



Diversity and prevalence of endosymbionts in populations of the two-spotted spider mite on different plant hosts in North, Razavi, and South Khorasan Provinces, Iran, and the effect of temperature on the vertical transmission of symbiotic bacteria

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ABSTRACT

Many bacteria associated with arthropods play important roles in host functional traits, and the structure of these bacteria can be influenced by intracellular symbionts. In this study, a survey of bacterial endosymbionts present in natural populations of the two-spotted spider mite, *Tetranychus urticae*, was conducted in North, Razavi, and South Khorasan Provinces. A total of 1440 spider mites collected from three localities associated with eight host plants were screened for endosymbionts. Among the three detected facultative endosymbionts, *Wolbachia*, *Cardinium*, and *Rickettsia*, different infection frequencies (91.6%, 9.72%, and 9.72%, respectively) were observed. None of the individuals carried *Arsenophonus* or *Spiroplasma*. In the majority of the studied populations, multiple infections by endosymbiont were detected and the prevalence of individuals with the *Wolbachia*-*Rickettsia* coinfection (9.72%) was higher than the frequency of the individual coinfection rates with other symbionts. The findings of the current study suggest that the frequencies of endosymbiont infections may be affected by collection site characteristics, including geographic location (latitude, longitude), altitude, and collection date, as well as host plant species. *Wolbachia* infection rates were higher in mites collected from Razavi Khorasan Province compared to those from other localities. The highest frequencies of *Cardinium* and *Rickettsia* were observed in North and South Khorasan Provinces. Host plants also significantly influenced the prevalence of endosymbionts in the present study. The results of vertical transmission experiments indicated that temperature influences vertical transmission in symbiotic bacteria.

KEYWORDS

Endosymbiont, facultative endosymbiont, infection pattern, *Tetranychus urticae*, multiple infections, vertical transmission

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INTRODUCTION

Spider mites belonging to the Tetranychidae family are known to feed on a wide range of plants and can cause significant economic damage (Grbić *et al.* 2011; Van Leeuwen *et al.* 2015). The name “spider mite” is derived from their webbing, and the species within this family are important herbivorous mites affecting agricultural crops worldwide, causing damage to crops, trees, and ornamental plants (Jeppson *et al.* 1975). Among the different species of spider mites, *Tetranychus urticae* Koch (Tetranychidae), also known as the two-spotted spider mite, is the most common species worldwide (Li *et al.* 2009). This



particular species feeds on over 1100 plant species, of which 150 are important agricultural products (Migeon and Dorkeld 2020; Santamaria *et al.* 2020). It is considered a serious pest for agricultural products due to its wide host range, short generation length, high number of progenies, and resistance to pesticides (Santamaria *et al.* 2020).

Endosymbiotic bacteria are highly prevalent and diverse among arthropods and are increasingly acknowledged as significant contributors to the ecology and evolution of their host organisms (Zhu *et al.* 2018). While certain symbiont-arthropod associations are critical for host survival, others are facultative and exhibit irregular distribution patterns (Zelev *et al.* 2020). Intensive field surveys of separate species of arthropods have revealed that the most common endosymbionts are *Wolbachia*, *Rickettsia*, *Cardinium*, *Arsenophonus*, and *Spiroplasma* (Duron *et al.* 2008; Weinert *et al.* 2015; Zélé *et al.* 2018).

Spider mites harbor a wide range of endosymbionts, with many species hosting multiple endosymbionts (Ros *et al.* 2012; Zhu *et al.* 2018) whose infection patterns frequently display spatial and temporal variation (Zhu *et al.* 2018). At least four distinct lineages of facultative endosymbionts, comprising *Wolbachia*, *Cardinium*, *Rickettsia*, and *Spiroplasma* have been documented heretofore in spider mites (Zhu *et al.* 2018). Despite the capacity of endosymbionts to elicit diverse effects facilitating their spread within natural populations, the frequencies of endosymbiont infections differ among geographic populations of spider mites. Nonetheless, without comprehensive and systematic surveys of endosymbionts in a region, it remains uncertain whether this variation in infection frequency is associated with ecological factors (Zhu *et al.* 2018).

Abiotic factors, including geographical variables such as latitude, altitude, and climate, have been shown to significantly affect the diversity and prevalence of endosymbiotic bacteria in arthropods, as well as the expression of symbiont-induced phenotypes (Ross *et al.* 2017; Clancy and Hoffman 1998; Toju and Fukatsu 2011; Liu *et al.* 2006). Biotic interactions, including host genetic variation and competition among co-infecting symbionts within the same host, further modulate infection dynamics (Chiel *et al.* 2007; Gueguen *et al.* 2010). For example, Zhu *et al.* (2018) investigated facultative bacterial symbiont distributions in natural populations of the spider mite *Tetranychus truncatus* in China and found differential infection frequencies of *Wolbachia*, *Cardinium*, and *Spiroplasma* correlated with environmental gradients such as temperature and host plant species. Their study emphasizes that multiple geographically determined factors, including climate and host plant associations, influence the patterns of host-endosymbiont interactions. Understanding the predominance and ecological impacts of endosymbiotic microbes in arthropod pests and their natural enemies holds promise for enhancing and optimizing biological and organic pest control strategies (Enigl and Schausberger 2007; Zhu *et al.* 2018). Endosymbionts can be manipulated, transferred, or genetically modified to exploit their beneficial traits or mitigate detrimental effects on host insects and their natural enemies (Floate *et al.* 2006).

The aim of the present study was to investigate the diversity and abundance of endosymbiont bacteria within natural populations of the two-spotted spider mite across various agricultural, horticultural, and ornamental host plants. The occurrence patterns and co-occurrence of five distinct endosymbiont lineages, namely *Wolbachia*, *Cardinium*, *Rickettsia*, *Arsenophonus* and *Spiroplasma*, were investigated. The effect of temperature on the vertical transmission of endosymbiont bacteria was also assessed.

MATERIAL AND METHODS

Spider-mite sampling

Foliage infected by *T. urticae* (green form) were collected from eight host plant species in three geographic localities across North-Eastern Iran (Table 1). Adult female mites were transferred from infected leaves to containers containing 96% ethanol and kept at -20°C until DNA extraction.

DNA extraction

Total genomic DNA was extracted from the whole body of a single individual mite using the Tissue Genomic DNA Extraction Mini Kit (Yekta Taghiz Azma), in accordance with the manufacturer's

protocol. This process was repeated for at least 10 individual mites per population. The resulting DNA samples were stored individually at -20°C until used for PCR.

Table 1. Samples of *Tetranychus urticae* (green form) used in this study.

Location	Collection date	Latitude (°N)	Longitude (°E)	Altitude (m)	Host plant	W*	C*	R*	W & C	W & R	W, C & R
North Khorasan, Bojnourd	2022.7	37.41074843	57.28855705	1181	cucumber	100	12.5	0	12.5	0	0
North Khorasan, Bojnourd	2022.7	37.41405997	57.29267263	1174	eggplant	87.5	0	0	0	0	0
North Khorasan, Esfarayen	2022.8	37.09231486	57.55316877	1376	cucumber	87.5	0	0	0	0	0
North Khorasan, Esfarayen	2022.8	37.09580645	57.55419874	1331	eggplant	87.5	0	0	0	0	0
North Khorasan, Esfarayen	2022.9	37.01360363	57.49901390	1185	cotton	100	0	0	0	0	0
North Khorasan, Esfarayen	2022.9	36.99402632	57.51849461	1203	corn	75	0	0	0	0	0
North Khorasan, Esfarayen	2022.8	36.98442832	57.54647541	1222	apple	100	87.5	0	87.5	0	0
North Khorasan, Esfarayen	2022.8	37.07967163	57.50398707	1262	<i>Alocasia sanderiana</i>	87.5	0	0	0	0	0
Razavi Khorasan, Neishabur	2022.8	36.23607793	58.76578617	1198	cucumber	100	0	0	0	0	0
Razavi Khorasan, Neishabur	2022.8	36.23121033	58.75707293	1191	eggplant	100	12.5				
Razavi Khorasan, Ghochan	2022.8	36.99635708	58.61498165	1329	cucumber	100	0	12.5	0	12.5	0
Razavi Khorasan, Ghochan	2022.8	37.01129967	58.62948704	1333	eggplant	100	0	0	0	0	0
Razavi Khorasan, Mashhad	2022.8	36.30919114	59.52787435	1038	bean	100	0	0	0	0	0
South Khorasan, Ferdows	2022.8	33.77894995	57.88714028	1169	cucumber	100	0	0	0	0	0
South Khorasan, Ferdows	2022.8	33.79592755	57.91546440	1202	eggplant	62.5	12.5	37.5	12.5	37.5	12.5
South Khorasan, Khusf	2022.8	32.87751360	59.02731514	1387	cucumber	87.5	0	0	0	0	0
South Khorasan, Khusf	2022.8	32.87535107	59.02971840	1395	eggplant	75	0	25	0	25	0
South Khorasan, Birjand	2022.8	32.74939800	59.37586900	1964	rose	100	50	100	50	100	50

* W = *Wolbachia*, C = *Cardinium*, R = *Rickettsia*

Polymerase chain reaction (PCR)

The five facultative endosymbionts belonging to the genera *Wolbachia*, *Cardinium*, *Rickettsia*, *Arsenophonus*, and *Spiroplasma*, which have previously been identified in spider mites, were screened in our study through PCR amplification employing specific primer sets (Table 2). PCR was performed using an Eppendorf thermal cycler in a final volume of 25 µl, containing of 12.5 µl of master mix, 1.5 µl of each forward and reverse primers, 4 µl of DNA, and 5.5 µl of sterile distilled water. The PCR conditions are outlined in Table 3. PCR products were then visualized on a 1% agarose gel stained with DNA Green Viewer. A negative control without DNA was included in each PCR cycle. To verify the identity of the amplified endosymbionts genes, for each detected endosymbiont, one positive PCR sample was haphazardly sent for sequencing (Jahad Daneshgahi, Mashhad, Iran).

Table 2. PCR primers used to identify the bacterial endosymbionts in *Tetranychus urticae* (green form).

Endosymbiont	Target gene	Primer	Primer sequence (5'-3')	Amplicon size (bp)	Reference
<i>Wolbachia</i>	Wsp	81-F 691-R	TGGTCCAATAAGTGAAGAAAC AAAAATTAACGCTACTCCA	600	Zhou <i>et al.</i> 1998
<i>Rickettsia</i>		16SA1 Rick16SR	AGAGTTTGATCMTGGCTC CATCCATCAGCGATAAATCTT	200	Fukatsu and Nikoh (1998) Fukatsu <i>et al.</i> (2001)
<i>Cardinium</i>	16S rRNA	Car-SP F Car-SP R	CGGCTTATTAAGTCAGTTGTGAAAT CCTAG TCCTTCCTCCCGCTTACACG	544	Nakamura <i>et al.</i> (2009)
<i>Arsenophorus</i>		Ars23S-1 Ars23S-2	CGTTTGATGAATTCATAGTCAAA GGTCCTCCAGTTAGTGTTACCCAAC	500	Thao and Baumann (2004)
<i>Spiroplasma</i>	16S rRNA	16SA1 TKSSpR	AGAGTTTGATCMTGGCTC TAGCCGTGGCTTTCTGGTAA	510	Fukatsu and Nikoh (1998)

Table 3. PCR conditions to detect bacterial endosymbionts in *Tetranychus urticae* (green form).

Endosymbiont	Primer	No. cycle	Denaturation		Annealing		Elongation	
			°C	S	°C	S	°C	S
<i>Wolbachia</i>	81-F 691-R	35	94	40	57	40	72	60
<i>Arsenophonus</i>	Ars23S-1 Ars23S-2	35	95	30	60	30	72	45
<i>Cardinium</i>	Car-SP F Car-SP R	35	95	30	57	30	72	60
<i>Rickettsia</i>	16SA1 Rick16SR	40	95	30	55	30	72	30
<i>Spiroplasma</i>	16SA1 TKSSpR	40	95	30	60	30	72	30

Phylogenetic analysis

The obtained chromatograms were checked manually using MEGA version 11 and the resulting sequences were subjected to homology searches using the BLAST algorithm of the NCBI database (<https://www.ncbi.nlm.nih.gov/blast>). Forward and reverse reads were assembled into contigs employing DNAbaser software to ensure sequence accuracy and completeness. All sequences were submitted to the GenBank under accession numbers PP868267, PP868268 (*Rickettsia*) PP868269, PP868270 (*Cardinium*), PQ419153, PQ419154 (*Wolbachia*).

The phylogenetic analyses of bacterial endosymbionts were performed using Beast v. 1.10.4 (Suchard *et al.* 2018). Beast was run using a Yule speciation process and two independent MCMC chains for 10,000,000 generations, sampling every 100th generation. The convergence to stationary and the effective sample size of the model parameters were evaluated with Tracer v.1.7.1 (Rambaut *et al.* 2018). The maximum clade credibility trees were generated with Tree Annotator (Drummond and Rambaut 2007). FigTree 1.4.0 software was utilized to display and edit the phylogenetic trees (Rambaut 2008).

Statistical analyses

To study the impact of host plant species on the infection frequency of endosymbionts inserting experiments Wilcoxon pairs with Chi-square statistics were used. All analyses were performed in JMP Pro 14 software (SAS Institute Inc.). Our focus was on two common host plants (eggplant and cucumber) for further analysis (Table 1).

The effect of temperature on vertical transmission of endosymbiont bacteria

Spider-mite sampling

Two-spotted spider mite populations were collected from cucurbit plants grown at the Faculty of Agriculture, Ferdowsi University of Mashhad, and subsequently transferred to and reared on bean plants.

Infected and uninfected lines

Adult females of the two-spotted spider mite were collected from cucurbit plants and individually screened for *Wolbachia* infection to establish infected and uninfected lines, as required for subsequent experiments. Genomic DNA was extracted from single adult mites using standard protocols, and the presence of *Wolbachia* was determined by PCR amplification targeting *Wolbachia* surface protein gene (*wsp*) (Table 2). Only populations with 100% confirmed infection prevalence were designated as infected lines. These infected lines were maintained by rearing mated females on bean leaf discs placed on moist cotton substrate under controlled environmental conditions: temperatures of 25, 30, and 35 °C, 60% relative humidity, and a photoperiod of 16 hours light and 8 hours darkness for at least four consecutive generations. This ensured stable vertical transmission of *Wolbachia* within lines under different temperature regimes. To generate uninfected lines, infected populations were subjected to antibiotic treatment by maintaining mites on common bean leaf discs placed on cotton substrates soaked with a tetracycline solution (0.1% w/v) for three consecutive generations, following the method detailed by Zhang *et al.* (2018). After antibiotic exposure, adult females (2 days old) were randomly sampled from each treatment group and re-screened by PCR to verify the complete absence of *Wolbachia* infection. The DNA concentration, primers, and PCR conditions used for all assays were consistent with those described previously.

To experimentally assess the effect of temperature on the vertical transmission fidelity of *Wolbachia*, it was necessary to generate defined infected and uninfected iso female lines. This approach controls for the host genetic background and provides a baseline 100% infection rate from which to accurately quantify any transmission failure induced by thermal stress.

RESULTS

PCR-based investigation of endosymbiosis

PCR tests were conducted to diagnose endosymbionts of *T. urticae* specimens from different populations collected from various host plants. The identity of PCR amplicons was confirmed by comparing nucleotide sequences with the Gene Bank Database (Table 1). Overall, three facultative endosymbionts, namely *Wolbachia*, *Cardinium*, and *Rickettsia*, were detected, while *Arsenophorus* and *Spiroplasma* were not found in any of the examined individuals.

Wolbachia was the most prevalent endosymbiont with the infection rate ranged from 62.5% to 100%. It was present in all the examined populations of *T. urticae*. *Rickettsia* endosymbiont was only observed in populations collected from cucumber, eggplant, and rose. The prevalence of *Rickettsia* infection varied significantly across plant species, with the lowest infection rate recorded at 12.5% in cucumbers and the highest at 100% in roses. *Cardinium*-infection rates in populations collected from the three observed hosts were 12.5% for eggplant, 50% for rose, and 87.5% for apple. Additionally, no *Arsenophorus* and *Spiroplasma* infections were observed in any of the samples taken from different hosts (Table 1).

Phylogenetic analysis

Phylogenetic analysis of the 16S rDNA sequences revealed a monophyletic clade for “*Cardinium*” symbionts sequenced in this study with 0.96 posterior probability value (Fig. 1). The two *Rickettsia* endosymbiont sequences obtained in the current study formed a well-supported sister group (posterior probability = 1.00) with the *Rickettsia* endosymbiont sequence AY753175 derived from *T. urticae*, confirming close evolutionary relatedness within this genus. This monophyletic group further clustered

with *Rickettsia* sequences from diverse hosts including MW114877 (*Rhipicephalus microplus* (Canestrini), Ixodidae), MW523993 (*Ixodes pacificus* Cooley & Kohls, Ixodidae), F362030 (*Aphis craccivora* C.L. Koch, Aphididae), and OP007141 (*Culex pipiens* L., Culicidae) with strong support (posterior probability = 0.915), suggesting phylogenetic affinity among *Rickettsia* strains infecting diverse arthropod hosts across different taxa (Fig. 2). These results indicate that our *Rickettsia* endosymbionts from the two-spotted spider mite share a recent common ancestor with symbionts of *T. urticae* and are part of a broader clade comprising tick, aphid, and mosquito-associated *Rickettsia* species. This phylogenetic clustering reflects the extensive host range and evolutionary diversification of *Rickettsia*, highlighting potential horizontal and vertical transmission pathways among arthropods. Such close relationships support the hypothesis that these *Rickettsia* endosymbionts may play similar ecological or evolutionary roles within their respective hosts. The phylogenetic tree constructed using *Wolbachia* wsp gene sequences revealed that the *Wolbachia* strains obtained in this study clustered together and formed a sister group with *Wolbachia* from *Tetranychus truncatus* (posterior probability 0.1) (Fig. 3). These sequences clustered with *Wolbachia* endosymbionts of other tetranychid mites including *T. urticae* (green and red forms), and *T. kanzawai* Kishida, albeit with low posterior probability (0.096). All *Wolbachia* from tetranychid mites clustered distinctly as a well-supported clade (posterior probability = 1), separate from the outgroup *Brugia malayi*. This grouping is consistent with placement within *Wolbachia* supergroup B, which is commonly associated with mite hosts, although low statistical support limits finer subgroup resolution. These results contribute to understanding *Wolbachia* diversity and host specificity in tetranychid mites.

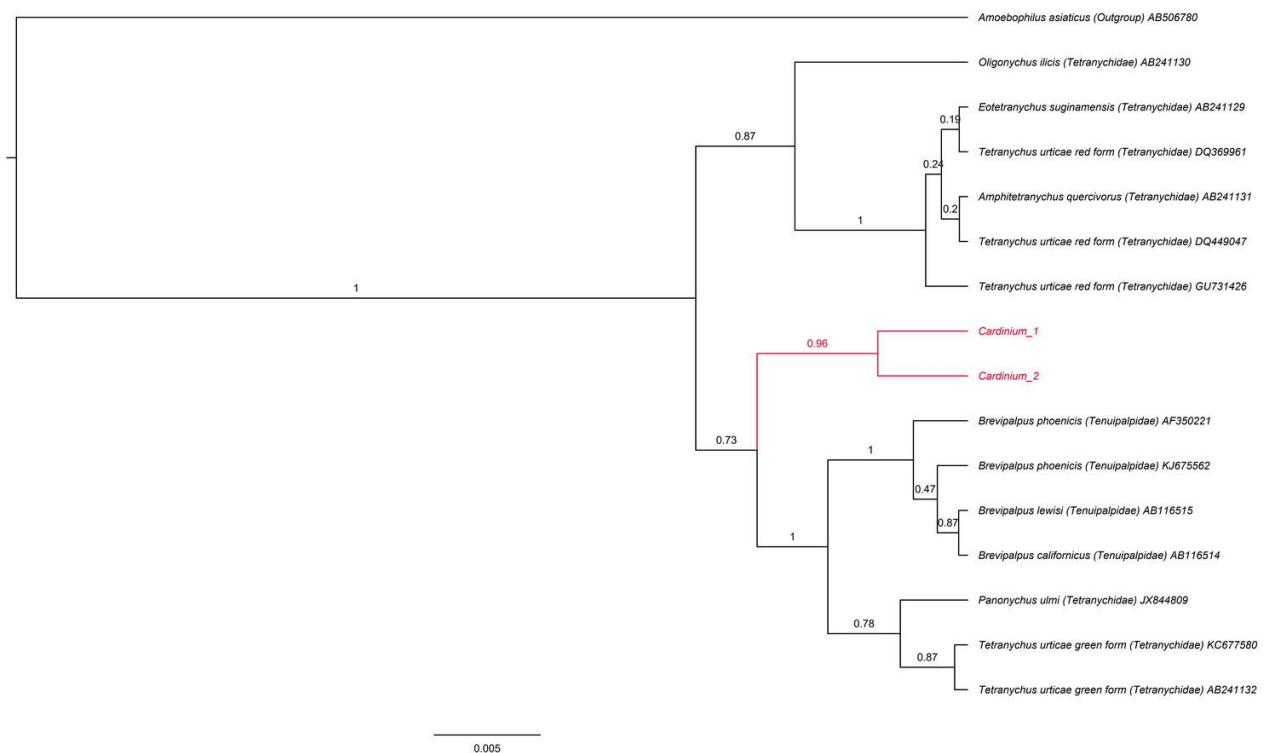


Figure 1. Phylogenetic tree of *Cardinium* symbionts associated with *Tetranychus urticae* based on 16S rRNA gene.

Geographic distribution of endosymbionts

Our analysis revealed significant heterogeneity in the geographic distribution of endosymbiont infections across the sampled regions of north-eastern Iran. *Wolbachia* was detected at high frequencies throughout the study area, reaching near-fixation within populations in Razavi Khorasan Province. In contrast, *Cardinium* and *Rickettsia* exhibited sporadic, low-frequency infection patterns, with their respective prevalence peaks localized to North and South Khorasan Provinces (Table 1). While the geographic scope of this study is limited to this specific agro-ecological region and precludes broad national-level conclusions, the stark contrasts in infection dynamics among these closely situated provinces are compelling. This pronounced sub-regional variation strongly suggests the influence of localized drivers –such as climatic gradients, host plant associations, or agricultural practices– on

endosymbiont epidemiology. Consequently, our findings provide a critical baseline for north-eastern Iran and generate testable hypotheses regarding the ecological forces shaping these symbioses, establishing a necessary foundation for future research employing expanded latitudinal and longitudinal transects across Iran.

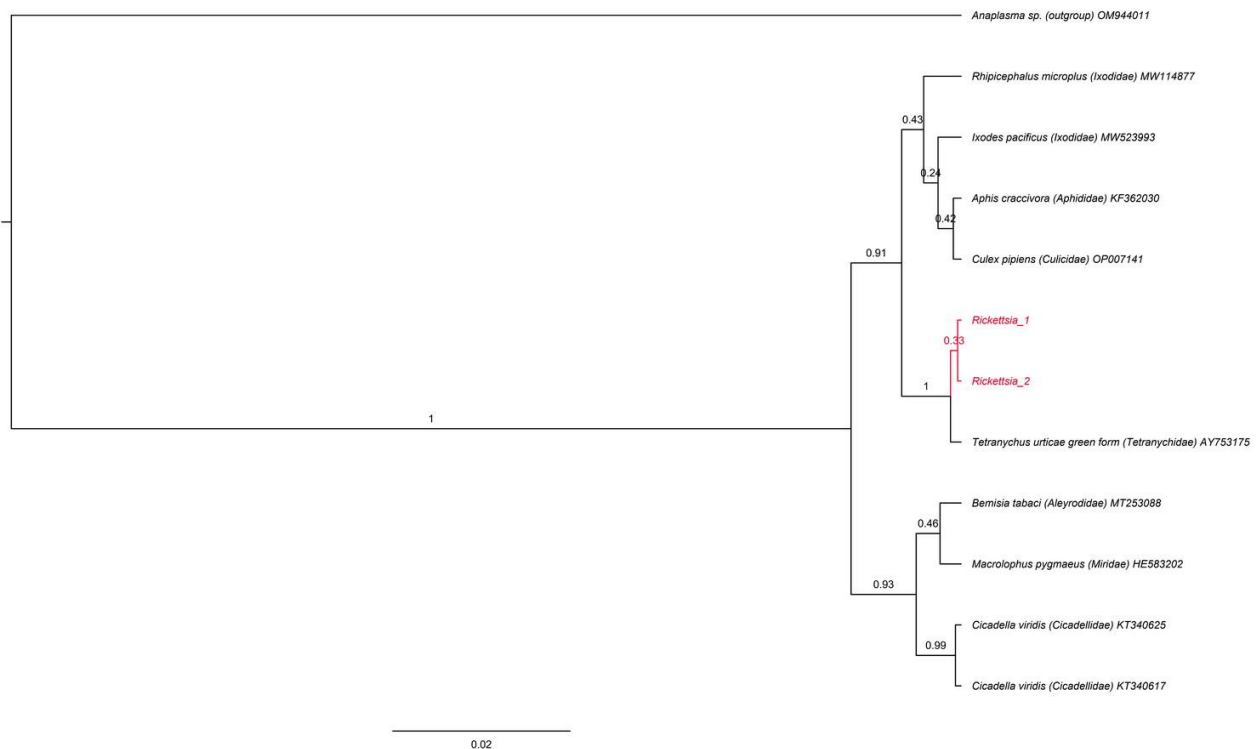


Figure 2. Phylogenetic tree of *Rickettsia* symbionts associated with *Tetranychus urticae* based on 16S rRNA gene.

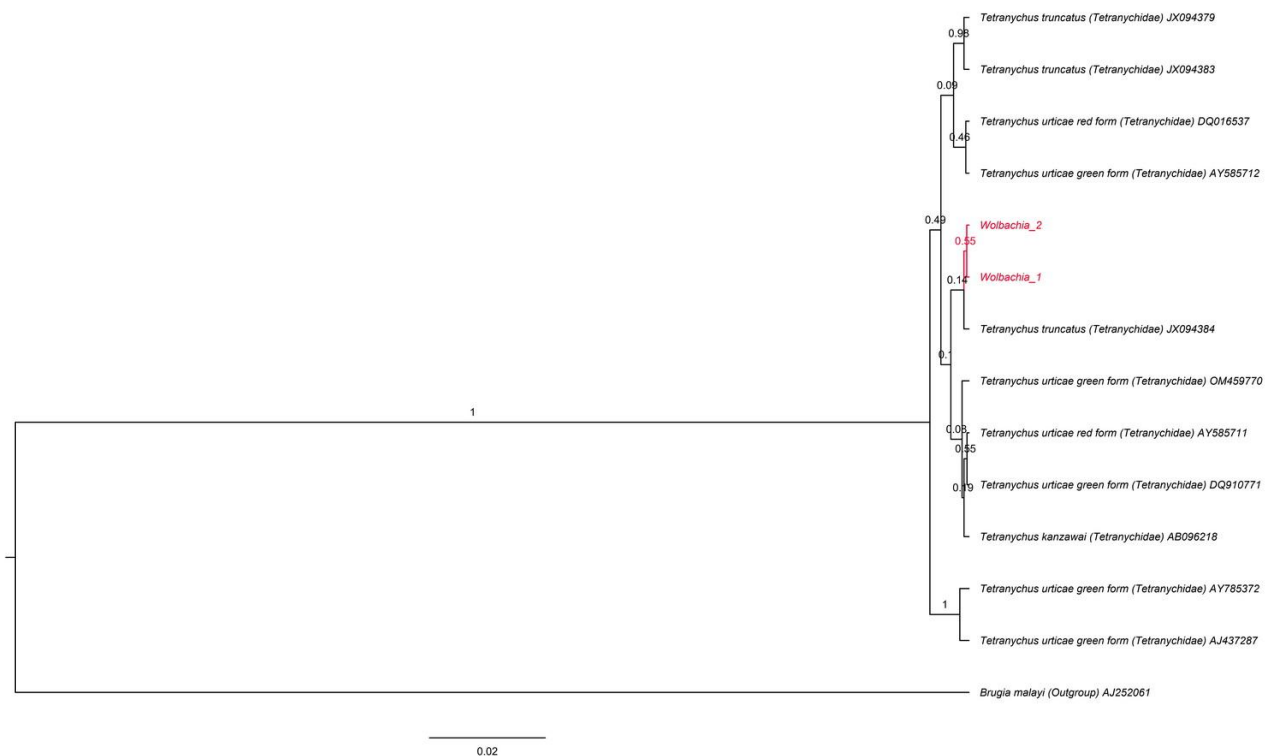


Figure 3. Phylogenetic tree of *Wolbachia* symbionts associated with *Tetranychus urticae* based on 16S rRNA gene.

Host plant and endosymbiont infections

To assess the effects of host plant on the incidence and frequency of endosymbionts, two common host plants (eggplant, cucumber) from the three areas were evaluated. Host plants significantly affect the infection frequencies of *Wolbachia* ($\chi^2 = 5.654$, $P = 0.01$). Infection frequencies in *T. urticae* collected from cucumber (mean, 95.83; 95% confidence interval, 87.5% to 100%) were significantly more than those collected from on eggplant (mean, 84.37; 95% confidence interval, 62.5 to 100%; $P = 0.01$) (Fig. 4). Nonetheless, the host had no significant influence on either *Cardinium* or *Rickettsia* infection.

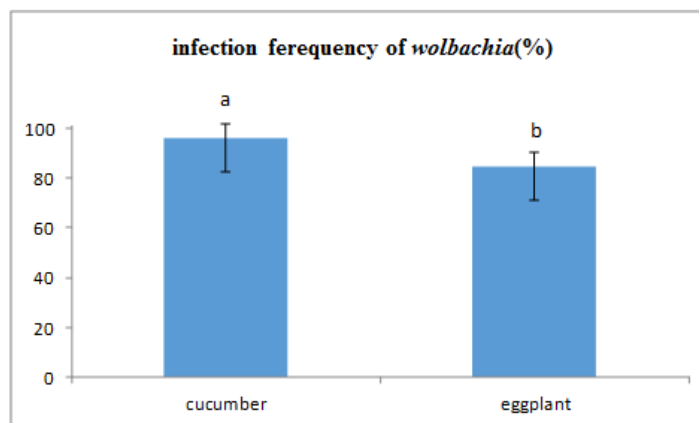


Figure 4. Infection frequencies of the endosymbiont *Wolbachia* infesting each of the host plants, cucumber and eggplant in natural populations of the spider mite *Tetranychus urticae*. Error bars indicate 99% confidence intervals. Different lowercase letters indicate significant differences ($P < 0.01$).

Occurrence of multiple infections

Co-infections of endosymbionts were detected in *T. urticae* individuals, including both double and multiple infections, although at relatively low infection frequencies. Wilcoxon pairs tests showed that the double-infection of *Wolbachia*-*Cardinium* ($\chi^2 = 15.716$, $df = 7$, $P = 0.02$) and the triple infection of *Wolbachia*-*Cardinium*-*Rickettsia* ($\chi^2 = 15.708$, $df = 7$, $P = 0.02$) had significant differences on different hosts. The highest infection rate for *Wolbachia*-*Cardinium* was observed in individuals collected from apple plants, while the highest triple infection rate of *Wolbachia*-*Cardinium*-*Rickettsia* was observed on rose plants. In contrast, the double infection of *Wolbachia*-*Rickettsia* ($\chi^2 = 7.214$, $df = 7$, $P = 0.4$) did not show any significant difference among different hosts (Table 1).

The effect of temperature on vertical transmission

The results of vertical transmission experiments at three different temperatures of 25, 30 and 35 °C showed that vertical transmission of bacteria is affected by high temperature, at 25 °C PCR experiments showed 100% infection, at 30 °C infection 62.5% and at 35 °C no infection with *Wolbachia* was found (Table 4). Also, the life span of the two-spotted spider mite at 35 °C was reduced from 14 days to 8 days compared to 25 °C. This was the same as what was found by Van Opijnen and Breeuwer (1999) and Margolies and Wrensch (1996).

Table 4. *Wolbachia* infection rate in *Tetranychus urticae*.

Location	Host plant	Temperature (°C)	<i>Wolbachia</i> (%)
Razavi Khorasan, Mashhad	bean	25	100
Razavi Khorasan, Mashhad	bean	30	62.5
Razavi Khorasan, Mashhad	bean	35	0

DISCUSSION

In this study, the diversity and abundance of endosymbionts in natural populations of the two-spotted spider mite in Iran (North-, Razavi-, and South Khorasan Provinces) were investigated using diagnostic PCR. The effects of the host plants on diversity and abundance of endosymbionts and the effect of temperature on vertical transmission of endosymbiont bacteria (*Wolbachia*) were also assessed.

Out of the five examined endosymbionts, three, including *Wolbachia*, *Cardinium* and *Rickettsia*, were found to contaminate spider mite populations, while *Arsenophorus* and *Spiroplasma* were not detected. Overall, infection frequencies of 62.5% to 100%, 12.5 to 87.5%, and 12.5% to 100 for *Wolbachia*, *Cardinium* and *Rickettsia* were observed, respectively.

The prevalence of *Wolbachia* was found to be quite high in the examined populations of the two-spotted spider mite. Infection rates ranged from 62.5% to 100% across the studied populations (Table 1). This high prevalence significantly exceeded that of the other detected endosymbionts and is consistent with the global pattern of *Wolbachia* being a dominant and widespread reproductive manipulator in arthropods (Gotoh *et al.* 2003, 2007; Zhang *et al.* 2016c; Zélé *et al.* 2018; Kashkouli *et al.* 2021). The success and persistence of *Wolbachia* in these populations can likely be attributed to two primary factors. First, as previously demonstrated in *T. urticae*, *Wolbachia* can induce cytoplasmic incompatibility (CI), conferring a reproductive advantage to infected females and thereby enhancing the relative fitness of the infected maternal lineage (Zhang *et al.* 2013). Second, the efficient vertical transmission of the symbiont from mother to offspring is crucial for its maintenance in a host population. Environmental temperature is a key factor modulating this transmission fidelity, as shown in other arthropod systems (Nasehi *et al.* 2022). The climatic conditions of the Khorasan Provinces, characterized by high temperatures, may therefore favor the high vertical transmission rates necessary to achieve and sustain the observed high infection frequencies.

Some earlier findings confirm a comparatively frequent incidence of *Cardinium* in mites (Nakamura *et al.* 2009; Zhang *et al.* 2016b). Nonetheless, in the current study, *Cardinium* prevalence was overall much lower in the studied mite populations compared to that of *Wolbachia*, an outcome that is not consistently encountered in spider mites (Zhang *et al.* 2016a; Zélé *et al.* 2018). There are several studies reporting *Cardinium*-induced reproductive alterations in mites (Wu and Hoy 2012; Zhao *et al.* 2013; Famah Sourassou *et al.* 2014). The occurrence of *Rickettsia* was exceedingly limited in our study, which was in accordance with the outcomes reported by Zhang *et al.* 2016 and Zélé *et al.* 2018.

Despite previous reports of *Spiroplasma* presence in *T. urticae* (Enigl and Schausberger 2007), our study did not reveal its existence in the examined mite populations. Our finding aligned with the results of Zhang *et al.* (2016) and Zélé *et al.* (2018), in which no mite population infected with *Spiroplasma* was observed. *Arsenophorus* was also not detected in our study. To the best of our knowledge, there have been no previous reports of *Arsenophorus* presence in spider mites, while its occurrence in other mites has been documented (Zélé *et al.* 2018).

Our study displayed that coinfections with more than one endosymbiont are common in the studied populations of *T. urticae*. The occurrence of multiple infections holds particular importance for studying the impacts of microorganisms on reproduction in arthropods since it is essential to ascertain which bacterium is responsible for any observed effects and, if so, the specific nature of those effects (Enigl and Schausberger 2007). Interactions between symbionts within a single host may also be a crucial factor influencing their predominance, either adversely (through competition) or beneficially (through assistance) (Vautrin *et al.* 2008; Vautrin and Vavre 2009; Hellard *et al.* 2015; Zélé *et al.* 2018). Coexisting endosymbionts are required to compete for limited resources and space within the same host, which may lead to the exclusion of the less competitive symbiont. In fluctuating environments, the most advantageous symbiont community can vary spatially or temporally due to the interactions among multiple genotypes and environmental factors. This dynamic may result in either the establishment of distinct communities within populations or a polymorphism of symbiont communities across those populations (Ferrari and Vavre 2011).

In our study, rearing infected isofemale lines at 35 °C for four consecutive generations resulted in the complete elimination of *Wolbachia*. This finding is consistent with the work of Van Opijnen and Breeuwer (1999), who demonstrated that prolonged exposure to elevated temperatures (32.5 °C for two generations) could eliminate *Wolbachia* from *T. urticae* and induce cytoplasmic incompatibility. The multi-generational thermal stress applied in our experiment appears to be a critical factor in achieving complete symbiont loss, likely by disrupting the bacterial cell division cycle or the maternal transmission machinery beyond a recoverable threshold. Field temperatures, particularly in greenhouse environments, can frequently surpass 30 °C and remain elevated for extended durations spanning multiple mite generations.

The thermal regime used in our study is, therefore, ecologically relevant. Our results demonstrate that such conditions are not merely stressful but can be profoundly curative, providing a plausible mechanistic explanation for the natural occurrence of both infected and uninfected individuals within populations, as previously observed (Breeuwer and Jacobs 1996). The persistence of *Wolbachia* in nature likely represents a dynamic equilibrium between its reproductive advantages and the counteracting selective pressure of high-temperature events.

However, it is important to acknowledge that conventional PCR methods have inherent limitations in detecting endosymbionts when bacterial DNA is present at low concentrations. As bacterial cell counts decrease due to heat treatment or other factors, the extracted DNA yield may fall below the detection threshold of standard PCR, potentially resulting in false negatives despite the continued presence of bacteria at low levels. Therefore, relying solely on conventional PCR could underestimate the infection status in such marginal cases. Quantitative real-time PCR (qPCR) offers improved sensitivity by detecting and quantifying low bacterial loads and should be considered in future studies to more accurately assess *Wolbachia* presence under conditions of decreased bacterial density.

Enhancing our understanding of the predominance and impacts of endosymbiotic microbes in pests and their natural enemies may improve and optimize organic pest control methods (Enigl and Schausberger 2007; Zhu *et al.* 2018). Symbionts can be manipulated, transferred or harnessed through genetic modification to exploit their benefits or mitigate their potential impacts on pests and/or their natural enemies (Floate *et al.* 2006).

In arthropods, the incidence of bacterial contamination may be influenced by abiotic factors, including geographical aspects (Toju and Fukatsu 2011; Liu *et al.* 2006) or biotic factors such as genetic variation of the host and competition with other endosymbionts in the same host (Chiel *et al.* 2007; Gueguen *et al.* 2010). Geographical factors such as latitude, altitude, and climate can significantly affect the diversity and abundance of microbial communities associated with arthropods, as well as the expression of symbiont phenotypes. In other words, there is a correlation between the environment and the abundance/incidence of endosymbionts (Clancy and Hoffman 1998; Ross *et al.* 2017).

Zhu *et al.* (2018) studied the distribution of facultative bacterial symbionts in natural populations of the spider mite *Tetranychus truncatus* in China, focusing on associations with the local environment and host plants. They found three lineages of facultative endosymbionts, *Wolbachia*, *Cardinium* and *Spiroplasma*, with different infection frequencies (52.5%) in Chinese populations of *T. truncatus*. Their results confirmed the association between symbiont infection rates and environmental factors in regions with higher average annual temperatures. Furthermore, their findings suggest that other geographically determined factors, as well as the host's food plants, may be related to host-symbiont interactions (Zhu *et al.* 2018).

Our results indicated that the host plant can have an effect on the prevalence of endosymbiont infections. Our study focused on two main host plants (cucumber and eggplant), showing that the rate of *Wolbachia* infection was higher in mites on cucumber than in those on eggplant, but the type of host plant had no significant effect on the infection rates of other endosymbionts. Ribeiro *et al.* (2020) examined the endosymbiont microbial diversity of two spider mite species, *Tetranychus evansi* Baker & Pritchard and *T. urticae*. Their results showed that bacterial diversity was higher in *T. evansi*. They attributed the observed higher bacterial diversity in *T. evansi* to the ability of this mite to manipulate plant defense systems. Two hypotheses have been proposed to elucidate the mechanisms by which host plants can influence the symbionts of herbivorous insects. The primary hypothesis suggests that plant phytotoxins or secondary metabolites have the capacity to either suppress or increase the population growth of the symbionts (Harborne 2014). The alternative hypothesis theorizes that the host may manipulate the titer of its endosymbiont to compensate for particular insufficiencies within the nutrient profile of its host plant (Zhang *et al.* 2016a; Zhu *et al.* 2018). In our study, it is not clear which hypothesis explains the higher prevalence of *Wolbachia* in cucumber compared with that.

In summary, this research offers a thorough overview of the diversity and infection prevalence of endosymbionts within natural populations of *T. urticae* in northeastern Iran. The findings demonstrate a correlation between changes in endosymbiont composition and factors such as temperature and host.

These insights suggest potential mechanisms influencing host-endosymbiont interactions and their possible links to local adaptation in different geographic contexts.

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تنوع و شیوع همزیست‌های داخلی در جمعیت‌های کنه تارتن دولکه‌ای روی میزبان‌های گیاهی مختلف در استان‌های خراسان شمالی، رضوی و جنوبی و تأثیر دما بر انتقال عمودی باکتری‌های همزیست

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چکیده

بسیاری از باکتری‌های همزیست داخلی مرتبط با بندپایان، نقش مهمی در تعیین ویژگی‌های عملکردی میزبان ایفا می‌کنند و ساختار جمعیت آن‌ها می‌تواند تحت تأثیر همزیست‌های داخلی قرار گیرد. در پژوهش حاضر، بررسی همزیست‌های داخلی موجود در جمعیت‌های طبیعی کنه دولکه‌ای (*Tetranychus urticae*) در سه استان خراسان شمالی، رضوی و جنوبی انجام شد. در مجموع، ۱۴۴۰ نمونه کنه از سه منطقه جغرافیایی و از روی هشت گونه گیاه میزبان جمع‌آوری و از نظر وجود همزیست‌های داخلی ارزیابی شدند. در میان سه همزیست داخلی اختیاری شناسایی شده شامل *Wolbachia*، *Cardinium* و *Rickettsia*، به ترتیب میزان آلودگی ۹۱/۶٪، ۹/۷۲٪ و ۹/۷۲٪ مشاهده شد. هیچ‌یک از نمونه‌ها حامل *Arsenophonus* یا *Spiroplasma* نبودند. در بخش عمده‌ای از جمعیت‌های مورد بررسی، آلودگی‌های چندگانه به همزیست‌های داخلی مشاهده شد و میزان هم‌زمانی آلودگی به *Wolbachia*-*Rickettsia* (۹/۷۲٪) بیش از سایر انواع آلودگی هم‌زمان بود. نتایج این مطالعه نشان داد که فراوانی آلودگی به همزیست‌های داخلی ممکن است تحت تأثیر ویژگی‌های زیست‌محیطی محل نمونه‌برداری، شامل موقعیت جغرافیایی (عرض و طول جغرافیایی)، ارتفاع از سطح دریا، تاریخ نمونه‌برداری و گونه گیاه میزبان قرار گیرد. میزان آلودگی به *Wolbachia* در نمونه‌های جمع‌آوری شده از استان خراسان رضوی بیشتر از سایر مناطق بود. همچنین بیشترین میزان آلودگی به *Cardinium* و *Rickettsia* به ترتیب در استان‌های خراسان شمالی و جنوبی مشاهده شد. نتایج به دست آمده همچنین نشان داد که نوع گیاه میزبان بر شیوع همزیست‌های داخلی تأثیری معناداری دارد. بررسی آزمایش‌های مربوط به انتقال عمودی نیز بیانگر آن بود که دما بر کارایی انتقال عمودی در باکتری‌های همزیست تأثیرگذار است.

واژگان کلیدی: همزیست‌های داخلی، همزیست‌های داخلی اختیاری، الگوی آلودگی، کنه تارتن دولکه‌ای، آلودگی چندگانه، انتقال عمودی

دریافت

۱۱ مرداد ۱۴۰۴

پذیرش

۱۸ آبان ۱۴۰۴

انتشار

۲۵ دی ۱۴۰۴

دبیر تخصصی

ع. صبور

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