



**Is the emerging mite pest *Aculops lycopersici* controllable?  
Global and genome-based insights in its biology and  
management.**

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# 1 Is the emerging mite pest *Aculops lycopersici* 2 controllable? Global and genome-based insights in its 3 biology and management. 4

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11  
12 **Keywords:** Eriophyidae, rust mite, effector, plant defence, biological control, predator

## 13 14 Abstract

15 Over the last decade, the tomato russet mite, *Aculops lycopersici*, has become a major pest in tomato  
16 crops worldwide, both in open-field and protected cultivation. Its minute size of 150-200µm  
17 complicates early detection and monitoring in tomato crops. Passive dispersal occurs via air currents,  
18 crop management practices and commercial trade. Chemical control of *A. lycopersici* is difficult.  
19 Altered product use from broad spectrum pesticides towards selective acaricides, to meet IPM  
20 standards, has created better conditions for the rapid expansion of this specialized eriophyid mite.  
21 Moreover, practical implementation of promising natural enemies is challenging due to the complexity  
22 of biological control in tomato crops. Trichomes on tomato negatively affect arthropod natural  
23 enemies, but provide a refuge for the tomato russet mite. Despite the cosmopolitan nature of *A.*  
24 *lycopersici*, knowledge associated with integrated pest management is limited and fragmented. This  
25 review describes fundamental biological data on *A. lycopersici* from the last 20 years and novel  
26 developments in the field of prevention, monitoring, chemical and biological control. The recent

1  
2  
3 27 analysis of the genome sequence will be helpful in the development of a sustainable control strategy  
4  
5 28 for *A. lycopersici*.

## 8 29 1 Introduction

10  
11 30 The tomato russet mite, *Aculops lycopersici* (Tryon), belongs to the superfamily of the Eriophyoidea  
12  
13 31 (Arthropoda: Chelicerata: Acari: Acariformes) that harbours some of the most economically important  
14  
15 32 mite pests around the world.<sup>1,2</sup> Eriophyoid mites have traditionally been considered a member of the  
16  
17 33 Trombidiformes, which includes many agriculturally important species such as spider mites  
18  
19 34 (Tetranychidae).<sup>3</sup> Recent work, however, including a phylogenetic analysis based on the genome  
20  
21 35 sequence of *A. lycopersici*, suggests that the Eriophyoidea belong to the Sarcoptiformes, which  
22  
23 36 includes species such as dust mites and scabies mites, or belong to a sister taxon.<sup>3</sup> The tomato russet  
24  
25 37 mite feeds on various plant species within the Solanaceae family including several wild species like  
26  
27 38 black nightshade (*Solanum nigrum* L.) and crop plants like pepper (*Capsicum annuum* L.), eggplant  
28  
29 39 (*Solanum melongena* L.), potato (*Solanum tuberosum* L.) and tomato (*Solanum lycopersicum* L.).<sup>4-7</sup> *A.*  
30  
31 40 *lycopersici* feeds and reproduces on cultivated tomato until high population densities are reached and  
32  
33 41 the plant suffers severe damage or dies.<sup>1</sup> The tomato russet mite has recently emerged as a serious  
34  
35 42 pest problem in European greenhouse and open-field tomatoes, for unclear reasons.<sup>2, 4, 8, 9</sup> The basic  
36  
37 43 morphology and biology of *A. lycopersici* has been described in detail by a range of authors in the mid-  
38  
39 44 20th century.<sup>6, 7, 10</sup> Although already mentioned as a minor pest since the 1930s, the first efforts to  
40  
41 45 control *A. lycopersici* only occurred in the late 20<sup>th</sup> century.<sup>1</sup> The most important knowledge on  
42  
43 46 eriophyoid mites, their biology, natural enemies and control, including on *A. lycopersici*, was compiled  
44  
45 47 in 1996.<sup>1</sup> As this key reference work dates back to more than 20 years ago, our aim was to complement  
46  
47 48 it with insights into new developments and research efforts to better understand the recent  
48  
49 49 emergence of *A. lycopersici* as a primary pest in tomato cultivation. Research on biological control of  
50  
51 50 *A. lycopersici* also started in the late 20<sup>th</sup> century, but was largely limited to laboratory experiments.<sup>4</sup>  
52  
53 51 Information on the chemical control of *A. lycopersici* has been compiled based on the products  
54  
55 52 available two decades ago.<sup>11</sup> However, the advent of switching from broad spectrum pesticides to

1  
2  
3 53 selective acaricides to meet IPM standards, and the elimination of many acaricides by pesticide review  
4  
5 54 programmes and ensuing regulations in the EU (Directive 91/414/EEC and Regulation 1107/2009) have  
6  
7 55 presented new challenges for the control of this eriophyid mite.<sup>2</sup> Based on an overview of the literature  
8  
9 56 on its biology and ecology from the last 20 years, together with new developments including the  
10  
11 57 recently published genome of *A. lycopersici*, possible strategies for the sustainable control of this  
12  
13 58 emerging pest of tomato will be discussed.

## 17 59 2 Morphology and biology

20 60 The tomato russet mite is one of the smallest plant-feeding arthropods known today.<sup>3</sup> Its minute size,  
21  
22 61 with adults measuring not more than 150-200µm in length (Fig. 1a), coincides with a very small genome  
23  
24 62 of only 32.5Mb and a unique derived body plan.<sup>3, 6, 7</sup> It has only two pairs of legs (Fig. 2a), which  
25  
26 63 terminate in a distinctive four-rayed feather-like empodium or feather-claw.<sup>6</sup> Genomic analysis  
27  
28 64 revealed that in contrast to other mite and tick species, *A. lycopersici* lacks the Hox gene  
29  
30 65 *proboscipedia*, which is expressed in the pedipalps and in the first to fourth pair of legs in most  
31  
32 66 Chelicerata.<sup>3</sup> Whether this lack of the *proboscipedia* gene is indeed related to a reduction in the  
33  
34 67 number of legs remains to be validated but this hypothesis seems plausible, as this gene is missing in  
35  
36 68 other ecdysozoan animals without legs, such as nematodes.<sup>3</sup> Additionally, although only a low rate of  
37  
38 69 gene family expansions are present in the genome of *A. lycopersici*, one of the expanded families  
39  
40 70 contains a troponin domain that has a conserved role in muscle contraction.<sup>3</sup> This expansion, together  
41  
42 71 with the loss of several other genes and gene families involved in conserved aspects of arthropod  
43  
44 72 development and physiology, may be related to the characteristic pronounced skeletal and peripheral  
45  
46 73 musculature and overall body plan of this mite.<sup>3</sup> Because of their characteristic fusiform abdomen,  
47  
48 74 they had been mistaken for tiny maggots instead of mites, in a study that later appeared to have been  
49  
50 75 the first to comment on galls and erineae associated with the action of arthropods.<sup>1</sup> Tomato russet  
51  
52 76 mites are white to orange and have dorsal half-rings (tergites) (Fig. 2b), which are broader but less  
53  
54 77 abundant than the ventral half-rings (sternites).<sup>6</sup> A pair of long setae (Fig. 2c) and large clinging lobes  
55  
56 78 (Fig. 2d) are located on the posterior end of the body. These anal lobes allow the mite to stand-up

1  
2  
3 79 while clawing the air, to initiate take-off for dispersal by wind, rain or attachment to a vector.<sup>7, 12</sup> The  
4  
5 80 adult genitalia are situated just behind the coxae.<sup>6, 7</sup> There is no pronounced sexual dimorphism and  
6  
7 81 no aedeagus for sperm transfer.<sup>1</sup> Fertilization is internal by transfer of spermatophores which are  
8  
9 82 deposited onto the plant substrate by males and subsequently picked up by females.<sup>1, 13</sup> Remarkably,  
10  
11 83 eriophyoids are the only known group of obligatory herbivores exhibiting this outcrossing non-pairing  
12  
13 84 mode of reproduction, since most other organisms with sex dissociation are aquatic or terrestrial,  
14  
15 85 often inhabiting soil or leaf-litter.<sup>12</sup> Eriophyidae have an arrhenotokous mode of reproduction and  
16  
17 86 short life cycle with three active postembryonic instars (Fig. 2).<sup>1</sup> Unfertilized eggs parthenogenetically  
18  
19 87 develop into haploid (n) males and diploid (2n) females develop from fertilized eggs. The spherical eggs  
20  
21 88 are approximately 55µm in diameter, and are opalescent–white when freshly laid but cloudy and  
22  
23 89 yellowish just before hatching after approximately 2 days.<sup>7</sup> The translucent white protonymphs attain  
24  
25 90 a maximum length of about 90-100µm and lack rings on the abdominal dorsum.<sup>7</sup> This stage is followed  
26  
27 91 by the first quiescent stage or nymphochrysalis.<sup>7, 13</sup> The yellow deutonymphs are completely beset with  
28  
29 92 rings and microtubercles and are about 140-160µm in length.<sup>7</sup> From the last quiescent stage or  
30  
31 93 imagochrysalis emerges the adult to complete the life cycle.<sup>7, 13</sup>

32  
33 94 Few life history studies on the tomato russet mite have been published.<sup>7, 10, 13, 14</sup> The lower threshold  
34  
35 95 temperature for development from egg to adult was estimated to be around 10°C with linearly  
36  
37 96 decreasing developmental durations from 15°C to 27.5°C and a thermal maximum close to 39°C.<sup>13, 14</sup>  
38  
39 97 At 8°C, eggs fail to hatch while at 39°C, no immatures succeed in reaching the adult stage.<sup>13</sup> Freezing  
40  
41 98 temperatures kill all stages within a few hours to a few days, there is no diapause.<sup>6</sup> Successful  
42  
43 99 development from egg to adult was reported between 11°C and 36°C at 55% R.H. (relative humidity),  
44  
45 100 with an optimal temperature for development between 28°C and 32°C.<sup>13</sup> However, survival decreased  
46  
47 101 from 90% at 27.5°C to only 53% at 30°C.<sup>14</sup> The life cycle can be completed in just 6 to 7 days at optimal  
48  
49 102 conditions of approximately 27°C and 30% R.H.<sup>4, 10</sup> Under these conditions, the egg, protonymph and  
50  
51 103 deutonymph stages take 2.8, 0.9 and 1.2 days, respectively.<sup>10</sup> With a pre-reproductive period of about  
52  
53 104 2 days and a longevity between 17 and 30 days, females can lay up to more than 50 eggs, depending

1  
2  
3 105 on temperature.<sup>7,10,14</sup> Together, this indicates that this mite is an exceptionally rapidly developing pest  
4  
5 106 that performs best at high temperatures and low humidity levels.  
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7  
8 107 All mobile life stages possess needle-shaped mouthparts with short stylets of approximately 10-15µm  
9  
10 108 long, which are used to inject the saliva into the pierced plant cell and suck up the cell contents.<sup>1,13,15</sup>  
11  
12 109 In contrast to for example spider mites that feed on cells within the leaf mesophyll<sup>16</sup>, these short stylets  
13  
14 110 only allows feeding on the epidermal cell content of all aerial plant parts.<sup>3,13</sup> The short generation time  
15  
16 111 of *A. lycopersici* while feeding on a nutritionally poor epidermis, might be a driver for the evolution of  
17  
18 112 genome miniaturization.<sup>3</sup> Tomato russet mites are usually found in greater abundance just ahead of  
19  
20 113 the damaged area and in depressions surrounding veins or near leaf petioles of tomato.<sup>1,4</sup> This  
21  
22 114 preference may be a response to greater nutritional content, but these areas also may provide a more  
23  
24 115 favourable microhabitat.<sup>1</sup> Their particular mode of feeding starts with feeding on single epidermal cells  
25  
26 116 for a short period of time, after which they attack distal cells, and leads finally to a massive destruction  
27  
28 117 of the epidermal cell layer.<sup>1,9,16</sup> Damage intensity varies between different hosts and among tomato  
29  
30 118 cultivars, but severe damage to plants other than tomato is rare.<sup>1,10,17</sup> Early symptoms of russet mite  
31  
32 119 damage include leaf silvering and discoloration and can be misdiagnosed as a nutritional deficiency,  
33  
34 120 plant disease or water stress.<sup>3,4,9</sup> Although Eriophyidae are known to vector viruses, this has never  
35  
36 121 been reported for the tomato russet mite.<sup>1,17</sup> From days to a week after infestation, the glandular  
37  
38 122 heads of the trichomes change colour from oblique to amber (Fig. 1b). This is followed by deterioration  
39  
40 123 and local but massive collapse of both glandular and non-glandular trichomes.<sup>15</sup> Later symptoms  
41  
42 124 include russetting and bronzing of leaves and stems.<sup>6,15</sup> This injury may occur near the top of the plant  
43  
44 125 but typically first appears at ground level from where it spreads upwards.<sup>7</sup> At high population densities  
45  
46 126 (Fig. 1c), leaves turn paper-like, eventually leading to serious foliage loss and only in the most severe  
47  
48 127 infestations the fruit becomes russeted (Fig. 1d).<sup>6,7</sup> The damage inflicted by *A. lycopersici* can be very  
49  
50 128 severe, but is often only noticed when population densities are already high and this complicates  
51  
52 129 effective control. Depending on the infestation level and control measures, damage can cause 25 to  
53  
54 130 100% yield losses of tomato production.<sup>7,13</sup>

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2  
3 131 The geographical origin and original host of *A. lycopersici* are unknown, but the mite was first described  
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5 132 as *Phyllocoptes lycopersici* Tryon as a pest of tomatoes in Queensland, Australia in 1917.<sup>1</sup> This  
6  
7 133 thermophilic species is distributed worldwide and present in almost all areas where solanaceous crops  
8  
9 134 are grown.<sup>4,6</sup> Having no dormant season, the tomato russet mite is unable to survive outdoor in areas  
10  
11 135 where unfavourable winter temperatures kill its host plants.<sup>6</sup> Therefore *A. lycopersici* generally does  
12  
13 136 not occur below and above 60 degrees southern and northern latitudes, respectively.<sup>4</sup> However,  
14  
15 137 certain types of refuges (shrubs, greenhouses or cold frames) could support winter survival.<sup>6</sup> This  
16  
17 138 species is exceptionally polyphagous for an eriophyid but most of its host plants belong to the  
18  
19 139 Solanaceae family. It has been suggested that the original host plant of the tomato russet mite was an  
20  
21 140 unproductive, small, wild solanaceous plant with native mite resistance genes which may have been  
22  
23 141 lost in the breeding process of productive tomatoes.<sup>12</sup> Whereas the unnatural relationship between *A.*  
24  
25 142 *lycopersici* and tomato is fatal for the host, a perennial host is of the essence for perpetuation of a  
26  
27 143 population.<sup>6,10</sup> At least 33 species are considered as alternate host plants with only seven being non-  
28  
29 144 solanaceous species (belonging to Convolvulaceae, Grossulariaceae and Rosaceae) (Supplementary  
30  
31 145 Table 1).

### 146 3 Plant-mite and tritrophic interactions

147 Plants have evolved a diverse set of defences to discourage or kill herbivores. These include  
148 constitutive chemical and physical defences that are present even when herbivores are absent,  
149 whereas induced defences are activated when feeding commences. Some induced defences include  
150 complex cocktails of volatiles to attract natural enemies to herbivore-infested plants.<sup>18,19</sup> However,  
151 some herbivores have developed means to overcome plant defences, either by detoxifying plant  
152 allelochemicals or interfering with their production in the plant.<sup>20</sup> Suppression of plant defences can  
153 be accomplished by secreting metabolites or proteins in saliva that is injected into plants.<sup>20</sup> There is a  
154 growing interest to integrate crucial knowledge on plant-herbivore interactions when devising  
155 integrated environmentally sustainable control strategies.<sup>21</sup>

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3 156 The genus *Solanum*, including the cultivated tomato *Solanum lycopersicum*, has a wide range of well-  
4  
5 157 studied constitutive and inducible defences against herbivores.<sup>15, 18, 19, 22, 23</sup> Chemically induced  
6  
7 158 defences include enzymes and compounds such as polyphenol oxidase and proteinase inhibitors that  
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9  
10 159 reduce the nutritional quality of the tomato plant to herbivores.<sup>19</sup> Furthermore,  $\alpha$ -tomatine, the main  
11  
12 160 glycosylated steroidal alkaloid that accumulates in leaves, green fruits and trichomes, plays an  
13  
14 161 important protective role in tomato. Tomato-mite interactions have been studied at the molecular  
15  
16 162 level for two-spotted spider mites (*Tetranychus urticae* (Koch))<sup>24</sup> and *A. lycopersici*.<sup>16, 25</sup> Mite feeding  
17  
18 163 induces plant defence responses that negatively affect mite performance, which are mediated by  
19  
20 164 jasmonate and salicylate hormone responses.<sup>16, 25</sup> *A. lycopersici* can, however, selectively suppress the  
21  
22 165 jasmonate mediated host defences downstream from phytohormone accumulation and  
23  
24 166 independently from antagonistic crosstalk between jasmonate and salicylate.<sup>16, 25</sup> Additionally, tomato  
25  
26 167 russet mites induce salicylate defences, to which they are not sensitive, but which have been shown  
27  
28 168 to inhibit the growth of the bacterial pathogen *Pseudomonas syringae*.<sup>25</sup> Field-grown tomatoes that  
29  
30 169 already suffered from a tomato russet mite infestation were often observed to be invaded with *T.*  
31  
32 170 *urticae* as well.<sup>25</sup> When tomato is co-infested with *A. lycopersici* and *T. urticae*, the latter takes  
33  
34 171 advantage of the suppression of the jasmonate defences and can establish larger colonies, presenting  
35  
36 172 a risk for secondary infestations for tomato growers.<sup>25</sup> The population growth of the tomato russet  
37  
38 173 mite decreases in the presence of two-spotted spider mites, indicating that the benefits of plant-  
39  
40 174 mediated indirect interactions thus depend on the community structure on the plant and can backfire  
41  
42 175 in the presence of competitors.<sup>25</sup> Moreover, jasmonate defences are typically modulated by drought  
43  
44 176 stress.<sup>26</sup> Tomato russet mite populations were observed to increase faster and caused more damage  
45  
46 177 on drought-stressed plants compared to well-irrigated tomato plants.<sup>9, 26</sup> Furthermore, the increase in  
47  
48 178 jasmonate can impact the density, chemistry or development of trichomes<sup>19, 21</sup> and the down-  
49  
50 179 regulation of trichome-localized terpenoid biosynthesis genes might be associated with the  
51  
52 180 deterioration of glandular trichomes.<sup>16</sup> Interestingly, *A. lycopersici* has a striking reduction in gene  
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54 181 families associated with host plant interactions and only a very limited number of chemosensory  
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3 182 receptor families are present.<sup>3</sup> This finding could be attributed to the loss of sensory structures during  
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5 183 miniaturization but might also be due to the specialized lifestyle of this herbivore. Whereas *A.*  
6  
7 184 *lycopersici* suppresses the defences of its host, the need for a large set of environmental response-  
8  
9  
10 185 detoxification and chemosensory genes might be decreased.<sup>3</sup> Using the available genome, the  
11  
12 186 underlying molecular mechanisms of mite-plant interactions can be investigated, for example by  
13  
14 187 identifying the potential effector proteins and their plant targets that can be used for resistance  
15  
16 188 breeding (S-genes).<sup>3, 27</sup>

189 The interactions between *A. lycopersici* and tomato trichomes are of special interest. These specialized  
190 extensions of the plant epidermis have been intensively studied given their strong relationship with  
191 resistance to herbivory as constitutive defences but also because they play an important role in  
192 induced defences.<sup>19, 28</sup> Trichomes are classified as either glandular or non-glandular.<sup>19, 21, 28</sup> Glandular  
193 trichomes have the capacity to synthesize, accumulate and secrete secondary metabolites in a head  
194 consisting of one to a few secretory cells of which the chemical content differs between the types.<sup>19</sup>  
195 These glandular trichome-borne metabolites, whether or not upregulated by herbivorous attack, can  
196 immobilize and/or exert toxic effects on herbivores leading to their death.<sup>23</sup> Non-glandular trichomes  
197 lack these heads and function as a mechanical barrier by obstructing herbivore movements, or  
198 preventing herbivores from reaching the nutritious tissues with their mouthparts.<sup>15, 19</sup> For example, in  
199 cultivated tomato, trichomes of type I, VI, VII (glandular) and III, V and VIII (non-glandular) can be  
200 present.<sup>19, 28</sup> Although only low densities occur in cultivated tomatoes, type I trichomes contain mostly  
201 non-volatile acyl glucosides.<sup>29</sup> Type VI trichomes, which are more abundant, accumulate monoterpenes  
202 and sesquiterpenes.<sup>19, 21, 23</sup> Additionally, this trichome type also produces tridecan-2-one (2-TD) and  
203 undecan-2-one (2-UD), which are toxic to *A. lycopersici* but more abundant in wild tomato species  
204 compared to cultivated tomato.<sup>30</sup>

205 For the plant, trichomes can be primarily defensive but secondarily harmful, either directly by  
206 entrapping and killing predators or increasing their predation time or indirectly by limiting

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3 207 development or modifying prey quality of natural enemies.<sup>5, 18</sup> For instance, the rate of prey attacks by  
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5 208 the phytoseiid *Euseius victoriensis* (Womersley) on *A. lycopersici* on tomato leaf discs was drastically  
6  
7 209 lower than that on other eriophyid species on non-tomato hosts.<sup>31</sup> This suggests that the host is  
8  
9 210 generally unsuitable, distasteful or toxic to the prey.<sup>12, 31</sup> Although trichome-mediated plant defences  
10  
11 211 generally negatively affect phytophagous mites, this is not necessarily the case for *A. lycopersici* as  
12  
13 212 their size allows them to move between the trichomes.<sup>5, 15</sup> Even when glandular trichomes entrap  
14  
15 213 tomato russet mites when invading a new tomato plant, once on the plant surface, the trichome  
16  
17 214 'forest' creates a shelter against most competitors and predators.<sup>15</sup> Findings with six tomato cultivars  
18  
19 215 (Dora, Etna, Grande, H2274, Jana and M1103) indicate that trichomes provide excellent shelter for  
20  
21 216 tomato russet mites whereas they form an obstacle for their predator, *Tydeus kochi* (Oudemans).<sup>5</sup>  
22  
23 217 However, *A. lycopersici* causes a local but massive collapse of the glandular and non-glandular  
24  
25 218 trichomes. It remains unclear whether this is an effect of the destruction of the epidermis or results  
26  
27 219 from mite-induced physiological changes in the plant via interference with jasmonate defences which  
28  
29 220 are known to have an impact on trichomes.<sup>3, 15</sup> Tomato russet mites seek refuge in trichome-dense  
30  
31 221 areas upwards on the plant, which hampers successful predation.<sup>15</sup> This was shown for the phytoseiid  
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33 222 predator, *Amblydromalus limonicus* (Garman and McGregor), which was only able to successfully  
34  
35 223 establish once the glandular trichomes collapsed as a result of the tomato russet mite infestation.<sup>15</sup>  
36  
37 224 Could trichome-related host plant resistance breeding potentially reduce pesticide use in tomato  
38  
39 225 production?<sup>22</sup> Most genes conferring herbivore resistance are present in wild species.<sup>22</sup> Even when the  
40  
41 226 presence of trichomes seems to benefit *A. lycopersici* in commercial tomato varieties by providing  
42  
43 227 shelter, resistance to *A. lycopersici* was linked to increasing densities of mainly type VI glandular  
44  
45 228 trichomes in wild type tomato (*Lycopersicon hirsutum*).<sup>30</sup> Wild species can be used to introgress  
46  
47 229 agriculturally relevant traits such as certain pest resistance genes into the cultivated tomato genome.<sup>22,</sup>  
48  
49 230 <sup>29</sup> However, this may lead to adverse effects on yield traits or unpredictable responses in the pest–  
50  
51 231 natural enemy complexes, negatively affecting biological control agents.<sup>29</sup> At the other end of the  
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53 232 spectrum, trichome free tomato plants might be less colonized by *A. lycopersici*, but prove to be more

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3 233 ideal hosts for the many other pests of tomato, which might or might not be compensated by better  
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5 234 overall performance of arthropod biological control agents. It would be interesting to also look for  
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7 235 potential shifts in commercial tomato cultivars over time, and rule out that modern cultivars are more  
8  
9 236 susceptible to *A. lycopersici* infestation, potentially contributing to the recent emergence of the species  
10  
11  
12 237 as a pest.

## 15 238 4 Management

### 18 239 4.1 Prevention

20 240 There is little knowledge on the effective prevention of tomato russet mite infestations. In protected  
21  
22 241 tomato cultivation, the ability of the mite to survive the period in between two cultivation cycles and  
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24 242 transfer from a removed infested crop to a newly planted tomato crop, may allow early infestation of  
25  
26 243 the crop. In many places around the world, the area of artificially lighted greenhouse crops has  
27  
28 244 increased exponentially during recent years.<sup>8</sup> This has led to situations of year round production in  
29  
30 245 tomato cultivation.<sup>8</sup> A clean start of the new crop is of utmost importance but has become a challenge.  
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32 246 Laboratory experiments with infested tomato leaves showed that all stages of *A. lycopersici* are killed  
33  
34 247 after a 4 day exposure of -5.5°C but at a constant temperature of 1°C, second instar nymphs could  
35  
36 248 survive up to 20 days.<sup>7</sup> Without food, adult mites survived 4 days in summer.<sup>7</sup> Furthermore,  
37  
38 249 solanaceous weeds surrounding a greenhouse could serve as a reservoir or shelter for *A. lycopersici* in  
39  
40 250 between two cultivation cycles. Consequently, the development of an adequate hygiene protocol for  
41  
42 251 *A. lycopersici* is highly warranted.

### 48 252 4.2 Monitoring

50 253 The microscopic size of *A. lycopersici* complicates adequate scouting. Populations often remain  
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52 254 undetected for too long and once detected, the densities are frequently underestimated. Various  
53  
54 255 efforts have been undertaken to develop efficient and accurate methods to make eriophyid sampling  
55  
56 256 and population estimations easier.<sup>8,9,32</sup> *A. lycopersici* can be detected by measuring changes in volatile  
57  
58 257 organic compounds (VOCs) emitted by the trichomes with a portable gas chromatograph.<sup>32</sup> Although

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3 258 proposed as an inexpensive and handy gas analysis instrument, this method still requires labour  
4  
5 259 intensive dabbling of the stem surface with sampling papers. In another study, visual assessments were  
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7 260 compared with sticky tape imprints and blue light-induced chlorophyll fluorescence measurements.<sup>9</sup>  
8  
9  
10 261 Although the sticky tape imprint technique achieved the best classification rate of the monitored plants  
11  
12 262 as either infested or healthy, this labour intensive method is unsuitable for large-scale monitoring. At  
13  
14 263 night or under stable and low light conditions, a classification based on stem fluorescence  
15  
16 264 measurements enabled differentiating infested from healthy plants. This method performed as least  
17  
18 265 as good as the visual assessment and was robust against drought stress symptoms as well. The  
19  
20 266 necessity of dark or low light conditions in the fluorescence measurements is definitely a limitation for  
21  
22 267 their practical use. On the other hand, measurements at the level of the stem may facilitate an  
23  
24 268 automated monitoring system as in a modern greenhouse most plants show uniform growth.<sup>9</sup> Further,  
25  
26 269 a binomial sampling plan for *A. lycopersici* has been proposed.<sup>8</sup> Instead of counting the actual number  
27  
28 270 of tomato russet mites on a tomato plant, this plan estimates the population densities. Pictures of the  
29  
30 271 upper leaf surface from the lower third of the tomato plant are processed using a smartphone with an  
31  
32 272 attached magnifying lens. Taking labour, cost and accuracy of the models in consideration, the authors  
33  
34 273 suggested to take at least fifteen pictures in which no more than nine mites should be counted. The  
35  
36 274 proportion of infested samples with at least nine individuals allowed for an acceptable prediction of  
37  
38 275 the population density of the tomato russet mite. Although further research needs to determine the  
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40 276 number of plants to be sampled and the spatial distribution of the sampling in the greenhouse, this  
41  
42 277 plan was deemed practical for glasshouse tomato growers.<sup>8</sup> Finally, the sequenced *A. lycopersici*  
43  
44 278 genome provides a resource for methods of early detection of mite infestations using molecular  
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46 279 markers, although this might not be practically applicable for tomato growers at the moment.<sup>3</sup>  
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### 53 280 *4.3 Chemical control*

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55 281 Chemical control of *A. lycopersici* is difficult and the efficacy of treatments is often perceived as  
56  
57 282 inconsistent and inadequate by growers.<sup>4, 15</sup> Many factors contribute to the difficulties in suppressing  
58  
59 283 tomato russet mite populations with acaricides. Tomato russet mites occur on all aerial plants parts,  
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3 284 generally hidden under trichomes, making them difficult to effectively reach with acaricide  
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5 285 applications, particularly when the spraying technique is not appropriate.<sup>1, 15</sup> An effective pesticide  
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7 286 application technique (such as proper nozzle type, pressure, spray volume, ... ) is crucial for complete  
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9  
10 287 coverage and penetration into the crop canopy. Translaminar properties of certain acaricides, such as  
11  
12 288 abamectin and spiromesifen, might increase efficacy towards tomato russet mites, provided that  
13  
14 289 enough active ingredient resides within the epidermis.<sup>33</sup> These compounds obtain a uniform spread in  
15  
16 290 the leaf without the need for complete coverage of the canopy. The chemical control of eriophyids  
17  
18 291 was first reviewed in 1996, listing a substantial set of compounds tested against *A. lycopersici*.<sup>11</sup> Several  
19  
20 292 classical acaricides and insecticides with miticidal activity have demonstrated effectiveness, including  
21  
22 293 monocrotophos, pyridanphenthion (organophosphates), cyhexatin, azocyclotin (organotin  
23  
24 294 compounds), chlorobenzilate, bromopropylate and dicofol (diphenyl carbinols).<sup>11, 34</sup> All of these  
25  
26 295 products have been prohibited by the pesticide review programmes in Europe. Many pesticides with  
27  
28 296 broad activity were used in alternation to control other pests, such as spider mites, leafminers, thrips,  
29  
30 297 caterpillars and whiteflies. Moreover, a number of fungicides, like dinocap, captafol and binapacryl,  
31  
32 298 exhibiting strong side-effects on *A. lycopersici*, were banned for use in Europe.<sup>11</sup> In addition, optimized  
33  
34 299 biological control strategies in tomato greenhouse crops against other key pests such as whiteflies and  
35  
36 300 two-spotted spider mites have led to fewer insecticide and acaricide applications.<sup>8</sup> The altered product  
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38 301 use over the last decade may be one of the reasons for the recent emergence of *A. lycopersici* as a  
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40 302 major tomato pest.

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45  
46 303 In 2010, the available acaricide portfolio was reviewed in light of the EU review program, yielding a list  
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48 304 of compounds which provide good eriophyoid control that would likely remain available.<sup>2</sup>

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50  
51 305 Table 1 presents an updated list of pesticides that are approved in the EU and some are currently used  
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53 306 to control the tomato russet mite. Nowadays, forms of sulphur are commonly used for tomato russet  
54  
55 307 mite control.<sup>35</sup> Although sulphur generally has a good acaricidal activity on Eriophyidae, applications  
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57 308 have proved to be inadequate for limiting *A. lycopersici* infestations and in some areas tolerance might  
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1  
2  
3 309 be evolving.<sup>4, 11</sup> Furthermore, due to undesired sulphur residues and the negative side-effects on  
4  
5 310 natural enemies the search for alternative control methods continues.<sup>36</sup> The macrocyclic lactones  
6  
7 311 abamectin and milbemectin are quite successful against a range of eriophyoids, including *A.*  
8  
9 312 *lycopersici*.<sup>11, 37-40</sup> However, extensive use of abamectin against other mite and insect species has led  
10  
11 313 to the evolution of high levels of resistance, for example in *T. urticae* across Europe.<sup>41</sup> Although  
12  
13 314 acaricide resistance has not been documented for *A. lycopersici*, a shift in susceptibility of eriophyoids  
14  
15 315 against abamectin has already been detected in citrus.<sup>42</sup> The relatively newly developed tetrionic acids  
16  
17 316 spirotetramat and spiromesifen provide good control of eriophyoid mites<sup>2</sup>, including *A. lycopersici*<sup>39</sup>,  
18  
19 317 by inhibiting lipogenesis as competitive inhibitors of acetyl coenzyme A carboxylase.<sup>43</sup> As these tetrionic  
20  
21 318 acids mainly kill juvenile stages and affect fecundity of adult females (at least in spider mites), it is of  
22  
23 319 utmost importance to intervene early in the infestation.<sup>43</sup> For a number of frequently used acaricides  
24  
25 320 such as acequinocyl, bifenazate, etoxazole, and the new class of complex II inhibitors cyenopyrafen,  
26  
27 321 cyflumetofen and pyflubumide, there is insufficient data to judge whether they might be useful in  
28  
29 322 controlling *A. lycopersici*. Under laboratory conditions at the field dose registered for *T. urticae*, we did  
30  
31 323 not observe sufficient activity of bifenazate, acequinocyl and cyflumetofen to potentially control *A.*  
32  
33 324 *lycopersici* (Vervaet, unpublished). Thus, the availability of acaricides with good activity against tomato  
34  
35 325 russet mite is limited.<sup>2</sup> In addition, IPM programs relying on natural enemies for the control of other  
36  
37 326 key tomato greenhouse pests (whiteflies, spider mites, aphids) place further limits on product use.<sup>8, 38</sup>  
38  
39 327 <sup>44</sup> Together this may speed up resistance evolution to the few products used today. This is especially  
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41 328 so for target-site resistance, caused by point mutations in the acaricide target. The population size of  
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43 329 the tomato russet mite can be enormous and the male haploid parthenogenesis allows early selection  
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45 330 of potential recessive resistance genes. This has also led to the rapid spread of resistance in spider  
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47 331 mites.<sup>27</sup> Many cases of resistance are at least partially caused by an increased detoxification, and  
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49 332 genomic analysis has shown that *A. lycopersici* has an extreme deficit in detoxification enzymes.<sup>3</sup>  
50  
51 333 Compared to the generalist herbivore *T. urticae*, dramatic reductions of the classic detoxification gene  
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53 334 families were observed with only 4 glutathione transferases, 8 carboxylcholinesterases and 23 P450  
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3 335 mono-oxygenases present in *A. lycopersici*, versus 31, 69 and 78, respectively, in *T. urticae*.<sup>3</sup> In contrast  
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5 336 to genes encoding “classic” detoxification enzymes, an extreme reduction was not observed in ABC  
6  
7 337 transporter genes and even an expansion was noted within three subfamilies of the large Major  
8  
9 338 Facilitator Superfamily that are involved in membrane-based transport of small molecules.<sup>3</sup> Additional  
10  
11 339 research is needed to assess whether these expansions in *A. lycopersici* are associated with host  
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13  
14 340 specialisation.<sup>3</sup>

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16  
17 341 In conclusion, the genome of *A. lycopersici* displays a remarkable reduction in detoxification potential,  
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19 342 which could impact the evolution of metabolic resistance and offer opportunities for resistance  
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21 343 management. In addition, insight in the genome may help the identification of molecular targets of  
22  
23 344 acaricides, which makes screening for target-site resistance much more feasible.<sup>45</sup> This might in time  
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25 345 allow the development of molecular markers that will inform rational resistance management  
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27 346 programs for the few effective compounds available.<sup>45</sup>

#### 31 347 *4.4 Biological control*

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34 348 *Aculops lycopersici* has only recently become one of the main problems in tomato cultivation.  
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36 349 Consequently, less is known regarding biological control of *A. lycopersici* compared to other key  
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38 350 tomato pests. Nonetheless, a growing number of studies has addressed this question. This resulted in  
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40 351 a long list of candidate natural enemies including a wide range of predatory mites, belonging to the  
41  
42 352 families Iolinidae, Phytoseiidae and Stigmaeidae (Supplementary table 2). In addition, a few  
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44 353 entomopathogenic fungi such as *Metarhizium anisopliae* (Metschinkoff) Sorokin and *Hirsutella*  
45  
46 354 *thompsonii* (Fisher) were reported to influence the survival of *A. lycopersici*.<sup>1, 9</sup> Although several  
47  
48 355 arthropod natural enemies show encouraging results under laboratory conditions, they fail to control  
49  
50 356 the pest in greenhouse tomatoes due in part to the morphological and chemical traits of the  
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52 357 trichomes.<sup>15</sup> Up to date, there is still no biological control agent for *A. lycopersici* commercially  
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55 358 available that shows satisfying results.

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3 359 A natural enemy to be used as an augmentative biological control agent against *A. lycopersici* should  
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5 360 meet several requirements. It should be effective under the environmental conditions conducive to *A.*  
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7 361 *lycopersici* outbreaks and should be able to perform on tomato, which may be cultivar dependent.<sup>38</sup>  
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10 362 An adequate mass production method should be available to enable cost effective commercialization.  
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12 363 Preventive releases may be necessary to prevent the pest from reaching economically damaging  
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14 364 numbers. This requires willingness from growers to make expenditures for a situation that may or may  
15  
16 365 not arise. In addition, supplemental nutrition may be needed to support the establishment of an  
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18 366 augmentatively released predator.<sup>46</sup> The ability to use alternative foods is thus an asset for a candidate  
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20  
21 367 predator.

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23  
24 368 Most attention goes to predatory mites, especially among the Phytoseiidae family (Supplementary  
25  
26 369 table 2).<sup>2</sup> Several phytoseiids reportedly feed on tomato russet mite. In a laboratory setting,  
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28 370 *Amblyseius swirskii* (Athias-Henriot) attacked all developmental stages of *A. lycopersici*.<sup>47, 48</sup> *A. swirskii*  
29  
30 371 developed faster on *A. lycopersici* than on pollen (4.97 and 6.16 days, respectively) and had higher  
31  
32 372 daily oviposition (2 eggs/day and 1.5 eggs/day resp.).<sup>47</sup> Based on the handling time in a functional  
33  
34 373 response experiment, it was estimated that an adult female predator could consume over one hundred  
35  
36 374 tomato russet mites per day (Table 2).<sup>47</sup> In a preliminary greenhouse experiment, the effect of a  
37  
38 375 preventive, simultaneous or curative release of *Amblyseius andersoni* (Chant) on a *A. lycopersici*  
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40 376 population in tomato was investigated.<sup>36</sup> The predator was able to slow down the population  
41  
42 377 development of *A. lycopersici*, but did not provide long-term regulation.<sup>36</sup> Similar findings were  
43  
44 378 reported for *Ambydromalus limonicus* (Garman and McGregor).<sup>15</sup> The latter phytoseiid could  
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46 379 reproduce on a diet of tomato russet mites alone and successfully established on plants that had been  
47  
48 380 previously infested with *A. lycopersici*.<sup>15</sup> Nevertheless, biological control was unsuccessful because the  
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50 381 tomato russet mites escaped predator control by moving up in the plants at a rate faster than their  
51  
52 382 predators.<sup>15</sup> The generalist *Euseius concordis* (Chant) is often found in association with tomato russet  
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54 383 mites or on Solanaceae species in general.<sup>49, 50</sup> A single *E. concordis* female killed on average 1.4 active  
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56 384 individuals of *A. lycopersici* per hour.<sup>49</sup> However, it was noted that the predator could be hindered by

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3 385 the webbing produced by *Tetranychus evansi* (Baker and Pritchard).<sup>49</sup> Based on development and  
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5 386 predation data from laboratory experiments under different conditions of temperature and relative  
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7 387 humidity, it was concluded that *Neoseiulus cucumeris* (Oudemans) could be an effective biological  
8  
9 388 control agent of *A. lycopersici* (Table 2).<sup>51</sup> Another phytoseiid, *Neoseiulus californicus* (McGregor),  
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11 389 successfully developed and reproduced on *A. lycopersici*.<sup>52</sup> Intrinsic growth rates of two *N. californicus*  
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13 390 strains with a different nutritional history (either reared on *Quercus* spp. pollen or on *T. urticae*)  
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15 391 decreased from F1 to F3 generations.<sup>52</sup> Neither strains were adapted to tomato or eriophyoid prey  
16  
17 392 which could explain their dwindling performance.<sup>52</sup> Previous experience with this predator suggests  
18  
19 393 that longer adaptation could improve its efficacy.<sup>52</sup> *Typhlodromus (Anthoseius) recki* (Wainstein) is  
20  
21 394 among the most frequently encountered phytoseiid species on Solanaceae in the West Palearctic  
22  
23 395 region.<sup>50</sup> Preliminary laboratory findings on its biological features and dispersal abilities are  
24  
25 396 encouraging to conduct further trials on plants (Table 2).<sup>53</sup> In the Stigmaeidae family, *Agistemus*  
26  
27 397 *exsertus* (Gonzalez) displayed excellent predation capacity towards *A. lycopersici* in the laboratory, but  
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29 398 again was never tested in the field (Table 2).<sup>54</sup>

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35 399 Furthermore, inconsistencies can occur between studies. For example, in one study<sup>44</sup> the iolinid mite  
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37 400 *Homeopronematus anconai* (Baker) could not develop to the adult stage using *A. lycopersici* as a food  
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39 401 source, whereas other studies<sup>55-57</sup> did suggest its potential as a biological control agent (Table 2).  
40  
41 402 *Pronematus ubiquitous* (McGregor), a member of the same Iolinidae family, was observed to prey on *A.*  
42  
43 403 *lycopersici* both in the laboratory and the field (Table 2).<sup>5, 55</sup> The adult size (~200-300µm) of these two  
44  
45 404 members of the Iolinidae family is only slightly bigger than that of *A. lycopersici*.<sup>55</sup> This enables them  
46  
47 405 to walk in between the trichomes. Their diet includes non-prey food such as pollen and fungi, which  
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49 406 offers potential towards mass rearing and supporting population establishment in the crop when prey  
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51 407 densities are low.<sup>46, 55</sup>

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56 408 Acaricides can affect the survival and performance of biological control agents. Five compounds  
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58 409 (dicofol, abamectin, sulphur, cyhexatin and thuringiensin) tested on *A. lycopersici* proved toxic to *H.*  
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3 410 *anconai*, but selective doses of abamectin showed good potential to control *A. lycopersici* without  
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5 411 reducing *H. anconai* numbers.<sup>35</sup>  
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8 412 Further, beneficial microorganisms like endophytic fungi might have potential to protect tomato plants  
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10 413 from tomato russet mite infestation. The endophytic non-pathogenic fungal strain *Fusarium solani* K  
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12 414 was found to affect both direct and indirect tomato defences against the two spotted spider mite, *T.*  
13  
14 415 *urticae*. The fecundity of the spider mite was negatively affected and the feeding damage was lower  
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16 416 compared to control plants.<sup>58</sup>  
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20 417 To summarize, the morphological and chemical traits of tomato complicate biological control of *A.*  
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22 418 *lycopersici* as they hamper the action of presently commercially available phytoseiid mite predators.  
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24 419 Encouraging results with other predatory mites (e.g. iolinids) in laboratory experiments should be  
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26 420 validated in the greenhouse. The inclusion of low risk, selective pesticides in an IPM programme holds  
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28 421 most promise. Assessing the effect of these compounds on the pest's natural enemies is thus of utmost  
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30 422 importance.  
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## 34 423 5 Conclusions

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38 424 The establishment of an effective IPM strategy against the tomato russet mite is complicated by  
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40 425 knowledge gaps related to the prevention of *A. lycopersici* outbreaks and the interaction between the  
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42 426 pest and its host plant, and by the limited availability of acaricides and a lack of effective biological  
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44 427 control agents. The recently available genome sequence will be of great help in understanding some  
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46 428 of the idiosyncrasies in the biology of this species. This offers opportunities for future control  
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48 429 strategies, for example by identifying the relevant genes and gene families involved in acaricide mode  
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50 430 of action and resistance. The detoxification toolbox of this species seems very limited, which is  
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52 431 potentially related to feeding on nutrient poor epidermis and the capacity to manipulate plant  
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54 432 defences. The genome also offers opportunities to identify effector proteins and peptides used to  
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56 433 avoid the toxic effect of JA-regulated plant defences. Interfering with this process, and improving our  
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3 434 understanding of the tritrophic interactions between the tomato russet mite, its host plant and  
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5 435 promising biocontrol agents, might be the best way forward.  
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For Peer Review

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595 **Table 1** Compounds with acaricidal activity, currently approved in the EU.

Common names	Primary target	MoA group	References
Carbamates: oxamyl, formetanate	Acetylcholinesterase inhibitors	1A	<sup>2</sup>
Pyrethroids : <b>cypermethrin</b> , fluvalinate	Sodium channel modulators	3A	<sup>2, 11, 34</sup>
Avermectins and milbemycins: <b>abamectin</b> , <b>milbemectin</b>	Glutamate-gated chloride channel allosteric modulators	6	<sup>35, 37, 39, 40</sup>
<i>Clofentezine</i> , <b>hexythiazox</b>	Mite growth inhibitors affecting CHS1	10A	<sup>37, 39</sup>
<i>Etoxazole</i>	Mite growth inhibitors affecting CHS1	10B	<sup>2</sup>
Benzoylureas : diflubenzuron	Inhibitors of chitin biosynthesis affecting CHS1	15	<sup>2</sup>
<i>Acequinocyl</i>	Mitochondrial complex III electron transport inhibitors	20B	<sup>2, 40</sup>
<i>Bifenazate</i>	Mitochondrial complex III electron transport inhibitors	20D	<sup>2</sup>
<b>Fenpyroximate</b> , fenazaquin, pyridaben, tebufenpyrad	Mitochondrial complex I electron transport inhibitor	21A	<sup>2, 40</sup>
Tetronic and Tetramic acid derivates : <b>spiromesifen</b> , <b>spirotetramat</b>	Inhibitors of acetyl CoA carboxylase	23	<sup>39, 40</sup>
Cyflumetofen	Mitochondrial complex II electron transport inhibitors	25A	
<b>Azadirachtin</b>	Compounds of unknown or uncertain MoA	UN	<sup>39</sup>
<b>Sulphur</b>	Compounds of unknown or uncertain MoA	UN	<sup>11, 35, 37</sup>

596 Compounds with good activity on *A. lycopersici* are in bold type. Compounds with no or limited activity on eriophyid mites  
597 and/or *A. lycopersici* are italicized. Efficacy classification is based on the doses tested in the corresponding references. MoA  
598 group refers to the classification provided by the Insecticide Resistance Action Committee (IRAC, [www.irac-online.org](http://www.irac-online.org))

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**Table 2** Predatory mites with potential to control *A. lycopersici*, based on the outcome of laboratory experiments on tomato substrates (with the exception of *T. recki* which was tested on *S. nigrum*). For a full overview of predators tested against *A. lycopersici* see supplementary table 2.

Family	Predatory mite species	Climatic conditions	Substrate	Predator stage	<i>A. lycopersici</i> stage	Predation efficacy (no. of prey attacked or % population reduction)	Predation Period	Reference					
<b>Iolinidae</b>	<i>Homeopronematus anconai</i>	25°C, - 25°C, 70% RH	Tomato leaf	1 adult	Deutonymphs	69	24h	<sup>59</sup>					
				1 adult female	Eggs	14	24h	<sup>57</sup>					
						Nymphs	22	24h					
						Adults	8	24h					
		25°C, 80-94% RH	Tomato leaf	2 adult females	Population development	Up to 85% reduction	18 days	<sup>55</sup>					
<b>Iolinidae</b>	<i>Pronematus ubiquitous</i>	25°C, 60% RH	Tomato leaf	1 adult female	Population development	Up to 78% reduction	5 days	(Vervae, unpublished)					
					<b>Phytoseiidae</b>	<i>Amblyseius swirskii</i>	25°C, 70% RH	Tomato leaf	1 adult female	Mobile stages	103 (theoretical)	24h	<sup>47</sup>
					<b>Phytoseiidae</b>	<i>Neoseiulus cucumeris</i>	25°C, 65% RH	Tomato leaf	1 ovipositing female	Mobile stages	152	24h	<sup>51</sup>
		30°C, 60% RH	Tomato leaf	1 ovipositing female	Mobile stages	175	24h	<sup>51</sup>					
		35°C, 55% RH	Tomato leaf	1 ovipositing female	Mobile stages	179	24h	<sup>51</sup>					
<b>Phytoseiidae</b>	<i>Typhlodromus recki</i>	25°C, 70% RH	<i>S. nigrum</i> leaf	1 young gravid female	unspecified	50	24h	<sup>53</sup>					
<b>Stigmaeidae</b>	<i>Agistemus exsertus</i>	30°C, 75% RH	Tomato leaf	1 adult female	Eggs	60	24h	<sup>54</sup>					
				1 adult female	Mobile stages	45	24h	<sup>54</sup>					

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3 603 **Figure 1** The tomato russet mite *Aculops lycopersici* is a major pest of tomato. Panel a. Two individuals  
4 of *A. lycopersici* on a leaf of *S. lycopersicum*. Panel b. Discoloration of the trichomes indicated by white  
5 604 arrows, the first visible sign of a tomato russet mite infestation. Panel c. Tomato russet mites rapidly  
6 605 develop and are able to reach extremely high population densities on tomato. Panel d. Severe damage  
7 606 including russeted fruits on cultivated tomato due to tomato russet mite infestation. Pictures from  
8 607 panels a and b by J. van Arkel (University of Amsterdam).  
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10 609 **Figure 2** A schematic representation of the life stages of the tomato russet mite (*Aculops lycopersici*):  
11 610 egg, protonymph, nymphochrysalis, deutonymph, imagochrysalis and adult. Tomato russet mites are  
12 611 white to orange and they have only two pairs of legs (A) and dorsal half-rings (tergites) (B) which are  
13 612 broader but less abundant than the ventral half-rings (sternites). A pair of long setae (C) and large  
14 613 clinging lobes (D) are located on the posterior end of the body.  
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Figure 1 The tomato russet mite *Aculops lycopersici* is a major pest of tomato. Panel a. Two individuals of *A. lycopersici* on a leaf of *S. lycopersicum*. Panel b. Discoloration of the trichomes indicated by white arrows, the first visible sign of a tomato russet mite infestation. Panel c. Tomato russet mites rapidly develop and are able to reach extremely high population densities on tomato. Panel d. Severe damage including russeted fruits on cultivated tomato due to tomato russet mite infestation. Pictures from panels a and b by J. van Arkel (University of Amsterdam).

179x179mm (150 x 150 DPI)

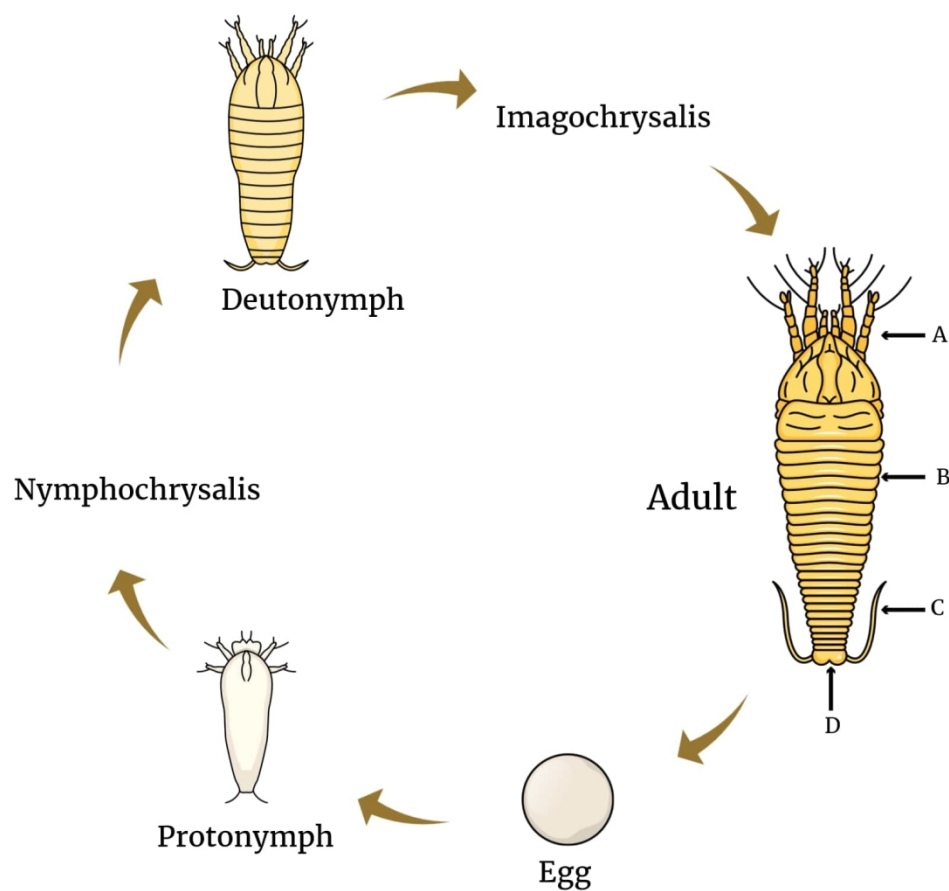


Figure 2 A schematic representation of the life stages of the tomato russet mite (*Aculops lycopersici*): egg, protonymph, nymphochrysalis, deutonymph, imagochrysalis and adult. Tomato russet mites are white to orange and they have only two pairs of legs (A) and dorsal half-rings (tergites) (B) which are broader but less abundant than the ventral half-rings (sternites). A pair of long setae (C) and large clinging lobes (D) are located on the posterior end of the body.

598x598mm (72 x 72 DPI)