



HAL
open science

In search of artificial domatia for predatory mites

Cecile Bresch, Lea Carlesso, Ricardo Suay, Louise van Oudenhove, Suzanne Touzeau, Hicham Fatnassi, Lydia Ottenwaelder, B. Paris, Christine Poncet, Ludovic Mailleret, et al.

► **To cite this version:**

Cecile Bresch, Lea Carlesso, Ricardo Suay, Louise van Oudenhove, Suzanne Touzeau, et al.. In search of artificial domatia for predatory mites. *Biocontrol Science and Technology*, 2019, 29 (2), pp.1-18. 10.1080/09583157.2018.1540030 . hal-01947693

HAL Id: hal-01947693

<https://inria.hal.science/hal-01947693>

Submitted on 7 Jan 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **In search of artificial domatia for predatory mites**

2 Bresch C. ^a, Carlesso L. ^{a,b}, Suay R. ^a, Van Oudenhove L. ^a, Touzeau S. ^{a,c},

3 Fatnassi H. ^a, Ottenwaelder L. ^a, Paris B. ^{a,d}, Poncet C. ^a, Mailleret L. ^{a,c},

4 Messelink G.J. ^e, Parolin P. ^{a,f}

5 ^aUniversité Côte d'Azur, INRA, CNRS, ISA, France

6 ^bRothamsted Research, Department of Sustainable Soils and Grassland Systems, West

7 Common, Harpenden, Hertfordshire AL5 2JQ, United Kingdom

8 ^cUniversité Côte d'Azur, Inria, INRA, CNRS, UPMC Univ Paris 06, BIOCORE, France

9 ^dAstredhor, 44 rue d'Alésia 75682 Paris cedex 14

10 ^eWageningen UR Greenhouse Horticulture; PO Box 20, 2265 ZG Bleiswijk, The

11 Netherlands

12 ^fHumboldt-Universität zu Berlin, Faculty of Life Sciences, Division Urban Plant

13 Ecophysiology, Lentzelallee 55-57, 14195 Berlin, Germany

14

15 Léa Carlesso

16 <https://orcid.org/0000-0002-6527-4112>

17 Ricardo Suay

18 <https://orcid.org/0000-0003-1604-8132>

19 Louise Van Oudenhove

20 <https://orcid.org/0000-0001-5251-7464>

21 Suzanne Touzeau

22 <https://orcid.org/0000-0001-5255-8960>

23 Hicham Fatnassi

24 <https://orcid.org/0000-0002-9729-0504>

25 Christine Poncet

26 <https://orcid.org/0000-0001-5800-5996>

27 Ludovic Mailleret

28 <https://orcid.org/0000-0001-7019-8401>

29 Gerben Messelink

30 <https://orcid.org/0000-0002-5196-1229>

31 Pia Parolin

32 <https://orcid.org/0000-0003-3947-7132>

33

34 Corresponding author: Cécile Bresch

35 <https://orcid.org/0000-0003-4056-0531>

36 E-mail address: cecile.bresch@inra.fr

37

38 Manuscript word count: 7370 words

39 **Abstract**

40 Banker plants can enhance biological pest control by providing both floral
41 resources and appropriate oviposition sites, e.g. through acarodomatia, to
42 predator species. The use of materials mimicking domatia i.e., artificial
43 domatia may be an economically favourable alternative to the use of
44 banker plants bearing domatia. The aim of the present study was to
45 identify materials that are able to host eggs of the *Neoseiulus californicus*
46 predatory mite but not those of the *Tetranychus urticae* pest mite. In a
47 laboratory experiment, the oviposition of predatory and phytophagous
48 mites were compared in Petri dishes containing leaves. The different
49 modalities compared were (i) natural domatia of *Viburnum tinus* or (ii) one
50 of twelve potential artificial domatia materials. The overall oviposition
51 response of predatory mites to all artificial domatia was similar to that of
52 the natural domatia. The oviposition of the *Tetranychus urticae* pest mite
53 did not increase in response to the artificial domatia. Five artificial
54 domatia hosted as many eggs of the predatory mite as observed in the
55 natural domatia. The effect of the physical properties of artificial domatia
56 was also tested and *N. californicus* was found to favour the artificial
57 domatia that had high heat retention capacities for oviposition. Three of
58 these artificial domatia were tested on rose plants in a greenhouse
59 experiment; none of which enhanced the biological control on the plants
60 under these conditions. The present study highlights the difficulty in
61 identifying and using suitable artificial domatia as substitutes to banker
62 plants in biological pest control efforts.

63 **Keywords:** *Neoseiulus californicus*; *Tetranychus urticae*; banker plant; domatia;
64 microhabitat; biological pest control.

65 **Introduction**

66 In integrated pest management, natural enemies such as predatory mites are frequently
67 used to control pests on crops (Gerson & Weintraub, 2012). *Neoseiulus californicus*
68 (MacGregor), (Acari: Phytoseiidae) also known as *N. chilensis* Dosse is a predatory

69 mite that may potentially be used in the biocontrol of the two-spotted spider mite
70 *Tetranychus urticae* Koch (Easterbrook, M. A., Fitzgerald, J. D., & Solomon, M. G.,
71 2001; García-Marí & González-Zamora, 1999). However, low establishment rates and
72 the persistence of natural enemies are sometimes observed in various cropping systems
73 (Messelink et al., 2014). Indeed, in order for a population to become established in a
74 crop without prey or with low prey density, predatory mites need alternative or
75 supplementary food sources, such as pollen or nectar (Kumar et al., 2014; McMurtry &
76 Croft, 1997) and oviposition and shelter sites with trichomes or domatia (Kreiter, S.,
77 Tixier, M. S., Croft, B. A., Auger, P., & Barret, D., 2002; Walter D. E. & O'Dowd J.R.,
78 1996).

79 Acarodomatia are tufts of hair or invaginations under the leaf surface (English-
80 English-Loeb, G.; Andrew, P. N. & Walker, M. A., 2002) usually on the main vein axils
81 (Adar, E., Inbar, M., Gal, S., Gan-Mor, S., & Palevsky, E., 2014). Parolin, P., Bresch,
82 C., Van Oudenhove, L., Errard, & A., Poncet, C. (2013) demonstrated that *N.*
83 *californicus* prefer to lay eggs on plants bearing domatia. They have been shown to
84 influence the distribution, to increase the abundance and to improve the reproduction of
85 predatory mites (Agrawal, A. A., Karban, R., & Colfer, R.G., 2000; Grostal & O'Dowd,
86 1994; Norton, A. P., English-Loeb, G., & Belden, E., 2001; Pemberton & Turner, 1989;
87 Walter, 1996; Walter & O'Dowd, 1992). Furthermore, domatia offer mites protection
88 from predators (Faraji, F., Janssen, A., & Sabelis, M. W., 2002; Norton et al., 2001;
89 Roda, A., Nyrop, J., Dicke, M., & English-Loeb, G., 2000). Domatia presumably also
90 buffer the effects of changes in relative air humidity (RH) (Grostal & O'Dowd, 1994;
91 O'Dowd & Willson, 1989), however, the microclimate benefits of domatia on mite
92 populations has not yet been clarified (Ferreira, J. A. M., Pallini, A., Oliveira, C. L.,
93 Sabelis, M. W., & Janssen, A., 2010; Norton et al., 2001).

94 As many crops cannot provide both floral resources and oviposition sites at all
95 stages of their development, it is challenging to maintain predatory mite populations on
96 crops when prey are scarce (Adar et al., 2014; Messelink et al., 2014). The use of
97 banker plants that provide oviposition sites and floral resources is one option to
98 overcome these problems. Banker plants form ‘a rearing and release system [that is]
99 purposefully added to or established in a crop for pest control in greenhouses or open
100 fields’ (Huang et al., 2011) and they may influence the establishment and reproduction
101 of released natural enemies (Frank, 2010; Huang et al., 2011; Parolin et al., 2013).
102 Crops such as rose plants are not suitable for predatory mite oviposition as they do not
103 bear domatia. Moreover, when rose stems are regularly harvested, a part of the
104 predatory mite population is removed from the greenhouse and this harvest may
105 consequently have a significant impact on pest suppression (Nundloll, S.; Mailleret, L.
106 & Grogard, F., 2008). In a greenhouse study, a rose crop was much less damaged by
107 the *T. urticae* pest when *Viburnum tinus* L. (Adoxaceae), a plant bearing acarodomatia,
108 was present as a banker plant (Parolin et al., 2013). The presence of *V. tinus* resulted in
109 increased numbers of *N. californicus* as well as a decreased population of *T. urticae*.
110 Another greenhouse study showed improved spider mite control by predatory mites
111 when plants containing many domatia (*V. tinus* L. and *Vitis riparia* Michx, Vitaceae)
112 were included amongst the rose plants (Parolin et al., 2015).

113 In the literature, various studies have reported the potential of plants with
114 acarodomatia to develop a significant and sustainable population of predatory mites,
115 inducing the decline of phytophagous mites and increasing crop health without pesticide
116 applications (Grostal & O’Dowd, 1994; Karban, R., English-Loeb, G., Walker, M.A., &
117 Thaler, J., 1995; Parolin et al., 2013; Walter & O’Dowd, 1992). Nevertheless, the use of
118 secondary plants that provide acarodomatia can be time-consuming and costly due to

119 the additional time needed for maintenance and pruning. The use of banker plants also
120 reduces the space available for the crops. These issues hamper the utilization of banker
121 plants by commercial plant producers.

122 Various studies have tried to mimic trichomes and to create artificial domatia on
123 crops. For example, Rozario (1994) observed higher reproductive outputs of the
124 predator *Galendromus occidentalis* Nesbitt (Acari: Phytoseiidae) when tufts of polyester
125 fibres were added to the vein axils of grape varieties with low natural domatia density.
126 Loughner, R., Wentworth, K., Loeb, G., & Nyrop, J. (2010) found that increased habitat
127 complexity on leaves, e.g. trichome density mimicked with cotton fibre patches,
128 reduced adult dispersal of *Typhlodromus pyri* Scheuten (Acari: Phytoseiidae) from
129 plants. Roda et al. (2001) tested the effect of the leaf surface topography on phytoseiid
130 behaviour. *T. pyri* and *Phytoseiulus persimilis* Athias-Henriot (Acari: Phytoseiidae)
131 were shown to spend more time and oviposit more frequently on leaf surfaces with
132 cotton fibres compared to surfaces without these microstructures. Loughner, R., Nyrop,
133 J., Wentworth, K., & Sanderson, J., (2011) showed that the application of both chopped
134 acrylic fibres and pollen on the canopy of plants improved the persistence and egg
135 production of *Amblyseius swirskii* (Athias-Henriot). In a laboratory trial, Kawashima,
136 M., Adachi, I., & Toyama, M. (2006) tested the colonization efficiency of 22 types of
137 artificial microstructures by *N. californicus* adults. Textured urethane foam and
138 polyethylene shading nets were preferentially colonized by adult predatory mites.
139 Kawashima, M., & Jung, C. (2011) studied the effects of sheltered ground habitat on *N.*
140 *californicus* populations in apple orchards and concluded that the presence of urethane
141 foam deposited on the ground may potentially improve the survival of the predatory
142 mite in winter. These findings are consistent with those of Zhao et al. (2014) who
143 demonstrated that natural ground cover had a positive effect on the biological control of

144 *Panonychus citri* McGregor (Acari: Tetranychidae). Adar et al. (2014) tested a solution
145 including pollen application, shelter and oviposition sites for predatory mites by
146 installing pollen coated twines on pepper plants. The combination of an artificial pollen
147 reservoir and oviposition and shelter sites increased the populations of *A. swirskii* and
148 *Euseius scutalis* (Athias-Henriot) (Acari: Phytoseiidae). Pekas and Wäckers (2017)
149 tested the impact of single and combined resources (fibres, pollen, and sugar) on the
150 oviposition of *Euseius stipulatus* (Athias-Henriot) (Acari: Phytoseiidae) on *Citrus*
151 *aurantium* L. (Rutaceae), and showed that the impact of the fibres was significant when
152 combined with pollen. The combination of the three resources resulted in the highest
153 oviposition of the predatory mite. All these studies tend to show that artificial domatia,
154 in particular when combined with a food resource (mostly pollen), favour the
155 development of predatory mites.

156 The main objective of this study was to identify materials that provide suitable
157 oviposition sites, i.e. artificial domatia, for the *N. californicus* predatory mite in a mild
158 climate area in Southern France. To achieve this goal, we conducted laboratory and
159 greenhouse experiments with various materials. Based on the literature, we not only
160 provided predatory mites with materials, but also with food resources to favour their
161 development.

162 More specifically, the following questions were addressed:

163 (1) Do materials act as artificial domatia and promote an overall oviposition of
164 the predatory mite similar to natural domatia in laboratory conditions? If so, which
165 materials are most suitable?

166 (2) Do these materials also increase the number of pest mites in the same
167 laboratory conditions?

168 (3) Under greenhouse conditions, does the presence of artificial domatia on rose
169 plants enhance the biological control of the pest mite by the predatory mite. If so, which
170 types of artificial domatia are most effective?

171 **Materials and methods**

172 We selected twelve different materials and assessed the oviposition of *N. californicus*
173 predatory mites and *T. urticae* pest mites on the different materials in experimental units
174 containing both predator and pest individuals, as well as the natural or artificial domatia
175 in laboratory experiments. Three of these materials were subsequently tested on rose
176 plants in a greenhouse experiment. The experiments were conducted in spring 2014 in a
177 laboratory setting and in summer 2015 in a greenhouse at the French National Institute
178 for Agricultural Research (INRA) Sophia Antipolis site in Southern France (43°36'44.9"
179 N latitude, 07°04'40.4" E longitude, 125 m altitude).

180 ***Selection of artificial domatia***

181 Materials were selected based on (i) characteristics that were similar to acarodomatia,
182 such as density, thickness, fibre diameter, and morphology; and (ii) structural
183 differences from natural domatia. We also considered that ideal materials should be
184 affordable; easy to remove; long-lasting; resistant to water, solar radiation and fungi;
185 and be easy to handle and maintain.

186 We assessed the structural characteristics (density, thickness, fibre diameter,
187 morphology) and trichome size of *V. tinus* acarodomatia using a binocular magnifier
188 (Fig. 1a). We then screened commercial and suitable materials to find those with similar
189 characteristics, with a preference for woven fibres instead of finely-chopped fibres for
190 easier manipulation, installation and removability from a crop system. In addition, we

191 looked for materials that offered different characteristics related to RH absorbency, heat
192 retention, morphology, thickness, fibre density and fibre diameter. These criteria led to
193 the selection of twelve artificial materials that were purchased from the TOTO TISSUS
194 outlet in Cannes, France: acrylic, acetate, linen, silk, viscose, wool and two types of
195 polyamide, polyester and cotton (Table 1).

196 RH absorbency ability can be defined as the capacity of fibres to reach moisture
197 balance. The heat retention capacity of fibres refers to their thermal-retaining properties
198 (Ishimaru, 2016). RH absorbency and heat retention capacities were obtained from the
199 literature (see Table 1). Materials were distinguished according to two types of
200 morphology: tightly woven fibres and more loosely woven fibres (Fig. 1b, 1c), with the
201 latter being more similar to acarodomatia (Fig. 1a). Thickness and fibre diameter were
202 measured using a binocular magnifier. Following Roda et al. (2001), the density of each
203 material (i.e., each artificial domatium) was measured by placing ten 2.5 mm lines
204 lengthwise along the grain of the fabric and recording how many times the fibres
205 crossed the 2.5 mm line.

206 Due to cost and technical constraints, all twelve artificial materials could not be
207 tested in the greenhouse experiment. Among the artificial domatia on which oviposition
208 rates were as high as natural domatia, we chose the two materials that were known to be
209 both resistant to abrasion and were at least 0.5 mm thick: wool and polyamide 1.
210 Organic wool, a non-woven material that did not receive any chemical treatments (in
211 contrast to the two other materials), was also included in the greenhouse experiment.

212

213 - INSERT Table 1 -

214

215 - INSERT Figure 1-a.b.c -

217 **Laboratory experiment**

218 The plant species used in the experiment were *Rosa Emera*®, *Decorosier*® and *V. tinus*
219 grown at INRA Sophia Antipolis, which were pest and pesticide free. The *T. urticae* pest
220 mites used as prey for predatory mites were reared on bean plants in growth chambers
221 (23 °C, 70% RH, 16–8 h D/N photoperiod). The Spical® commercial strain of *N.*
222 *californicus* predatory mites (KOPPERT, B.V. The Netherlands) was released onto the
223 experimental arenas within two days of their delivery. The sex ratio of *N. californicus*
224 was ~3:2 females:males (KOPPERT). Both mite species showed a range of instars.
225 *Typha angustifolia* L. pollen (Nutrimite™, BIOBEST Group, Westerlo, Belgium) was
226 supplied *ad libitum* as alternative food for the predator population (Marafeli et al.,
227 2014).

228 Experimental units were 14 cm diameter Petri dishes containing both the
229 predator and the pest, as well as the natural or artificial domatia, pollen and leaves (Fig.
230 2a). On day 1, moistened filter paper and a 12 cm long rose plant leaf (on top of the
231 filter paper) were placed in each Petri dish. In addition, either a 4 mm² piece of one type
232 of artificial domatia or a 7 cm *V. tinus* leaf providing 4 mm² natural domatia was
233 introduced in the experimental unit. The 4 mm² area of natural domatia was determined
234 from photographs using ImageJ software. On day 2, each experimental unit was
235 inoculated with bean leaves infested with *T. urticae*. Each Petri dish received 140 units
236 of prey (Castagnoli, M.; Simoni, S. & Nachman, Gö, 2001); a unit of prey was defined
237 as either one nymph or two eggs of *T. urticae*. On day 3, 40 *N. californicus* adults and
238 100 mg of pollen were added to each Petri dish. Pollen was placed next to the filter
239 paper to avoid influencing the oviposition inside artificial or natural domatia. Petri

240 dishes were sealed with Parafilm and randomly placed on tables in a laboratory. The
241 experiment included ten repetitions for each modality, artificial and natural domatia,
242 which resulted in a total of 130 Petri dishes.

243

244 - INSERT Figure 2-a.b -

245

246 The laboratory was maintained under controlled climatic conditions with a 16 h
247 D/N photoperiod, to produce stable microclimatic conditions in the Petri dishes.
248 Temperature and RH were measured simultaneously every second and averaged every 5
249 minutes throughout the 8-day experiment, in control Petri dishes (without mites) to
250 confirm the microclimatic homogeneity. Average conditions inside the Petri dishes were
251 23.34 °C [\pm 0.88 standard deviation (SD)] and 91.81 % RH (\pm 4.52 SD).

252 On day 8, all predatory and phytophagous mite eggs were counted. We
253 distinguished two locations for the eggs in the Petri dishes: (i) 'inside', defined as
254 within the natural or artificial domatia; and (ii) 'outside', defined as anywhere else on
255 the Petri dish. The locations of motile stages, i.e. nymphs and adults, were not recorded.

256 ***Greenhouse experiment***

257 The experiment was performed in two compartments of a glass greenhouse. The
258 biological control effect of the three artificial domatia was tested on rose plants. As
259 described for the laboratory experiment, the same Spical® commercial strain and the
260 alternative food Nutrimite™ were used. The rose plants *Rosa rekord* 'Pink Emely'® =
261 *Rosa kordes*® 'Korselary' were planted in 1.3 L pots filled with Agrilit 3® perlite and
262 Humomot compost, in a 1:2 ratio, at 6.5 pH and with 1.08 mS/cm electrical
263 conductivity (EC). Before the beginning of the experiment, the rose plants were

264 acclimated in the greenhouse for one week at 21 °C (± 3.9 °C SD) and 66 % RH (± 13
265 % SD). Planted pots were placed in a balanced design on tables in the greenhouse,
266 without touching each other. A strip of polyamide, wool, or organic wool (16.0×0.5
267 cm) was installed on each rose plant in direct contact with the leaves from the top to the
268 bottom of the rose plants (Fig. 2b). Plants without strips were also included as controls.
269 The experiment included 16 repetitions for each treatment except for polyamide (i.e. 15
270 repetitions).

271 To prevent mite dispersal between plants, each pot was placed on a Petri dish in a tray
272 filled with water reaching up to 5 mm below the base of the 10 cm diameter pots. The
273 mean temperature of the greenhouse was 24 °C (± 3.7 °C SD) and mean RH was 72 %
274 (± 12 % SD) throughout the experiment.

275 On day 1, each rose plant was inoculated with adults ($n = 10$) and nymphs ($n =$
276 10) of the *T. urticae* pest mite using a thin brush. On day 6, each plant was inoculated
277 with *N. californicus* adults ($n = 10$).

278 On day 33, eggs, nymphs and adults of both mite species were counted under the
279 stereomicroscope (magnifying power $\times 20$) and their locations were recorded. In this
280 study, “on” refers to the location being on and under the leaves of the rose plant and
281 “inside” refers to the location being on and under the artificial domatia strip.

282 ***Statistical analyses***

283 All analyses were conducted using R software (R Core Team 2014).

284 *Laboratory experiment*

285 We used the following 3-step analysis:

286 (i) The effect of the artificial domatia was determined based on the total
287 oviposition by *N. californicus*. The response variable was the total number of
288 eggs, laid both inside + outside, and the factor was the treatment, with levels
289 corresponding to the twelve artificial domatia and natural domatia. A quasi-
290 Poisson generalized linear model (GLM) was used for the *N. californicus*
291 analyses and a non-parametric Kruskal-Wallis test was used for the *T.*
292 *urticae* analyses. The latter test was chosen because parametric models did
293 not provide adequate fits.

294 A Wilcoxon signed rank test was conducted to determine whether *N.*
295 *californicus* preferred to lay eggs inside or outside. For this test, we
296 calculated the density of eggs by dividing the number of eggs laid inside by
297 0.04 cm^2 , i.e. the natural or artificial domatia area, and the number of eggs
298 laid outside by 402.93 cm^2 , which is the area of the Petri dish and the leaves
299 minus the natural/artificial domatia.

300 (ii) Comparisons were then made between the number of eggs laid inside the
301 artificial and natural domatia using a negative binomial generalized linear
302 model for *N. californicus*. Two treatments (i.e. cotton 2, polyamide 2)
303 yielded no eggs inside and were, therefore, removed from the analyses. The
304 natural domatia was used as the reference level for the treatment factor.

305 (iii) The effect of the physical properties of artificial domatia on the number
306 of *N. californicus* eggs laid inside the artificial domatia was tested on the
307 remaining artificial domatia. Properties that had no significant relationship
308 (Pearson's correlation) with the number of eggs laid inside were excluded.
309 Generalized linear models could not be fit to the data, due to the number of

310 factors and zeros values, therefore, Hurdle negative binomial models were
311 used. Different models that combined the remaining factors with and without
312 their two-way interactions were tested. The best model was selected based
313 on Akaike's information criterion. The AIC is an estimator of the relative
314 quality of statistical models for a given set of data: the best model is the one
315 with the lowest AIC (Akaike, 1973).

316 *Greenhouse experiment*

317 The effect of the artificial domatia strips was tested on the populations of predatory and
318 pest mites. Given that very few eggs were laid (see Results section), we considered the
319 total number of individuals: eggs + nymphs + adults, as the response variable per plant
320 for each population. Two independent factors were considered: the artificial domatia
321 strip treatment (polyamide, wool, organic wool, control) and the greenhouse
322 compartments. A negative binomial generalized linear model was fitted to data. The full
323 model, which included both factors and their two-way interactions, and a backward
324 selection were used.

325 **Results**

326 *Laboratory experiment*

327 *Predatory mites*

328 No significant difference in the total number of eggs (inside + outside) laid by *N.*
329 *californicus* was observed among the artificial and natural domatia in the experimental
330 units (GLM: $df = 12$, $p = 0.59$; Fig. 3a). A mean of 13 eggs per replicate was laid by *N.*
331 *californicus* (± 13 SD).

332

333 - INSERT Figure 3-a.b -

334

335 *Neoseiulus californicus* showed an oviposition preference inside natural domatia
336 rather than outside ($V = 55$, $p < 0.001$). A mean of $3.6 (\pm 2.7 \text{ SD})$ eggs per Petri dish
337 was laid inside natural domatia. *Neoseiulus californicus* egg density was 100 times
338 higher inside natural domatia than outside. This level was similar for wool, viscose, silk,
339 polyamide 1 and polyester 2 (Table 2, Fig. 4). The remaining artificial domatia, i.e.
340 acetate, acrylic, cotton 1, linen and polyester 1, hosted significantly fewer eggs than the
341 natural domatia (Table 2, Fig. 4).

342

343 - INSERT Figure 4 -

344

345 - INSERT Table 2 -

346

347 *Phytophagous mites*

348 No significant difference in the total number of eggs (inside + outside) laid by *T. urticae*
349 was observed between the artificial and natural domatia of *V. tinus* (Kruskal-Wallis test:
350 $\chi^2(12) = 18.76$, $p = 0.09$; Fig. 3b).

351 No eggs were laid by *T. urticae* inside the natural or the artificial domatia, and
352 thus no further analyses were conducted. Pest mites only oviposited outside the artificial
353 and natural domatia.

354 *Physical properties of the artificial domatia*

355 No significant correlations were found between the number of eggs laid by *N.*

356 *californicus* inside the artificial domatia and the three physical properties of the artificial
357 domatia: fibre density (correlation coefficient $r = -0.10$, $p = 0.33$), fibre diameter ($r =$
358 0.07 , $p = 0.47$) and thickness ($r = 0.05$, $p = 0.64$).

359 These three factors were excluded from the analysis and Hurdle models were
360 built based on the three remaining factors, i.e. RH absorbency, morphology and heat
361 retention. Different models that combined the remaining factors with and without their
362 two-way interactions were tested.

363 The Hurdle model using the heat retention factor produced the lowest AIC (AIC
364 = 268.5196). There were two other Hurdle models with slightly higher AIC. Both
365 included the heat retention factor and either RH or breath, so we chose the simplest
366 model with the heat retention factor only. The oviposition probability of *N. californicus*
367 was significantly higher inside artificial domatia with a high heat retention capacity
368 (Zero model: $p = 7.88e-05$).

369 According to these findings, the most favourable artificial domatia in terms of
370 oviposition probability had high heat retention.

371 ***Greenhouse experiment***

372 The mean total population of eggs, nymphs and adults per rose plant was: 12 (± 23 SD)
373 *N. californicus* and 15 (± 63 SD) *T. urticae*. The oviposition mean inside polyamide was
374 0.53 (SD 0.50) for *N. californicus* and 0.47 (SD 0.62) for *T. urticae*.

375 Fitting the data to the negative binomial generalized linear model raised the
376 following issues: residuals were not acceptable for *N. californicus* and the model did not
377 converge for *T. urticae*. Two outliers (two replicates) that could have been due to
378 inoculation errors were removed: one was for the polyamide treatment ($n = 50$ *N.*
379 *californicus*, $n = 326$ *T. urticae*) and one for organic wool treatment ($n = 10$ *N.*

380 *californicus*, n = 382 *T. urticae*). Data excluding these replicates were used for
381 subsequent analyses.

382 Without outliers, the mean total population was, per rose plant, 11 (\pm 23 SD)
383 individuals for *N. californicus* (Fig. 5a) and 4 (\pm 7 SD) individuals for *T. urticae* (Fig.
384 5b).

385 The analysis for *N. californicus* data showed that neither the treatment nor the
386 compartment factor had a significant effect on the population. The treatment factor was
387 the only factor that had a significant effect on the *T. urticae* population (df = 3, residual
388 deviation = 57.85, p = 0.02; Fig. 5b).

389

390 - INSERT Figure 5-a.b -

391

392 The pest mite population per plant was significantly higher for the polyamide
393 treatment than for the wool or the control treatment (respectively df = 1, Z = -2.49, p =
394 0.01; df = 1, Z = -2.79, p = 0.005). The pest population on the plants was composed of
395 41% eggs and 59% mobile stages for the polyamide treatment, which compares with the
396 48% eggs and 52% mobile stages for all treatments.

397 In conclusion, no artificial domatia strip increased the predator mite population
398 in this greenhouse experiment. In contrast, an undesired side effect was observed, i.e.
399 polyamide promoted an increase in the pest mite population.

400 **Discussion**

401 In the laboratory experiment, the total oviposition of *N. californicus*, i.e. inside +
402 outside, was the same on all artificial domatia as was on the natural domatia. However,
403 *N. californicus* clearly preferred to oviposit inside the natural domatia and five artificial

404 domatia (wool, silk, polyamide, viscose and polyester). This preference occurred in
405 spite of favourable environmental factors outside the artificial and natural domatia, i.e.
406 absence of predators, high temperature and high RH. By providing mites with a narrow
407 physical place to be in close contact (Gerson & Weintraub, 2012), the artificial domatia
408 appeared to favour the thigmotaxis behaviour of the predatory mites. Among the five
409 artificial domatia found to be as attractive as natural domatia in this study, two of the
410 same materials had also previously been tested, i.e. wool by Kawashima et al. (2006)
411 and viscose (rayon) by Adar et al. (2014).

412 Kawashima et al. (2006) found the highest number of *N. californicus* adults
413 inside wool in a choice test among eight artificial microstructures in a laboratory setting.
414 Adar et al. (2014) observed that a twine made of rayon (80%) and jute fibres (20%) had
415 a positive effect on *A. swirskii* and *E. scutalis* populations, with the majority of
416 predatory mite eggs laid on the thin rayon fibres rather than on the thick jute.

417 No *T. urticae* eggs were laid either inside artificial or natural domatia in the
418 laboratory experiment. Moreover, none of the artificial domatia favoured the pest mite
419 total oviposition, i.e. inside + outside. A likely explanation is that spider mites do not
420 need domatia to protect their eggs because they make their own webbing. However,
421 whether this webbing also protects eggs against desiccation at low RH levels is not
422 known.

423 In the laboratory experiment, the probability of *N. californicus* oviposition
424 inside artificial domatia was best explained by a high capacity for heat retention of the
425 materials, although it was not a perfect predictor. Among the five artificial domatia that
426 were found to be as attractive as natural domatia in our study, wool, silk, viscose and
427 polyamide 1 had this feature. Polyester 2 was the only artificial domatia as attractive as
428 natural domatia that had a low heat retention capacity. This result suggests that other

429 factors, other than the heat retention capacity of artificial domatia, may have been
430 involved in oviposition site selection. *N. californicus* is a natural enemy found in both
431 humid and arid climate zones (Castagnoli & Simoni, 2003) and is known to thrive at
432 high temperatures (Castagnoli, M., & Simoni, S., 1991). Therefore, an artificial
433 domatium characterized by a high heat retention capacity can be beneficial to *N.*
434 *californicus* by providing warmer temperatures and a buffer to temperature fluctuations.
435 A similar test with other predatory mite species may produce different results.
436 Furthermore, different life stages of the same mite species may possibly respond
437 differently to different climatic conditions.

438 The other tested physical properties of the artificial domatia were unable to
439 explain our data. Indeed, RH absorbency, domatia mimicking morphology (or
440 otherwise), fibre density, fibre diameter, and material thickness did not discriminate
441 favourable artificial domatia.

442 RH absorbency capacity of artificial domatia had no impact on oviposition
443 inside, which may be explained by the high level of RH maintained in the laboratory
444 experiment. In addition, other studies have reported contrasting results regarding the
445 microclimate benefits of domatia on mite populations (Ferreira et al., 2010; Grostal &
446 O'Dowd, 1994; Norton et al., 2001; Rowles & O'Dowd, 2009; Walter, 1996).

447 In the laboratory experiment, the morphology of artificial domatia had no effect
448 on the number of eggs laid inside by *N. californicus*. The predatory mite did not favour
449 a specific morphology type whether it was similar to or different from the natural
450 domatia. Our findings are not corroborated by Nishida, S., Naiki, A., & Nishida, T.
451 (2005) who demonstrated that domatia may be more or less adapted depending on the
452 ecological contexts. For example, different mite species inhabit domatia with different
453 opening sizes.

454 In our study, fibre density did not correlate with the number of eggs laid inside
455 artificial domatia by the predatory mite. However, Roda et al. (2001) showed that *T.*
456 *pyri* preferred to live and lay eggs in the highest density of available cotton fibres. In
457 addition, an experiment on bean seedlings showed that a higher cotton fibre density was
458 associated with a higher number of *T. pyri* (Loughner et al., 2010).

459 Similarly, in the laboratory experiment, thickness of artificial domatia had no
460 impact on the number of eggs laid inside artificial domatia. However, this factor might
461 play an important role in greenhouse or field conditions, particularly in conjunction with
462 artificial domatia density. Indeed, phytoseiids are known to prefer micro-environmental
463 conditions in the inner canopy leaves rather than in the outer ones (Allen & Syvertsen,
464 1981). Moreover, Tachi and Osakabe (2012) reported that *N. californicus* actively
465 avoided both solar UV and visible light radiation. Therefore, thicker and more dense
466 materials are expected to provide better protection to all life stages of *N. californicus*.

467 Most of the physical and morphological properties of the artificial domatia
468 tested in the laboratory experiment could not explain our data. However, even if several
469 studies have demonstrated the role of these factors on the development of Phytoseiidae
470 populations, the results may be dependent on the mite species studied. The present study
471 is the first to test the effect of artificial domatia on *N. californicus* oviposition.

472 In addition to the major physical and morphological factors tested in this study,
473 other factors such as volatile components, fibre microstructure, UV absorbency
474 (possibly linked to material thickness) may have an impact on *N. californicus*
475 oviposition and interact with heat retention, the only significant factor identified in this
476 study.

477 In the greenhouse experiment, the presence of artificial domatia strips on the
478 rose plants had no effect on the total number of *N. californicus* individuals. Even wool,

479 characterized by the favourable physical property identified in the laboratory
480 experiment, i.e. a high capacity to retain heat, did not boost the predatory mite
481 population. Four explanations are possible. First, in comparison to the stable laboratory
482 conditions, the fluctuating climatic conditions in the greenhouse were probably
483 constraining. Predatory mites probably preferred the climatic conditions at the boundary
484 layer of the plants rather than the wool. Indeed, the boundary layer is a thin zone of air
485 that surrounds each leaf. Its thickness influences how quickly gasses and energy are
486 exchanged between the leaf and the surrounding air (Runkle, 2016). Boundary layers
487 are known to improve biological control efficiency, in particular by providing more
488 stable RH conditions (Boulard et al., 2004; Fatnassi et al., 2014). Second, Loughner et
489 al. (2011) demonstrated that the way materials are applied to the plant strongly
490 influences their effectiveness. Although Adar et al. (2014) successfully used a
491 combination of uncoated 15 cm twines and pollen on the leaves of pepper plants for *A.*
492 *swirskii*, Loughner et al. (2011) sifted finely-chopped acrylic fibres on impatiens leaves.
493 The material strips are practical but may not be adequate as oviposition shelters. Third,
494 the inability of the artificial domatia strips to adequately mimic the spatial distribution
495 of leaf domatia on the rose plants. Situngu, S., & Barker, N. (2017) showed that mites
496 were more abundant and diverse on lower and internal parts of the canopy, characterized
497 by old leaves bearing more domatia, for two tree species [*Ocotea bullata* (Lauraceae)
498 and *Gardenia thunbergia* (Rubiaceae)]. This suggests that the distribution of
499 microhabitats is a crucial factor for the population dynamics of predatory mites.
500 Optimizing the spatial distribution and the application method for artificial domatia in
501 cropping systems may improve the establishment of predatory mites. Lastly, providing
502 pollen or another resource may also interact positively with the presence of artificial

503 domatia and improve the predatory mite establishment, as recently evidenced by Pekas
504 and Wäckers (2017).

505 *Neoseiulus californicus* did not lay any eggs inside the organic wool. The lanolin
506 grease present in the organic wool is secreted by the sebaceous glands of wool-bearing
507 animals (López–Mesas, M., Carrillo, F., Gutiérrez, M. C., & Crespio, M., 2007) and it
508 produces a specific odour (Lisovac & Shooter, 2003) which may repel arthropods.

509 In contrast with the laboratory experiment, the presence of polyamide strips on
510 rose plants greatly promoted the population of *T. urticae*, although polyamide also
511 favoured *N. californicus* in the greenhouse experiment (Fig. 5a). Polyamide 1 hosted a
512 significant number of predatory mite eggs in the Petri dishes, which were characterised
513 by stable and saturated RH conditions. In contrast, this artificial domatium did not
514 perform as well under the fluctuating RH conditions of the greenhouse experiment. It
515 could be due to the low RH absorbency capacity of the material.

516 **Conclusions**

517 The aim of this study was to identify artificial microhabitats to host *N. californicus* eggs
518 as effectively as natural domatia do. The results of the laboratory experiment supported
519 our hypotheses that artificial domatia, such as fabrics, could constitute artificial
520 oviposition sites for the predatory mite, but would not improve the reproduction of the
521 *T. urticae* phytophagous mite. Five of the twelve investigated artificial domatia were
522 particularly attractive for *N. californicus* oviposition. It was found that *N. californicus*
523 favoured artificial domatia with a high heat retention capacity for oviposition, such as
524 those composed of wool. However, testing the most efficient artificial domatia on whole
525 plants under greenhouse conditions produced different results. None of the tested
526 materials enhanced biocontrol by *N. californicus* and one (polyamide) even favoured the
527 *T. urticae* pest population.

528 Improving predatory mite habitat suitability is essential to sustainably improve
529 their establishment in a cropping system. Our findings highlighted the difficulty in
530 identifying selection criteria for artificial domatia that were likely to ensure a
531 sustainable establishment of the *N. californicus* predatory mite. They also underlined
532 the difficulty in finding a trade-off between an efficient, yet practical way for growers to
533 apply the artificial domatia in greenhouse conditions. This study further demonstrated
534 that artificial domatia should be specifically selected according to the life history and
535 behaviour of each predatory mite species.

536

537 **Acknowledgements**

538 We are grateful to Besma Khelil and Lionel Salvy for their assistance during the experiment.
539 The study was conducted with partial funding from the European Union Seventh Framework

540 Program (FP7/2007-2013) under grant agreement n° 265865 (project PURE), from the
541 European INTERREG ALCOTRA Programme (2007-2013) under the grant agreements n° 178
542 (FIORIBIO 2 project) and n° 264 (ECOLEGO project), and from DEPHY EXPE ECOPHYTO
543 (OTELHO Project). This research has been integrated in the framework program of UMT
544 FioriMed since 2015. The manuscript was proofread by a professional English Language
545 Editing service.

546

547 **Conflicts of Interest**

548 The authors declare that there are no conflicts of interest.

549 **References**

- 550 Hirotugu Akaike. (1973). Information theory and an extension of the maximum
551 likelihood principle. *Proceedings Second International Symposium on*
552 *Information Theory*, pp. 267-281
- 553 Allen J, Syvertsen JP (1981). The world of the citrus rust mite: a microclimate
554 prediction problem. In Kommedahl, T. (Eds.). *Proceedings of symposia: IX*
555 *International Congress of Plant Protection*, Washington, 1, (pp. 138–140).
- 556 Adar, E., Inbar, M., Gal, S., Gan–Mor, S., & Palevsky, E. (2014). Pollen on–twine for
557 food provisioning and oviposition of predatory mites in protected crops.
558 *BioControl*, 59, 307–317.
- 559 Agrawal, A. A., Karban, R., & Colfer, R.G. (2000). How leaf domatia and induced plant
560 resistance affect herbivores, natural enemies and plant performance. *Oikos*, 89,
561 70–80.
- 562 Boulard, T., Fatnassi, H., Roy, J.C., Lagier, J., Fargues, J., Smits, N., ..., & Jeannequin,
563 B. (2004). Effect of greenhouse ventilation on humidity of inside air and in leaf
564 boundary-layer. *Agricultural and Forest Meteorology*, 125, 225–239.
- 565 Castagnoli, M., & Simoni, S. (2003). *Neoseiulus californicus* (McGregor) (Acari,
566 Phytoseiidae): survey of biological and behavioural traits of a versatile predator.
567 *Redia*, 86, 1–12
- 568 Castagnoli, M.; Simoni, S. & Nachman, Gö. (2001). Short–term changes in consumption
569 and oviposition rates of *Neoseiulus californicus* strains (Acari: Phytoseiidae)
570 after a diet shift. *Experimental & Applied Acarology*, 25, 969–983.

- 571 Castagnoli, M., & Simoni, S. (1991). Influence of temperature on population increase of
572 amblyseius californicus McGregor acari phytoseiidae. *Redia*, 74, 621–640
573
- 574 Easterbrook, M. A., Fitzgerald, J. D., & Solomon, M. G. (2001). Biological control of
575 strawberry tarsonemid mite *Phytonemus pallidus* and two-spotted spider mite
576 *Tetranychus urticae* on strawberry in the UK using species of *Neoseiulus*
577 (*Amblyseius*) (*Acari: phytoseiidae*). *Experimental & Applied Acarology*, 25, 25–
578 36.
- 579 English-Loeb, G.; Andrew, P. N. & Walker, M. A. (2002). Behavioral and population
580 consequences of acarodomatia in grapes on phytoseiid mites (*Mesostigmata*)
581 and implications for plant breeding. *Entomologia Experimentalis Et Applicata*,
582 104, 307–319.
- 583 Faraji, F., Janssen, A., & Sabelis, M. W. (2002). Oviposition patterns in a predatory mite
584 reduce the risk of egg predation caused by prey. *Ecological Entomology*, 27,
585 660–664.
- 586 Fatnassi, H., Boulard, T., Poncet, C., Bartzanas, T., Katsoulas, N., Kacira, M. (2014).
587 CFD modeling of microclimate in the leaf boundary layer. *Ecological Niche of*
588 *Pests. Acta Hort (ISHS)*, 1037, 1027–1034.
- 589 Ferreira, J. A. M., Pallini, A., Oliveira, C. L., Sabelis, M. W., & Janssen, A. (2010). Leaf
590 domatia do not affect population dynamics of the predatory mite *Iphiseiodes*
591 *zuluagai*. *Journal of Basic and Applied Ecology*, 11, 144–152.
- 592 Frank, S. D. (2010). Biological control of arthropod pests using banker plant systems:
593 past progress and future directions. *Biological Control*, 52(1): 8–16.
- 594 García-Marí, F., & González-Zamora, J. E. (1999). Biological control of *Tetranychus*
595 *urticae* (*Acari: Tetranychidae*) with naturally occurring predators in strawberry
596 plantings in Valencia, Spain. *Experimental & Applied Acarology*, 23, 487–495
- 597 Gerson, U., & Weintraub, P. (2012). Mites (*Acari*) as a factor in greenhouse
598 management. *Annual Review of Entomology*, 57, 229–47.
599
- 600 Grostal, P., & O’Dowd, D. J. (1994). Plants, mites and mutualism – leaf domatia and the
601 abundance and reproduction of mites on *Viburnum tinus* (*Caprifoliaceae*).
602 *Oecologia*, 97, 308–315.
- 603 Huang, N., Enkegaard, A., Osborne, L. S., Ramakers, P. M. J., Messelink, G.J.,
604 Pijnakker, J., & Murphy, G. (2011). The banker plant method in biological
605 control. *Critical Reviews in Plant Sciences*, 30, 259–278.
606

607 Ishimaru S. (2016). Heat–Controllable Man–Made Fibers. In: The Society of Fiber
608 Science and Techno J. (Ed.), *High–Performance and Specialty Fibers* (pp. 261–
609 269). Tokyo: Springer.

610 Karban, R., English-Loeb, G., Walker, M.A., & Thaler, J. (1995). Abundance of
611 Phytoseiid mites on *Vitis* species: effects of leaf hairs, domatia, prey abundance
612 and plant phylogeny. *Experimental and Applied Acarology*, 19, 189–197.

613 Kawashima, M., Adachi, I., & Toyama, M. (2006). Artificial microstructure encouraging
614 the colonization of the predacious mite, *Neoseiulus californicus* (McGregor)
615 (Acari: Phytoseiidae). *Applied Entomology and Zoology*, 41, 633–639.

616 Kawashima, M., & Jung, C. (2011). Effects of sheltered ground habitats on the
617 overwintering potential of the predacious mite *Neoseiulus californicus* (Acari:
618 Phytoseiidae) in apple orchards on mainland Korea. *Experimental and Applied*
619 *Acarology*, 55, 375–88.

620 (2002). Plants and leaf characteristics influencing the predaceous mite *Kampimodromus*
621 *aberrans* (Acari: Phytoseiidae) in habitats surrounding vineyards. *Environmental*
622 *Entomology*, 31, 648–660.

623 Kumar, V., Wekesa, V. W., Avery, P. B., Powell, C. A.; McKenzie, C. L., & Osborne, L. S.
624 (2014). Effect of pollens of various ornamental pepper cultivars on the
625 development and reproduction of *Amblyseius swirskii* (Acari: Phytoseiidae).
626 *Florida Entomologist*, 97, 367–373.

627 Lisovac, A., & Shooter, D. (2003). Volatiles from sheep wool and the modification of
628 wool odour. *Small Ruminant Research*, 49, 115–124.

629 López–Mesas, M., Carrillo, F., Gutiérrez, M. C., & Crespio, M. (2007). Alternative
630 methods for the wool wax extraction from wool scouring wastes. *Grasas y*
631 *aceites*, 58, 402–407.

632 Loughner, R., Wentworth, K., Loeb, G., & Nyrop, J. (2010). Leaf trichomes influence
633 predatory mite densities through dispersal behavior. *Entomologia*
634 *Experimentalis Et Applicata*, 134, 78–88.

635 Loughner, R., Nyrop, J., Wentworth, K., & Sanderson, J. 2011. Towards enhancing
636 biocontrol of thrips: effects of supplemental pollen and fibres on foliar
637 abundance of *Amblyseius swirskii*. *IOBC/WPRS Bulletin*, 68, 105–109.

638 Mac Murtry, J. & Croft, B. (1997). Life–styles of Phytoseiid mites and their roles in
639 biological control. *Annual Review of Entomology*, 42, 291–321.

640 Messelink, G. J., Bennison, J., Alomar, O., Ingegno, B.L., Tavella, L., Shipp, L., ..., &
641 Wäckers, F.L. (2014). Approaches to conserving natural enemy populations in
642 greenhouse crops: current methods and future prospects. *Biological Control*, 59,
643 377–393.

644 Nishida, S., Naiki, A., & Nishida, T. (2005). Morphological variation in leaf domatia
645 enables coexistence of antagonistic mites in *Cinnamomum camphora*. *Canadian*
646 *Journal of Botany*, 83, 93–101.

647 Norton, A. P., English-Loeb, G., & Belden, E. (2001). Host plant manipulation of
648 natural enemies: leaf domatia protect beneficial mites from insect predators.
649 *Oecologia*, 126, 535–542.

650 Nundloll, S.; Mailleret, L. & Grogard, F. (2008). The effect of partial crop harvest on
651 biological pest control. *The Rocky Mountain Journal of Mathematics*, 38, 1633–
652 1661

653

654 O'Dowd D. J., & Willson, M. F. (1989). Leaf domatia and mites on Australasian plants:
655 ecological and evolutionary implications. *Biological Journal of the Linnean*
656 *Society*, 37, 191–236.

657 Parolin, P., Bresch, C., Van Oudenhove, L., Errard, & A., Poncet, C. (2015).
658 Distribution of pest and predatory mites on plants with differing availability of
659 acarodomatia. *International Journal of Agricultural Policy and Research*,
660 3,267–278.

661 Parolin, P, Bresch, C., Ruiz, G., Desneux, N., & Poncet, C. (2013). Testing banker
662 plants for biological control of mites on roses. *Phytoparasitica*, 41,249–262.

663 Pekas, A. & Wäckers, F. L. (2017). Multiple resource supplements synergistically
664 enhance predatory mite populations. *Oecologia*, 184, 479–484.

665 Pemberton, R., & Turner, C. E. (1989). Occurrence of predatory and fungivorous mites
666 in leaf domatia. *American Journal of Botany*, 76, 105–112.

667 R Core Team (2014) A language and environment for statistical computing. R
668 Foundation for Statistical Computing, Vienna, Austria. URL [http://www.R-](http://www.R-project.org/)
669 [project.org/](http://www.R-project.org/)

670 Roda, A., Nyrop, J., Dicke, M., & English-Loeb, G. (2000). Trichomes and spider-mite
671 webbing protect predatory mite eggs from intraguild predation. *Oecologia*, 125,
672 428–435.

673 Roda, A., Nyrop, J., English-Loeb, G., & Dicke, M. (2001). Leaf pubescence and two-
674 spotted spider mite webbing influence phytoseiid behavior and population
675 density. *Oecologia*, 129, 551–560.

676 Rozario, S.A. (1994). *Domatia and mites: effects of leaf morphology on beneficial mites*
677 *in semi-natural and managed systems* (Doctoral dissertation). Retrieved from
678 <https://catalogue.nla.gov.au/Record/2275037>. Monash University.

679 Rowles, A. D., & O'Dowd, D. J. (2009). Leaf domatia and protection of a predatory
680 mite *Typhlodromus dereenae* Schicha (Acari: Phytoseiidae) from drying
681 humidity. *Australian Journal of Entomology*, 48, 276–281.

682 Runkle, E. (2016). The boundary layer and its importance. GPNMAG.COM. Retrieved
683 from <http://flor.hrt.msu.edu/assets/Uploads/Boundary-layer.pdf>.
684 Situngu, S., & Barker, N.(2017). Position, position, position: mites occupying leaf
685 domatia are not uniformly distributed in the tree canopy. *South African Journal*
686 *of Botany*, 108, 23–28.
687 Tachi, F., & Osakabe, M. (2012). Vulnerability and behavioral response to ultraviolet
688 radiation in the components of a foliar mite prey–predator system.
689 *Naturwissenschaften*, 99, 1031–1038.
690 Walter D. E. & O'Dowd J.R. (1992). Leaves with domatia have more mites. *Ecology*,
691 73,1514–1518.
692 Walter, D. E. (1996). Living on leaves: mites, tomenta, and leaf domatia. *Annual*
693 *Review Of Entomology*, 41, 101–114.
694
695 Zhao, W., Zheng, W., Zhang, B., Yu, G., Hu, S., Xu, X. & Zhanga, H. (2014). Effect of
696 different ground cover management on spider mites (Acari: Tetranychidae) and
697 their phytoseiid (Acari: Phytoseiidae) enemies in citrus orchards. *Biocontrol*
698 *Science and Technology*, 24, 705–709.