmos, M. Teresa-Gorris, E. Bertolini, M. Carmen-Martinez, E.A Carbonell, A. Hermoso De Mendoza and M. Cambra. 2004. Estimation of the number of aphids carrying Citrus tristeza virus that visit adult citrus trees. Virus Res. 100 (1): 101–108.

Mostefaoui, H., L. Allal-Benfekih, Z.E. Djazouli, D. Petit and G. Saladin. 2014. Why the aphid *Aphis spiraecola* is more abundant on clementine tree than *A. gossypii*. C. R. Biol. 337 (2): 123–133.

Mukhopadhyay, S. 2004. Citrus: Production, postharvest, disease and pest management. Science Publisher, Inc., Enfield, NH.

Muller, C.B. and H.C.J. Godfray. 1997. Apparent competition between two aphid species. J. Animal Ecol. 66: 57–64.

Norman, P.A. and T.J. Grant. 1953. Preliminary studies of aphid transmission of Tristeza virus in Florida. Proc. Fla. State Hort. Soc. 66: 89–92.

Nowierski, R.M., A.P. Gutierrez and J.S. Yaninek. 1983. Estimation of thermal thresholds and age-specific life table parameters for the walnut aphid (Homoptera: Aphididae) under field conditions. Environ. Entomol. 12: 680–686.

Olivares-Fuster, O., G.H. Fleming, M.R. Albiach-Marti, S. Gowda, W.O. Dawson and J.W. Crosser. 2003. *Citrus tristeza virus* (CTV) resistance in transgenic citrus based on virus challenge of protoplasts. In Vitro Cell. Dev. Biol. Plant 39: 567–572.

Petersen, M.K. and J.P. Sandström. 2001. Outcome of indirect competition between two aphid species mediated by responses in their common host plant. Funct. Ecol. 15: 525–534.

Potts, G.R. and G.P. Vickermam. 1974. Studies on the cereal ecosystem. Adv. Ecol. Res. 8: 107–197.

Rocha-Peña. M., R.F. Lee, R. Lastra, C. Niblett, F.M. Ochoa-Corona, S.M. Garnsey and R. Yokomi. 1995. *Citrus tristeza virus* and its aphid vector *Toxoptera citricida*: Threats to citrus production in the Caribbean and Central and North America. Plant Dis. 79: 437–444.

Schmidt, M.H., A. Lauer, T. Purtzuf, C. Thies, M. Schaefer and T. Tscharntke. 2003. Relative importance of predators and parasitoids for cereal aphid control. Proc. Royal Soc. Lond. B 270: 1905–1909.

Sekkat, A. **1987.** Etude bioécologique des aphides du Saïs et du Moyen Atlas (Maroc). Implications agronomiques. PhD Dissertation. Univ. des Sciences et Technologies de Lille, Montpellier, France.

Smirle, M.J., C.L. Zurowski D.T. Lowery and R.G. Foottit. 2010. Relationship of insecticide tolerance to esterase enzyme activity in *Aphis pomi* and *Aphis spiraecola* (Hemiptera: Aphididae). J. Econ. Entomol. 103: 374–378.

Southwood, T.R.E. and M.J. Way. 1970. Ecological background to pest management, Pp. 6–28. *In* Rabb, R.L. and F.E. Guthrie (eds.), Concepts of Pest Management. North Carolina State Univ., Raleigh.

Stadler, B. **2004.** Wedged between bottom-up and top-down processes: Aphids on tansy. Ecol. Entomol. 29: 106–116.

Thomson, L.J., S. Macfadyen and A.A. Hoffmann. 2010. Predicting the effects of climate change on natural enemies of agricultural pests. Biol. Control 52: 296–306.

Tremblay, E. and S. Barbagallo. 1983. *Lysiphlebus testaceipes* (Cr.), a special case of ecesis in Italy, Pp. 65–68. *In* Cavallaro, R. (ed.), Aphid Antagonists. Balkema, Rotterdam.

Tremblay, E., S. Barbagallo, L. Micieli-de-Biase, R. Monaco and S. Ortu. 1980. Compositione dell'entomofauna parasitica vivente a carico degli afidi agrumi in Italia. Boll. Lab. Entomol. Agr. Portici 37: 209–216.

Tunisian Ministry of Agriculture. **2017.** Global Agricultural Information Network. Record citrus crop highlights market constraints, 31/05/2017, Tunis, USDA (United States Department of Agriculture) Foreign Agric. Serv.

Van Emden, H.F. and R. Harrington. 2007. Aphids as Crop Pests. CABI Publishing, London, UK.

Vickerman, G.P. and S.D. Wratten. 1979. The biology and pest status of cereal aphids (Hemiptera: Aphididae) in Europe: A review. Bull. Entomol. Res. 69: 1–32.

Walters, R.J. and M. Hassall. **2006.** The temperature-size rule in ectotherms: May a general explanation exist after all? Am. Nat. 167: 510–523.

Wang, J.J. and J.H. Tsai. **2000.** Effect of temperature on the biology of *Aphis spiraecola* (Homoptera: Aphididae). Ann. Entomol. Soc. Am. 93: 874–883.

Wang, J.J. and J.H. Tsai. **2001.** Development, survival and reproduction of black citrus aphid, *Toxoptera aurantii* (Hemiptera: Aphididae), as a function of temperature. Bull. Entomol. Res. 91: 477–487.

Wu, G.M., M. Barette, G. Boivin, J. Brodeur, L.A. Giraldeau and T. Hance. **2011.** Temperature influences the handling efficiency of an aphid parasitoid through body size-mediated effects. Environ. Entomol. 40: 737–742.

Zhou, X., R. Harington, I.P. Woiwod, J.N. Perry, J.S. Bale and S.J. Clark. **1995.** Effects of temperature on aphid phenology. Glob. Change Biol. 1: 303–313.

Ziska, L. and G.B. Runion. 2007. Future weed, pest and disease problems for plants, Pp. 261–279. *In* Newton, P.C.D., R.A. Carran, G.R. Edwards and P.A. Niklaus (eds.), Agroecosystems in a changing climate. Taylor & Francis, New York.