



Prevalence and Effects of Endosymbiotic Bacterium *Wolbachia* in Spider Mites: Interactions and Implications for Pest Management

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Authors' contributions

This work was carried out in collaboration among all authors. All authors read and approved the final manuscript.

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ABSTRACT

Spider mites are pests of crops and ornamental plants. It has a cosmopolitan distribution and causes huge economic loss by yield reduction. *Wolbachia* is a prevalent endosymbiont in spider mites. *Wolbachia* imparts cytoplasmic incompatibility, parthenogenesis, mitochondrial DNA variation, behavioural changes, and varied effects on fecundity and longevity in spider mites. Co-infection with other endosymbiotic bacteria such as *Cardinium*, *Spiroplasma* and *Rickettsia* are also

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common with profound effects on host mites, host bacterial flora and host plants. 32 species of spider mites belonging to 9 genera are reported to have infected with *Wolbachia*. Highest infection is reported in tetranychus genera followed by bryobia. The detection, effects and applications of *Wolbachia* infection in spider mites are discussed. *Wolbachia* prevalence in the spider mite host is greatly dependent upon the host genotype, *Wolbachia* density and environmental factors. Dissecting the *Wolbachia*-spider mite interactions may enhance knowledge on evolutionary and ecological aspects of animal microbe interactions. This study will contribute to understand the *Wolbachia*- spider mite interactions and may pave way to the control of this agricultural pest.

Keywords: *Wolbachia*; biological control; endosymbiont; pest.

ABBREVIATIONS

CI : Cytoplasmic Incompatibility
MtDNA : Mitochondrial DNA
FISH : Fluorescent insitu hybridization
PCR : Polymerase chain reaction
Rdna : Ribosomal DNA

1. INTRODUCTION

Microbial symbiosis is a significant phenomenon in the biosphere, since it lead to the origin of eukaryotic cells and species formation, influencing the ecological, behavioural, and physiological activities of animals and plants. The most prevalent symbiotic microbe in the animal world is the alpha proteobacterium *Wolbachia* [1,2]. Current estimates suggest that 52% of arthropods and several filarial nematode species harbor *Wolbachia* [3]. This success is mainly attributed to its ability to induce various types of reproductive manipulation in hosts to increase the reproductive success of infected females, thereby increasing its own transmission [4]. The *Wolbachia* system serves as a model for inquiry-based science education that incorporates lessons on biotechnology, biodiversity, and bioinformatics.

Wolbachia has effects on the evolution of the host genome and speciation. It has applications in biological pest control through population replacement strategy (which provides a mechanism for the autonomous spread of desired genes into targeted populations), incompatible insect technique (to suppress target pest populations by repeated sweeps with infected individuals) and genetic manipulation. Anti-*Wolbachia* drug therapy is being successfully used to treat filarial diseases since *Wolbachia* is an obligate mutualist in filarial nematodes. *Wolbachia* can protect its hosts against a wide array of pathogens, including viruses, protozoan parasites, fungi, or pathogenic bacteria [1]. In contrast it can also infect any

beneficial arthropod species and may dramatically affect the outcome of a biological control program [5].

Spider mites (Acari: Tetranychidae) represent a distinctive evolutionary group that is comprised of about 1200 species, including many closely related species [6]. They are so named because some species utilize silk in constructing webbing on leaves or pads for oviposition and also for dispersal via ballooning much in the manner of some spiders. Spider mites have two reproductive strategies (bisexual and parthenogenetic). Many species of them have a wide host range, whereas others are highly host-specific [7]. They are notorious pests of many cultivated plants, causing massive economic losses worldwide, with approximately 0.9 billion Euros being spent annually for their control [8]. Due to the rapid evolution of pesticide resistance, effective control strategies are less. The presence of *Wolbachia* is most common in spider mites, although reproductive parasites such as *Cardinium*, *Rickettsia* and *Spiroplasma* also occur. A deeper understanding of *Wolbachia* impact on spider mite hosts may facilitate the development of intervention tools for controlling them. Manipulation of bacteriome could lead to future opportunities to decrease agricultural loss. Also, spider mites are considered a suitable model organism for studies related to *Wolbachia* to unravel the mysteries of animal microbe interactions [9]. We synthesize in this review the current knowledge accumulated on *Wolbachia* prevalence and effects in the spider mites.

2. PREVALENCE OF WOLBACHIA

The influential insider *Wolbachia* was first described in 1924 by Hertig and Wolbach [10] in the ovaries of the mosquito *Culex pipiens*. Tsagkarakou et al. [11] was the first to report *Wolbachia* in spider mite, *Tetranychus urticae*. Later studies confirmed a high prevalence of *Wolbachia* in spider mites across the globe. To

date, 32 species belonging to 9 genera of tetranychidae are infected with *Wolbachia*. Lack of incidence in others can be due to fewer sampling attempts because they are polymorphic for the infection; the absence of infection in the selected sample does not mean that the entire species is uninfected. In *T. urticae*, a cosmopolitan agricultural pest coming under spider mites, *Wolbachia* is detected in all the

surveyed populations, with the infection rate varying from 2.5 to 80% [12].

A total of 32 species of spider mites belonging to 9 genera is reported to have infected with *Wolbachia*. Highest infection is reported in the *Tetranychus* genera, with 12 species infected. Second highest infection is reported in the *Bryobia* genera, with 9 species infected.

Table 1. *Wolbachia* infection in tetranychid mites

S.No	Spider mite species	Country/region	Reference
1.	<i>Aplonobia histricina</i> Berlese	Spain	[69]
2.	<i>Amphitettranychus viennensis</i> Zacher	China	[52,45]
3.	<i>Bryobia berlesei</i> Eynhoven	Netherlands	[57]
4.	<i>B. graminum</i> Schrank	Netherlands	34
5.	<i>B. kissophila</i> Eynhoven	Netherlands, Belgium, Portugal, South Africa, Spain USA, France, Greece, Italy	[34,57]
6.	<i>B. neopraetiosa</i> Meyer	Netherlands	[34]
7.	<i>B. praetiosa</i> Koch	Netherlands	[34,57,73]
8.	<i>B. rubrioculus</i> Scheuten	Austria, Netherlands, France, Poland	[34,57,58]
9.	<i>B. sarothamni</i> Geijskes	Netherlands, Belgium, France	[56,57,73]
10.	<i>B. species1</i>	Netherlands	[57,73]
11.	<i>B. species V</i>	Netherlands	[57,73]
12.	<i>Eutetranychus banksi</i> McGregor	Spain	[71]
13.	<i>E. orientalis</i> Klein	Spain, Egypt	[69,74]
14.	<i>Oligonychus biharensis</i> Hirst	Bangladesh	[74]
15.	<i>O. castaneae</i> Ehara & Gotoh	Japan	[75]
16.	<i>O. gotohi</i> Ehara	Japan	[27,55]
17.	<i>Panonychus citri</i> McGregor	China, Spain	[69,76]
18.	<i>P. mori</i> Yokoyama	Japan	[16,17,27,55]
19.	<i>Petrobia harti</i> Ewing	California, China	[7,51]
20.	<i>Schizotetranychus cercidiphylli</i> Ehara	Japan	[27]
21.	<i>Tetranychus cinnabarinus</i> Boisduval	China	[12,52,53]
22.	<i>T. evansi</i> Baker & Pritchard	Brazil, Portugal, Spain	[9,69,77]
23.	<i>T. kanzawai</i> Kishida	Japan, China, Indonesia	[17,67,78,27,28,30,55,7,79,74]
24.	<i>T. ludeni</i> Zacher	Portugal	[9,79]
25.	<i>T. neocaledonicus</i> Andre	Louisiana	[74]
26.	<i>T. parakanzawai</i> Ehara	Japan	[27,57]
27.	<i>T. phaselus</i> Ehara	China	[67,7,64,79]
28.	<i>T. piercei</i> McGregor.	China	[7,20]
29.	<i>T. pueraricola</i> Ehara & Gotoh	Japan, China	[7,67,27,54,55]
30.	<i>T. truncatus</i> Ehara	China	[7,8,52,67,80,15,81,44,46,49,60,61,62,63,82,79,83]
31.	<i>T. turkestanii</i> Ugarov & Nikolskii	Gainesville, Netherlands, France, Greece, Spain, Poland, Turkey	[84,21,69,74,85]

S.No	Spider mite species	Country/region	Reference
32.	<i>T. urticae</i> Koch	Athens, Netherlands, Gainesville, Japan, California, Austria, China, South Korea Florida, France, Greece, Brazil, Portugal, Spain, Korea, France, Switzerland, Italy, England, Turkey	[7,9,11,12,65,52, 67,37,86,78,84, 87,18,19,21,23, 24,26,29,31,32, 35,38,88,45,48, 88,51,54,55,57, 69,71,72,89,77, 90,79,73,74,85]

3. EFFECTS OF WOLBACHIA

Four classical phenotypes induced by *Wolbachia* are CI, parthenogenesis, male killing and feminization. Of these only CI and parthenogenesis are detected in spider mites.

3.1 Cytoplasmic Incompatibility (CI)

CI is the most frequently found *Wolbachia*-induced phenotype and has been described in several arachnids, isopods and insect orders. Here the sperm from *Wolbachia*-infected males is incompatible with eggs from females that do not harbour the same *Wolbachia* type (or types). CI comprises two distinct components: *Wolbachia*-induced modification of sperm during spermatogenesis and rescue of this modification in embryos infected with the same strain. If the sperm is modified, but the appropriate *Wolbachia* are not present in the developing embryo, embryonic development is disrupted [4]. In the arrhenotokous (a form of parthenogenesis seen in spider mites, in which unfertilized eggs develop into males) species, two CI types are found in incompatible crosses. Egg haploidization and male production, referred to as 'male development' and aneuploidy and female mortality, referred to as 'female mortality' [13]. But in spider mites, only female mortality type of CI is produced by *Wolbachia* [14,15] and it is apparent by a reduced egg hatchability and a lower daughter: son ratio [15,16,17,18, 19,20]. The first report on CI in spider mites (*T. urticae* & *T. turkestanii*) is given by Breeuwer [21]. Then a variable level of CI ranging from no CI to complete CI is reported from spider mites [15,19,22, 23,24,25,26].

No effect in reproductive incompatibility is reported in *T. urticae* [27] and *T. kanzawai* [28,29,30]. Varied level of CI is reported in many other populations of *T. urticae* but no CI is reported in *T. kanzawai* in any populations tested. This is proposed to be due to the host

genotype or low bacterial density in the gametes [30]. Wybow et al. [31] reported that there is striking variation in CI with different host genetic backgrounds by transferring a single CI-inducing *Wolbachia* isolate into multiple host nuclear backgrounds of *T. urticae*.

The tripartite associations among *WO*, *Wolbachia*, and CI were analyzed by Lu et al. [32]. *WO* is a Bacteriophage widespread in the genus and harbored by 89 % of *Wolbachia*. According to Phage Density Model [33], when phage *WO* is lysogenic and titers of *Wolbachia* are high in male reproductive tissues, CI intensity is high after mating with an uninfected female; when phage *WO* becomes lytic, *Wolbachia* cell titers decrease as a result of cell lysis and cause the CI intensity also decreased. *WO* may alternate between lytic and lysogenic life cycles or change phage production under certain conditions including temperature, host age and host species background. The results of Lu et al. [32] confirm the effect of temperature and host age in the life cycle of *WO* and consequently in *Wolbachia* and the host.

3.2 Parthenogenesis

Wolbachia-induced female parthenogenesis (Thelytoky) is present in species with arrhenotokous development. Instead of producing sons from unfertilized eggs, infected females produce daughters, which unlike males can transmit the bacteria to their offspring. Like CI, *Wolbachia*-induced parthenogenesis is caused by disruption of the cell cycle during early embryonic development, which results in diploid development in unfertilized eggs. *Wolbachia*-induced parthenogenesis is reported in two species of the genus *Bryobia* [34].

3.3 Behavioural Changes

T. urticae females evolved avoidance of incompatible males to escape CI by oviposition

and mating behavior [35]. Uninfected females preferred uninfected males and infected females aggregated their offspring to promote sib mating. But a later study [36] divulge that there is no such preference for infected or uninfected males. Zhao et al. [37] also observed no difference in mating competitiveness between infected and uninfected males. A combined effect of host-associated incompatibilities and *Wolbachia*-induced post mating isolation contributing to host population divergence and the subsequent evolution of intrinsic reproductive barriers is demonstrated by Cruz et al [38]. A subsequent study by the same authors [39] showed that pre-mating isolation matches both host-associated and *Wolbachia*-induced post-mating isolation. So it is clear that *Wolbachia* may have a considerable effect in the processes of speciation currently ongoing in spider mites.

Evolution of CI driven polyandry is reported in spider mites [40]. Although spider mites shows first sperm precedence, to avoid CI, They break sperm priority pattern in favour of the second male, only when the first mating is incompatible. In addition, mutation fixation and hybridization caused by *Wolbachia* or *Cardinium* are proposed to result in the evolutionary success of asexual spider mites [41].

3.4 Life History Parameters

Wolbachia can influence life history traits differentially across populations. Fecundity varies distinctly amongst different species and populations of spider mites with *Wolbachia* infection including deleterious [23,24,42], neutral [15,24,25] and beneficial effects [25,26,37]. Similarly positive, negative and neutral effects of *Wolbachia* infection on longevity are reported from spider mites [15,25]. Vala et al. [23] reported *Wolbachia* causing hybrid breakdown in the f_2 generation and it is confirmed in two populations of *T. urticae* [43].

3.5 Effects at the Transcriptional Level

With the advent of advanced molecular techniques, some of the mechanisms underlying *Wolbachia* mediated phenotypes in the host is revealed. It has been shown to regulate several reproduction-related host genes and pathways. To identify genes involved in the *Wolbachia*-induced effects, RNA interference and transcriptome analysis is used. However, the genes regulated by *Wolbachia* in different hosts are diverse and complex. *Chorion protein S38*, an important component protein in the early

stage of egg shell formation and *Ras* opposite gene (*Rop*) (mediate cell division in *Drosophila*) were down-regulated by *Wolbachia* in *T. truncatus* and resulted in oviposition decrease. Differentially expressed genes showed the effect of *Wolbachia* infection on energy, nitrogen, and oxygen metabolism [44]. Zhang et al. [45] found that *Wolbachia* responses are sex-specific with the transcription of 251 genes being affected in females and 171 genes being affected in males in *T. urticae*. More profoundly affected genes in both sexes were lipocalin genes and genes involved in oxidation-reduction, digestion and detoxification. Lipocalins are small extracellular proteins that typically bind hydrophobic molecules. In spider mites, they may bind pesticides or allelochemicals, resulting in the sequestration of these toxic, generally hydrophobic compounds. This may be the reason for *T. urticae* resistance to a variety of plant chemicals and pesticides. Two genes encoding vitellogenin were upregulated in infected females. Vitellogenins are important for the growth and differentiation of oocytes and for transporting metallic ions, lipids and vitamins into the oocytes, hence, these genes might have a role in enhancing female fecundity. In *T. truncatus* co-infected with *Wolbachia* and *Spiroplasma*, detoxification genes, lipocalin genes, histone-related genes, vitellogenin genes, immune-related genes and genes related to lipid metabolic processes are differentially expressed [46]. Detoxification genes such as P450, glutathione-S-transferase (GST), ABC transporters, and carboxyl/cholinesterases are found to be upregulated in *Wolbachia* infected *T. urticae* [47]. This has increased mite survival after exposure to the insecticides abamectin, cyflumetofen, and pyridaben. Bing et al. [48] revealed that *Wolbachia*-infected mites upregulated the gene expression levels of many *T. urticae* salivary proteins including a cluster of *Tetranychidae*-specific, functionally uncharacterized SHOT1s (secreted host-responsive proteins of Tetranychidae). RNA interference experiments showed that knockdown of *SHOT1s* significantly decreased *Wolbachia* density, increased the number of deposited eggs and decreased the egg hatching rate. Zhu et al. [49] identified 177 putative salivary proteins from *T. truncatus*. Of these 14 proteins were only found in *Wolbachia*-*Spiroplasma* infected spider mites, and 6 proteins were only found in *Wolbachia*-*Spiroplasma* uninfected spider mite, indicating that *Wolbachia* and *Spiroplasma* can affect the salivary secretion of spider mites.

Rong et al. [50] recognized the involvement of miRNA in *Wolbachia*-spider mite interactions. miRNA's are non coding small RNA's that play significant roles in regulating cellular processes. They integrated the mi RNA and mRNA transcriptome data to predict the candidate target genes and their biological functions were analyzed using the gene ontology annotations of the *T. urticae* genes. The team revealed that the *Wolbachia* infection affected 91 miRNAs in females and 20 miRNAs in males. Genes related to apoptosis, sphingolipid metabolism, lysosome function, and lipid transporting in both sexes, as well as reproduction in females were found to be affected. Authors raise the possibility of a symbiotic relationship between *Wolbachia* and spider mites.

4. CO-INFECTIONS

Multiple endosymbiont infections are common in spider mites. They have a range of phenotypic effects; some have no additional impact over single infections, whereas others appear to enhance the effects of single infections or lead to novel phenotypic effects. *P. harti* [51], *T. cinnabarinus* [52,53], *T. pueraricola* [54,55], *T. viennensis* [52], *B. sarothamni* [56,57], *T. urticae* [9,57], *B. rubrioculus* [57,58], *T. evansi* [9], *T. piercei* [20], *O. gotohi* and *P. mori* [55] are reported to have co-infected with *Wolbachia* and *Cardinium*. In *T. urticae*, *Cardinium* enhancing the severity of CI induced by *Wolbachia* is reported [59]. *T. truncatus* and *B. sarothamni* co-infected with *Wolbachia* and *Cardinium* were reported to have higher fecundity [15,56].

T. truncatus [46,60,61] and *T. urticae* [58] are co-infected with *Wolbachia* and *Spiroplasma*. *T. truncatus* shows higher egg deposition and faster developmental rate, compared with singly infected and uninfected spider mite strains. Doubly infected mites could induce incomplete CI, whereas *Wolbachia* singly infected mites could not induce CI [62]. *T. truncatus* co-infected with *Wolbachia* and *Spiroplasma* showed higher thermal tolerance than uninfected and singly infected mites [63]. This co-infection also protects them from pathogenic bacteria [46]. *T. truncatus* co infected with *Wolbachia* and *Spiroplasma* showed lower expression levels of jasmonic acid and salicylic acid-responsive genes than those damaged by uninfected spider mites. Also, they consumed more tomato amino acids compared to uninfected spider mites. These may be the reason for the reproductive benefits conferred by endosymbionts [8].

Wolbachia and *Spiroplasma* could influence the bacterial community of *T. truncatus*. It did alter the abundance of many bacterial genera, such as *Megamonas* and *Bacteroides* [60]. Decreased fecundity with co-infection is also reported in *T. truncatus* [46].

Co-infection with *Wolbachia* and *Rickettsia* is reported in *T. evansi* and *T. urticae* and triple infection with *Wolbachia*, *Cardinium* and *Rickettsia* is reported in *T. ludeni* [9]. Co-infection with *Cardinium* and two strains of *Wolbachia* detected in *T. phaseolus* displayed a high level of CI with reduced egg hatchability and male-biased sex ratio and showed greater depression of fecundity [64].

Wolbachia have a domination over other symbionts in the co-infected spider mites. In the co-infected *T. truncatus*, *Wolbachia* had significantly higher density than *Spiroplasma*. The gene expression patterns of the *Wolbachia* singly infected strain were similar to the doubly infected strain, which showed a stronger effect of *Wolbachia* in the co-infected strain [46]. *Wolbachia* boosted the expression of *Cardinium*-induced CI in *T. piercei*, the strength of CI induced by doubly infected males also was found to be higher than that induced by the singly infected males [20].

5. DETECTION METHODS

Wolbachia is an intracellular symbiotic bacterium that cannot be cultured outside of host cells. Thus, the detection of its presence in mites is done mainly using PCR-based techniques, sometimes aided by bioassays (crossing breeding studies). PCR amplification and sequencing of a fragment of ribosomal DNA and any of the protein-coding genes *ftsZ* [16], *groEL* [65], *wsp* [17] and citrate synthase (*gltA*) [66] is the generally used technique for the detection of infection. Long PCR which uses two enzymes (Taq and Pwo), is a highly sensitive method [65]. It gives the highest incidence of *Wolbachia* (76%) in arthropods but is not generally used because of false positives due to the detection of environmental contaminants. Multiplex PCR is a rapid, reliable and highly sensitive method to detect multiple endosymbionts simultaneously. Chen et al. [67] used the technique in four strains of *T. cinnabarinus* co-infected with *Wolbachia* and *Cardinium*. Zele et al. [68] also developed a multiplex PCR method for the rapid identification of *T. urticae*, *T. evansi* and *T. ludeni*, and the detection of their endosymbionts, namely *Wolbachia*, *Cardinium* and *Rickettsia*.

Wolbachia strain diversity is determined by multilocus sequence typing, which overcomes the recombination issue and provides an expanded data set for comparative analyses [69]. To date, 17 *Wolbachia* supergroups (from A to R, except for supergroup G, which is controversial) have been established [70]. FISH is used for localization of *Wolbachia*. It is found mainly located in the gnathosoma and ovaries of females and testes of males [8,37].

6. APPLICATIONS FOR PEST CONTROL

Wolbachia-based incompatible insect technique (IIT), pathogen blocking technique (PBT) and anti-*Wolbachia* drug therapy have been shown to be effective at protecting humans from mosquito-borne diseases. Similar strategies have been put forth to shield plants from agricultural pests and the diseases they cause. CI induced by *Wolbachia*, can be used as a population suppression strategy, analogous to the IIT that reduces or eliminates the population, or/and as population replacement, using the bacteria as a vehicle to drive desired phenotypes into natural populations [71]. Still, the requirement for techniques to create insect lines that are transinfected with *Wolbachia* represents a barrier to the widespread use of *Wolbachia*-based pest management solutions. Gong et al. [72] considered the following five qualities as prerequisites for this kind of strategy to be successful in agriculture. (1) stable *Wolbachia* interspecific transinfection in a target insect line, (2) little or no fitness cost in the transfected line, (3) an ability of the transinfected line to induce strong CI (necessary) and pathogen blocking (optional) phenotypes, (4) establishment of an effective sex sorting method for the target species, and (5) an ability of the transinfected line to be artificially maintained and mass-reared.

Zele et al. [73] infers that despite reports of *Wolbachia* induced pathogen resistance in arthropods, the effectiveness of biological control with entomopathogenic fungi is not hampered and may even be enhanced by it in spider mite *T.urticae*. Studies on endosymbionts in pest mites are considered significant as they can be used to optimize control programs or to explain resistance in pests against certain control agents [5,58,74].

7. CONCLUSION

Although spider mites are serious agricultural pests with more than 1200 species, only 32

species are reported to have been infected with *Wolbachia*. This is because there haven't been as many investigations done in this area. The prevalence and effects of their infection depend upon various factors such as the host genotype, host-microbial flora, host plant, and environmental factors. While considering their effects on evolution, genetics and biological control, investigation of *Wolbachia* infection in spider mites across the globe will be fruitful. Moreover, spider mites being a suitable model organism for studies related to *Wolbachia*, investigations will help to understand and unravel host-microbe interactions.

DISCLAIMER (ARTIFICIAL INTELLIGENCE)

Authors hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

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COMPETING INTERESTS

Authors have declared that no competing interests exist.

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